Modelling the effects of seed mussel collectors on the western Dutch Wadden Sea ecosystem

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Summary

The Dutch Wadden Sea, Oosterschelde and the Voordelta are Natura-2000 areas and nature protection is a key issue; all intended activities have to be screened on their effects on a number of nature targets. One of the major activities in the Wadden Sea concerns the fishery for seed mussels: in autumn and spring young mussels are fished from the sediment and laid on culture lots in the Wadden Sea and the Oosterschelde where they grow to consumption sized mussels, fished again and brought to the auction in Yerseke.

This bottom fishery for seed mussels is bound to be replaced by alternative methods of seed collection. This change is a result of an agreement between the Dutch Government, fishermen and nature protection organisations.
Seed mussel collectors (abbreviated: MZI) are most promising as an alternative for the bottom fishery: ropes or nets are placed in the water column in spring, and form a good substrate for settling mussels in late spring and early summer.

It has to be tested what seed mussel collectors mean for the western Dutch Wadden Sea ecosystem. Seed mussel collectors are meant to replace the bottom fishery completely, and thus, yearly about 40 million kg of seed mussels (fresh mass) have to be harvested from these MZI-systems. This amount is for Wadden Sea, Oosterschelde and Voordelta together..

Effects studied in this model research concern the impact on the carrying capacity of the western Dutch Wadden Sea. The main question of this study is: to what extend is shellfish stock in the system affected by the introduction of MZI's?

The present study has been performed by using EcoWasp-ecosystem model computations and includes natural and cultured shellfish biomass development in the Wadden Sea with varying MZI-seed mussel harvests.

The current harvest of consumption mussels from culture lots has been taken into account. This is simulated by assuming a yearly auction target: the amount that mussel fishermen want to harvest from the culture lots. Three different auction targets have been assumed (20, 40 and 60 Mkg fresh mass of consumption mussels), plus a fourth, pristine, situation without any mussel culture.

In the model computations it is assumed that mussels attaching to MZI-nets have a much better survival chance than shellfish settling on natural substrates on the sea floor. Also, growth of mussels at the nets may be a bit better and mortality a bit lower, compared to the natural situation.

The model computations finally provide the following conclusions

1. MZI’s have a positive effect on the total shellfish biomass in the modelled system compared to the situation where –in absence of MZI’s- a certain amount of mussels is fished from natural beds. This conclusion is valid as long as the number of MZI’s stays below an upper limit; this upper limit is related to the original shellfish mass harvested from the system.
2. The effect on total *mussel* biomass is even more positive with increasing number of MZI’s.
3. Non-mussel shellfish biomass is negatively affected by an increasing number of MZI’s.
4. This negative effect is mainly established in the early period of MZI-mussels at the nets.
5. Under the assumption that growth and survival of culture mussel does not differ from natural mussels, the model computes that harvesting of mussels from the Wadden Sea has a negative effect on the total shellfish biomass. The model computes highest shellfish biomass in a situation with no harvest.
6. MZI practice has a positive effect on shellfish biomass available as food for birds compared to a reference situation with 60 Mkg auction target.
7. Positive effects are all caused by the fact that withdrawal of natural mussel biomass is replaced by mussels originating from MZI-systems.
8. Explaining conclusion (3) in more detail: In summer, a higher mortality of shellfish seed is computed; a result of competition for food. Shellfish seed grows a bit less fast, and since in the model mortality is coupled to the animals’ size (the smaller the higher the mortality) animals decreasingly survive this period with increasing numbers of MZI’s.
9. With an increasing number of MZI’s, an increasing part of mussel larvae goes into the MZI-route. This does affect the development of natural mussel stock a bit in a negative sense, but this effect is minor compared to the increasing natural mussel stock that is not fished anymore with increasing MZI-practice.

Overall, the model results indicate that the amount of food available for mussel eating birds increases with increasing MZI practice, a consequence of the increasing amount of mussels.

Finally, it is suggested to study the effect of culture lot efficiency. In this study, it is assumed that shellfish losses on culture lots were not different from the other –natural- losses; in reality these losses probably are less than on natural beds. The ratio (mussels brought to the auction)/(MZI seed mussels needed) will largely determine the conclusions drawn in this report. The larger this efficiency, the less MZI seed mussels and thus MZI’s are needed to arrive at a desired yearly mass of mussels brought to the auction. Also, the negative effects linked to an increased mortality of shellfish seed mention in chapter 5 will become less important with a decreasing amount of MZI seed mussels needed.

1 Introduction

The Dutch Wadden Sea, Oosterschelde and the Voordelta are Natura-2000 areas and nature protection is a key issue; all intended activities have to be screened on their effects on a number of nature targets. One of the major activities in the Wadden Sea concerns the fishery for seed mussels: in autumn and spring young mussels are fished from the sea floor and laid on culture lots in the Wadden Sea and Oosterschelde where they grow to consumption sized mussels, fished again and brought to the auction.

This bottom fishery for seed mussels is bound to be replaced by alternative methods of seed collection. This change is a result of an agreement between the Dutch government, fishermen and nature protection organisations. Seed mussel collectors (abbreviated: MZI) are most promising as an alternative for the bottom fishery: ropes or nets are placed in the water column in spring, and form a good substrate for settling mussels in late spring and early summer. After the seed mussels reach a sufficient size, they are harvested and laid on culture lots where they grow to consumption size.

The seed mussel collectors are meant to replace the sediment fishery completely, and thus, yearly about 40 million kg of seed mussels (fresh mass) have to be harvested from these MZI-systems. Part of this 40 million kg will be harvested in the Oosterschelde and the Voordelta It is also meant to transport (a part of) the seed mussels collected in the Oosterschelde and Voordelta to the culture lots in the Wadden Sea.

In this study, it has to be tested what seed mussel collectors mean for the western Dutch Wadden Sea ecosystem. Relevant ecosystem characteristics that are studied are primary and secondary production, phytoplankton and shellfish biomass, grazing rate of shellfish on phytoplankton, and the amount of shellfish available for birds.

Since the amount of MZI-seed mussels will roughly equal the amount fished –which usually exceeds 50% of all seed mussels in the system (Smaal et al, 2013)- one might expect as one of the possible effects that MZI's will affect the establishment of natural mussel beds. Mussel larvae that attach to the nets are not available any more for natural settlement. *The first question to be answered in this study is: what is the effect of MZI's on natural settlement of mussels on the sea floor?*

The keyword here is *mussel larvae utilization*. The part of mussel larvae that attaches onto the MZI-nets should be only a small part of all mussel larvae. In a first report (Brinkman, 2011), the MZI-mussel larvae in the model were subtracted directly from the total amount of available mussel larvae and thus, a production of each Mkg of MZI-seed mussels implied an almost equally lower amount of naturally settled mussels. This was considered to be unrealistic by a number of experts, and therefore, this process is investigated further in the present study.

A second potential effect concerns the phytoplankton species composition. Very large and very small phytoplankton is hardly filtered by mussels (and other shellfish species) (Riisgard, 1988). Since MZI's will be placed there where settlement of larvae and growth of the young mussels is optimal, it may be possible that other shellfish are negatively affected by the MZI's. It may be 'on the second row' because of a lower amount of food, and/or a larger part of smaller and /or larger less edible phytoplankton. *The second question to be answered in this study is: is the phytoplankton size composition altered when (a large number of) MZI's is placed in the western Wadden Sea?.*

A third potential effect is that food may become limiting in the system when more shellfish is brought into the system as a result of a successful MZI-exploitation. A keyword here is *carrying capacity* of the system and is related to the situation where competition for food is limiting the amount (biomass, numbers) of organisms. 'Carrying capacity' can be read as the amount of shellfish the system can produce in a year, or the maximum possible standing stock of shellfish. Whatever definition is chosen, it always reflects, somehow, the limits of the system to produce biomass; in the present case: shellfish biomass. Coming close to these limits, the amount of food available for shellfish growth gets depleted, average sizes of shellfish individuals become smaller, and addition of more shellfish will reduce the amount of other shellfish. *The third question to be answered thus is: is shellfish growth or the development of the shellfish population affected by the MZI's?*

The mechanisms from mussel larvae production to the largest mussels have been implemented into the model. Thus, parameters have been estimated, and the results are reported here for the whole trajectory from pelagic organisms, including larvae mortality, via sediment or MZI-seed mussels, including their growth and mortality characteristics, to the largest mussels.

The effects of the amount of MZI-mussels on the ecosystem have been expressed in several ways, such as the amount of natural shellfish present in the system, the primary production of the (western Dutch Wadden Sea) system related to the total amount of harvested MZI-mussels and the total amount of harvested mussels originating from MZI's.

Framework

The questions mentioned above and the work reported here are part of a larger project on seed mussel collectors. Other parts concern, among others, monitoring seed mussel growth at the nets, development of cultured mussels, deposition of organic matter nearby MZI-nets and the influence on local sediment composition, phytoplankton size preference of filtering seed mussels and the interaction with microzooplankton (Kamermans et al, 2010). For the Oosterschelde, Deltares performs a similar model study (Troost & Van Duren, 2011).

Methods

The work reported here is completely based on model research, and concerns the western part of the Dutch Wadden Sea.

Terminology

In order to avoid naming the *western Dutch Wadden Sea* each time, in the report *Wadden Sea* is written. In an exceptional case where the whole (Dutch) Wadden Sea is meant, it is explicitly written as whole (Dutch) Wadden Sea.

Set-up of the model research

The model computations are set up as realistic as possible, within limitations.
It is assumed that in the Wadden Sea each year a certain amount of shellfish is harvested from the culture lots and brought to the market. This amount is the auction target, and it is initially set to 60 Mkg fresh mass.

In the *reference* situation there are no seed mussel collectors, and the auction target is completely originating from natural mussels.

In all further scenarios such a target is harvested from the system. This harvest can completely concern mussels originating from natural beds (the reference situation) to mussels completely originating from MZI's (there are many seed mussel collectors in the system). The scenarios run cover the whole trajectory from very few MZI's to many.
Each year it is calculated what fraction of the harvested biomass from the culture lots originate from the MZI's. If there are many MZI's in the system, the harvest of MZI-mussels may exceed the pre-set auction target and then the total amount of mussels withdrawn from the system is larger than the reference.

Finally, scenarios have been run with 40 and 20 Mkg as intermediate auction targets, including a scenario without any harvest at all of natural mussels. The reason for this is first that the assumed target of 60 Mkg is not always the real harvest, and second, varying the target value also gives better insight in the underlying mechanisms that determine the effects of MZI's and mussel culture on the Wadden Sea.

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Jenny Cremer, Elze Dijkman, Carola van Zweden and Margriet van As (IMARES) did many data preparations; the Helpdesk of the waterbase.nl (Rijkswaterstaat) provided us with all needed water quality data. Rob Dekker (NIOZ) kindly provided data needed to tune mussel mortality parameters. Jeroen Wijsman and Roel Riegman (IMARES) carefully checked the text and gave many useful comments. Pauline Kamermans, Han Lindeboom (IMARES) and the 'convenantgroep' of the MZI-project provided critical remarks and questions resulting in improvements of this report.

2 Model and Data

2.1 Introduction

Modelling effects of seed mussel collectors on an ecosystem requires a couple of explanations of applied models and data. First, the overall model is explained, next the typical part related to the mussel dynamics, third the set-up for the western part of the Dutch Wadden Sea, and fourth the data used plus the necessary data compilations.

2.2 Overall model setup

The basic ecosystem model EcoWasp (see Brinkman (1993), Brinkman & Smaal (2003) for a detailed overview, and Smit et al (2010) for a short overview) contains descriptions of key processes in the Wadden Sea ecosystem. In this report, appendices I-IX give more detailed information on a couple of key processes for this study.
The key processes include biological processes (such as growth of algae and fauna), biochemical processes (e.g. breakdown of dead organic matter and bacterial oxidation of ammonium), chemical processes (mainly adsorption onto and desorption from solid particles) and physical processes (horizontal advective and dispersive transport and vertical dispersive transport across the sediment-water interface and the atmosphere-water interface).

Figure 1 gives a schematic overview of the model used in this study. Included are three or four phytoplankton groups: diatoms, non-diatoms ('flagellates') and pico-phytoplankton. In appendix II differences between the present model and previous versions are explained.

Diatoms and flagellates are grazed by filter feeding organisms, of which mussels is the overall presentations. *So, mussels actually are shellfish in general*. In reality, this group mainly consists of Blue mussels (*Mytilus edulis*), Cockles (*Cerasteroderma edule*), Sand gapers *(Mya arenaria*), and the last years also American razorclams *(Ensis directus*) and Pacific oysters (*Crassostrea gigas*).
Picophytoplankton is the group of <2 µm algae that and cannot be filtered by larger shellfish. In the model, picophytoplankton can only be grazed by microzooplankton (typical size assumed in this study 35 µm) and by mussel larvae (80-230µm). The accompanying PhD-study of Pascalle Jacobs has to reveal to what extend seed mussels are capable of filtering picophytoplankton.
In the model it is assumed that large shellfish are also capable to feed on microzooplankton and mussel larvae. As such they are not only primary, but also secondary consumers.

For the present study, wild shellfish and seed collector mussels are distinguished. Both groups have the same characteristics, but they follow a different route of development. This is explained below.

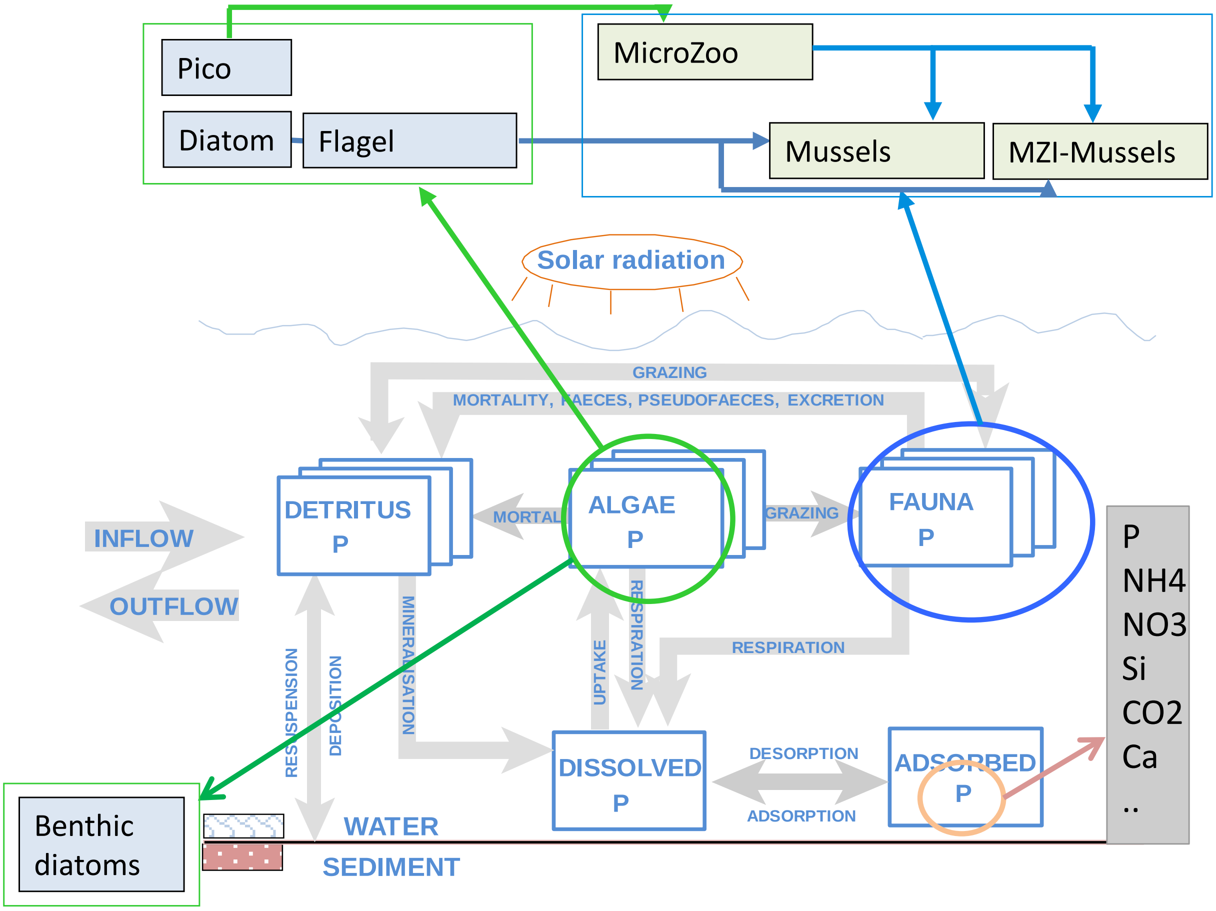


Figure 1 Schematic representation of the extended EcoWasp ecosystem model. ‘P’ represents all dissolved components, as mentioned in the grey box. As explained in the text: “Mussels” comprised all filter feeding shellfish in the system.

2.3 The model life of natural shellfish and of MZI-mussels

2.3.1 The model-mussel: (natural shellfish)

A schematic overview of EcoWasp-animals is given in Figure 2 and Figure 3. This scheme basically is valid for all animal types in the model. Several classes are distinguished, starting with larvae and ending with large (‘consumption’) mussels. Animals within a class are assumed to be identical. They increase in mass and size as a result of feeding (Figure 3) and decrease in number as a result of mortality. Mortality is a synonym for predation by other animals, fishing and ‘natural’ mortality (age, physical processes, etc). Each class is also characterized by its own set of parameters that define, for example, where the animal lives (e.g. water column for larvae and MZI-mussels at the nets, sediment for natural seed mussels and next classes), where it feeds (for natural shellfish: the water column), where it respires (also: water column), where it puts its faeces (the sediment top-layer for benthic mussel classes, the water column for larvae), etc. MZI- mussels have a bit different set of characteristics (regarding mortality and growth), see below. In fact, animals are followed during their lives (*cohorts* are followed, from egg to adult), and the model set-up is some version of a simplified structured population model. However, during their live, cohorts 'jump' from one class to a next one.

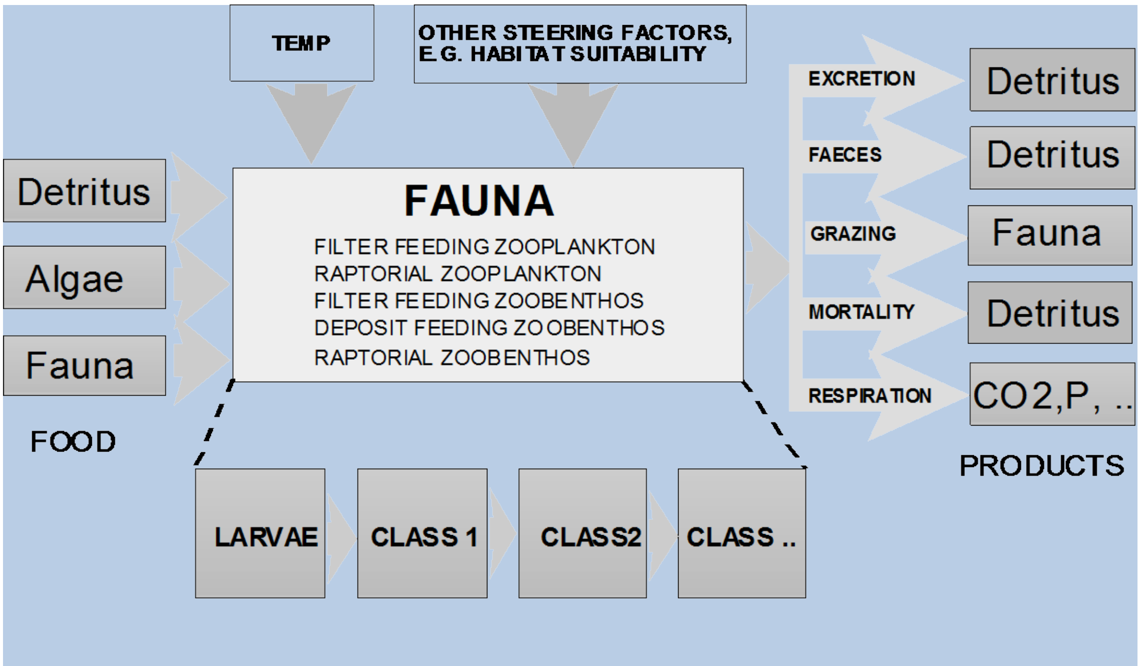


Figure 2 Representation of generic fauna in EcoWasp. Each fauna group consists of one or more classes. In case of more than one, the first contains larvae. Upon reproduction, classes shift to the next class. Fauna feeds on detritus, phytoplankton, other fauna. It produces faeces, adds to detritus when dying, and may serve as food for other fauna. Respiration produces carbon dioxide, but also phosphate, ammonium, etc, according to the stoichiometric ratios. The fauna description is generic.

When a cohort changes from class i to i+1, also its properties change. Mussel larvae are born (in the water column) each year in a certain period with initial size of about 80 µm, and grow until they reach a 230 µm size (Bayne, 1976). Then they settle (and shift to the next class), and change their characteristics.

The description of the fauna processes is generic, and follows the processes illustrated in Figure 3. All the mentioned processes are size-related; equations and parameter values are mentioned briefly in section 2.5, and in more detail in appendices III and XI. Mortality is also size-related: relative mortality decreases with increasing size.

All processes also depend on temperature, described in section 2.5.8.

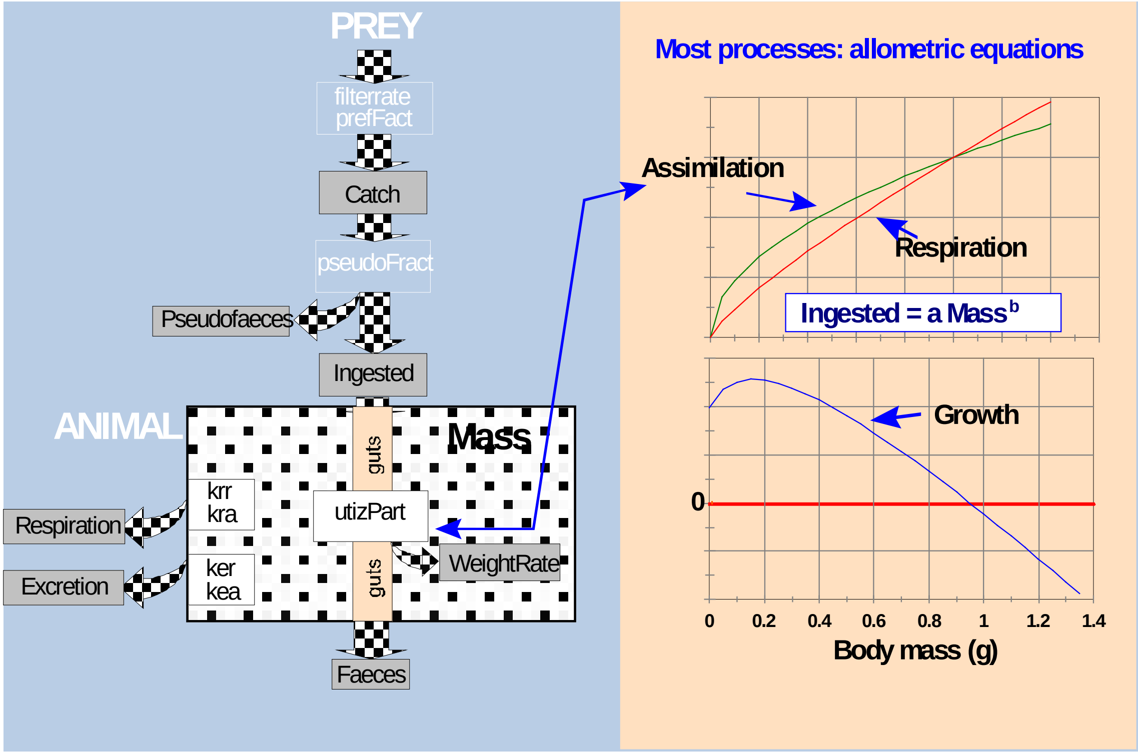


Figure 3 The model mussel. Physiological processes are size-related (allometric). A mussel filters water and catches solid particles (algae, detritus, silt). A preference (0 ≤ preference ≤ 1) is used first to select particles, and next, the size of the particles may be important. A part of the catch may be laid aside as pseudofaeces. A part of the ingested food is assimilated (assimilation efficiency), the rest is excreted as faeces. The net growth (mass rate) depends on the assimilated food and extra losses as maintenance respiration, activity related respiration and digestion costs.

2.3.2 The MZI-mussel

Mussels that attach to the MZI-nets are the same species as natural mussels (= natural shellfish), but follow a different route. In the model, this has been solved by introducing a new fauna type: the MZI-mussel. It has almost the same characteristics as the 'normal' shellfish; there are a few differences. Seed MZI-mussels are attached to the MZI-nets, and therefore they live in the water column (*not* at the sediment), and produce faeces etc in the water column. After harvesting, the MZI-mussels change to (benthic) class 3. So, two classes are needed to describe the phase of class 2 of 'natural' mussels. Therefore, MZI-mussels have five classes (Figure 4).

2.4 Key parameters defining the MZI-mussels and natural shellfish

In Figure 4, the life-span of natural shellfish and of MZI-mussels is illustrated. After a couple of discussions, the presumed critical parts are the efficiency of reproduction, the losses at the moment of settling and the losses when harvesting the MZI-seed mussels from the nets.

These are illustrated in Figure 4:
δ_{1i} are the efficiencies of larvae production for natural mussels (i=1) and MZI-mussels (i=2),
δ_{2i} are the losses upon settlement,
δ_{3i} are the losses when changing from class 2 to class 3 . For natural mussels, nothing happens, but for MZI-mussels it denotes the losses when harvested from the nets and laid on the culture plots,
δ_{4i} and δ_{5i} give the losses when changing from class 3 to class 4 and from 4 to 5. Normally these values are 1, but for MZI-mussels it can be used to include extra mortality culture mussels are fished sometimes and laid on other culture lots.

The parameter α is used to divide the new-born larvae between natural shellfish and MZI-mussels.

Δt reflects a possible advantage of MZI-mussels over natural mussels when searching a substrate to attach to. One of the ideas is that, since MZI-nets are a very good substrate, natural mussels may take more time to find a substrate, and thus undergo more losses than the mussels following the MZI-route.
MZI-mussels may be harvested from the nets during several events. In the model maximal three moments of harvesting MZI-seed mussels are possible (t_1-t_3 in Figure 4), and each time a fraction β_1-β_3 of the mussels then present is harvested; by this definition, β_3=1 (all remaining mussels are harvested). The times t_1-t_3 are fixed, but a minimum size is needed; if this minimum size is not reached for the moments t_1 and t_2, harvesting takes place later.
Consumption-sized MZI-mussels (MZIMUSS4 and MZIMUSS5) are harvested in a certain period. MZIMUSS5 is always harvested in such a period, MZIMUSS4 may be harvested, but then they have to be larger than a minimum size.

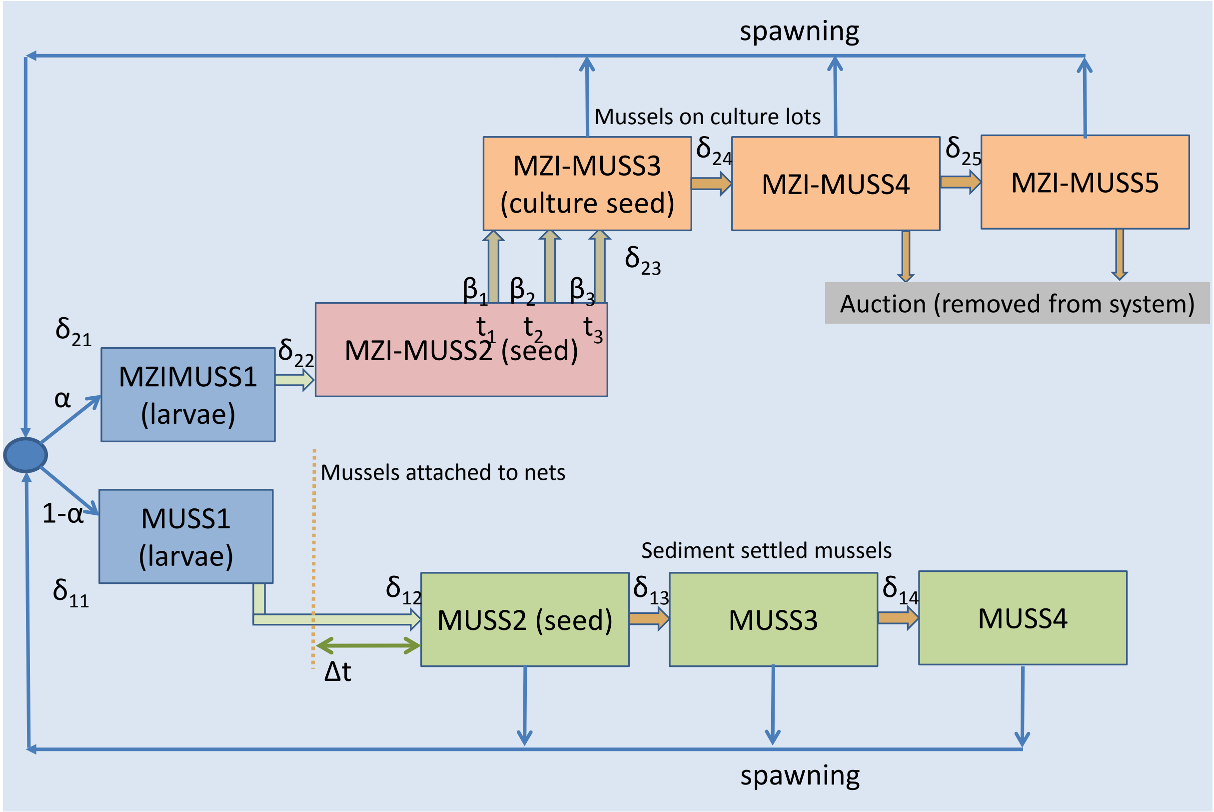


Figure 4 Route of mussels (MUSS) and seed collector mussels (MZIMUSS) as implemented in the version of the EcoWasp-model for MZI's. MUSS1 and MZIMUSS1-larvae are considered separately, and both the cohorts are filled by both MZIMUSS2-5 and MUSS2-4. Part α of all the larvae goes to MZIMUSS1 and consequently, (1-α) to MUSS1. Upon settlement, a fraction δ_{12} and δ_{22}, respectively, dies instantaneously. Such an extra mortality is defined for all classes now (e.g. δ_{21} .. δ_{25} for MZI-mussels) but is only relevant for the change from MZIMUSS2 to MZIMUSS3: after harvesting the MZI-mussels a part will die as a result of mechanical damage or of bringing the young mussels to culture lots. Finally, δ_{11} and δ_{21} may get a value<1 describing a loss upon larvae production.

2.5 Key processes in the present model application

2.5.1 Introduction

For this MZI-application, a number of processes had to be tuned (better), or had to be adapted:

- Feeding behaviour of natural mussels
- Gain and losses of shellfish
- Shellfish reproduction
- Growth and mortality of mussel larvae
- Mortality and growth of MZI-mussels
- Costs of digestion (this was neglected in previous model studies)
- Growth of picophytoplankton
- Parameters for microzooplankton, including its feeding behaviour on picophytoplankton

- Mortality of natural mussels
- Losses (mortality) when spawning: only a part of the spawned biomass also becomes mussel (shellfish) larvae
- Losses upon settling: a part of the larvae that settles dies (is not able to find an appropriate substrate or undergoes other losses).
- Temperature dependencies

2.5.2 Feeding behaviour of natural shellfish

Shellfish can only filter algae that are large enough. Very small phytoplankton cannot be caught: pico-phytoplankton escapes from being filtered. Thus, at high grazing rates, the system might become enriched with small, not-filtered algae. This is one of the hypotheses of the MZI-study (chapter 1).

These small algae are a prey for small zooplankton (micro-zooplankton); this small zooplankton can be filtered by mussels.
Thus, the relative amount of picophytoplankton may increase since the larger species are eaten by shellfish, and picophytooplankton is not, and because the picophytoplankton *predator* is eaten as well by shellfish.
Only shellfish larvae may be capable of filtering picophytoplankton.

Not all the food can equally be digested by shellfish. This *assimilation efficiency* of ingested food (Figure 3) differs per type of food. For example: even detritus may be used, but the fraction of detritus that can be assimilated is low compared to fresh phytoplankton.

Filtration parameters are not changed for this MZI-application, but are compared to literature data. Appendix III (“*Fauna filtration and respiration parameters a first estimates*”) gives a method that can be used to come to a first estimate of filtration (and respiration) parameters. Comparison with literature data is described in appendix V.

2.5.3 Gain and losses

Assimilation is the only process that contributes positively to the animal’s energy budget; all other processes concern losses. Assimilation is expressed as g AFDW ind^{-1} d^{-1}, assimilation efficiency is expressed as a fraction of food ingested. This efficiency depends on the type of food.
Maintenance respiration is always needed, expressed as g AFDW ind^{-1} d^{-1}. Digestion costs are relative to the amount of food ingested, and total costs are expressed as g AFDW ind^{-1} d^{-1}.
There is a standard excretion possible, similar to the maintenance respiration.

The amount of water filtered may be a cost factor (although is generally is assumed that these costs are minor); expressed as g AFDW m^{-3} filtered.
The production of pseudofaeces is accompanied by the excretion of mucus, and thus, it is a negative contribution to the energy budget. Expressed in g AFDW g^{-1} pseudofaeces.
High silt contents in the water column may have negative consequences for the filtration success and supposed to be one of the reasons that suspended mussels (like those at the MZI-nets) grow better than those at the sea floor (see e.g. the review by Wijsman et al, 2012). Silt content in the water is modelled as a cost for shellfish. Expressed in g AFDW d^{-1} $(g\ m^{-3})^{-1}$ silt content.

Respiration parameters are not changed tor this MZI-application, but are compared to literature data. See Appendix III ("*Fauna filtration and respiration parameters, a first estimate*") for a method that can be used to come to a first estimate of filtration (and respiration) parameters, and appendix (V) for a comparison with literature data.

2.5.4 Reproduction, growth and mortality of mussel larvae

A substantial part of the work was needed to tune the reproduction of the mussels, and the growth and survival of mussel larvae. As presented above, in previous applications it was assumed that reproduction was 100% efficient, as was the settlement of seed mussels. Assuming a much lower efficiency of both processes implied that also the mortality parameters had to be adjusted. This is described in detail in appendix VIII ("*Mussel larvae and mussel spawning*").

2.5.5 Mortality of natural mussels

Mortality is the sum of all loss processes such as predation, fishery and physical processes (e.g. ice winters, storms). In some cases these processes are taken into account, in others cases they have to be parameterized. In the latter case, the mortality rate parameter depends of the size of the animal:

$$\text{mortality rate} = \frac{dN}{dt} = mort \cdot N \qquad (\text{nrs } d^{-1}) \qquad (1)$$

and for the mortality rate parameter mort:

$$\text{mort} = \text{mora} \cdot M^{\text{morb}} \qquad (d^{-1}) \qquad (2)$$

with M as individual animal mass, and morb<0. Thus: the smaller the animal, the larger the mortality rate parameter.
In this application, settlement of shellfish larvae (from a pelagic stage to a benthic one) occurs with a large loss. As a result, also the mortality rate parameters for seed (MUSS2) and also the adult

shellfish (MUSS3 and MUSS4) had to be adjusted. This is mainly based on a) a comparison with existing data on total shellfish content in the western Dutch Wadden Sea, and b) data on the ratio of seed mussel numbers to total mussel numbers on the Balgzand area (the tidal flats in the south-western part of the western Wadden Sea). Data were kindly supplied by R Dekker (NIOZ). Results are illustrated in appendix V.

2.5.6 Picophytoplankton and microzooplankton

In the present application, picophytoplankton and microzooplankton have been included. For both populations, a new set of parameters was needed. A first guess for microzooplankton parameters was achieved following the description in appendix III, and fine tuning was done using literature data and data from the on-going PhD-work of Pascalle Jacobs (IMARES). This is described in appendix X ("*Picophytoplankton and microzooplankton*").

2.5.7 Mortality and growth of MZI-mussels

Advantages of mussels that are attached to the MZI-nets mainly concern a lower predation risk and better growth conditions.
The predation risk is lowered because shrimps, starfish and crabs are mainly epibenthic. The experiences with the MZI-nets support this (Troost et al, 2011). Although the predation will be lower, the competition for space is larger than on the sediment, and many mussels die because they are overgrown by other mussels. The ratios between numbers at the beginning of the settlement and the numbers of harvested mussels are roughly known, and are used to tune the MZI-mortality. See appendix IV.
Conditions for growth are assumed to be better at the nets than on the sediment, mainly because of the fact that the silt and sand content of the filtered water is lower. The intention was to compute the vertical profile of all particulate matter and to use it for a better description of this process. However, time was lacking to complete this part of the modelling task. Instead, the food ingestion was increased a bit for MZI-mussels at the nets. See also appendix IV.

2.5.8 Temperature dependency

Many processes depend on temperature. A very flexible optimum function is implemented in the EcoWasp-model (see Textbox 1); parameter values completely determine the shape of the relationship. Parameter values used are listed in appendix XII.

Temperature and other possible dependencies

The function used for all the biological processes reads

$$F(T)=\left[\frac{(T-T_1)^2}{(T-T_2)^2+(T-T_1)^2}\right]\quad (if\ \ T<T_2)$$

$$F(T)=\left[\frac{(T-T_3)^2}{(T-T_2)^2+(T-T_3)^2}\right]\quad (if\ \ T>T_2)$$

and

$$F(T)=0\quad (if\ \ T<T_1\ \ or\ \ T>T_3)$$

with exceptional cases

$$F(T)=1\ \ (if\ \ T<T_2\ \ and\ \ T_1=T_2)\ \ or\ \ (if\ \ T>T_2\ \ and\ \ T_3=T_2)$$

where F(T=T_2) =1.0. For T<T_1 and T>T_3 F(T)=0. When (T2-T1)= (T3-T2), then the function is symmetric around T2. Also, the area under the curve is 1.0, which is useful in a couple of cases. Important is that the shape of this function is very different for different parameter combinations (), thus allowing temperature dependent species competition, or optimum temperatures for species occurrence. .

Textbox 1 Temperature dependency in EcoWasp. The function has an optimum of 1 at T=T2. The same function may be applied to other dependencies, e.g. the relationship between processes and salinity. A second type of this function includes an intermediate area between (T_{2low} and $T_{2\ high}$) where F(T)=1. Parameter values applied are listed in appendix XII.

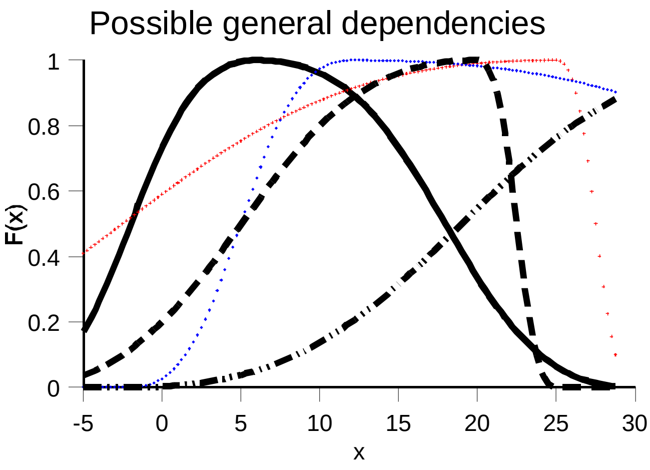


Figure 5 Possible shapes of the temperature dependency function. Parameter values defining what function actually has been used are listed in appendix XII

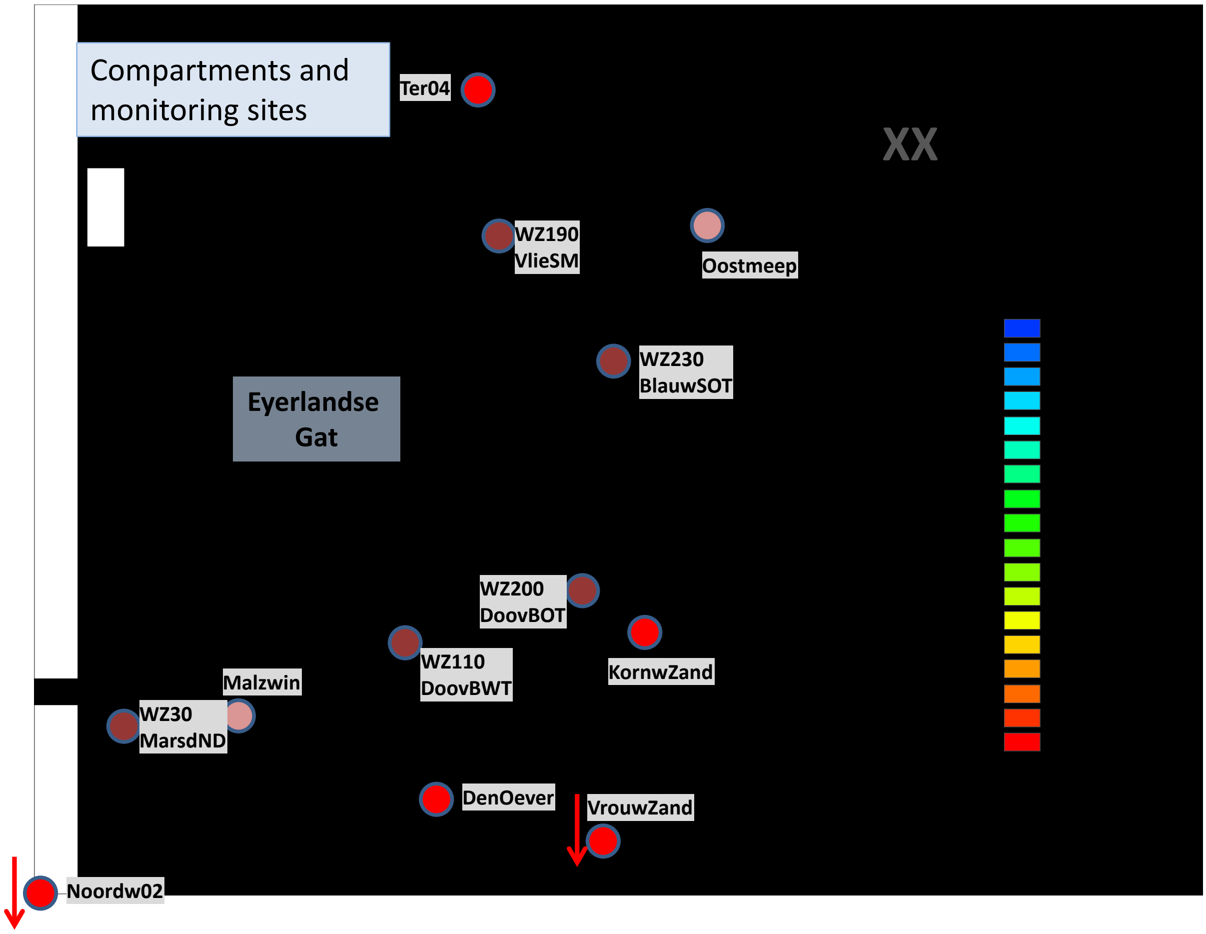


Figure 6 Western Dutch Wadden Sea compartments in the EcoWasp ecosystem model. Each compartment has a tidal area (above low water level, numbered 1-6), a subtidal area (below low water level down to -5 m NAP, numbered 7-12) and a channel part (below -5 m NAP, numbered 13-18). Red circles represent boundary condition sites. Dark-red sites denote monitoring sites used for comparison. Compartment number 1 on the map thus includes sub-compartments 1, 7 and 13, compartment 2 the sub-compartments 2, 8 and 14, etc... until nr 6 with sub-compartments 6, 12 en 18. This numbering is used thoughout the report. The Eyerlandse Gat-area (between Texel and Vlieland) and the area east of the tidal division of Terschelling are outside the modelled area. Abbreviations: WZ30/MarsdND= Marsdiep Noord; WZ110/DoovBWT= Doovebalg West; WZ200/DoovBOT= Doovebalg Oost; WZ190/VieSM= Vliestroom; WZ230/BlauwSOT= Blauwe Slenk Oost; DenOever= Den Oever; KornwZand= Kornwerderzand; Noordw02= Noordwijk02, 2 km off the coast; Ter04= Rerschelling 04, 4 km off the coast. The areas 1-3 together are the Marsdiep basin; the areas 4-6 the Vlie basin.

2.6 Compartment set-up for the western Dutch Wadden Sea

The spatial set-up for the Wadden Sea model is illustrated in Figure 6. Six compartments are assumed, each with a tidal flat area (down to low-water level), a sub-tidal area (down to NAP-5 m) and a channel area (the deepest parts). There is advective and dispersive transport between the compartments and with the North Sea, and there is freshwater inflow from Lake IJssel. Physical data (flow, waves) are similar to the data used for the composition of the mussel habitat maps (Brinkman & Bult, 2003), and are obtained from model computations by Alkyon (http://www.alkyon.nl/). Exchange of water between compartments and the exchange between the system and the adjacent North Sea has been taken from Ridderinkhof (1988) and EON-I and –II (1988), although the parameter values have been adapted after a comparison between salinity measurements and model results.

More details are given in appendix I (“*Spatial set-up of the Wadden Sea model…*”).

2.7 Sediment data and morphology

Morphological data are obtained from Rijkswaterstaat. Data on sediment composition are from the Sedimentatlas (Min VWS, 1998).
Tables are listed in appendix I (“*Spatial set-up of the Wadden Sea model ….”*)

2.8 Water quality data, meteorological data and necessary data compilations

Running the model needs a lot of boundary condition data (conditions at the edges of the modelled system). For comparison, data for the modelled compartments have to be known (inside the modelled system).
Water quality data are obtained from Rijkswaterstaat (live.waterbase.nl) as are the water quantity data describing the fresh water input from Lake IJssel.
Meteorological data are obtained from the Royal Netherlands Meteorological Institute (KNMI, www.knmi.nl).

The Netherlands Rijkswaterstaat (Netherlands Water Board) collects water quality data for so-called Rijkswateren in The Netherlands: marine water bodies as well as fresh water systems. These data are primarily collected because of the ‘Wet Verontreiniging Oppervlaktewateren’ (WVO) from 1969 and, from December 2009, the ‘Waterwet’ (Water Act), that replaces the WVO. The data serve as indicators whether water quality targets are achieved or not.

These data also are an important source of information for ecosystem modeling activities; the data give information for boundary conditions, and are very useful as comparison to model results.

From the available data other quantities were derived that are not directly measured. Especially an estimate for the amounts of algae, diatoms/non-diatoms, refractory organic matter (ROM) and labile organic matter (LOM) may be computed. A first computation concerns the estimation of the phytoplankton content from chlorophyll-a data, the composition of algae (N & P) and the composition of the remaining fractions: detritus (N & P) and inorganic matter (P).

A second computation concerns the composition of the dissolved organic fraction (DOM = dissolved organic matter). It appeared from a first check that probably two fractions may be distinguished: one type of DOM that is more or less always present (a more refractory type of DOM), and one type that appears in the summer period (a more labile type of DOM).

A third computation concerns the estimation of missing data. Especially for the boundary conditions it is important that there are no large caps in the data series. Therefore, missing data have been estimated based on existing data for the same site plus neighbour sites. Thus, time series for dissolved components, phytoplankton, detritus, e.g. produced for the whole period relevant for ecosystem simulations.

These computations are illustrated in appendix X ("*WaterQuality Data variables. elaboration of Waterbase data*").

2.9 Set-up of the calculations

With the model as described above, it is calculated what an increasing amount of MZI-mussels could mean for the Wadden Sea ecosystem, with emphasis on the natural shellfish stock, the ratio picophytoplankton to total phytoplankton, primary production of the system and the size of adult natural mussels.

Varying the MZI-harvest
Since it is hard to start with the amount of MZI-mussels after harvesting, the simulations were run with a varying α-parameter: α describes the division between mussel larvae and MZI-mussel larvae at spawning. When α=0, no MZI-mussels are born, and at α=1, all shellfish larvae are MZI-mussels. The computations are performed for α-values: 10^{-5}, 10^{-4}, $5\ 10^{-4}$, 10^{-3}, $3\ 10^{-3}$, $7\ 10^{-3}$, 10^{-2}, $2\ 10^{-2}$ and $3\ 10^{-2}$, thus covering the whole range of almost no MZI's in the system to a very intense MZI-mussel culture. In the last case, 3% off all shellfish larvae go to MZI's. By this, the total MZI harvest varies between 0 and 120 Mkg year^{-1}. In this report, the harvests>60 Mkg have been omitted.

Varying some MZI-mussel characteristics

The mortality rate parameter and the growth parameter for the MZI-mussels at the nets have been varied a bit. The mortality rate parameter was taken as 1 and 0.9 times the value of the natural shellfish, and the growth parameter as 1 and 1.1 time the value of the natural shellfish.

Not all shellfish is mussel

Only a part of the natural shellfish stock is *real* mussel, next to cockles, sand gapers, razorshells and others. Therefore, α must be much smaller than 1. For example, in case *Mytilus edulis* is about 20% of the total biomass (which presently roughly is the case) is , then α=0.1 implies that half of the mussel larvae go into the MZI-route. Consequently, the value of α (the part that goes into the MZI-route) cannot exceed 0.2.

Present mussel fishery

The basic situation at the moment is that natural seed mussels are fished from the sea floor and laid on the mussel culture lots. In case of seed mussel harvest from the MZI-nets, part of the consumption mussels originate from the MZI-nets, and thus, the natural amount that has to be fished is lowered.

The way this has been implemented in the model is as follows:

- A target is set: that is the *desired* biomass of consumption mussels to be harvested from the culture lots. This is called here the *auction target*. Since the amount of mussels harvested is not always the same, this *auction target* is varied: 0, 20, 40 and 60 Mkg consumption mussels, each year.
- The harvest of MZI-seed mussels varies per scenario since the α-parameter varies, as described above (see also sections 2.3 and 2.4). These MZI-seed mussels grow to consumption size MZI-mussels, and are harvested (withdrawn from the system and brought to the auction) as soon as they are large enough. There is a certain period in the year that this harvest takes place. If this harvest of MZI consumption mussels is lower than the target, then the rest is taken from the natural stock. The larger the target the more natural mussels have to be fished in order to reach this target. But, in case the total amount of consumption size mussels originating from the MZI's exceeds the target, simply more mussels are brought to the auction.
- No flexible fishery behaviour is taken into account. Usual business will be that mussel fishermen themselves will regulate the amount of mussels brought to the market, based on whatever considerations. Here, a 100% strict procedure is followed: the amount that cannot be harvested as MZI consumption sized mussels will be harvested from the natural stock; any surplus will be brought to the auction as well.

In the graphs presented, a MZI seed mussel harvest target of 40 Mkg seed mussels is used, but this is just for presentation and does not affect the results of the computations.

3 Validation

For validation of the results the reader is referred to the appendices. Flow and dispersion characteristics are discussed in appendix I. Growth and mortality of mussels is described in appendix IV. Respiration and uptake by mussels and the relationship with mussel size is described in appendix V. Mussel larvae parameters are discussed in appendix IX. Picophytoplankton and microzooplankton are discussed in appendix X.
For computed dissolved components, the reader is referred to Brinkman (2012).

4 Results

4.1 Introduction

In the next sections results of the simulations are presented. They all are shown as function of the amount of seed mussels harvested from the MZI-nets. Next to absolute values also the difference relative to the reference situation is shown. All computed harvest values are averages for the seven years 2006-2012. Stock values are expressed in Mkg fresh mass.

4.2 Harvest from the collector nets, harvest from the culture lots and harvest of natural mussels

By varying the fraction of larvae that go into the MZI-route, the number of MZI's in the system is simulated, as explained above. The amount of MZI-seed mussels harvested from the nets, and the corresponding amount of MZI-consumption mussels finally harvested from the culture lots is shown in Figure 7.

Roughly spoken, each kg of MZI-seed mussels results in 1.5 kg of MZI-consumption mussels harvested from the culture lots. The computations have been performed for all four auction-targets, and there is only a small difference between the results.

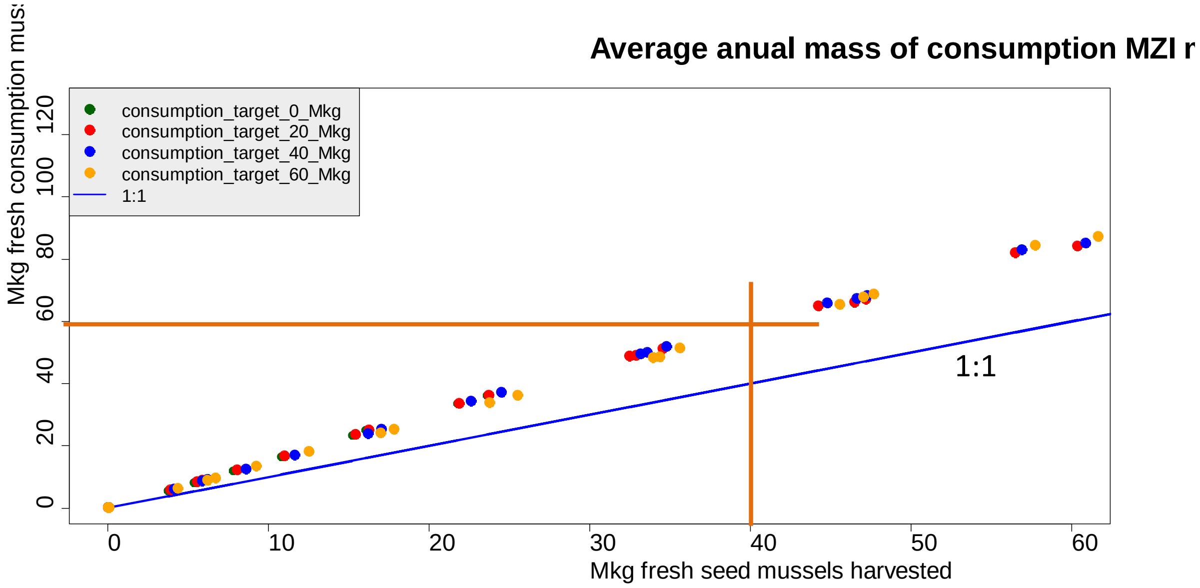


Figure 7 Amount of consumption mussels harvested related to the amount of seed mussels harvested from the nets. Average values for a 7-years simulation (period 2006-2013). The model results give an about 50% increase in mussel biomass after harvesting the MZI-mussels from the nets.

In Figure 8, the amount of mussels harvested from the culture lots is shown for all four different auction targets. The part that originates from the MZI-nets and the part that still had to be harvested from natural beds are both shown.

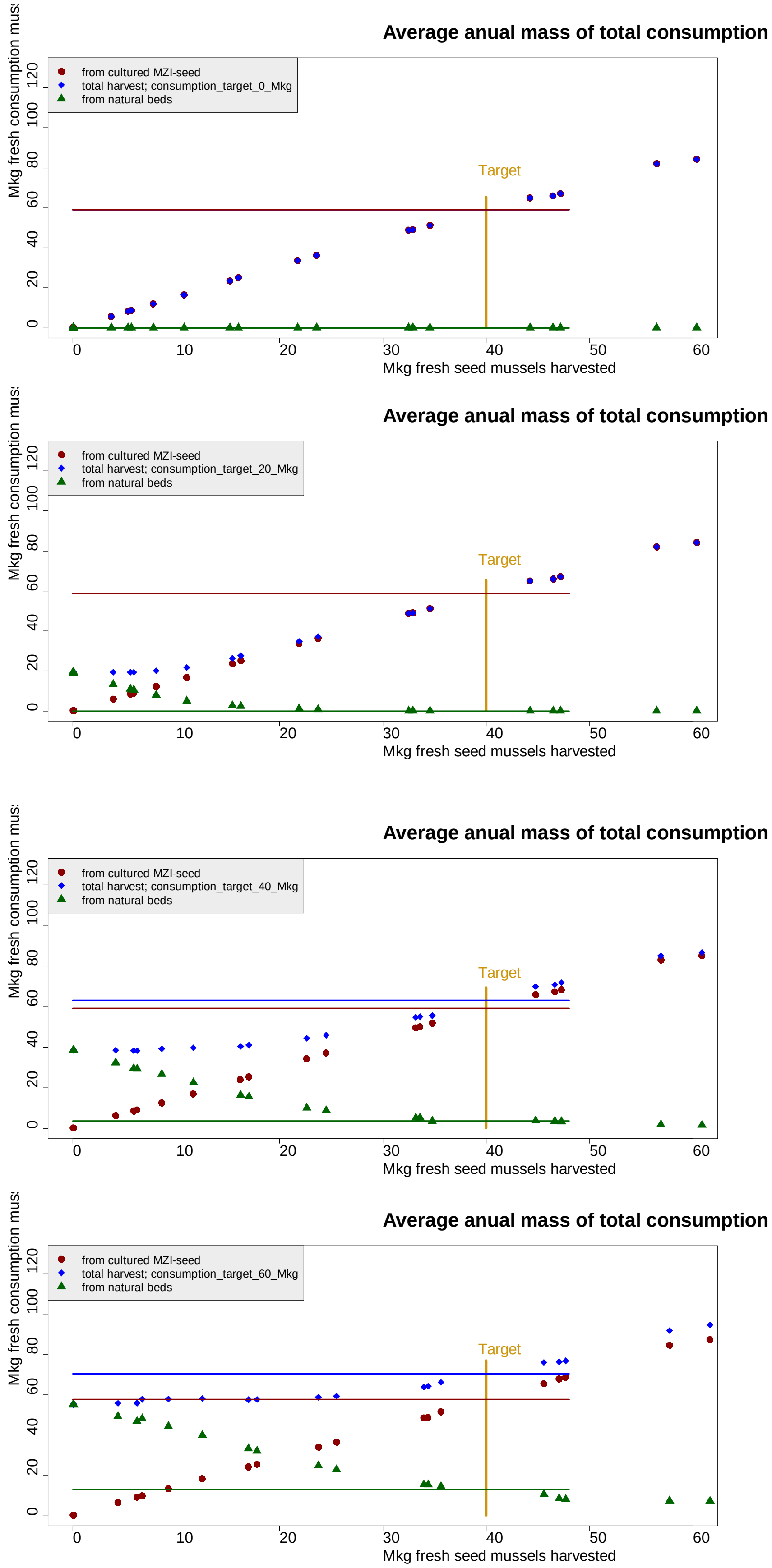


Figure 8 Total harvest from the culture lots (Y-axis), and contribution of mussels originating from MZI's, and from natural beds. On the X-axis the total amount harvested from the MZI-nets is shown. Top: there is no harvest of natural mussels.

Second, the auction target (== target for the culture lots) is 20 Mkg fresh mass. The graph shows that if 20 Mkg seed mussels are harvested from the nets, (almost) no harvest of natural mussels is needed anymore.

Third: the auction target is 40 mkg fresh mass. At 30-40 Mkg seed mussels from the MZI-nets, almost no natural harvest is needed anymore.

Bottom: the auction target is 60 Mkg. Also if over 40 Mkg seed mussels are harvested, still some natural fishery sometimes is needed.

If no MZI's are present, all mussels brought to the auction originate from natural beds.
If the auction target is set to low values, the amount of mussels needed from natural beds is also low, and thus, fewer MZI's are needed to supply the culture lots with enough seed mussels in order to finally reach the auction target. For example:

- In case the auction target is 20 Mkg consumption mussels there are no more natural mussels needed if 20 Mkg seed mussels (fresh mass) are harvested from the MZI-nets.
- In case the auction target is 40 Mkg consumption mussels the contribution from natural beds becomes zero at about 30-40 Mkg MZI-seed mussel harvest.
- In case the auction target is 60 Mkg and the MZI-seed mussels harvest is 40 Mkg, then still about 15 Mkg mussels are needed from natural beds.

The reason for the latter is that there are still some years that the harvest from the lots is not enough to get to the desired 60 Mkg harvest from the culture lots. It also implies that on average the total culture lot harvest (and thus the amount brought to the auction) exceeds this 60 Mkg (Figure 8, bottom graph). Remaining needed harvests from natural beds are summarized in Figure 9.

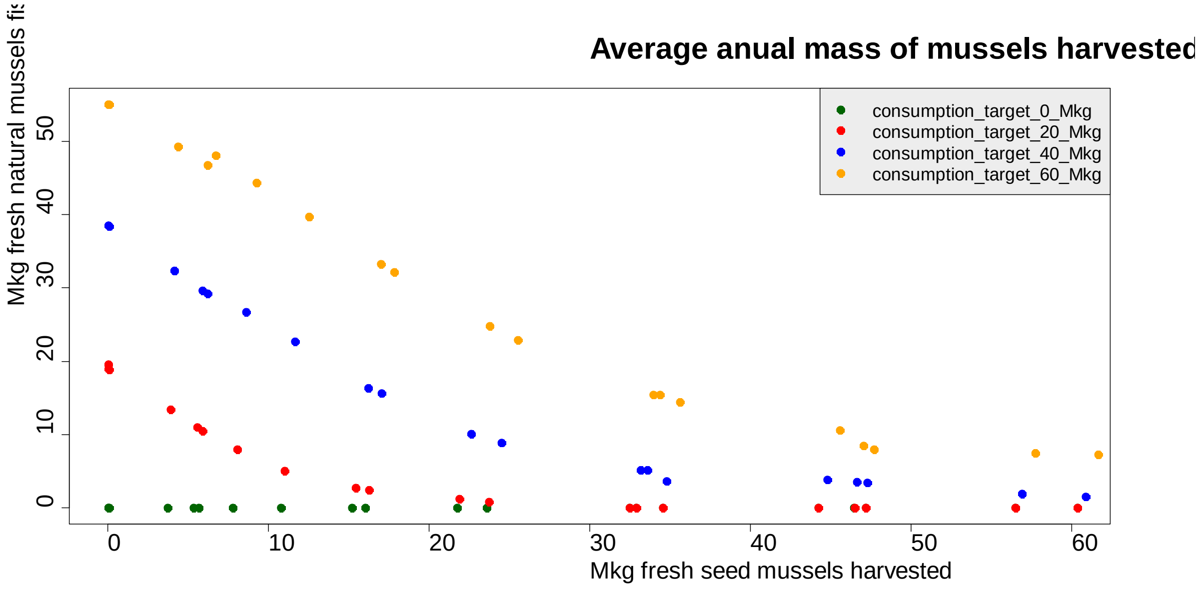


Figure 9 Average annual mass of mussels originating from natural beds, needed to reach the several auction targets (0-60 Mkg fresh mass mussels). The amount decreases with increasing amount of mussels originating from the MZI-nets (X-axis).

4.3 Shellfish stock, natural and total

The model results for the total shellfish stock are given in Figure 10; all computed possible combinations are shown: four auction targets, ranging from no to a large amount of MZI-seed mussels harvested. According to these model results, the largest amount of shellfish in the systems is found when fishery is absent (at a 2006-2013 average of 440-450 Mkg fresh mass).

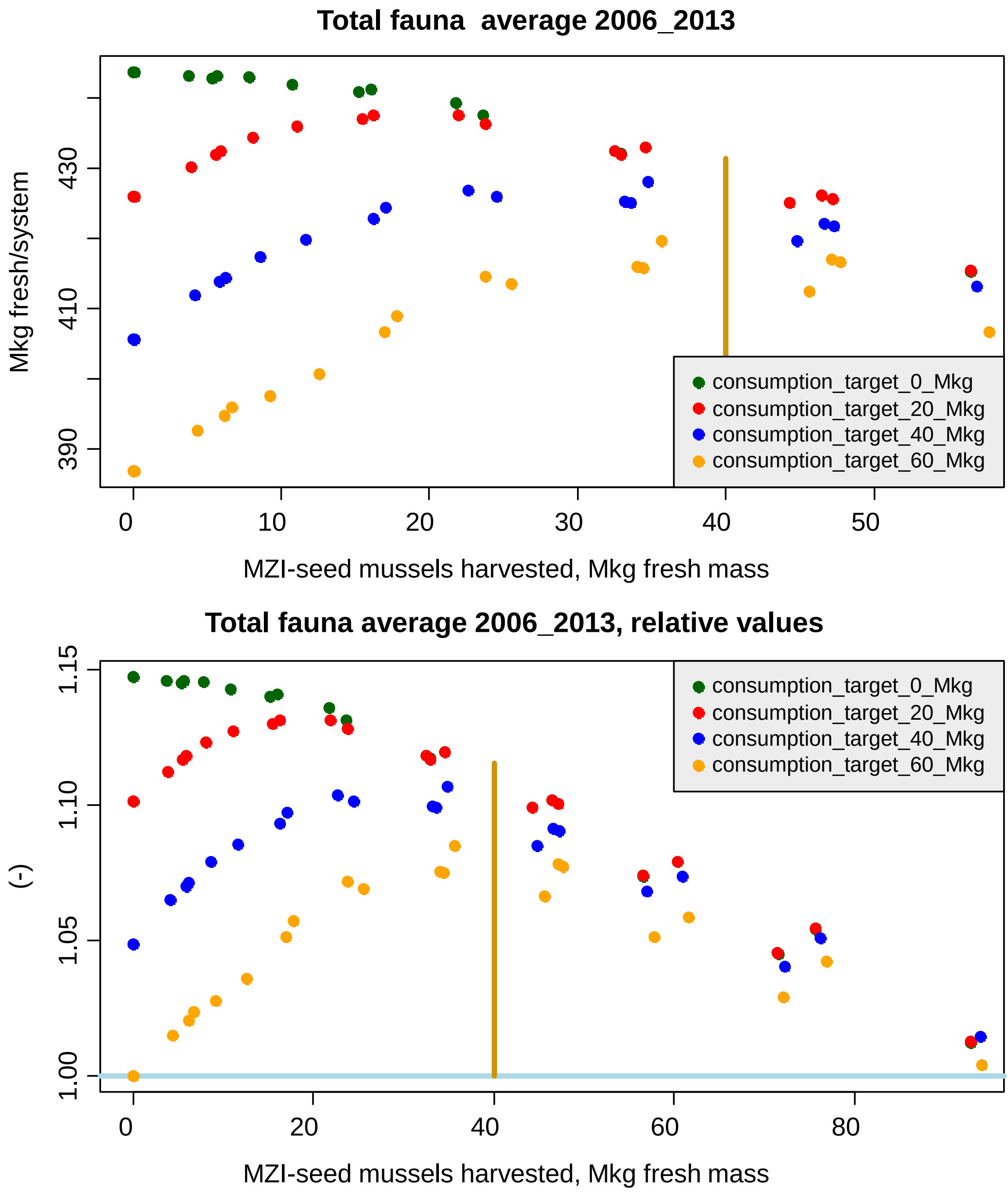


Figure 10 Total shellfish fauna in the system, depending of the amount of seed mussels harvested from the nets (X-axis), for four different auction targets (0..60 Mkg fresh mass). Average values for the whole period 2006-2013. The variation of the mortality and the uptake parameter for seed mussels at the nets causes the small variations in the results. Total shellfish includes natural shellfish, MZI-nets and culture lots. Upper: absolute values, lower: all values relative to the reference situation: 60 Mkg target harvest from the culture lots, and no MZI's present.

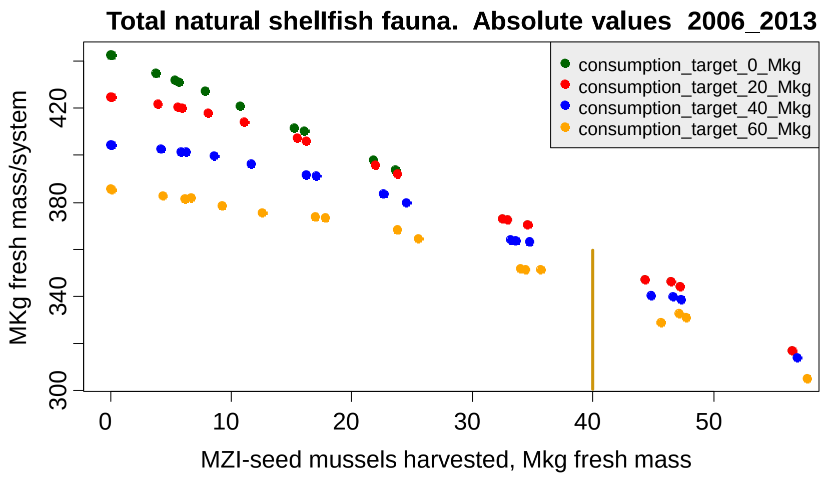
In case there is fishery present (which is the actual situation) MZI's have a positive effect on total shellfish stock. An increasing amount of seed mussels harvested from the nets increases the total amount of shellfish in the system, until a maximum is reached. Further increase of seed mussels harvested from the MZI-nets causes a decrease of the total shellfish stock.

This maximum is connected to the auction target. If this target is set at 20 Mkg fresh mass consumption mussels, the maximum shellfish biomass is reached at about 20 Mkg MZI-seed mussels harvested from the nets. If the auction target is 40 Mkg, the stock maximum is reached at about 30 Mkg MZI-seed mussels; at 60 Mkg auction target, this value is about 40 Mkg MZI-seed mussels harvested.

In Figure 11, the shellfish stock is divided into natural shellfish and MZI-related mussels (MZI-nets + culture lots). From the lower graph in Figure 11 it is clear that e.g. at 40 Mkg seed mussels harvested from the MZI-nets, there are about 70 Mkg MZI-mussels in the system (and 60 Mkg are harvested each year (Figure 7).

From the upper graph in Figure 11 it can be concluded that although the total shellfish stock initially increases with an increasing amount of MZI-nets (Figure 10), the stock of natural shellfish always decreases with an increasing amount of MZI's in the system.
It could have been expected that the natural shellfish stock would increase a bit, since fishery from these stocks decreases with increasing MZI-seed mussel harvest.

There are two possible reasons for this effect: competition for food (and related processes) and the fact that an increasing part of the shellfish larvae goes into the MZI-route. At 40 Mkg MZI-seed mussels, the latter fraction is about 1.5% (not shown here). From Figure 13, where the absolute data from the upper Figure 11-graph are presented as relative values, it can be seen that the natural shellfish stock reduction is about 12%. Of this 12%, 1.5% can be explained by that fraction of larvae going into the MZI-route, and the larger part (the remaining 10.5%) is a result of other causes. This is explained later in more detail.



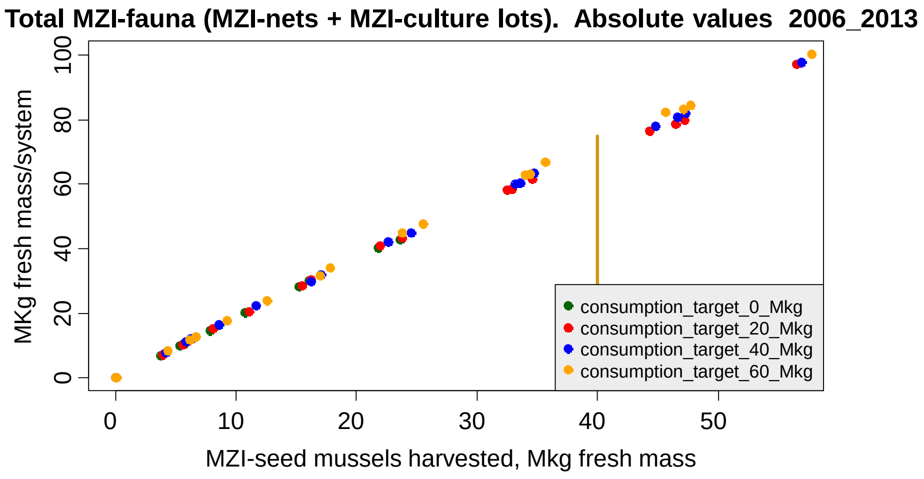


Figure 11 Shellfish stock in the system, natural stock (top) and MZI-related stock (bottom). . MZI includes MZI-nets and MZI-mussels presented at culture lots. Absolute values.

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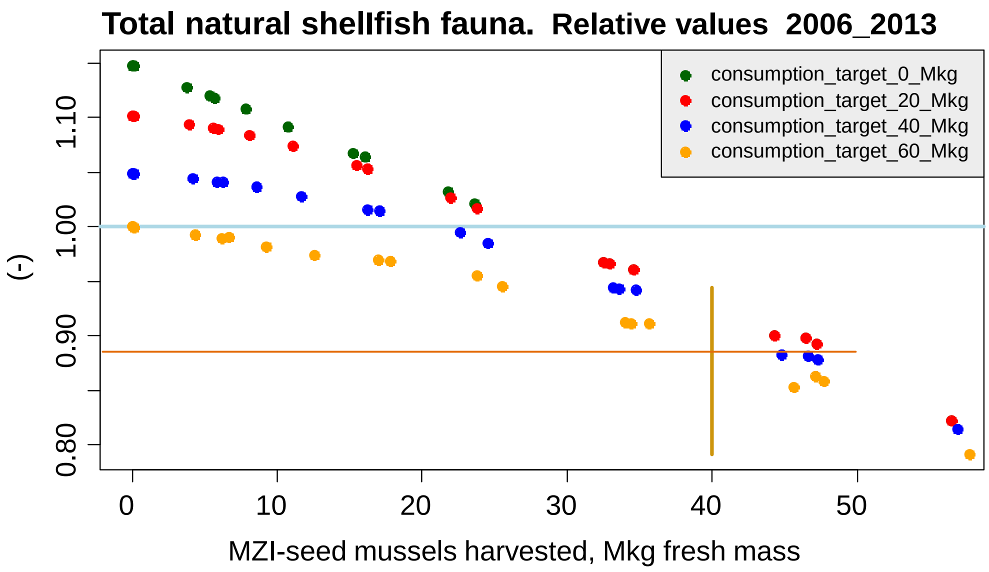


Figure 13 Natural shellfish stock in the system, relative to a situation without MZI's in the system. The reference situation is the one with an auction target of 60 Mkg fresh mass (the yellow dots). Absolute values are in Figure 11.

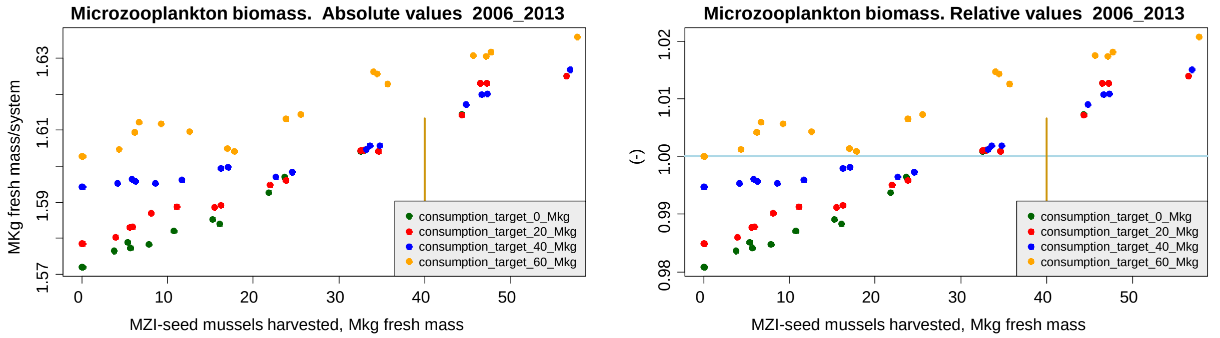


Figure 12 Microzooplankton biomass (Mkg fresh in the system). Left: absolute values, right (values relative to the reference situation: 60 Mkg auction target without MZI's in the system).

4.4 Microzooplankton

In Figure 12 the computed microzooplankton biomass is shown: microzooplankton contributes less than 0.5 percent to total fauna biomass. With increasing MZI-seed mussel harvest, microzooplankton amounts increase as well, but differences are not more than about 1-2% in the 60 Mkg auction target case with 40 Mkg MZI-seed mussels harvest.

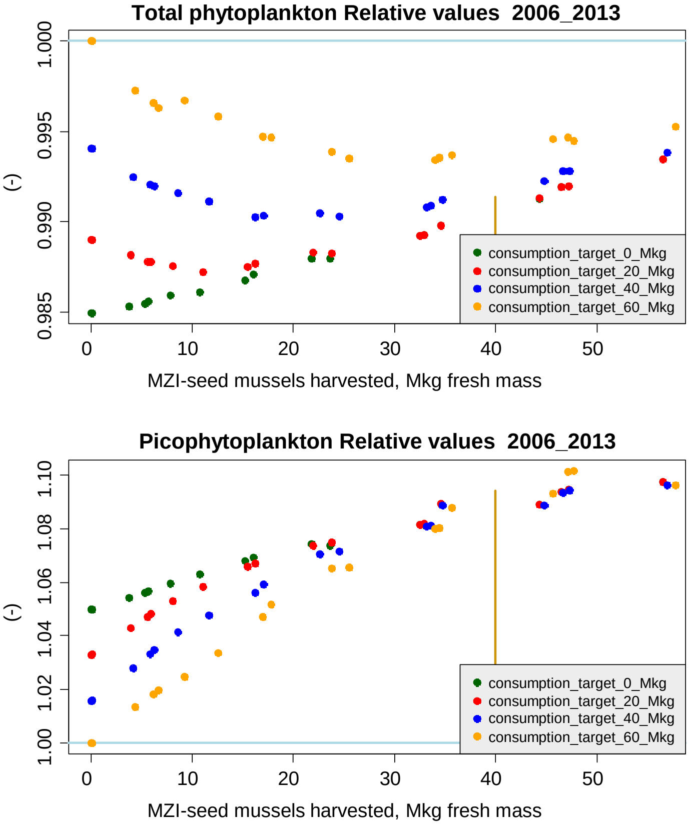


Figure 14 Relative changes in biomass of total algae (upper) and of picophytoplankton (lower), averaged for the period 2006-2013. All values relative to a 60 Mkg auction target (yellow dots) and without MZI's (X-axis=0). Orange & blue lines represent a target net harvest of 40 Mkg fresh mass. Note the different scales.

4.5 Phytoplankton

Relative changes in total phytoplankton and picophytoplankton abundance are shown in Figure 14. Whereas average total phytoplankton content is almost constant, some increase of picophytoplankton is computed with increasing amount of MZI-mussels.

4.6 Primary and secondary production

With increasing MZI-seed production, both primary and secondary production increase. In Figure 15 results are shown for all scenarios; all values relative to a situation without MZI's. The reference value chosen is the 60 Mkg fresh mass auction target.

Primary production increases only slightly with increasing MZI-seed mussels harvested from the nets. For the reference situation this is about 4% for 40 Mkg seed mussel harvest.

Secondary production increases about 7-8% for a 60 Mkg auction target and 40 Mkg seed mussel harvest. It does not show a maximum as total fauna stock does (Figure 10).

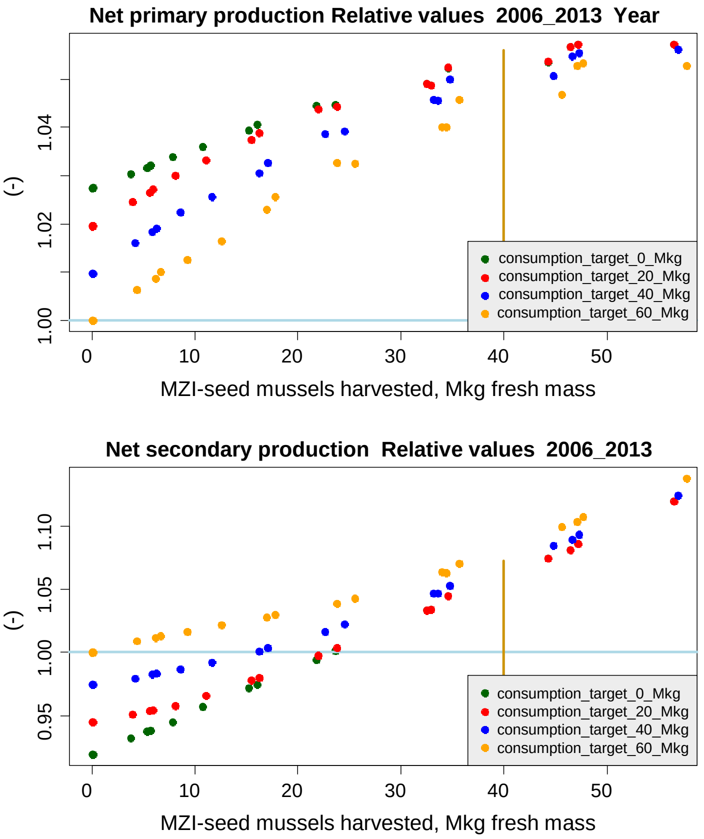


Figure 15 Average yearly net primary (upper) and secondary (lower) production in the system for the period 2006-2013. All relative to a situation without MZI's in the system (X-axis==0). The reference situation here is the one with an auction target of 60 Mkg fresh mass (the yellow dots).

4.7 Grazing pressure

Grazing pressure is to be seen as the rate at which the water column is filtered by fauna. A value of 0.1 (d^{-1}) means that every day 1/10th of the water volume is cleared from phytoplankton. Grazing pressure varies a lot during a year with highest values in the summer period and lowest during winter.

Grazing pressure by all fauna together, by natural shellfish, by MZI-mussels (culture plus net-mussels) and by microzooplankton is presented in Figure 16. Natural shellfish grazing pressure decreases a bit (about 0.04 d^{-1} at 40 Mkg net harvest) and is replaced by 0.06 d^{-1} MZI-grazing pressure. Microzooplankton grazing increases slightly (about 0.03 d^{-1}). These together explain the slight increase in total grazing pressure (about 0.04 d^{-1}) completely. Grazing pressure by natural shellfish decreases about 17% (at 40 Mkg MZI-seed mussel harvest) relative to the reference situation). This is a bit larger than the natural shellfish biomass decline of about 10-12% (Figure 13).

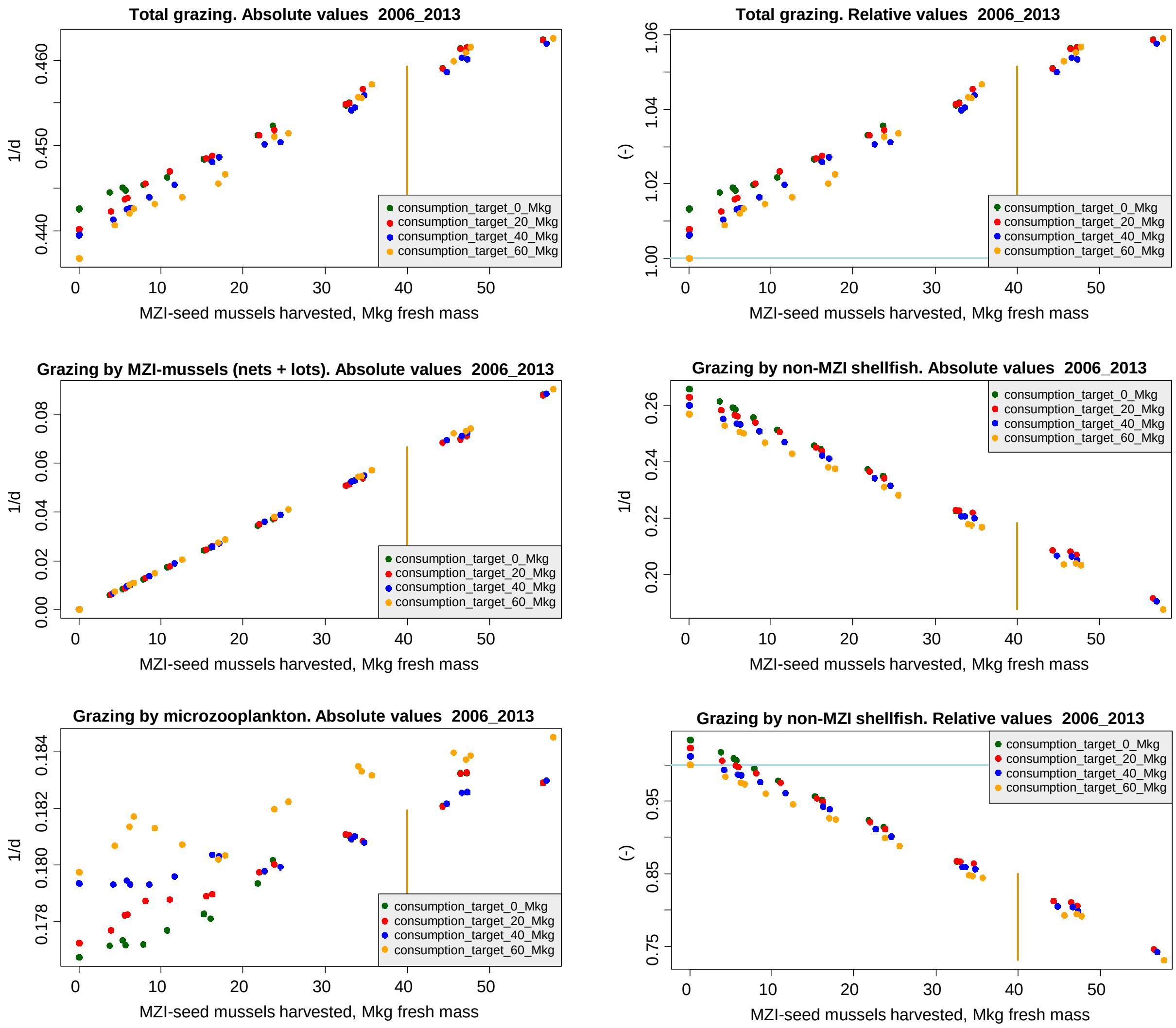


Figure 16 Grazing pressure, related to the net harvest. Averages for the period 2006-2013. Upper left: total grazing pressure, including microzooplankton. Upper right: ditto, but now relative to the reference situation: 60 Mkg auction target without MZI's in the system (X-axis =0). Middle left: grazing pressure by MZI-mussels (nets+lots), middle right: grazing pressure by non-MZI shellfish. Lower right: same as middle right, now relative to the refrence situation. Lower left: grazing pressure by microzooplankton.

This difference is caused by the fact that with increasing MZI-contribution less adult natural shellfish are removed from the system: the size distribution of natural shellfish moves a bit to the larger animals.

4.8 What happens during the MZI-period, some details

In the previous sections it was explained what the model computations tell about the effects of the MZI-process as a whole, thus combining the period of MZI-nets plus the periods the MZI-mussels are on the culture lots.
In this section, characteristics of the model results are restricted to the period the nets are present: from spawning to the moment shortly after the seed mussels are harvested from the nets. The results concern a first year: all the previous years no MZI's have been present in the model simulation. And, similar to the other computations, a certain fraction of all shellfish larvae is supposed to attach to the MZI-nets. At the moment of harvest, the MZI-seed mussels have grown; the biomass harvested from the nets is mentioned here in all the graphs. This harvest is not the same as in the other computations, since here it concerns just one first year; in the other computations the harvests mentioned concern the average harvest for the whole period 2006-2012. Before the net harvest, no MZI-mussels are present at the culture lots.

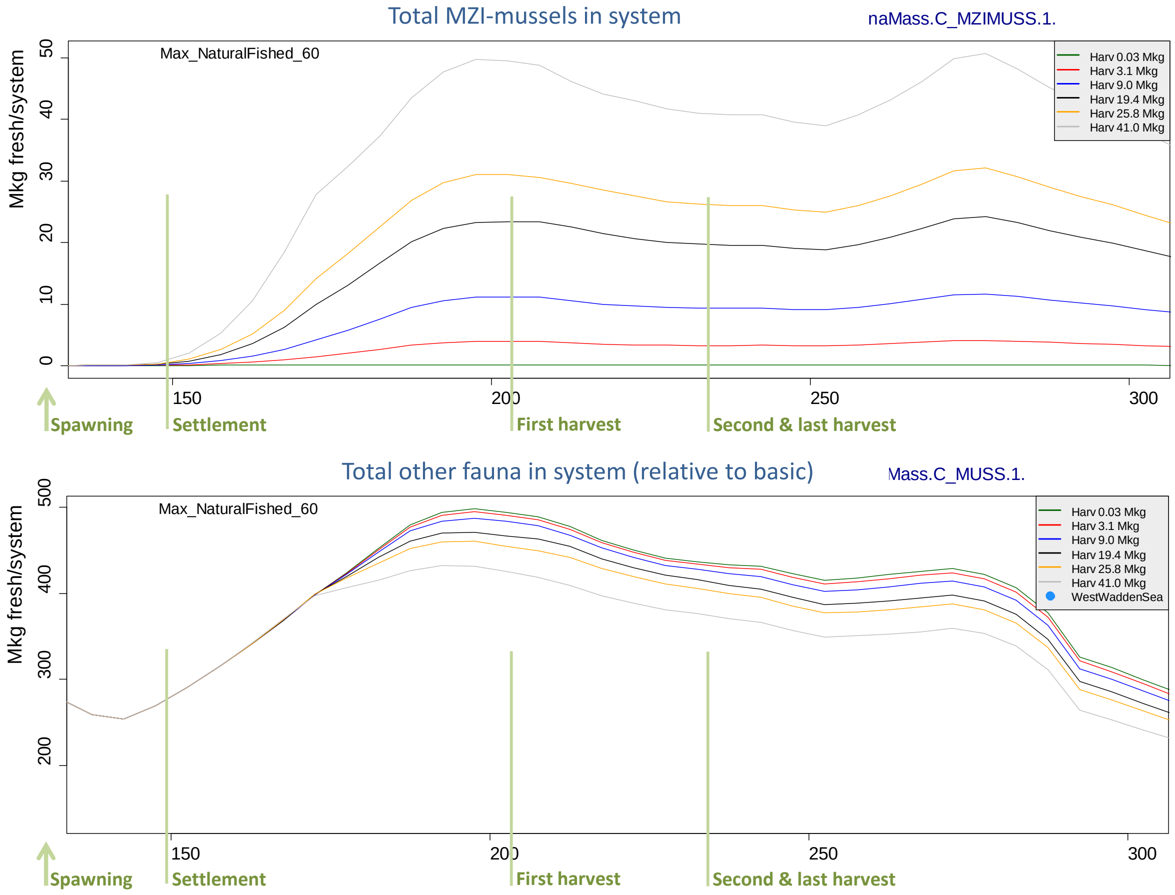


Figure 17 Shellfish biomass in the system. Above: MZI-mussels alone, below: total other shellfish (no MZI-mussels included). Data in Mkg fresh mass. At the moment of settlement, MZI-mussels have a better chance for survival, and biomass at the nets increases fast. After the second harvest (which is also the last harvest; it takes place around mid august) no more mussels are present at the nets. Before the net harvest, no MZI-mussels are present at the culture lots.

The computed development of biomass in the western Dutch Wadden Sea is shown in Figure 17. First all shellfish biomass increases, but roughly halfway the MZI-period natural shellfish starts to be affected by the strong increase of the mussels at the nets.

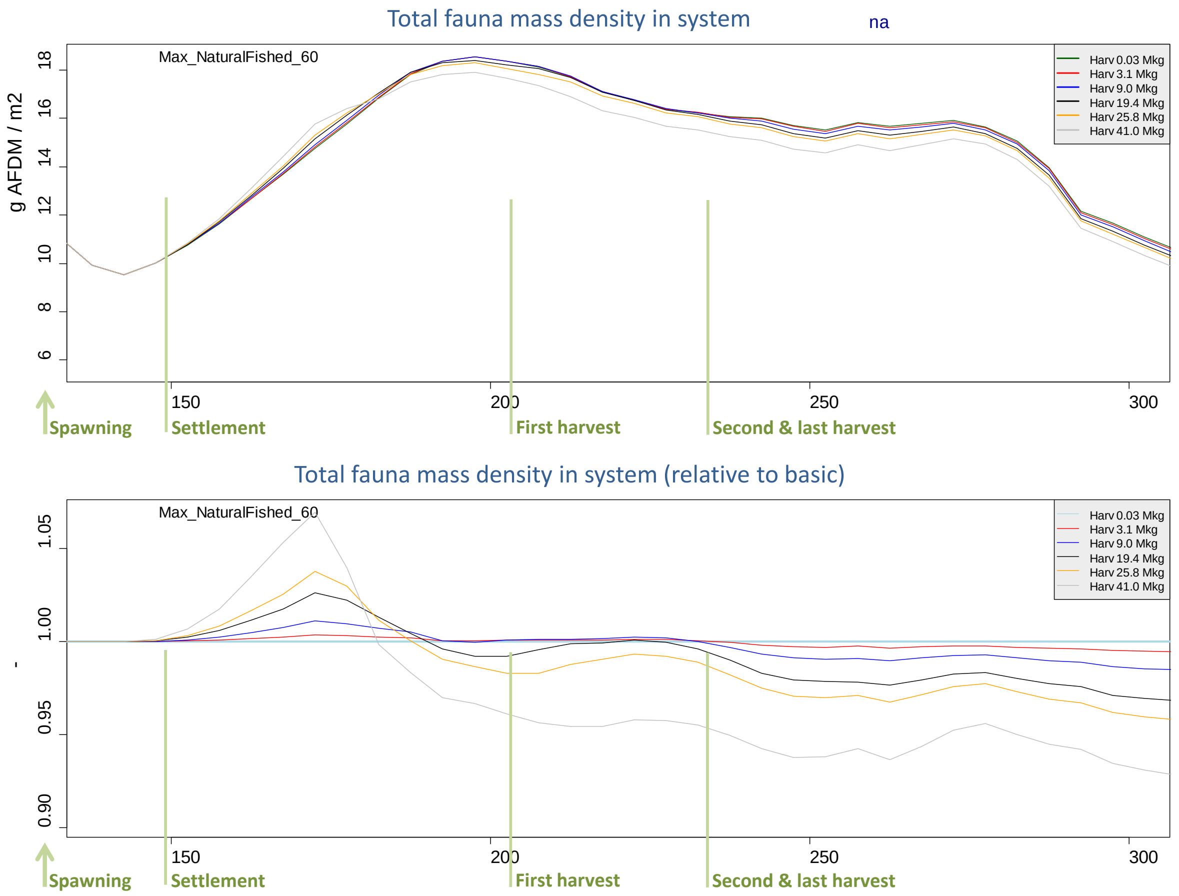


Figure 18 total fauna density in the system. Upper: absolute values computed (g AFDW/m2), lower: densities relative to the situation (almost) without MZI's.

This is also the message from Figure 18: first total shellfish biomass increases from the moment of settlement, but later this turns into a negative effect. The reason why is explained by Figure 19: grazing pressure by MZI-mussels at the nets increases rapidly, and as a result, the grazing pressure by other shellfish decreases, but less than this increase. Consequently, less food becomes available, as shown in Figure 20, and shellfish size development starts to lay behind a bit (Figure 21).

Later on (between first and second harvest, see Figure 19), grazing rates decrease, phytoplankton biomass increases (to values even larger than the case without MZI's, Figure 20), but this is not enough to eliminate all effects of the period before the first harvest. Other shellfish development stays behind as it was (Figure 21).

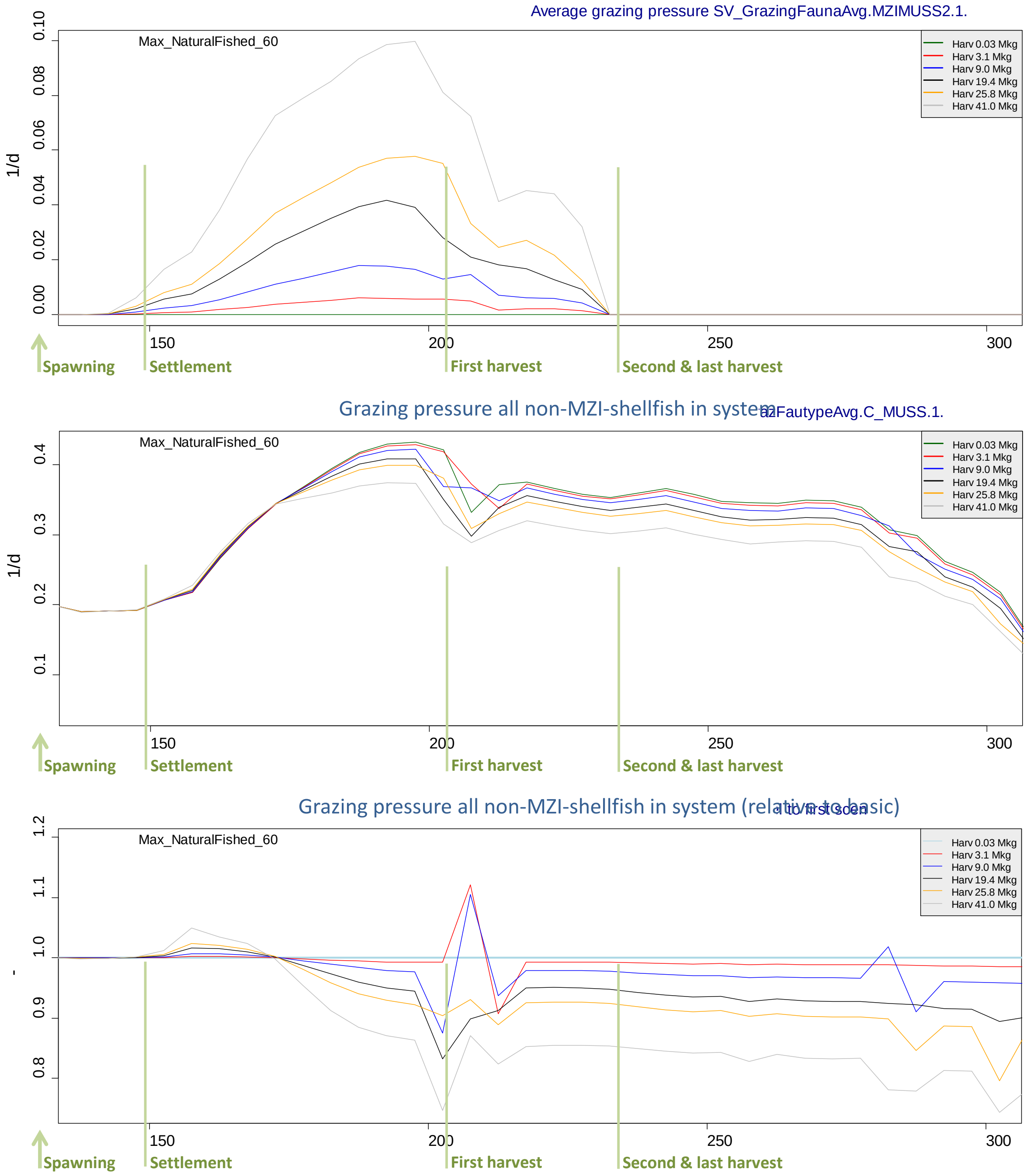
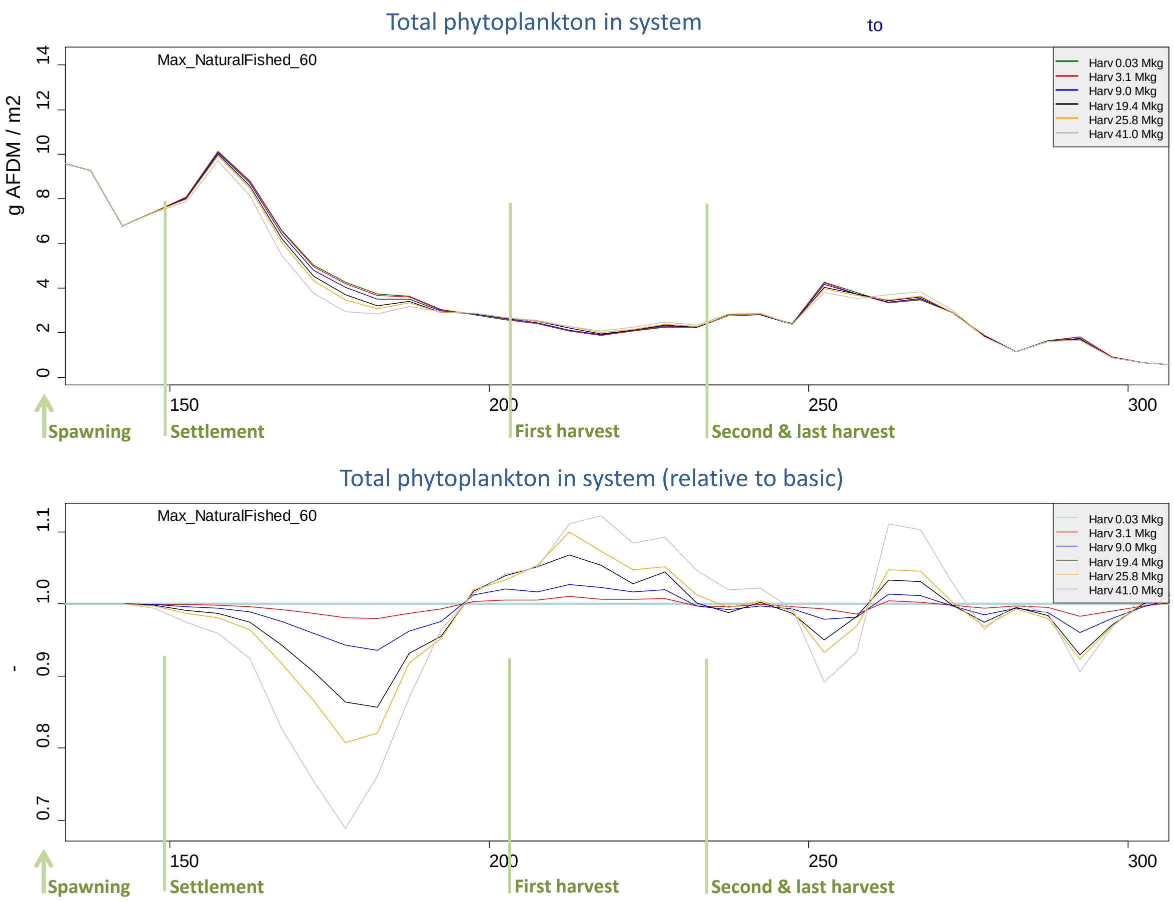


Figure 19 Grazing pressure in the system (average whole western Dutch Wadden Sea). Upper: grazing by the MZI-seed mussels while at the nets. Middle: grazing by all non-MZI shellfish, absolute values (d^{-1}). Lower: as middle, but relative to the situation without MZI's.



Total phytoplankton in system

Total phytoplankton in system (relative to basic)

Figure 20 Total computed phytoplankton biomass in the system of the western Dutch Wadden Sea (as g AFDW/m2).

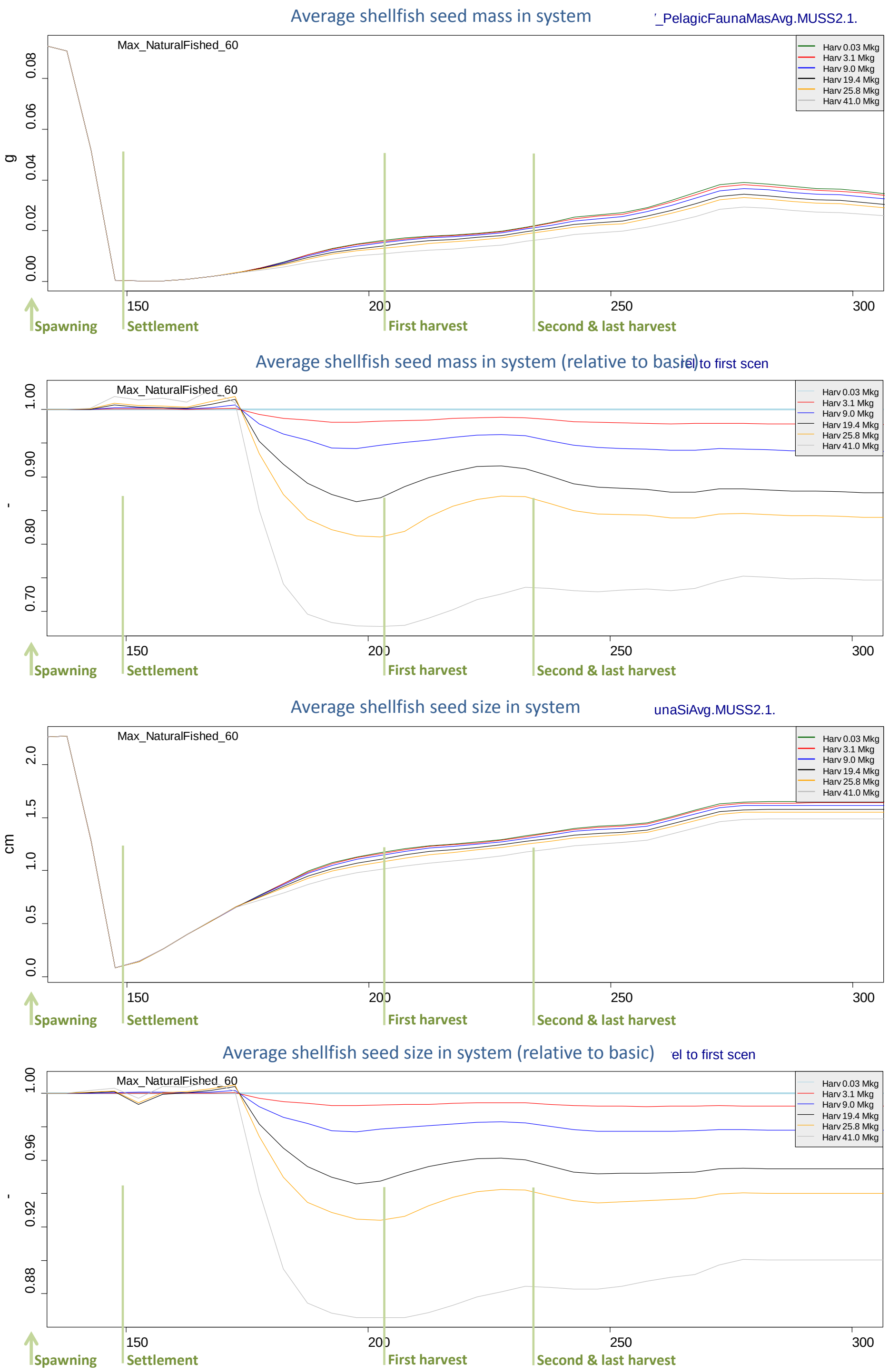


Figure 21 Development of non-MZI shellfish seed. Upper two: individual biomass (g) and biomass relative to the situation without MZI's; lower two: individual length (cm) and length relative to a situation without MZI's. Average values for whole western Dutch Wadden Sea.

4.9 Total shellfish stock and real mussels

In the previous sections, there was no difference made between the total shellfish stock and mussels, except for the MZI-mussels. "*Model-mussels"* represented all other shellfish. In reality, only a part of the natural shellfish stock consists of real mussels (*Mytilus edulis*), and a larger part is other shellfish, with species like cockle (*Cerasteroderma edule*), razor shell (*Ensis directus*), sandgaper (*Mya*

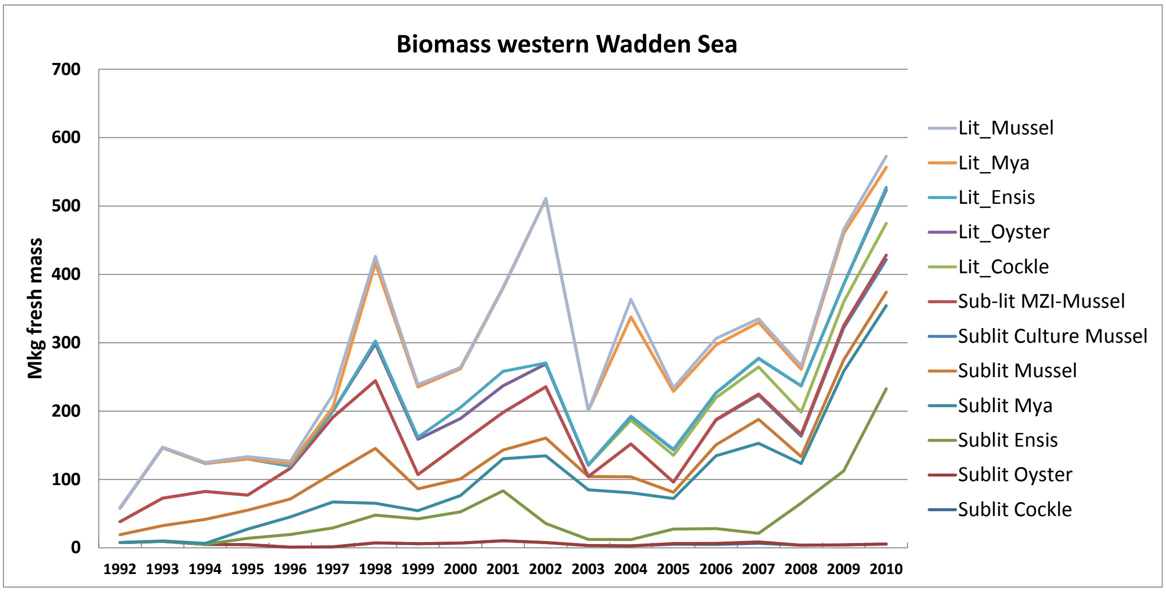


Figure 22 Estimated western Wadden Sea biomass. Taken from an overview by Schellekens (2012) . Lit== litoral, Sub-lit = sublitoral. After measurements by IMARES and after a data compilation by Schellekens (2012). Data are cumulative.

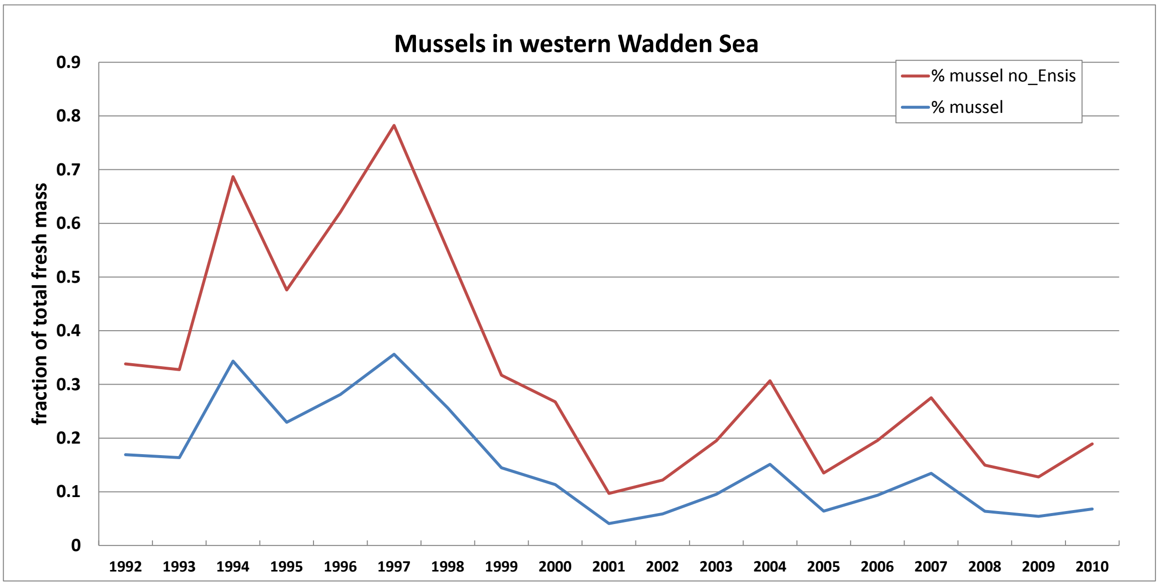


Figure 23 Part of the western Wadden Sea biomass that is mussel (*Mytilus edulis*). After a data compilation by Schellekens (2012). In blue: % 'real' mussel if the estimates for Ensis are taken into account; if not: this % is represented by the red line represents the % 'real' mussels.

arenaria) and pacific oyster (*Crassostrea gigas*). According to the estimations made by Schellekens (2012, see Figure 22) mussels only make out 10-20% of the western Wadden Sea biomass. In Figure 22 and Figure 23, the estimated amount of *Ensis directus* and *Mya arenaria* make up a large part of the total shellfish stock, and especially these two estimates have a large uncertainty. Thus, the estimated part that is really *Mytilus edulis* also has a large uncertainty. Nevertheless, it is expected that especially *Ensis directus* makes up a considerable part of the Wadden Sea biomass (comm. Dekker, NIOZ).

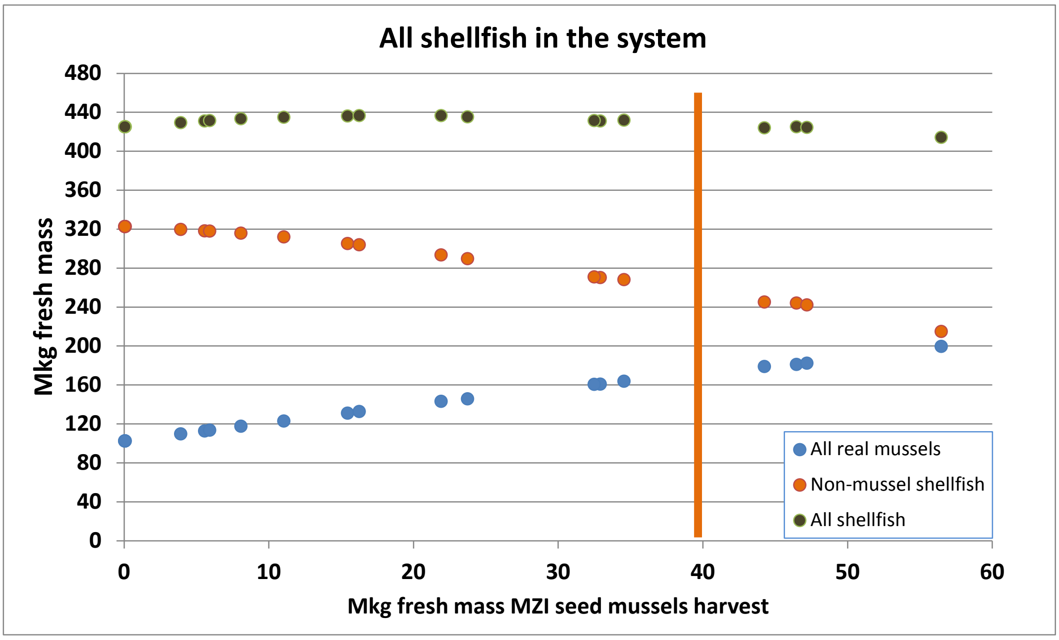
This has implications for the interpretation of the results. For example , if –as assumed in one of the scenarios- that 1% of the shellfish larvae goes into the MZI-route, and only 10% of these shellfish larvae really is a mussel, than about 10% of all mussel larvae will settle onto the MZI-nets.

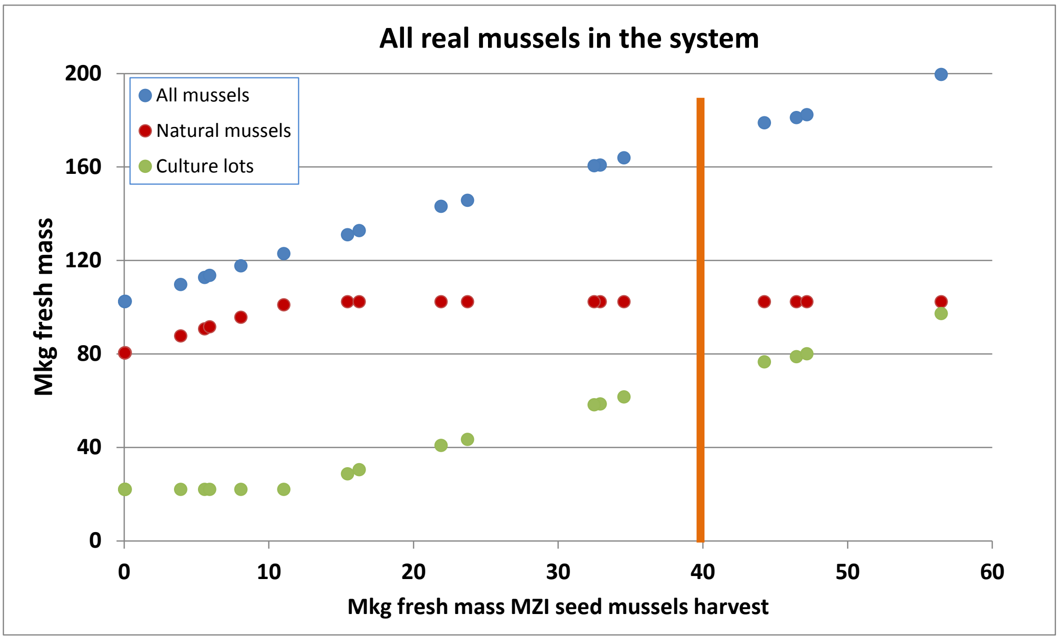
The question now is to estimate what this all means for the 'real' mussels in the system.

As an example, the reference situation (60 Mkg auction target) and 20 Mkg MZI-seed mussel harvest is taken.
For the 60 Mkg auction target situation: without MZI's present, total stock was 390 Mkg shellfish (Figure 11).
Of this 390 Mkg, 60 Mkg (about) is real mussel on the culture lots and thus, 330 Mkg is natural shellfish.
Of this remaining 330 Mkg, about 10% (according to the IMARES surveys, Schellekens, 2012) is real mussel (=33 Mkg), that makes a total of 99 Mkg of real mussels. That is 99/390=25% of all shellfish.
With an increasing number of MZI's (expressed as Mkg MZI seed mussels harvested), the amount of natural mussels fished will decline, and the percentage of mussel larvae that goes into the MZI-route increases (and the percentage going into the natural route decreases). The latter is just a minor effect: at 40 Mkg MZI seed mussel harvest, and 25% of all shellfish is real mussel (natural mussel plus mussels on the culture lots) only 4% of all mussel larvae are needed for the MZI's (under the present model conditions).

These calculations have been done for all the MZI-seed mussel harvests, for two auction scenarios. In Figure 24, the 20 Mkg and in Figure 25, the 60 Mkg auction targets are shown.
In both cases, the model computes an increase in real mussel stock from about 100 Mkg (no MZI's) to about 160-170 Mkg (at 40 mkg MZI seed mussel harvest). Thus, according to the model computations, replacing the natural seed mussel fishery by seed mussel supply from MZI's enhances the mussel stock in the system.

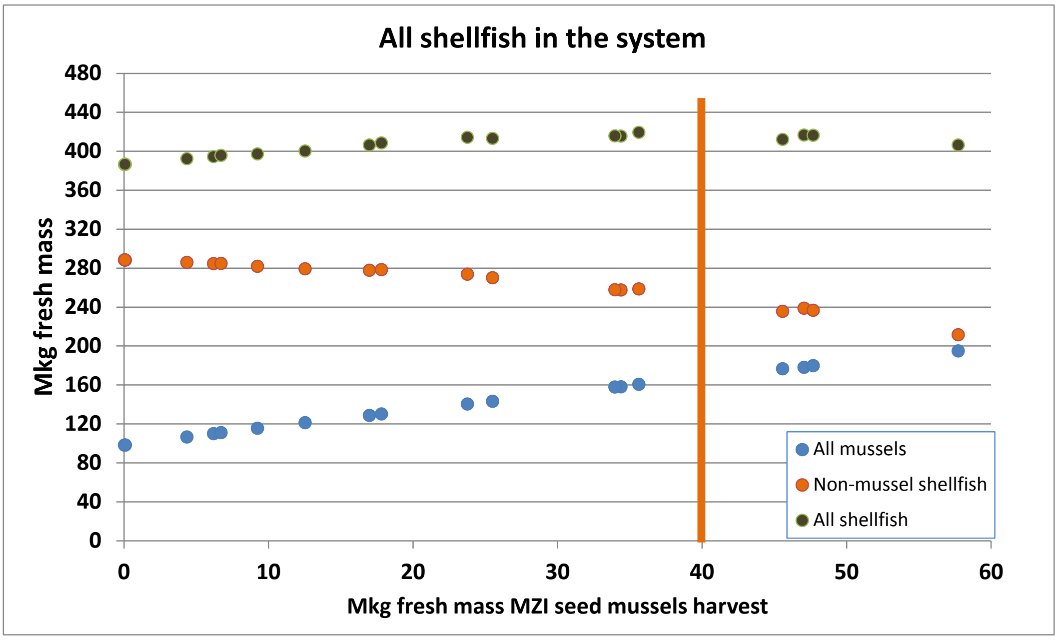
The model also computes a decreasing stock of other shellfish with increasing MZI harvest. This

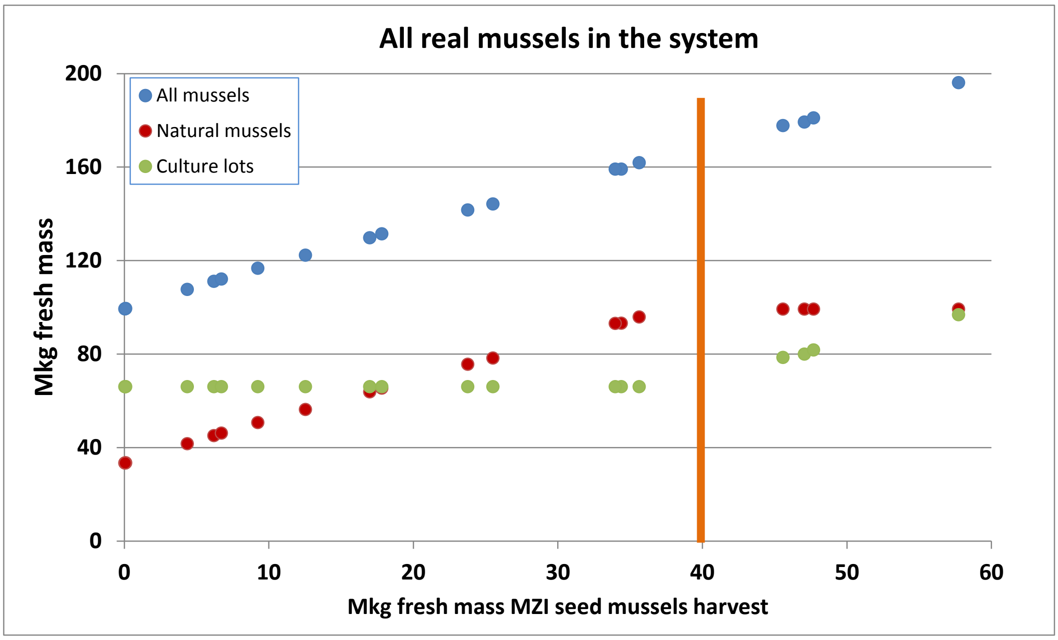




Scenario 20 Mkg auction target

Figure 24 What is real mussel in the system, and what is other shellfish; model results for the situation with an auction target of 20 Mkg (fresh mass). Upper: All shellfish, divided into real mussels and other species. Lower: real mussels in the system, divided into natural mussels and mussels on the culture lots. With increasing amount of MZI seed mussel harvest (X-axis), the amount of natural mussels fished and brought to the auction decreases (and finally becomes zero) (see Figure 9).





Scenario 60 Mkg auction target

Figure 25 What is real mussel in the system, and what is other shellfish; model results for the situation with an auction target of 60 Mkg (fresh mass). Upper: All shellfish, divided into real mussels and other species. Lower: real mussels in the system, divided into natural mussels and mussels on the culture lots. With increasing amount of MZI seed mussel harvest (X-axis), the amount of natural mussels fished and brought to the auction decreases (and finally becomes zero) (see Figure 9).

is due to i) a competition for food and ii) a slightly increased predation upon larvae. The real mussels also suffer from this increasing competition and larvae predation, but the positive changes due to the increasing MZI-harvest are much larger than these two negative effects.

4.10 Amount of larvae and larvae activity

Average computed numbers of shellfish larvae (partly as ‘MZI’-larvae and the rest of all shellfish larvae) are shown in Figure 26. De Vooijs (1999) mentioned up to 100000 mussel larvae per m^3. The model computes a bit higher values. The computed values thus are not very unrealistic. The larvae settle as soon as they are large enough; and those larvae that go into the MZI-route (MZIMUSS1) become MZI-seed mussels (lower graph in Figure 26). In Figure 28, biomass density (g DW m^{-3}) is shown: the MZI-biomass increases a lot in a few weeks. The size development is tested against the MZI-data (Janssen, 2012; data by Jacobs, pers. comm.): the MZI-seed length reaches about 2 cm at the moment of harvest from the nets.

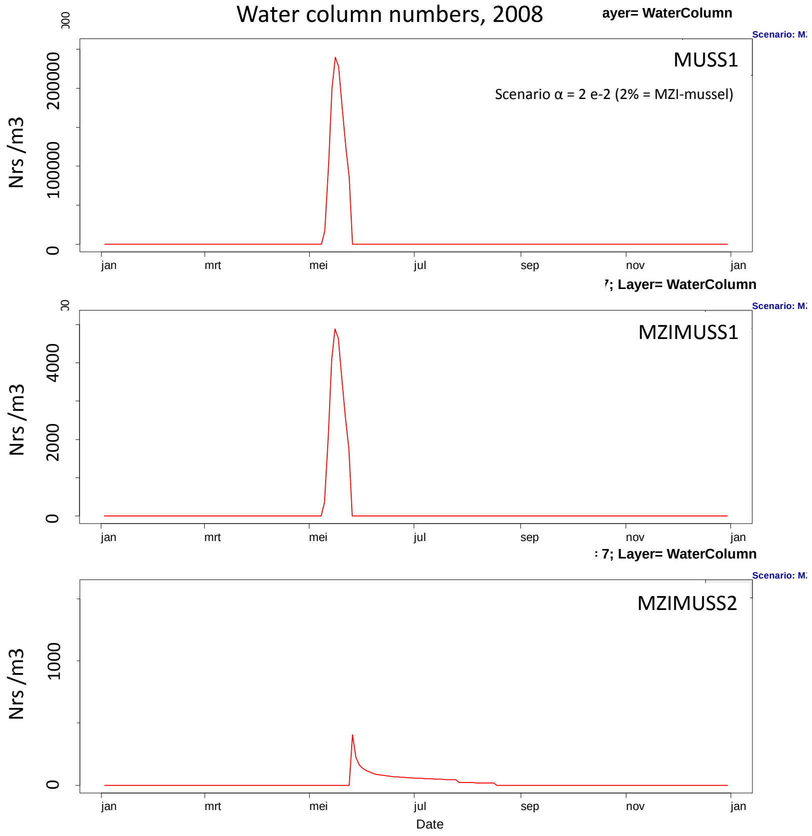


Figure 26 Numbers of mussel and MZI-mussel larvae in the water column, and MZI-mussels at the nets. All in nrs m^{-3}

Grazing pressure by shellfish larvae on the system is much lower than that of all shellfish together (Figure 27).

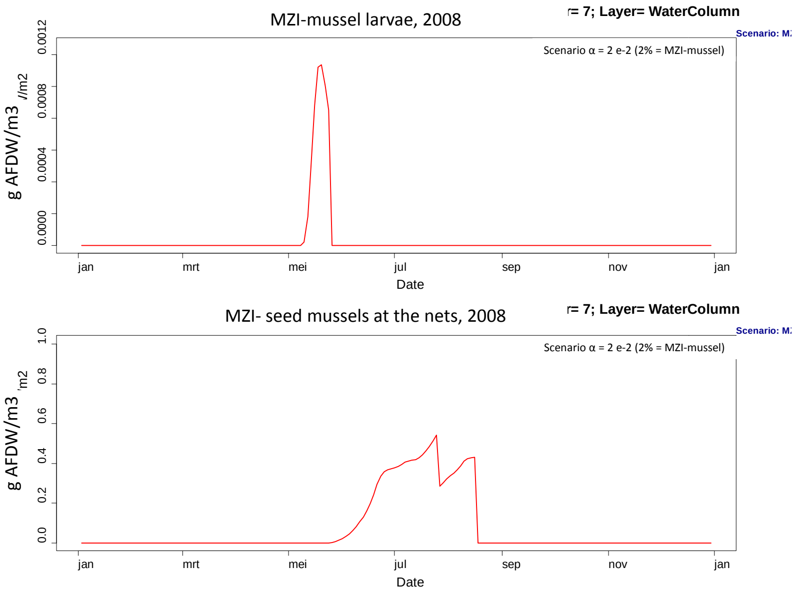


Figure 28 Computed biomass density of MZI-larvae and of MZI-seed mussels at the nets, results for the year 2008.

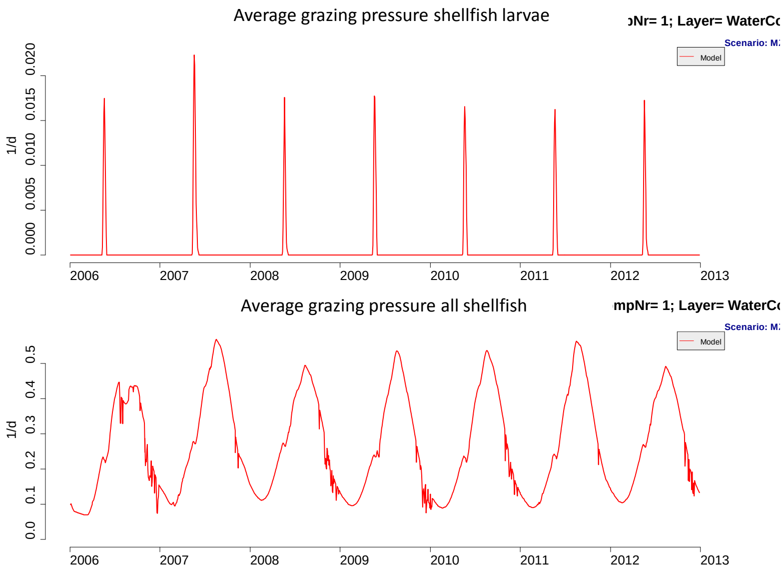


Figure 27 Computed grazing pressure of shellfish larvae and of all shellfish together

4.11 Food for birds, all shellfish

The model calculates the total amount of shellfish that dies (as explained in appendix IV). It is assumed that mortality is nothing else than predation by some other organism: the mortality gives the amount of food produced by the shellfish population for predators, including birds.

The amount of shellfish that dies is grouped into size classes; the upper boundaries are given in Table 1.

Total fauna mortality –including all size classes- is given in Figure 29. An increase is computed from 365 (at 0 kg MZI-seed harvest) to 385 Mkg fresh mass yearly (at 40 Mkg MZI-seed harvest). This is exclusive the yearly withdrawal of mussels from the culture lots (amounts given in Figure 8, lower graph), but including the mortality of the MZI-mussels during their stay on the culture lots.

Upper size class boundary (m)
SizeClasses[1] = 1.0e-5;
SizeClasses[2] = 1.0e-4;
SizeClasses[3] = 1.0e-3;
SizeClasses[4] = 5.0e-3;
SizeClasses[5] = 1.0e-2;
SizeClasses[6] = 0.02;
SizeClasses[7] = 0.03;
SizeClasses[8] = 0.04;
SizeClasses[9] = 0.05;
SizeClasses[10] = 0.06;
SizeClasses[11] = 0.08;
SizeClasses[12] = 1.0;

Table 1 Upper size class boundary (m) for fauna mortality. For example; the amount of shell fish that died while it was between 3 and 4 cm large is summed in class 8. See appendix IV for details.

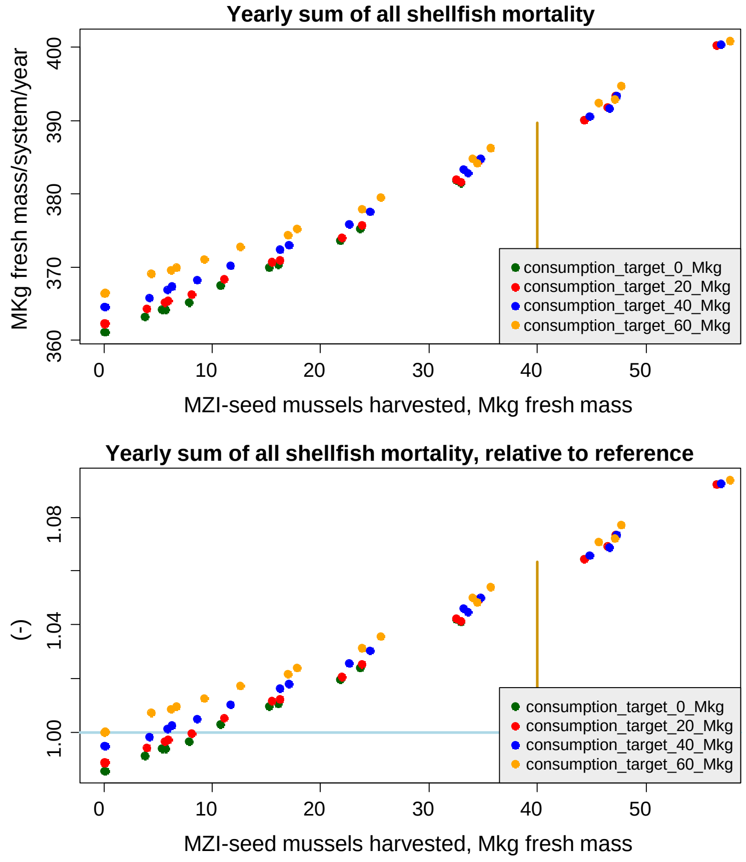


Figure 29 Total yearly shellfish mortality. Upper: absolute, lower: relative to the reference scenario (60 Mkg auction target –yellow dots- and no MZI's present). X-axis: total MZI-seed mussel harvest.

There seems to be only a minor effect of the auction target: whether this is zero or 60 Mkg mussels, the yearly mortality is almost the same.

Some more detail is illustrated in Figure 29. For example, for the reference situation (an auction target of 60 Mkg mussels) the model computes a decrease in the yearly average mortality in the 4-5 cm size class from 61 to 54 Mkg fresh mass (with an optimum of 66 Mkg at 5 Mkg MIZ seed harvest), and a decrease in the 5-6 cm size class (from 85 to 45 Mkg fresh mass) .

The amount needed for 80000 Oystercatchers plus 40000 Eider Ducks (see Smit et al, 2011) is 100 Mkg fresh mass yearly. And thus, the results shown in Figure 30 would indicate that there is enough food for these birds produced: the amount of 3-6 cm reaches an annual value of about 180 Mkg at a zero-MZI situation, and about 200 Mkg at an average yearly MZI seed mussel harvest of 40 Mkg fresh mass.

However,

- only a part of this amount can be eaten by birds since not all shellfish (Ensis, Mya, Pacific Oyster) are available for birds
- birds are not the only predator: also starfish and crabs predate upon these shellfish size classes.

The numbers mentioned here should be taken as qualitative indications of what happens in the system with increasing MZI-seed harvest and different auction targets.

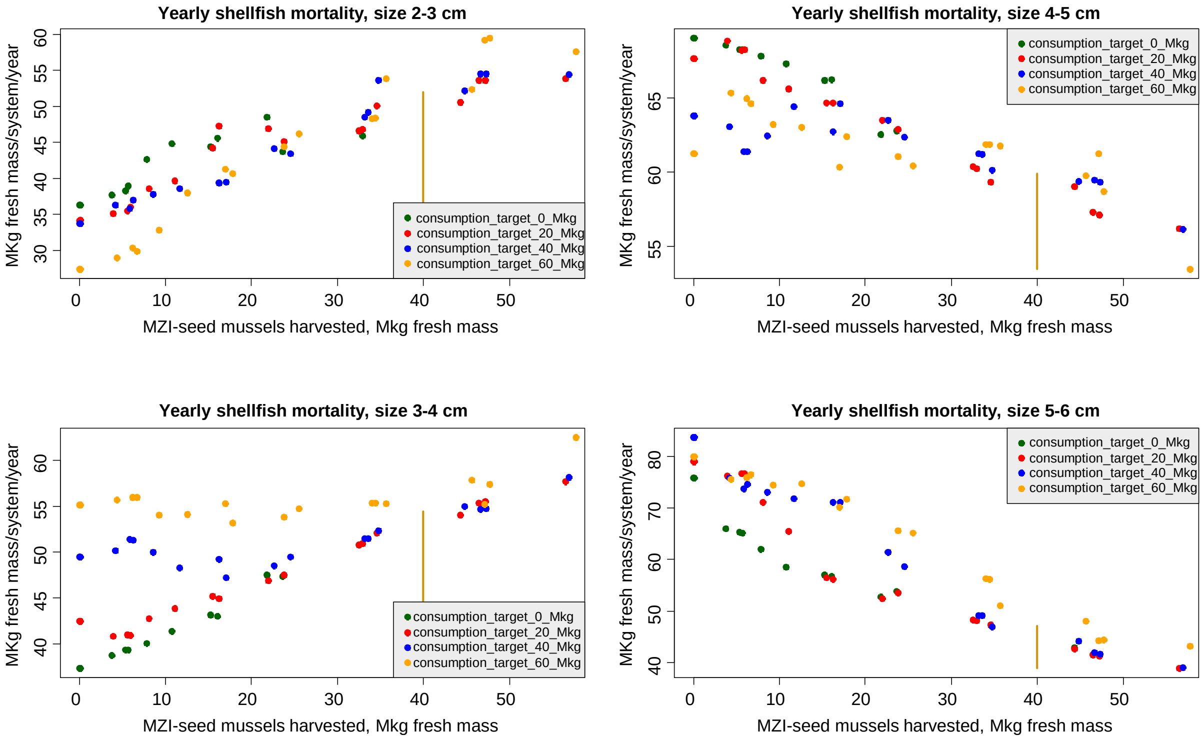


Figure 30 Illustration of shellfish larger size class mortality changes. There is an increasing mortality computed in smaller size classes, and decreasing mortality in larger size classes.

4.12 Food for birds, real mussels alone

In the previous section, the mortality of all shellfish was discussed. Since only a part of the shellfish actually is available to birds, it is hard to interpret such results correctly.

Another possibility is to regard the computed stock of real mussel s (Figure 24 Figure 25). Real mussels are available to Eider Ducks and/or Oystercatchers.

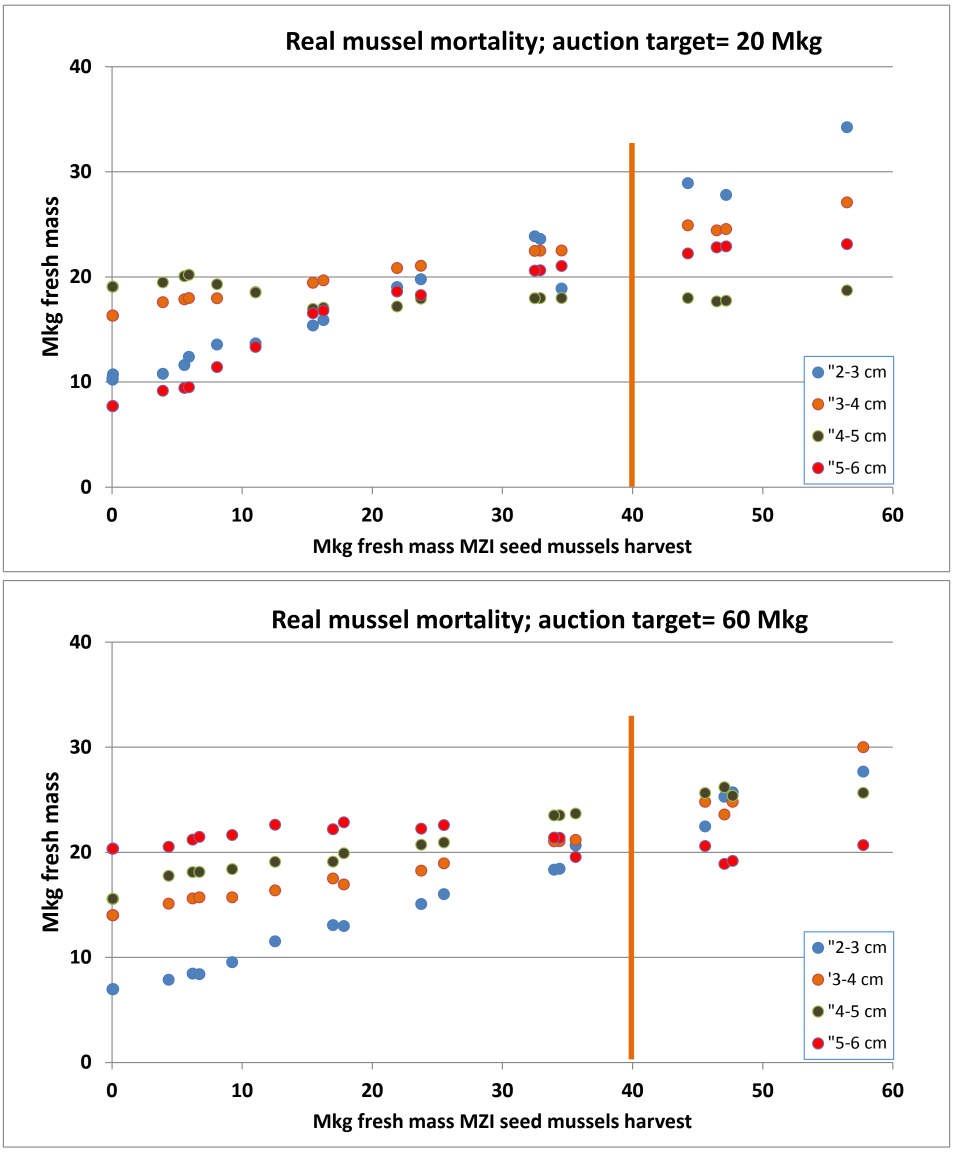


Figure 31 Estimated mortality of ‘real’ mussels (size classes 2-6 cm) in the system, as a function of the amount of MZI-seed mussels harvested. In Mkg fresh mass per year. Upper: auction target= 20 Mkg fresh mass, lower: auction target= 60 Mkg fresh mass.

In Figure 31, an estimate for the amount of real mussels, size between 2 and 6 cm, that died per year. This is the amount that is assumed to be eaten by birds and other large predators (crabs, starfish). Results are shown for two auction targets (20 resp. 60 Mkg fresh mass). It can be concluded that total mussel food available for birds increases with increasing MZI-harvest. Without MZI's, the model computes about 55 Mkg mortality (=food available for Eiders and Oystercatchers) for both auction targets. At 40 Mkg MZI seed mussel harvest this values becomes about 90 Mkg.

This estimate probably is better than the one in section 4.11, although

- it now may be an underestimate in terms of biomass available for birds, since not only mussels (*Mytilus edulis*), but also cockles (*Cerasteroderma edule*), and the smaller *Mya arenaria* and some of the *Ensis directus* are edible by birds,
- the change with increasing MZI's will be different if the decline of non-mussel shellfish (cockles and the edible part of Mya and Ensis) is taken into account

The latter remark implies a somewhat different trend with increasing number of MZI's, but, for the reference situation (60 Mkg auction target) still an increase in food for birds results.

4.13 Differences between Vlie basin and Marsdiep basin

The next question now is whether there are differences between the two basins in the western Dutch Wadden Sea: the Marsdiep-basin (compartments 1-3 in Figure 6) and the Vlie-basin (compartments 4-6 in Figure 6).
This is *not* the case. The reason is that in each compartment, the part of the larvae that goes to the MZI's is the same, and also, larvae, shellfish seed and seed mussels from MZI's stay in the same compartment: there is no transport between compartments. Thus, in each compartment, the relative effects are similar.

4.14 Seasonal differences

Are there seasonal differences? The idea behind that question was that for example birds have a higher food demand in autumn and spring, compared to summer.
In Figure 32, amounts of total shellfish mass are shown relative to the reference situation (no MZI's, 60 Mkg auction target). The shape of all lines is very similar for all seasons, but the relative changes show some differences. These are smallest in summer and largest in autumn and in winter. That means that the increase in fauna biomass relative to the reference situation is largest in winter and smallest in summer. But also, relative to a pristine situation (no fishery at all), effects of mussel fishery are largest in autumn and in winter. This probably has to do with the fact that withdrawal of culture mussels takes place in autumn.

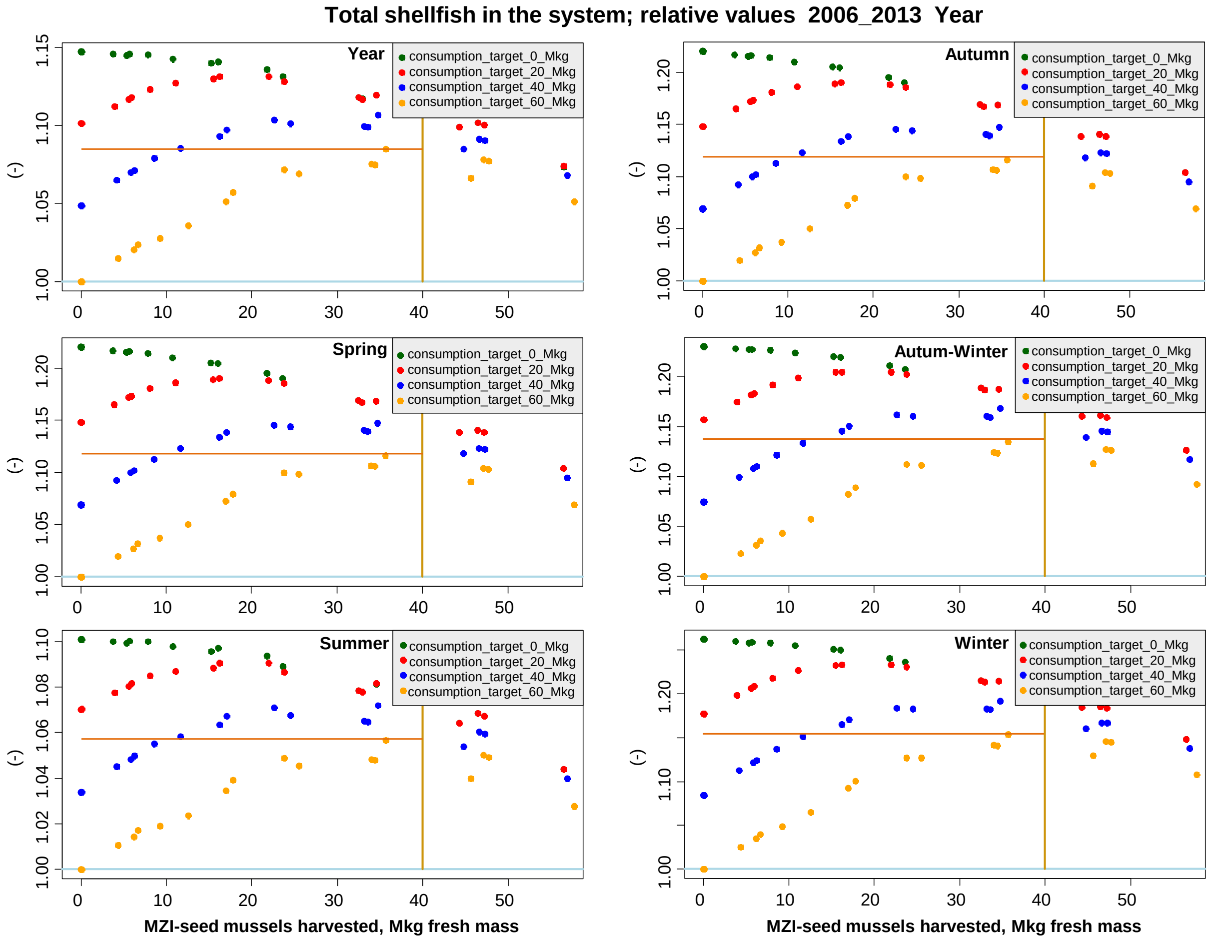


Figure 32 MZI-effect on total shellfish in the system, for several seasons and auction targets. All values relative to the reference situation: no MZI (X-axis=zero), 60 Mkg auction target (yellow dots). Auction targets in the figures: 0 Mkg fresh mass (green dots), 20 Mkg (red), 40 Mkg (blue), 60 Mkg (yellow). Upper left: year-average effect (same graph as Figure 10, but now relative values), middle left: spring (months 1,2,3,4), lower left: summer (months 4,5,6,7,8,9), upper right: autumn (months 8,9,10,11), middle right: autumn-winter (months 10,11,12,1,2), lower right: winter (months 1,11,12).

4.15 Conclusions

The major model results are

- MZI's have a positive effect on the total shellfish biomass in the modelled system compared to the situation where –in absence of MZI's- a certain amount of mussels is fished from natural beds. This conclusion is valid as long as the number of MZI's stays below an upper limit; this upper limit is related to the original amount of shellfish harvested from the system.
- The effect on total *mussel* biomass is even more positive with increasing number of MZI's.
- Non-mussel shellfish biomass is negatively affected by an increasing number of MZI's.
- This negative effect is mainly established in the early period of MZI-mussels at the nets

- Mussel culture activity itself has a negative effect on total shellfish biomass, mainly due to the yearly withdrawal of consumption mussels: the model computes the highest shellfish biomass in a pristine situation without any mussel culture. An important assumption here is that natural shellfish and mussels on culture lots have the same growth and mortality characteristics. In reality, mussels on culture lots probably have a lower mortality and have better growth conditions.
- MZI practice has a positive effect on shellfish biomass available as food for birds compared to a reference situation with 60 Mkg auction target
- Positive effects are all caused by the fact that withdrawal of natural mussel biomass is replaced by mussels originating from MZI-systems.

5 Discussion

5.1 Introduction

The major model results, mentioned in section 4.14, are coupled to mussel culture activities. The difference between a situation with and without mussel culture is mainly caused by the yearly withdrawal of mussels from the culture lots. But also, non-mussel shellfish biomass decreases with increasing harvest of seed mussels from these MZI's.

The reason for this is briefly discussed in the next sections.

5.2 Decline of non-mussel shellfish in the system

The amount of non-mussel shellfish in the system is presented in Figure 33 as a function of MZI harvest.

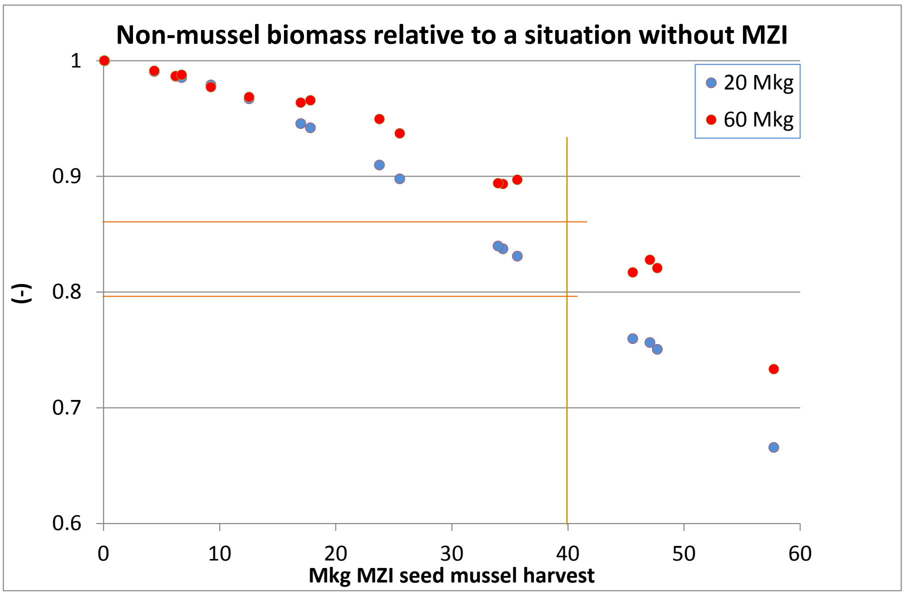


Figure 33 Biomass of non-mussel shellfish in the system, relative to a situation without MZI's. For an auction target of 20 Mkg fresh mass (blue dots) and of 60 Mkg fresh mass (red dots).

The cause for this behaviour has to be found in the activity of the animals. What happens with an increasing amount of MZI's in the system is that the number of small individuals increases: larvae settling on MZI-nets escape from dying upon settlement (this is an assumption made for these model simulations) contrary to larvae settling onto the sediment.

The activity of small animals per unit of biomass is much higher than of larger animals. This is illustrated in Figure 34.

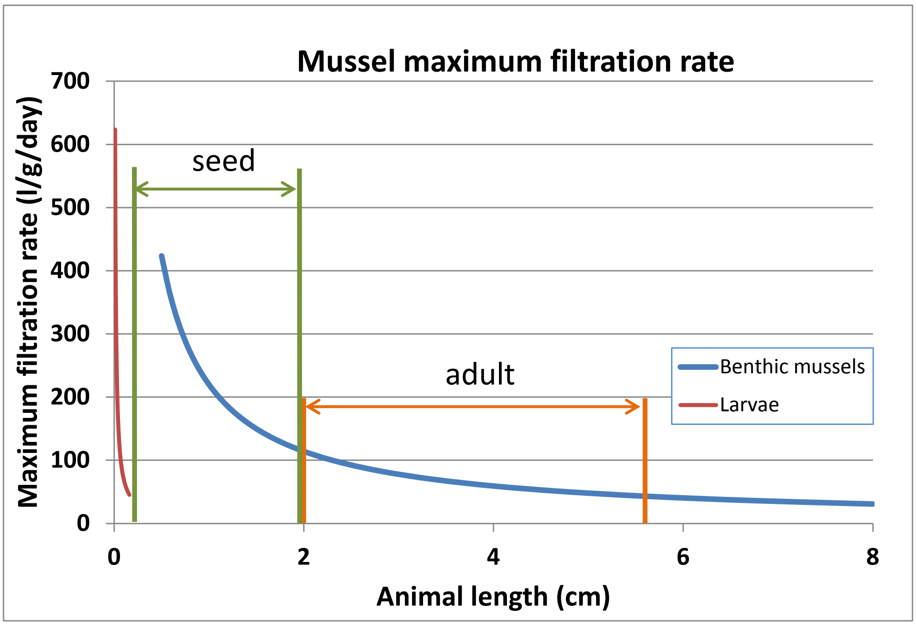


Figure 34 Maximum filtration rates per unit of DW body mass of shellfish larvae and of adult shellfish in the EcoWasp-model. Microzooplankton (40 um, 2 10^{-9} g) has a mass specific maximum filtration rate of 11 m^3 g^{-1} d^{-1} in the EcoWasp computations. The relevant regions for seed and adult shellfish are roughly indicated.

Seed mussels (MZI ánd natural) have a 4-10 times as high specific filtering activity compared to adult mussels. It is explained in appendix VIII that shellfish larvae have a much lower mass specific foraging activity than adult shellfish (including seed) has. This is illustrated in Figure 34.

The overall effect (larger shellfish replaced by a higher number of more active smaller animals) was already illustrated in Figure 16, and it can be viewed in more detail, see Figure 35. From this figure it can be seen that natural seed activity decreases with increasing MZI-seed amount, and drops roughly from 0.075 d^{-1} to 0.058 d^{-1} (=-22%) at 40 Mkg MZI-seed harvest and 60 Mkg auction target.
The absolute decrease in natural seed filtration activity is roughly 0.017 d^{-1}. However, the filtration rate of the benthic MZI-seed mussels increases about 0.03 d^{-1}, and that of seed mussels at the nets 0.008 d^{-1} (not shown here). Together an increase that is more than twice as high. Moreover, and this is illustrated in Figure 36, this process takes place in July-August, a period where phytoplankton content is relatively low (Figure 37). The scenario used for Figure 35 comes close to the grey lines in Figure 37.

The relevant effect to be observed is the decline in phytoplankton content just before day 200 in Figure 37. Phytoplankton content drops then with increasing amount of MZI-seed, and as a result,

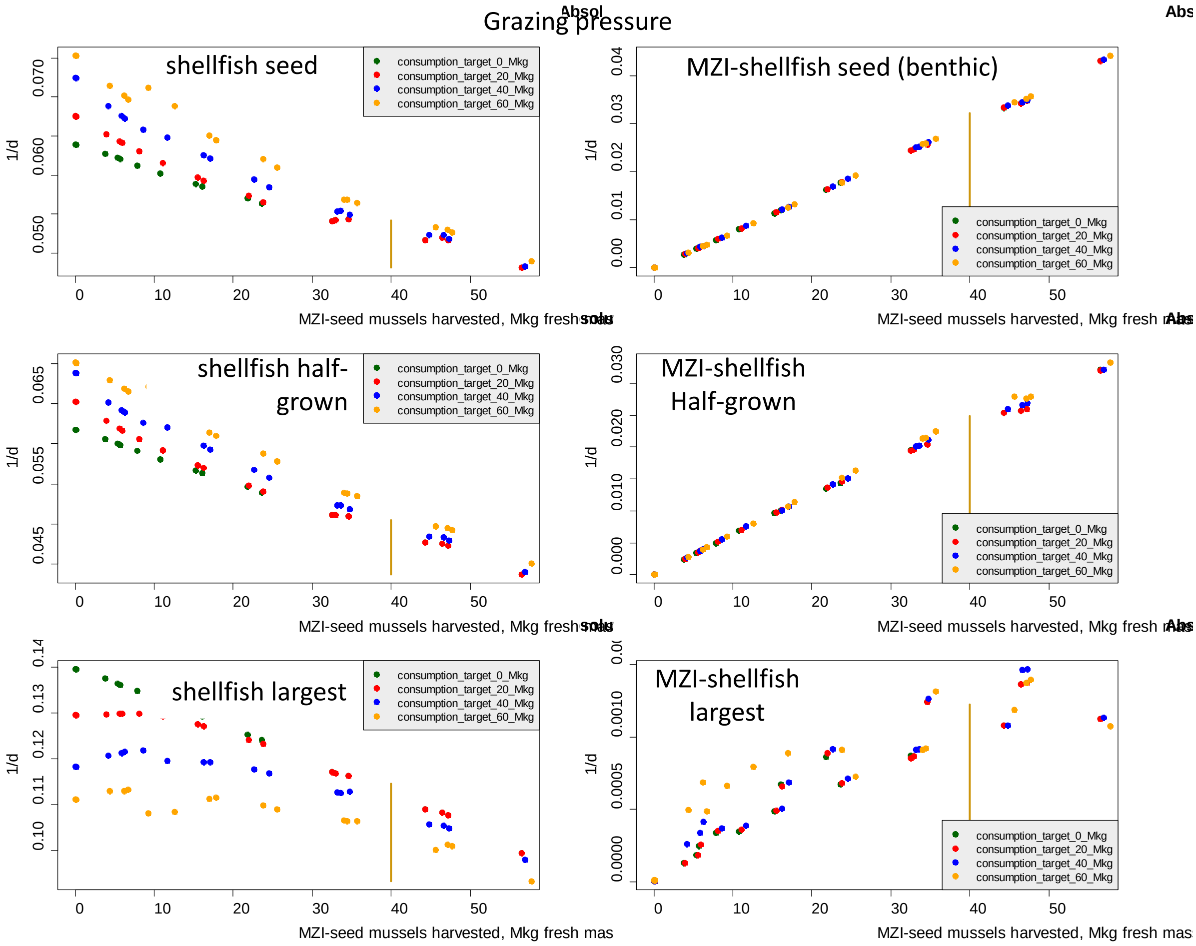


Figure 35 Grazing pressure by shellfish on the system. Y-axis: grazing pressure (d^{-1}), X-axis: fresh mass of seed harvested from the MZI's. All averaged over the period 2006-2013. Left: natural shellfish, left: shellfish originating from MZI's. Upper: benthic seed, middle: half-grown, lower: consumption size shellfish. Note that in the computations, 'half-grown' MZI-originating mussels most times are large enough to be harvested and brought to the auction. All computations for four auction targets: 0 Mkg (green), 20 Mkg (red), 40 Mkg (blue), 60 Mkg (yellow).

the average mass of seed shellfish decreases a bit (Figure 38). Note that larger shellfish does not show this characteristic. Next, the result of this lower individual mass of shellfish seed is that seed mortality increases (Figure 39). In the model, mortality is coupled to the size of the individuals: the smaller, the larger the mortality. This results in lower numbers (Figure 40). Adult shellfish sizes do nót decrease (Figure 38), typically showing that adult shellfish sizes do not necessarily give information on food availability or carrying capacity.

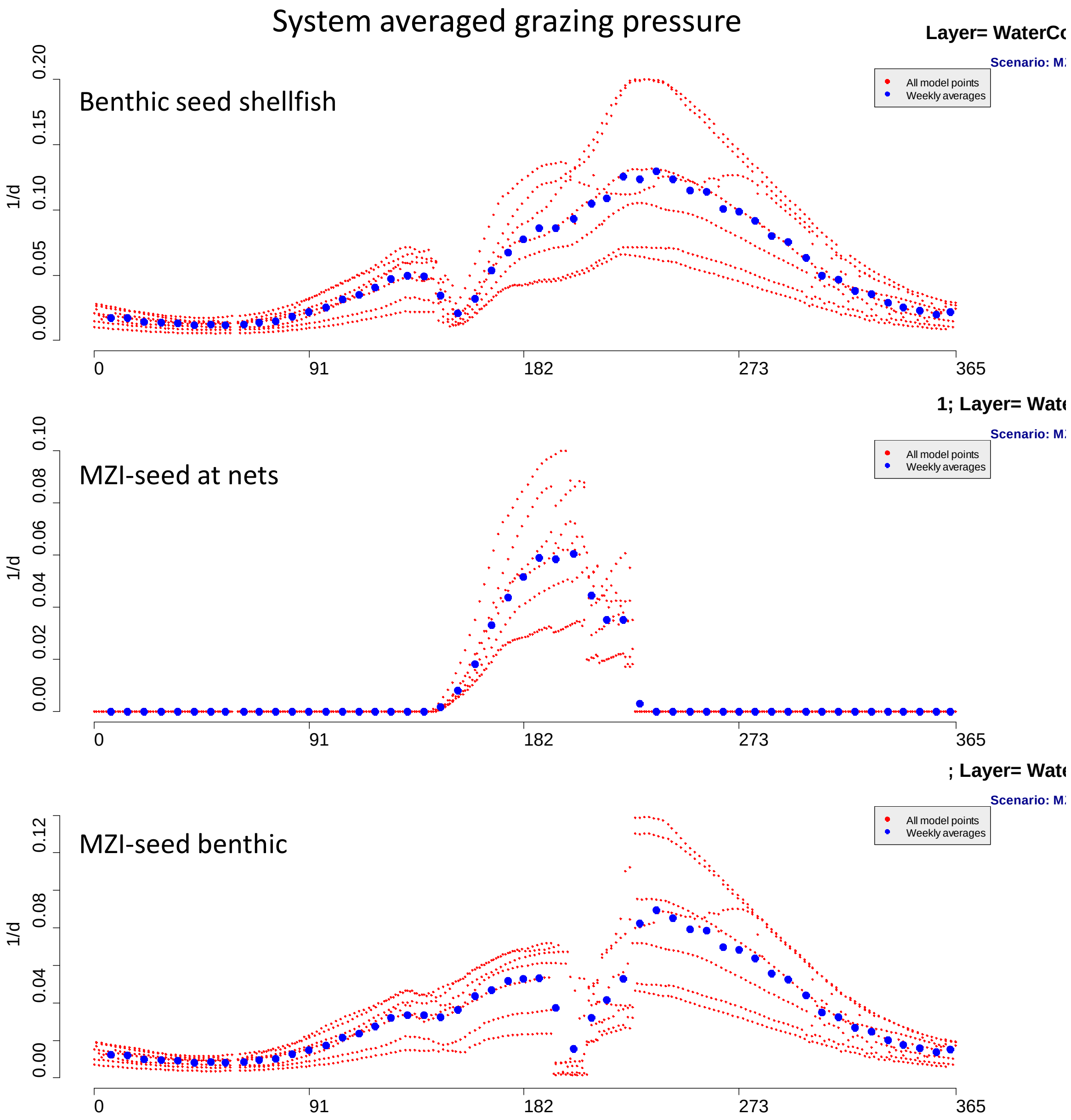


Figure 36 Grazing pressure by seed shellfish, system averaged and averaged per week for all years 2006-2013 together. Scenario with an auction target of 60 Mkg fresh mass, at a MZI-seed mussel harvest of 45 Mkg fresh mass. Upper: natural shellfish seed, middle: MZI-seed at the nets, and lower: benthic MZI-seed. Note that there are two phases for MZI-seed at the nets and on the sediment since there are two harvests from the nets.

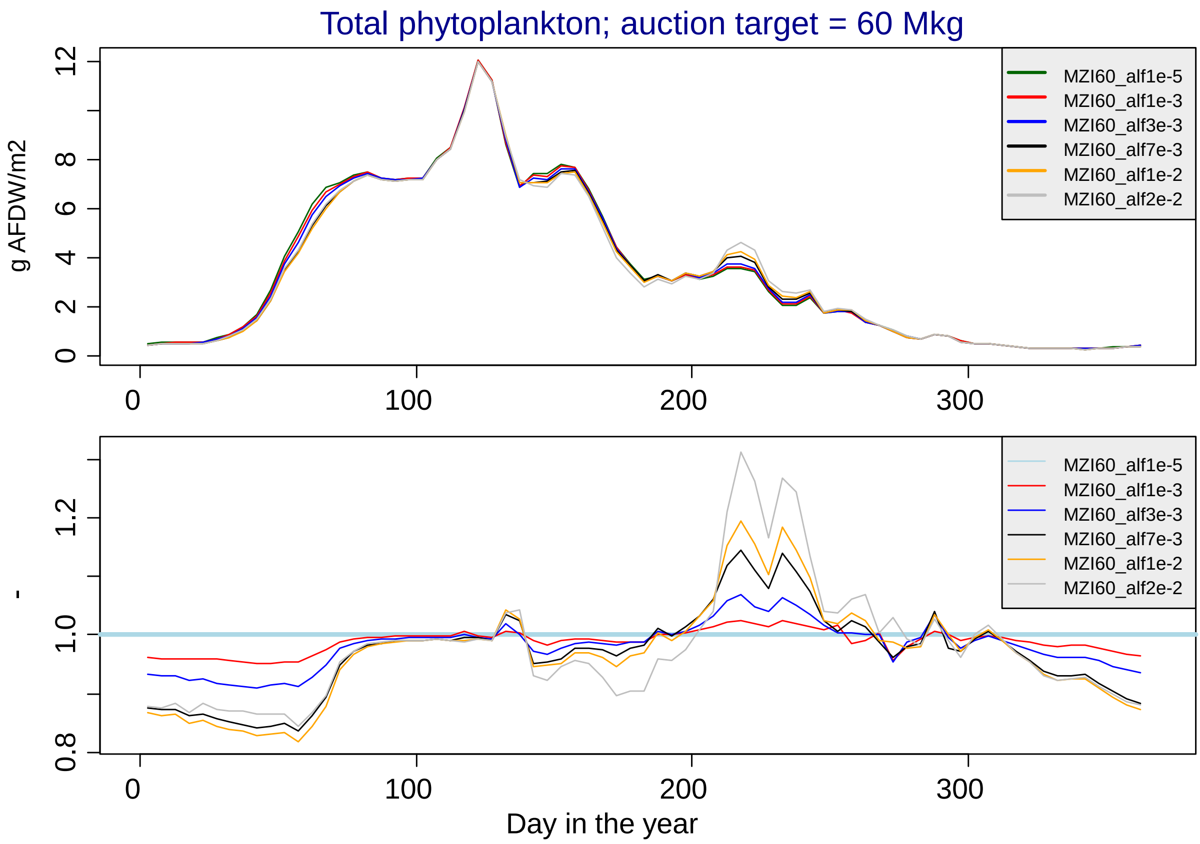


Figure 37 Phytoplankton biomass, absolute (upper) and relative (lower) to the reference situation (no MZI's, and the present auction target of 60 Mkg fresh mass). Averages for every week for all years 2006-2013. Simulations for almost no MZI's (green) to a seed harvest of about 47 Mkg MZI (grey line).

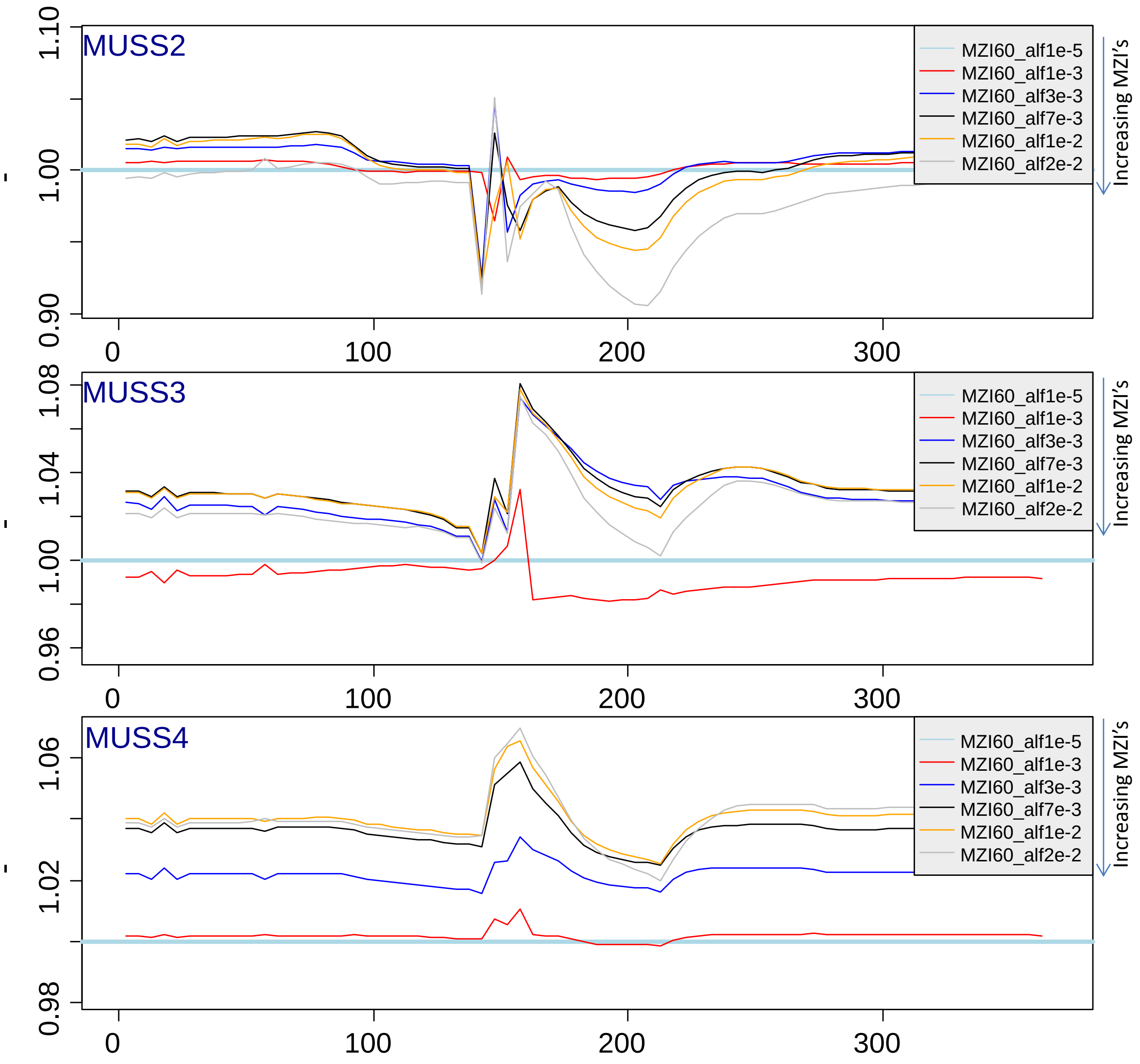


Figure 38 Size of natural shellfish, relative to the reference situation (no MZI's, 60 Mkg auction target). Upper: seed mussels, mid: class 3 (MUSS3), lower : largest shellfish (MUSS4).

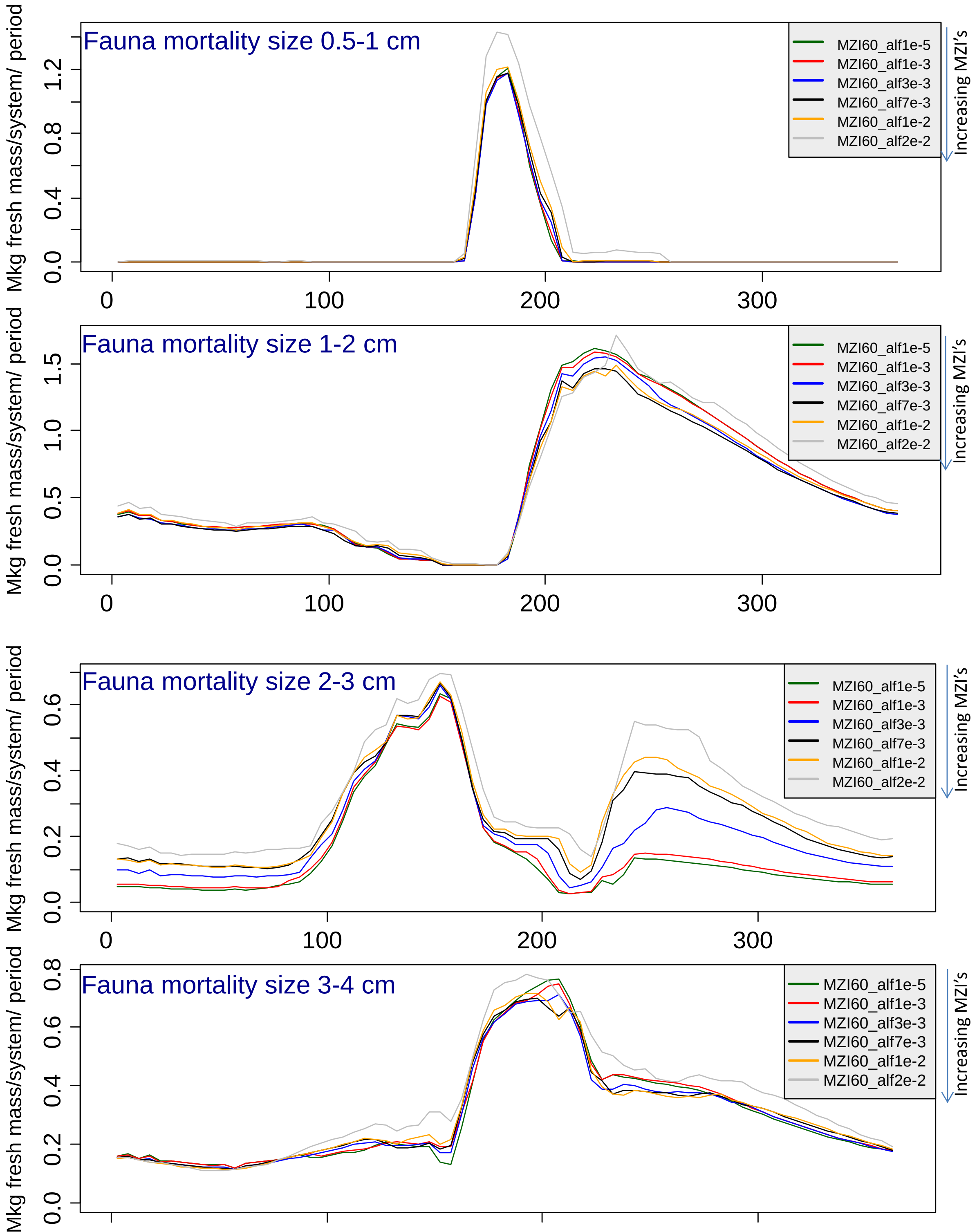


Figure 39 Computed fauna mortality. Scenario with 60 Mkg fresh mass auction target, from almost no MZI's to about 47 Mkg MZI seed harvest (grey lines). Data averaged per week, all years 2006-2013 taken together. X-axis: day in the year, Y-axis: Mkg fresh mass died during each output period (=2 days). Upper: shellfish seed 0.5-1.0 cm; second: shellfish seed 1-2 cm; third: half-grown shellfish 2-3 cm; lower: half-grown shellfish 3-4 cm.

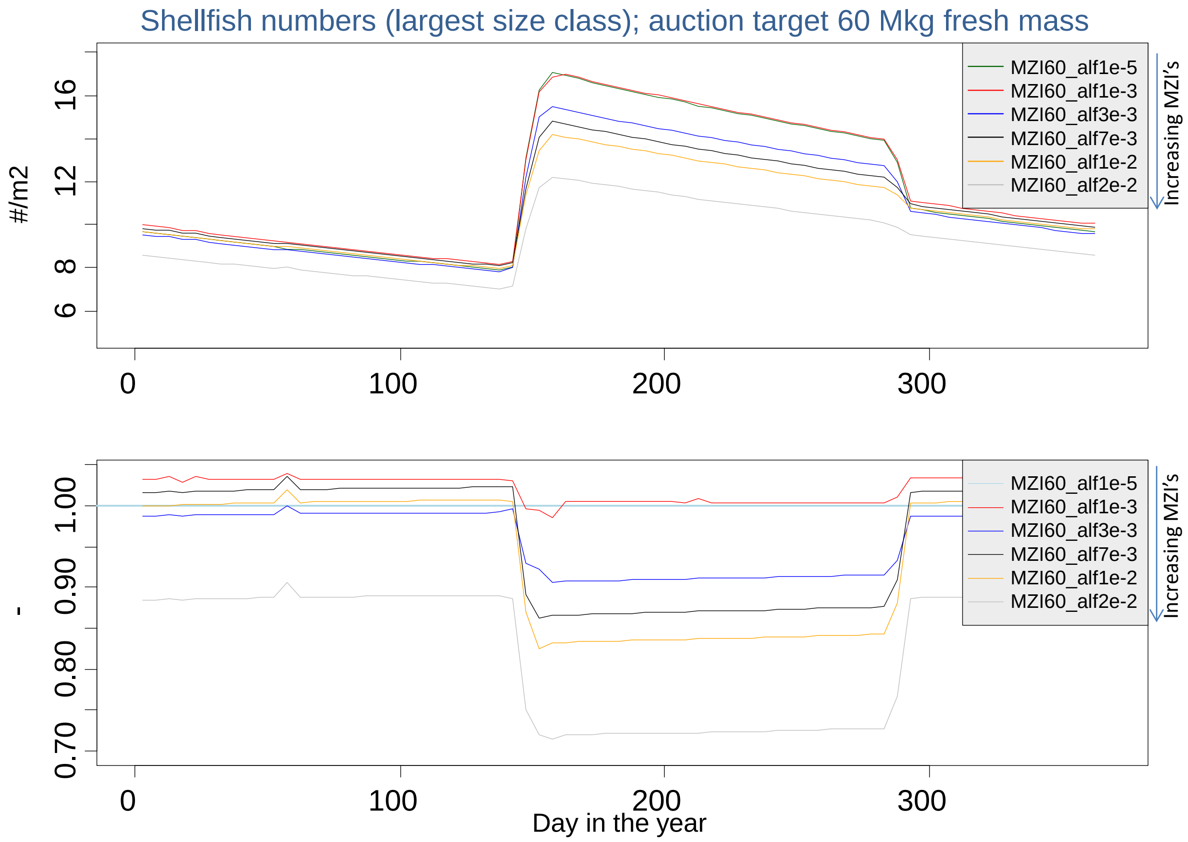


Figure 40 Adult shellfish numbers. Scenario with auction target of 60 Mkg fresh mass and ranging from almost no MZI's to a MZI-seed harvest of about 47 Mkg fresh mass (grey lines). Upper: absolute values, lower: values relative to the reference situation (no MZI's in the system).

5.3 Conclusions

This leads to the conclusions that next to the computed increase of total biomass, as a result of MZI practice, natural shellfish populations decline as a result of food competition, leading to smaller individuals shortly after settling and to a higher mortality. As a final result: shellfish numbers decrease and because of that: total natural shellfish biomass. The effect of decreasing number of larvae (since part is going to the MZI's) is not zero, but less important than this increased mortality. At the end, the individual biomass of older individuals does not decrease.

6 Conclusions

Introducing MZI-nets into the system has as result that a considerable part of shellfish larvae is ‘saved’ from dying; something what normally happens at or shortly after the moment of settlement. Physical processes as well as predation by e.g. shrimps (e.g. Beukema & Dekker, 2006) may be responsible for such losses.

The model computations finally provide the following conclusions
Chapter 4:

1. MZI’s have a positive effect on the total shellfish biomass in the modelled system compared to the situation where –in absence of MZI’s- a certain amount of mussels is fished from natural beds. This conclusion is valid as long as the number of MZI’s stays below an upper limit; this upper limit is related to the original amount of shellfish harvested from the system.
2. The effect on total *mussel* biomass is even more positive with increasing number of MZI’s.
3. Non-mussel shellfish biomass is negatively affected by an increasing number of MZI’s.
4. This negative effect is mainly established in the early period of MZI-mussels at the nets.
5. Under the assumption that growth and survival of culture mussel does not differ from natural mussels, the model computes that harvesting of mussels from the Wadden Sea has a negative effect on the total shellfish biomass. The model computes highest shellfish biomass in a situation with no harvest.
6. MZI practice has a positive effect on shellfish biomass available as food for birds compared to a reference situation with 60 Mkg auction target.
7. Positive effects are all caused by the fact that withdrawal of natural mussel biomass is replaced by mussels originating from MZI-systems.

Chapter 5:

8. Explaining conclusion (3) in more detail: In summer, a higher mortality of shellfish seed is computed; a result of competition for food. Shellfish seed grows a bit less fast, and since in the model mortality is coupled to the animals’ size (the smaller the higher the mortality) animals decreasingly survive this period with increasing numbers of MZI’s.
9. The fact that an increasing part of mussel larvae goes into the MZI-route does affect the development of natural mussel stock in a negative sense, but this effect is minor compared to the increasing natural mussel stock that is not fished anymore with increasing MZI-practice.

On a whole, the model results indicate that the amount of food available for mussel eating birds increases with increasing MZI practice, a consequence of the increasing amount of mussels.

Suggestions

The effect of culture lot efficiency was not studied. In this study, shellfish losses on culture lots were not different from the other –natural- losses; in reality these losses probably are less than on natural beds (Bult et al, 2004; Wijsman et al, in prep). The ratio (mussels brought to the auction)/(MZI seed mussels needed) will largely determine the conclusions drawn in this report. The larger this efficiency, the less MZI seed mussels and thus MZI’s are needed to arrive at a desired yearly mass of mussels brought to the auction. Also, the negative effects linked to an increased mortality of shellfish seed mention in chapter 5 will become less important with a decreasing amount of MZI seed mussels needed.

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Appendix I Spatial set-up of the Wadden Sea model, exchange parameters and sediment composition

General

The western Dutch Wadden Sea is divided into six large compartments. In each compartment a tidal, a sub-tidal and a channel area is distinguished. Boundaries are the low-water level (lwl) and lwl-5 m. The EcoWasp-model is based on daily averages for input, temperature, solar radiation, etc, and does not distinguish the tidal variations. However, as many processes have a daily variation, the effect of the daily variation is computed if possible: for algal growth the length of the light an dark periods are accounted for. Also, the effect of tidal variation is accounted for. Not only the fraction of the time a tidal flat runs dry, but also the variation in water depth and the effect of that on pelagic and benthic primary production is computed. See Brinkman (1993) for a more detailed overview.
The sediment compartment is 20-40 cm deep. Primary production occurs on the bentic toplayer. Degradation of organic matter needs oxygen or nitrate as electron acceptor, and as a result phosphorus, ammonia and other components are produced. These are transported as a result of diffusion and bioturbation. Phosphate and silicate may adsorb onto solids. See Brinkman (1993) for a detailed overview of bentic processes.

Spatial setup and transport

In Figure 41, the EcoWasp set-up of Wadden Sea compartments and advective and dispersive exchanges between the distinguished Wadden Sea compartments are depicted. In Figure 42, the pathway of fresh water from Lake IJssel is shown.
The data for advection and dispersion have been taken from Ridderinkhof (1988), but were found to be too high for the EcoWasp simulations. Reason for that is the numerical dispersion that is characteristic for box-models. Simply spoken: suppose a number particle is released in compartment 4. The next timestep, a part of these particles are transported into the adjacent compartments. The second next timestep, a part is already transported to the next adjacent compartment. Thus, the transport through the system is much too fast. It is also clear from this example that the numerical dispersion increases with increasing box-size and decreasing time-steps for the numerical integration.

The solution for this numerical phenomenon is simple: decrease the dispersion and advection parameters (in certain cases, these even may get negative values). This is not evaluated further, here. Just Ridderinkhof's results have been used, and adapted after fitting chloride-data from the Rijkswaterstaat montly monitoring programme.

Modelled and measured chloride values (from the Rijkswaterstaat monthly monitoring programme live.waterbase.nl) are shown in Figure 43 & Figure 44. The fit is far from perfect, but it is the best that could be found for this tidal system where the fresh water moves to and from over a distance of more then 10 km each tide, and also local differences occur.
It appeared that multiplying the advective terms with 0.5 and the dispersive terms with 0.3 gave a satisfactory result.

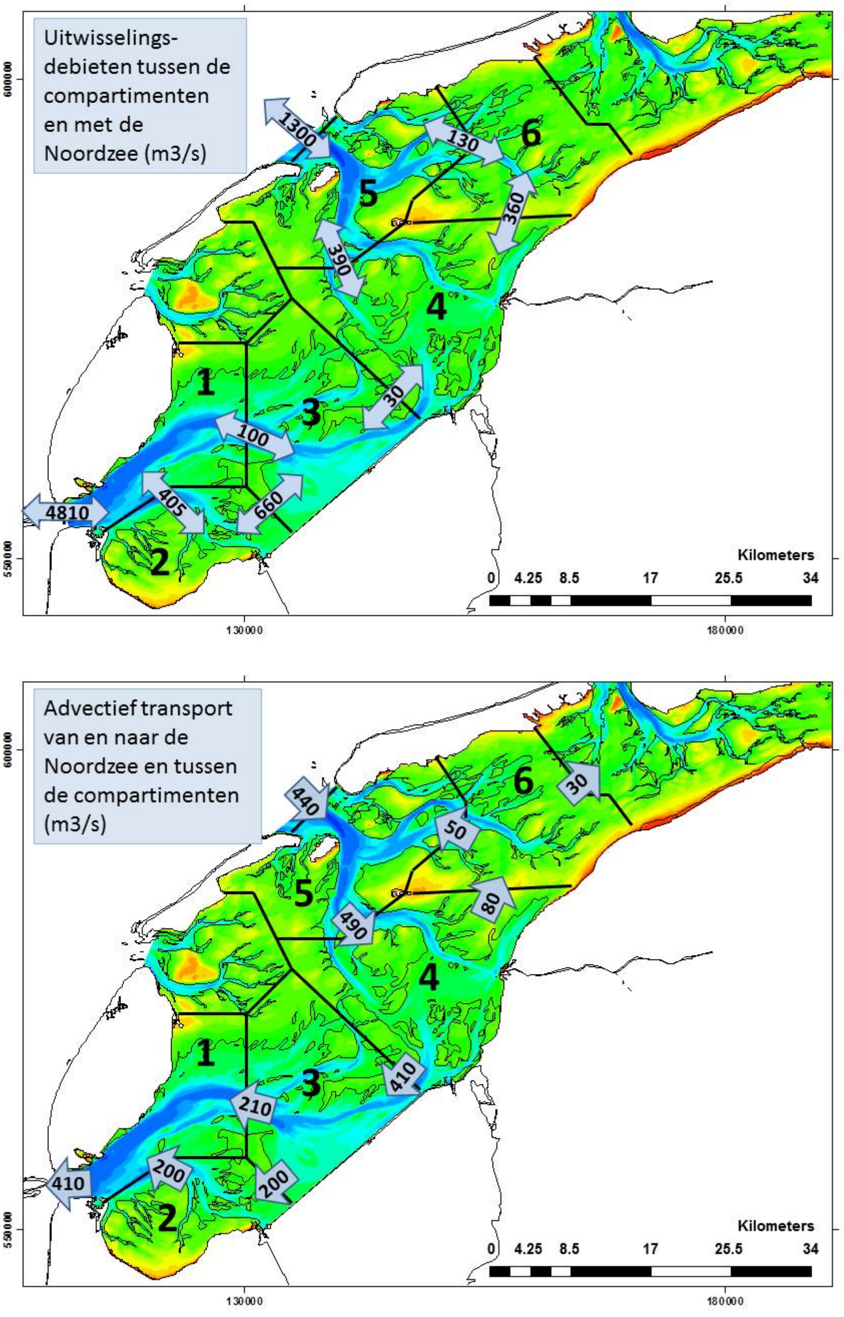
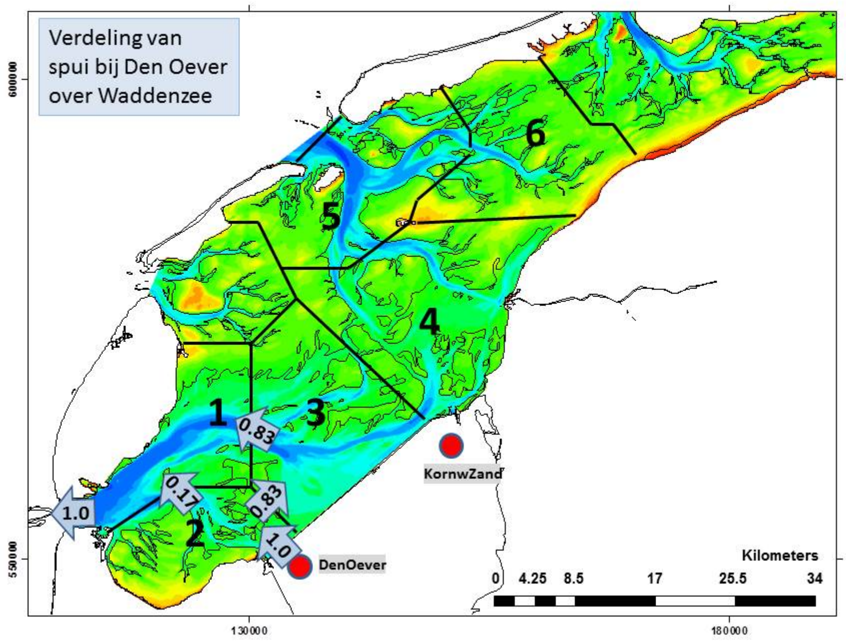


Figure 41 EcoWasp-compartments and the North Sea, and exchange with North Sea and between compartments. Lower: rest flow of water (advective transport,m^3 s^{-1}). Upper: exchange (dispersive transport, m^3 s^{-1}) between compartments and North Sea (both following Ridderinkhof, 1988). The Eyerlandse Gat-area (between compartment 1, 3 and 5) is relatively independent from the other compartment since the exchange of water is low; therefore it is not part of the model computations. In the model application, these mentioned values for flow and dispersion have been adjusted based on known salinity data: in the model all the flow values are multiplied by 0.5 and all the dispersion values by 0.3.



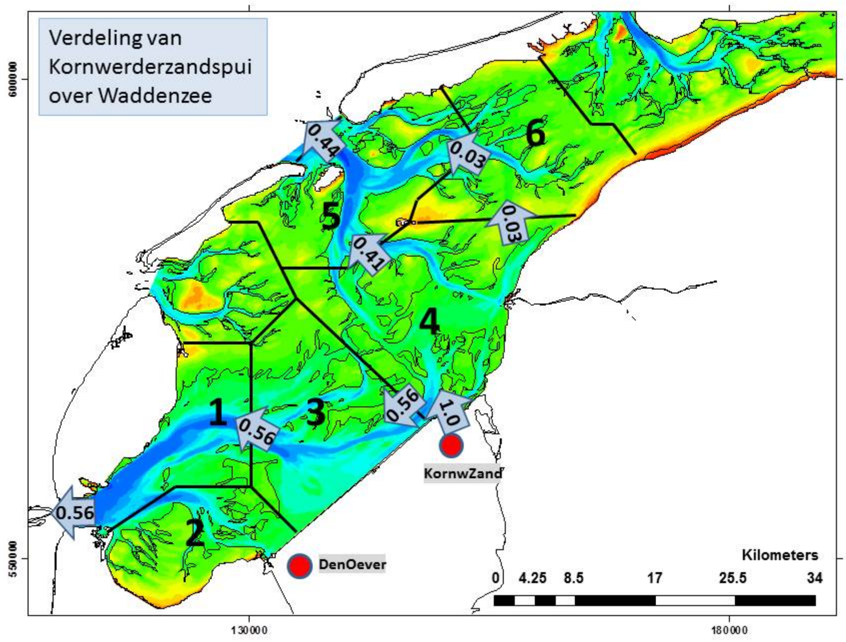


Figure 42 Overview of the distribution of fresh water from both the IJsselmeer-inlets. Upper: input at Den Oever, lower: input at Kornwerderzand. The numbers give the fraction of the inlet water adding to the advective transport data from Figure 41. As an example: each m^3 Den Oever inlet implies an increase in the advective flow from compartment 2 to 3 of 0.83 m^3.

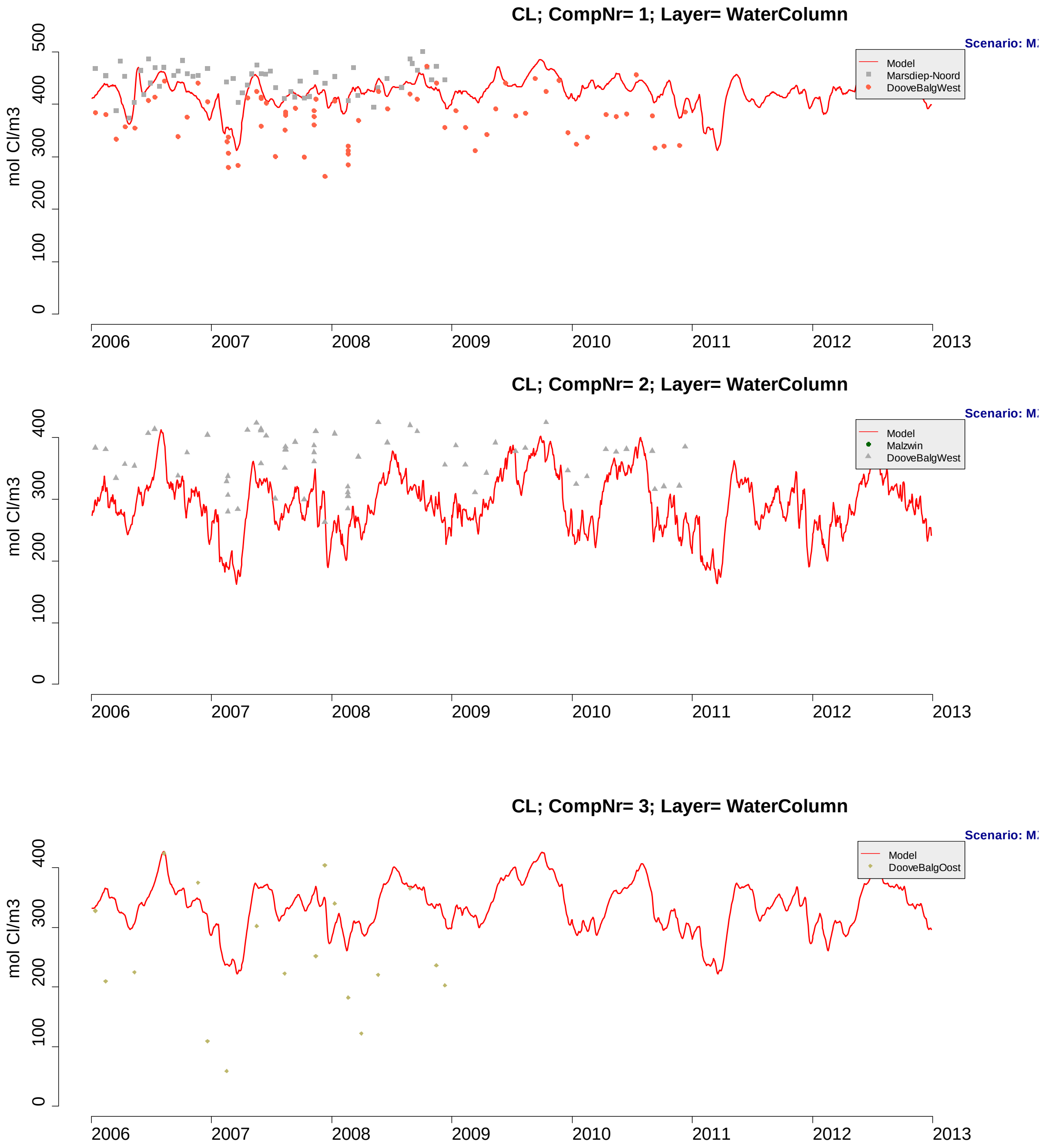


Figure 43 Chloride concentrations in the Marsdiep-compartments, with measurements by Rijkswaterstaat (www.waterbase.nl)

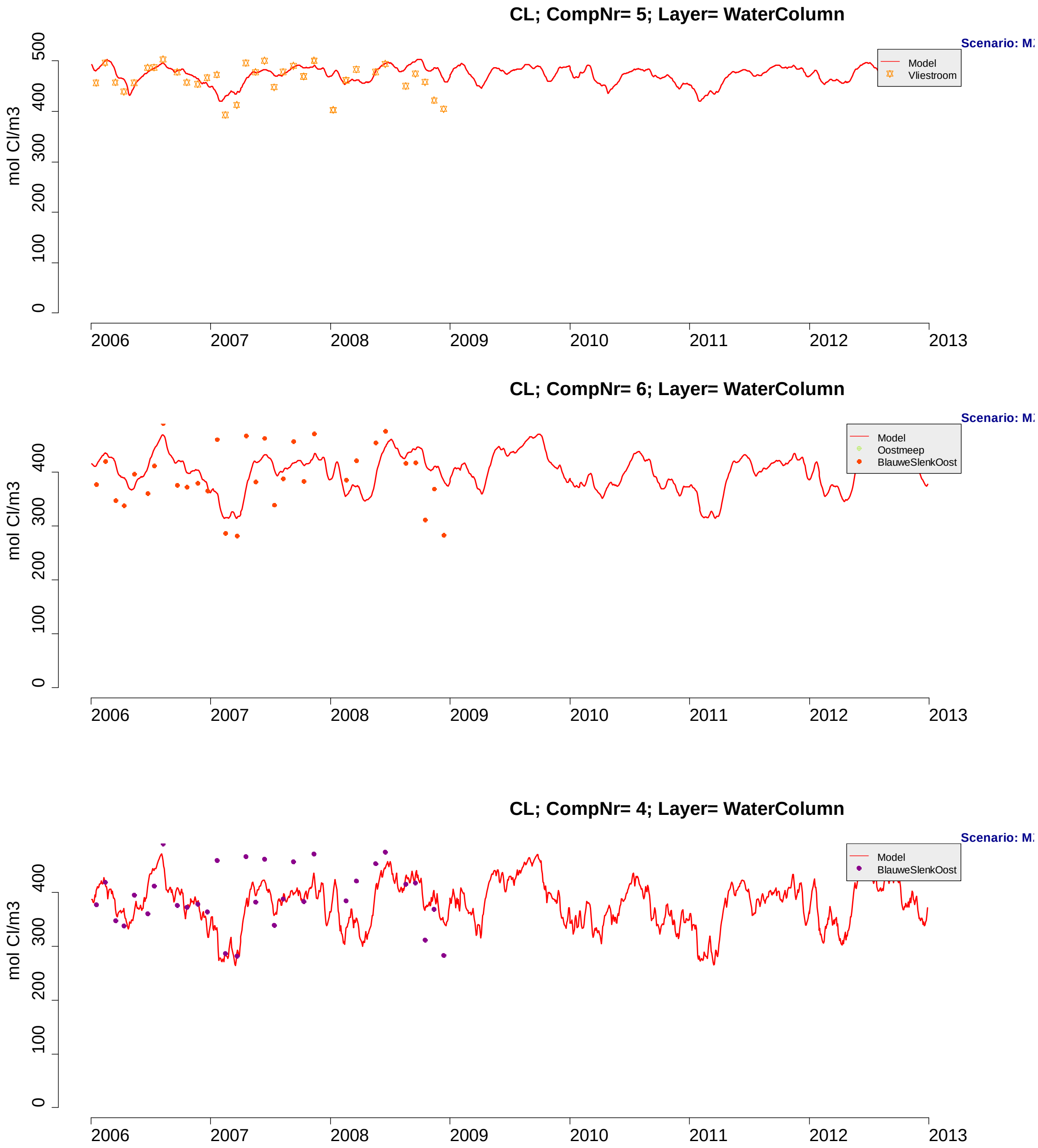


Figure 44 Chloride concentrations in the Vlie-compartments, with measurements by Rijkswaterstaat (www.waterbase.nl)

System depths, areas, sediment composition and some other physical properties

In the model, the area is divided into tidal flats (part above mean low water level, MLWL), the subtidal area (between MLWL and -5 m) and channels (everything below -5 m). Data after Rijswaterstaat. Sediment data are after Zwarts (2004).

Table AI.1 Area (m2) of the compartments (height relative to NAP)

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Sum Tidal flats m2*	Sum all m2
1	1.42E+04	2.06E+06	2.90E+07	5.68E+07	8.02E+07	3.10E+07	1.68E+08
2	0.00E+00	9.25E+06	9.44E+07	8.04E+07	2.07E+07	1.04E+08	2.05E+08
3	0.00E+00	0.00E+00	6.99E+07	1.12E+08	5.65E+07	6.99E+07	2.38E+08
4	3.36E+05	5.31E+06	8.68E+07	1.03E+08	1.76E+07	9.25E+07	2.13E+08
5	3.27E+05	7.31E+06	1.69E+08	6.74E+07	7.70E+07	1.77E+08	3.21E+08
6	1.81E+05	1.94E+07	1.87E+08	4.61E+07	1.97E+07	2.07E+08	2.73E+08
SUM	8.58E+05	4.33E+07	6.36E+08	4.65E+08	2.72E+08	6.81E+08	1.42E+09

Table AI.2 *Average depth (cm relative to NAP)*

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Avg tidal flats cm*	*Avg* all cm
1	53.0	16.9	-93.7	-264.7	-1459.2	-86.3	-801.8
2		33.9	-63.2	-247.3	-721.7	-54.5	-197.7
3			-104.1	-274.9	-869.6	-104.1	-365.8
4	89.0	25.6	-77.2	-229.5	-670.3	-70.7	-196.8
5	102.7	18.2	-69.4	-245.2	-1056.1	-65.5	-340.8
6	89.5	23.9	-71.6	-236.3	-568.8	-62.5	-128.5
						Mean all	-316.6

Tabel AI.3 Average orbital velocity (from file UBWAV.MRD (m/s) (Brinkman & Bult, 2002)

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Avg Tidal flat m/s*	Avg all m/s
1	2.88E-02	2.09E-01	3.08E-01	3.51E-01	9.32E-02	0.30	0.22
2		2.64E-01	3.28E-01	3.00E-01	1.26E-01	0.32	0.29
3			3.66E-01	3.17E-01	1.37E-01	0.37	0.29
4	2.50E-01	3.20E-01	3.38E-01	2.81E-01	8.89E-02	0.34	0.29
5	3.46E-01	3.51E-01	3.33E-01	3.12E-01	1.36E-01	0.33	0.28
6	2.39E-01	3.21E-01	3.22E-01	2.66E-01	1.42E-01	0.32	0.30
						Avg all	0.28

Tabel AI.4 *Average silt content (% silt, particles < 16 µm) (%)*

	> +60cm	+60 cm – 0 cm	0 cm -- LW-lijn	LW-lijn -- -5m	< -5m	*Gem plaat %*	Gem alles %
1	6.26	4.99	1.48	0.87	0.30	1.72	0.75
2		9.81	4.51	3.28	1.51	4.98	3.96
3			1.59	2.39	1.44	1.59	1.93
4	4.98	4.35	2.71	3.12	1.74	2.81	2.87
5	5.58	4.10	2.63	2.51	1.39	2.69	2.34
6	5.98	6.83	3.31	2.85	2.44	3.65	3.42
						Avg all	2.61

Tabel AI.5 Average lutum content = 0.66 * silt (%)

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Avg Tidal flat %*	Avg all %
1	4.13	3.29	0.98	0.57	0.20	1.13	0.50
2		6.47	2.97	2.17	1.00	3.29	2.62
3			1.05	1.57	0.95	1.05	1.27
4	3.29	2.87	1.79	2.06	1.15	1.86	1.90
5	3.68	2.70	1.73	1.66	0.92	1.78	1.55
6	3.94	4.51	2.19	1.88	1.61	2.41	2.26
						Avg all	1.72

Tabel AI.6 Content organic matter = 0.17 * lutum *(%)*

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Avg Tidal flat %*	Avg all %
1	0.702	0.560	0.167	0.097	0.033	0.19	0.08
2		1.101	0.505	0.368	0.170	0.56	0.44
3			0.179	0.268	0.161	0.18	0.22
4	0.559	0.488	0.304	0.350	0.196	0.32	0.32
5	0.626	0.460	0.295	0.282	0.156	0.30	0.26
6	0.671	0.766	0.372	0.320	0.274	0.41	0.38
						Avg all	0.29

Tabel AI.7 Fine sand (<63 um)=5 * silt *(%)*

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Avg tidal flat %*	Avg all %
1	31.295	24.935	7.420	4.342	1.491	8.59	3.77
2		49.043	22.525	16.417	7.574	24.89	19.81
3			7.972	11.931	7.180	7.97	9.64
4	24.892	21.747	13.546	15.596	8.718	14.06	14.36
5	27.901	20.482	13.144	12.555	6.950	13.47	11.72
6	29.880	34.145	16.574	14.250	12.195	18.23	17.12
						Avg all	13.03

All mentioned contents were in weight-%. With a mean specific mass = 1.5 kg dm^{-3} = 1.5 e6 g m^{-3} , everything can be transferred into g m^{-3} (next four tables)

Tabel AI.8 Content refractory organic matter (ROM) in gram/m3

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line-- -5m	< -5m	*Avg Tidal flat*	Avg all
1	1.05E+04	8.39E+03	2.50E+03	1.46E+03	5.02E+02	2.89E+03	1.27E+03
2		1.65E+04	7.58E+03	5.53E+03	2.55E+03	8.38E+03	6.67E+03
3			2.68E+03	4.02E+03	2.42E+03	2.68E+03	3.25E+03
4	8.38E+03	7.32E+03	4.56E+03	5.25E+03	2.93E+03	4.73E+03	4.83E+03
5	9.39E+03	6.89E+03	4.42E+03	4.23E+03	2.34E+03	4.54E+03	3.94E+03
6	1.01E+04	1.15E+04	5.58E+03	4.80E+03	4.10E+03	6.14E+03	5.76E+03
						Avg all	4.39E+03

Tabel AI.9 Silt content in gram/m3

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Avg tidal flat*	Avg all
1	9.39E+04	7.48E+04	2.23E+04	1.30E+04	4.47E+03	2.58E+04	1.13E+04
2		1.47E+05	6.76E+04	4.93E+04	2.27E+04	7.47E+04	5.94E+04
3			2.39E+04	3.58E+04	2.15E+04	2.39E+04	2.89E+04
4	7.47E+04	6.52E+04	4.06E+04	4.68E+04	2.62E+04	4.22E+04	4.31E+04
5	8.37E+04	6.14E+04	3.94E+04	3.77E+04	2.09E+04	4.04E+04	3.52E+04
6	8.96E+04	1.02E+05	4.97E+04	4.27E+04	3.66E+04	5.47E+04	5.14E+04
						Avg all	3.91E+04

Tabel A1.10 Content fine sand in gram/m3

	> +60cm	+60 cm – 0 cm	0 cm -- LW-line	LW-line -- -5m	< -5m	*Avg Tidal flat*	Avg all
1	4.69E+05	3.74E+05	1.11E+05	6.51E+04	2.24E+04	1.29E+05	5.65E+04
2		7.36E+05	3.38E+05	2.46E+05	1.14E+05	3.73E+05	2.97E+05
3			1.20E+05	1.79E+05	1.08E+05	1.20E+05	1.45E+05
4	3.73E+05	3.26E+05	2.03E+05	2.34E+05	1.31E+05	2.11E+05	2.15E+05
5	4.19E+05	3.07E+05	1.97E+05	1.88E+05	1.04E+05	2.02E+05	1.76E+05
6	4.48E+05	5.12E+05	2.49E+05	2.14E+05	1.83E+05	2.73E+05	2.57E+05
						Avg all	1.95E+05

Tabel A1.11 Content medium-course sand in gram/m3.
Computed als rest (1.5e6-ROM-silt-fine sand)

	above NAP +60cm	between NAP + 60 cm and NAP	between NAP and LW-line	between LW-line and NAP-5m	below NAP-5m	Avg tidal flat	Avg all
1	9.26E+05	1.04E+06	1.36E+06	1.42E+06	1.47E+06	1.34E+06	1.43E+06
2		6.01E+05	1.09E+06	1.20E+06	1.36E+06	1.04E+06	1.14E+06
3			1.35E+06	1.28E+06	1.37E+06	1.35E+06	1.32E+06
4	1.04E+06	1.10E+06	1.25E+06	1.21E+06	1.34E+06	1.24E+06	1.24E+06
5	9.88E+05	1.12E+06	1.26E+06	1.27E+06	1.37E+06	1.25E+06	1.29E+06
6	9.52E+05	8.74E+05	1.20E+06	1.24E+06	1.28E+06	1.17E+06	1.19E+06
						Avg all	1.26E+06

Appendix II Choices for the MZI-model set-up

The mussel model: the old one and the new one, overall-scheme

Mussels, if large enough, produce pelagic larvae especially in the early summer period (April-May). During roughly a month, the larvae grow and develop a shell and a foot. Already after two days, the shell development starts; after 2-6 weeks, they lose their velum, develop foot and gills and try to settle onto a substrate. Hard substrates are preferred (such as rocks, stones, other shells, ropes, ships). In the Wadden Sea soft substrates are dominant, and it often happens that mussel beds are newly formed on sandy substrates. The young seed mussels have a size of less than a millimetre at the moment they settle, and grow to a size of about 20 mm at the end of the growing season (roughly September).

In the model, it is assumed that one year old mussels and older produce larvae. In the ‘old’ model, a fixed percentage (mostly 25%) of their body mass is used and transferred into pelagic larvae. Also, it was assumed that this happens with 100% efficiency. Also, settlement of seed mussels was assumed to occur with 100% efficiency (0% loss). This was also assumed for MZI-mussels. Consequently, in the old model, the only advantage of MZI-mussels over natural mussels was their better growth rate and lower mortality.

In the new model, a number of improvements is implemented: production of larvae is not 100% efficient, and neither is the settlement of seed mussels. In both cases a part of the mussels dies instantaneously. In case larvae decide to settle on the sediment, they probably face a large loss as a consequence of simple mechanical processes like getting buried under sand; a result of sedimentation or simply bed movements. At MZI-nets, mussels have a lower settling mortality. Thus, in Figure 45: $loss_2 > loss_1$.

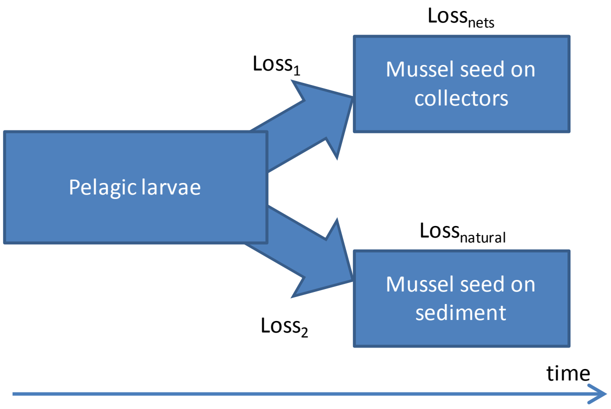


Figure 45 Transition of mussel larvae to mussel seed. Settlement takes place at the same time for both routes. $Loss_2 >> Loss_1$. The losses at the nets and those as natural mussels ($Loss_{nets}$, $Loss_{natural}$, respectively) may differ or not.

A second possible mechanism is that larvae seeking for a suitable substrate may encounter a collector net or not. In case they do not, they have to continue with their search and thus, stay in the water column for a longer period. The losses during the pelagic phase may be relatively larger than the losses later on as settled seed, and thus, a shorter stay in the water column for those mussels that attach to collector nets may result in a (much) better survival of mussel larvae that follow the collector net route.

A third mechanism may be that the loss of collector mussels due to predation by shrimps, starfish, fish and crabs ($Loss_{nets}$ in both Figure 45 and Figure 46) is (a lot) lower than the loss of seed mussels that settled on sediments or natural mussel beds ($Loss_{natural}$) The reason probably is that collector mussels can hardly be reached by shrimps, starfish or crabs.

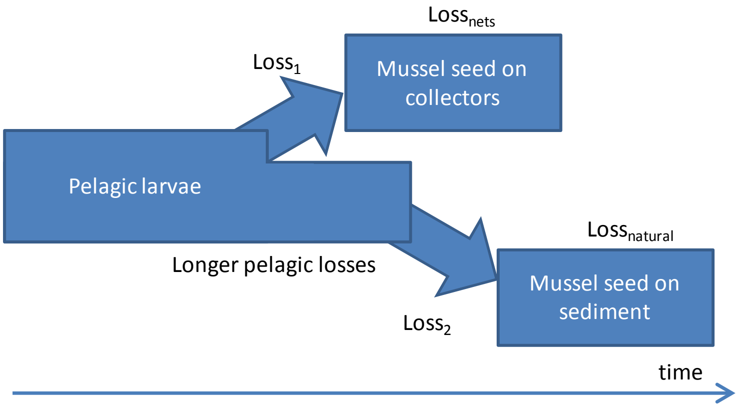


Figure 46 Transition of mussel larvae to mussel seed. Settlement on to seed collectors takes place some time before settlement on to sediment, and therefore, pelagic losses of collector mussels are reduced. $Loss_2$ still may be larger $Loss_1$ (as in Figure 45), but this is not necessarily the case. The losses at the nets and those as natural mussels ($Loss_{nets}$, $Loss_{natural}$, respectively) may differ or not.

Finally, growing conditions at the nets may be better. At the sediment, mussels have to cope with larger concentrations of silt and sand, and sometimes even large extra loads may appear.

At the end, harvesting from the nets however causes an additional, unavoidable, mortality.

One of the tasks of the modelling project is to investigate the fate of several of the possible 'larvae-saving'- mechanisms. In all cases, a smaller amount of mussel larvae will settle in a natural way.
In the model runs, the fraction of mussel larvae that attaches to the nets and the assumed losses $Loss_1$, $Loss_2$ and the pelagic losses are used to vary the number of MZI-mussels.

The ecosystem model: the old one and the new one

In the basic ecosystem model food web (see Brinkman (1993), Brinkman & Smaal (2003) for a larger overview, and Smit et al (2011) for a short overview) mussels (four age cohorts) are included that filter pelagic phytoplankton. A schematic overview of the model is given Figure 47.

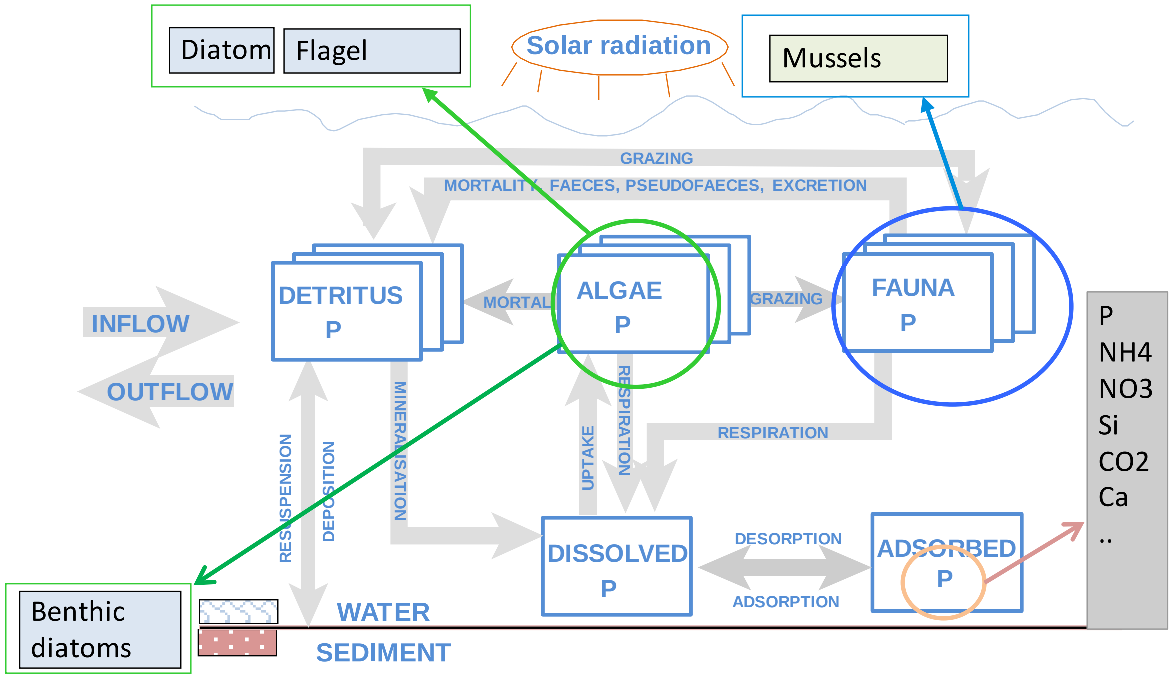


Figure 47 Schematic representation of the basic EcoWasp ecosystem model. Fauna==mussels, with four cohorts; algae is phytoplankton plus phytobenthos. 'P' represent all dissolved components, among those mentioned in the grey box.

For a complete description of the model, the reader is referred to Brinkman (2013, in prep). The age cohorts each have their own characteristic regarding where the animals live, where they feed, defecate, respire, etc. Thus, when a cohort changes from class 1 to 2, also its properties change. For example, the mussels in the model have a pelagic larval phase (with all the related properties), followed by a transition to benthic seed mussels (and thus, different properties).

Dealing with a situation where a part of the mussels does not attach to the sediment but to collector nets, this alternative route via the nets had to be implemented; this is shown in Figure 48 (same as Figure 1). Another extension that is implemented is the property of mussels that they only can filter algae that are large enough. Very small phytoplankton cannot be caught: pico-phytoplankton escapes from being filtered. Thus, the system might be enriched with small, not-filtered algae. These small algae are a prey for small zooplankton (micro-zooplankton) that in turn does serve as food shellfish. So, mussels omit picophytoplankton as a food source and thus enhance their presence by reducing their competitors for nutrients as a food source, and also, mussels predate upon microzooplankton being a predator upon picophytoplankton. Thus, indirectly mussels do profit from the presence of picophytoplankton but also enhance their presence.

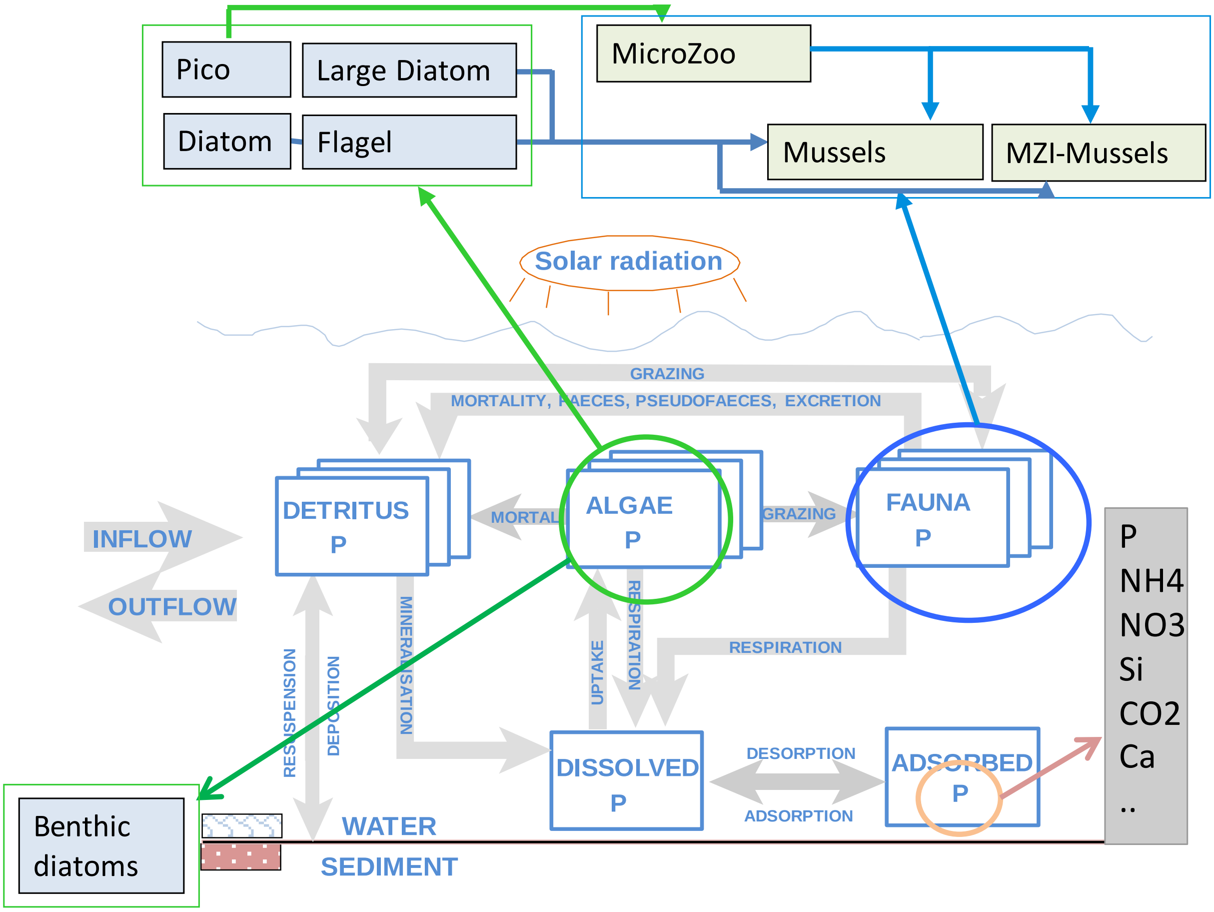


Figure 48 Schematic representation of the extended EcoWasp ecosystem model. As Figure 47, but now also MZI-mussels(see below) and microzooplankton is included. Extra algae are added (pico-phytoplankton, only eaten by microzooplankton) and large (slowly growing and slowly dying) diatoms. ‘P’ represent all dissolved components, as mentioned in the grey box.

The mussel model: the old one and the new one, detail-scheme

Another improvement appeared to be necessary. It was concluded in the past that the life span of a mussel could be represented by four cohorts. Of course, the more cohorts, the more precise the description of a mussel life, but four cohorts seemed to be a sufficient number. For MZI-mussels it appeared that an extra cohort had to be included. For ‘natural’ mussels, the second fauna class exists until the next reproduction takes place. As collector (MZI-) mussel, this second phase ends at the moment the seed mussels are collected from the nets, and thus their benthic phase already is the third one. Therefore, for MZI-mussels, an extra class is introduced, illustrated in Figure 49.

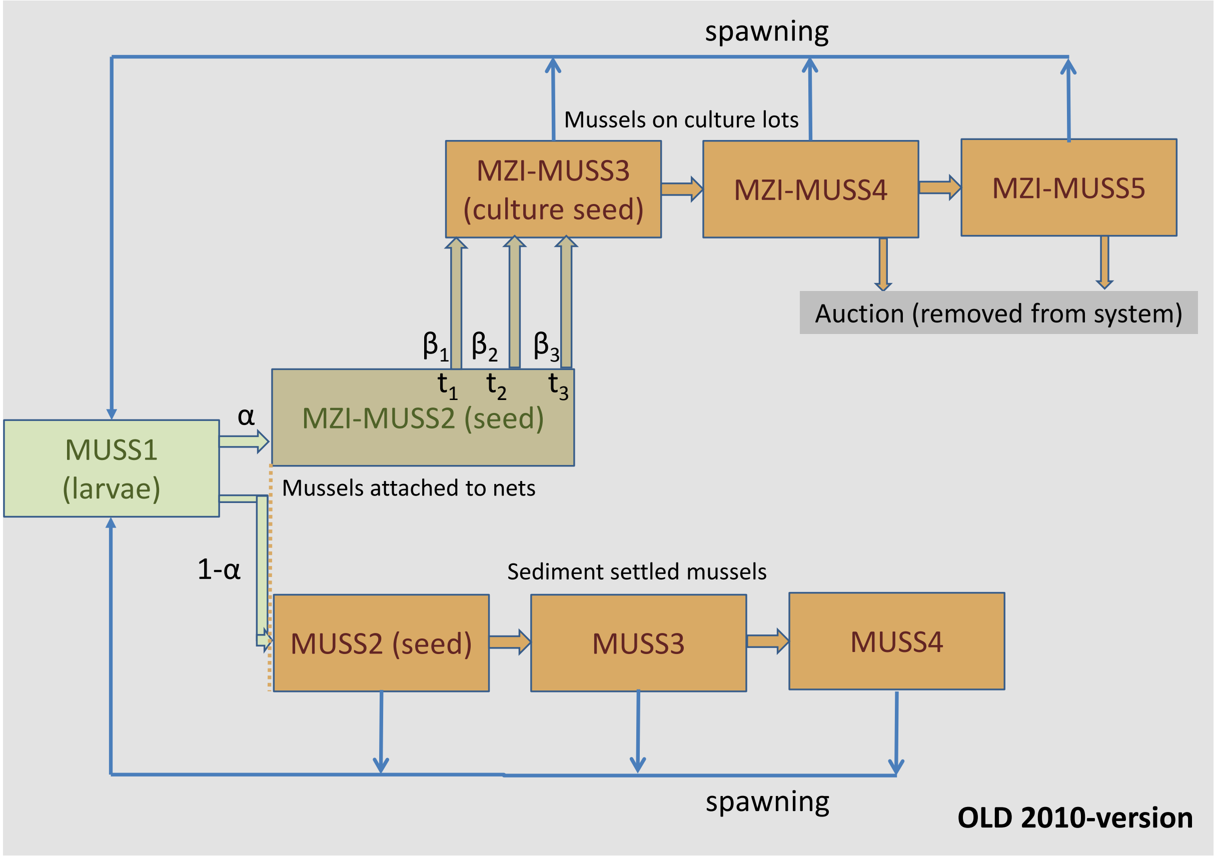


Figure 49 Route of mussels (MUSS) and seed collector mussels (MZIMUSS) as implemented in the 2010-version of the EcoWasp-model for MZI's. Natural mussels and MZI-mussels (on culture lots) both contribute to mussel larvae (MUSS1). On settlement, a part of the larvae goes to MZI-nets (α) and the rest to natural mussel beds (1-α). From that moment, MZIMUSS have their own route. There may be more than one harvesting from the nets (parts β_i). As explained in the text, MZI-mussels have five cohorts. By this, growth to an appropriate harvesting size of these culture lot mussels is better accounted for. Adult MZIMUSS4 or MZIMUSS5 is harvested and brought to the market as soon as these mussels are large enough, or after a certain maximum period. Spawning outside the Dutch Wadden Sea and subsequent import to the Wadden Sea is not part of the model (yet)

Next to that, the mussel culture process itself has to be described. It is also illustrated in Figure 49 how the 2010-version looked like.

In Figure 50 the present version is shown. It is included that

- mussel larvae that will settle naturally may stay longer in the water column than mussels that settle onto MZI-nets. As modelled now, larvae settle as soon they have reached a certain size. To distinguish between a fast settlement onto nets and a delayed settlement as natural mussels, a trick had to be found. The moment of the settlement at the MZI-nets is stored, and the natural settlement can only take place after the delay-period. The length of this period (days) has to be set in advance.

- There is a possible instantaneous mortality when changing from larvae to settled mussels. For natural mussels, this mortality may be different from the one for MZI-mussels. Defined as survival.
- There is a possible instantaneous mortality at harvesting MZI-MUSS2 from the MZI-nets. Defined as survival.
- In the old version (and all previous versions) all the reproductive effort (biomass converted into larvae) was 100% efficient. However, a part of the larvae will never be generated, and from now on, it is possible to introduce a loss at reproduction. Defined as survival.

The three last characteristics are modelled in the same way: entrance into the new class is combined with an instantaneous mortality of the fraction (1-survival). All the fauna that died is assigned to a certain detritus type ('DeadSub' in the EcoWasp-model).

The first mechanism, a delayed attachment to natural substrate compared to attachment to MZI-nets, is modelled as follows:
as soon as the larvae are large enough: attachment to MZI-nets is allowed (transfer from MZIMUSS1 to MZIMUSS2), but transfer from MUSS1 to MUSS2 (attachment to natural substrate) is only possible a certain number of days later. At attachment to MZI-nets, a flag ("*MZI_Flag*") is set to TRUE, and only if (*present day minus the day the flag was set to TRUE*)> *AttachmentDelay*, the natural settlement takes place. The parameter *AttachmentDelay* (days) has to be set in advance, and thus is one of the parameters that needs to be tuned. Since larvae growth differs per compartment, the flag is set per compartment.

By this, the way the specific mechanisms concerning the larvae settlement onto the MZI-nets as well as natural settlement onto the sediment are explained.

Harvesting of MZI-mussels from the nets

After a while, harvesting takes place. This is modelled such that three harvesting moments are possible. The real moment of harvesting and what amount to harvest is decided upon by the fishermen based on what is actually on the nets. Because of that, it is difficult to build in a rule that tells the model when to harvest what and/or which amount. Therefore, we simply modelled three possible moments of harvesting and also the relative amount of mussels harvested each moment.

The moments of harvesting depend on
- the maximum number of days after settlement
- a minimum size

and the amount harvested
- is simply set as parameters (e.g. 50% first, 80 of the rest later, and the remaining part at the third and last moment of harvesting =100%).

As soon as the size of MZI-MUSS2 is > the minimum size, than harvesting takes place, and if not, then harvesting takes place after the mentioned maximum number of days after settlement. MZI-MUSS2 is the class of the mussel s that settled onto the nets.

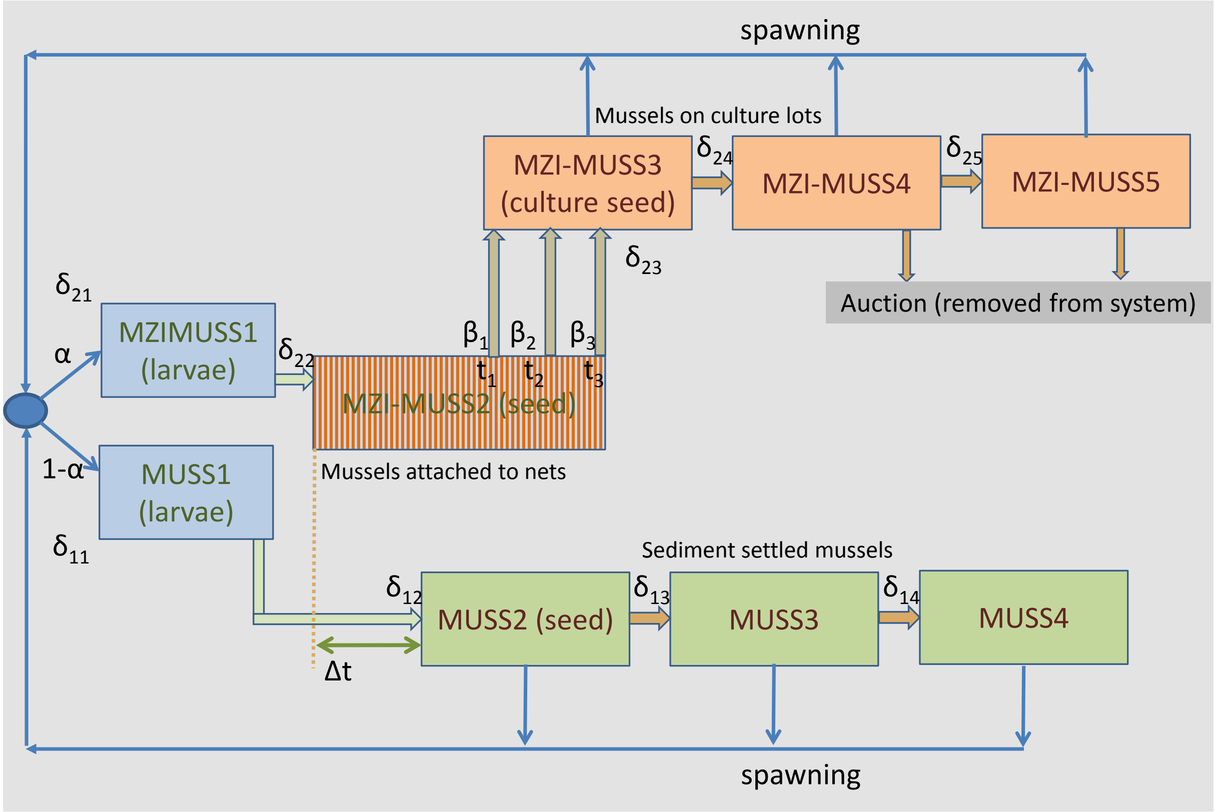


Figure 50 Route of mussels (MUSS) and seed collector mussels (MZIMUSS) as finally implemented in 2011-version of the EcoWasp-model for MZI's. MUSS1 and MZIMUSS1-larvae are considered separately, and both the cohorts are filled by both MZIMUSS2-5 and MUSS2-4. Part α of all the larvae goes to MZIMUSS1 and consequently, (1-α) to MUSS1. Upon settlement, a fraction δ_{12} and δ_{22}, respectively, dies instantaneously. Such an extra mortality is defined for all classes now (e.g. δ_{21} .. δ_{25} for MZI-mussels) but is only relevant for the change from MZIMUSS2 to MZIMUSS3: after harvesting the MZI-mussels a part will die as a result of mechanical damage or of bringing the young mussels to culture lots. Finally, δ_{11} and δ_{21} may get a value<1 describing a loss upon larvae production.

Culture lots

Mussels that are harvested from the nets are brought to culture lots. In the model, it is possible to transport mussels from the compartment where the nets are to another compartment. This possibility is implemented in the EcoWasp-model, but not used in the present computations: culture lots are in the same compartment as the MZI-nets are.

Mussels from culture lots are harvested in a certain period (set by model parameters). There is a possibility to harvest MZIMUSS4, but there is a restriction: the mussel should have a sufficient size. MZIMUSS5 is *always* harvested in the predefined period.

Appendix III. Fauna filtration and respiration parameters, a fast first estimate

Fauna filtration and respiration parameters, a fast first estimate

All fauna parameters have to be tuned. Mussel growth (change in individual biomass M) is one of the characteristics that is used to find best values for uptake and respiration parameters. But, mostly, a first guess is needed and can be arrived at by a few simple considerations. These are based on the simplified growth equation of an animal.
The general formula for growth is, with just uptake (first right hand term) and respiration (second right hand term) as relevant processes and all others neglected, and with a, b, r and q as allometric parameters:

$$\frac{dM}{dt} = a\,M^{-b}M - r\,M^{-q}M \qquad (\text{g DW d}^{-1}) \qquad (1)$$

The maximum mass M (g AFDW) is reached when dM/dt=0 thus:

$$a\,{M_{max}}^{-b} = \;r\,{M_{max}}^{-q} \qquad (2)$$

or

$$\frac{a}{r} = {M_{max}}^{-q+b} \qquad (3)$$

This formula sets the relative values of a and r.

A second characteristic is the moment where a certain fraction of the maximum mass is achieved. Therefore, the differential equation

$$\frac{dM}{aM^{1-b} - r\,M^{1-q}} = dt \qquad (4)$$

has to be solved.
The primitive of the left hand term is a bit easier to obtain when q=0 is substituted; this is a normal value for q. In that case (se e.g. Handbook of Chemistry & Physics, Table of integrals; Weast , 1970):

$$P\left(\frac{dM}{aM^{1-b} - r\,M^{1-q}}\right) = P(\left(\frac{dM}{(aM^{-b} - r)M}\right) = \frac{1}{b \cdot r}\,\ln\left(\frac{M^{-b}}{-r + aM^{-b}}\right) \qquad (5)$$

Thus, the general solution for eq.4&5 is

$$\frac{1}{b \cdot r} \ln\left(\frac{M^{-b}}{-r+aM^{-b}}\right) = t \tag{6}$$

or:

$$\ln\left(\frac{M^{-b}}{-r+aM^{-b}}\right) = b \cdot r\, t \tag{7}$$

To describe the growth of animal from t=t$_0$ and M(t=t$_0$)=M$_0$ one needs the definite integral:

$$\left[\ln\left(\frac{M^{-b}}{-r+aM^{-b}}\right)\right]_{t=0}^{t=t} = [b \cdot r\, t\,]_{t=0}^{t=t} \tag{8}$$

or, since t$_0$=0,

$$\ln\left(\frac{{M_t}^{-b}}{-r+a{M_t}^{-b}}\right) - \ln\left(\frac{{M_0}^{-b}}{-r+a{M_0}^{-b}}\right) = b \cdot r \cdot t \tag{9}$$

or :

$$\ln\left[\frac{\left(\frac{{M_t}^{-b}}{-r+a{M_t}^{-b}}\right)}{\left(\frac{{M_0}^{-b}}{-r+a{M_0}^{-b}}\right)}\right] = b \cdot r \cdot t \tag{10}$$

Now, some substitutions can be done. First, eq. (3), with q=0

$$\frac{a}{r} = {M_{max}}^{+b} \quad \rightarrow r = \frac{a}{{M_{max}}^{+b}} = a \cdot\ {M_{max}}^{-b} \tag{11}$$

Eq.(11) can now be substituted into the left- and the right-hand term of eq.(11). It gives

$$\ln\left[\frac{\left(\frac{{M_t}^{-b}}{-a \cdot {M_{max}}^{-b}+a{M_t}^{-b}}\right)}{\left(\frac{{M_0}^{-b}}{-a \cdot {M_{max}}^{-b}+a{M_0}^{-b}}\right)}\right] = b \cdot a \cdot\ {M_{max}}^{-b} \cdot t \tag{12}$$

It is easy to see that a in the left-hand term disappears, leaving:

$$\ln\left[\frac{\left(\frac{M_t{}^{-b}}{-M_{max}{}^{-b}+M_t{}^{-b}}\right)}{\left(\frac{M_0{}^{-b}}{-M_{max}{}^{-b}+M_0{}^{-b}}\right)}\right] = b\cdot a\cdot\ M_{max}{}^{-b}\cdot t$$

And thus, rearranging a bit:

$$a = \frac{M_{max}{}^{b}}{b\cdot t}\cdot ln\left[\frac{\frac{M_t{}^{-b}}{-M_{max}{}^{-b}+M_t{}^{-b}}}{\frac{M_0{}^{-b}}{-M_{max}{}^{-b}+M_0{}^{-b}}}\right] \qquad (13)$$

And for r (eq.12 substituted):

$$r = \frac{1}{b\cdot t}\cdot ln\left[\frac{\frac{M_t{}^{-b}}{-M_{max}{}^{-b}+M_t{}^{-b}}}{\frac{M_0{}^{-b}}{-M_{max}{}^{-b}+M_0{}^{-b}}}\right] \qquad (14)$$

The equations tell us that

- the maximum biomass is defined by the ratio between uptake and respiration (eq.3)
- the moment at which e.g. 50% of the maximum biomass is reached determines the respiration parameter r (eq.14), ánd the uptake parameter a (eq.13). The faster the maturity occurs, the larger a and r. Since usually the smaller the animal, the faster the maturity, a will increase less than r .

Now a quick method is available to estimate the uptake and respiration parameter from two data points: the maximum biomass of an animal (species) and the moment a certain percentage of that maximum size is reached, e.g. 50% of the maximum biomass.

Note, in EcoWasp, a is the parameter upt_facta, b= upt_factb, r is resp_facta.

Appendix IV Growth and mortality of natural mussels and of MZI-mussels at the nets

Growth of natural mussels: data

Based on the old mussel data gathered by the former RIN, analysed by Brinkman (1993), data are available on the growth of mussels in the system. In Figure 51, sites (numbered 1-8) are shown on the western Wadden Sea map, and in Figure 52, sampling dates and frequencies are summarized. Most data are available for 1984, 1985, 1988 and 1989. In 1986 and 1987 fewer data are available, and for 1990, only one sampling date is available.

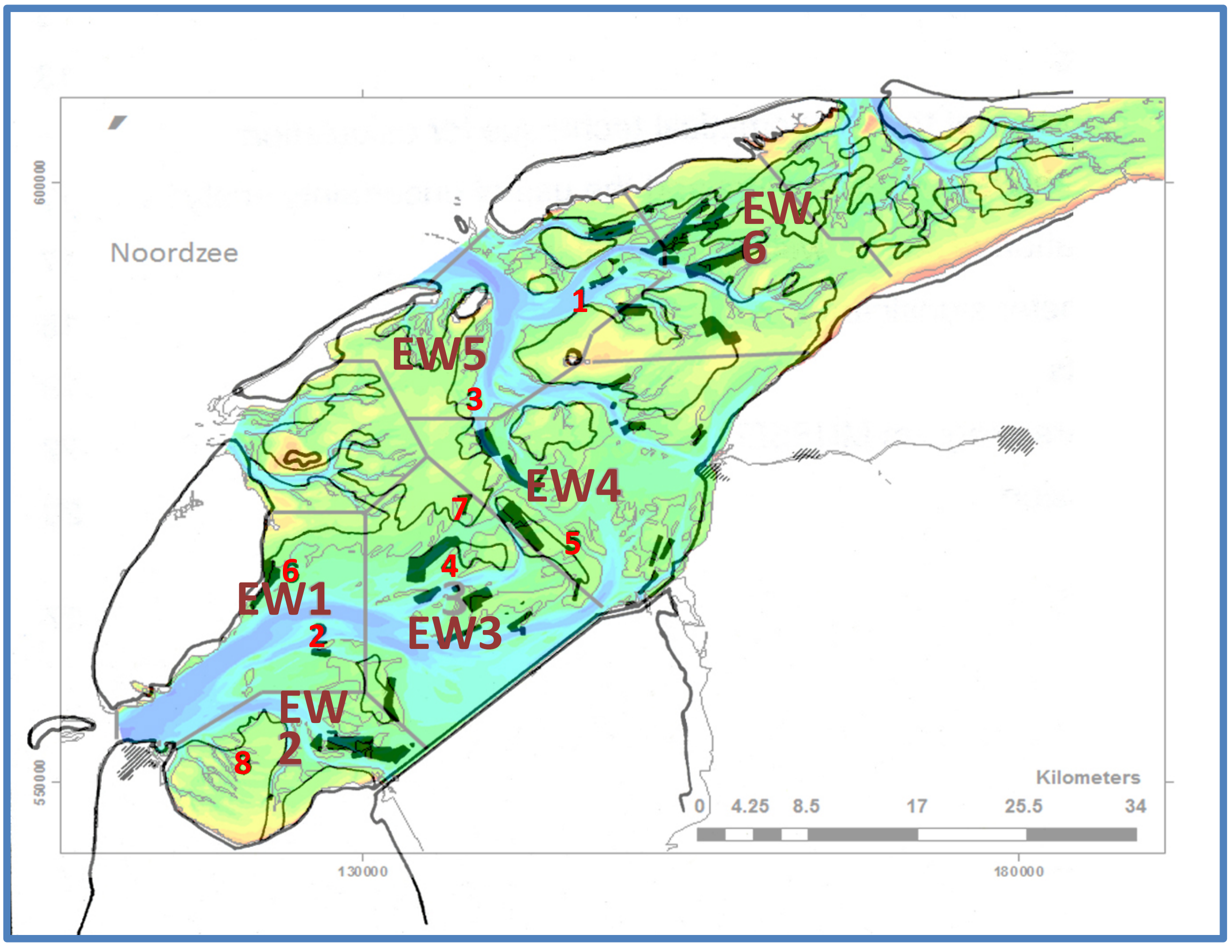


Figure 51 Measurement sites for RIN-data in the period 1984 – 1990 (numbers in red), and corresponding EcoWasp-compartments (EW-numbers in red-brown).

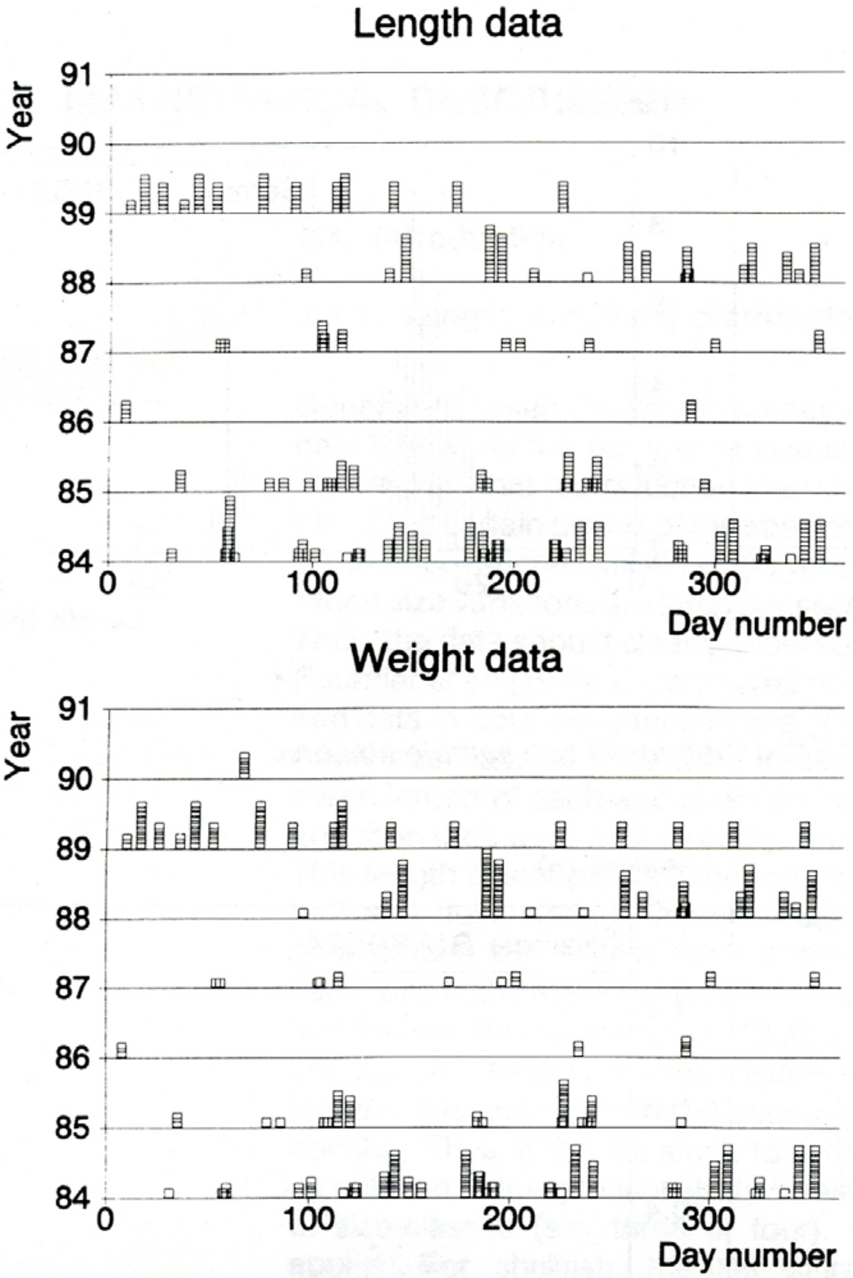


Figure 52 RIN-measurements, sampling dates and frequency

Table 2 Description of abbreviations

Number	Letter	Name	EcoWasp-compartment	Lit/Sublit
1	K, L, M	Meep	11	Culture lots, Sublitoral
2	A, B	Scheer	7	Culture lots, Sublitoral
3	I	Inschot	12	Culture lots, Sublitoral
4	S	Scheurrak	10	Culture lots, Sublitoral
5	Z	Zuidoostrak	11	Culture lots, Sublitoral
6	U, T	Texel	7	Culture lots, Sublitoral
7	V	Oude Vlie	3	Mussel beds, Tidal areas
8	X, Y	Mosselgaatje	2	Mussel beds, Tidal areas
Basin	R	RIN-Mesocosms	Not relevant	Model systems at the Institute (20 m^2 tidal systems)
	E	NIOZ-wad	1	Mussel beds, Tidal areas
	P	PAN		
	F	NIOZBL	1	Mussel beds, Tidal areas
	G	NIOZGE	1	Mussel beds, Tidal areas
	W	W100		

For most samples, length frequency measurements have been performed, and length-mass measurements, although not always both measurements for each sample. Thus sometimes only the first data are available, sometimes only the last type, and sometimes both.

The process of data elaboration and analysis has been described in Brinkman (1993[b]), for more detail the reader is referred to that report. Basic results have also been described in that report.
The length-frequency data result –for each sample- in average lengths of maximal three cohorts. Since samples have been taken four to six times per season, growth of each cohort during the season could be followed. Thus, per year, and per sample site, the increase in individual biomass and length during spring and summer, and the decrease during the winter period is known, by approximation.

Growth of Wadden Sea mussels has been tuned such that the model results are –as good as possible- similar to the field observations. Seed mussels (MUSS2) grow to almost 2 cm length in the first season, MUSS3-mussels to about 4-4.5 cm in the next season, and MUSS4 mussels to about 5-5.5 cm in the last phase.

Presently, resulting lengths and masses of all samples are listed in a couple of tables, and plotted together with individual biomasses of the three benthic mussel classes.

However, success is limited, basically since it a result had to be assigned to one of the three classes, and obviously, choices probably are not always correct. Time was lacking to improve this part of the data elaboration.

A summary of results for mussel body condition is presented in Figure 53. The summary contains all those measurements where length and mass data have been available. It will clear that in spring and early summer body masses are relatively high, whereas winter periods show low values. Also, there is more than a factor 2 between highest and lowest spring time values.

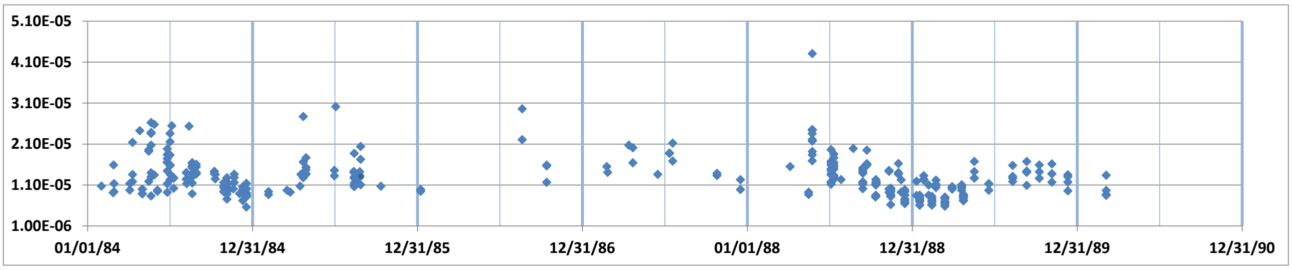


Figure 53 Body condition of mussels from the RIN-measurements. a-values from the equation mass=a Length$^{2.8}$. Note the large spread in values in summer, the low values in winter/early spring and the sudden drop after spawning.

Computed and measured body masses are presented in Figure 54 - Figure 63.

Seed mussel development is illustrated in Figure 54- Figure 55. Tidal area data for mass development are scarce, but both model results and data show that sub-tidal mussels have a larger mass than those on tidal flats; caused by the shorter feeding possibilities for tidal flat mussels. Computed lengths are roughly in line with the data.

Results and data for MUSS3 (the third mussel class) are shown in Figure 56 - Figure 59. Here, it is clear that some of the data assigned to MUSS3 probably are more related to MUSS2. As said above, time was too short to come to a better assignment. In some cases (e.g. compartment 11; Figure 57) modelled mass development is faster than the data suggest. Also here, one might wonder whether the data shown might better be connected to class 2 instead of to class 3. Sizes and masses for mussels on tidal flats are smaller/lower than for subtidal mussels.

MUSS4 development is shown in Figure 60 - Figure 63. Mass development (Figure 60 - Figure 61) is computed well for mussels on tidal flats, but for some sub-tidal areas the model seems to be a bit too optimistic. Results for compartment 11 and 12 (Figure 61) suggest that some of the data shown actually belong to MUSS3. The same remarks can be made on MUSS4-lengths (Figure 62 - Figure 63). Also for MUSS4, the tidal mussels are smaller than the sub-tidal mussels are.

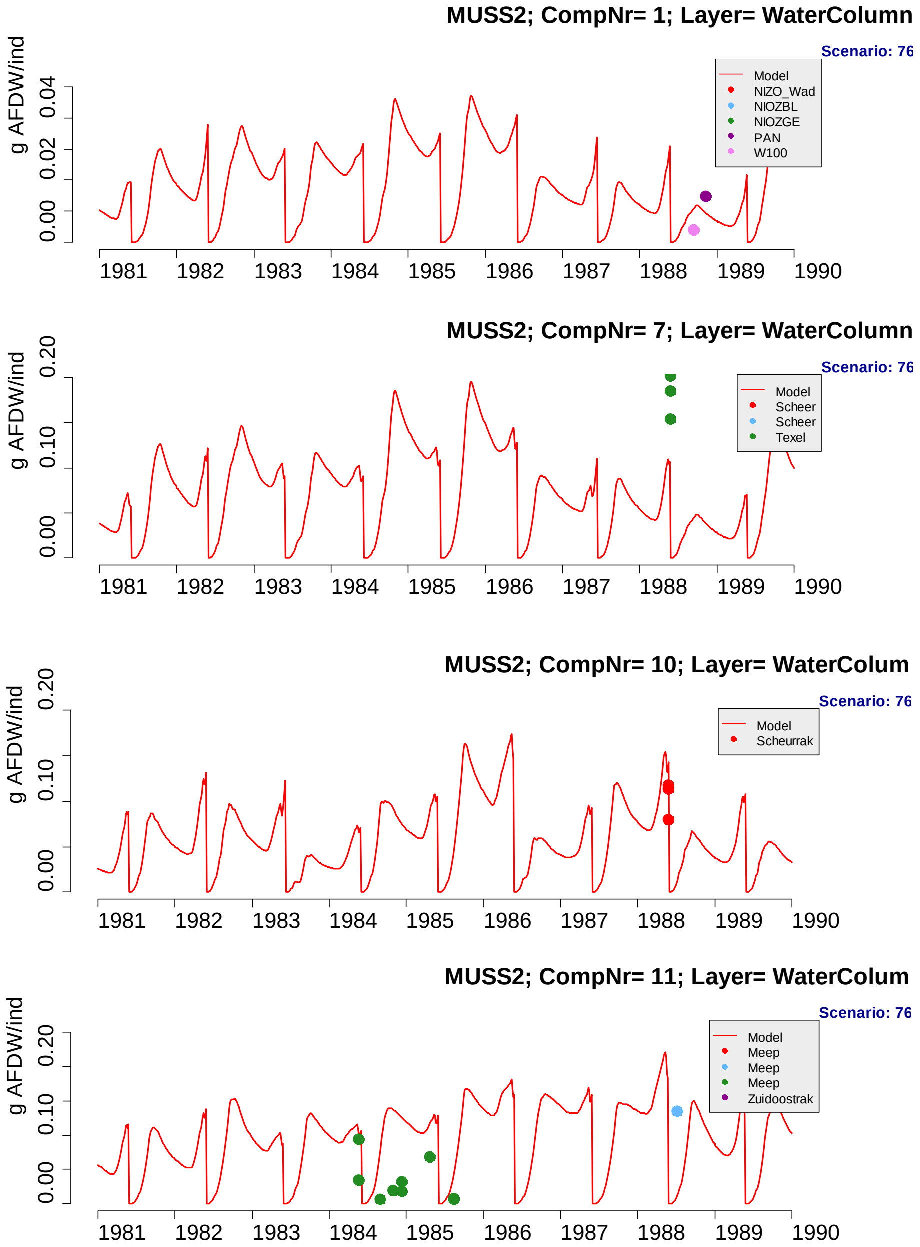


Figure 54 Individual body mass of seed mussels in several compartments. Compartment numbers in Figure 6. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Only, without MZI-mussels.

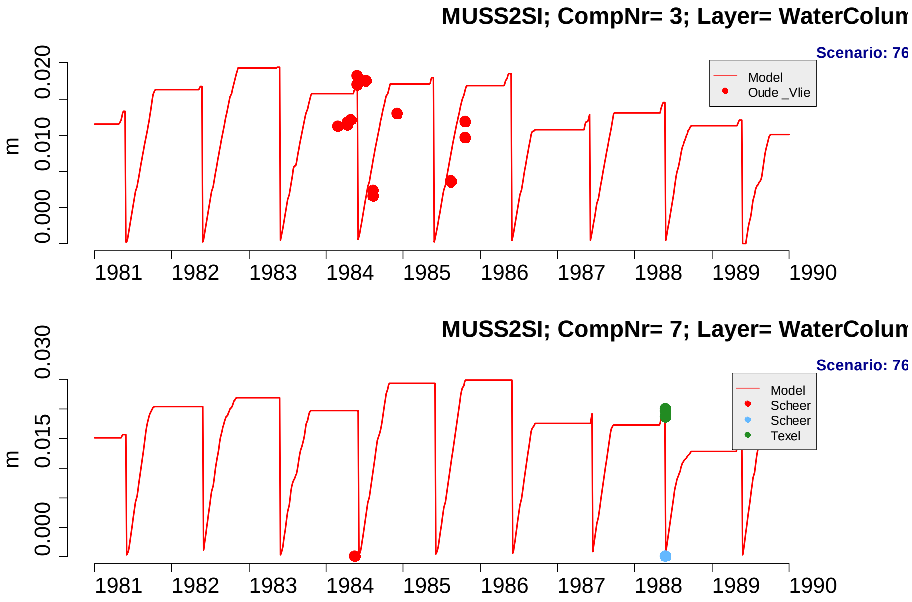


Figure 55 Individual lengths of seed mussels in several compartments. Compartment numbers in Figure 6. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Only, without MZI-mussels.

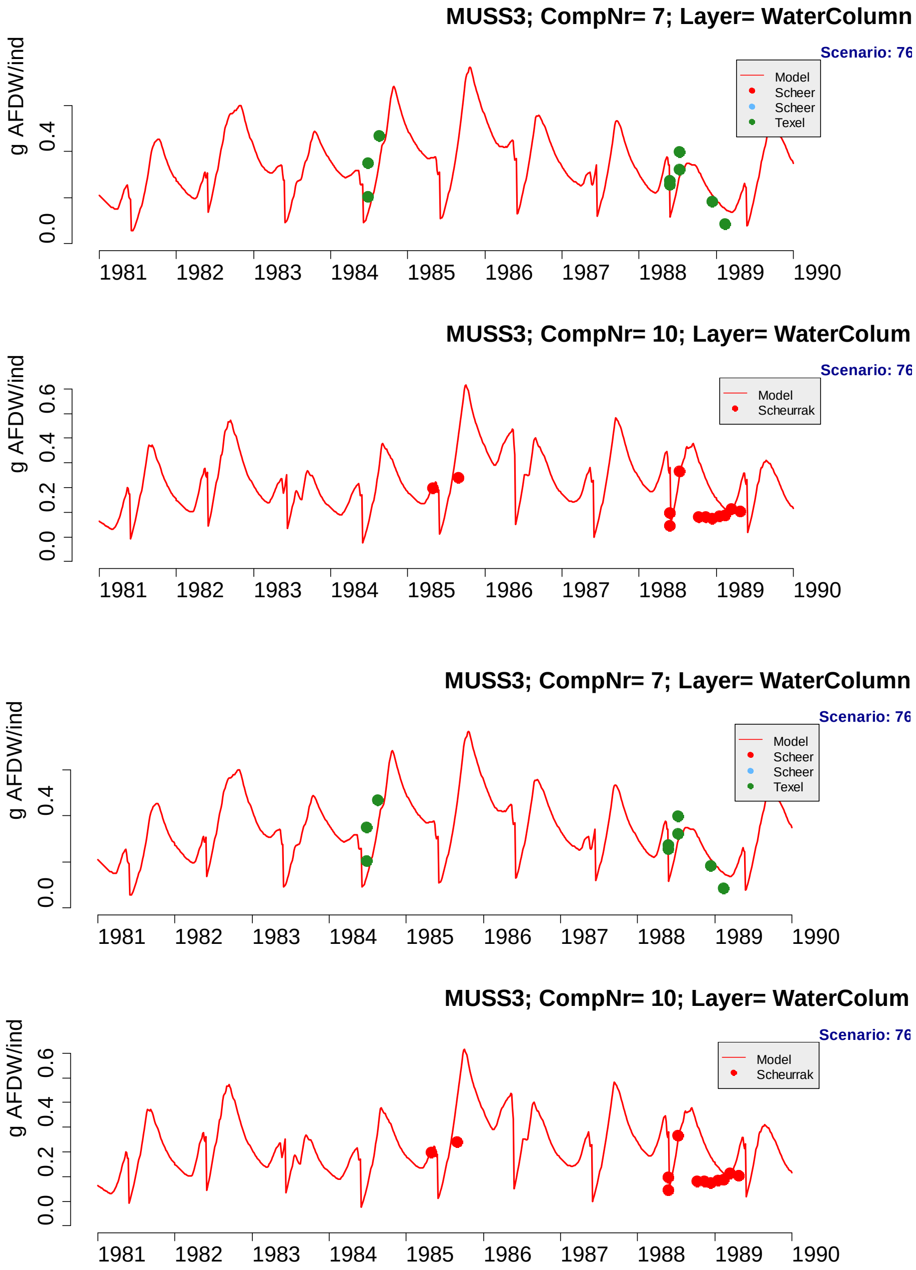


Figure 56 Individual body mass of class 3 mussels (MUSS3) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Only, without MZI-mussels.

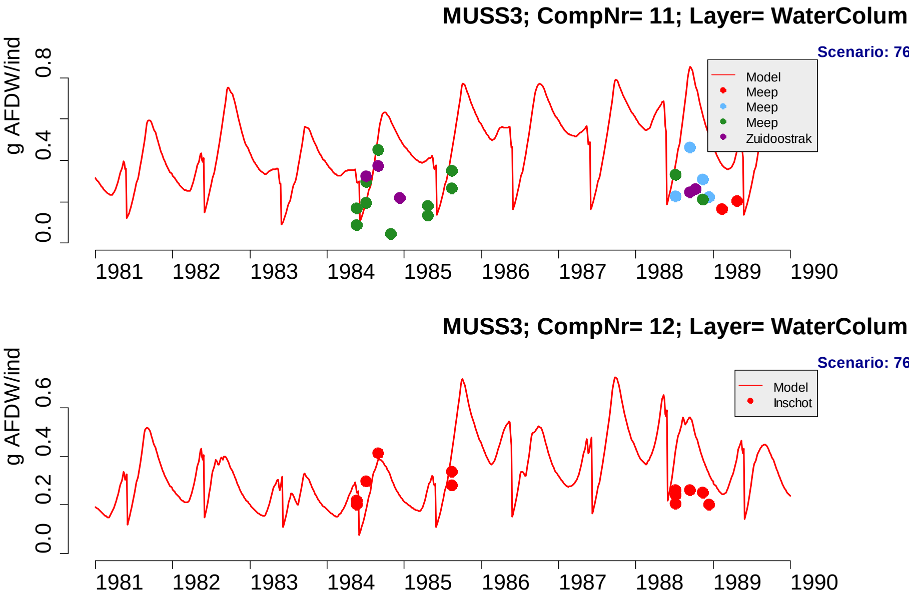


Figure 57 Individual body mass of class 3 mussels (MUSS3) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Only, without MZI-mussels.

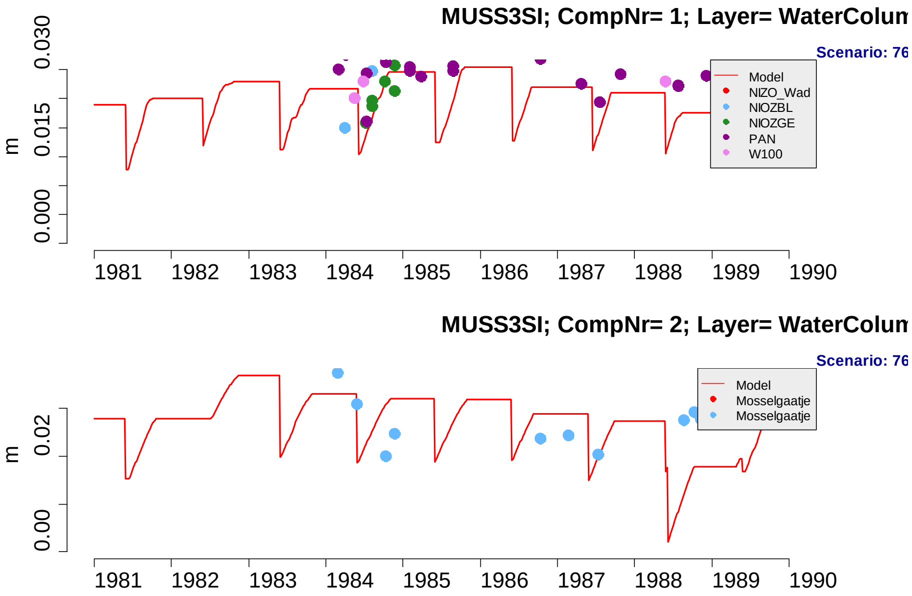


Figure 58 Individual lengths of class 3 mussels (MUSS3) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Only, without MZI-mussels.

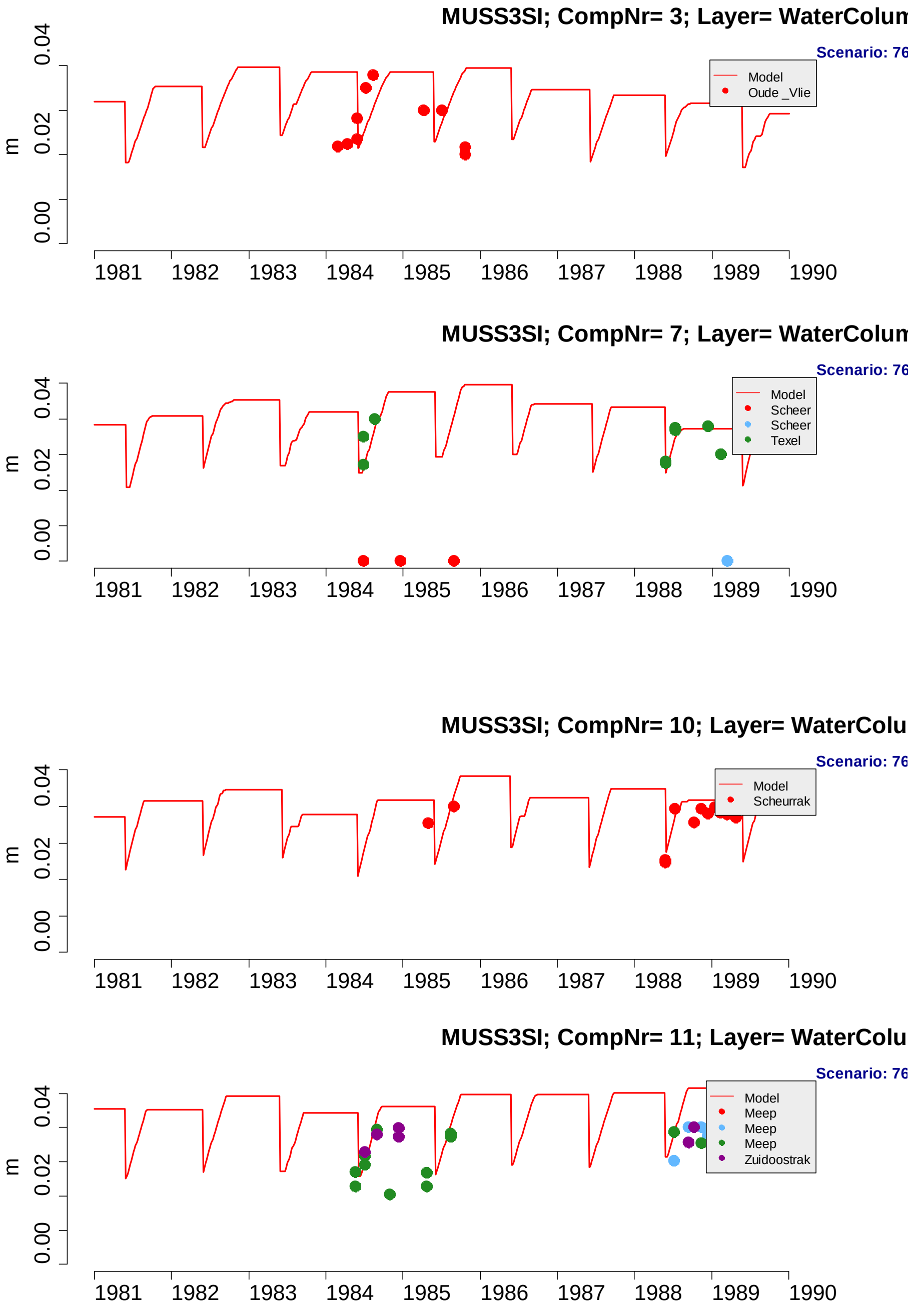


Figure 59 Individual lengths of class 3 mussels (MUSS3) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Without MZI-mussels. Note: the few zero-values in the second graph are dummies.

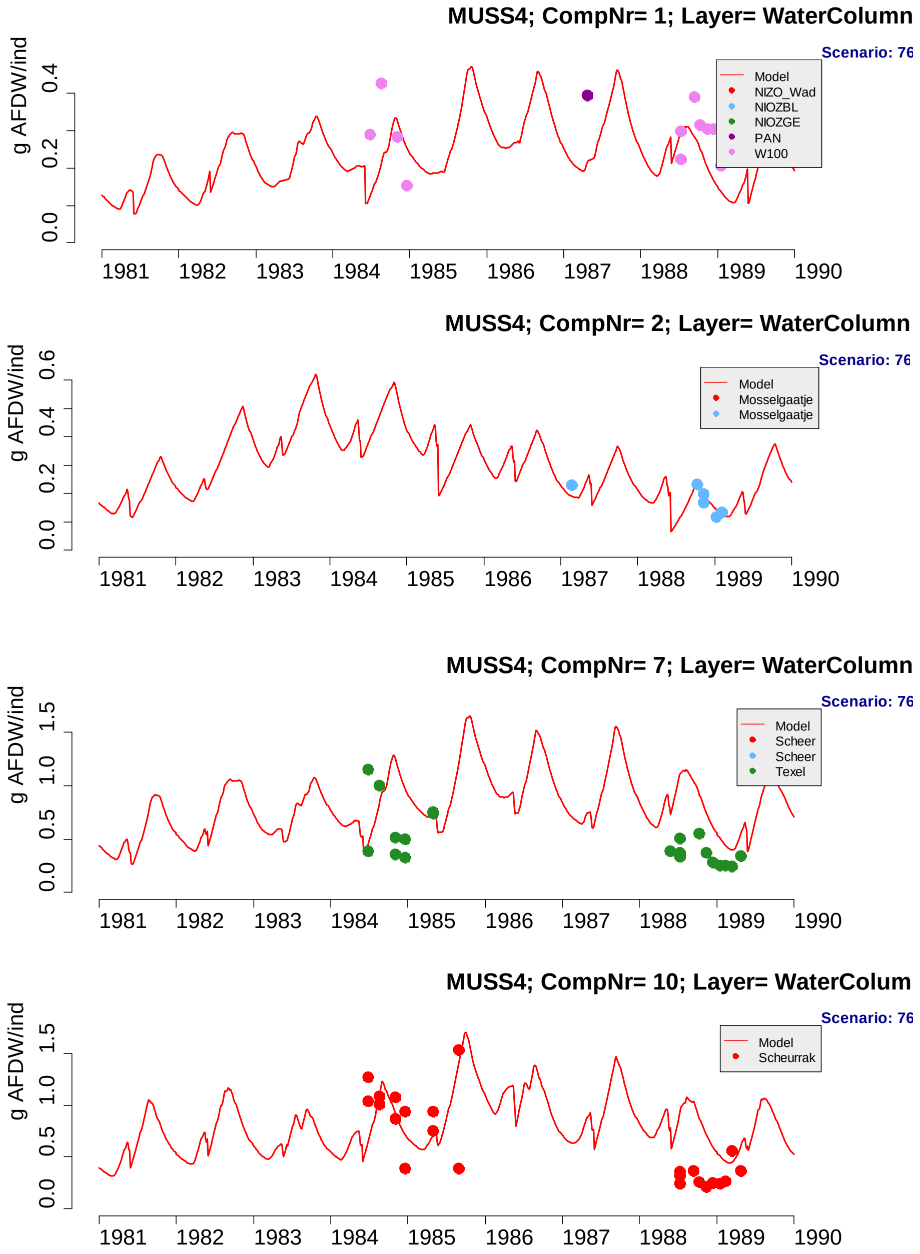


Figure 60 Individual body mass of class 4 mussels (MUSS4) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Without MZI-mussels in the system.

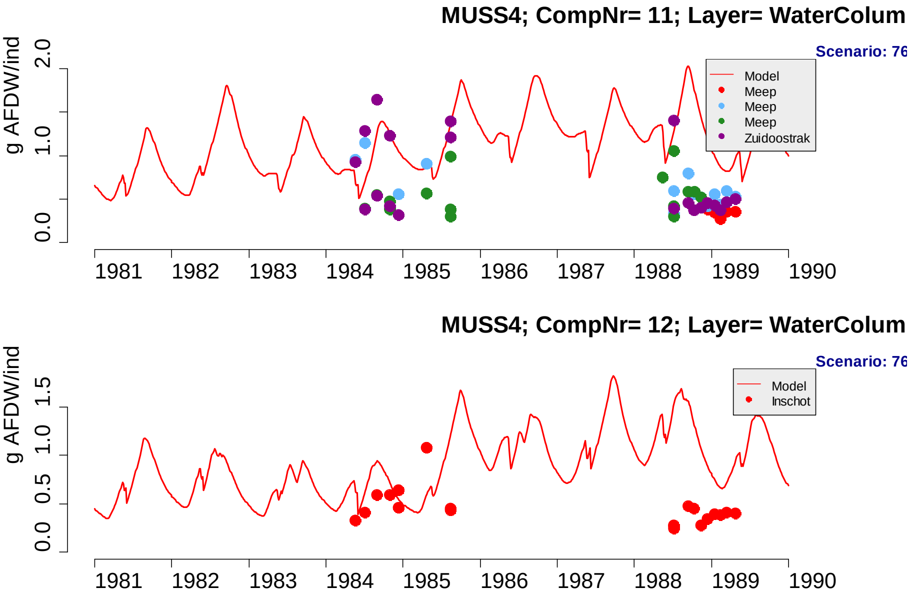


Figure 61 Individual body mass of class 4 mussels (MUSS4) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Without MZI-mussels in the system.

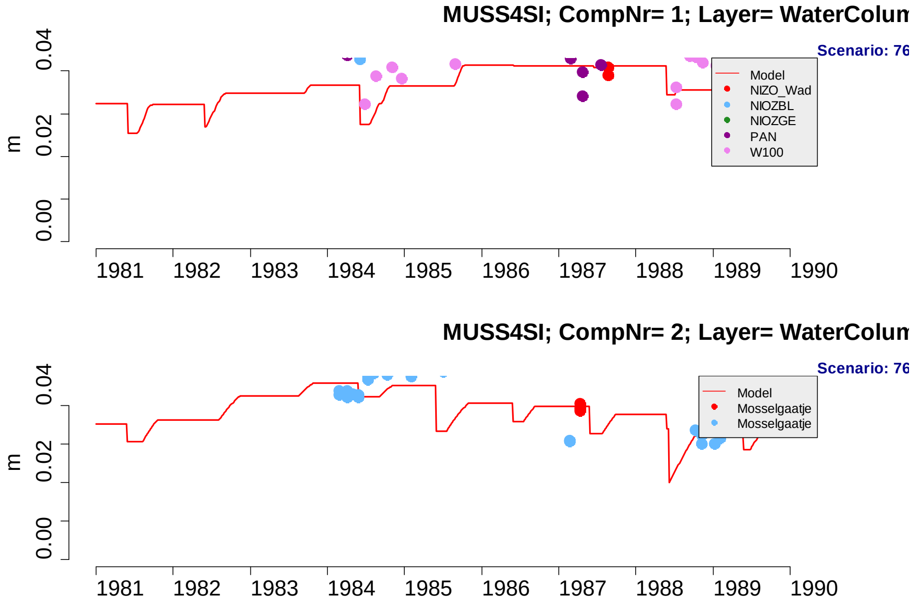


Figure 62 Individual lengths of class 4 mussels (MUSS4) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Without MZI-mussels in the system.

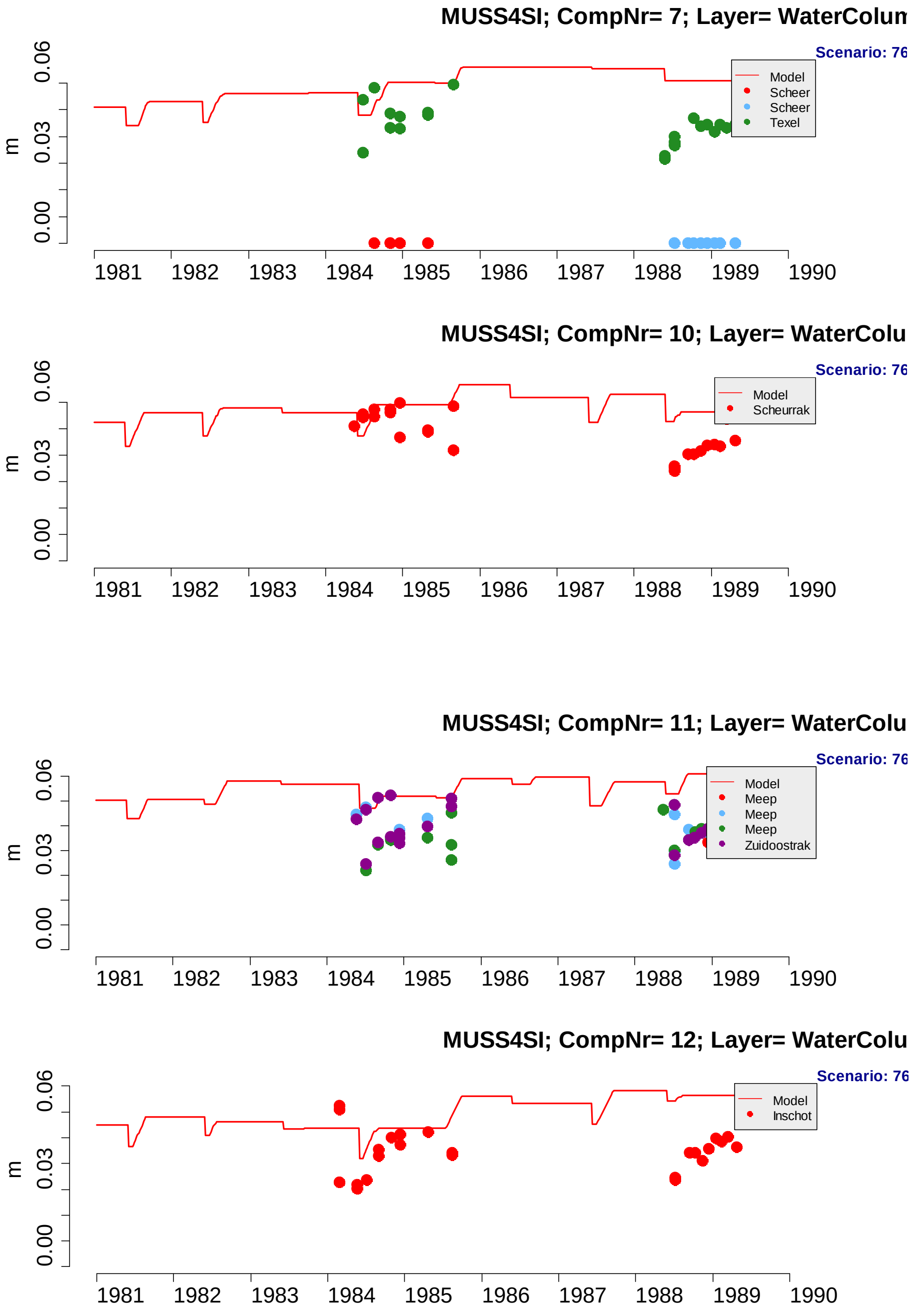


Figure 63 Individual lengths of class 4 mussels (MUSS4) in several compartments. Compartment numbers in Figure 5. Scenario mor2a3_6 has the same parameter setting as the final MZI-simulations had. Without MZI-mussels in the system. Note: the few zero-values in the upper graph are dummies.

Mortality of mussels

Modelling mussel mortality is a crucial part when calculating the development of mussel size and biomass development. It appeared from previous modelling that when mortality of the seed mussels was too high, the development of the larger (and older) classes was erroneous, especially because the computed sizes of classes 3 and 4 then were too high. Also, total shellfish biomass turned out to be too low in most cases. On the other hand, when a too low mortality was assumed, total shellfish biomass also turned out to be too low. In that case, too many seed mussels stayed alive, and out-competed the larger mussels.
All shellfish mortality is modelled following:

$$\frac{dN}{dt} = aW^bN \qquad (\#\ d^{-1})$$

with b<0. Thus the number decrease rate is largest for small animals and decreases with increasing mass. A and b are mentioned in appendix XII as mortalityfacta and mortalityfactb.

Important in that respect is what is called the zero-net growth isocline (Figure 64). The line illustrates that small mussels still can grow at food levels that are insufficient for large mussels to grow.

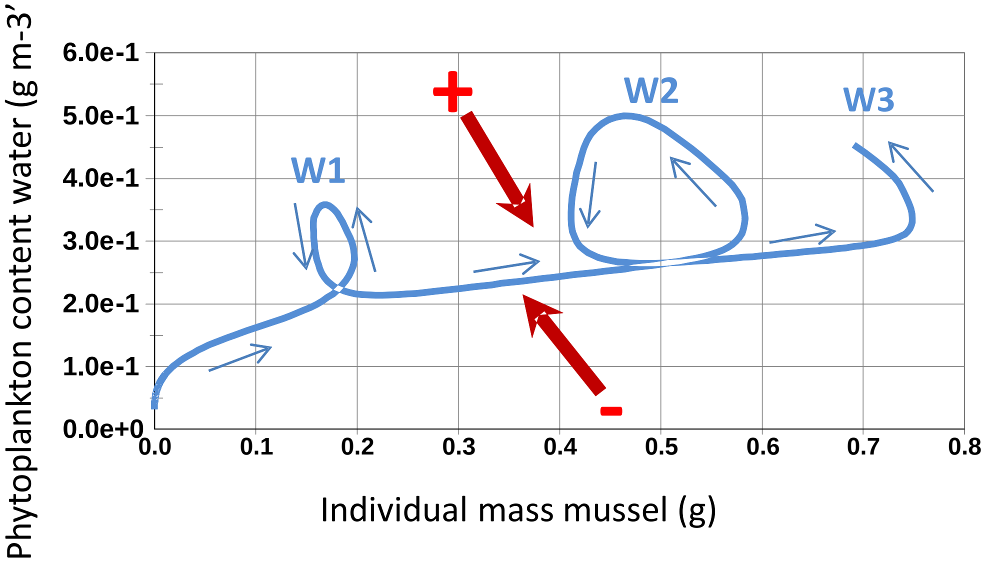


Figure 64 ‘Zero nett–growth isocline’ of the (model-) mussel: depending on mussel mass, the food concentration at which no more growth is possible is drawn. The line is computed for a simple system (so: not the EcoWasp-simulation, but a simpler set-up with varying temperature and food concentration. The thin arrows denote the time path. W1..W3 mark the winter periods. In case the phytoplankton content is higher than the blue line denotes, then the mussel still can grow. In case it is lower, the mussel will lose mass. In winter periods the desired food level increases, and the individual mass gets lower. In case of a lower food content first the individual biomass will decrease, but, since the mortality is coupled to this individual mass, also the mortality will increase. As a result, both the population biomass and the reproduction will decrease. The remaining animals can grow and finally, the food content will return to a value that is in agreement with the individual shellfish biomass. See also Brinkman (2012).

Thus, when MUSS2 mortality is too high, too few mussels survive and standing stock of adult mussels will not develop. If MUSS2 mortality is too low, too many seed mussels (MUSS2) will survive and will out-compete the adult mussels.

Extra data available to tune mortality come from the NIOZ-surveys done by Beukema and Dekker. They both sampled the Balgzand area for many years and counted and measured the numbers and individual masses of –among others- tidal flat mussels. Their survey was conducted twice a year: in springtime (dated mid March) and in autumn (dated mid August), average values were kindly made available.
Based on their results data for the ratio seed mussels to total mussels are available.

In Figure 65, data and model results are shown. Autumn ratios mostly are higher than March ratios. On average, the agreement is –although far from perfect- not too bad; but the model has difficulties with predicting very low ratios.

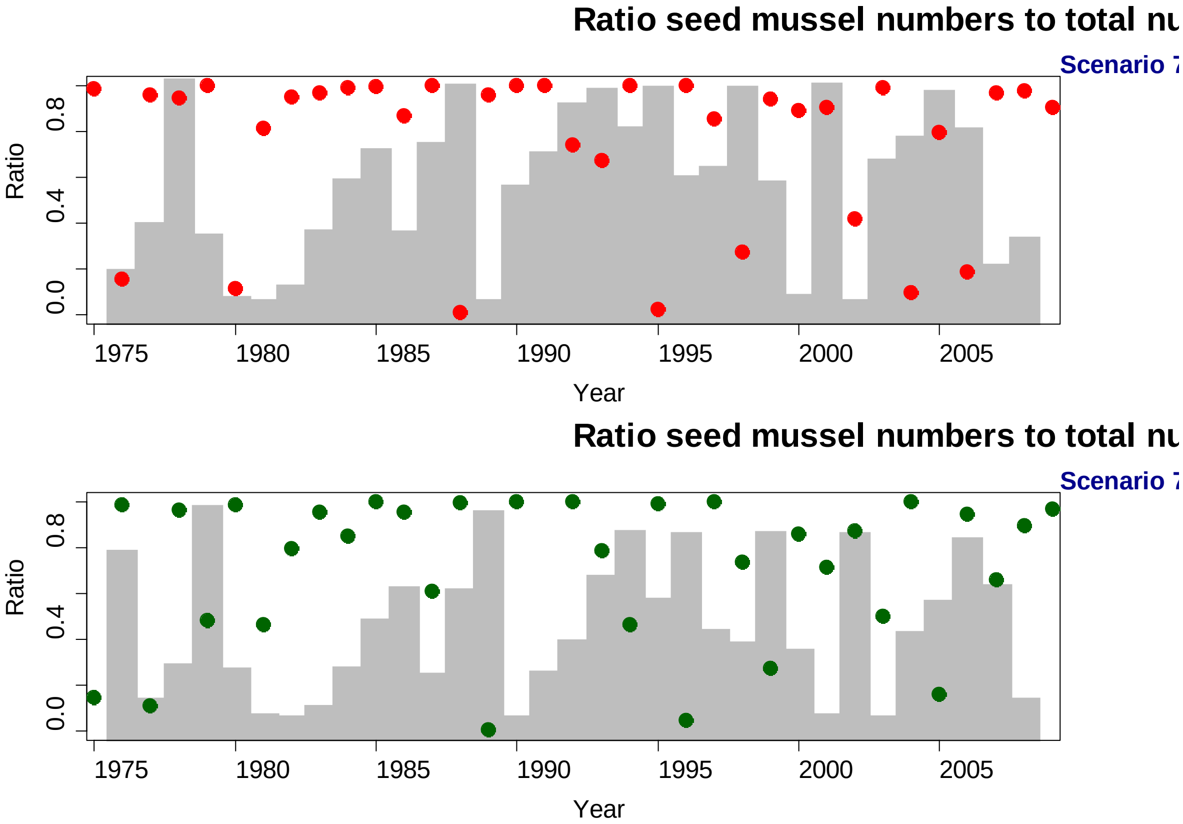


Figure 65 Ratio seed mussels to total mussels (numbers) on the Balgzand area during the period 1975-2009. Upper: August, lower: March. Dots: data by Beukema and Dekker. Bars: as computed by the EcoWasp-model.

Special attention is needed for the years around 1990. In reality, almost the complete mussel population disappeared from the Wadden Sea, caused by continuous fishing in a period where nutrient conditions were poor. In the model situation, this fishing is not occurring, and thus, low ratios are computed. In the real world, no adult mussels were available, which results in very high ratio values.

Mortality of MZI-mussels at the nets

Previous data by Kamermans (comm) showed that the number of MZI-mussels at the nets decreased to about 10-20% of the initial numbers.

Growth of MZI-mussels at the nets

Data for growth of MZI-mussels follow from Jansen et al (2012) and data by P Jacobs. At the end of the growing season, MZI-mussels reached a 20 mm length (about).

Kamermans et al (2012) showed a MZI-mussel biomass increase from 10 to 30 kg fresh mass m^{-2} from week 33 to 40, in 2011. For 2010, data were more scattered.

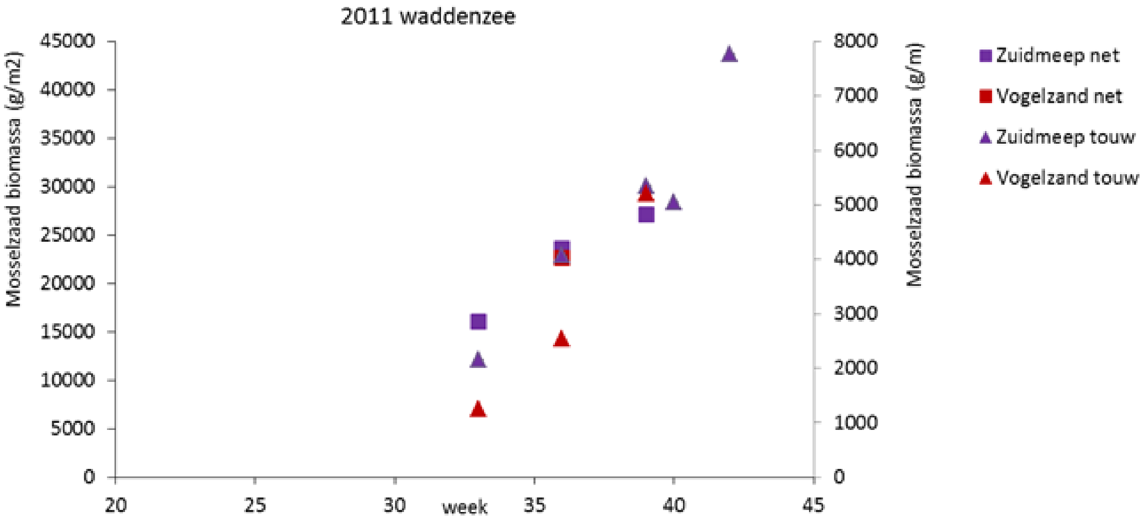


Figure 66 Biomass increase at MZI-nets in the Wadden Sea, 2011. From week 33 to week 40, biomass roughly increased twice to three times. Maximum value is about six times increase for ropes at 'Vogelzand'. Taken from Kamermans et al, 2012

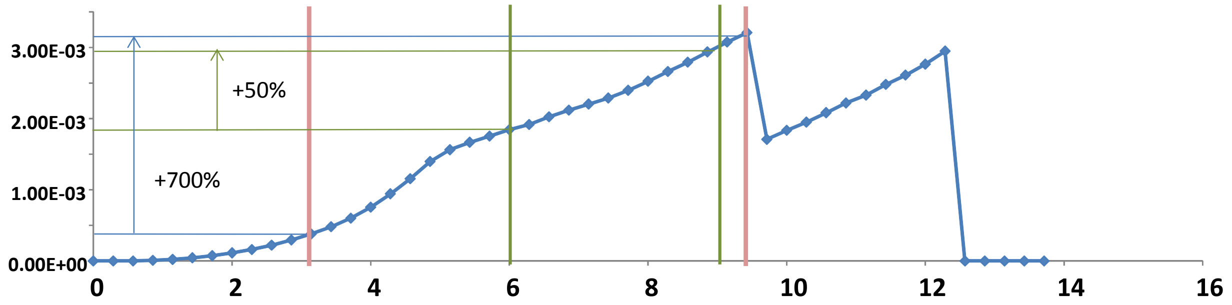


Figure 67 Biomass increase at MZI-nets in compartment 7 in the Wadden Sea. Example of model results. X-axis: weeks from settlement. Y-axis: g AFDW/m3 (water column) in this compartment. Since these values depend on the number of MZI-nets, these values can only be compared with those from Figure 66 in a relative sense. Biomass roughly increased 6-fold from week 3 to week 9, and about 1.5 fold between week 6 and week 9.

Growth and mortality of MZI-mussels at the culture lots

For MZI-mussels at the culture lots the same parameters for filtration, growth and mortality have been used as for natural mussels. See appendix XII for parameter values.

Appendix V Tuning the fauna parameters

Filtration and respiration compared to literature data

Uptake and respiration parameters have been estimated first following a procedure as sketched in the previous section. Next, field and literature data have been used to come to better final values. Field data on natural mussels growth –found for the Wadden Sea- are mentioned in the next appendix (IV).
Several literature data are available: Sprung (1984^{a-c}), Riisgard et al (1980, 1981), Riisgard & Randløv (1981), Bayne (1979), Thompson (1984), Smaal (1985,1997), Cranford et al (2011). Smaal (1985, 1997) also provided an overview.

From Figure 68 it can be seen that most of the literature data for filtration give much larger results than the EcoWasp model computes. The experience was that mussels would grow much too fast in the model if the literature data had been applied. It appeared that the data by Cranford et al (2011) are best in agreement with the model. Mussel respiration rates (Figure 69) had to be chosen in the model to be somewhere between the (wide) range of literature results.

The model results have been tested against Wadden Sea data. These were obtained as mentioned in Appendix IV.

A second way is to compare the model results with field and experimental data as provided by the work of Asmus et al (1992), Asmus & Asmus (1997,1998a, 1998b), Dame & Dankers (1988), Dankers et al (1989). They measured uptake or release of components by mussel beds, compared to bare Wadden Sea sediment (Asmus & Asmus) or to mussels beds consisting of dead shells (Dame & Dankers). Variables measured have been chlorophyll-a, particulate matter, oxygen, phosphorus, nitrogen, ammonium. In Figure 70, results are shown. Mostly, the computed fluxes of the several compounds are within the range measured in the field and the experimental situations, and the similarity is seen as confirmation that the modelled processes are tuned satisfactorily.

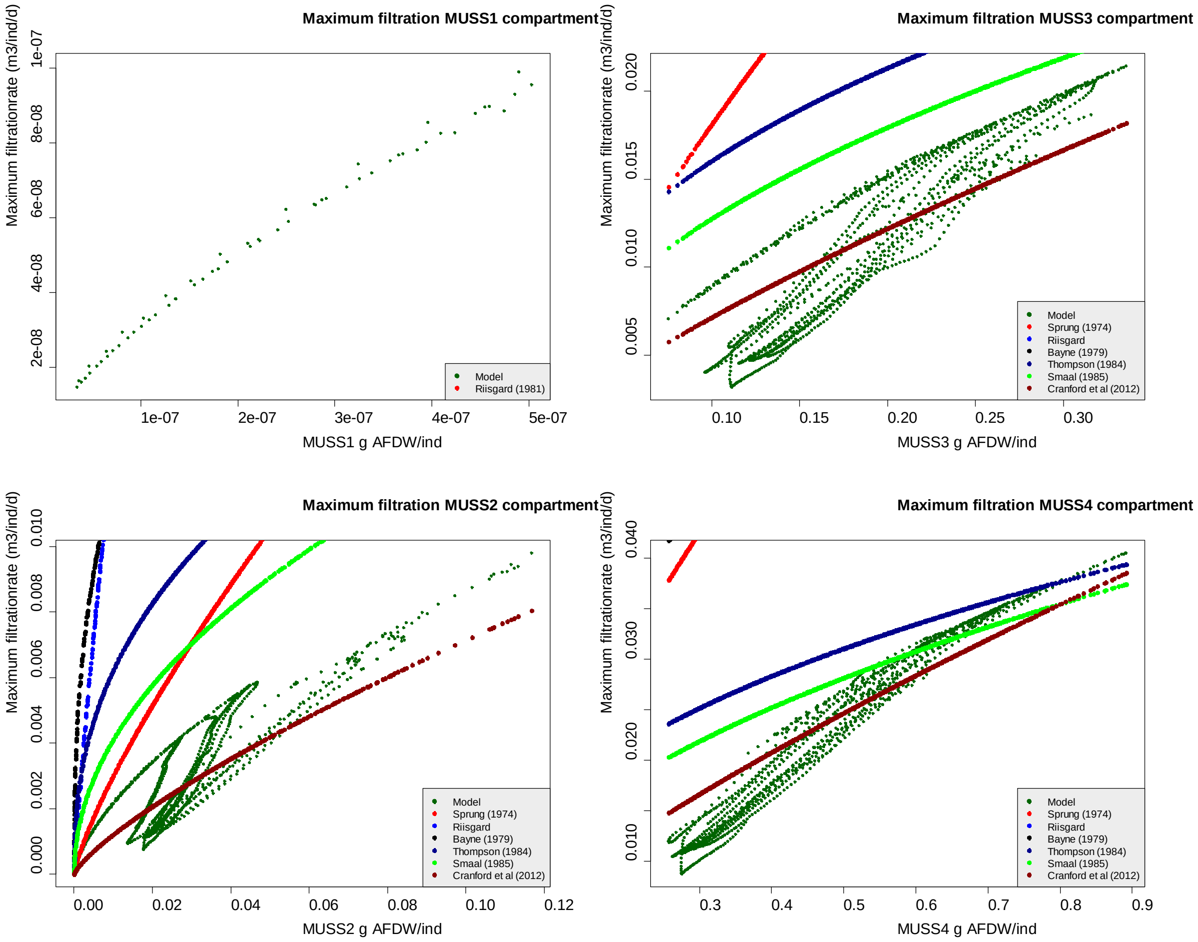


Figure 68 Maximum filtration rates (m^3 ind^{-1} day^{-1}) for mussel larvae, seed mussels (lower left), and adult mussels (MUSS3, upper right and MUSS4, lower right). Green dots represent EcoWasp-model results; lines are from literature data. Note that most of the literature data have been measured for a shorter size range than used here; part of the extrapolation thus is not valid. Larvae filtration rates are outside the range of the graph (literature data are much higher than model setting).

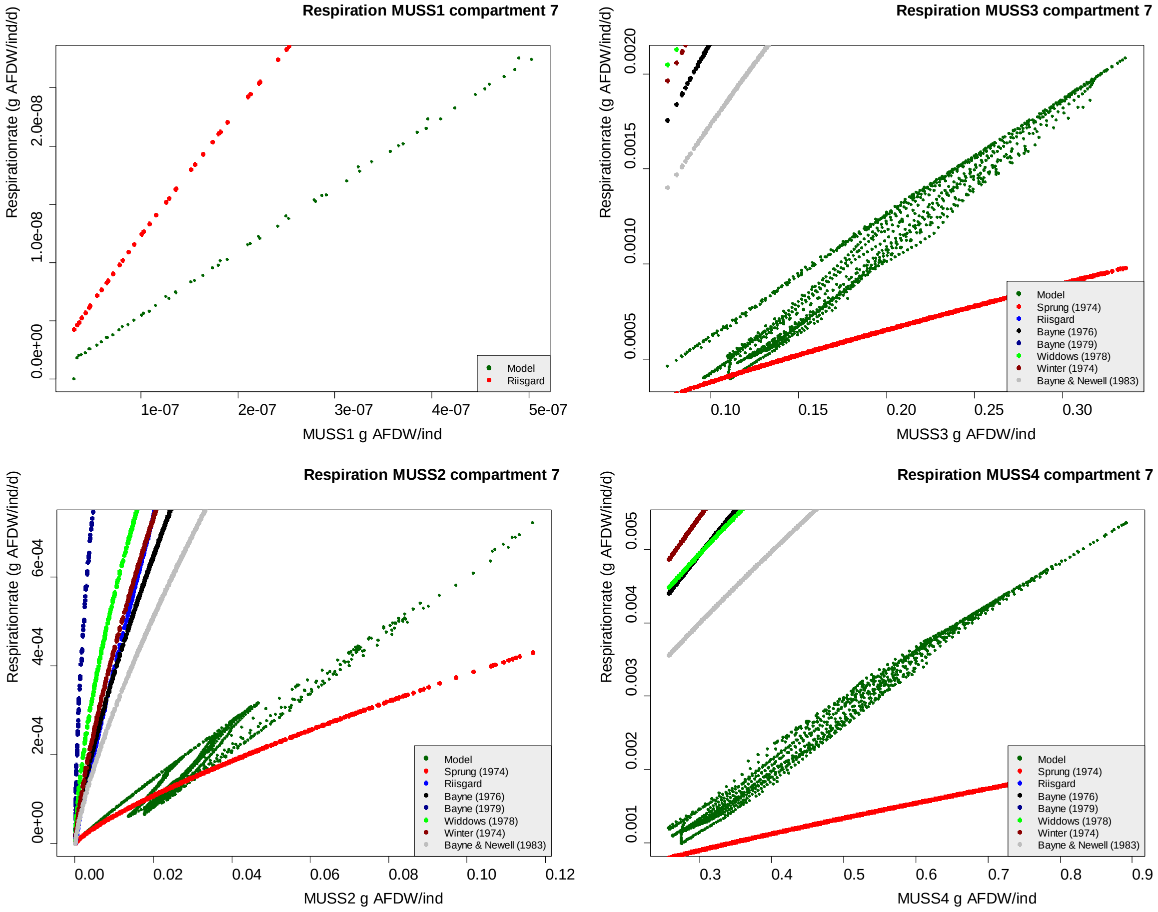


Figure 69 Respiration rates (g AFDW ind-1 day-1) for mussel larvae, seed mussels (lower left), and adult mussels (MUSS3, upper right and MUSS4, lower right). Model results for compartment 7 (Marsdiep). Green dots represent EcoWasp-model results; lines are from literature data. Note that most of the lite of the literature data have been measured for a shorter size range than used here; part of the extrapolation thus is not valid.

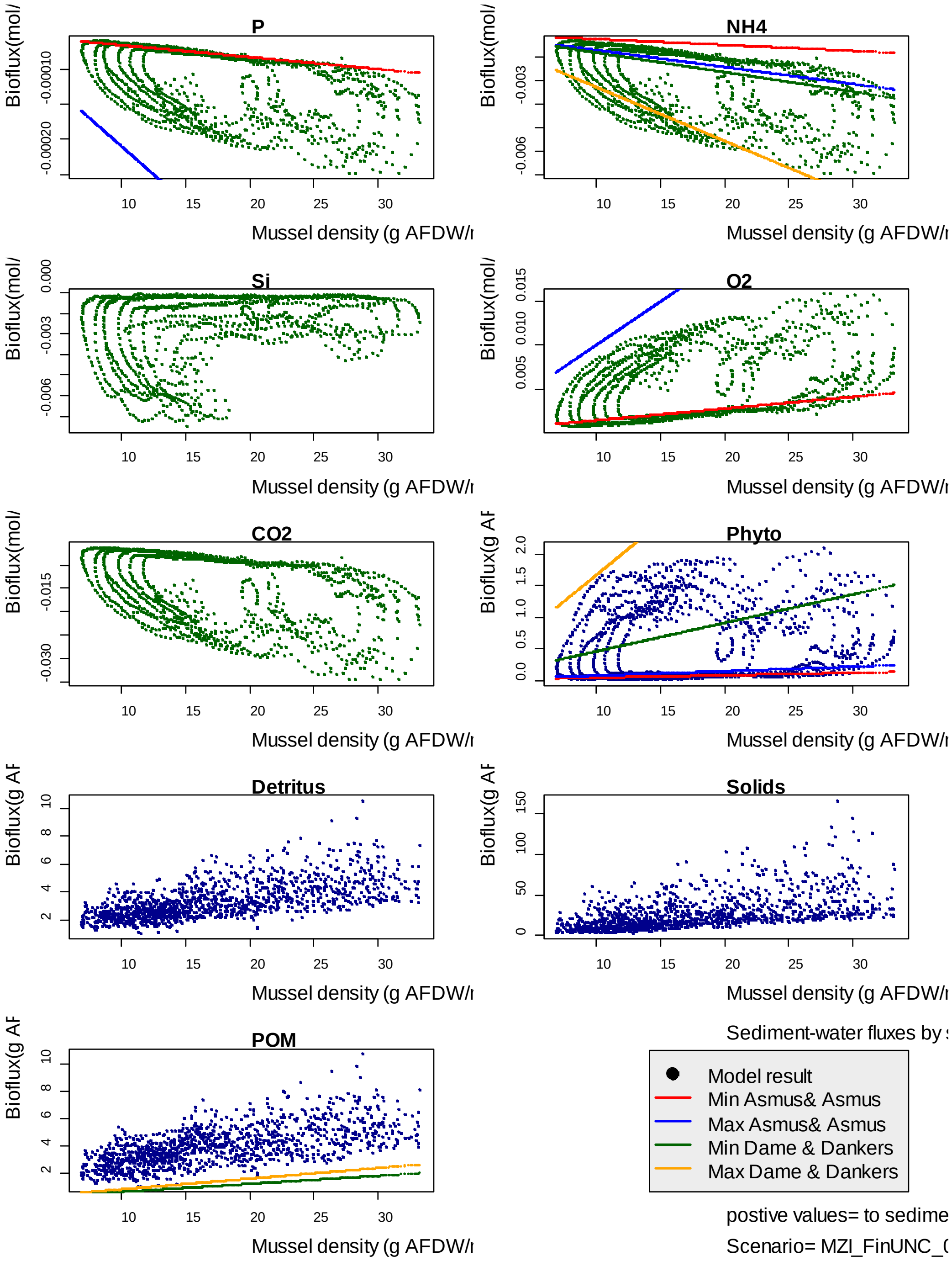


Figure 70 Exchange between a mussel bed and the water column, measured by Asmus & Asmus, and Dame & Dankers (refs see text) (lines) and computed by the EcoWasp-simulations (green dots).

Appendix VI. Energy budget for fauna

Based on the uptake by and energetic losses of mussels (as representative Wadden Sea shellfish species), an energy budget can be computed. For mussels present in compartment 7 results are presented in Figure 71 and Figure 72. Assimilation is the only food source, and minus the several losses a nett gain results. This net gain, relative to the total flow of energy, decreases from MUSS1 -> MUSS4. Thus, a MUSS4-mussel of about 0.6 g AFDW on average assimilates two to three times its mass per year.

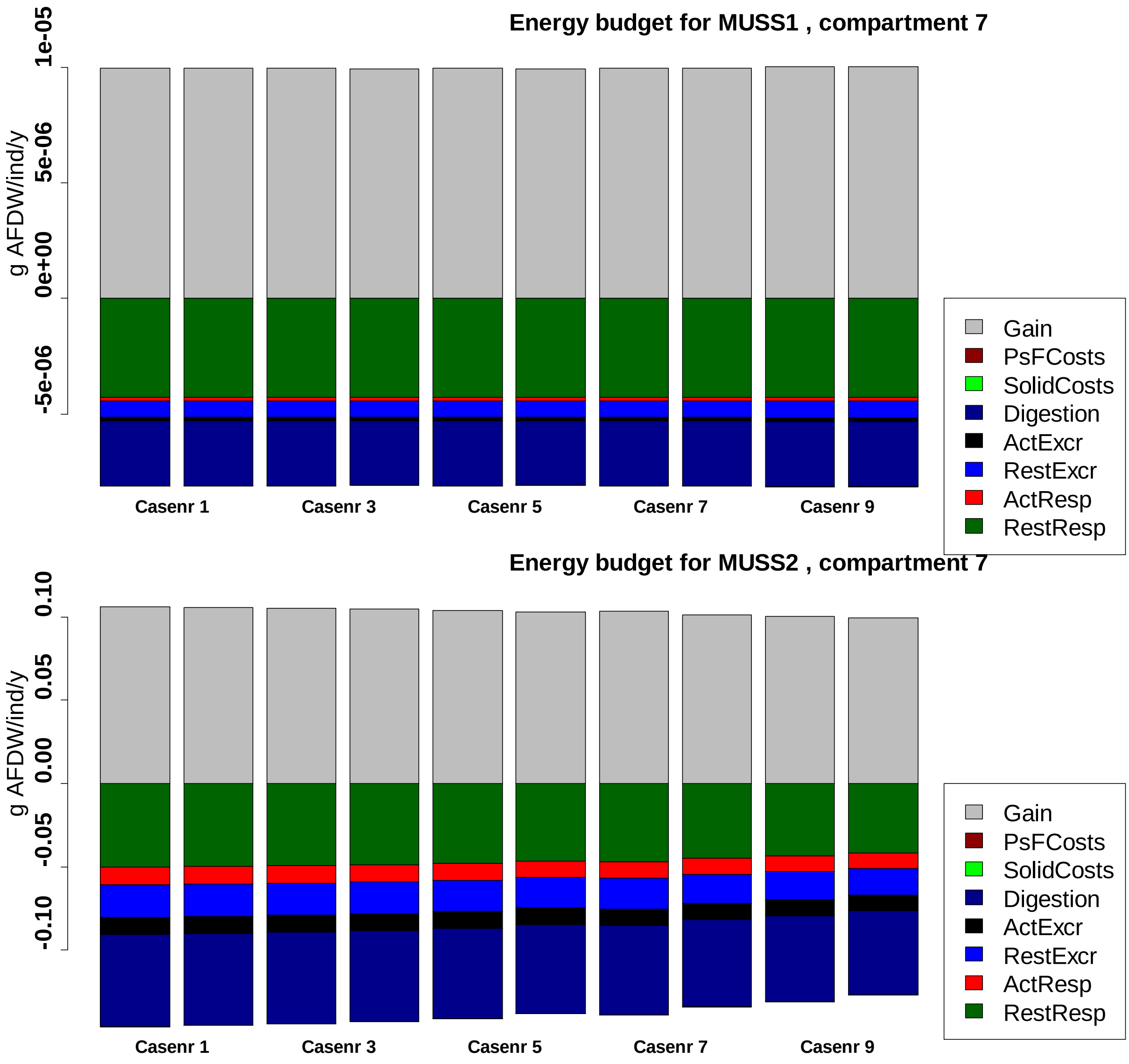


Figure 71 Energy budgets for mussel larvae (upper) and seed mussels (lower), in compartment 7 (sub-tidal Mardiep-area; see Figure 6 for situation). Average values for the whole 2006-2013 simulation period. There is one source: food assimilation, and several losses. Gain is the difference between source and losses and equals net growth rate.

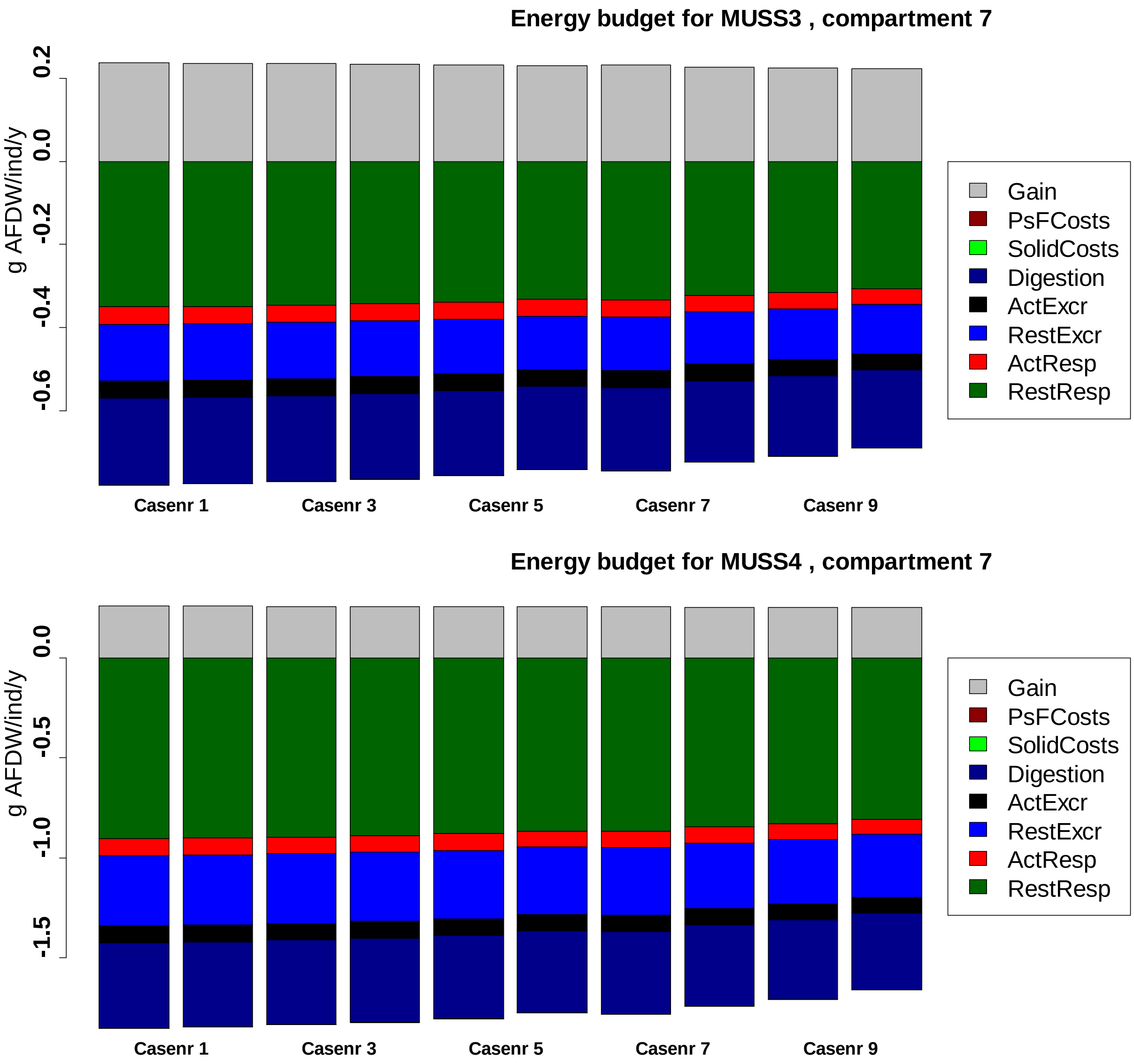


Figure 72 Energy budgets for larger mussels: MUSS3 (upper) and MUSS4 (lower), in compartment 7 (sub-tidal Mardiep-area; see Figure 6 for situation). Average values for the whole 2006-2013 simulation period. There is one source: food assimilation, and several losses. Gain is the difference between source and losses and equals net growth rate.

Appendix VII. Prey-size selection for fauna

Particle retention by shellfish

There are two parameters that can be used for prey size selection.
The first, PP_Pref[prey], is straight-forward. It simply gives the chance that a prey, although it can be caught, also really is caught by an animal. If =1, than the catch is equal to the filtration rate times the concentration of an animal in the medium. If =0, than a prey is never caught by the shellfish, although the prey may be abundant. PP_Pref[prey] may get any values from 0 to 1.
The second possibility is related to the sizes of prey and predator/grazer. It can be relative: the prey size selection depends on the size of the predator/grazer, and absolute: a certain prey size range is grazed/predated. The ranges can be chosen very wide (all sizes are caught) or narrow (specific prey choice).
Thus, prey-size selection is not always really necessary. It is only relevant in case a specific prey choice based on size selection has to be included.

In the final EcoWasp-simulations, the size range that can be captured by shellfish depends (or: may depend) on the animal size. Basically, the selection efficiency (-) for a certain size L (m) is described using the equation:

$$\text{Efficiency}(L) = \begin{bmatrix} \frac{(L-L_1)^2}{(L-L_1)^2+(L-L_2)^2} & for\ L_1 < L < L_2 \\ \frac{(L-L_4)^2}{(L-L_3)^2+(L-L_4)^2} & for\ L_3 < L < L_4 \end{bmatrix} \qquad \text{(-)} \qquad (1)$$

and Efficiency(L)=1 for $L_2 \leq L \leq L_3$ and =0 for $L<L_1$ and $L>L_4$. L is the prey length (m), and $L_1..L_4$ are the size parameters.
Thus, for $L_2 \leq L \leq L_3$, the catch is 100% efficient, and it drops to 0 from $L_2 \rightarrow L_1$ and $L_3 \rightarrow L_4$.
Depending on the choices such a drop can be very steep or not, an example is given in Figure 73.

The values for $L_1..L_4$ can be made depend on the size of the animal, and thus describe the catch sizes changing during the growth of the animal:

$$L_i = L_{i0} \cdot Size + Xa_i \cdot Size \qquad \text{(m)} \qquad (2)$$

Few data are available on particle retention. Vahl (1973, cited by Winter, 1978) gave some values for a few shellfish species (Figure 74). These values have been found for the larger shellfish sizes. Small animals, such as seed mussels, are able to catch small algae with higher efficiency.

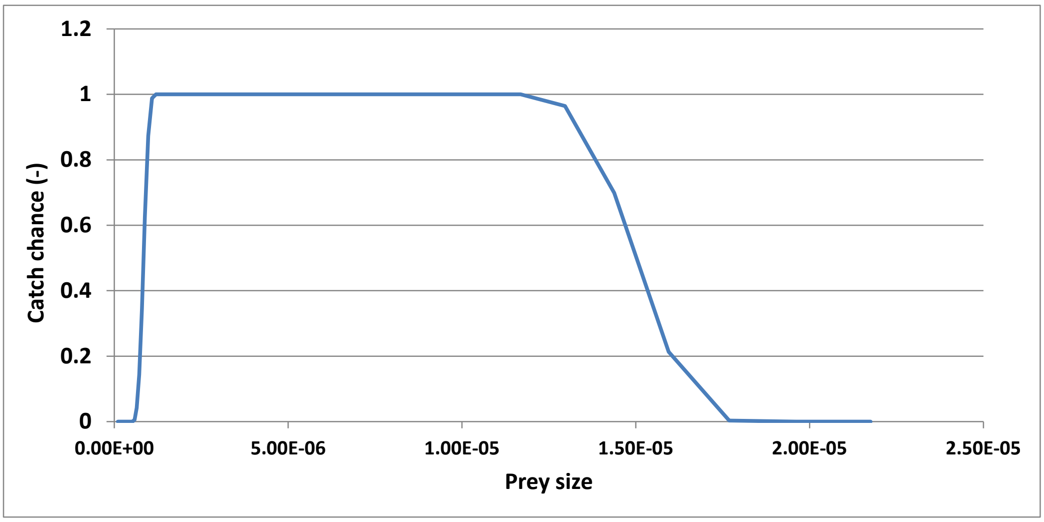


Figure 73 Particle size selection efficiency (“catch chance”) depending on prey size. Illustrative example.

Implementation in the model

In the model, L_1..L_4 are called PP_preysz_x1.. PP_preysz_x4, and Xai are called psz-ia. Note that the parameter L_{i0} in eq. 2 is the same as the L_i in eq. 1.

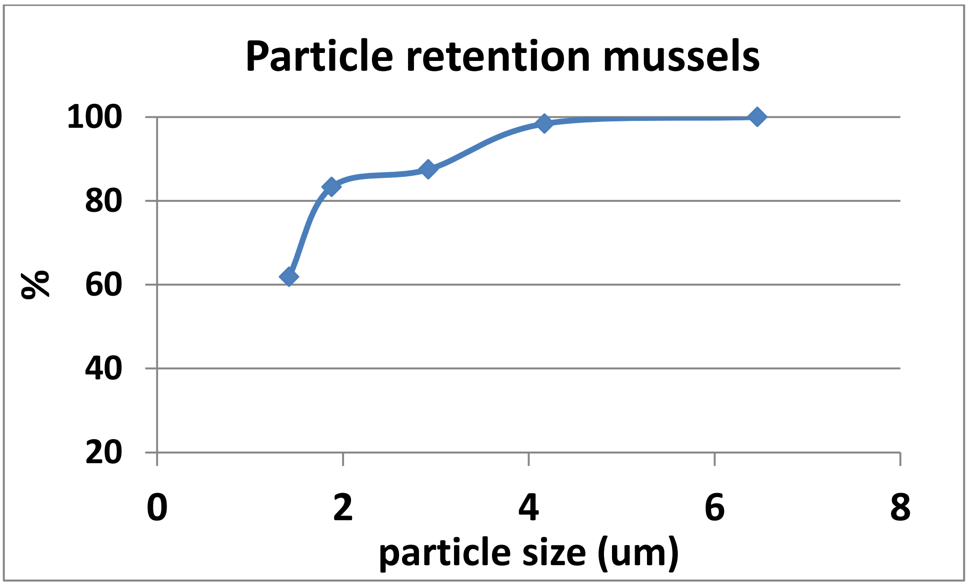
For mussels (class 3 &4) and MZI-mussels (class 4 & 5), there's no need for a size selection. The animals filter diatoms, non-diatoms and microzooplankton. For picophytoplankton the preference-parameter (PP_Pref[PICOPHYTO]) is simply set to 0.

For these mussels and MZI-mussels, the parameters PP_preysz_x1 .. PP_preysz_x4 (the boundaries) and PP_psz_x1a – PP_psz_x4a (change of the boundaries with the size of the animal) have to be chosen such that no limitations for the prey selection occurs. Thus, all psz-ia values can be set to 0; preysz_x1 and _x2 can be set to very low values: 1e-7 & 1e-6, and preysz_x3 and x4 can be set to large values: 1 & 2. Note that if the first two are equal, all values below x2 will give a prey selection of 1, as is the case for the upper boundaries: if x3==x4, everything above x3 is caught (prey-selection=1). If the parameter PP_preysz_relative ==1, then all the absolute values of the boundaries are computed as xi*animal size, else the values xi *are* the boundaries.

For the mussel larvae, it also is not needed to use preysz_xi for particle selection: only the picophytoplankton is used and this can be governed by the prey-preference parameter.

The only case where it is needed, concerns the seed mussels. From the PhD-work of Pascalle Jacobs it appeared that seed mussels can catch very small algae, but this capability changes with their size.

Seed mussels (MUSS2 cq MZIMUSS2) start at 230 µm size, and grow until about 20 mm. In the beginning they still can catch 2 µm picophytoplankton → the lower boundary is computed according to preysz_x1= 5e-3 and preysz_x2= 1e-2. These choices imply that algae<1.15 µm are not caught, and algae> 2.3 µm are fully caught. Later on, the lower boundary gets larger, and at 20 mm length, algae<3 µm cannot be caught anymore, and algae> 5 µm are fully caught. That means a x1-value of 1.5e-4 and a x2-value of 2.5e-4. These changes mean that the x1a-parameter is -5e-4 and the x2-a parameter -4.93e-4.



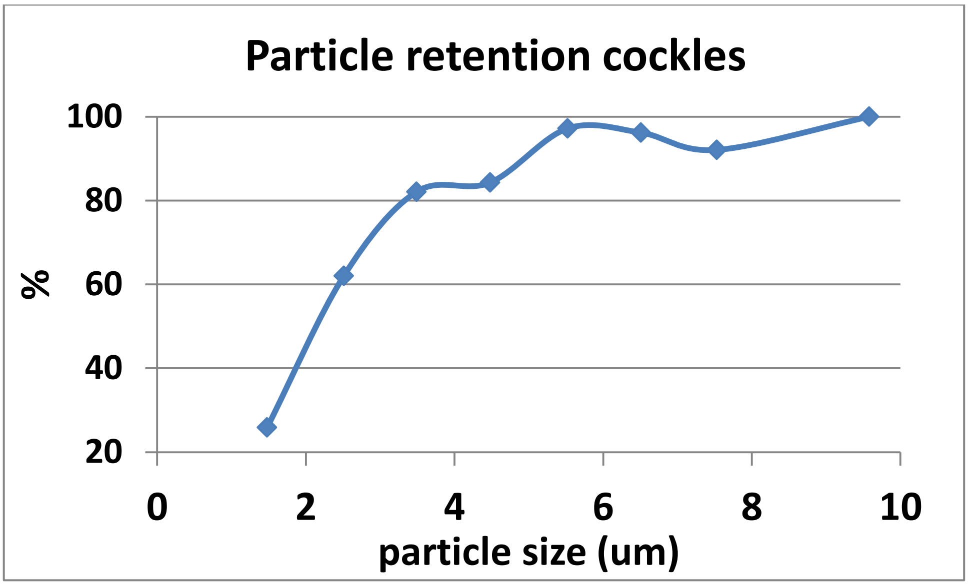


Figure 74 Particle retention by mussels (upper) and cockles (lower), according to Vahl (1973, cited by Winter, 1978).

We also have set upper boundaries. This is not relevant for the phytoplankton, but it is for the mussel larvae. Larvae are between 80 and 230 µm in size, and the largest ones cannot be caught by mussels of a few mm in size. The upper boundary therefore has been set to 0.1; this is an arbitrary figure.

That leads to the following parameter setting:

par	MUSS2 & MZIMUSS2&MZIMUSS3	Rest
preysz_x1	5e-3	0
preysz_x2	1e-2	1e-3
preysz_x3	0.1	1
preysz_x4	0.15	2
psz_x1a	-5e-4	0
psz_x2a	-4.93e-4	0
psz_x3a	0	0
psz_x4a	0	0

These parameters appeared to be, unfortunately, not in agreement with the results of Pascalle Jacobs; there was not enough time to implement her data. In a follow-up the particle selection can be made consistent with her data.

Appendix VIII. Phytoplankton, detritus and fauna composition

Phytoplankton composition

In the present EcoWasp-setup, phytoplankton still has a fixed composition. This composition is computed as follows.

The “chemical equation” of phytoplankton production is generally:
$aCO_2 + bNH_3 + c\ H_3PO_4 + d\ H_2O + s\ SiO_2 = C_aH_zO_eN_bP_c(SiO_2)_s + q\ O_2$

with 'usual' values: $a=5$, $b=1$, $c=1/30$, $e=2$, $z=h+c+b$ with $h=6$.

With this reaction, charge neutrality is ensured, and the oxidation number of the C-atoms is determined by the choice of the a, b, c, e and h values.

The H-budget gives:
$3b + 3c + 2d = z = h + c + b$.
Since we need d, it follows that
$2d = z - 2b - 2c \rightarrow d = (h - 2b - 2c)/2$

The oxygen balance gives:
$2a + 4c + d + 2s = e + 2s + 2q$
Since we need q, it follows that
$2q = 2a + d + 4c - e \rightarrow q = (2a + d + 4c - e)/2$

The “molar mass” of the phytoplankton formula is $M = 12a + 17b + 30.07c + 16e + z + 60.09s$.
In EcoWasp-terms: each gram DW contains 1/M mol phytoplankton.
The molar composition of phytoplankton (mol element g^{-1} DW) thus is
CO_2 = a /M
NH_4 = b/M
P = c/M
O_2 = - q/M
Si = s/M
H = z/M
Restcharge = 0
Note that the oxygen coupled to Si is left out of the molar composition for oxygen.

The oxidation number of the carbon in phytoplankton hereby is fixed. The total charge of P N, O and H is
$+5c - 3b - 2e + z = 5/30 - 3 - 4 + 7\ 1/30 = +6/30$. Thus the average C-oxidation number is -6/30/5, so close to 0.

Detritus composition

For detritus, the same chemical reaction formula is used, with a different stoichiometry. Generally, the more degraded the organic matter is the lower the N- and P content. On the lower end, humic matter has a typical composition of about 0.03 gN g^{-1}DW, or 2 10^{-3} mol N g^{-1} DW (Swift & Posner, 1972; Schnitzer & Khan, 1972, 1978); lower than the phytoplankton value of about 7 10^{-3} mol N g^{-1} DW (0.1 g N g^{-1} DW phytoplankton). This is similar for phosphorus, where a typical phytoplankton value is 2.2 10^{-4} molP g^{-1} DW, or 7 10^{-3} gP g^{-1} DW. Humic matter has a lower P-content of about 0.05% (Swift & Posner, 1972), or 0.5 mg P g^{-1} DW = 1.6 10^{-5} mol P g^{-1} DW. Thus, in an end-product of mineralization, the nitrogen content drops to 30%, and the phosphorus content to 14% of a typical phytoplankton value.

The detritus compounds in EcoWasp are defined as degradation matter of phytoplankton and fauna, and simply contain less P and N than the sources. Two steps are used: phytoplankton and fauna that dies goes immediately to DeadSub (with –roughly- the same composition as the source), and then, degradation takes place to Frac2 and ROM (refractory organic matter). Frac2 thus is an intermediate type. For diatoms, the same procedure is followed, only Frac2Dia contains some SiO_2, and finally frustules form and end product next to ROM.

Composition of fauna

Nadaffi et al (2009) come up with typical C:N and C:P-ratios (for Zebra mussels, *Dreissena polymorpha*) of 6 and 180, respectively; thus an overall formula without H and O would look like $C_6NP_{1/30}$. This is close to the 'general' stoichiometry given above for phytoplankton. Nadaffi et al (2009) state that Zebra mussels have a relatively low nutrient content, and are capable to grow under relatively low nutrient supply. Also, young mussels appeared to have a higher P content and these animals require food with a higher P content than adult mussels do; this is to maintain optimal growth and reproduction.

EcoWasp model

Phytoplankton: in the model, the composition of all phytoplankton groups is chosen to be the same, albeit that for diatoms the Si-fraction is accounted for.

Fauna: in the model, the composition of fauna is kept the same for all fauna types, and the nutrient content is chosen to be a bit above the phytoplankton levels.

Detritus: the N- and P- content of the breakdown products decrease towards the end-products.

All the composition data are summarized in the fauna-, phytoplankton and detritus parameter tables.

Appendix IX. Mussel larvae and mussel spawning

Introduction

In the EcoWasp-simulations so far, larvae development has been based on the assumptions that all tissue used for spawning is really converted into larvae. These larvae grow according to the same equations used for the other mussel classes and when settling, it was assumed that all mussel larvae turn into seed mussels.

For the present MZI-research, it was necessary to adjust this picture, because differences between natural mussels and MZI-mussels will mainly be due to the better conditions for settlement and growth at the MZI-nets. And, when the success of settlement has to be estimated, the number of larvae available is evenly important.

Thus, characteristics for mussel larvae are described here, including their survival in the water column.

Length-mass relationship

The standard relationship used in the EcoWasp model is mass=a. length^b. Values for blue mussels are a= 2.57 10^3, b= 2.7.

Sprung (1984a) mentions values for a and b . Both relationships are shown in Figure 75, and are almost the same. Therefore, the 'standard' values for a and b have been used for the EcoWasp computations.

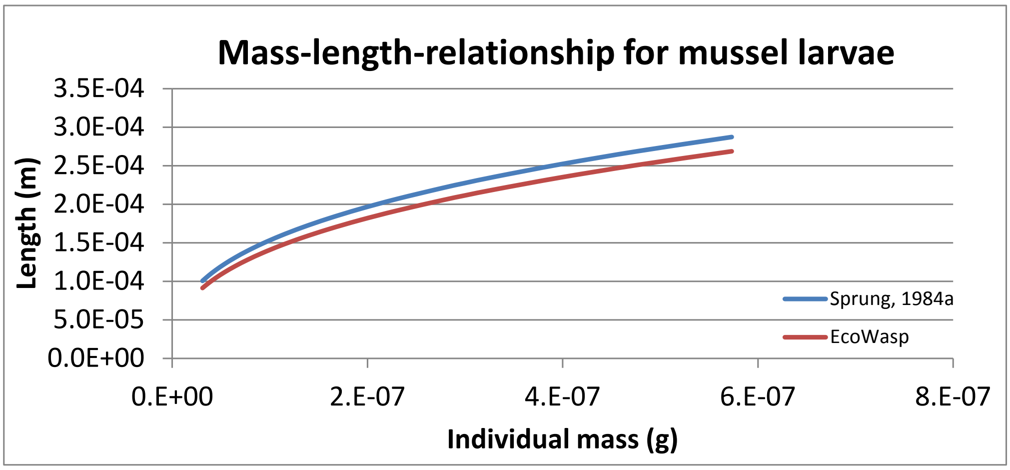


Figure 75 Mass-length relationship for mussel larvae. In blue according to Sprung (1984a); in red: the one used for EcoWasp, which is based upon average adult mussel data for the Wadden Sea.

Larvae food

Food resource of planktonic larvae probably is quite similar to that of microzooplankton of the same size, being small phytoplankton, whilst larger phytoplankton that may serve as food for adult shellfish may be too large to ingest. Widdows (1991) states that larvae exclusively feed upon small phytoplankton; particles > 9 μm are not retained by the larvae (Riisgard et al, 1980); and according to Sprung (1984b) the maximum retention efficiency is for particles 2-6 μm. Mussel larvae clearance rates were highest at low food concentrations, and clearance rates declined with increasing food concentrations. The low food concentrations were 0.6 mg AFDW dm^{-3}; in Sprung's (1984) measurements the food consisted of *Isochrysis galbana*, a widely used phytoplankton type (about 5 μm size) for bivalve cultures.

Bacteria are assumed to have little nutritional value for molluscs (Widdows, 1991: citing Davis, 1953; Millar and Scott, 1967; Chu et al, 1987) since they are lacking in long-chained polyunsaturated fatty acids which are considered essential for bivalve growth.

EcoWasp

In the model, diatoms, non-diatoms ('flagellates') and picophytoplankton are distinguished. The latter cannot be filtered by adult mussels (and a bit by seed mussels, depending on their size; see appendix VII).

Mussel larvae do feed upon picophytoplankton (as does microzooplankton), diatoms and non-diatoms.

In the model, mussel larvae appear to have no or hardly any food shortage, and thus, the choice for the food resources is not very critical: the larvae simply grow at their 'normal' rate.

Larvae filtration and respiration rates

Data on mussel larvae filtration and respiration rates are scarce. Riisgard et al (1981) give clearance rates CR for mussel veligers: CR= 220 $M^{0.846}$, μl h^{-1}, M in ug. In g, m and day as units, it follows that CR = 0.63 10^{-1} $M^{0.846}$ (m^3 ind^{-1} d^{-1}), see Figure 77.

As an example, for a 3 10^{-7} g animal it follows that it filters 1.9 10^{-6} m^3 d^{-1}, ingests (if the food content of the water is 1 g m^{-3}, which is a normal value) 1.9 10^{-6} g food, while the rest respiration costs (see below) are 2.5 10^{-8} g d^{-1}. Digestion costs (also see below) may then be around 0.3 10^{-6} g food. This ingestion rate is –intuitively- far too high. It can hardly be understood that larvae ingest over 6 times their mass as food per day. Also, as a consequence, the larvae would explode. It also contradicts the observation of slow growth of about 5 μm d^{-1} (see below, section on larval growth). This is supported by Sprung (1984b) saying that the maximum ingestion rate is roughly 60-70% of the body mass per day, thus, about 2 10^{-7} g ind^{-1} d^{-1} for this 3 10^{-7} g example individual, instead of the 10 times as high value mentioned before. For the present EcoWasp-computations, filtration parameters have been chosen much lower than mentioned here; see Appendix XI for the chosen values.

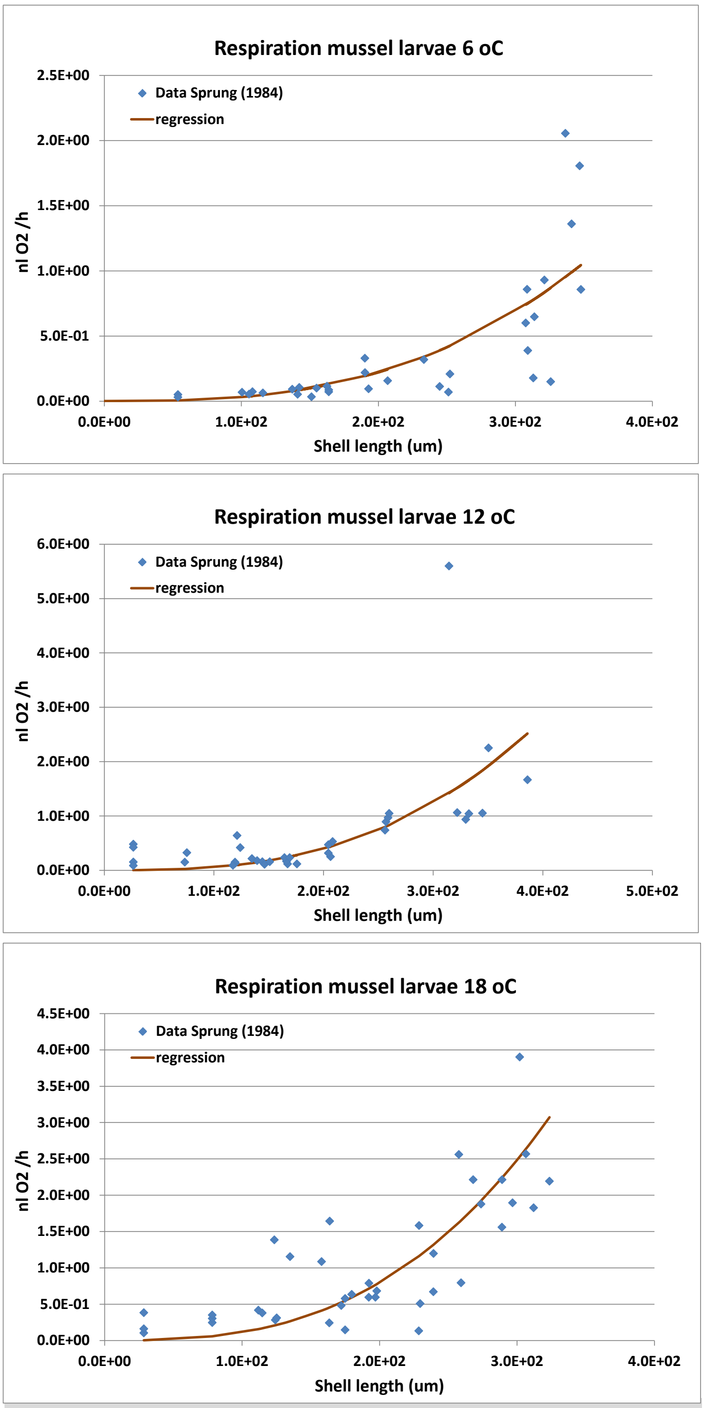
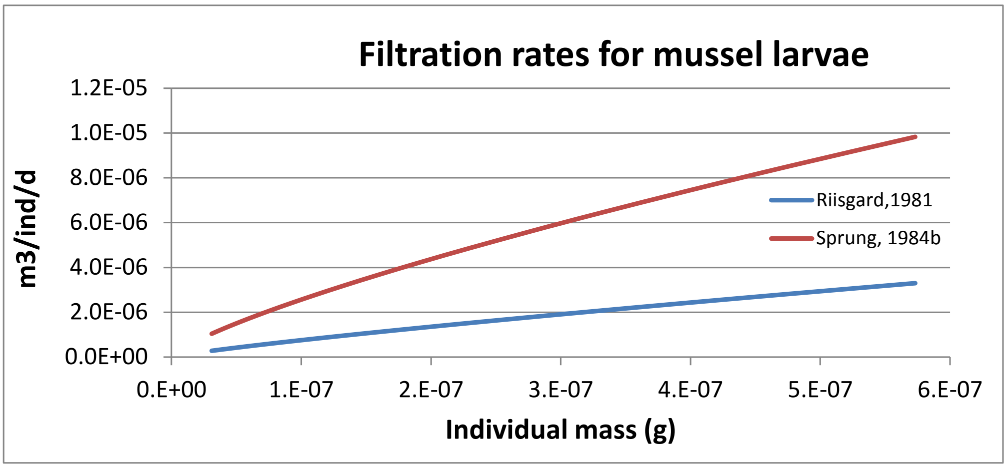


Figure 76 Mussel larvae respiration rates. Data from Sprung (1984^c) have been digitized, and the regression has been recalculated with a constant exponent of 2.8 for the length-dependency. Sprung data digitized using PlotReader (Bruggeman). Respiration = a $L^{2.8}$, with a=8e-8, 1.44e-7 and 2.88e-7 for6, 12 and 18 ^{o}C respectively.

Riisgard et al (1980) give data on respiration rates. Mussel larvae of 150 µm, at 12 ^{o}C 11 µl O_2 h^{-1} and 31 µl O_2 h^{-1} at 15 ^{o}C. In general: Oxygen uptake = 3.10 $M^{0.902}$. M in ug, O_2 in nl h^{-1}. Recalculated (I l O_2= 1/22.4 mol O_2= 1.42 g O_2 == 1.33 g CH2O ➔ 1 nl/h = 1.33 1e-9*24 = 32.14 e-9 = 3.2e-8 g AFDW d^{-1}) it follows that the respiration rate RR= 1.92 10^{-2} $M^{0.902}$ (g AFDW ind^{-1} d^{-1}). See Figure 77 for a graph.

Widdows (1991) also gives heat dissipation rates, showing that heat dissipation is highest (relative to the body mass) at the veliconcha-stage of larval development; his 80 mW g^{-1} equals 0.3 g g^{-1} d^{-1} (assuming a 22 10^4 J g^{-1} energetic value of AFDW body tissue). This is higher than the 'normal' respiration losses that range around 0.1 g g^{-1} d^{-1}. The 300 µm pediveligers (1 µg mass) have a 20 mW g^{-1} dissipation (== 8.6 g ind^{-1} d^{-1}), which is in line with Riisgard (1981) and Sprung (1984c).

For the present application, the data by Sprung (1984c) have been recalculated (Figure 76). Sprung comes up with relationships for mussel respiration with shell length for three different temperatures, and each of the regression lines given has its own allometric exponent. This makes the regression coefficients incomparable to each other. Recalculation with a fixed exponent (2.8, in this case) gives a result that is easier to use later on (see section on temperature effects). The results shown in nl O_2/h have to be translated into g ind^{-1} d^{-1} (not shown here). Sprung uses 20.1 J / ml (O_2) as a conversion factor, originating from Crisp (1971); it is the same value used by Widdows (1991).



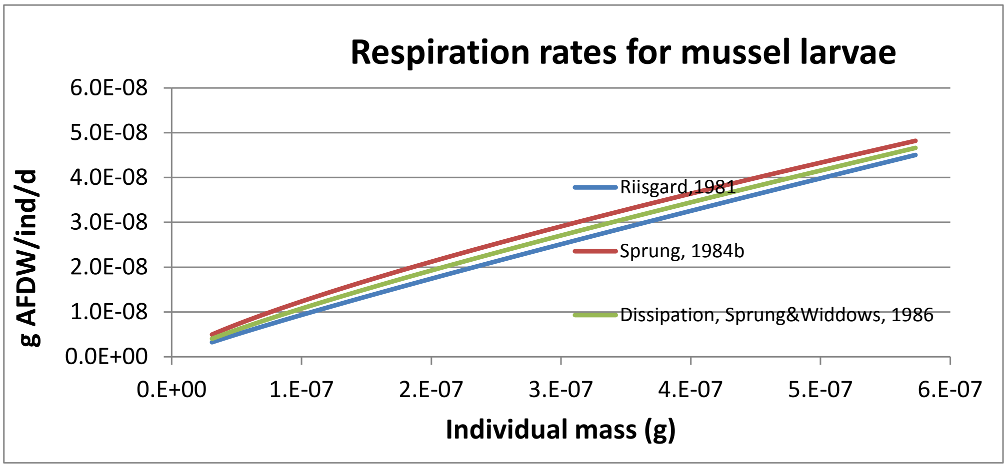


Figure 77 Relationships for mass<->filtration and mass<->respiration rate for mussel larvae. In red according to Sprung (1984b); in blue: according to Riisgard, 1981. In green the dissipation energy curve according to Sprung & Widdows, 1984.

Larvae growth

Mussel larvae have an initial size of about 70-90 µm (Widdows, 1991), although other shellfish species may have different initial larvae sizes. *Macoma balthica* (Baltic Tellin) larvae, for example, have an initial size of about 140 µm (Bos et al, 2007; deduced from their data: they give as size 160 µm at day 3, and a growth rate of about 5 µm d^{-1}); Honkoop & Van der Meer (1997) give *Macoma* eggs sizes of 100-110 µm, while Honkoop et al mention a mussel (*Mytilus edulis*) larva size of 73 µm, and a cockle (*Cerasteroderma edule*) larva size of 77 µm.

From the beginning, the larvae grow, and numbers decrease because of several loss processes. Bos et al (2007) give Macoma larvae growth rates of about 5.7 µm d^{-1}, and Drent (2002) found 5.2 µm d^{-1}, both found in an experimental set-up. Macoma larvae reach their critical size at metamorphosis after about 20 days, depending on food availability. In their experimental situations, both Drent (2003) and Bos et al (2007) found that lower food concentrations led to an earlier metamorphosis and thus settlement, the explanation being that the larvae stay longer in the water column at high food concentrations because they can better profit from the good feeding conditions.

On the other hand, they leave the environment earlier when food conditions are worse. At high food levels, growth rates may be up to 6.9 µm d^{-1} (Bos et al, 2007), and down to 4.4 µm d^{-1} at low food concentrations. Blue mussel larvae, starting at 80 µm length, and a metamorphosis after about 4 weeks at 200-250 µm length have to have a growth rate of about 5-6 µm d^{-1}. Thus, mussels show a growth rate similar to the one of Baltic Tellins.

It should be noted that most of these published growth rates have been computed based on (length at end – length at begin)/(time), and thus, a linear size development with time is assumed. However, it appears that based on allometric equations as often used for animal growth (see e.g. Kooijman, 1993), growth does not differ a lot from a linear development with time (see also Figure 79 later on as an example). Thus the way the published growth rates are computed corresponds to the real larvae size development.

Widdows (1991) reports maximum growth rates of about 12 µm d^{-1}, occurring under optimal food conditions and also, growth sometimes slows down considerably at the end of the larval stage: the mean maximum growth rate thus is lower than this 12 µm d^{-1}.

Jørgensen (1981) reports a growth from 0.017 µg -> 0.77 µg DW/larvae within about a month.

The ‘old’ EcoWasp-model.

In the EcoWasp-model until now it was assumed that i) the initial body mass is 10^{-5} g, it equals a 0.7 mm body length, ii) larvae settle at the moment the maximum mass of 1 mg, iii) larvae filtration and respiration parameters were similar to those for seed and adult mussels. The reason to choose a higher birth mass and thus length in the old model set-up had to do with numerical problems that appeared. However, these have been solved already some time ago, and it appeared now that choosing a smaller birth mass did not cause numerical errors.

Larvae growth in the ‘old’ model was much too fast, since the parameters for filtration and food uptake were close to the ones for the seed and adult mussels. In the present model set-up, these parameters have been reduced drastically.

The EcoWasp-model used for the present MZI-study

A birth mass of 3.1 10^{-8} g (91 µm) is chosen. This comes close to the ‘real’ birth value of 80 µm.

The model is tuned is such a way that the growth rate is about 5 µm d^{-1}.

A maximum larvae mass of 0.5 µg DW is assumed (250 µm); as soon as this mass is reached, the larvae will start to settle. This value is reached normally after about four weeks, thus in line with the Jørgenson (1981)-data (0.77 g after four weeks).

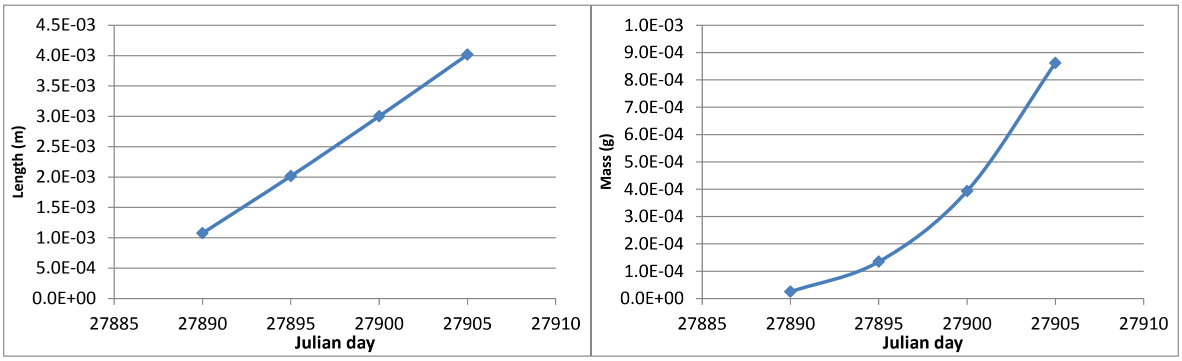


Figure 78 Development of mussel larvae in the old model. Left: length (m); right: AFDW (g)

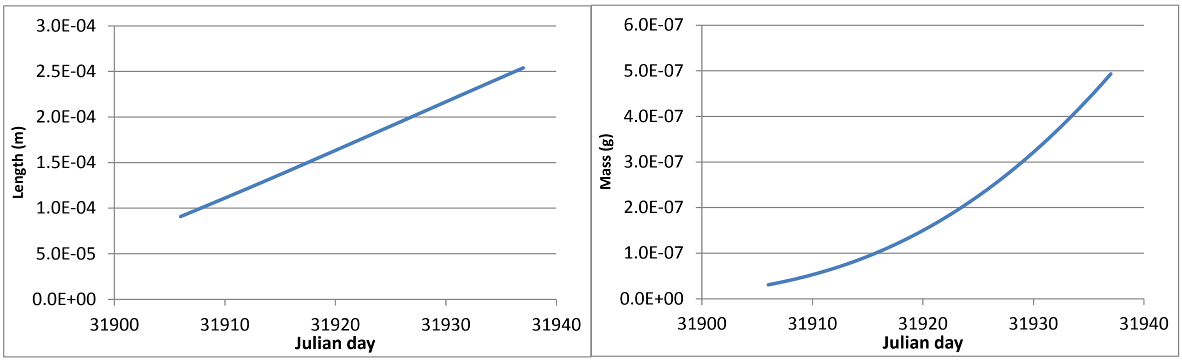


Figure 79 Development of mussel larvae in the final model. Left: length (m); right: AFDW (g). Note that the ‘new’ development comes close to a growth rate of 5 µm day^{-1}.

The new development looks as depicted in Figure 79. It implies that mussel larvae feed very differently from the older mussels: their intake rate per unit of biomass is roughly 5% of the relative intake rate of settled mussels. It also means that the contribution to the overall grazing rate upon phytoplankton is much lower than was computed according to the old parameter settings. This is also a necessary condition: a much larger larvae number showing the same filtration characteristics as before would seriously deplete the phytoplankton biomass.

The description of spawning

The way spawning is computed has not changed, compared to the existing model (Brinkman & Smit, 1983a), except for the spawning efficiency.

In the model versions so far, a 100% efficient shellfish reproduction was assumed. This percentage is reduced considerably, and in the present version 10% efficiency is assumed.

The moment of spawning is fixed: a 14 days period starting at day 130, with a maximum spawning rate after 7 days. A certain fraction of the adult body mass is converted into larvae, this fraction is 0.25 in the present application. These values are model parameters, and may be changed in the parameter files.

The birth rate was clock-shaped modelled according to

$$\frac{dN}{dt} = \frac{F_b \cdot mass_{repr}}{birth_{mass}} \qquad \text{(number d}^{-1}\text{)} \qquad (1)$$

With

$mass_{repr}$ as the reproductive mass, $birth_{mass}$ as the mass of the larvae, and for the rate parameter F_b:

$$F_b = \frac{2}{(t_3 - t_1)} \cdot F(t) \qquad (\text{-}) \qquad (2)$$

The factor F(t) is characteristic for the way the larvae production depends on the time:

$$F(t) = \begin{bmatrix} \frac{(t-t_1)^2}{(t-t_1)^2+(t-t_2)^2} & for\ t < t_2 \\ \frac{(t-t_3)^2}{(t-t_3)^2+(t-t_2)^2} & for\ t > t2 \end{bmatrix} \qquad (\text{-}) \qquad (3)$$

F(t) = 0 for t<t1 and t>t3. See Figure 80, with $t_2=0.5(t_3+t_1)$ the result is clock-shaped. The characteristic of eq(2) is that

$$\int_{t_1}^{t_3} F_b\, dt = 1 \qquad (\text{-}) \qquad (4)$$

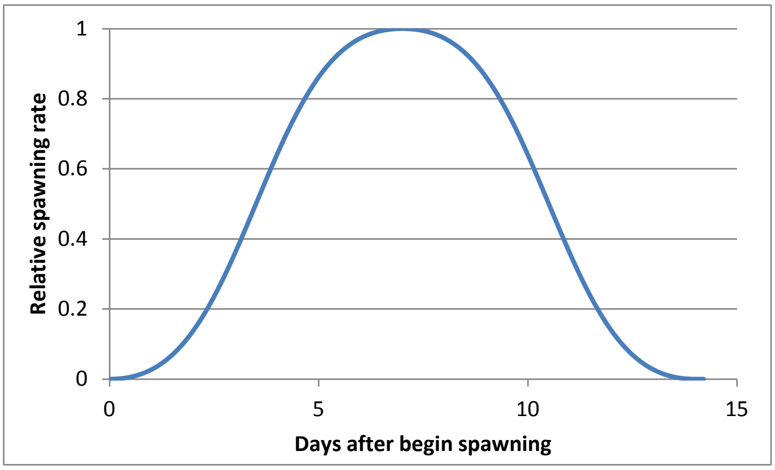


Figure 80 F(t) as a function of the day during the spawning period

In the beginning of the spawning period, the larvae get the birth mass ($birth_{mass}$) of 3.1 10^{-8} g, as mentioned above. During the spawning period, existing larvae already are growing: the later born larvae get the mass of the larvae already present, this avoids other difficulties. This affects the larvae *number* negatively and in fact, it is a kind of hidden mortality.

The chosen spawning period is close to the natural spawning period, although in nature this period varies per year. Also, it is clear from the available larvae data that also later on still larvae are produced, although often in numbers that are considerably lower.

Applying some temperature-related rule, that would probably increase the reliability of the chosen reproductive period, would be too time-costly at the moment.

Larvae mortality

Mortality of larvae may be due to starvation (in case of food depletion), predation and physical processes as dispersion to the North Sea (in the Wadden Sea situation). In their experimental set-up, Bos et al (2007) found only a low mortality due to starvation. After 20 days, still 35-40% of all larvae were still alive, and food depletion was hardly a relevant cause. Larvae seem to be able to survive for many days without food supply (Widdows 1991, citing Bayne 1965 & His et al, 1989). The mortality rate parameter was 0.02 to 0.04 d^{-1} in the experiments of Bos et al (2007); Philippart et al (2003) concluded at an egg-to-recruit mortality of 0.05 d^{-1}. A review of Rumrill (1990) mentioned 0.13 – 0.28 d^{-1} as first-order mortality parameter for natural meroplanktonic larvae. The resulting differences in terms of percentage of larvae still alive after say 20 days are large: the percentage of larvae still alive after 20 days is 45 (mortality rate parameter= 0.04 d^{-1}), 37 (0.05 d^{-1}),7.5 (0.13 d^{-1}) resp. 0.37 (0.28 d^{-1}). And after 30 days, these values are 30, 22, 2 and 0.02 % respectively. Hendriks (2004) gives a daily mortality of 4-4.7% for *Macoma balthica* larvae and 5.2% for Pacific oyster (*Crassostrea gigas*) larvae, thus more or less the same values as Philippart et al (2003) and Bos et al (2007). Widdows (1991) mentions a mortality of 0.1-0.2 d^{-1} for mussel larvae.

Physical processes may affect the larvae number: Philippart et al (2003) mention wind direction as possibly an important factor, but their remark was not supported by physical model computations. Dispersive processes will contribute to larvae losses in the Wadden Sea, because of the exchange with the North Sea. For the western Dutch Wadden Sea, a residence time of about two –three weeks is a likely value (Ridderinkhof, 1988). The residence period in a well-mixed system implies that at t=residence time the loss equals (1-1/e) = 0.63 (==63%); the daily loss factor is then 0.07 (two weeks residence time) to 0.05 (three weeks residence time).

Predation by adult shellfish (larviphagy) is considered as an important mortality factor.
Shellfish inhalant inflow velocities often exceed the swimming capacities of the larvae as illustrated by Troost (2009): mussel larvae swim at 0.6-2.2 mm s^{-1}, and oyster larvae swimming speed is about 0.7 to 6.5 mm s^{-1}. Inhalant velocities depends on body size, and of course on the distance from the siphon opening. Oyster inhalant velocities are larger than those of mussels (Troost, 2009), and thus, it seems plausible that Oyster larvae might escape from the inhalant yet stream of adult shell fish and mussel larvae might not, or at a lesser extent. However, Troost et al (2008), Troost (2009) also

concluded that the larvae did *not* show an escape reaction to such an inhalant water current. Thus, adult feeding behaviour probably is not discriminating between larvae species, and all larvae are equally filtered. Then, since accumulated grazing pressure by bivalves may be up to 0.5 d^{-1} in a shallow system like the Wadden Sea, larvae mortality may mainly be due to larviphagy. The data of Rumhill (1990) come close to these larviphagy based mortality rates.

De Vooys (1999) argues that the lower phytoplankton content in the water column in the 80's may be a cause for the lower number of larvae in the water column. This would imply that in the 80's, with its much larger nutrient supply, shellfish content was larger than in the 90's (also relative to the possibilities as provided by this nutrient input) and thus, grazing pressure was relatively large, phytoplankton concentration was relatively low, and shellfish individual body mass was lower than in the 90's. This is in agreement with and could explain the observations on primary production: the NIOZ-pole data give 80's-primary production data that are only slightly above the data from the 90's (Cadée & Hegeman, 2002; Philippart et al, 2000; Philippart et al, 2007; Riegman, 2011), despite that nutrient supply was much larger (Brinkman & Smaal, 2003); and the same goes for the chlorophyll-a content, as an (rough) indicator for the phytoplankton content. A consequence would be the lower production of larvae per animal, but also a higher mortality due to larviphagy.

Temperature effects

A few temperature data are available. First the recalculated respiration data (see also appendix III) by Sprung (1984c); he measured the relationship between larvae length and respiration rates at three different temperatures (6,12, and 18 °C).

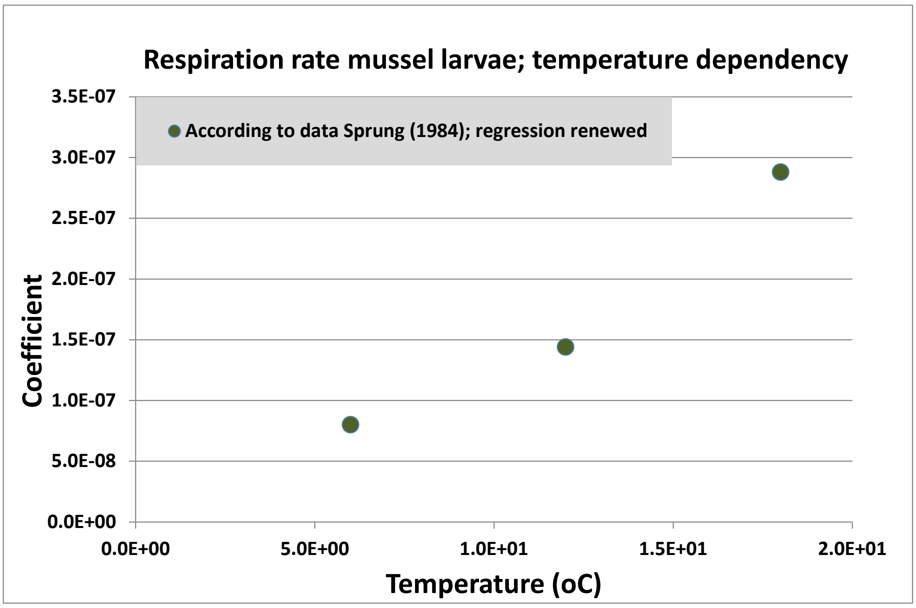


Figure 81 Respiration rates of mussel larvae. The coefficient is the a-value in the equation respiration rate=a $Length^{2.8}$, with Length in um and respiration in nl O_2 h^{-1}).

Data

A few observations on shellfish larvae in the Wadden Sea have been done, among those by De Vooys (1999; figure 2 from this paper is copied and shown in Figure 82), Bos et al (2006[a,b], 2007) and Philippart et al (2003). Both latter datasets were digitally available; de data by De Vooys (1999) were gone (pers. comm.), and retrieved by digitizing the graphs from the 1999-paper (using Jorn Bruggemans PlotReader, http://jornbr.home.xs4all.nl/plotreader/).

The data as mentioned above by De Vooys (1999), Bos et al (2007) and Philippart et al (2003) have been used. All three papers show larvae presence during a much longer period than the model allows for. This is a model simplification, but at the moment there is no simple solution to solve this. But, all three papers also show that larvae numbers are largest in the model reproduction period. Therefore, this is not adjusted in the model.

A lower larvae production efficiency means a smaller initial larvae number. At the moment of settlement, the number of mussel larvae still present has to be higher than assumed until now (Figure 83) since at the moment of settling comes with a (large) loss. This all is in line with the larvae number observations (De Vooys, 1999; Bos et al, 2007; Philippart et al, 2003). The computed larvae numbers in the 'new'-version are illustrated in Figure 84. Larvae numbers of several ten thousands of larvae per m^3, as given by De Vooys (1999) are reached as well.

The new set/up alters the grazing activity of the larvae class. Originally, there was a large grazing pressure shortly after the moment of reproduction that declined rapidly to relatively low values at the moment of settlement. In the new case, this grazing pressure pattern is much less steep. This is illustrated Figure 84. It implies that the contribution of the larvae to the overall grazing rate, which is of the order of 0.1-0.4 d^{-1}, is only minor.

Model and examples of larvae development

Based on the considerations above, new parameter values have been found; these are listed in Table 3. As an example, some simulation results for larvae growth and number development are shown in Figure 84. Data for 1993 were shown in Figure 82, and for the new model in Figure 84. The difference between the old model and the new set-up (Figure 83 cq Figure 84) does not seem very large, but this is masked by the choices for the old model: the larvae grow very fast *and* the new born get the mass of the larvae already present and already. As said, it is a hidden mortality, and largely affects the number of larvae put into the (model-) environment. Since in the new model set-up larvae settlement comes with a large loss, the number of larvae prior to settlement has to be larger than in the old model. That is the reason that the larvae number in Figure 84 is larger than in Figure 83.

Table 3 Initial and final larvae sizes and allometric model parameters for mussel larvae growth. Allometric equations all are $a \cdot mass^b$. Allometric b-values are -0.35 for uptake and filtration, and 0 for respiration and excretion.

Model parameters	Old	New	Comment
Birth mass	10^{-5}	$3.1\ 10^{-8}$	g (AFDW). Larvae born after the spawning onset get the size of the larvae already present.
Birth length	700	91	µm
Mass at settlement	$1\ 10^{-3}$	$5\ 10^{-7}$	g (AFDW)
Length at settlement	4250	250	µm
Uptake-a	$2\ 10^{-2}$	$8\ 10^{-4}$	Food intake as gram per gram individual mass per day
VIndw_a	$5\ 10^{-2}$	$1.6\ 10^{-3}$	Filtration as m^3 per gram individual mass per day
Resp-a	$8\ 10^{-3}$	$2\ 10^{-2}$	Respiration as gram respired per gram individual mass per day
Excr-a	$1\ 10^{-3}$	$2\ 10^{-2}$	Excretion as gram excreted per gram individual mass per day

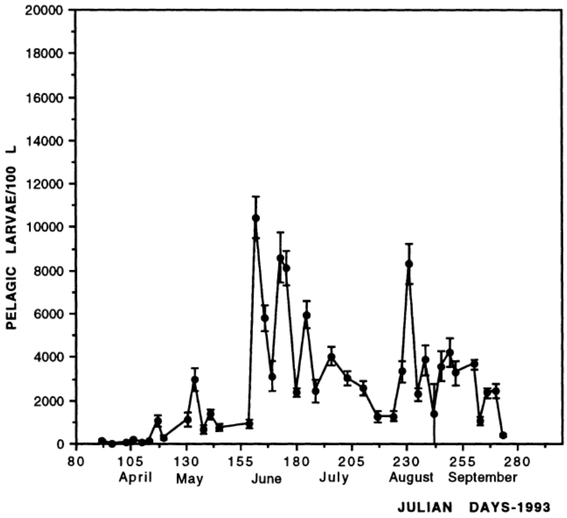


Fig. 2. Numbers of pelagic larvae (mean ± s.d.) in 100 dm^3 water during the spring and summer of 1993.

Figure 82 Larvae in the Wadden Sea water column, 1993. Copied from De Vooys, 1999

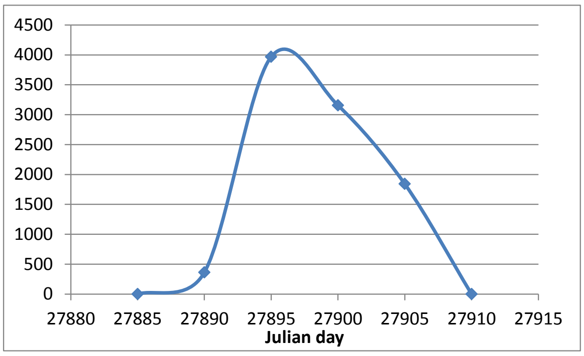


Figure 83 The EcoWasp-model 'old'-version: number of mussel larvae in a certain year. At or shortly after day number 27885 spawning starts, and around day 27895 the larvae number is maximal. Between day 27905 and 27910 settlement occurs. Example, for the year 1976.

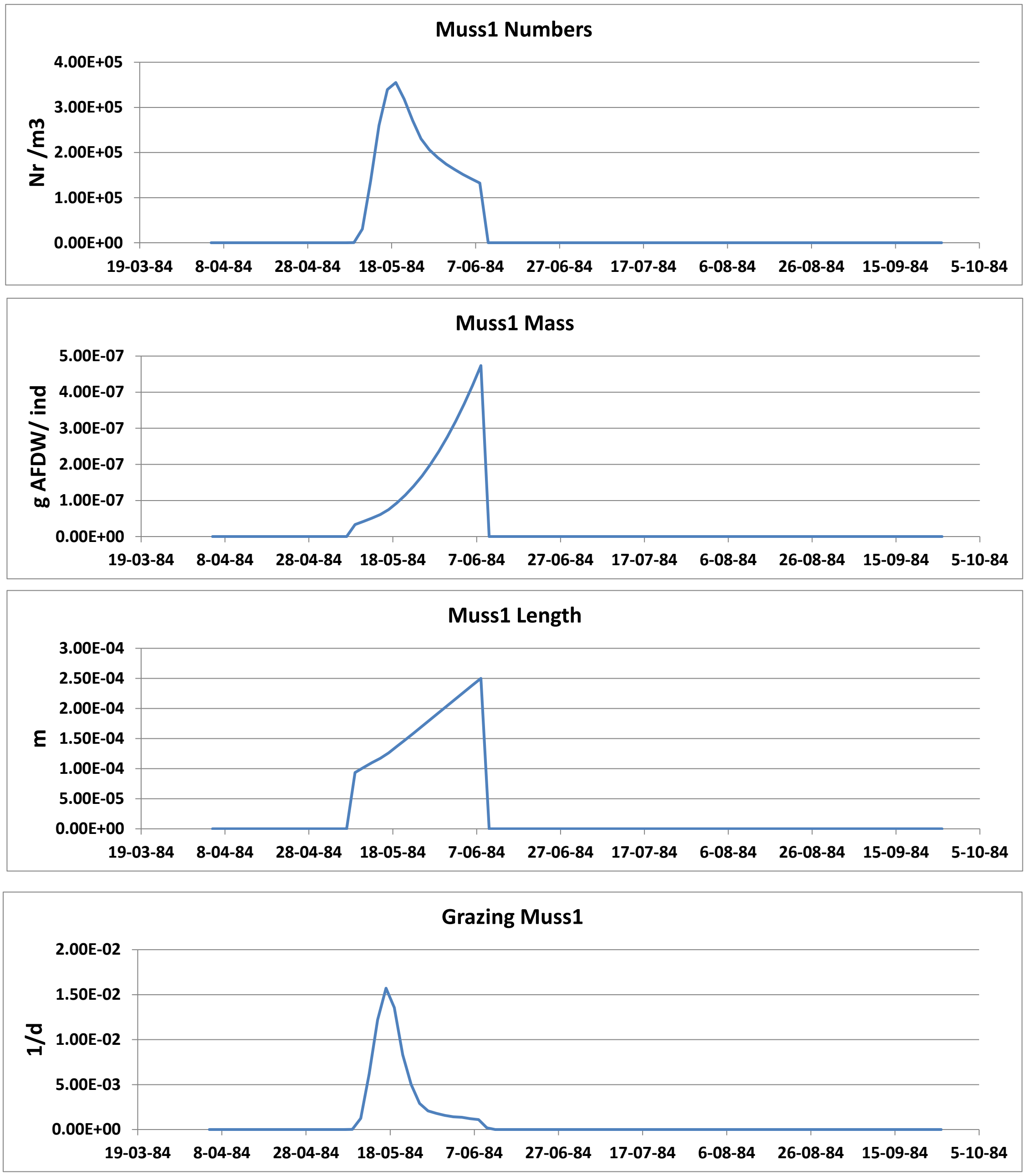


Figure 84 On the route to the best parameter settings: mussel larvae numbers, mass, length and grazing rate. The latter illustrates that mussel larvae do not affect the phytoplankton content of the water column to a large extend.

From Figure 84 it can be seen that larval size development is almost linear with time. The period larvae occur in the water column is much shorter than in reality (Figure 82). Larvae numbers come close to the data given by De Vooys (Figure 82) (note the difference in scaling: De Vooys gives nrs/100 l, the model produces nrs/m^3).

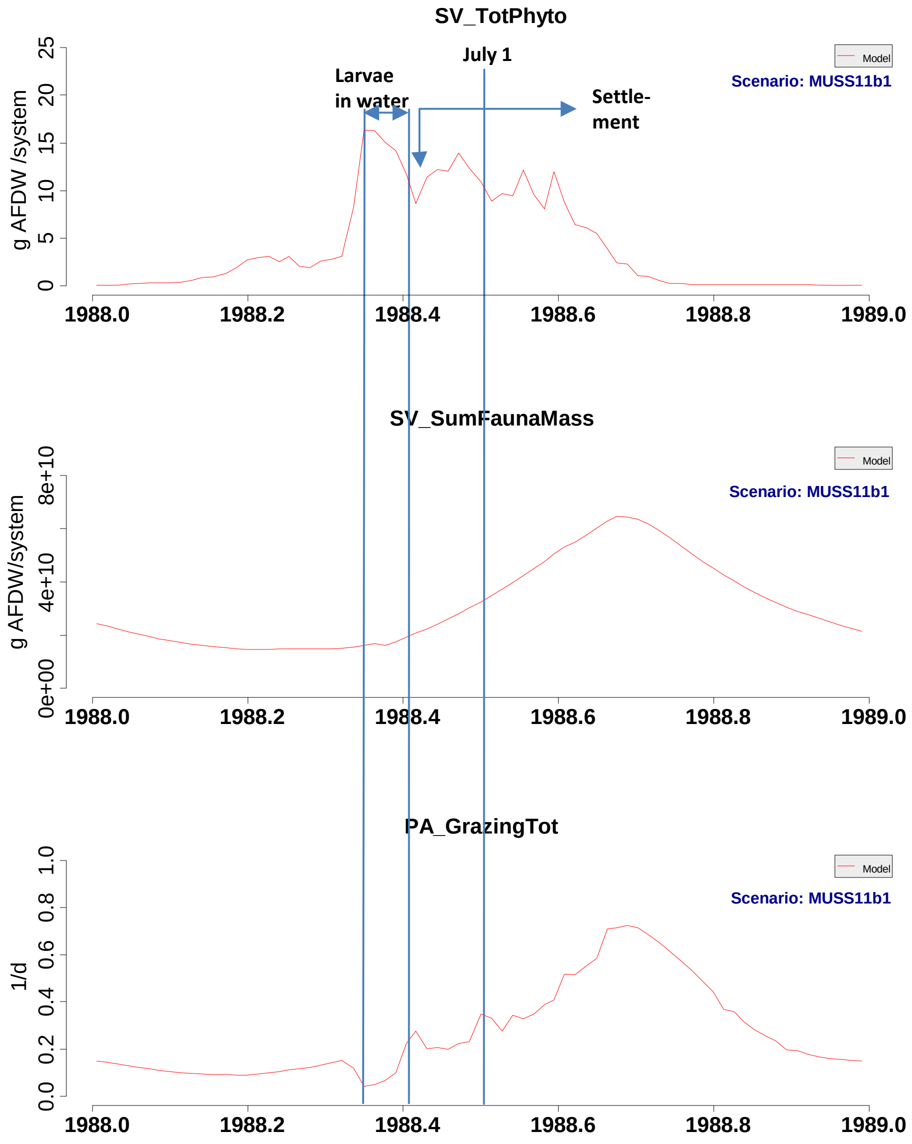


Figure 85 Illustration of characteristics during the short period of larvae production and growth; example for 1988. As soon as larvae are produced, the total filtration pressure (lower graph) is reduced. Larvae feeding is much less intense in the model than filtration by benthic shellfish. The total biomass (middle figure) is affected just a little bit by reproduction: although 25% of total biomass goes into larvae biomass, and of the newly born larvae 90% dies immediately, growth is that fast that a nett fauna biomass change is hardly detectable. Grazing activity, however, is reduced a lot in the larval period; this increases a lot shortly after seed settlement and during seed development.

Appendix X. Picophytoplankton and microzooplankton

Picophytoplankton and microzooplankton

Introduction

In the model, microzooplankton and picophytoplankton are added. The underlying idea is that mussels and other shellfish are not capable to ingest phytoplankton cells < 2 µm in size, and thus, a drastic increase in very active seed mussel at the MZI-nets might affect the phytoplankton composition: the proportion of the smallest phytoplankton species may drastically increase. Such an effect might be visible in the Oosterschelde, where picophytoplankton may consist of about 20% of the phytoplankton biomass (Wetsteyn et al, 2003; Geurts van Kessel, 2004). Picophytoplankton is grazed by microzooplankton (mainly ciliates) and shellfish larvae. Shellfish larvae are between 80 and 230 µm in size. Size of microzooplankton range between 20-200 µm. Here, a 35 µm animal is assumed. Both shellfish larvae and microzooplankton are eaten by benthic shellfish. The prey size selection by benthic (and MZI-net) shellfish is explained in the relevant shellfish section (Appendix VII). The relevant structure has been pictured in Figure 1.

Data

Few data are available. Brussaard et al (1995, 1996) measured picophytoplankton, micro- and mesozooplankton, nanoflaggellates in the Marsdiep area. Jacobs in her present PhD-research measured picophytoplankton and microzooplankton close to the MZI-nets and at the NIOZ-jetty, in the Marsdiep just in front of the Institute. For the data of Jacobs, the reader is referred to (Jacobs, 2013, publications in prep).

Model adjustments

In the first model simulations, microzooplankton solely had picophytoplankton as food source. Loss processes were an autonomous mortality (which was chosen rather low) and grazing by benthic shellfish.

Picophytoplankton in the model had similar characteristics as non-diatoms, only grazing by benthic shellfish was absent. Thus, it had good possibilities to grow in spring an early summer, where non-diatoms soon were reduced in biomass as a result of intensive shellfish grazing.

However, it appeared that in the model each year picophytoplankton first came up with high biomass densities (see e.g. Figure 86, middle and lower graph, but then much more pronounced), followed quickly by a microzooplankton boost. Neither the first, nor the second is visible in the available data (Brussaard et al, 1995, 1996; Jacobs (2013, in prep)).

This problem was tackled (partly) by assuming that microzooplankton also could feed upon detritus (in this case refractory organic matter ROM). ROM is always present and as such, microzooplankton does not have a long period without any food. It says in fact that microzooplankton can feed upon the nanoflaggellates that in their turn feed upon bacteria that are associated with the detritus (see also Brussaard et al, 1995, 1996). A low preference factor and a low utilization factor had to be chosen.

The “problem” with the high picophytoplankton content and the directly following microzooplankton boost decreased a lot, although they did not disappear completely. This is something to be improved later on.

For these tests the model was run for the years 1983-1988. In Figure 86 and Figure 87, results of the model test are presented. Finally, the combination Pref07 and upt40 has been chosen. In Figure 88

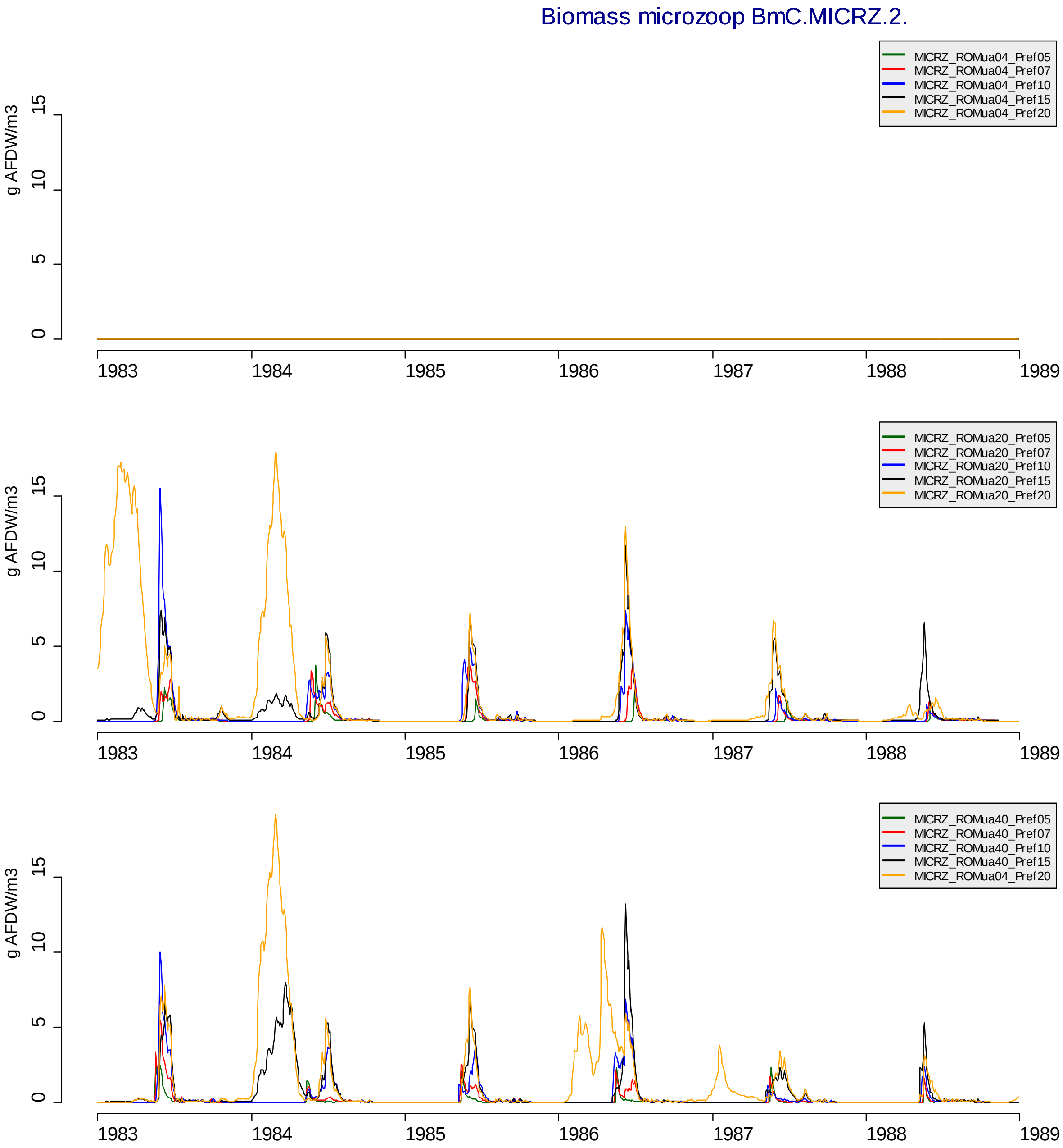


Figure 86 Computed biomass of microzooplankton for a couple of parameter settings.

(lower), two examples for the years 1983 and 1987 are shown in more detail, Figure 88 (upper) gives data from Brussaard et al (1995 & 1996).

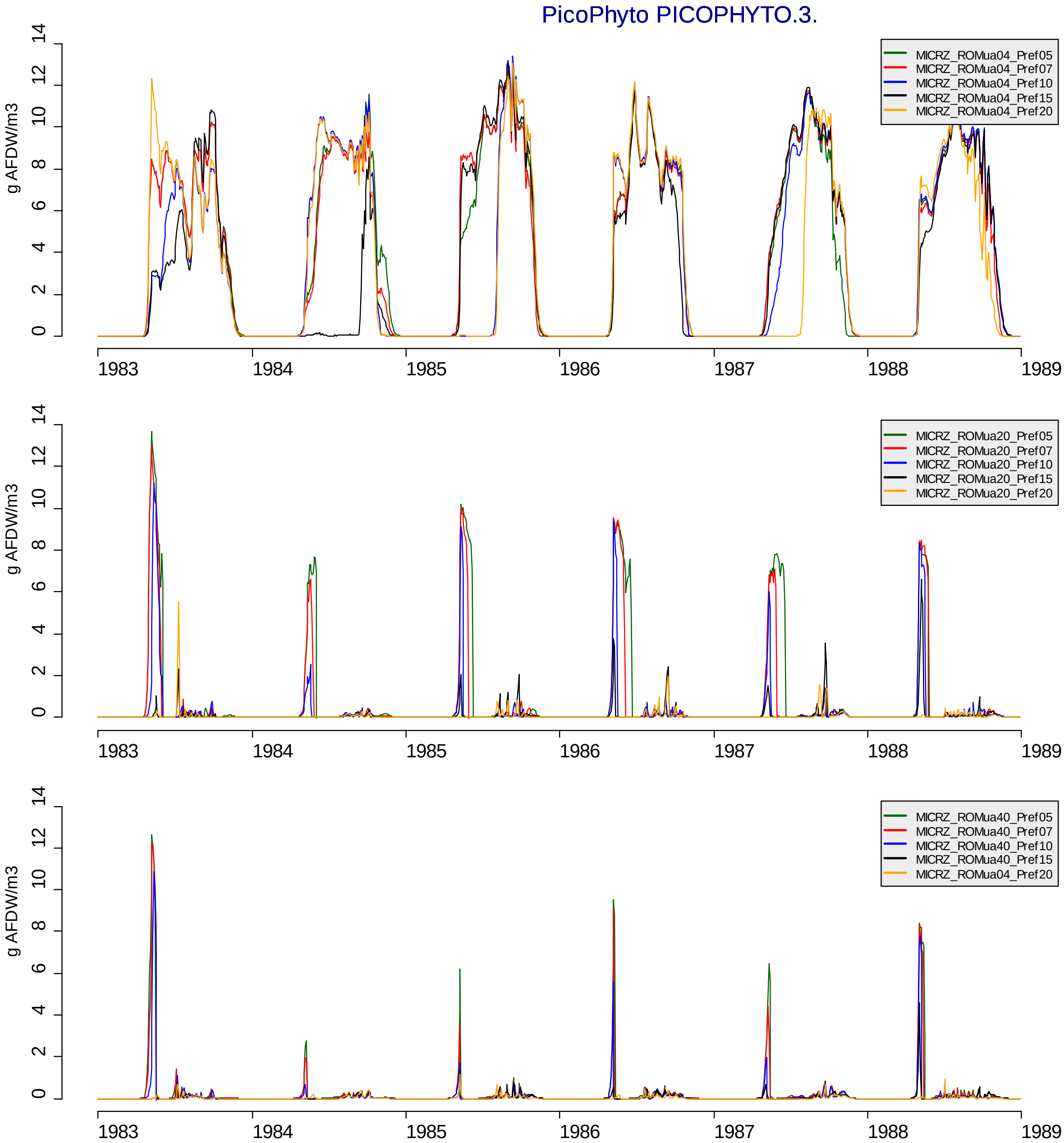
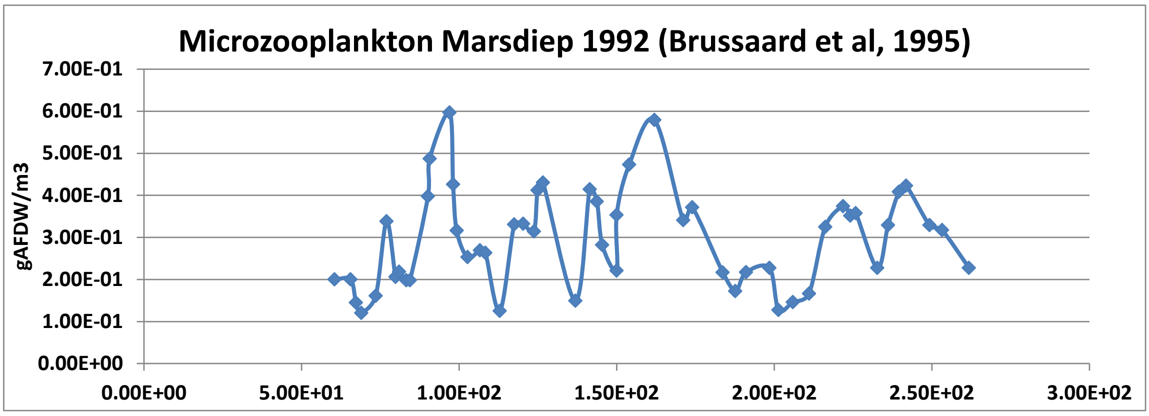
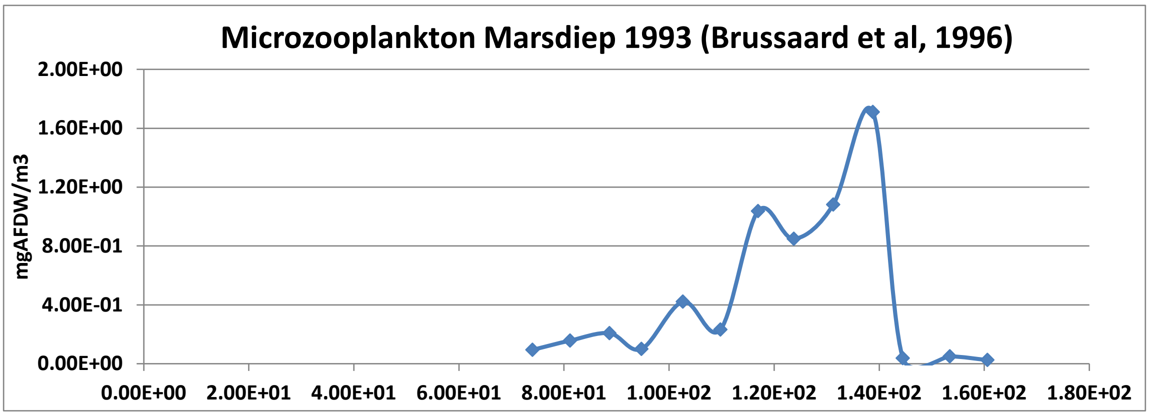
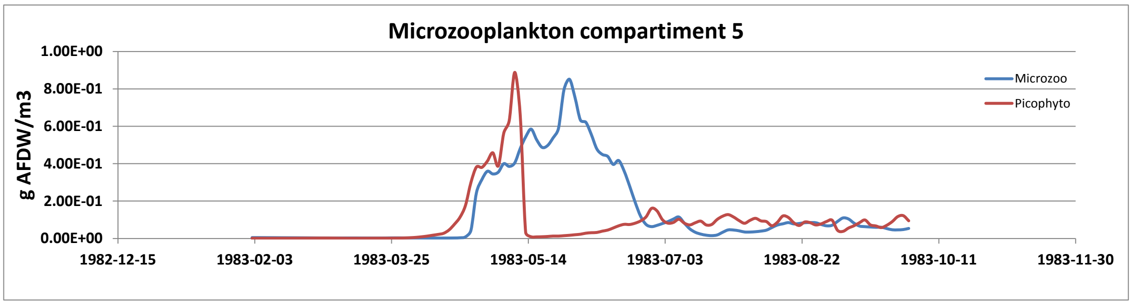


Figure 87 Computed biomass of picophytoplankton for a couple of parameter settings.







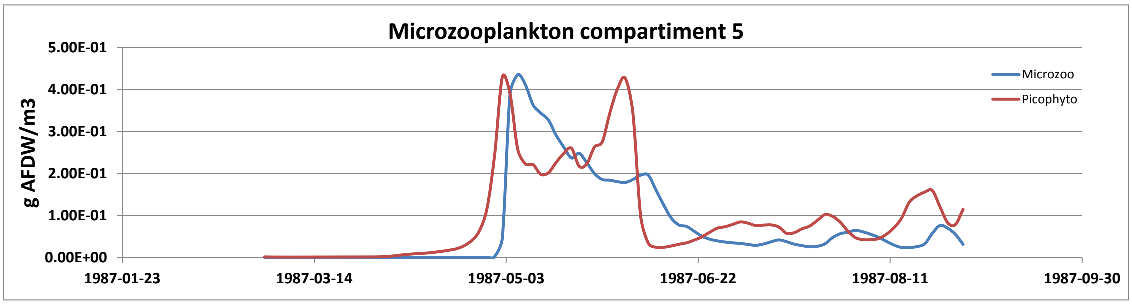


Figure 88 Upper: microzoplankton data from Brussaard et al (1995,1996), lower: Example of computed picophytoplankton and microzooplankton content in the testrun "MICRZ_ROMua40_Pref07" from Figure 87. The parameter settings for this run have been used for the following MZI-simulations.

Appendix XI. Water quality variables, elaboration of Waterbase data

Introduction

The Netherlands Rijkswaterstaat (Netherlands Water Board) collects water quality data for so-called Rijkswateren in The Netherlands, from marine water bodies as well as from fresh water systems. These data are primarily collected because of the ‘Wet Verontreiniging Oppervlaktewateren’ (WVO) from 1969 and, from December 2009 the ‘Waterwet’ (Water Act), which replaces the WVO. The data serve as indicators whether the water quality targets are achieved or not.
These data also are an important source of information for ecosystem modeling activities; the data give information for boundary conditions, and are very useful as comparison to model results.

The idea is that from the available data some other quantities may be derived that are not directly measured. Especially an estimate for the amounts of algae, diatoms/non-diatoms, humics (refractory organic matter, ROM) and labile organic matter (LOM) may be computed. A first computation concerns the estimation of the phytoplankton content from chlorophyll-a data, the composition of algae (N & P) and the composition of the remaining fractions: detritus (N & P) and inorganic matter (P).

A second computation concerns the composition of the dissolved organic fraction (DOM = dissolved organic matter). It appeared from a first check that probably two fractions may be distinguished: one type of DOM that is more or less always present, and one type that appears in the summer period.

A third computation may concern an estimation of the presence of phytoplankton, detritus and the one or two dissolved organic compounds for the whole period relevant for ecosystem simulations. Both the above mentioned two computations concern existing data, this third one implies that for periods where no data exist so far, estimates for DOM, phytoplankton and detritus are produced.

Data consistency check and completion

The data as they are present in the Rijkswaterstaat files (Rijkswaterstaat) are not applicable without a check on errors and inconsistencies. Also data completion is needed.

Data completion may be necessary because of the way the data have been stored. As an example, of the four phosphorus components (ortho-phosphate, dissolved organic phosphate, particulate phosphate and total phosphate) usually not all four are mentioned. If three of these four components have been measured, the fourth can be computed; the practice however is that not always the same three are stored (and also, not always three of the four have been analyzed at all), so for each monitoring point it has to be checked which ones have been stored, and thus, which one can be computed. Especially for the nitrogen compounds this concerns a couple of possible combinations.

Thus, if possible, lacking values have computed and added to the tables. This has been done for the combinations:
TOC – POC – DOC : total, particulate and dissolved organic carbon
TP, partP, Pnf, PO4Pnf : total, particulate, total dissolved after filtration and ortho-phosphate
TN, partN, KjN, Nnf, NH_4, NO_2, NO_3, NO_2NO_3 : total, particulate, Kjeldahl-N, total dissolved N after filtration Ammonium, nitrite, nitrate and the sum of NO_2 and NO_3
Sal, geleid, Cl : Salinity, Conductivity and chloride-concentration.

Details, and the way it was done is described below. Not mentioned in the list is the content of organic dissolved N and –P; computed data are added to the table. Also, from suspended solids and data on glowing rests provide a possibility to compute POC as well. These data have been added as well.

Also, data consistency is checked. It appeared that sometimes typo's occur. For example, total phosphorus may be lower than ortho-phosphorus in the monitoring records. Sometimes it is possible to repair such an error (when it is obvious what typo was made), and sometimes it is a reason to replace the value by a NA.

Phosphorus compounds

Tot_P	sum of all P-compounds (TP)
Part_P	all P present in particulate matter (PP)
Pnf	all P in solution after filtration over a 0.45 u millipore membrane filter
PO4Pnf	ortho-P, all inorganic dissolved P (DIP).

Not mentioned, but added to the data is

DOP	all dissolved organic P: the difference between P_nf and PO4Pnf

Pnf is analyzed after destruction. Since ortho-P is analysed after adding acid to the solution, the distinction between DOP and DIP is not very precise, and probably a part of DOP is measured as DIP.

In all cases Tot-P= Part-P+Pnf is used to complete one of the three variables if two of the others are present in the table, and also, DOP=Pnf-PO4Pnf is used to find values for DOP.

Nitrogen compounds

Tot_N	sum of all N-compounds (TN)
Part_N	all N present in particulate matter (PN)
Nnf	all N in solution after filtration over a 0.45 u millipore membrane filter
KjN	Kjeldahl-N, this is all the oxidizable N, thus the sum of part-N + NH4+DON (dissolved organic N)
NH4_N	dissolved ammonium (NH_4^+)
NO2	nitrite
NO3	nitrate
NO2+NO3	sum of nitrate en nitrite.

Not measured, but present is

DON	dissolved organic N (also the difference Nnf-NH4-NO2NO3)

Completed is:

NO2+NO3 = NO2NO3

PartN = Tot-N – Nnf

Added is

DON = Nnf – NH4 – NO2NO3

Carbon compounds

TOC	total organic carbon
POC	particulate organic carbon
DOC	dissolved organic carbon

Completed is

TOC = POC + DOC

Added is

POM_1 = TOC / $\alpha_{C,POM}$. $\alpha_{C,POM}$ is the mass ratio of C to total organic matter. For Organic matter as CH_2O, $\alpha_{C,POM}$ is strictly 0.4, but for natural matter, $\alpha_{C,POM}$ has a bit lower value.

POM_2 = ZS*(100-perGR)/100. ZS = the content of suspended solids, and perGr the percentage glowing rest. If POM_1 is absent, POM_2 is added.

Conductivity, salinity and chloride content

These values are related, and can be used to convert the one into the other.

Chlorinity concerns, based on the method of analysis, the sum of chloride, bromide and jodide in water –expressed as gram per kilogram. But, the two latter forms are of minor importance, and thus is the measured value similar to the chloride content.

Salinity is the total of dissolved matter in water (g kg^{-1}); the relationship with chlorinity is (Wooster, Lee, and Dietrich, 1969):

$$S = 1.80655[Cl^-] \qquad \text{g kg}^{-1}$$

[Cl-] is expressed in g kg^{-1}.

The conductivity strongly depends on the content of conducting anions and cations, and thus on salinity.

There are precise conversion (UNESCO-standard; Fofonoff & Millard, 1983), but for the present situation a more simple conversion as the one by Williams (1986) is satisfactory:

$$Salinity = 0.4665\, cond(25)^{1.0878}$$

with

$$cond(25) = \frac{cond(T)}{1 + ft \cdot (T - 25)}$$

Salinity g kg^{-1},
Cond (=conductivity) in mS cm^{-1}
T °C.
In many cases, salinity is expressed in µS cm^{-1}, thus a factor 1000 higher.

Williams gives ft =0.02, but he used salinity as g l^{-1} (not per unit of mass). At T=30 °C the values are more or less the same, but deviate for lower temperatures. By choosing ft=0.0185 these deviations disappear.

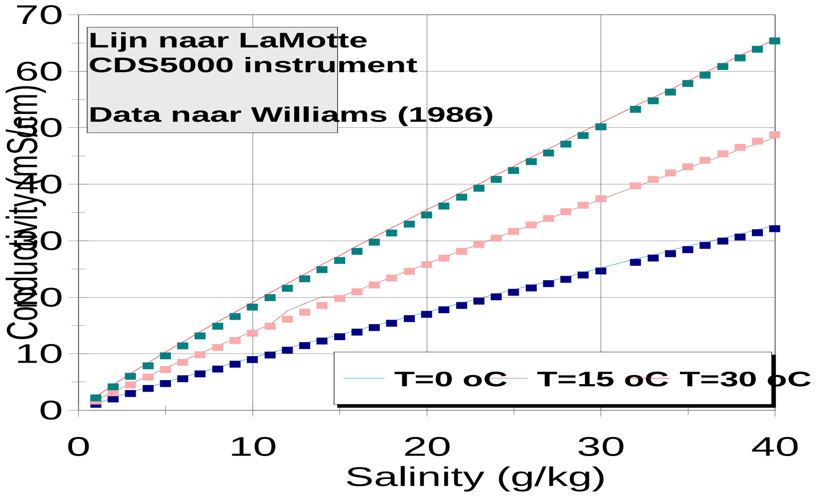


Figure 89 Conductivity and salinity after Williams (1986)

In the Netherlands 20 °C is used as als standard temperature for the conductivity measurements. The ration between cond(20) en cond(T) is:

$$cond(T) = cond(20) \cdot \frac{1 + ft \cdot (T - 25)}{1 + ft \cdot (20 - 25)}$$

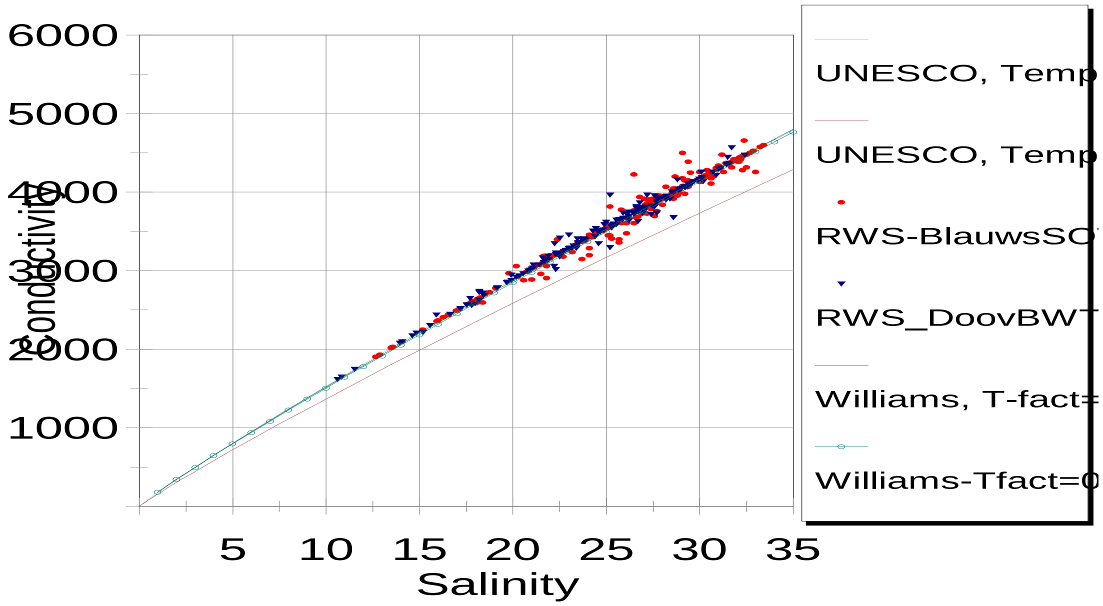


Figure 90 Salinity and conductivity according to UNESCO (Fofonoff & Millard1983), Williams (1986) and RWS-measurements in the western Dutch Wadden Sea (Blauwe Slenk-Oost and Doove Balg-West)

Rijkswaterstaat uses in its tables conductivity at 20 °C. RWS uses the UNESCO-method (Fofonoff & Millard, 1983) as temperature relationship. The relationship are given in Figure 90. Additions based on salinity and chlorinity are shown in Figure 89 showing that these additions are consistent with the other data.

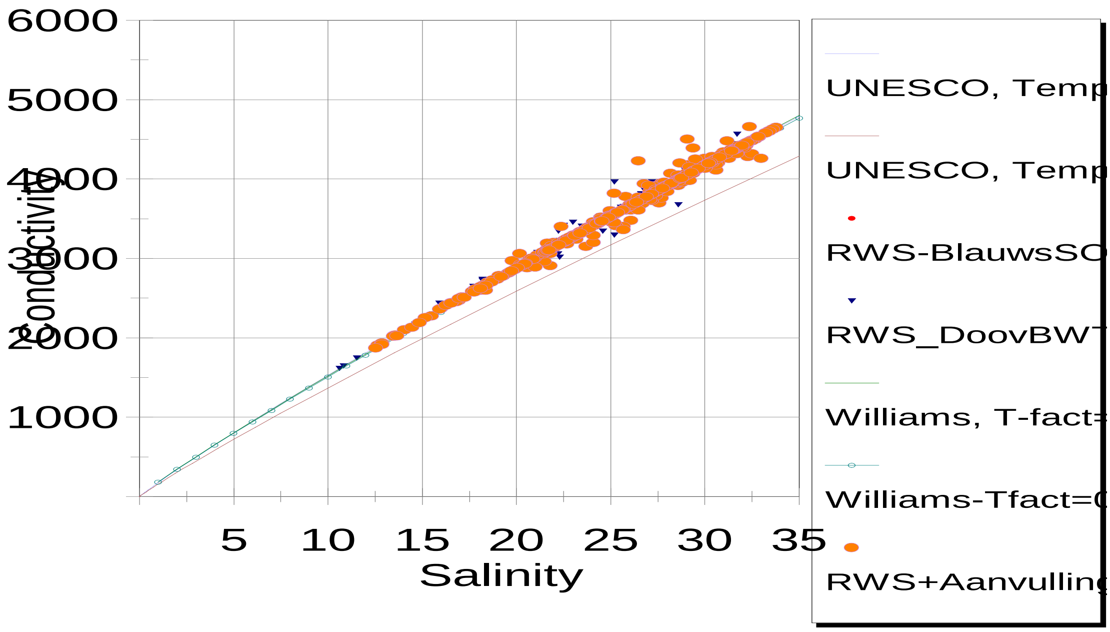


Figure 91 Conductivity and salinity, including the addition to the Rijkswaterstaat dataset.

P and N-stoichiometry of particulate matter, first phytoplankton, detritus and inorganic solid

The basic rule is that algae, detritus and inorganic suspended solids (SS) have their own stoichiometric composition.

So, let $\alpha_{chl,phyto}$ be the amount of chlorophyll-a in phytoplankton, then the amount of phytoplankton can be estimated:

$$Phyto = \frac{CHLFA}{\propto_{chl,phyto}} \qquad 1$$

Let $\alpha_{p,comp}$ be the amount of P in each of the components (comp=phyto, detritus, SS), and $\alpha_{N,comp}$ be the amount of N in each of the components (comp=phyto, detritus), then it follows for P that

$$part_{orgP} \quad = \propto_{P,Phyto} Phyto + \propto_{P,Det} Detritus \qquad 2$$

$$part_{inorgP} = \propto_{P,SS} SS \qquad 3$$

and for N

$$part_{orgN} \quad = \propto_{N,Phyto} Phyto + \propto_{N,Det} Detritus \qquad 4$$

For total particulate P it follows

$$part_P \quad = part_{orgP} + \ part_{inorgP} \qquad 5$$

and N

$$part_N \quad = part_{orgN} \qquad 6$$

For part-P and part-N, M measurements are available, and the minimization routine will minimize the sum-of-squares of the differences between the computed and the measured values of part-P and part-N.

Since the values of part-P and part-N differ in value by roughly an order of magnitude, a weight parameter is introduced in order to give both differences the same importance: suppose the average values of each monitored variable Y_i is $\bar{Y}$, then the weight to be assigned to each monitoring variable i (in this case just part-P and part-N):

$$weight_i = \frac{1}{\bar{Y}} \qquad 7$$

Then, each monitoring day j, the sum-of-squares

$$SQ_j = \sum_{i=1}^{7}(\widehat{Y_i} - Y_i) \cdot weight_i \qquad 8$$

should be minimized, in which $\hat{Y}$ is the computed value for part-P (i=1) and part-N (i=2), and Y_i the observation.

Next, for all M measurements together, the total sum-of-squares TSQ can be computed:

$$\boldsymbol{TSQ} = \sum_{j=1}^{M} \boldsymbol{SQ_j} \tag{9}$$

This TSQ is to be minimized. This is performed by R-routine nlm (R 2010; Dennis & Schnabel, 1983; Schnabel et al, 1985) and thus, best values for all the parameters α can be estimated. Nlm applies a kind of Newton-Raphson method and uses computed first-order derivatives (Jacobian matrix) to approach the minimum value of TSQ. After the calculation, the second-order derivatives (Hessian matrix) are stored, which gives the opportunity to compute confidence interval for the resulting parameters (the α–values) from the equations 1-4.
The α-parameters are assumed to be constant during the whole period.

P and N-stoichiometry of dissolved organic matter, a first and simple approach

For dissolved matter (DOM) first it is assumed it has a constant stoichiometric composition (C, N, P). So, let $\alpha_{i,DOM}$ be the amount of component i in DOM (g g^{-1}), then the value of the α's follows from a simple linear regression on the equation

$$DOP = \propto_{P,DOM} \cdot DOM \tag{10}$$

The regressions are performed using R and the linear regression routine lm (R, 2010; Wilkinson & Rogers, 1973; Chamber, 1992).
Next, a gam-analysis is performed, assuming that there might be seasonal and yearly variations. After a few trials, the gam-model applied is

$$DOP = gam(DOC + s(Year, k1) + s(Month, k2)) \tag{11}$$

s(Year,k1) and s(Month,k2) are smoothers with k1 and k2 degrees of freedom. Thus Year and Month

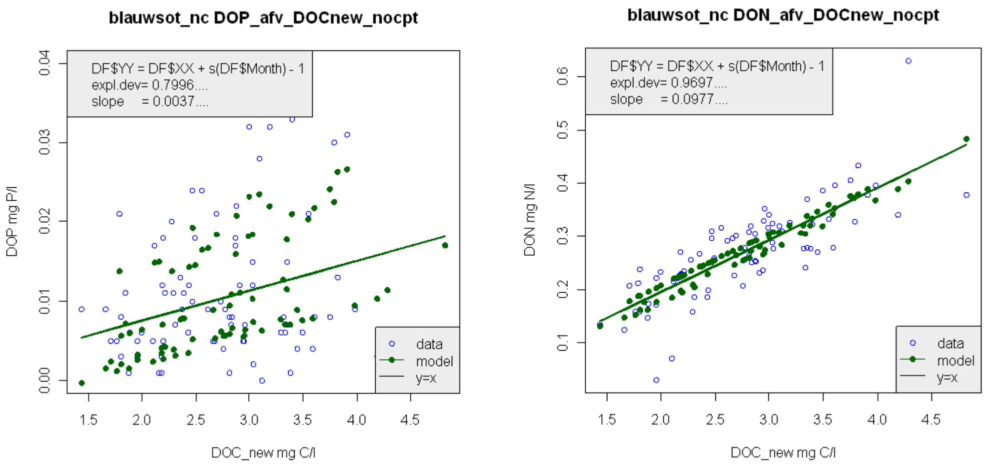


Figure 92 Relationship between dissolved organic phosphorus and nitrogen with dissolved organic carbon at monitoring site Blauwe Slenk Oost. Left: phosphorus, right: nitrogen. It is obvious that for N most data points are close to the average value; and that for P there are large differences. The model with also Year as a explaining variable gives similar results. 'DF' in the heading of both figures refers to the sub-dataframe used for the analysis.

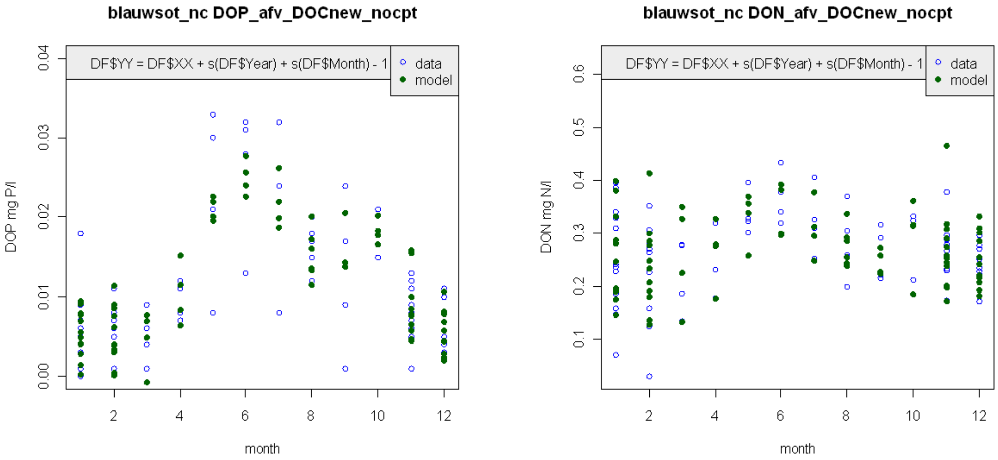


Figure 93 Concentration of dissolved organic phoshorus and nitrogen at monitoring site Blauwe Slenk Oost. Left: phosphorus, right: nitrogen, showing the seasonal variations. Open circles= data points, solid green circles= according to the gam-model xxx. It is obvious that for N there is a slight seasonal variation with somewhat higher values in summer, and for P values in summer are much higher than in winter. DF in the heading of both figures is the sub-dataframe used for the analysis.

are treated as numerical variables and not as factors. The slope of the average line as presented in Figure 92 is similar to the value α in equation 10, the differences are contributions of Year and Month. The difference between average and real values, as depicted in Figure 92, gets clearer when plotted against Month (Figure 93). It is obvious that the summer period plays an important role: especially the phosphorus content of the dissolved organic fraction has much higher values in summer than in winter, compared to a more constant level for dissolved organic nitrogen. Although the latter is not completely constant: late summer values are somewhat higher than late winter ones.

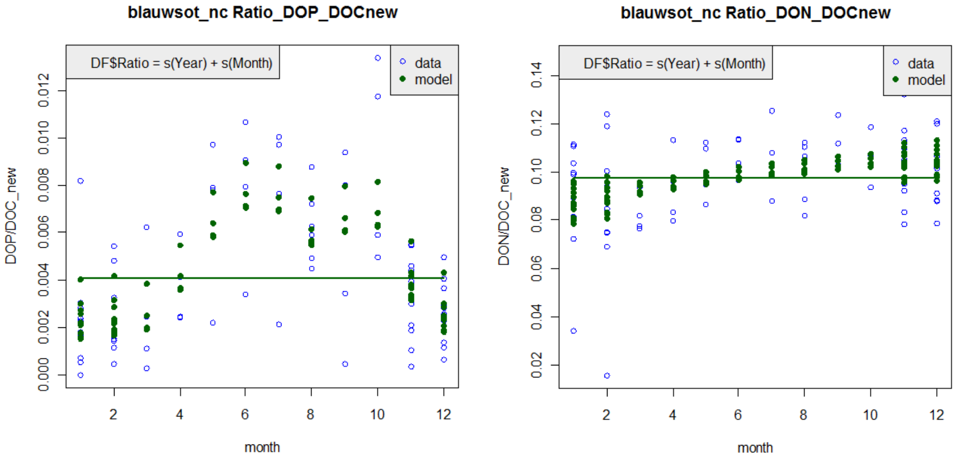


Figure 94 Composition of dissolved organic matter at monitoring site Blauwe Slenk Oost. Left: phosphorus, right: nitrogen, showing the seasonal variations. Open circles= data points, solid green circles= according to the gam-model xxx. It is obvious that especially for N there is a strong seasonal pattern with much higher values in summer. DF in the heading of both figures is the sub-dataframe used for the analysis

The question now is how to deal with such variations.

Estimating time series for the whole period 1976-now for all variables

Background

When simulating the ecological behavior of an ecosystem, boundary values should be as good as possible. In a number of cases, some elaboration of existing data is necessary in order to obtain best possible time series. For example, the Lake IJssel-data exist for three monitoring sites: two close to the outlet-sluices, and one in the centre of the lake. For the two first ones, monitoring stopped around 1993. Since these values are most relevant for the Wadden Sea as they reflect the characteristics of the outflowing fresh water better than the centre values it is worthwhile trying to examine the relationships between the conditions at the three sites. Using these relationships, best estimates for the outflow characteristics may be computed.

The used R-model could be

$$Val_{DenOever} = a + b \cdot Val_{Vrouwezand} + factor\ (Month)$$

here, a linear relationship is assumed, with some variation allowed per month. This variation implies that per month another offset (the value for parameter a) is allowed. In a previous exercise, it has proved to be rather successful (Brinkman, 2008), but the fixed value for the offset appeared to be a disadvantage, especially when state variables were considered that showed a large change in concentration with time. A second model

$$Val_{DenOever} = a + b \cdot Val_{Vrouwezand} * factor\ (Month)$$

has proven itself to suit better. Instead of Vrouwezand as basic data set and Den Oever as data set to be predicted, other stations may be handled as well. In Table 4 Monitoring stations (third column) that have been completed by using values from basic sets available (stations mentioned in first column). All the stations that have been elaborated in this way are mentioned.

Table 4 Monitoring stations (third column) that have been completed by using values from basic sets available (stations mentioned in first column).

Basic data set available	Years	Data set to be completed	Years that were available
Vrouwezand (Lake IJssel)	1975-2008	Den Oever	1975-1993
Vrouwezand (Lake IJssel)	1975-2008	Kornwerderzand	1975-1993
Noordwijk -1 km Finally, Noordwijk was used.	1975-2008	Callantsoog - 1 km	1975-1993

Appendix XII Parameter values for the model

Appendix Parameter values

In this appendix all parameter values for processes regarding ions, phytoplankton, detritus, fauna (including spawning) and solids are listed.

Table 5 Values for ion parameters

Ion/Element_Names	NH4	P	CO2	O2	NO3	NO2	Si	Ca	Chloride	ReducedComp	RestCharge
Chemical_Formula	NH3	H3PO4	CO2	O2	HNO3	HNO2	SiO2	Ca2+	Cl-	CH4	H+
Transport_tr	1	1	1	1	1	1	1	1	1	1	1
Mixing	1	1	1	1	1	1	1	1	1	1	1
MolarMass_g	17	97.97	30	32	63	47	60.09	40	35.45	16	1
ElementMolarMass_g	14	30.97	12	16	14	14	28.09	40	35.45	12	1
Charge	0	0	0	0	0	0	0	2	-1	0	1
Elemental Charge	-3	5	4	-2	5	3	4	2	-1	-4	1
ElektronAccCap_(mol/mol)	0	0	0	4	5	3	0	0	0	0	0
DiffusionCoeff_m2/s	1.90E-09	7.43E-10	1.18E-09	3.47E-09	1.18E-09	1.10E-09	1.00E-09	7.90E-10	2.00E-09	1.90E-09	2.90E-09
DiffusionFactor	1.90E+00	7.43E-01	1.18E+00	1.00E+00	1.18E+00	1.10E+00	1.00E+00	7.90E-01	5.76E-01	1.90E+00	2.90E+00
AirExchange_(1/0)	0	0	1	1	0	0	0	0	0	0	0
Adsorption parameters ============================== Detritus											
AdsorptionDetritus-?(1/0)	----	----	----	----	----	----	----	----	----	----	----
DetritusSubstrate	----	----	----	----	----	----	----	----	----	----	----
Rate_parameter_Vads_(1/d)	----	----	----	----	----	----	----	----	----	----	----
MaxAds_Aerobe_(mol/g)	----	----	----	----	----	----	----	----	----	----	----
MaxAds_Anaerobe_(mol/g)	----	----	----	----	----	----	----	----	----	----	----
Max_AdsOccupation_Theta	----	----	----	----	----	----	----	----	----	----	----
Adsorption_parameter_a	----	----	----	----	----	----	----	----	----	----	----
Adsorption_parameter_b	----	----	----	----	----	----	----	----	----	----	----
Adsorption_parameter_c	----	----	----	----	----	----	----	----	----	----	----
Adsorption_parameter_d	----	----	----	----	----	----	----	----	----	----	----
Adsorption_parameter_e	----	----	----	----	----	----	----	----	----	----	----
Ion/Element_Names	NH4	P	CO2	O2	NO3	NO2	Si	Ca	Chloride	ReducedComp	RestCharge
Adsorption_parameter_f	----	----	----	----	----	----	----	----	----	----	----

Adsorption parameters ============================== Solids											
AdsorptionSolids-?(1/0)	----	1	----	----	----	----	1	----	----	----	----
SolidSubstrate	----	IronHydrox_P_Comp	----	----	----	----	IronHydrox_P_Comp	----	----	----	----
Rate_parameter_Vads_(1/d)	----	2.93E-02	----	----	----	----	3.00E-02	----	----	----	----
MaxAds_Aerobe_(mol/g)	----	2.00E-03	----	----	----	----	2.00E-03	----	----	----	----
MaxAds_Anaerobe_(mol/g)	----	5.00E-04	----	----	----	----	5.00E-04	----	----	----	----
Max_AdsOccupation_Theta	----	----	----	----	----	----	----	----	----	----	----
Adsorption_parameter_a	----	4.00E-01	----	----	----	----	-4.00E-01	----	----	----	----
Adsorption_parameter_b	----	-5.80E-01	----	----	----	----	-5.80E-01	----	----	----	----
Adsorption_parameter_c	----	-1.50E-02	----	----	----	----	-1.50E-02	----	----	----	----
Adsorption_parameter_d	----	----	----	----	----	----	----	----	----	----	----
Adsorption_parameter_e	----	1.09E+01	----	----	----	----	1.20E+01	----	----	----	----
Adsorption_parameter_f	----	6.50E+00	----	----	----	----	8.50E+00	----	----	----	----
Reaction parameters =======================================											
Oxidation_RateParameter	1.00E-01	----	----	----	----	3.00E-01	----	----	----	3.00E-01	----
Oxidation_Temp01	0.6	----	----	----	----	4	----	----	----	-1	----
Oxidation_Temp02	55	----	----	----	----	15	----	----	----	20	----
Oxidation_Temp03	70	----	----	----	----	20	----	----	----	70	----
Monod_Conc_own	1.00E-02	----	----	----	----	1.00E-02	----	----	----	3.00E-02	----
Monod_Conc_O2	5.00E-02	----	----	----	----	5.00E-02	----	----	----	6.00E-02	----
Monod_Conc_NO3	----	----	----	----	----	----	----	----	----	2.00E-02	----

Table 6 Parameter values for phytoplankton and phytobenthos

Phyto_Names	Non-diatoms	Diatoms	Benthic-diatoms	Pico-Phyto
Transport_tr	1	1	1	1
Mixing	1	1	1	1
IK Wm-2	20	8	3	25
rcgrow d-1	3	3	2	3
rcresp d-1	0.25	0.25	0.15	0.3
rcexcr d-1	----	----	----	----
rcmort d-1	----	----	0.1	----
ExtinctionContribution m-1/(g/m3)	0.07	0.045	0.06	0.103
Length m	1.20E-05	5.00E-06	5.00E-06	2.50E-06
Chla mg/g	12	9	9	0.01
Maximum_conc g DW/m3	----	----	2.00E+02	----
MolarMass g	149.47	233.6	233.6	149.47
sinking_velocity md-1	2.00E-06	2.00E-06	2.00E-05	2.31E-06
float_velocity md-1	----	----	----	----
Resuspension-r	2.00E-09	1.50E-09	1.60E-10	1.60E-10
Resusp_power-r3	1.4	1.4	1.4	1.4
Resusp_UWI_0 m/s	0.5	0.5	4	0.5
LiveDepth m	-1.00E-01	-1.00E-01	1.00E-03	-1.00E-03
Temp01_growth oC	-5	-5	-30	-5
Temp02_growth oC	30	15	15	25
Temp03_growth oC	40	40	40	40
Temp01_Respiration oC	-5	-5	-20	-20
Temp02_Respiration oC	25	25	25	25
Temp03_Respiration oC	40	40	40	40
Temp01_Mortality oC	----	----	-20	----
Temp02_Mortality oC	----	----	40	----
Temp03_Mortality oC	----	----	45	----
Composition mol NH4/g DW	6.69E-03	4.28E-03	4.28E-03	6.69E-03

Composition mol P/g DW	2.23E-04	1.43E-04	1.43E-04	2.23E-04
Composition mol CO2/g DW	3.35E-02	2.14E-02	2.14E-02	3.35E-02
Composition mol O2/g DW	-1.78E-02	-1.14E-02	-1.14E-02	-1.78E-02
Composition mol Si/g DW	----	5.99E-03	5.99E-03	----
Composition mol RestCharge/g DW	4.71E-02	3.01E-02	3.01E-02	4.71E-02
C Oxidation number	-0.04	-1.16	-1.16	-0.04
Monod_Factor mol NH4/m3	5.00E-03	5.00E-03	5.00E-03	3.00E-03
Monod_Factor mol P/m3	2.00E-04	1.50E-04	1.50E-04	1.50E-04
Monod_Factor mol CO2/m3	8.00E-03	8.00E-03	8.00E-03	8.00E-03
Monod_Factor mol NO3/m3	1.50E-03	1.50E-03	1.50E-03	1.50E-03
Monod_Factor mol Si/m3	----	6.00E-03	6.00E-03	----
MortDestination	Dead_Substance	Dead_Diatoms	Dead_Diatoms	Dead_Diatoms
ExcretionDestination	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter

Table 7 Parameter values fauna

Fauna_Names	Mussel_ Larvae	Mussel_ Seed	Mussel_3	Mussel_4	Micro Zooplankton	MZIMussel_ Larvae	MZIMussel_ Seed_Net	MZIMussel_ Seed_Benth	MZIMussel_3	MZIMussel_4
Transport_tr	0	0	0	0	0	0	0	0	0	0
Mixing	1	0	0	0	1	1	0	0	0	0
IndwFacta	1.60E-03	4.40E-02	4.40E-02	4.40E-02	1.00E-02	1.60E-03	4.40E-02	4.40E-02	4.40E-02	4.40E-02
IndwFactb	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35
UptakeFacta	1.60E-03	2.20E-02	2.33E-02	2.44E-02	4.00E-03	1.60E-03	2.64E-02	2.20E-02	2.33E-02	2.44E-02
UptakeFactb	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35	-0.35
RespirationFacta	6.00E-02	5.60E-03	5.60E-03	5.60E-03	3.00E-01	6.00E-02	5.60E-03	5.60E-03	5.60E-03	5.60E-03
RespirationFactb	0	0	0	0	0	0	0	0	0	0
ExcretionFacta	1.00E-02	2.18E-03	2.18E-03	2.18E-03	0.00E+00	1.00E-02	2.18E-03	2.18E-03	2.18E-03	2.18E-03
ExcretionFactb	0	0	0	0	0	0	0	0	0	0
Activity_respiration	0.01	0.01	0.01	0.01	----	0.01	0.01	0.01	0.01	0.01
Activity_excretion	0.01	0.01	0.01	0.01	----	0.01	0.01	0.01	0.01	0.01
Morta	----	1.40E-03	1.44E-03	1.44E-03	1.00E-07	----	1.12E-03	1.40E-03	1.44E-03	1.44E-03
Mortb	----	-0.5	-0.5	-0.5	-0.5	----	-0.5	-0.5	-0.5	-0.5
sedArea_indw_a	----	----	----	----	----	----	----	----	----	----
sedArea_indw_b	----	----	----	----	----	----	----	----	----	----
ShiftMortality (-)	0.9	0.9	----	----	----	0.9	0.05	0.07	----	----
DigestionCosts (gDW/gFood ingested)	1.50E-01	1.50E-01	1.50E-01	1.50E-01	1.50E-01	1.50E-01	1.50E-01	1.50E-01	1.50E-01	1.50E-01
Costs_SuspendedSolids gDW/(gSS/m3)	----	----	----	----	----	----	----	----	----	----
PseudoFaecesCosts gDW/gPSF	----	----	----	----	----	----	----	----	----	----
MaximumPseudoFaecesFactor	----	2	2	2	----	----	2	2	2	2
ExtinctionContribution	----	----	----	----	----	----	----	----	----	----
Length_Mass_a	2.57E+03	2.57E+03	2.57E+03	2.57E+03	2.57E+03	2.57E+03	2.57E+03	2.57E+03	2.57E+03	2.57E+03
Length_Mass_b	2.703	2.703	2.703	2.703	2.703	2.703	2.703	2.703	2.703	2.703
MolarMass g	1.52E+02	1.52E+02	1.52E+02	1.52E+02	1.52E+02	1.52E+02	1.52E+02	1.52E+02	1.52E+02	1.52E+02
MaxWeight	5.00E-07	-9.00E+00	-9.00E+00	-9.00E+00	-9.00E+00	5.00E-07	-9.00E+00	-9.00E+00	-9.00E+00	-9.00E+00

Fauna_Names	Mussel_ Larvae	Mussel_ Seed	Mussel_3	Mussel_4	Micro Zooplankton	MZIMussel_ Larvae	MZIMussel_ Seed_Net	MZIMussel_ Seed_Benth	MZIMussel_3	MZIMussel_4
LiveDepth m	-1.00E-01	5.00E-03	5.00E-03	5.00E-03	-1.00E-01	-1.00E-01	-1.00E-01	5.00E-03	5.00E-03	5.00E-03
PreyDepth m	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01
RespirationDepth m	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01	-1.00E-01
FaecationDepth m	-1.00E-01	5.00E-03	5.00E-03	5.00E-03	-1.00E-01	-1.00E-01	-1.00E-01	5.00E-03	5.00E-03	5.00E-03
PseudoFaecationDepth m	-1.00E-01	5.00E-03	5.00E-03	5.00E-03	-1.00E-01	-1.00E-01	-1.00E-01	5.00E-03	5.00E-03	5.00E-03
LiveLayer	1	1	1	1	1	1	1	1	1	1
PreyLayer	1	1	1	1	1	1	1	1	1	1
RespirationLayer	1	1	1	1	1	1	1	1	1	1
FaecationLayer	1	1	1	1	1	1	1	1	1	1
PseudoFaecationLayer	1	1	1	1	1	1	1	1	1	1
PreySize_Relative	1	1	1	1	1	1	1	1	1	1
MinRelSize	1.00E-06	1.00E-06	1.00E-06	1.00E-06	1.00E-06	1.00E-06	1.00E-06	1.00E-06	1.00E-06	1.00E-06
MaxRelSize	1.00E+00	1.00E+00	1.00E+00	1.00E+00	1.00E+00	1.00E+00	1.00E+00	1.00E+00	1.00E+00	1.00E+00
MinPreySize_X1	----	----	----	----	----	----	----	----	----	----
MinPreySize_X2	1.00E-04	1.00E-04	1.00E-04	1.00E-04	1.00E-04	1.00E-04	1.00E-04	1.00E-04	1.00E-04	1.00E-04
MinPreySize_X3	4.00E+00	1.00E-01	4.00E+00	4.00E+00	4.00E+00	4.00E+00	1.00E-01	1.00E-01	4.00E+00	4.00E+00
MinPreySize_X4	4.00E+01	1.50E-01	4.00E+01	4.00E+01	4.00E+01	4.00E+01	1.50E-01	1.50E-01	4.00E+01	4.00E+01
Shift_X1_withLength	----	----	----	----	----	----	----	----	----	----
Shift_X2_withLength	----	----	----	----	----	----	----	----	----	----
Shift_X3_withLength	----	----	----	----	----	----	----	----	----	----
Shift_X4_withLength	----	----	----	----	----	----	----	----	----	----
Fixed mass	----	----	----	----	2.00E-09	----	----	----	----	----
Temp01_Filtration oC	-7	-8	-10	-15	-5	-7	-8	-8	-10	-15
Temp02_Filtration oC	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5
Temp03_Filtration oC	45	45	45	45	45	45	45	45	45	45
Temp01_Respiration oC	-20	-20	-20	-20	-5	-20	-20	-20	-20	-20
Temp02_Respiration oC	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5
Temp03_Respiration oC	45	45	45	45	45	45	45	45	45	45

Fauna_Names	Mussel_ Larvae	Mussel_ Seed	Mussel_3	Mussel_4	Micro Zooplankton	MZIMussel_ Larvae	MZIMussel_ Seed_Net	MZIMussel_ Seed_Benth	MZIMussel_3	MZIMussel_4
Temp01_Mortality oC	-20	-20	-20	-20	-5	-20	-20	-20	-20	-20
Temp02_Mortality oC	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5	21.5
Temp03_Mortality oC	45	45	45	45	45	45	45	45	45	45
Compostion Mol NH4 /g DW	7.23E-03	7.23E-03	7.23E-03	7.23E-03	7.23E-03	7.23E-03	7.23E-03	7.23E-03	7.23E-03	7.23E-03
Compostion Mol P /g DW	2.41E-04	2.41E-04	2.41E-04	2.41E-04	2.41E-04	2.41E-04	2.41E-04	2.41E-04	2.41E-04	2.41E-04
Compostion Mol CO2 /g DW	3.29E-02	3.29E-02	3.29E-02	3.29E-02	3.29E-02	3.29E-02	3.29E-02	3.29E-02	3.29E-02	3.29E-02
Compostion Mol O2 /g DW	-1.74E-02	-1.74E-02	-1.74E-02	-1.74E-02	-1.74E-02	-1.74E-02	-1.74E-02	-1.74E-02	-1.74E-02	-1.74E-02
Compostion Mol RestCharge /g DW	4.69E-02	4.69E-02	4.69E-02	4.69E-02	4.69E-02	4.69E-02	4.69E-02	4.69E-02	4.69E-02	4.69E-02
C Oxidation number	0	0	0	0	0	0	0	0	0	0
CatchPref of Mussel_Larvae	----	1	1	1	----	----	1	1	1	1
CatchPref of MicroZooplankton	----	1	1	1	----	----	1	1	1	1
CatchPref of MZIMussel_Larvae	----	1	1	1	----	----	1	1	1	1
CatchPref of Non-diatoms	1	1	1	1	----	1	1	1	1	1
CatchPref of Diatoms	1	1	1	1	----	1	1	1	1	1
CatchPref of Benthic-diatoms	1	1	1	1	----	1	1	1	1	1
CatchPref of Pico-Phyto	1	----	----	----	1	1	----	----	----	----
CatchPref of Labile_Org_Matter	----	1	----	1	----	----	1	1	----	1
CatchPref of Frac2	----	1	1	1	----	----	1	1	1	1
CatchPref of Refract_Org_Matter	----	1	1	1	0.07	----	1	1	1	1
CatchPref of Dead_Substance	1	1	1	1	----	1	1	1	1	1
CatchPref of Dead_Diatoms	1	1	1	1	----	1	1	1	1	1
CatchPref of Frac2_Diat	----	1	1	1	----	----	1	1	1	1
CatchPref of Frustules	----	1	1	1	----	----	1	1	1	1
Fraction assimilated of Mussel_Larvae	----	0.8	0.8	0.8	----	----	0.8	0.8	0.8	0.8
Fraction assimilated of MicroZooplankton	----	0.8	0.8	0.8	----	----	0.8	0.8	0.8	0.8
Fraction assimilated of MZIMussel_Larvae	----	0.8	0.8	0.8	----	----	0.8	0.8	0.8	0.8

Fauna_Names	Mussel_ Larvae	Mussel_ Seed	Mussel_3	Mussel_4	Micro Zooplankton	MZIMussel_ Larvae	MZIMussel_ Seed_Net	MZIMussel_ Seed_Benth	MZIMussel_3	MZIMussel_4
Fraction assimilated of Non-diatoms	0.56	0.56	0.56	0.56	----	0.56	0.56	0.56	0.56	0.56
Fraction assimilated of Diatoms	0.28	0.28	0.28	0.28	----	0.28	0.28	0.28	0.28	0.28
Fraction assimilated of Benthic-diatoms	0.28	0.28	0.28	0.28	----	0.28	0.28	0.28	0.28	0.28
Fraction assimilated of Pico-Phyto	0.56	----	----	----	0.4	0.56	----	----	----	----
Fraction assimilated of Labile_Org_Matter	----	----	----	----	----	----	----	----	----	----
Fraction assimilated of Frac2	----	----	----	----	----	----	----	----	----	----
Fraction assimilated of Refract_Org_Matter	----	----	----	----	0.1	----	----	----	----	----
Fraction assimilated of Dead_Substance	0.1	0.1	0.1	0.1	----	0.1	0.1	0.1	0.1	0.1
Fraction assimilated of Dead_Diatoms	0.05	0.05	0.05	0.05	----	0.05	0.05	0.05	0.05	0.05
Fraction assimilated of Frac2_Diat	----	----	----	----	----	----	----	----	----	----
Fraction assimilated of Frustules	----	----	----	----	----	----	----	----	----	----
MortDestination	Dead_Substance	Dead_Substance	Dead_Substance	Dead_Substance	Dead_Substance	Dead_Substance	Dead_Substance	Dead_Substance	Dead_Substance	Dead_Substance
FaecesDestination	Frac2	Frac2	Frac2	Frac2	Frac2	Frac2	Frac2	Frac2	Frac2	Frac2
ExcretionDestination	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter	Labile_Org_Matter

Table 8 Parameter values detritus

Detritus parameters							
Detritus_Names	Labile_Org_Matter	Frac2	Refract_Org_Matter	Dead_Substance	Dead_Diatoms	Frac2_Diat	Frustules
Transport_tr	2	2	2	2	2	2	2
Mixing	1	1	1	1	1	1	1
kmax d-1	1.00E+00	8.00E-02	1.50E-03	3.00E-01	3.00E-01	1.20E-01	3.00E-02
totalpha	----	----	----	----	----	----	----
totminer	----	----	----	----	----	----	----
ExtinctionContribution m-1/(g/m3)	5.00E-03	4.50E-02	4.50E-02	4.50E-02	4.50E-02	3.00E-02	2.00E-02
Length m	1.00E-05	1.00E-05	1.00E-05	1.00E-05	1.00E-05	1.00E-05	1.00E-05
MolarMass g	133.09	108.12	114.85	142.38	220.5	1	1
sinking_velocity md-1	----	2.20E-05	2.20E-05	2.20E-05	2.20E-05	2.20E-05	2.20E-05
Resuspension-r	3.00E-10	6.00E-10	4.00E-10	6.00E-10	6.00E-10	3.00E-10	3.00E-10
Resusp_power-r3	1.4	1.4	1.4	1.4	1.4	1.4	1.4
Resusp_UWI_0 m/s	1	0	0.5	0	1	1	1
Temp01_Breakdown oC	-2	-2	-2	-2	-2	-2	-50
Temp02_Breakdown oC	30	30	30	30	30	30	5
Temp03_Breakdown oC	60	60	60	60	60	60	5
Composition Mol NH4/gDW	4.51E-03	1.85E-03	2.61E-03	5.62E-03	3.63E-03	1.07E-03	----
Composition Mol P/gDW	1.50E-04	1.23E-04	4.35E-05	1.87E-04	1.21E-04	7.16E-05	----
Composition Mol CO2/gDW	3.76E-02	4.63E-02	4.35E-02	3.51E-02	2.27E-02	2.69E-02	----
Composition Mol O2/gDW	-2.02E-02	-2.53E-02	-2.37E-02	-1.88E-02	-1.21E-02	-1.47E-02	----
Composition Mol Si/gDW	----	----	----	----	5.90E-03	6.98E-03	1.20E-02
Composition Mol RestCharge/gDW	4.97E-02	5.75E-02	5.49E-02	4.80E-02	3.10E-02	3.34E-02	----
C Oxidation number	-0.18	-0.34	-0.29	-0.11	-1.15	-1.38	0
Destination g/g-Labile_Org_Matter	----	----	----	0.3	0.15	----	----
Destination g/g-Frac2	0.05	----	----	0.2	0.1	----	----

Detritus_Names	Labile_Org_Matter	Frac2	Refract_Org_Matter	Dead_Substance	Dead_Diatoms	Frac2_Diat	Frustules
Destination g/g-Refract_Org_Matter	----	0.15	----	----	----	0.05	----
Destination g/g-Dead_Substance	----	----	----	----	----	----	----
Destination g/g-Dead_Diatoms	----	----	----	----	----	----	----
Destination g/g-Frac2_Diat	----	----	----	----	0.4	----	----
Destination g/g-Frustules	----	----	----	----	----	0.35	----
FaecesDestination	Frac2	Refract_Org_Matter	Refract_Org_Matter	Labile_Org_Matter	Frac2_Diat	Frustules	Frustules

Table 9 Parameter values for solids

Solid parameters				
Solid_Names	IronHydrox_P_Comp	Silt	FineSand	MediumSand
Transport_tr	0	0	0	0
Mixing	0	0	0	0
ExtinctionContribution m-1/(g/m3)	5.00E-02	5.00E-02	3.00E-02	1.00E-02
Length m	1.00E-04	1.00E-05	4.00E-05	2.00E-04
MolarMass g	1	1	1	1
sinking_velocity md-1	8.33E-05	5.00E-05	2.80E-04	2.20E-03
Resuspension r	----	1.00E-09	2.00E-10	1.00E-11
Resusp_power r3	1.4	1.4	1.4	1.4
Resusp UWI_0 m/s	2	2	5	10

Table 10 Parameter values spawning (note that microzooplankton does not spawn, so it does not appear in this table)

Spawning parameters		
Fauna_Type	Mussel	MZI_Mussels
Number_spawndays	1	1
Spawnday 1	130	130
Biomass fraction for spawning day 1	0.25	0.25
Minimum age for spawning (days)	210	210
Length spawning period (days)	14	14
Birth mass (g)	3.10E-08	3.10E-08

Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 124296-2012-AQ-NLD-RvA). This certificate is valid until 15 December 2015. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Fish Division has NEN-EN-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.

Justification

Rapport : C061/13
Project Number: 4308301022

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

Approved : Dr. Ir. J. Wijsman

Function : Senior Scientist

Signature :

Date : December 2013

Management being responsible for the scientific content of this report

Approved : Drs. J. Asjes

Function : Head of Department Ecosystems

Signature :

Date : December 2013