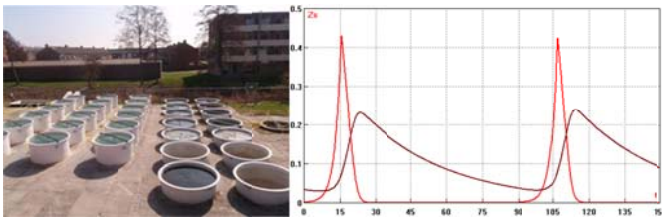


Marine Mesocosm Model, Development of phyto- and zooplankton under elevated copper concentrations

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Summary

A 'minimal' model was constructed to simulate the development of phyto- and zooplankton communities with and without the presence of elevated copper concentrations and to investigate if there is a food web effect in addition to the direct effect of copper. Data from a mesocosm experiment carried out in 2009 studying the effect of copper were used to compare model output.

It was decided to separate the phyto- and zooplankton groups according to their size since it is believed that individual size has important implications for the physiology, ecology and potential food web effects. The micro-phytoplankton group consisted of species $<8\text{ }\mu\text{m}$ in size, the macro-phytoplankton group of species $>8\text{ }\mu\text{m}$ in size. The micro-phytoplankton could only be consumed by the micro-zooplankton being $<200\text{ }\mu\text{m}$ in size. The macro-phytoplankton could only be consumed by meso-zooplankton, $>200\text{ }\mu\text{m}$ in size which also predated the micro-zooplankton community. The model consisted of a set of differential equation in which food intake was modelled using a modified Holling type II equation. Parameter values were set assuming that micro-phytoplankton can utilize resources more efficient than macro-phytoplankton, have lower maintenance cost and background mortality and a higher maximum growth rate. Micro-zooplankton has higher background mortality and maximum growth rate than meso-zooplankton. The effect of copper was incorporated into the model by adjusting the food intake.

The model was able to simulate the major direction of the phyto- and zooplankton as observed in the mesocosm data. Initial peaks in the different groups and the decline of the species observed in the blank treatment were both predicted by the model. In the (modelled) equilibrium situation macro-phytoplankton was not able to sustain itself when micro-phytoplankton was present. In nature extinction of macro-phytoplankton could be prevented by seasonal effects which are not incorporated in the model.

Three copper situations were modelled, by reducing the food intake, affecting each group of species equally; a high effect (decline of food intake by 70%), low effect (decline of 10%) and intermediate effect (decline of 50%). Next to a direct effect of copper on the development of the species also a food web effect was found. When zooplankton peaks decrease by a factor of 0.5, phytoplankton peaks were only reduced by a factor 0.75 – 0.9. The negative effect of copper for phytoplankton was partly compensated for by a decrease in predation pressure. At the highest copper treatment modelled meso-zooplankton was not able to sustain itself, this was observed in the mesocosm data as well. Mesocosm data show that macro-phytoplankton is able to re-establish itself in the copper treatments. This was not observed in model-output.

Even though model output is able to qualitatively predict most observations from the mesocosm experiment it is not known to which level individual species contribute to the observed development in biomass of the clusters. It is expected that by looking at the dynamics of individual zoo-/ phytoplankton species the effect of copper on the population can be assessed in greater detail. However the time span of this project didn't allow to conduct an in depth data analysis. It is therefore recommended to perform a data analysis to study the mechanisms with which the different plankton species are affected by the copper further together with the biology of the species (feeding behaviour etc). This could result in an alternative division of the plankton species ultimately resulting in even better model predictions and better understanding the effect copper has on the lower part of the food web.

1. Introduction

Ecosystems consist of very complex interactions between different species and their physical environment. Alterations on one part of the ecosystem can cause, via food web interactions, unexpected changes somewhere else. Translation of effects on one end of the organisational level, for instance individuals, to other levels of organisation, population or community, are complex and not obvious. In general measurements are mainly carried out for short periods of time and on individual level because of budget and practical reasons.

Unique exceptions are the salt water mesocosm experiments carried out by IMARES. In these systems the effect of mainly toxic substances are studied on a more complex ecosystem and represent therefore a more environmental relevant situation. 18 mesocosm tanks are available in total with a capacity of 4 m³ each. In each experiment several species of different trophic levels, linked by feeding interactions and competition for resources, are added. The development of the community is monitored over a longer period of time in which species grow, reproduce and die. From the monitoring activities a database is constructed. Combination of the available data from these studies with the result of an ecosystem model is a unique chance to extrapolate effects on individual level to effects on population- and ecosystem level.

Problem definition

A model is by definition a simplified form of the real world, but they differ in complexity. Existing applied ecosystem models are in general very complex, resulting in a great number of parameters. It is not uncommon that for certain parameters an independent measured value is lacking. This lack of data leads in practice to complex estimation procedures with the aim to synchronise model output with available time series. In the attempt to construct a model that include almost all existing relations known a system is made that resembles to great extent the natural world but at the same time makes it very hard to relate outcome to responsible ecological mechanisms. Model predictions have to be taken as it is without getting true insight in the system.

The challenge therefore is to construct a model that is simple enough to relate model output with model assumptions made and at the same time consist of sufficient complexity to deliver output relevant for the 'real' system, the outside world.

Project aim

By developing a model capable of describing a simple ecosystem several objectives can be reached;

- making a model available for IMARES that describes the interactions and succession of phyto- and zooplankton groups in a marine environment;
- extend our knowledge of complex interactions between different trophic level groups as they occur in marine ecosystems;
- exploring the effect of copper on the development of phyto- and zooplankton groups, both direct and indirect via food web interactions.

Next to extending our knowledge about the dynamic interactions that occur in the marine environment, model expertise at IMARES is increased and becomes more readily available for the different departments.

2. Research questions and method

Studies in which a model is linked to repeatable experiments on population- and community level are rare in ecological literature. As far as they occur they are usually statistical models which describe observed patterns rather than explain them.

In this study we try to formulate, on the basis of commonly accepted theory about ecological interactions and specific knowledge about the role individuals and groups play in the mesocosm, a model that creates time series which can be compared to observed results. Next we also try to examine how copper pollution/poisoning affects communities both directly and indirectly via food web interactions.

Independent of the extent in which the model can predict the development of phyto- and zooplankton as observed in the mesocosm experiments this research will lead to more insight in understanding the aspects and interactions of mesocosm ecosystems.

Research question

This study intends to answer the following question:

"Is it possible, on the basis of ecological mechanisms, to capture the dynamics of phyto- and zooplankton communities in the IMARES saltwater-mesocosms in an independently constructed and relative simple model and is it possible to assess the food web effect of copper toxicity on both groups with this tool?"

Methodology

In this study a model is developed and analysed describing the food web interactions as observed in a marine mesocosms experiment. In the experiment, carried out in 2009 by Edwin Foekema, the effect of copper is determined. Data from this experiment is very useful for several reasons:

- the mesocosm communities consist of roughly 3 trophic levels (phyto- / zooplankton, snails and worms);
- a semi-natural environment is created in the mesocosms;
- development of the systems are monitored (both chemical- as biological parameters) for an extended period of time (100 days);
- treatments are carried out in triplicate, replicas don't show big differences in development (Foekema et al., in prep).

Although in the mesocosms also snails and worms (a somewhat third level species) were present these were not considered because the life history of these species was too long (or duration of experiment too short) to show dynamics in numbers. Therefore only the interactions of phyto- and zooplankton groups are mathematically described in this study.

To compare the development of the measured and modelled plankton groups the available biomass data from the experiment must be converted into the same unit (mg C/l) first. The amount of carbon per individual (zooplankton) or ml (phytoplankton) will be derived from values found in literature. When no data can be found for a species an average value will be used. Note: this can lead to an over- or underestimation of the carbon content. Although meso-zooplankton is as small as micro-zooplankton in their early life stages differences between life stages within species are not accounted for.

First mesocosm without elevated copper concentrations (the blank treatments) are compared with model output. Next effects of copper is incorporated into the model and compared with experimental data. The results and set up of the mesocosm experiment is described by Foekema et al., (in prep.). A short description is given in chapter 3.

3. Short description of mesocosm experiment(s)

The development of a relatively simple ecosystem consisting of three trophic levels (primary producers, primary consumers and secondary consumers) is monitored for a period of 100 days under the influence of five different copper concentrations (the treatments) together with a system without an elevated copper concentration (the blank). Each treatment, including the blank, was carried out in triplicate, therefore 18 mesocosm systems were followed over time in total.

The mesocosm are made of round glass fiber tanks with a height of 180 cm and an internal diameter of 190 cm (top) and 175 cm (bottom). These tanks were partly buried. Approximately 20 cm of North sea sediment and 140 cm of saltwater (Eastern Scheldt) were added to each system. In order to obtain a similar development of species in each tank, the water of all tanks was continuously exchanged between the tanks in the acclimatization period lasting for 3 to 4 weeks. After this period the tanks were hydraulically isolated. Water movement was created in each tank by aeration. Loss of water due to evaporation was compensated for by additions with tap water. To minimize the influence of precipitation the tanks were shielded with a transparent screen.

Plankton and invertebrates were introduced via the sediment and water added to the system. As addition several other species were introduced as can be seen in Table 1.

Table 1: Introduced species to the mesocosm tanks.

Group	Species – Latin name	Specie – common name
Macro algae	<i>Ulva Lactuca</i>	Sea lettuce
Sponge	<i>Halichondria panicea</i>	Bread-crumbs sponge
Crustaceans	<i>Corophium volutator</i>	Mud shrimp
Molluscs	<i>Littorina Littorea</i>	Periwinkle
	<i>Hydrobia ulvae</i>	Laver spire shell
	<i>Cerastoderma edule</i>	Cockle
Annelid	<i>Arenicola marina</i>	Lugworm

Several biological and chemical parameters were regularly monitored during the 100 days in which the systems could develop. In Table 2 an overview of the measured biological parameters and the frequency of measurement is given, in Table 3 an overview of the chemical analyses is given.

Table 2: Overview and frequency of monitored biological parameters.

Parameter	Sort measurement	Frequency
Phytoplankton	chlorophyll –a	two times a week
Phyto- and zooplankton	density and composition	first 28 days; every week after 28 days; every two weeks
Pheriphyton	Biomass	every 28 days
Sponge	Biomass	At the start of the experiment, after acclimatization period and at the end of the experiment
Crustaceans	amount, length and weight	At the end of the experiment
Molluscs	amount, length and weight	At the end of the experiment
Annelid	amount, length and weight	At the end of the experiment

Table 3: Overview and frequency of monitored chemical parameters.

Parameter	Sort measurement	Frequency
Cu	dissolved water concentration	two times a week
DOC, NH ₃ , NO ₂ , NO ₃ , PO ₄ , Si	dissolved water concentration	once every week
CaCO ₃ , Zn, Cd, Pb, Ni, Fe, Mn	dissolved water concentration	once every two weeks
Cu, AVS, SEM en TOC	sediment concentration	At the start and the end of the experiment
Cu	concentration in biota	At the start and the end of the experiment

4. Model outline and assumptions

As can be seen in chapter 3 no fish-species were added to the mesocosm systems, experience has learned that addition of fish makes the systems very unstable: the addition of even a single fish can lead to the annihilation of zooplankton (E. Foekema, pers. comm.). Pheriphyton, sponges, crustaceans, molluscs, annelids, phytoplankton and zooplankton groups were present and monitored during the 100 days duration of the experiment. The development of the plankton community (both phyto- and zooplankton) was measured most frequent resulting in a good dataset. The life-history of the 'higher trophic level species' such as snail and worms, were too long so dynamics were not studied. Since phyto- and zooplankton groups form the basis of almost all marine ecosystems it was decided to focus on these functional groups for development of the model. A lot of papers are published in which plankton interactions and dynamics are studied in the marine environment. The model was constructed based on several hypotheses found in literature which are described here.

Phyto- and zooplankton interactions

Autotrophic communities (such as planktonic, periphytic-, micro- and macro algae) are responsible for the primary production and form the basis of the food web leading (via zooplankton) to fish and birds. The composition and dominance of these communities differ however due to an array of factors such as exposure to waves and currents, substratum composition, grazing, light and nutrient availability. These factors can determine alone the abundance of a species, but also via complex interactions, (Sand-Jensen and Borum 1991).

Phytoplankton is the major contributor to algal biomass and primary production in the North Sea (Mackinson and Daskalov 2007). Individual size has important implications for the physiology and ecology of the phytoplankton. Individual size effect processes such as nutrient uptake, light affinity, photosynthesis and respiration, settling rates and physical transport and plant herbivore interactions (Sabetta et al. 2008). Riegman and others suggest a size differential control of phytoplankton structuring the plankton communities resulting from nutrient and light competition of the phytoplankton. Four factors were proposed determining the food web structure under oligotrophic and eutrophic conditions (Riegman et al. 1993);

1. Small algae are better competitors for light and nutrients than larger algae;
2. The potentially high reproduction rate of their predators makes the smaller algae more susceptible to grazing control by micro-zooplankton than the larger algae;
3. Larger algae escape from micro-zooplankton grazing, due to their size, but experiences losses through sedimentation;
4. Micro-zooplankton is an important food source for meso-zooplankton in oligotrophic areas.

Modelled processes

Based on these assumptions the following model outline is proposed consisting of two phytoplankton groups and two zooplankton groups structured by their size, see Figure 1. We have assumed that nutrient concentration and grazing is most important for the phytoplankton dynamics in the mesocosms, and have ignored other factors such as waves and currents. In a meeting with employees of IMARES working with models and/or with expertise on nutrient, phyto-, zooplankton dynamics, it has been decided not to model nutrient dynamics explicitly. Instead resources, not further specified, are available for the phytoplankton groups.

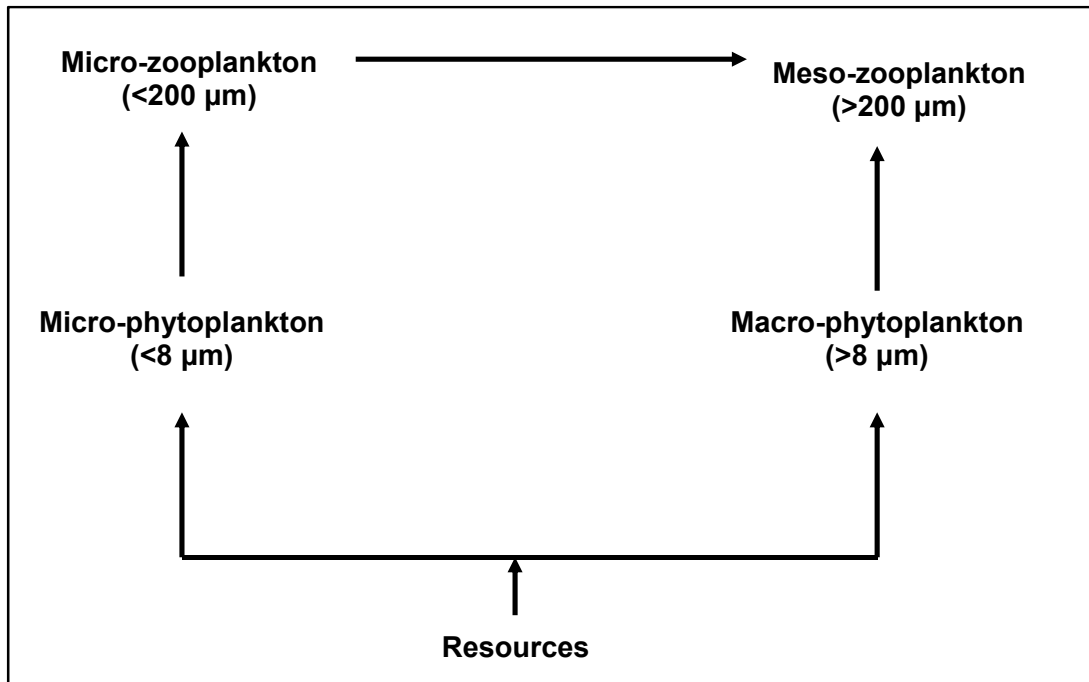


Figure 1: Modelled processes.

5. Model equations and parameter values

The different processes depicted in Figure 1 are modelled using a set of ordinary differential equations. Biomass (phyto- and zooplankton) is expressed as mgC/l. While in reality phytoplankton growth can be limited by a number of resources (N/P/light etc), we assume that only a single resource limits growth of phytoplankton. . To parameterize this limiting resource, we have used nitrogen data. We use the modelling framework developed by Yodzis & Innes to model the change in biomass of populations on the basis of individual-level processes (Yodzis & Innes, 1992).

First objective was to model the blank treatments, without the presence of elevated copper concentration. In a follow up the effect of copper was incorporated into the model and compared with measurements from the experiment.

The software package *Content* was used to solve the differential equations and visualize model output. *Content* was developed by Yu. A. Kuznetsov and V.V. Levitin at the 'Centrum voor wiskunde en informatica' in Amsterdam and is freely available on the internet.

Resources

Resources (nutrients) enter the mesocosm water column via both mineralization processes in the water column and in the sediment. Factors affecting the mineralization rate are not incorporated into the model, the mineralization rate is considered constant. Resources that become available for utilization by both micro-phytoplankton (P_S) and macro-phytoplankton (P_L) is modelled as a continuous flux, representing both sediment and water mineralization processes, see equation 1.

Uptake of resources by phytoplankton is determined from the amount of nitrogen needed per unit carbon growth of phytoplankton, using carbon to nitrogen ratio of 250:40, see equation 2.

$$\frac{dN}{dt} = N_{flux} - (P_S \cdot I_{ps} \cdot Cf) - (P_L \cdot I_{pl} \cdot Cf) \quad \text{Equation 1}$$

$$Cf = \frac{\left(\frac{40}{250}\right) \cdot Molair_mass_N}{Molair_mass_C} = 0.187 \quad \text{Equation 2}$$

N	Nitrogen concentration	(mgN/l)
N_{flux}	Flux of nitrogen into the system	(mgN/l/d)
I_{ps}	Intake rate resources by micro-phytoplankton	(d ⁻¹)
P_S	Micro-phytoplankton biomass	(mgC/l)
I_{pl}	Intake of resources by macro-phytoplankton	(d ⁻¹)
P_L	Macro-phytoplankton biomass	(mgC/l)
C_f	Conversion factor from C to N	(mgN/mgC)

Micro-phytoplankton (<8 µm)

The rate of micro-phytoplankton (P_S) change is determined by growth, cell maintenance, cell death and grazing. The growth of phytoplankton is determined by the intake of resources (I) and the food assimilation efficiency (ϵ) which express how efficient resources are converted to biomass. Cell death is expressed as mortality (M) and cell maintenance as (T), and both represent the fraction of the phytoplankton community that dies or is used for maintenance every day. Grazing depends on the micro-zooplankton (Z_S) specific ingestion rate which itself depends on the phytoplankton density, see equation 3.

$$\frac{dP_S}{dt} = P_S \cdot (\epsilon_{ps} \cdot I_{ps} - T_{ps} - M_{ps}) - (Z_S \cdot I_{zs}) \quad \text{Equation 3}$$

The intake rate by phytoplankton is resources limited according to a (modified) Holling type II functional response with maximum growth rate I_{\max} , a half saturation value (H) (at which concentration growth is half of its maximum) and available resources (N), see equation 4. For computational reasons we set an arbitrary threshold for nutrient uptake to prevent nutrient concentration to approach zero slowing down the model computations. , see equation 5.

$$I_{ps} = \frac{N_{psEff} \cdot I_{ps\max}}{H_{ps} + N_{psEff}} \quad \text{Equation 4}$$

$$N_{psEff} = \max(N - N_{psTH}, 0) \quad \text{Equation 5}$$

P_S	Micro-phytoplankton biomass	(mgC/l)
ϵ_{ps}	Assimilation efficiency	(-)
I_{ps}	Intake rate resources by micro-phytoplankton	(d ⁻¹)
T_{ps}	Mass specific maintenance rate	(d ⁻¹)
M_{ps}	Loss rate due to sedimentation	(d ⁻¹)
Z_S	Micro-zooplankton biomass	(mgC/l)
$I_{ps\max}$	Maximal intake rate	(d ⁻¹)
H_{ps}	Half saturation constant for nitrogen intake	(mgN/l)
N_{psEff}	Available nitrogen for micro-phytoplankton	(mgN/l)
N_{psTH}	Threshold concentration for nitrogen uptake by micro-phytoplankton	(mgN/l)
N	Nitrogen concentration	(mgN/l)

Macro-phytoplankton (>8 µm)

Macro-phytoplankton dynamics is governed by the same processes as for the micro-phytoplankton with the only difference that macro-phytoplankton (P_L) is grazed by meso-zooplankton (Matsumura-Tundisi et al.), see equation 6, 7 and 8.

$$\frac{dP_L}{dt} = P_L \cdot (\epsilon_{pl} \cdot I_{pl} - T_{pl} - M_{pl}) - (Z_L \cdot I_{zpl}) \quad \text{Equation 6}$$

$$I_{pl} = \frac{N_{PIEff} \cdot I_{pl \max}}{H_{pl} + N_{PIEff}} \quad \text{Equation 7}$$

$$N_{PIEff} = \max(N - N_{PITh}, 0) \quad \text{Equation 8}$$

P_L	Macro-phytoplankton biomass	(mgC/l)
ϵ_{pl}	Assimilation efficiency	(-)
I_{pl}	Intake rate resources by macro-phytoplankton	(d ⁻¹)
T_{pl}	Mass specific maintenance rate	(d ⁻¹)
M_{pl}	Loss rate due to sedimentation	(d ⁻¹)
Z_L	Meso-zooplankton biomass	(mgC/l)
I_{zpl}	Intake rate macro-phytoplankton by meso-zooplankton	(d ⁻¹)
$I_{pl \max}$	Maximum intake rate	(d ⁻¹)
H_{pl}	Half saturation constant for nitrogen intake	(mgN/l)
N_{PIEff}	Available nitrogen for micro-phytoplankton	(mgN/l)
N_{PITh}	Threshold concentration for nitrogen uptake by micro-phytoplankton	(mgN/l)
N	Nitrogen concentration	(mgN/l)

Micro-zooplankton (<200 µm)

The rate of micro-zooplankton (Z_S) change is determined by growth, maintenance, death and grazing. The growth of micro-zooplankton is determined by the intake rate of phytoplankton (I) and the food assimilation efficiency (ϵ) which express how efficient consumed phytoplankton is converted into biomass. Cell death is expressed as mortality (M) and cell maintenance as (T), both represent the fraction of the micro-zooplankton community that dies or is used for maintenance every day. Micro-zooplankton is subject to grazing itself as well by meso-zooplankton (Matsumura-Tundisi et al.). The grazing rate is depending on the meso-zooplankton (Matsumura-Tundisi et al.) specific ingestion rate which itself depends on the macro-phytoplankton and micro-zooplankton density, see equation 9. The intake rate of micro-phytoplankton is determined by a Holling type II functional response see equation 10.

$$\frac{dZ_S}{dt} = Z_S \cdot (\epsilon_{zs} \cdot I_{zs} - T_{zs} - M_{zs}) - (Z_L \cdot I_{zls}) \quad \text{Equation 9}$$

$$I_{zs} = \frac{P_S \cdot I_{zs \max}}{H_{zs} + P_S} \quad \text{Equation 10}$$

Z_S	Micro-zooplankton biomass	(mgC/l)
ϵ_{zs}	Assimilation efficiency micro-zooplankton	(-)
I_{zs}	Intake rate micro-phytoplankton by micro-zooplankton	(d ⁻¹)
T_{zs}	Mass specific maintenance rate	(d ⁻¹)
M_{zs}	Mortality rate micro-zooplankton	(d ⁻¹)
Z_L	Meso-zooplankton biomass	(mgC/l)

I_{zls}	Intake rate micro-zooplankton by meso-zooplankton	(d ⁻¹)
P_S	Micro-phytoplankton biomass	(mgC/l)
I_{zsmax}	Maximum intake rate of micro-phytoplankton by micro-zooplankton	(d ⁻¹)
H_{zs}	Half saturation constant for phytoplankton intake	(mgC/l)

Meso-zooplankton (>200 µm)

The rate of meso-zooplankton (Matsumura-Tundisi et al.) change is determined by growth, maintenance and death. In the model it is assumed that there is no predation of meso-zooplankton. Cell death is expressed as mortality (M) and cell maintenance as (T), both represent the fraction of the meso-zooplankton community that dies or is used for maintenance every day. The growth of meso-zooplankton is determined by the food assimilation efficiency (ε) and the intake rate of both macro-phytoplankton (I_{pl}) and micro-zooplankton (I_{zs}). Food assimilation efficiency is considered the same for both food sources, see equation 11.

The intake rate of macro-phytoplankton and micro-zooplankton is modelled as a Holling type II functional response depending on both the macro-phytoplankton and micro-zooplankton densities. If the macro-phytoplankton density is high, the main food-source for meso-zooplankton will be phytoplankton, when the micro-zooplankton density becomes high meso-zooplankton will gradually to micro-zooplankton becoming its main food source, see equation 12 and 13.

In the mesocosm experiments, each zooplankton group consists of many species and individuals of different sizes. This has consequences for their food particle size selection which we have chosen, for simplicity, not to deal with in this study.

$$\frac{dZ_L}{dt} = Z_L \cdot (\epsilon_{zl} \cdot (I_{zpl} + I_{zls}) - T_{zl} - M_{zl}) \quad \text{Equation 11}$$

$$I_{zpl} = \frac{P_L \cdot I_{zplmax}}{H_{zpl} + P_L + Z_S} \quad \text{Equation 12}$$

$$I_{zls} = \frac{Z_S \cdot I_{zlsmax}}{H_{zls} + P_L + Z_S} \quad \text{Equation 13}$$

Z_L	Meso-zooplankton biomass	(mgC/l)
ϵ_{zl}	Assimilation efficiency by meso-zooplankton	(-)
I_{zpl}	Intake rate macro-phytoplankton by meso-zooplankton	(d ⁻¹)
I_{zls}	Intake rate micro-zooplankton by meso-zooplankton	(d ⁻¹)
T_{zl}	Mass specific maintenance rate	(d ⁻¹)
M_{zl}	Mortality rate meso-zooplankton	(d ⁻¹)
P_L	Macro-phytoplankton biomass	(mgC/l)
I_{zplmax}	Maximum intake rate macro-phytoplankton by meso-zooplankton	(d ⁻¹)
H_{zs}	Half saturation constant for macro-phytoplankton and micro-zooplankton intake	(mgC/l)
Z_S	Micro-zooplankton biomass	(mgC/l)
I_{zlsmax}	Maximum intake rate micro-zooplankton	(mgC/l)

Parameter values

A literature search was carried out to find initial parameter values which could be used in the model. The result is shown in Table 4.

Table 4: Initial parameter values as found in literature, note: these are not the values used in the modelling work.

Parameter	Symbol	Value	Unit	Reference
<i>Resources</i>				
Flux of nitrogen	N_{flux}	0.015	(mgN/l/d)	(Kristensen and Blackburn 1987)
Conversion factor from C to N	Cf	0.187	(mgN/mgC)	-
<i>Micro-phytoplankton</i>				
Assimilation efficiency micro-phytoplankton	ϵ_{ps}	0.98	(-)	-
Mass specific maintenance rate	T_{ps}	0.0005	(d ⁻¹)	-
Maximal intake rate of resources	$I_{ps\ max}$	2	(d ⁻¹)	(O'Brien 1974)
Half saturation constant for resources intake	H_{ps}	0.008406	(mgN/l)	(Klausmeier et al. 2004)
Loss rate micro-phytoplankton	M_{ps}	0.01	(d ⁻¹)	-
Threshold for micro-phytoplankton	N_{psth}	0.0028	(mgN/l)	(Gentleman and Neuheimer 2008)
<i>Macro-phytoplankton</i>				
Assimilation efficiency macro-phytoplankton	ϵ_{pl}	0.9	(-)	-
Mass specific maintenance rate	T_{pl}	0.0006	(d ⁻¹)	-
Maximal intake rate of resources	$I_{pl\ max}$	2	(d ⁻¹)	(O'Brien 1974)
Half saturation constant for resources intake	H_{pl}	0.008406	(mgN/l)	(Klausmeier et al. 2004)
Loss rate macro-phytoplankton	M_{pl}	0.02	(d ⁻¹)	-
Threshold for micro-phytoplankton	N_{pith}	0.0028	(mgN/l)	(Gentleman and Neuheimer 2008)
<i>Micro-zooplankton</i>				
Assimilation efficiency micro-zooplankton	ϵ_{zs}	0.75	(-)	(Nugraha et al. 2010)
Mass specific maintenance rate	T_{zs}	0.006	(d ⁻¹)	(Yodzis & Innes, 1992)
Mortality rate micro-zooplankton	M_{zs}	0.055	(d ⁻¹)	(Nugraha et al. 2010)
Maximum intake rate of micro-phytoplankton by micro-zooplankton	I_{zsmax}	4	(d ⁻¹)	(Leising et al.)
Half saturation constant for phytoplankton intake	H_{zs}	0.0075	(mgC/l)	(Leising et al.)
<i>Meso-zooplankton</i>				
Assimilation efficiency meso-zooplankton	ϵ_{zl}	0.75	(-)	(Nugraha et al. 2010)
Mass specific maintenance rate	T_{zl}	0.006	(d ⁻¹)	(De Roos et al. 2008)
Mortality rate meso-zooplankton	M_{zl}	0.02	(d ⁻¹)	(Corkett et al. 1979)
Maximum intake rate of macro-phytoplankton by meso-zooplankton	$I_{zsplmax}$	0.17	(d ⁻¹)	(Saage et al. 2009)
Half saturation constant for phytoplankton intake	H_{zpl}	0.027	(mgC/l)	(Saage et al. 2009)
Maximum intake rate micro-zooplankton by meso-zooplankton	$I_{zizsmax}$	1.07	(d ⁻¹)	(Saage et al. 2009)
Half saturation constant for micro-zooplankton intake	H_{zizs}	0.141	(mgC/l)	(Saage et al. 2009)

Not all parameter values could be defined separately. For some parameters the same values were found for the different phytoplankton/zooplankton groups. The parameters were slightly altered with the following conditions, based the hypotheses and conditions described in chapter 4, in mind:

Phytoplankton groups

- Micro-phytoplankton can utilize resources more efficient than macro-zooplankton (*expressed by a lower N -threshold and half-saturation constant*)
- Micro-phytoplankton has lower maintenance cost than macro-phytoplankton
- Micro-phytoplankton has lower background mortality due to lower sedimentation rates
- Macro-phytoplankton has a higher maximum growth rate than micro-phytoplankton

Zooplankton groups

- Micro-zooplankton has higher background mortality than meso-zooplankton
- Micro-zooplankton has higher maximum growth rate than meso-zooplankton
- Micro-zooplankton can become an important food-source for meso-zooplankton

The parameter values as used in the model are presented in Table 5.

Table 5: Parameter values used in the model

Parameter	Symbol	Value	Unit
<i>Resources</i>			
Flux of nitrogen	N_{flux}	0.015	(mgN/l/d)
Conversion factor from C to N	C_f	0.187	(mgN/mgC)
<i>Micro-phytoplankton</i>			
Assimilation efficiency micro-phytoplankton	ϵ_{ps}	0.9	(-)
Mass specific maintenance rate	T_{ps}	0.0008	(d ⁻¹)
Maximal intake rate of resources	I_{ps_max}	1.2	(d ⁻¹)
Half saturation constant for resources intake	H_{ps}	0.01	(mgN/l)
Loss rate micro-phytoplankton	M_{ps}	0.1	(d ⁻¹)
Threshold for micro-phytoplankton	N_{psTH}	0.002	(mgN/l)
<i>Macro-phytoplankton</i>			
Assimilation efficiency macro-phytoplankton	ϵ_{pl}	0.8	(-)
Mass specific maintenance rate	T_{pl}	0.0012	(d ⁻¹)
Maximal intake rate of resources	I_{pl_max}	1.5	(d ⁻¹)
Half saturation constant for resources intake	H_{pl}	0.02	(mgN/l)
Loss rate macro-phytoplankton	M_{pl}	0.2	(d ⁻¹)
Threshold for micro-phytoplankton	N_{plTH}	0.004	(mgN/l)
<i>Micro-zooplankton</i>			
Assimilation efficiency micro-zooplankton	ϵ_{zs}	0.7	(-)
Mass specific maintenance rate	T_{zs}	0.006	(d ⁻¹)
Mortality rate micro-zooplankton	M_{zs}	0.06	(d ⁻¹)
Maximum intake rate of micro-phytoplankton by micro-zooplankton	I_{zsmax}	0.8	(d ⁻¹)
Half saturation constant for phytoplankton intake	H_{zs}	0.0075	(mgC/l)
<i>Meso-zooplankton</i>			
Assimilation efficiency meso-zooplankton	ϵ_{zl}	0.6	(-)
Mass specific maintenance rate	T_{zl}	0.008	(d ⁻¹)
Mortality rate meso-zooplankton	M_{zl}	0.02	(d ⁻¹)
Maximum intake rate of macro-phytoplankton by meso-zooplankton	I_{zslmax}	0.35	(d ⁻¹)
Half saturation constant for phytoplankton intake	H_{zlipl}	0.027	(mgC/l)
Maximum intake rate micro-zooplankton by meso-zooplankton	I_{zlsmax}	0.7	(d ⁻¹)
Half saturation constant for micro-zooplankton intake	H_{zlsz}	0.2	(mgC/l)

Effect of copper

It is assumed that all species which are modelled are equally (negatively) affected by elevated copper concentrations. In the model the intake rate (I) is reduced by a factor (CC) see equation 14. Hence, the presence of copper leads to that a fraction of the food acquired by individuals is 'wasted', and the usable fraction of the intake is reduced. In this way the overall effect for the development of the modelled species could easily be tested for several values for CC. The value for CC is not altered over time since in the mesocosm experiment copper is, in different quantities to obtain different treatments, continuously added throughout the duration of the experiment to obtain a constant copper concentration. We assume that it is this 'background concentration' of copper which determines the magnitude of the effect on intake.

$$I_{with_copper} = I_{xx} \cdot CC \quad \text{Equation 14}$$

I_{with_copper}	Reduced intake rate with the presence of copper	(d ⁻¹)
I_{xx}	Original intake rate without the presence of copper	(d ⁻¹)
CC	Factor at which intake rate is reduced	(-)

6. Development in the mesocosm (blank treatments)

In this chapter the development of the phytoplankton and zooplankton groups as observed in the mesocosm experiment is presented.

Measurement of phyto- and zooplankton

For the determination of the phytoplankton community composition during the experiment, water samples were collected every week. The samples were preserved with Lugol and stored in the dark. Samples collected at days -2, 12, 26, 54 and 82 were analysed by visual microscopic determination and counting of the various taxa Foekema et al., (in prep).

For the determination of the zooplankton community, five water samples of about 1.5 L each were collected using a core water sampler and pooled together per mesocosm. The zooplankton was collected using a 55 µm plankton net and preserved in a formaldehyde solution until visual microscopic analysis. Zooplankton samples collected at days -0, -5, -2, 12, 26, 54 and 82 were analysed Foekema et al., (in prep).

Separation according to size

Phytoplankton is modelled as gram C/l while measured in the experiment as cells/ml, therefore the density is converted using data from Table 6. The phytoplankton community is separated according to their size specified in the model (Figure 1); <8 µm being micro-phytoplankton, >8 µm being macro-phytoplankton, see Table 7.

Table 6: Carbon content of various phytoplankton species.

Species	Carbon content cell (pico gram C/cell)	Reference
Chroococcus turgidus	225*	(Watanabe et al. 2000)
Micro flagellate < 3 µm	0.4	(Menden-Deuer and Lessard 2000)
Medium Flagellate 3-10 µm	100	(Menden-Deuer and Lessard 2000)
Macro flagellates >10 µm	4000	(Menden-Deuer and Lessard 2000)
Nitzschia closterium	1000	-
Peridinium sp.	1270	(Mullin et al. 1966)

* estimated according to Strathmann equation

Table 7: Division of phytoplankton species in two size classes; micro- and macro- phytoplankton.

Species	Size (µm)	Phytoplankton size class
Micro flagellate < 3 µm	< 3	Micro phytoplankton
Medium Flagellate 3-10	3 - 10	Micro phytoplankton
Macro flagellates >10 µm	> 10	Macro phytoplankton
Nitzschia closterium	33	Macro phytoplankton
Peridinium sp.	45	Macro phytoplankton
Chroococcus turgidus	8 - 32	Macro phytoplankton

The zooplankton community is separated into micro-zooplankton, being <200 µm in size, and meso-zooplankton, being >200 µm in size. The zooplankton community is measured as individuals per liter while modelled as gram C/l, therefore also the zooplankton density is converted, see Table 8.

Table 8: Division of zooplankton species in size two classes; micro-, and meso-zooplankton.

Species	size (μm)	Carbon ($\mu\text{gC/indv}$)	Reference*	Zooplankton size class
Keratella cochlearis	100 - 150	0.014	(Telesh et al. 1998)	Micro-zoopl.
Keratella quadrata	180 - 220	0.058	(Telesh et al. 1998)	Micro-zoopl.
Mytilina sp?	150	0.036	-	Micro-zoopl.
Acartia clausi	880	2.19	(Cataletto and F. Umani 1994)	Meso-zoopl.
Bivalve larvae		3.51	-	Meso-zoopl.
Centropagus hamatipes	+/- 1000	11.0	(Costa et al. 2006)	Meso-zoopl.
Cladocera species (Podon)	0 - > 5000	1	(Bamstedt 1998)	Meso-zoopl.
copepoda nauplii	150 - 350	0.54	(Fernández 1979)	Meso-zoopl.
copepodites		3.51	-	Meso-zoopl.
Cypris larvae	200 - 300	3.51	-	Meso-zoopl.
Gastropoda larvae	650	3.51	-	Meso-zoopl.
Harpacticide copepoda	650	2	(Bamstedt 1998)	Meso-zoopl.
Nematodes	500	3.51	-	Meso-zoopl.
Ostracode sp.		2	(Bamstedt 1998)	Meso-zoopl.
Polychaeta larvae	200 - 1200	3.51	-	Meso-zoopl.
Temora longicornis	1000 - 1350	3.51	-	Meso-zoopl.

* Reference for carbon content. '-' means no data could be found about the carbon content, instead an carbon content of 3.51 $\mu\text{gC/individual}$ was used in case of the meso-zooplankton and 0.036 $\mu\text{gC/individual}$ for the micro-zooplankton. This are average values calculated from the species were the carbon content was found in literature.

7. Model results

Both model outcome for the blank treatments and for the treatments with elevated copper concentrations are presented in this chapter.

Blank treatments

The modelled development of the phytoplankton and zooplankton groups in the blank treatments (without elevated copper concentrations) over a duration of 100 days calculated and compared to results from the mesocosm experiments. Because in the experiment the three replicas had different start conditions each replica is modelled individually and compared to model output.

Model outcome for blank treatment 1

Initial values are set as found by mesocosm blank treatment 1, see Table 9. Figure 2 and Figure 3 show both measured and model results for the first 100 days.

Table 9: Initial values of mesocosm blank treatment 1 as found in the mesocosm data.

Parameter	Symbol	Value	Unit
Nitrogen	N	0.6	mgN/l
micro-phytoplankton	P _S	1.4	mgC/l
macro-phytoplankton	P _L	2.5	mgC/l
micro-zooplankton	Z _S	0.00001*	mgC/l
meso-zooplankton	Z _L	0.21	mgC/l

* there wasn't found any micro-zooplankton, therefore a very low value of 0.00001 mgC/l is used.

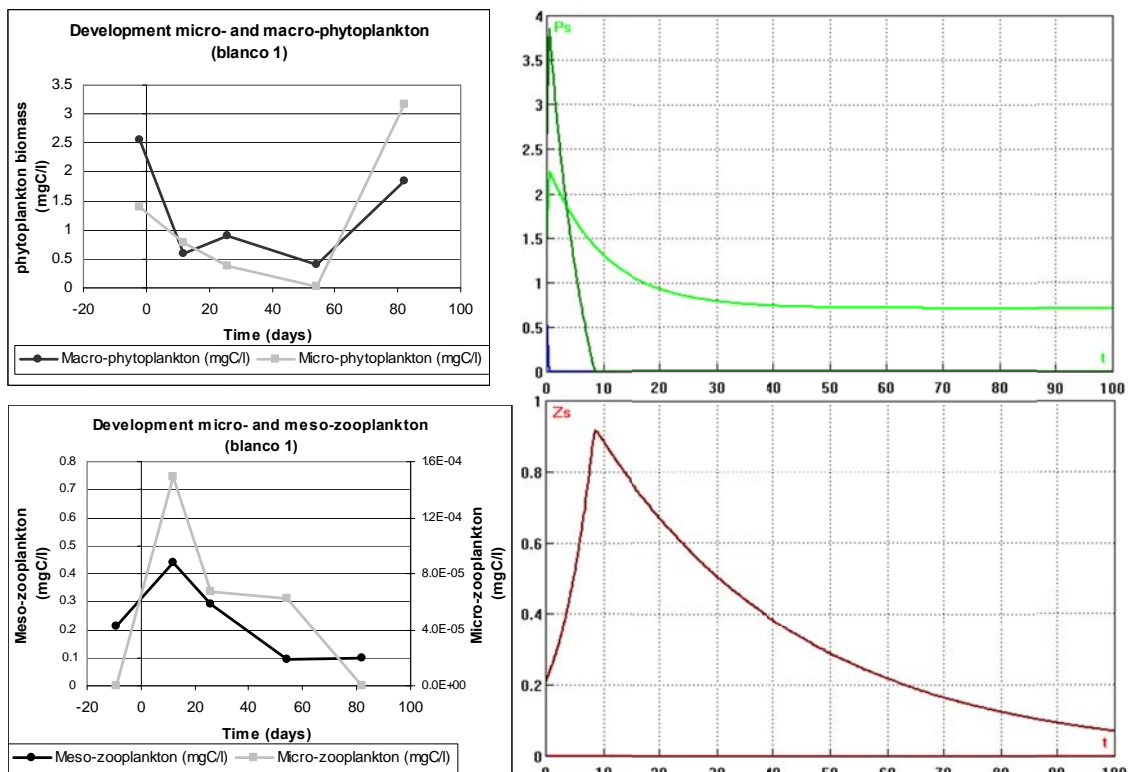


Figure 2: Measured values (left graphs) and modelled results (right graphs) for the first 100 days of mesocosm 1. Top graph micro-phytoplankton (light green line) and macro-phytoplankton (dark green line). Bottom graph shows zooplankton groups, meso-zooplankton (dark red line), micro-zooplankton (light red line). Both modelled as observed biomass expressed as mgC/l.

Model results for phytoplankton fluctuations show a peak in both micro- and macro-phytoplankton after one day. Micro-phytoplankton stabilizes after 40 days to a density of 0.7 mgC/l while macro-phytoplankton density decline to very low levels. Measured phytoplankton communities show an initial decrease of both micro- and macro-phytoplankton. The lowest density were observed at day 54, in the last measurement at day 82, the phytoplankton densities have increased greatly.

Model results for zooplankton fluctuations show an increase of meso-zooplankton just before day 10, moving to a more or less stable density of around 0.1 mgC/l. This corresponds well with measured meso-zooplankton, only the peak in density is less pronounced (this peak could have been missed due to the low frequency of measurements). When zooming in on the micro-zooplankton community, see Figure 3, a peak in density can be observed at day 6 after the micro-zooplankton density drop to very low densities. The peak in micro-zooplankton is also observed in data from the mesocosm experiment, but the density doesn't drop as fast and to such low levels in the mesocosm.

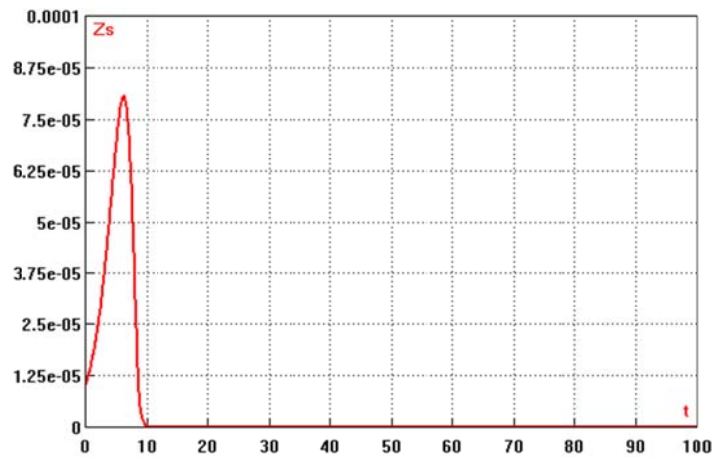


Figure 3: Fluctuation of the micro-zooplankton community (in mgC/l) for the first 100 days, blank treatment 1.

Model output blank treatment 2

Initial values are set as found by mesocosm blank treatment 2, see Table 10. Figure 4 and Figure 5 show both measured and model results for the first 100 days.

Table 10: Initial values of mesocosm blank treatment 2 as found in the mesocosm data.

Parameter	Symbol	Value	Unit
Nitrogen	N	0.6	mgN/l
micro-phytoplankton	P_s	1.33	mgC/l
macro-phytoplankton	P_L	0.62	mgC/l
micro-zooplankton	Z_s	0.0000528	mgC/l
meso-zooplankton	Z_L	0.37	mgC/l

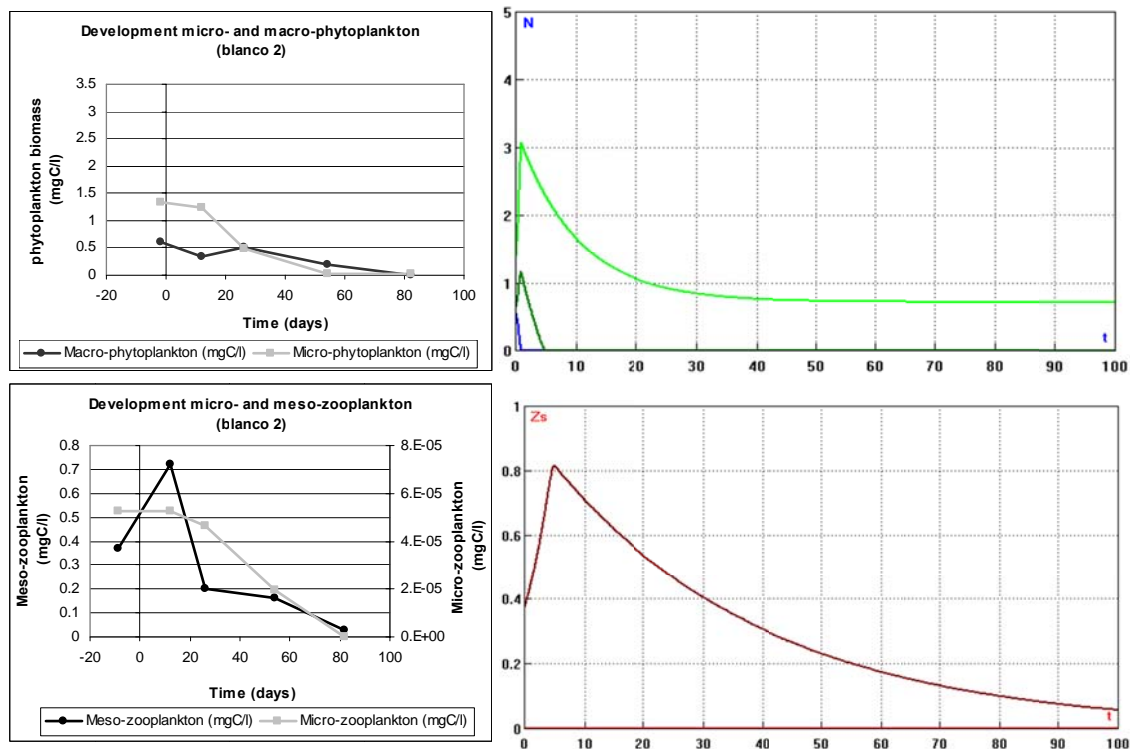


Figure 4: Measured values (left graphs) and modelled results (right graphs) for the first 100 days of mesocosm 2. Top graph micro-phytoplankton (light green line) and macro-phytoplankton (dark green line). Bottom graph shows zooplankton groups, meso-zooplankton (dark red line), micro-zooplankton (light red line). Both modelled as observed biomass is expressed as mgC/l.

Model results show first an increase in both micro- and macro-phytoplankton densities followed by a decrease. The micro-phytoplankton community becomes stable with a density of around 0.8 mgC/l after 40 – 50 days. Measured phytoplankton densities show also a stabilizing micro-phytoplankton but with much lower densities. No peak in micro- and macro-phytoplankton is measured.

Model results show a meso-zooplankton peak at around the 5th day and decrease densities afterwards. The micro-zooplankton community is declining rapidly from the start to very low densities. For meso-zooplankton the same trend is observed in the mesocosm, including the peak in macro-zooplankton (although occurring later, around the 15th day). When zooming in on the micro-zooplankton a peak in density is found after the 3rd day after which micro-zooplankton community declines to near extinction, see Figure 5.

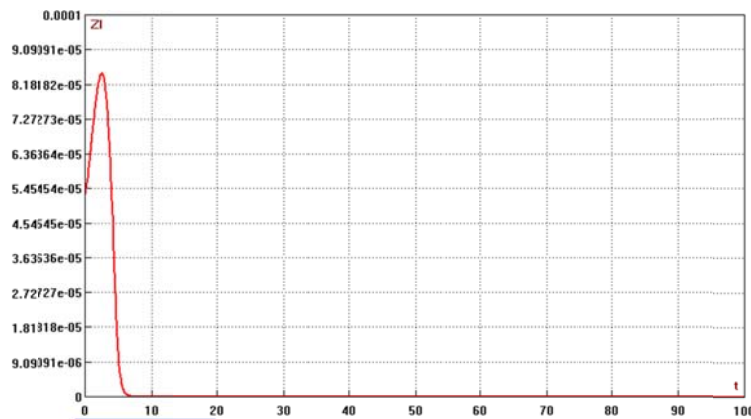


Figure 5: Fluctuation of the micro-zooplankton community (in mgC/l) for the first 100 days, blank treatment 2.

Model output blank treatment 3

Initial values are set as found by mesocosm blank treatment 3, see Table 11. Figure 6 and Figure 7 show both measured and modelled results for the first 100 days.

Table 11: Initial values of mesocosm blank treatment 3 as found in the mesocosm data.

Parameter	Symbol	Value	Unit
Nitrogen	N	0.73	mgN/l
micro-phytoplankton	Ps	0*	mgC/l
macro-phytoplankton	Pl	1.7	mgC/l
micro-zooplankton	Zs	0.000013	mgC/l
meso-zooplankton	Zl	0.25	mgC/l

* There was no micro-phytoplankton present.

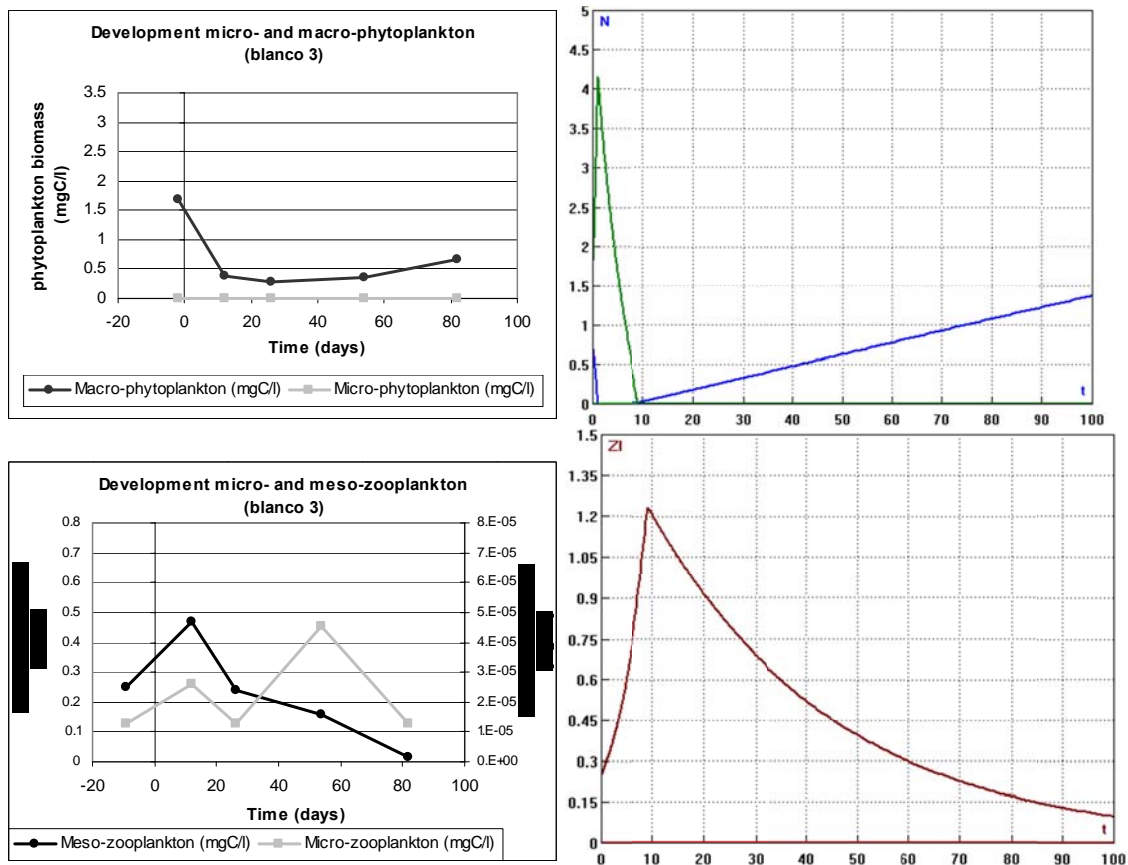


Figure 6: Measured values (left graphs) and modelled results (right graphs) for the first 100 days of mesocosm 3. Top graph micro-phytoplankton (light green line) and macro-phytoplankton (dark green line). Bottom graph shows zooplankton groups, meso-zooplankton (dark red line), micro-zooplankton (light red line). Both modelled as observed biomass is expressed as mgC/l.

As can be seen in Figure 6 the macro-phytoplankton density declines in the model output due to zooplankton predation. Since no micro-phytoplankton is present the micro-zooplankton cannot exist. Modelled micro-zooplankton density declines rapidly to extinction, see Figure 7.

Mesocosms results show an increase in macro-phytoplankton after day 50, this is not observed in model output. The micro-zooplankton community can even increase while model output show extinction. This is due to the model-set up where micro-zooplankton only feeds upon micro-phytoplankton.

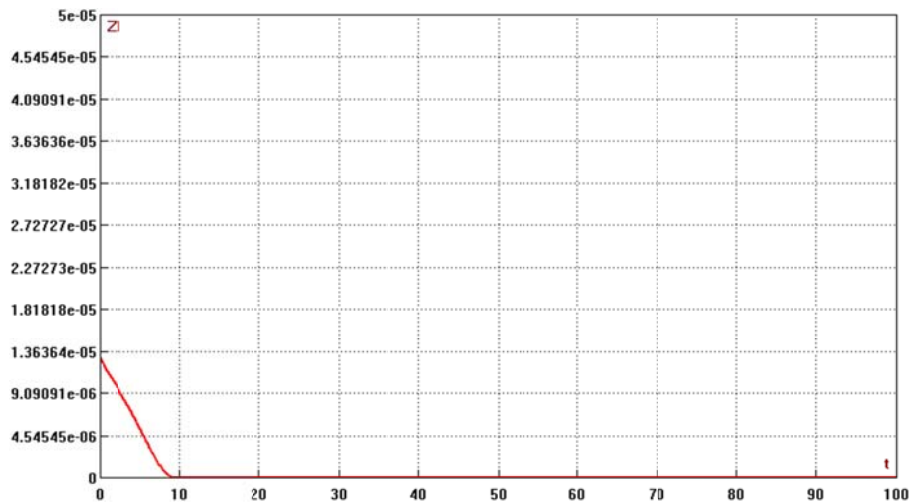


Figure 7: Fluctuation of the micro-zooplankton community (in mgC/l) for the first 100 days, blank treatment 3.

Equilibrium

When the time is extended stable limit cycles of the modelled system can be explored. In the situation where all phytoplankton species are present (blank treatment 1 and 2) the equilibrium situation is reached after around 400 - 600 days. At the equilibrium point no macro-phytoplankton can exist. It will not win the competition for nutrients from the micro-phytoplankton and is effectively grazed down by meso-zooplankton. There are stable micro-phytoplankton and micro-/meso zooplankton oscillations, see Figure 8.

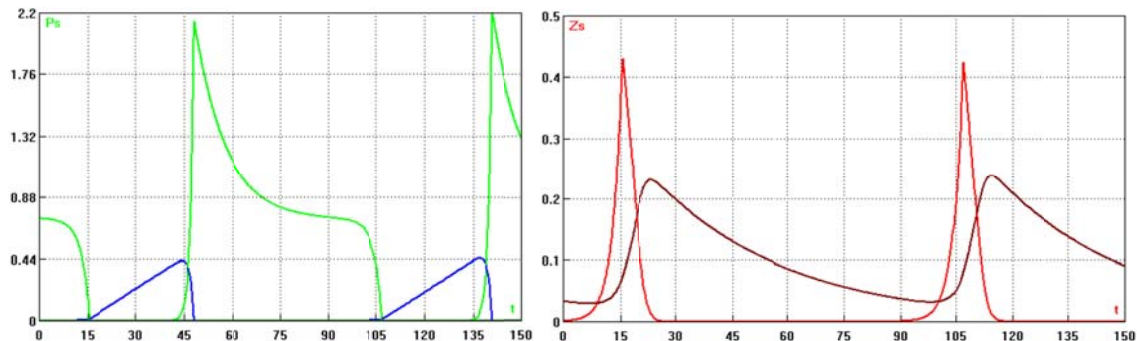


Figure 8: Stable limit cycles of the micro-phytoplankton, micro- and meso-zooplankton communities in the 'equilibrium' situation.

Without the presence of micro-phytoplankton also micro-zooplankton cannot exist (situation in mesocosm blank 3). Figure 9 shows stable oscillations with macro-phytoplankton and meso-zooplankton in the stable limit cycles.

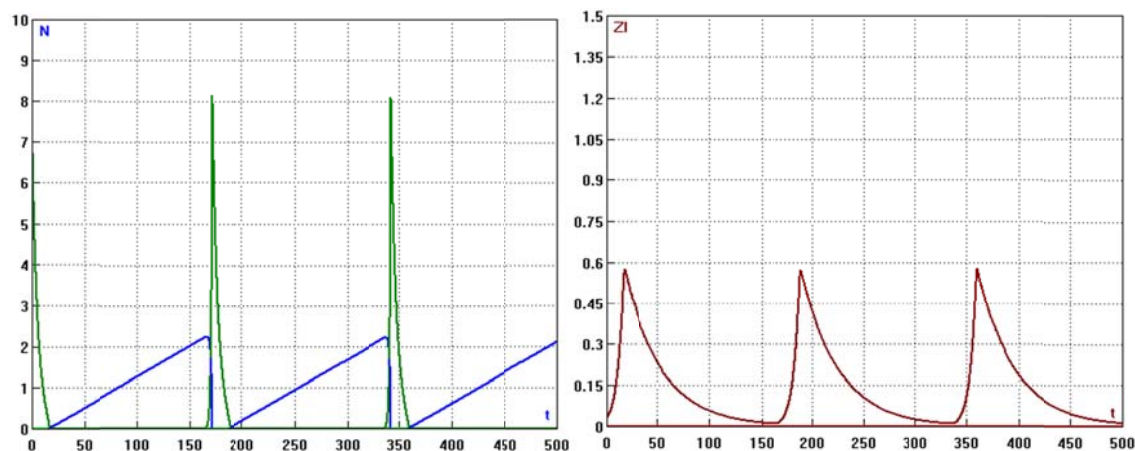


Figure 9: Stable limit cycles of the macro-phytoplankton and meso-zooplankton communities when no micro phytoplankton is present.

Treatments with elevated copper concentration

Copper has a direct negative effect on the plankton communities. However due to food web interactions the effect on specific groups can be positive (when predation pressure or competition is reduced). Based on simple food web interactions we can hypothesize ' the food web level effect of copper.

The meso-zooplankton community (Z_S) is negatively affected as a direct effect of copper. Since this group does not suffer losses due to predation in the model no positive food web interaction can take place resulting in a negative effect for all treatments, see also overview in Table 12. Due to the negative copper effect for meso-zooplankton, densities are lower and predation pressure on both macro-phytoplankton (P_L) and micro-zooplankton (Z_S) decline for all scenarios. Under low copper concentration, this food web effected might outweigh the negative copper effect that all groups of species suffer equally, in the end resulting in better survival conditions for both macro-phytoplankton and micro-zooplankton (indicated as '+/-' in Table 12). Under these conditions the micro-phytoplankton community is expected to suffer due to a higher density of micro-zooplankton, increasing predation pressure on top of the direct negative copper effect. In the other extreme, in the 'high' copper treatment, it is expected that the negative effect of copper on the individual group of species is such that this cannot be compensated for by positive food web interactions resulting in negative results for all groups of species. In intermediate copper conditions however micro-phytoplankton might experience an overall positive effect. The reasoning behind this is as follows: micro-zooplankton densities decline because the positive food web effect is overruled by the negative copper effect. Lower micro-zooplankton densities result in lower predation pressure for micro-phytoplankton overall resulting in a positive effect.

Table 12: Hypothesis on the overall effect of copper for the different plankton communities. '-' means overall negative affect, '+/-' indicates that an overall positive effect might be possible.

Species/Cu-level	Low	Intermediate	High
Meso-zooplankton	-	-	-
Macro-phytoplankton	+/-	-	-
Micro-zooplankton	+/-	-	-
Micro-phytoplankton	-	+/-	-

Development of phytoplankton and zooplankton in mesocosm experiment

In the experiment five different copper concentrations were tested, 2.9, 5.7, 9.9, 16 and 31 $\mu\text{g/l}$. The development (average of the 3 replica treatments) of the phyto- and zooplankton community of the 2.9, 9.9 and 31 $\mu\text{g/l}$ treatments are shown in Figure 10.

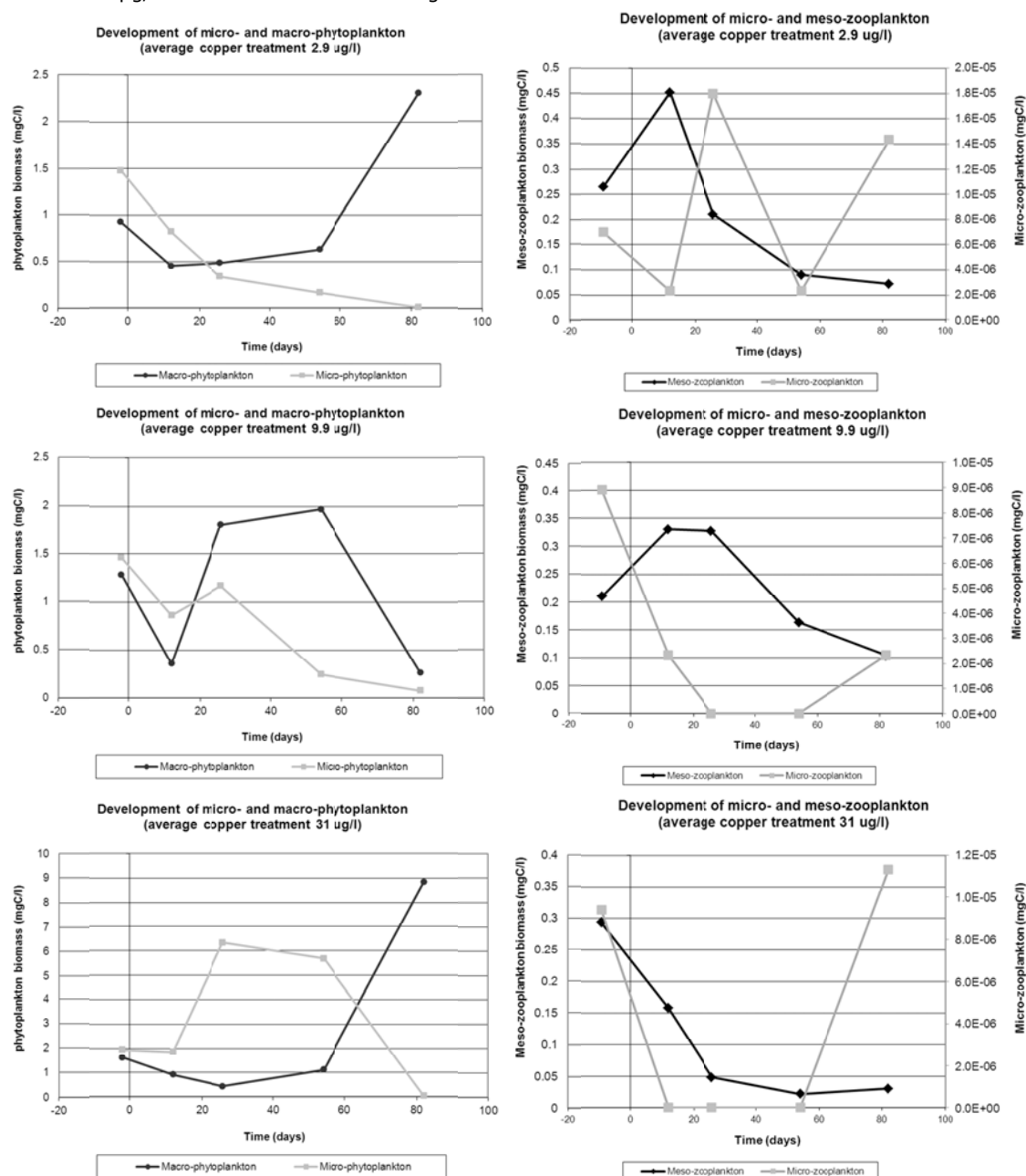


Figure 10: Development of phytoplankton (graphs on the left) and zooplankton (graphs on the right) in the mesocosm experiment under elevated copper concentrations. Average copper concentration of 2.9 $\mu\text{g/l}$ in upper graphs, average copper concentration of 9.9 $\mu\text{g/l}$ in middle graphs, average copper concentration of 31 $\mu\text{g/l}$ in bottom graphs. Graphs show average values of the replicates

As can be seen in Figure 10 the starting point for the phytoplankton community is approximately the same, a little bit more micro-phytoplankton than macro-phytoplankton. In the lowest copper treatment tested (2.9 µg/l) micro-phytoplankton declines gradually to near extinction. In this treatment meso-zooplankton shows a small peak after which it declines as well to very low concentrations while micro-zooplankton biomass fluctuates. Macro-phytoplankton can re-establish itself (after day 54) which could be due to lower grazing pressure.

In the 9.9 µg/l copper treatment the micro-phytoplankton declines gradually as well but the macro-phytoplankton seems to behave differently with a peak in biomass between day 20 – 60 with very low biomass as well on day 82. Meso-zooplankton shows a peak in between day 12 and 26 although less high compared to the 2.9 µg/l treatment, after this peak the declines gradually while micro-zooplankton declines rapidly from the beginning showing a small increase at the end.

In the 31 µg/l copper treatment micro-phytoplankton shows a peak in biomass in between day 20 – 60 but declines near to extinction at the end of the experiment. Macro-phytoplankton biomass declines from the beginning but can increase at the end of the experiment (day 82) to even very high concentrations namely 8.9 mgC/l. Both zooplankton groups decline rapidly in biomass from the beginning, no peak is observed, although micro-zooplankton biomass is able to increase at the end.

Model output for increased copper concentration

The effect of copper on the phyto-/zooplankton development is modelled as well. The influence of copper is incorporated into the model via the factor CC (see chapter 5), reducing (when below 1) the usable fraction of food which is taken up by the organisms (I) equally for all four groups of species.

To explore if a small (copper) effect could be enlarged via food web interactions and if a large effect might be reduced three situations were simulated: A slight effect of copper (factor CC = 0.95), a large effect of copper (factor CC = 0.3) and a situation in between (factor CC = 0.5).

The starting point for all three situations with elevated copper concentration were similar, the average biomass for the copper treatments was taken as found after the acclimatization period, see Table 13. Development of the (modelled) phytoplankton and zooplankton biomass can be seen in Figure 11 and Figure 12.

Table 13: Initial values set in the model.

Parameter	Symbol	Value	Unit
Nitrogen	N	0.73	mgN/l
micro-phytoplankton	P _S	1.6	mgC/l
macro-phytoplankton	P _L	1.3	mgC/l
micro-zooplanktom	Z _S	0.0000084	mgC/l
meso-zooplankton	Z _L	0.26	mgC/l

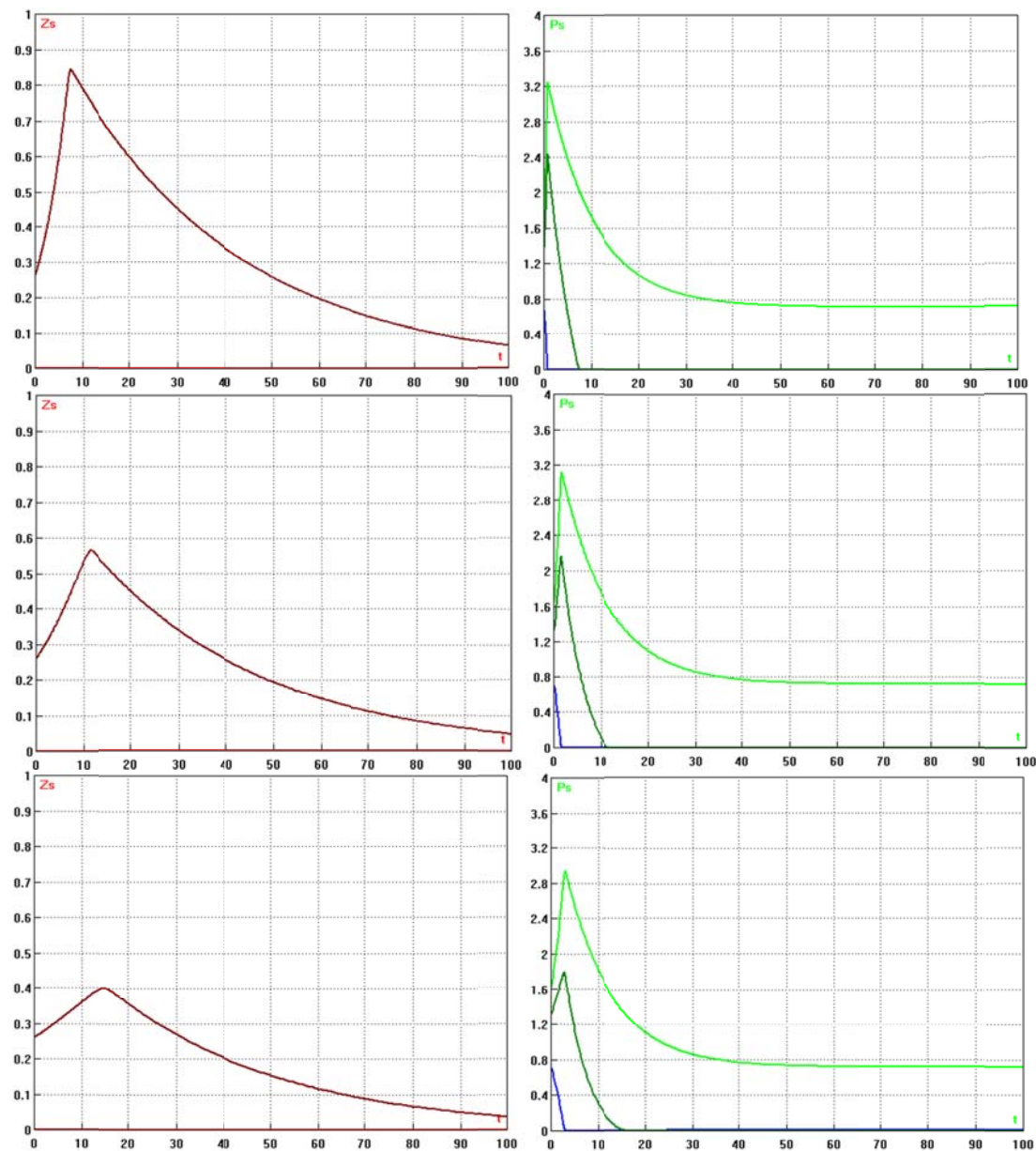


Figure 11: Modelled effect of copper, development of meso-zooplankton (left graphs) and phytoplankton (right graphs). Micro-phytoplankton (light green lines), macro-phytoplankton (dark green lines). Upper graphs represent the situation with factor CC of 0.95 (representing a minor copper influence), middle graphs the CC factor is 0.5 and in the bottom graphs the CC factor was set at 0.3 (representing major copper influence).

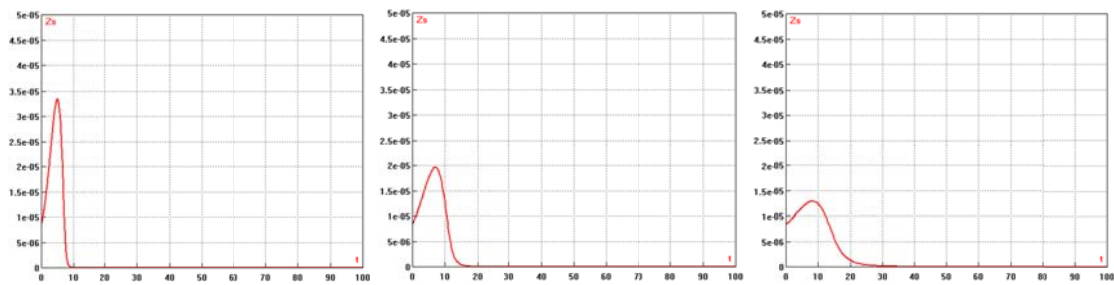


Figure 12: Development of micro-zooplankton at different copper influence intensity. Factor CC is set at 0.95 in the left graph, at 0.5 in the middle graph and at 0.3 on the right graph.

As can be seen in Figure 11 and Figure 12 the peak in zooplankton (both micro and meso) is, although present, less pronounced with increasing copper influence. Between the high ($CC=0.3$) and low ($CC = 0.95$) copper effect the peak is reduced by more than a factor 2. The peaks are also occurring somewhat later in time by increasing copper influence. The phytoplankton peaks show the same pattern (smaller and later peaks by increasing copper influence) but the decline in the peak is less pronounced than for the zooplankton groups. Between the two most extreme situations only a difference of about 0.9 in peak intensity is observed for the micro-phytoplankton and 0.75 for the macro-phytoplankton. The phytoplankton seems thereby less negatively affected by the copper than the zooplankton. Next to the direct (negative) effect, a food web effect (less grazing pressure), results overall in suppressed copper effects for the phytoplankton groups.

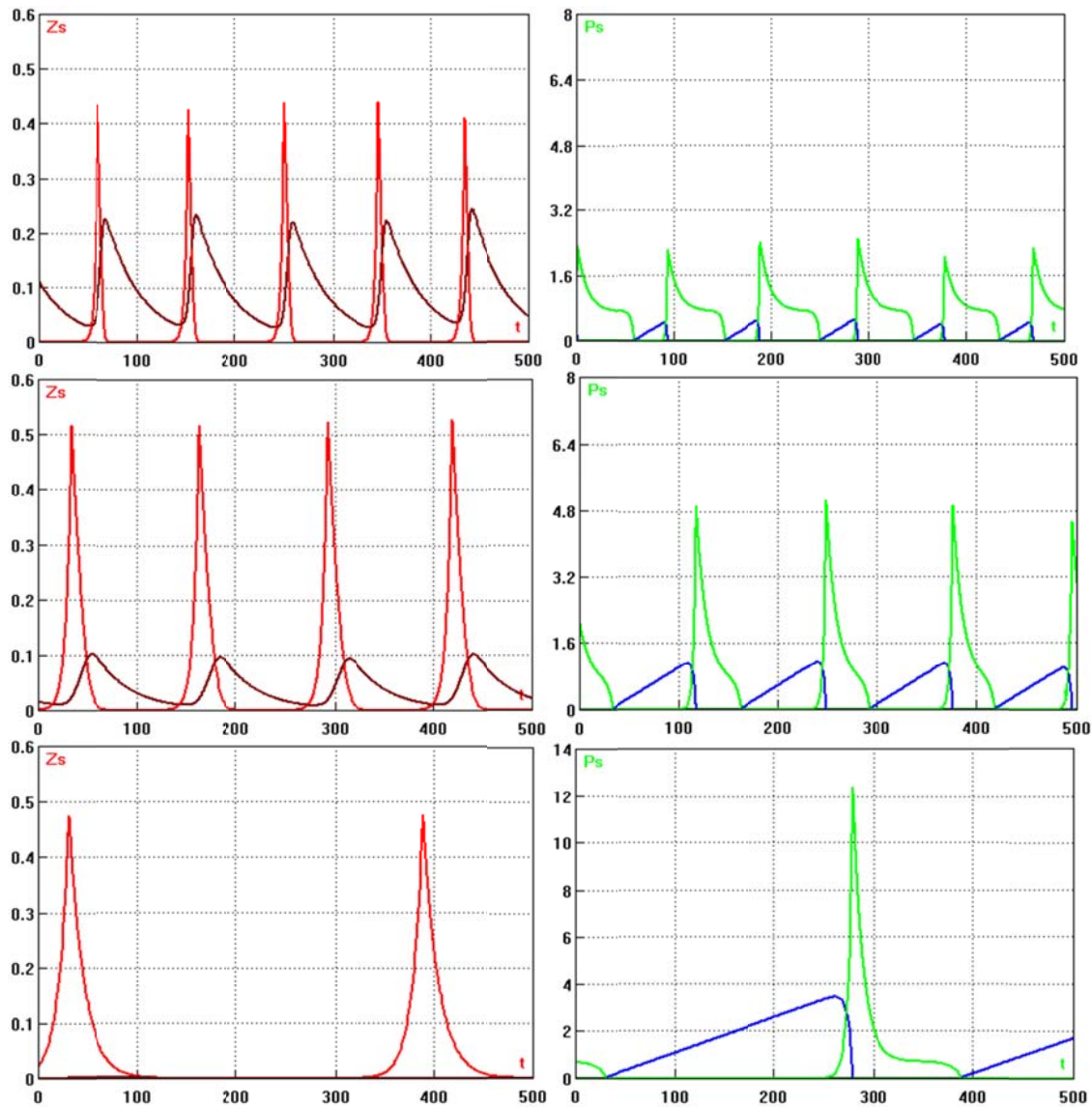


Figure 13: Stable oscillations for zooplankton (left graphs) and phytoplankton (right graphs) for the different copper treatments. Meso-plankton (dark red lines), micro-zooplankton (light red lines) in left graphs, resources (blue lines) and micro-phytoplankton (light green lines) in right graphs. Upper graphs represent the situation with factor CC of 0.95 (small copper effect), middle graphs the CC factor is 0.5 (intermediate effect) and in the bottom graphs the CC factor was set at 0.3 (large copper effect).

In Figure 13 the stable oscillations are shown for the different copper treatments. In none of the treatments macro-phytoplankton can exist (was also observed equilibrium situation for the blank treatments). With increasing copper influence peaks are becoming more extreme and repeating cycles become longer. In the small and intermediate copper treatments ($CC = 0.95$ and 0.5) a peak in micro-phytoplankton is followed by a peak in micro-phytoplankton that can support a meso-zooplankton population. In the highest copper situation ($CC = 0.3$) meso-zooplankton cannot exist anymore.

8. Conclusion & Discussion

Relations were made as simple as possible in the model, only the major processes were incorporated. For instance meso-zooplankton is not able to consume micro-phytoplankton in the model. In reality this division will probably not be so strict. Other processes that will influence phytoplankton development were excluded such as weather conditions (temperature, light intensity etc.) and the influence of seasons. These processes affect nutrient- and light availability and thereby the development of the different groups of species in the mesocosms. But the goal of this study was not to incorporate all processes that could be important and predict the development of the different species with great quantitative accuracy but to investigate major trends in development and possible food web effects by exposure to elevated copper concentrations. Constructing a 'minimal model', leaving out all unnecessary processes, made it easier to understand observed change in model output by changing parameter values (copper effect) and initial conditions (blank treatments).

The model was able to simulate the major direction of the phyto- and zooplankton development as observed in the blank treatments despite its simple set up. Initial peaks in the different groups and the decline of the species observed in the blank treatment were both predicted by the model. What the model couldn't predict was the observed increase in phytoplankton after day 80 or so. An increase eventually occurred in the model, but after a much longer time than observed in the mesocosms (as can be seen in the equilibrium situation). Investigating the stable limit cycles, macro-phytoplankton was not able to sustain itself. Only when no micro-phytoplankton was present, macro-phytoplankton was able to exist in the stable limit cycles (blank treatment 3). In reality macro-phytoplankton is able to sustain itself also with the presence of micro-phytoplankton. The reason for this could be that in the model seasonal influences, that set the system back in succession, are not incorporated.

The effect of copper was incorporated into the model affecting each modelled group of species equally by reducing the food intake (I) by a copper factor (CC). To investigate if food web effects were occurring three situations were modelled; a low copper effect ($CC = 0.95$), a high copper effect ($CC = 0.3$) and a situation in between ($CC = 0.5$).

Model results show that both phytoplankton and zooplankton groups were affected by the presence of copper, resulting in lower biomass. Although the direct effect was the same for each group of species, the zooplankton groups were affected more than the phytoplankton groups. When the 'low' copper treatment was compared to the 'high' copper treatment peaks in zooplankton biomass were decreased by a factor 0.5, while peaks in phytoplankton were reduced by only a factor 0.75 – 0.9. A food web effect was thereby found; it seems that direct negative effect of the copper on the food intake by phytoplankton was more or less compensated for by the decrease in predation pressure by zooplankton. At the highest copper effect modelled, meso-zooplankton was no longer able to sustain itself. By increasing copper effects peaks in micro-phytoplankton become higher and oscillations become longer as well.

A sharp decline in meso-zooplankton was also observed in the mesocosm experiment under the highest copper treatment. Micro-zooplankton was able to increase in biomass at this treatment while meso-zooplankton was not, corresponding with model output. Macro-phytoplankton was also able to re-establish itself in the experiment, this was not observed in model output. This could be due to spatial complexity not incorporated into the model. Some macro-phytoplankton could be escaped from predation pressure by its specific location in the system.

Overall it can be concluded that the model, although very simple in its set-up, is able to predict the development of the plankton species reasonably well according to the data measured in the mesocosm experiment for both the blank- and the copper treatments. We believe that this preliminary model is a

useful tool to study food web effects (for plankton species) resulting from pressures such as elevated copper concentrations.

Recommendation for further research

In order to extend our knowledge about food web effects of elevated copper concentrations and to develop the model further a thorough literature review and data analysis is proposed to investigate the importance of the assumed interactions made here. A literature review will help to understand the mechanisms in which copper affects the different plankton species. This might lead to a different separation of the plankton groups as is made currently in this study. Instead groups could be divided for instance in the way they feed (filter feeders versus predators) or according to the same toxic mechanism in which they are affected by the copper. Once groups are defined based on new insight an extended data analysis can be performed to check these assumptions with observed data from the mesocosms. Questions that could be answered are: What aspects underline the increase or decline in biomass for certain species under elevated copper concentrations? Are observed peaks in biomass a result of the development of one single species? And if so what kind of species is it and how is it dealing with the copper. After the literature review and data analysis the model can be altered according to the newly obtained insight.

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Justification

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

Approved: Dr. T. Schellekens
Researcher



Signature:

Date: 8th of March 2011

Approved: Drs. F.C. Groenedijk
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Date: 8th of March 2011