

LINKING CARBON-NITROGEN-PHOSPHORUS CYCLE AND FOODWEB MODELS OF AN ESTUARINE LAGOON ECOSYSTEM

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Abstract. In this study, an NPZD model and a trophic network model that contains organism groups on the higher trophic levels were developed and linked using the “bottom-up control” approach. Such a linkage of models provides the possibility to use the advantages of both models; reproducing of the erratic behaviour of nutrients and plankton as realistic as possible, while still taking the more complex organisms in the trophic network, which respond to external forcing in a larger time scale. The models developed in this study were applied to the Curonian Lagoon that is an important estuarine ecosystem for Lithuania. The tests and simulations have proven that the results of the NPZD model were accurate enough for representing the nutrient and phytoplankton dynamics in the Curonian Lagoon as well as spatial differences which are of ecological interest. Linkage with trophic network model demonstrated NPZD model results to be consistent with the Curonian Lagoons ecosystem. The modelling results showed that primary production is relatively high in the Curonian Lagoon and is unlikely to be controlled by the organisms that are on the higher trophic levels of the food web. Analysis of the NPZD model scenarios with different nutrients inputs revealed that phosphorus is the main limiting nutrient for primary production in the Curonian Lagoon. However, different combinations of nitrogen and phosphorus inputs control the relative abundance of different phytoplankton groups. Investigation of reaction of ecosystem to water temperature increase showed that the temperature increase finally leads to decrease of available phytoplankton to upper levels of the food web.

1. Introduction

Among aquatic ecosystems, estuarine lagoons are generally more complex than inland waters because of the combined effect of the land and the sea. These systems are under the influence of land through the rivers and have a restricted and temporally variable water exchange with the seas or the oceans. Estuarine lagoons are generally productive ecosystems, which offer habitats for many species. Many coastal and estuarine lagoons are known to be important components of the natural capital providing opportunities for aquaculture. These ecosystems are difficult to analyze. Like most of the transitional waters, their trophic and ecological status cannot be defined easily because of their complexity. Most of them are usually under strong human influence or already modified heavily, which

makes this task even more difficult. Nutrient Phytoplankton Zooplankton Detritus (NPZD) models can help scientists to analyze the full picture of an aquatic system, together with physical, chemical and biological processes focused on carbon, nitrogen and phosphorus cycles, to fill in the gaps of data between samplings and to forecast environmental changes and use this output for planning. Traditionally, these models have been developed and used by engineers extensively, usually with the aim of water resources and quality management. However, different needs may arise in ecological studies with different aims such as better understanding how an aquatic ecosystem works or analyze the interactions in an aquatic food web. In this case, different state variables may be needed than the conventional ones, which are used by more general water quality models that are available. In ecological studies, related to coastal lagoon ecosystems organism groups on the higher trophic levels can be of interest.

The Curonian Lagoon is an estuarine lagoon located in Lithuanian and Russian Federations territory latitude N 55°30' and longitude E 21°15' (Fig. 1). It is a shallow estuarine lagoon, connected to the south-eastern Baltic Sea through the narrow Klaipėda Strait (Fig. 2). The narrow sandy Curonian spit separates the Curonian lagoon from the Baltic Sea. The lagoon is of triangular shape with a surface area of 1584 km². The broadest part, up to 46 km wide, is in the southern part of the lagoon; while in the most northern part (Klaipėda Strait) is only 550 m wide. The length from the southern to the northern part is more than 90 km (Umgiesser et al., 2004a).

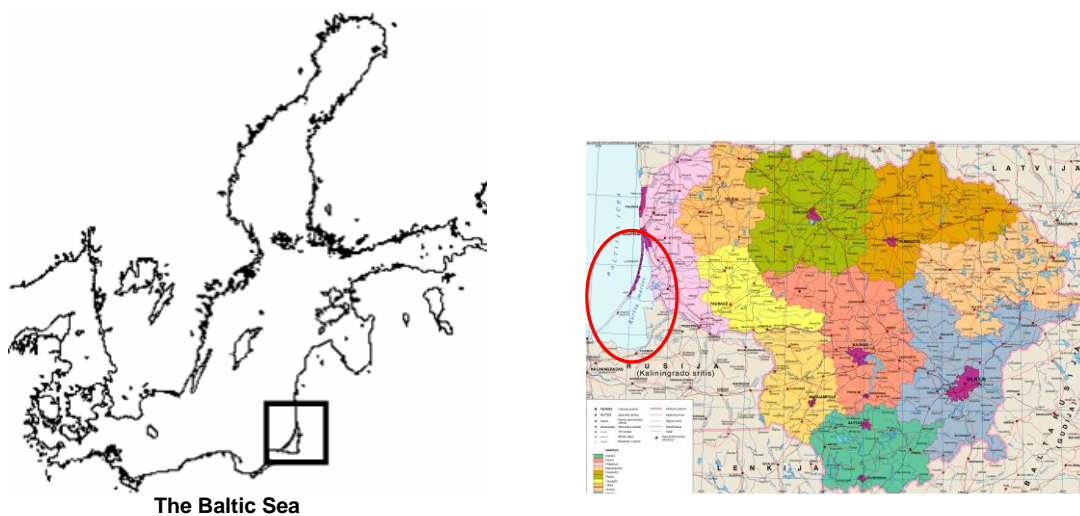


Figure 1. Location of the Curonian Lagoon

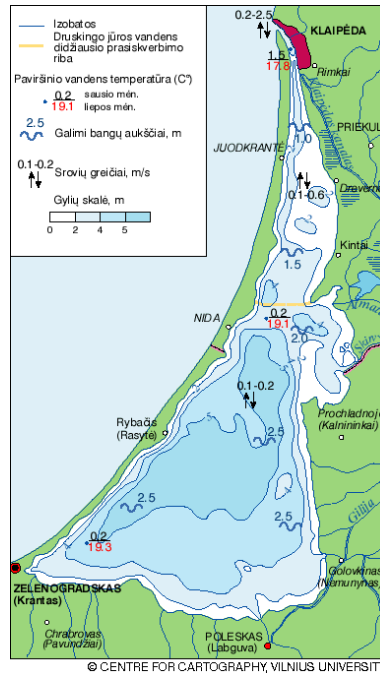


Figure 2. Curonian Lagoon and its vicinity

The lagoon is very shallow with a mean depth of 3.8 m; while the maximum depth reaches 5.8 m in the southern part and 10-14 m in the artificially deepened Klaipėda Strait harbour area. The lagoon has a volume of approximately 6.2 km³ (Ferrarin et al., 2004). It is an important water body for Lithuania, especially for the western part because of its productivity, contribution to fishery and the recreational value.

Like most of the other temperate estuarine lagoons, the Curonian lagoon has a relatively dynamic ecosystem that is complex to analyze. Biogeochemical models can help scientists to analyze the full picture of an aquatic system, together with physical, chemical and biological processes. They are also useful to fill in the gaps of data between two samplings. Another advantage using the models is the opportunity to forecast environmental changes and use this output for planning and management. Traditionally, these models have been developed and used by engineers extensively, usually with the aim of water resources and quality management. However, different needs may arise in ecological studies with different aims such as better understanding how an aquatic ecosystem works or analyze the interactions in an aquatic food web. In this case, different state variables may be needed than the conventional ones, which are used by more general water quality models that are available. In ecological studies, organism groups on the higher trophic levels can be of interest. In this case, two types of control approached could be used of the “top-down control” or “the bottom-up control” approaches. The prior necessitates simulating all the organism groups in one model. The latter approach provides the possibility to run the biogeochemical or NPZD (Nutrient Phytoplankton, Zooplankton and Detritus) models first and use their results as inputs to trophic network models, which contain organism groups on the higher trophic levels. Such a linkage of models provides the possibility to use the advantages of both models; reproducing of the erratic behaviour of nutrients and

plankton as realistic as possible, while still taking the more complex organisms in the trophic network, which respond to external forcing in a larger time scale.

Several ecological studies are made in the Curonian Lagoon (Gasiūnaitė et al., 2004; Razinkovas et al., 2005; Pilkaitytė and Razinkovas, 2006, 2007). Several ecological models were developed for the Curonian Lagoon as well. A trophic network model was developed by Razinkovas and Zemlys (2000) for the Curonian Lagoon using Ecopath (Christensen et al., 2000) to generate mass balance for the organic matter. The same version of Ecopath was also utilized by Jankauskienė (2001) for investigating the trophic relations of the ponto-caspian, higher crustaceans and fish larvae in the litoral zone of the Curonian Lagoon. Hydrodynamic models were developed for the Curonian Lagoon by Davulienė et al. (2002), Ferrarin et al. (2007) and Raudsepp and Kouts (2002). An ecological model was developed by Zemlys et al. (2003) to simulate the effect of the pre-ingestive selection efficiency for suspension feeding bivalves on the material fluxes.

Even though, several transport and ecological modelling studies had been already conducted for the Curonian Lagoon; a modelling system, which can analyze the system from the nutrients through the primary production up to the zooplankton and higher trophic levels was not developed so far. This study is an attempt to develop a bottom-up control approach based modelling framework and apply it to the Curonian Lagoon for analyzing its response to nutrient inputs by using ecological models, which simulate different levels of the trophic network.

2. The nutrient phytoplankton zooplankton and detritus (NPZD) model

The NPZD model consists of two modules; a transport module taking care of all the mass balances and an ecological module, where the kinetics of all the state variables related to nutrients, phytoplankton, zooplankton and detritus that represent the lower levels of the trophic network in the Curonian Lagoon are handled.

2.1 The Transport Module

The transport module called ESTAS (EcoSystem and TrAnsport Simulator) is a box type model that solves the advection-dispersion equations with several additional terms,

$$\begin{aligned} \frac{\partial C}{\partial t} = & -u \frac{\partial C}{\partial x} + D_x \frac{\partial^2 C}{\partial x^2} - v \frac{\partial C}{\partial y} + D_y \frac{\partial^2 C}{\partial y^2} - w \frac{\partial C}{\partial z} + D_z \frac{\partial^2 C}{\partial z^2} \\ & + f_{\text{settling}}(v_{\text{settling}}, C) + f_{\text{sediment}}(D_{\text{water-sediment}}, C, C_{\text{sediment}}) \\ & + f_{\text{external}}(Q_{\text{external}}, C_{\text{external}}, M_{\text{external}}) + f_{\text{kinetics}}(k_1, \dots, k_n, C) \end{aligned} \quad (\text{Eq. 1})$$

where x, y are the lateral coordinates [L]; z is the coordinate in the direction from the bottom to the water surface [L]; u, v and w are the velocities in x, y and z directions [$L \cdot T^{-1}$]; $v_{\text{water-settling}}$ is the settling velocity [$L \cdot T^{-1}$], $D_{\text{water-sediment}}$ is the dispersion coefficient for the mass transfer between the sediment and the water column [$L^2 \cdot T^{-1}$], C_{sediment} is the concentration in sediment [$M \cdot L^{-3}$], Q_{external} is the external inflow rate entering the system [$L^3 \cdot T^{-1}$], C_{external} is the concentration in external inflow entering the system [$M \cdot L^{-3}$], M_{external} is the material

entering the system in form of mass $[M \cdot T^{-1}]$ and k_1, \dots, k_n are coefficients which define the kinetic behaviour of the related constituent. The first additional term (f_{settling}) is the effect of settling on the concentration in the water column. The second additional term (f_{sediment}) is the effect of sediment flux on the concentration in the water column. It is modelled as a dispersive flux. The third additional term (f_{external}) is the effect of external inputs on the concentration in the water column. The fourth additional term (f_{kinetics}) is the effect of NPZD kinetics on the concentration in the water column. This part includes all the chemical and biological processes defined for the user developed NPZD model.

The ESTAS model network for the Curonian Lagoon is given in Fig 3. ESTAS divides the ecosystem into cells laterally and layers vertically. Equation 1 is rewritten for these boxes using a finite difference scheme that defines all the lateral neighbourhoods. Hence, it is reduced to a one dimensional transport equation that is solved for the vertical direction for each cell and to time functions that are responsible for horizontal material transfer between these cells. For the Curonian Lagoon, cells are divided into layers that are 1 m deep initially. ESTAS includes an adaptive algorithm that generates new layers when water surface elevation increases and removes them when water surface elevation decreases. The flow rates that are needed for the calculation were obtained from SHYFEM (SHYFEM, <http://www.ismar.cnr.it/shyfem>) that is a finite element hydrodynamic model. SHYFEM was successfully applied to many coastal environments (Umgiesser et al., 2004b; Ferrarin and Umgiesser, 2005; Ferrarin et al, 2010; Bellafiore et al. 2011; De Pascalis et al, 2011; Zemlys et al., 2013; Ferrarin et al, 2014; Umgiesser et al. 2014). ESTAS and SHYFEM are coupled externally using a hydrodynamic linkage file (Fig. 3).

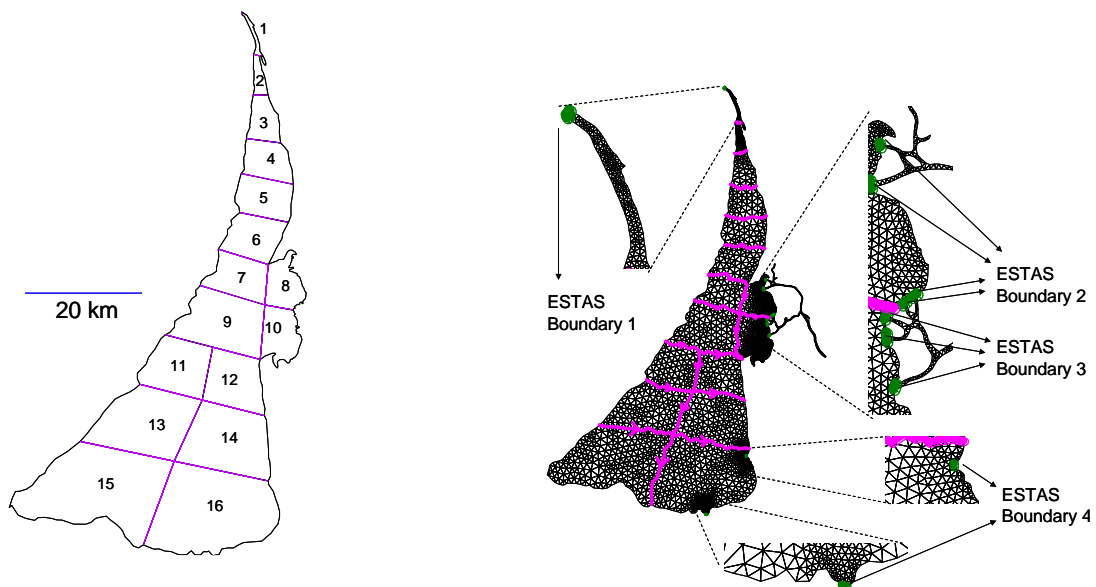


Figure 3. ESTAS model network for the Curonian Lagoon

ESTAS has additional capabilities such as to include the material transfer from the sediments, calculate vertical dispersion, waves and include the effects of resuspension for any state variable.

2.2 The Ecological Module

The ecological module called ALUKAS (Advanced Level nUtrient Kinetics for Aquatic ecoSystems) is a pelagic NPZD model that is fully integrated with ESTAS. ALUKAS includes 22 state variables and a detailed representation of the carbon, nitrogen and phosphorus biogeochemical cycles. It is a completely new sub model that is developed considering the experiences gained during the development of a preliminary model by Zemlyš et al (2008) for the Curonian Lagoon. ALUKAS consists of three main parts; a nutrient cycle (Fig. 4), plankton dynamics (Fig. 5) and a non-living organic matter cycle that also contains dissolved oxygen kinetics (Fig. 6).

The nutrient cycle contains nitrogen, phosphorus and silicon species and inorganic carbon. Nitrogen is assumed to be in three main pools. The first of them is ammonia nitrogen, the second is the nitrate nitrogen and the third is nitrogen bound to molecules found in living (phytoplankton and zooplankton) and dead organic matter. Phosphorus is assumed to be in two main pools. The first of them is phosphate phosphorus and the second is phosphorus bound to molecules found in living (phytoplankton and zooplankton) and dead organic matter similar to nitrogen. Silicon is assumed to be in two main pools. The first of them is available silicon (dissolved inorganic silicon) and the second is silicon found with living (diatoms and zooplankton feeding on diatoms) and dead (diatoms and zooplankton based organic carbon and detritus) organic matter.

Plankton dynamics is represented by three phytoplankton groups; diatoms, cyanobacteria and other planktonic algae and one zooplankton group. Zooplankton are assumed to be herbivorous and detritivorous. Carnivorism and cannibalism among zooplankton are not included into ALUKAS.

Non-living organic matter cycle is modelled extensively in ALUKAS. External labile dissolved organic carbon, external labile particulate detritus carbon, external refractory dissolved organic carbon and external refractory particulate detritus carbon are used to model the allochthonous organic and detritus carbon. The autochthonous detritus carbon is simulated using diatoms based dissolved organic carbon, diatoms based particulate detritus, cyanobacteria based dissolved organic carbon, cyanobacteria based particulate detritus, other planktonic algae based dissolved organic carbon, other planktonic algae based particulate detritus, zooplankton based dissolved organic carbon and zooplankton based particulate detritus.

The NPZD model was calibrated and validated using data from the years 1999 and 2000, those had different hydrological characteristics. More information related to calibration and validation is given in Section 5.1.

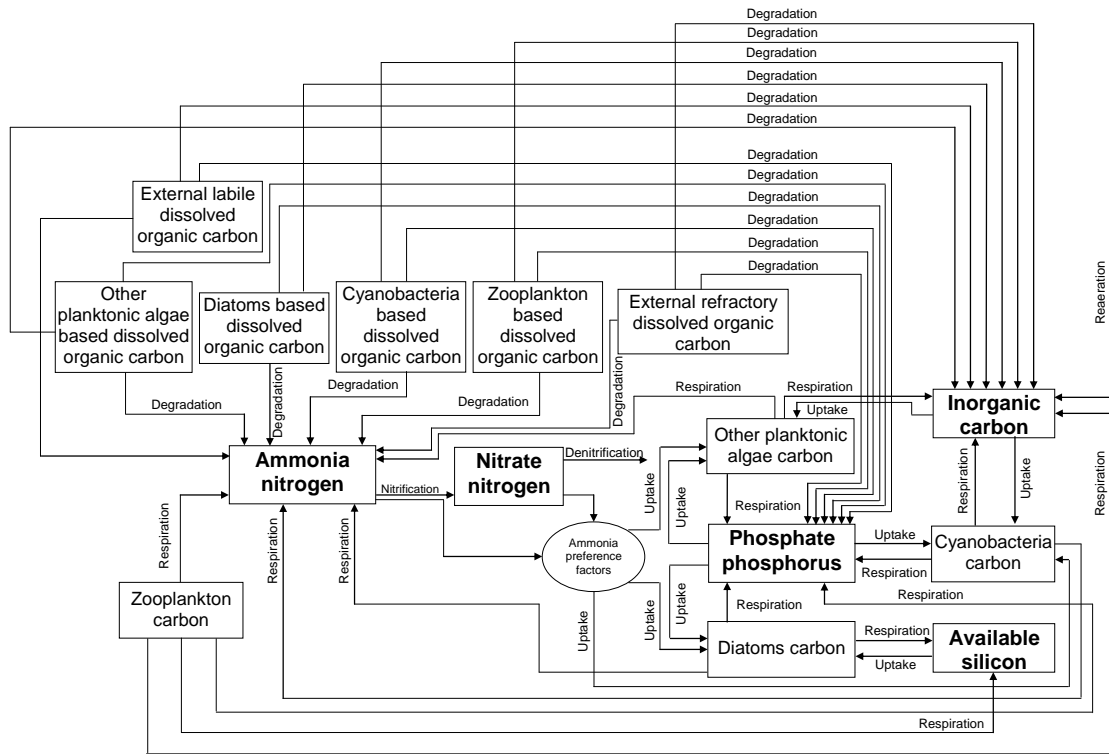


Figure 4. Nutrient cycles in ALUKAS

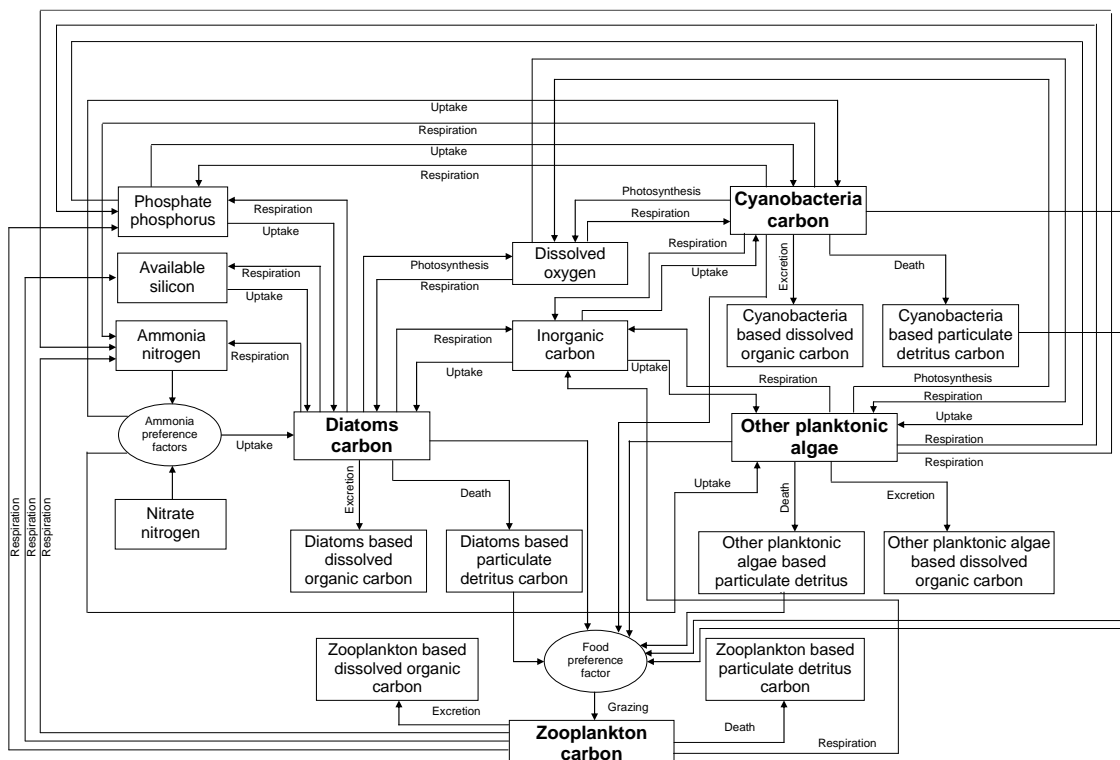


Figure 5. Plankton dynamics in ALUKAS

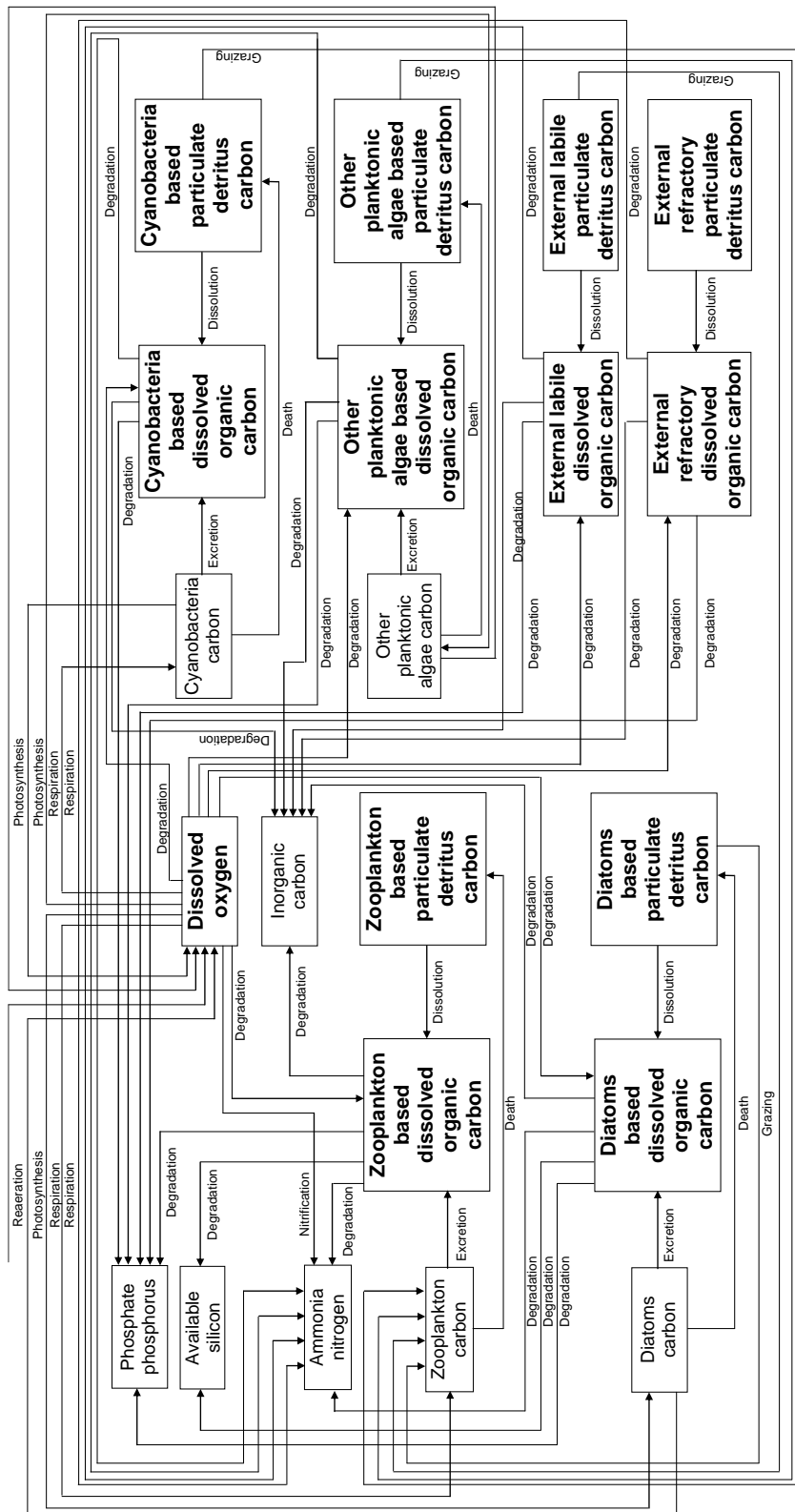


Figure 6. Non-living organic matter cycle in ALUKAS

3. The trophic network model

3.1 Model Description

The Curonian Lagoon trophic network model used in this study is based on the trophic network model developed by Razinkovas and Zemlys (2000) using Ecopath version 4. However, it has been enhanced to be compatible with ESTAS/ALUKAS and a newer version of Ecopath (Version 6) is used instead of version 4. Ecopath with Ecosim is designed for straightforward construction, parameterization and analysis of mass-balance trophic models for various ecosystems. The core of Ecopath is derived from ECOPATH program developed by Polovina and Ow (1983). However, Ecopath does not work under the steady state assumption any more. Instead, it bases the parameterization on an assumption of mass balance of an arbitrary period (Christensen et al., 2005). This period is usually one year, but modelling an ecosystem seasonally is also possible.

Since the original ECOPATH from early 1980s, Ecopath has undergone a long development process for both; the theory, ideas and as well as the software itself. The system has been optimized for direct use in fisheries assessment as well as for addressing other more general environmental questions through the inclusion of the temporal dynamic model Ecosim and spatial dynamic model Ecospace. Furthermore, tools such as Ecoranger (tool for addressing uncertainty), Ecoempire (tool for calculation of empirical relationships of production over biomass ratios), Flow diagram (tool for plotting the defined trophic network) or Ecowrite (reporting tool) ease and enhance the model development (Christensen et al., 2005).

Different versions of Ecopath with Ecosim are used for various studies with topics such as analyses of trophic interactions (Opiz, 1996; Okey and Pauly, 1999; Harvey et al. 2003), trophic modelling for aquatic ecosystems (Aydin et al., 2003; Mohamed et al, 2005), fisheries management and fish stock assessment (Pauly, 1998; Zuchetta et al., 2003; Fayram, 2005) in different aquatic ecosystems. Being applied to different aquatic ecosystems from the tropics up to Arctics, Ecopath with Ecosim is proven to be reliable. Detailed information related to methods used in, Ecopath, Ecosim and Ecospace as well as capabilities and limitations of these models is given by Walters et al. (1999), Walters et al. (2000), Pauly et al. (2000), Christensen and Walters (2004), Kavanagah et al. (2004) and Christensen et al., (2005).

Version 6.0 that is the most recent version of Ecopath with Ecosim software is used in this study. This version extends the capabilities of the previous versions. It is expandable by user developed plug-ins and is supplied with a programmable core. Its source code is available on demand. For the aim of this study, use Ecopath was sufficient and therefore Ecosim and Ecospace modules were not used.

Ecopath has two master equations. The first master equation (Eqs. 2-5) describes how the production term for each group modelled can be split into components.

$$\text{Production} = \text{catches} + \text{mortality by predation} + \text{biomass accumulation} + \text{net migration} + \text{other mortality} \quad (\text{Eq. 2})$$

In mathematical terms Equation 2 (the first master equation), for *i*-th group is written as,

$$P_i = Y_i + B_i M_{2i} + E_i + BA_i + P_i(1 - EE_i) \quad (\text{Eq. 3})$$

where, i is the index for each group (1 to number of groups), P_i is the total production rate of group i , Y_i is the total fishery catch rate of group i , M_{2i} is the total predation rate for group i , B_i the biomass of the group i , E_i the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate for group i , while $M_{0i} = P_i(1 - EE_i)$ is the ‘other mortality’ rate for group i and EE_i is the ecotrophic efficiency of group i . Eq. 3 can be rearranged and rewritten as Eq. 4.

$$B_i \left(\frac{P}{B} \right)_i EE_i - \left(\sum_{j=1}^n \left(B_j \left(\frac{Q}{B} \right)_j \right) DC_{j,i} \right) - Y_i - E_i - BA_i = 0 \quad (\text{Eq. 4})$$

where n is the number of groups modelled, j is the index for prey, P/B_i is the production/biomass ratio, Q/B_j is the consumption/biomass ratio and $DC_{j,i}$ is the fraction of prey j in the average diet of predator i (diet composition). A system of n linear equations (Eq. 5) is obtained from Eq. 3 for a trophic system with n groups. Ecopath includes algorithms to solve this system of linear equations. $DC_{j,i}$, Y_i and E_i must always be supplied by the user. Entry is optional for any of the four main variables for each group: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B) or ecotrophic efficiency (EE). Ecopath applies the generalized inverse method to solve the linear set of equations using the approach of Mackay (1981). Situations, when the set of equations is over-determined (more equations than unknowns) or underdetermined (more unknowns than equations) can be handled. If the set of equations is over-determined and the equations are not consistent with each other, the generalized inverse method based on least squares provides an estimate that minimizes the discrepancies. If the system is underdetermined, an answer that is consistent with the data will still be possible. However, it will be not a unique answer (Christensen et al., 2005). Equations 4 for all system components can be rewritten as follows:

$$\begin{aligned} B_1 \left(\frac{P}{B} \right)_1 EE_1 - B_1 \left(\frac{Q}{B} \right)_1 DC_{1,1} - B_2 \left(\frac{Q}{B} \right)_2 DC_{2,1} - \dots - B_n \left(\frac{Q}{B} \right)_n DC_{n,1} - Y_1 - E_1 - BA_1 &= 0 \\ B_2 \left(\frac{P}{B} \right)_2 EE_2 - B_1 \left(\frac{Q}{B} \right)_1 DC_{1,2} - B_2 \left(\frac{Q}{B} \right)_2 DC_{2,2} - \dots - B_n \left(\frac{Q}{B} \right)_n DC_{n,2} - Y_2 - E_2 - BA_2 &= 0 \\ \vdots & \\ B_n \left(\frac{P}{B} \right)_n EE_n - B_1 \left(\frac{Q}{B} \right)_1 DC_{1,n} - B_2 \left(\frac{Q}{B} \right)_2 DC_{2,n} - \dots - B_n \left(\frac{Q}{B} \right)_n DC_{n,n} - Y_n - E_n - BA_n &= 0 \end{aligned} \quad (\text{Eq. 5})$$

The energy input and output of all living groups must be balanced in a model. When balancing the energy for a living group additional terms, which do not exist in the first master equation, are needed and with their incorporation, the second master equation of Ecopath (Eq. 6) is formed.

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (\text{Eq. 6})$$

3.2 Model Inputs

The trophic network model used in this study for the Curonian lagoon contains 23 groups; 3 of them (Diatoms, Cyanobacteria and other planktonic algae) being producers, 17 of them being consumers (bacteria, grazing zooplankton, carnivorous zooplankton, planktivorous fish, deposit feeder gastropods, chironomids, oligochets, filtrators bivalves, meiobenthos, mysids, demersal fish, predatory fish, grey heron, seagull, goosander, great crested grebe, cormorants) and the last 3 (POC, DOC and Detritus) being detritus. POC (particulate organic carbon) and DOC (dissolved organic carbon) groups represent the pelagic detritus, while the group Detritus represents the benthic detritus. No multi stanza groups were included in the Curonian Lagoon model. The trophic network defined for the Curonian Lagoon for this study is illustrated in Fig. 7.

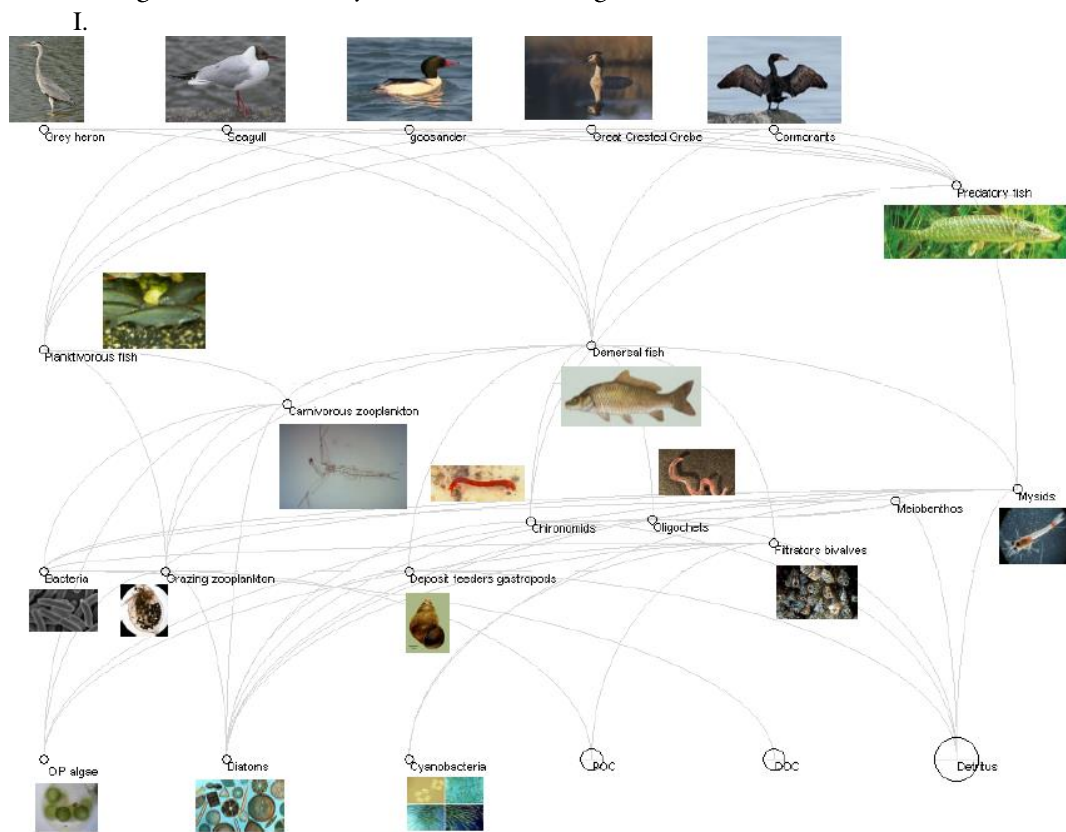


Figure 7. The trophic network model for the Curonian Lagoon

Most of the data related to higher trophic levels about the Curonian Lagoon were obtained as spatially averaged. Therefore, Curonian Lagoon was assumed to be homogeneous for the trophic network model setup. The basic model inputs and the diet composition given in Tables 1 and 2 were generated using the available data and some results from the NPZD model (Section 4.1) as it was linked with the trophic network model. Missing parts of the basic data were compiled from literature as referred in the Table 1, where the values used for similar ecosystems and the Baltic Sea were taken and incorporated into the trophic network model.

Table 1. Basic inputs for the ECOPATH model

II.

Group name	Biomass (gCm ⁻²)	P/B	C/B
Other planktonic algae	0.87 ¹	54.17 ¹	
Diatoms	0.98 ¹	52.43 ¹	
Cyanobacteria	1.78 ¹	133.98 ¹	
Bacteria	0.11 ²	189.00 ⁷	247.62 ⁸
Grazing zooplankton	0.30 ¹	49.72 ⁷	237.60 ⁹
Carnivorous zooplankton	0.08 ¹	37.80 ⁷	237.60 ¹⁰
Planktivorous fish	0.01 ³	0.70 ⁷	10.13 ⁸
Deposit feeders gastropods	0.15 ⁴	8.64 ⁷	40.50 ¹¹
Chironomids	0.22 ⁴	10.80 ⁷	59.40 ¹¹
Oligochets	0.40 ⁴	5.11 ⁷	10.40 ¹²
Demersal fish	1.78 ⁴	0.70 ⁷	3.00 ¹²
Grey heron	0.00 ⁵	0.30 ⁷	30.94 ⁵
Seagull	0.02 ⁵	0.30 ⁷	12.38 ⁵
goosander	0.00 ⁵	0.30 ⁷	45.35 ⁵
Great Crested Grebe	0.00 ⁵	0.30 ⁷	56.88 ⁵
Cormorants	0.01 ⁵	0.30 ⁷	15.84 ⁵
Predatory fish	0.42 ³	0.76 ⁷	2.71 ¹³
Filtrators bivalves	10.44 ⁴	0.27 ⁷	10.00 ¹²
Meiobenthos		18.90 ⁷	44.42 ¹²
Mysids	0.02 ⁶	8.00 ⁷	14.50 ²
POC	7.19 ¹		
DOC	8.53 ¹		
Detritus	35.20 ¹		

¹ Results from the NPZD model, results form 1999, for the year 2000 next year's simulation results were used.

² Space and time averaged monitoring data from Marine Research Department

³ Repecka, 1997

⁴ Olenin, 1997

⁵ Zarankaite personal communication

⁶ Lesutiene personal communication, unpublished data

⁷ Zaika, 1983

⁸ Harvey et al, 2003

⁹ Suchenia, 1975

¹⁰ Monakov and Sorokin, 1959

¹¹ Monakov, 1998

¹² Witek, 1995

¹³ Rudzianskiene, 1994

Table 2. Diet Composition

Ecopath Group No	Prey \ predator	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Other planktonic algae		37.0%	10.0%												10.0%		5.0%
2	Diatoms		9.0%	10.0%		10.0%	30.0%	15.0%								11.0%	10.0%	5.5%
3	Cyanobacteria															19.0%		9.5%
4	Bacteria			10.0%												15.0%	10.0%	10.0%
5	Grazing zooplankton			60.0%	80.0%				1.4%									20.0%
6	Carnivorous zooplankton			10.0%	20.0%				0.6%									
7	Planktivorous fish									0.5%	0.5%	0.5%	0.5%	0.5%				
8	Deposit feeders gastropods								15.0%									
9	Chironomids								35.0%						1.4%			
10	Oligochets						10.0%		10.0%									
11	Demersal fish									65.5%	65.5%	65.5%	65.5%	65.5%	50.0%			
12	Grey heron																	
13	Seagull																	
14	goosander																	
15	Great Crested Grebe																	
16	Cormorants																	
17	Predatory fish									14.0%	14.0%	14.0%	14.0%	14.0%	12.5%			
18	Filtrators bivalves								3.0%									
19	Meiobenthos						10.0%	20.0%									20.0%	10.0%
20	Mysids								0.5%						5.5%			
21	POC		54.0%													45.0%		
22	DOC	100.0%																
23	Detritus					90.0%	50.0%	65.0%									60.0%	40.0%

As the model included three forms of the non-living organic carbon compartments – POC, DOC and sedimentary detritus, we assumed that the most of the DOC was produced by the algae and bacteria, while the share between POC and detritus was mostly following the planktonic or benthic origin of living compartments.

The other production data consists of immigration, emigration and bioaccumulation. Immigration and emigration data for the phytoplankton groups and herbivorous zooplankton were obtained from the NPZD model via the linkage. Related details are given in Section 4.2. In this study, immigration and emigration were assumed zero for the other groups in the trophic network model. Another assumption made during the development of the trophic network model is that there was no bioaccumulation during the period of simulation.

4. Linkage of NPZD and trophic network models

4.1 Linkage on the State Variable Level

The first step of linking the NPZD (ESTAS/ALUKAS) model with the trophic network model (Curonian Lagoon trophic network model developed under Ecopath) was to generate derived variables from the state variables of the NPZD model and to adapt time scales of NPZD models derived variables with the trophic network model, which bases the parameterization on an assumption of mass balance of an arbitrary period that was one year in this study. This is the so-called “hand-shaking” stage of the linkage. Spatial averaging was also conducted. The transport module ESTAS can give averaged results for user defined time periods. The procedure for creating the derived variables from the NPZD models state variables were hard-coded into ESTAS for this study.

ESTAS/ALUKAS is a dynamic model with 22 state variables, which include nutrients, detritus and plankton groups. ALUKAS state variables related to plankton groups (three phytoplankton groups and one zooplankton) are directly interfaced with Curonian Lagoon trophic network model. Curonian Lagoon trophic network model includes two groups for pelagic detritus compartment, the dissolved organic carbon (DOC) and the particulate organic carbon (POC), whereas ALUKAS contains 12 state variables, 6 of them for dissolved organic carbon and 6 more for particulate detritus carbon. Therefore; the sum of external labile dissolved organic carbon, external refractory dissolved organic carbon, other planktonic algae based dissolved organic carbon, diatoms based dissolved organic carbon, cyanobacteria based dissolved organic carbon and zooplankton based dissolved organic carbon was defined as dissolved organic carbon, whereas the sum of external labile particulate detritus carbon, external refractory particulate detritus carbon, other planktonic algae based particulate detritus carbon, diatoms based particulate detritus carbon, cyanobacteria based particulate detritus carbon and zooplankton based particulate detritus carbon was defined as particulate organic carbon. The linkage between ESTAS/ALUKAS and Curonian Lagoon trophic network model is illustrated in Fig 8.

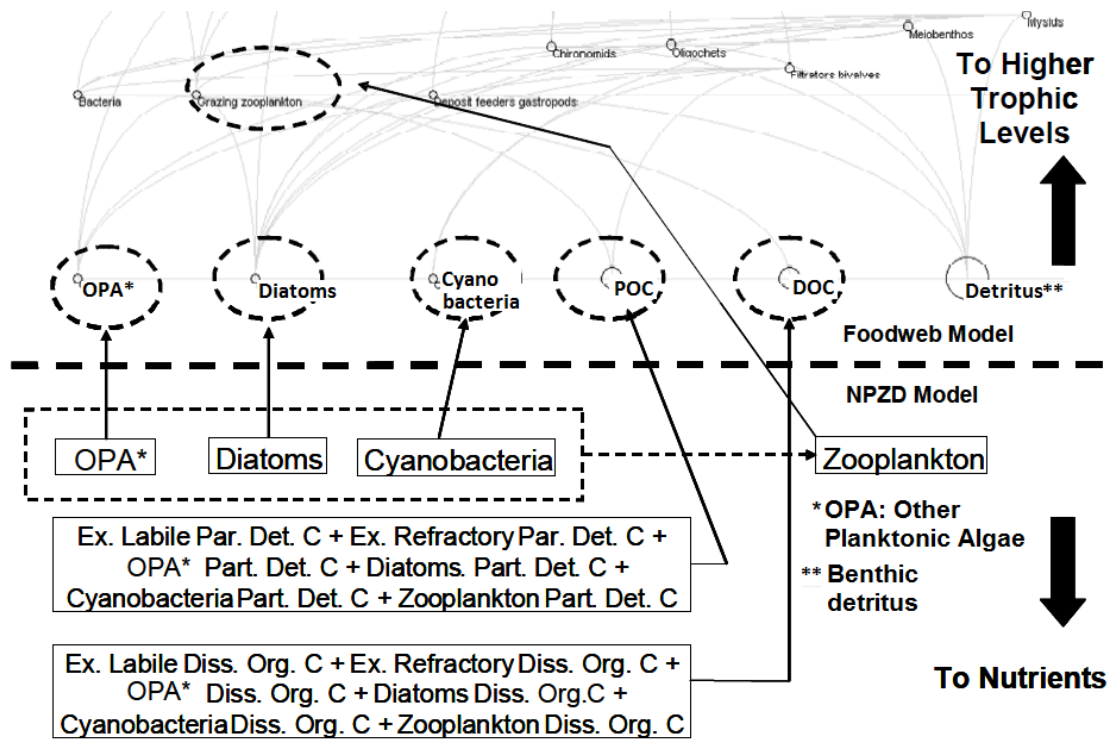


Figure 8. Linkage between ESTAS/ALUKAS state variables and Ecopath groups

4.2 Linkage on the Mass Balance Level

After the derived variables of the NPZD model were defined to be compatible with the groups of the trophic model network, incoming, outgoing and in-pool masses of the ecological variables related to linkage must be correctly transferred from the NPZD model to the trophic network model. This is utmost important since both models were based on mass balance.

Linking of incoming, outgoing and in-pool masses generated by the NPZD model to the trophic network model was straightforward. In ESTAS that is the host for the NPZD model, the mass of any state or derived variable is represented for unit volume as concentration whereas Ecopath, therefore the trophic network model, considers the mass per unit area. There are several standard averaging subroutines in ESTAS that are independent from the ecological model structure developed for this purpose. The only technical burden is that, the user needs to reprogram several subroutines of ESTAS that are supplied empty in the standard code for defining the masses related to derived state variables.

4.3 Linkage on the Process Level

Linkage of the process level was a relatively complicated task. This step of the linkage is necessary for several components of basic model inputs (P/B and detritus import) and diet composition. The P/B values for the phytoplankton groups and herbivorous zooplankton are calculated by dividing the time-averaged production rates to their time-averaged

biomasses. In the NPZD model, zooplankton consumes different groups of phytoplankton and particulate detritus and therefore gains biomass from different carbon sources. All of these were accounted to calculate the production rates. Filtrating bivalves and mysids were assumed to consume 40% and 20% phytoplankton in their diet respectively without distinguishing the groups. Therefore the diet composition percentages of individual phytoplankton groups related to the consumption by filtrating bivalves and mysids were taken directly proportional to their biomasses. All these specific procedures for the linkage between the NPZD model (ALUKAS) and the Curonian Lagoon food web model were needed to be programmed into a subroutine that is supplied empty in the standard code. The same subroutine is also responsible for generating an output file with the linkage information that must be entered to Ecopath manually and therefore programmed accordingly.

5. Results and discussion

5.1 Model Calibration and Validation

The NPZD model results changing parameter values were compared with available data for different stations until field data was acceptably well reproduced (Figures 9, 11). Model performance after calibration was compared to box plots summarising the performance of various biogeochemical models (153 studies published from 1990 to 2002) analysed in the review by Arhonditsis and Brett (2004) and to a former study results by Zemlys et al. (2008), where a simple nutrient dynamics model of the Curonian Lagoon (Figure 10) as well.

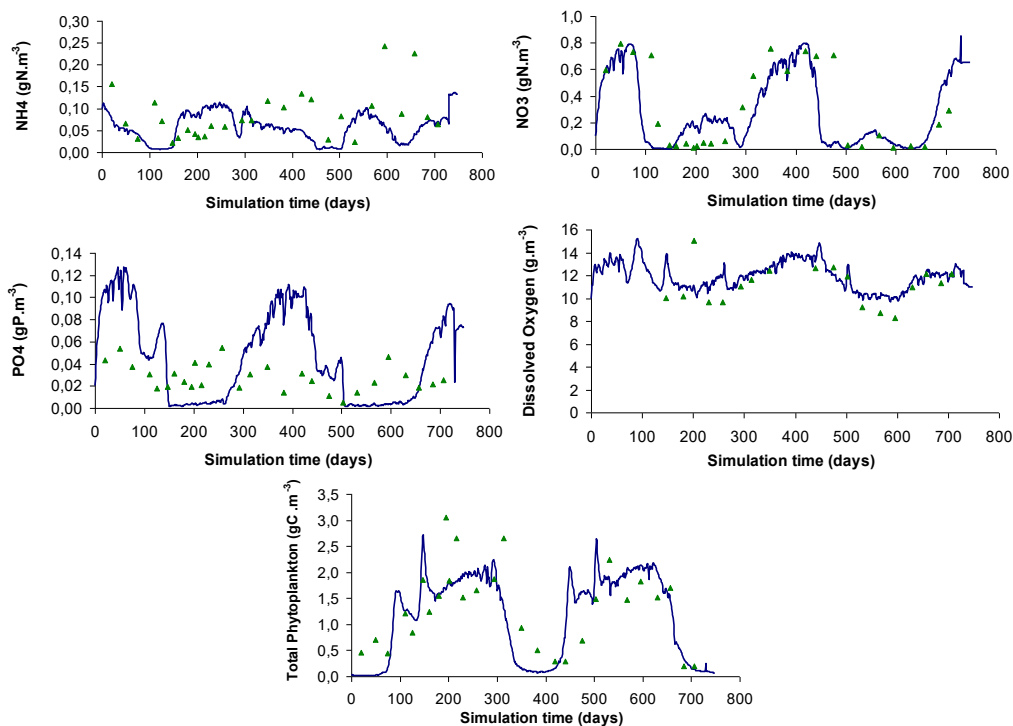


Figure 9. Model performance after calibration for nutrients

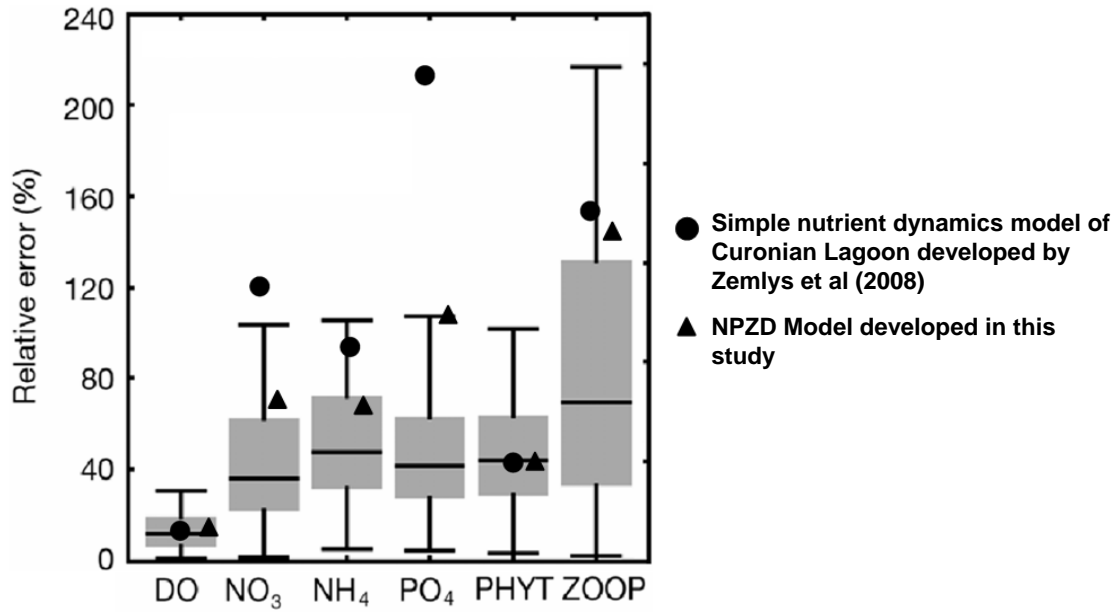


Figure 10. Comparison of NPZD calibrated model performance with performance of other biogeochemical models

The performance of the calibrated model for three different phytoplankton groups is shown in Figure 11. The NPZD model is found adequate at this stage of development, where its aim is to evaluate the general response of Curonian Lagoon to nutrient inputs and its results will be transferred to the foodweb model of the Curonian Lagoon for further analysis of the carbon cycle. Figure 12 illustrates the simulated distribution of primary producers biomass as carbon.

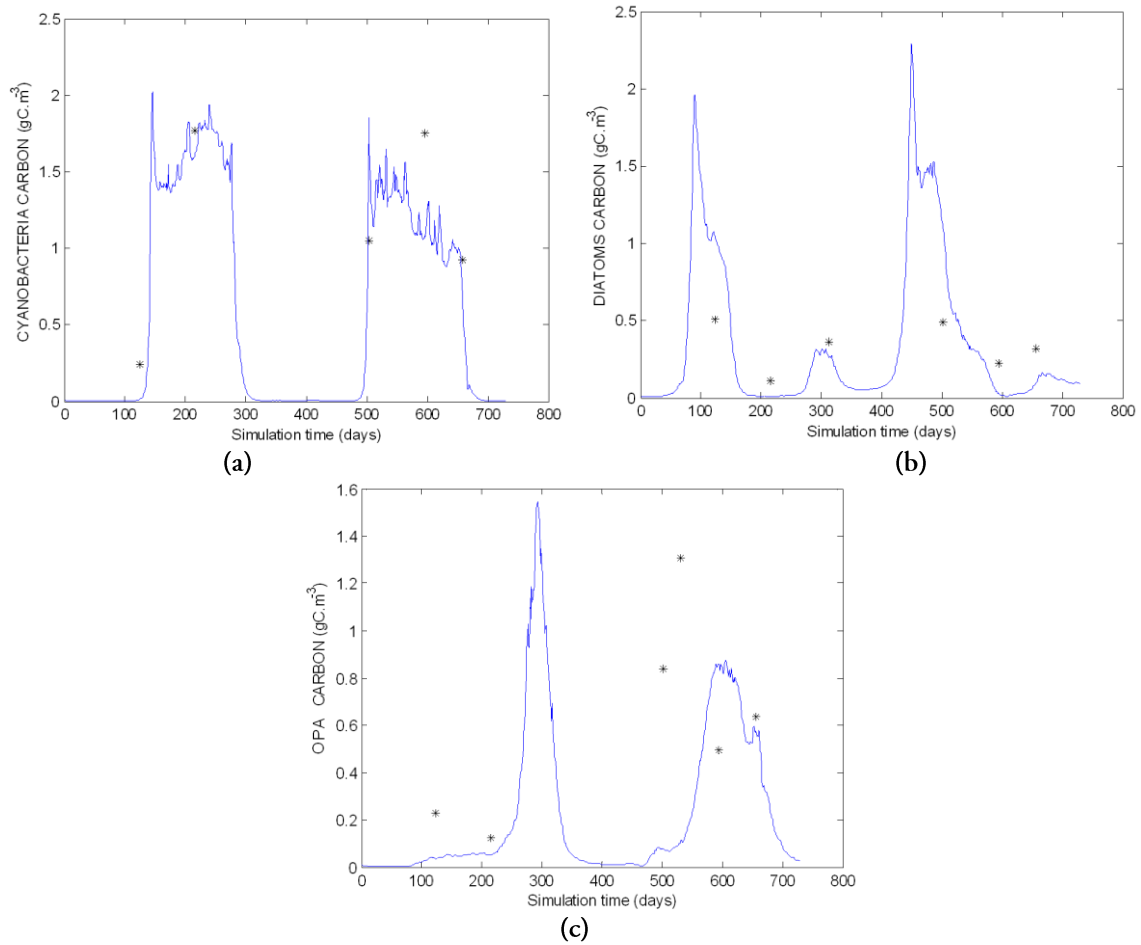


Figure 11. Performance of calibrated model for three different phytoplankton groups: (a) Cyanobacteria, (b) Diatoms, (c) Other planktonic algae.

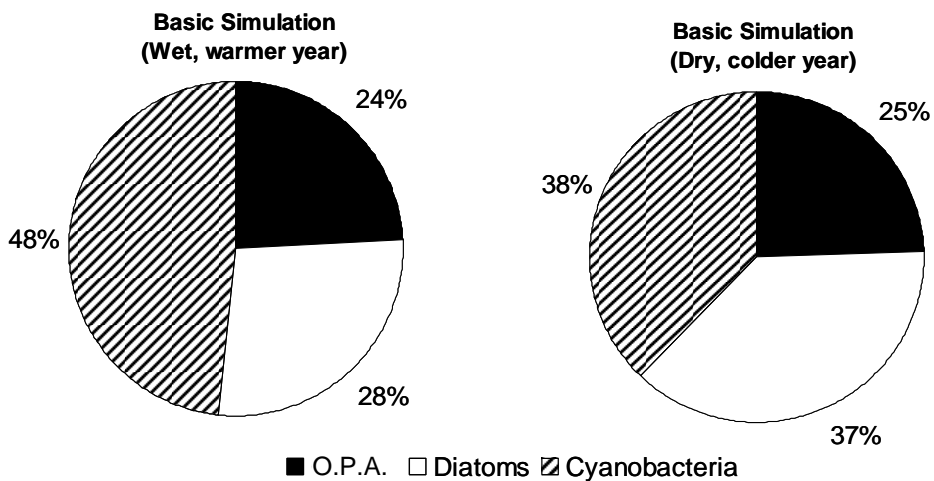


Figure 12. Distribution of primary producers carbon

5.2 Ecopath model as an extension of NPZD model

Even though the NPZD model reproduced the spatial and temporal variations for relevant state variables at an acceptable goodness of fit, the entire model calibration can be considered as a sort of advanced curve fitting procedure so far. Wrong set of model coefficients may produce results, which are acceptable close to field data. The consistency of the NPZD model was checked with a trophic network model developed under Ecopath.

The NPZD model calculated the diet compositions which correspond to phytoplankton and pelagic organic carbon and detritus. The advanced NPZD model also calculated yearly inflowing and outflowing biomasses of three phytoplankton groups, the zooplankton and the mass of particulate and dissolved pelagic detritus. All these outputs were used for the trophic network model as well. After the calibration of the advanced NPZD model, its results were transferred to the Curonian Lagoon trophic network model Ecopath was run for the years 1999 and 2000. The results are given in Table 3.

Table 3. Basic output from the Curonian Lagoon trophic network model

Ecopath group	Trophic Level	Ecotrophic Efficiency		Production / consumption	
		Year 1999	Year 2000	Year 1999	Year 2000
Other planktonic algae	1.00	0.77	0.78	Not defined	Not defined
Diatoms	1.00	0.50	0.34	Not defined	Not defined
Cyanobacteria	1.00	0.03	0.07	Not defined	Not defined
Bacteria	2.00	0.33	0.33	0.76	0.76
Grazing zooplankton	2.00	0.80	0.46	0.21	0.22
Carnivorous zooplankton	2.89	0.65	0.65	0.16	0.16
Planktivorous fish	3.18	0.30	0.30	0.07	0.07
Deposit feeders gastropods	2.00	0.60	0.60	0.21	0.21
Chironomids	2.27	0.78	0.78	0.18	0.18
Oligochets	2.28	0.92	0.92	0.49	0.49
Demersal fish	3.20	0.98	0.98	0.23	0.23
Grey heron	4.35	0.00	0.00	0.01	0.01
Seagull	4.35	0.00	0.00	0.02	0.02
Goosander	4.35	0.00	0.00	0.01	0.01
Great Crested Grebe	4.35	0.00	0.00	0.01	0.01
Cormorants	4.35	0.00	0.00	0.02	0.02
Predatory fish	4.05	0.80	0.80	0.28	0.28
Filtrators bivalves	2.15	0.24	0.24	0.03	0.03
Meiobenthos	2.38	0.95	0.95	0.43	0.43
Mysids	2.44	0.49	0.49	0.55	0.55
POC	1.00	0.55	0.82	Not defined	Not defined
DOC	1.00	0.11	0.13	Not defined	Not defined
Detritus	1.00	0.50	0.38	Not defined	Not defined

Curonian Lagoon trophic network model was balanced successfully for both of the simulation years. Ecotrophic efficiencies for all the groups were between 0 and 1 indicating that Ecopath was balanced successfully. Among the three phytoplankton groups, ecotrophic efficiency of the other planktonic algae was the highest (0.77 for the year 1999 and 0.78 for

the year 2000), followed by diatoms (0.50 for the year 1999 and 0.34 for the year 2000). Cyanobacteria have the lowest ecotrophic efficiency because they are not grazed by most of the organisms. As the only difference in the inputs between years 1999 and 2000 was in the inputs from the NPZD model, Ecopath revealed differences mostly related to lower trophic chains between these years. The double difference in the ecotrophic efficiency in cyanobacteria was mostly due to the fact of higher biomass in more warmer 1999 than 2000, while the differences in ecotrophic efficiency of diatoms appeared to be the opposite (Table 3). There was also a significant difference in ecotrophic efficiency of grazing zooplankton: 0.80 for the year 1999 and 0.46 for the year 2000, when the zooplankton was more abundant. However the production/consumption ratios calculated for grazing zooplankton weren't much different (0.21 for the year 1999 and 0.22 for the year 2000) pointing towards the fact that despite differences in the autotrophic plankton composition between years the diet has remained the same.

Yearly average biomass from three algal groups, the zooplankton group and yearly average mass from two detritus groups that were derived from 12 organic/detritus carbon based state variables of the NPZD model were used as inputs for the Curonian Lagoon trophic network model. Moreover production rates of phytoplankton groups and zooplankton groups were entered to the same model as production/biomass (P/B) ratios. P/B ratios were compared with literature values and were found to be in range.

The diet compositions which correspond to phytoplankton and pelagic organic carbon and detritus were calculated by NPZD model. Also yearly inflowing and outflowing biomasses of three phytoplankton groups, the zooplankton and the mass of particulate and dissolved pelagic detritus were calculated by the advanced NPZD model. All these outputs were used for the trophic network model as well.

Ecopath successfully balanced the Curonian Lagoon trophic network model, which was partly generated with the outputs (biomass, mass flow and several process rates) from the advanced NPZD model and partly with field data for the organism groups which were not included in the NPZD model. Therefore, the NPZD model results were considered to be consistent with the trophic network of the Curonian Lagoon. The present Ecopath model was more detailed than one published before (Razinkovas and Zemlys, 2000), and, what is more important, was using the more reliable time and space integrated inputs (autotrophic and heterotrophic plankton parameters) from the NPZD model. However, as the Curonian lagoon ecosystem appeared to be hyperretrophic, system producing the excess of organic matter in the autotrophic plankton compartments, not much of variation in higher trophic levels was found between climatically different years 1999 and 2000.

5.3 Estimating the response of Curonian Lagoon to Changes in Nutrient Inputs

Estimating the response of a eutrophic waterbody such as the Curonian Lagoon can answer important management question. To investigate the effects of the external nutrient inputs on the Curonian Lagoon's internal system behaviour, 16 scenarios with different combinations of total nitrogen (inorganic and organically bound compounds) and phosphorus (inorganic and organically bound compounds) inputs (Table 4) were conducted.

Table 4. Combinations of nitrogen and phosphorus input variations in different scenarios

Simulation no	Nitrogen	Phosphorus
1	25% increased	Not changed
2	50% increased	Not changed
3	Not changed	25% increased
4	Not changed	50% increased
5	25% increased	25% increased
6	25% increased	50% increased
7	50% increased	50% increased
8	50% increased	50% increased
9	25% decreased	Not changed
10	50% decreased	Not changed
11	Not changed	25% decreased
12	Not changed	50% decreased
13	25% decreased	25% decreased
14	25% decreased	50% decreased
15	50% decreased	50% decreased
16	50% decreased	50% decreased

In these scenarios, the same kinetic and stoichiometric model coefficients, which were obtained during the calibration and validation of the NPZD model, were assumed to be valid.

As expected, nutrients were more sensitive to nutrient input changes than the state and derived variables discussed in this section so far. This situation was expected since the nutrient mass is directly affected by nutrient inputs and indirectly affected by uptake and recycle processes. Inorganic phosphorus responses were stronger than the responses of inorganic nitrogen

The responses to each individual combination of nutrient input change are illustrated in Figures 13 to Figure 15. As seen in Figures 13 to 15, the responses to changed nutrient inputs in the dry year are stronger than the responses in the wet year. The reason is that the water residence times are longer in the dry year and therefore the effect of outflows on total mass of nutrients and other components such as organic matter or plankton is considerably lower. These conditions increase the utilization of nutrients before they are exported from the Curonian Lagoon and hence influence the biogeochemical processes. Cyanobacteria are affected differently, because the dry year is based on the year 2000, at which water temperature was lower than the wet year that is based on 1999.

Ammonia and nitrate nitrogen gave a positive response to either nitrogen or phosphorus input increase and a negative response to the decrease of any of these nutrients. However, phosphate phosphorus had a different response. In four combinations, where amounts of nitrogen inputs were changed and amount of phosphorus inputs were not changed, yearly average of phosphate phosphorus was decreased when the nitrogen inputs were increased and vice versa. This situation can be explained by the different behaviour of the phytoplankton groups. Other planktonic algae produce potentially faster than diatoms and cyanobacteria and they are more efficient. All these groups are competing for two nutrients; nitrogen and phosphorus. Cyanobacteria grow potentially slower than the other planktonic algae; however they have an important advantage, being able to fix nitrogen from gaseous

form if it gets scarce in the water. In this case, phosphorus is expected to have a stronger effect on the total phytoplankton biomass produced in the Curonian Lagoon. If phosphorus inputs are not changed, it is plausible to expect that the total phytoplankton in the relevant scenario should be at least the same as in the basic simulation if nitrogen is increased. Increasing nitrogen however had an important effect on the phytoplankton. The cyanobacteria need to fix less nitrogen, and other planktonic algae and the diatoms are less limited by nitrogen. The other planktonic algae and diatoms are growing potentially faster than the cyanobacteria and cyanobacteria are growing faster in non nitrogen fixing state if compared with nitrogen fixing. In this case, the plankton community is expected to be more advantageous against the outflow in total and the other planktonic algae and diatoms can resist zooplankton grazing more; hence the total phytoplankton biomass is expected to increase. Increase in total phytoplankton has another effect, more uptake of phosphorus if it is available. As seen in Figure 15, phosphorus was not enough to support all the potential extra biomass that could be gained according to the mechanisms explained above, therefore a small increase in total phytoplankton biomass not exceeding 2.5% occurred (Figure 15) that resulted in slightly more phosphorus uptake. The same mechanism proceeds in the opposite direction if nitrogen inputs were decreased. Decrease in nitrogen inputs generates more advantageous conditions for cyanobacteria; however they grow potentially slower and can compensate less to the same rate of outflow as potentially faster growing phytoplankton groups (diatoms and the other planktonic algae) do. Under low nitrogen conditions, the phytoplankton community shifted to cyanobacteria, but the total phytoplankton biomass was less than the basic simulation results (Figure 15) as expected and therefore less phosphate phosphorus was up taken by the phytoplankton.

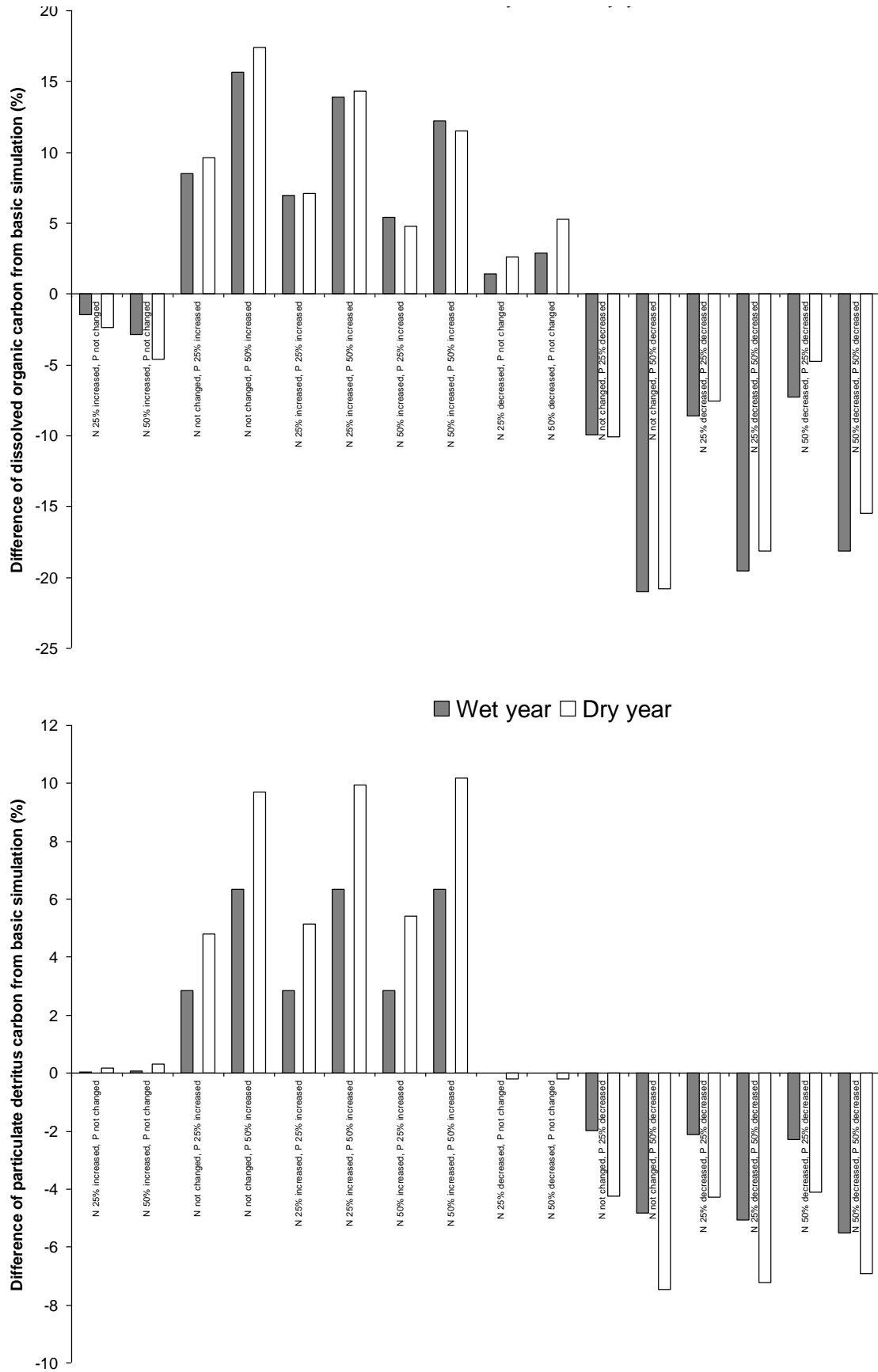


Figure 13. Yearly averaged response of DOC and Detritus Carbon to various nutrient inputs

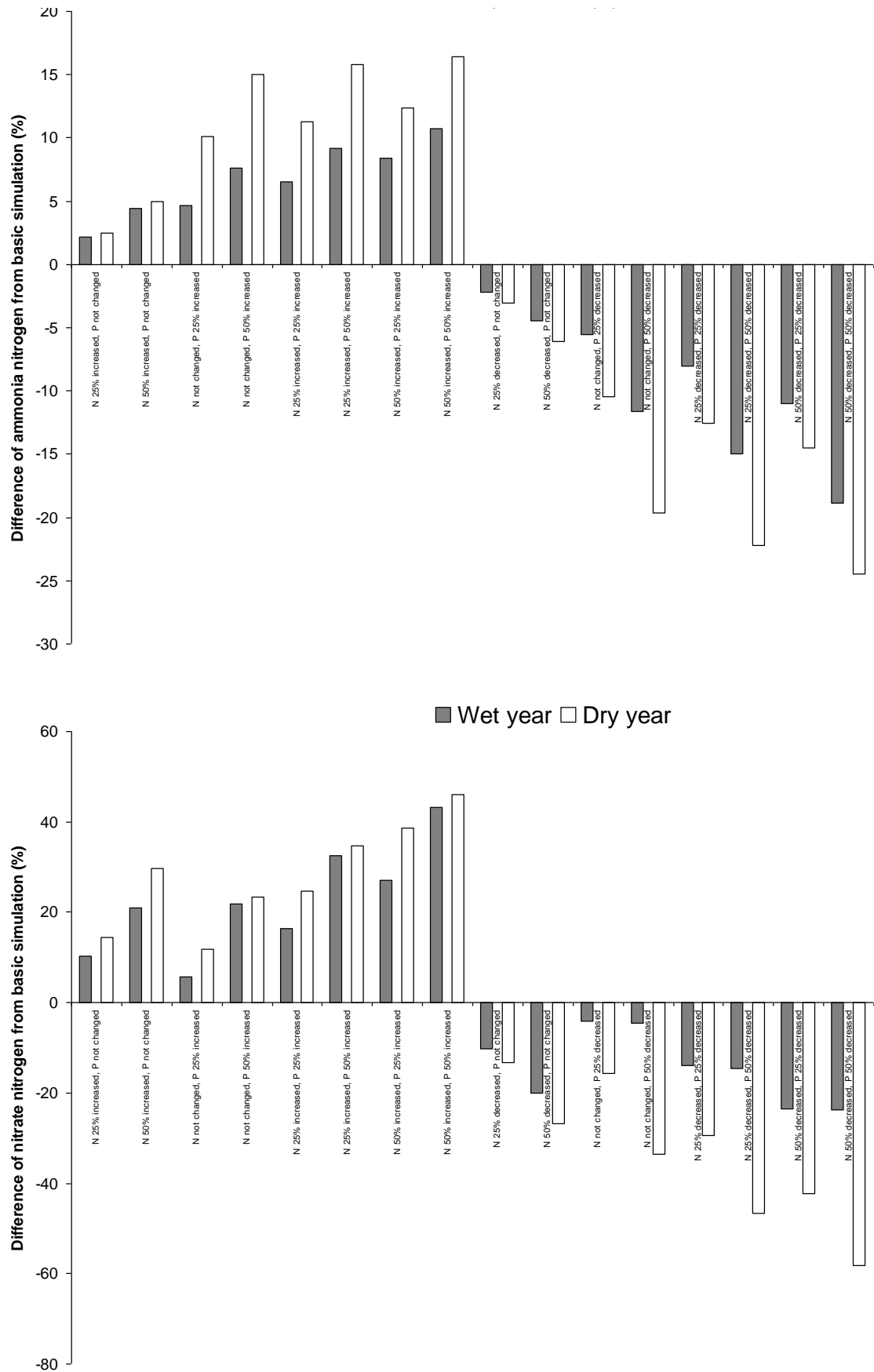


Figure 14. Yearly averaged response of ammonia and nitrate nitrogen to various nutrient inputs

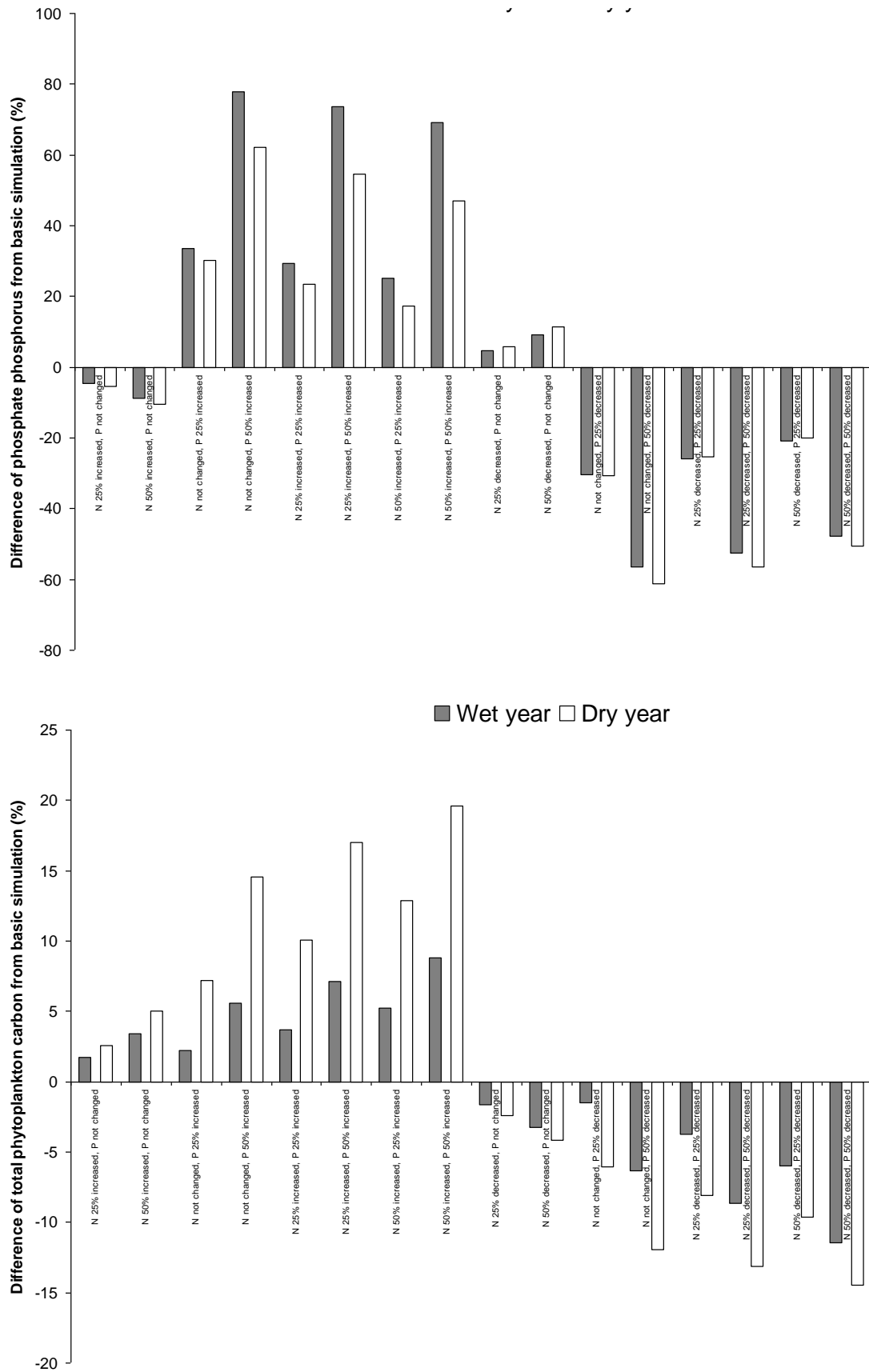


Figure 15. Yearly averaged response of phosphate phosphorus and phytoplankton carbon to various nutrient inputs

The yearly averaged compositions of phytoplankton according to three groups in case of change of nitrogen inputs only are illustrated in Figure 16. Increase of nitrogen caused decrease in cyanobacteria dominance, because their advantage of nitrogen fixation became less important for competition with the other two phytoplankton groups. The more the nitrogen inputs were increased without changing the phosphorus, the less advantaged the cyanobacteria became. The percentage of the other planktonic algae decreased slightly. Diatoms increased because they became more advantageous for competition with the other planktonic algae. The ratio of the other planktonic algae biomass to total phytoplankton biomass tended to increase under nutrient scarcity because of their ability of faster growth and nutrient uptake than the other two groups (Figure 19). Decrease of nitrogen increased cyanobacteria dominance. Cyanobacteria can compete better with the other two groups. The other planktonic algae had also better opportunities for competition with the diatoms, also in the dry year which is colder even though cold environment is more advantageous for diatoms.

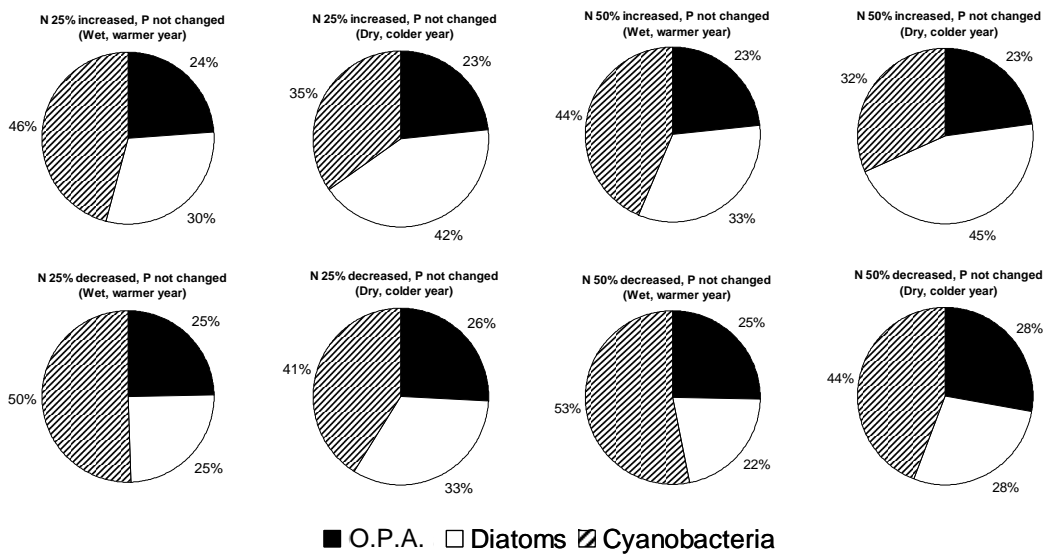


Figure 16. Yearly averaged compositions of phytoplankton according to three groups in case of change of nitrogen inputs only

Yearly averaged compositions of phytoplankton according to three groups in case of change of phosphorus inputs only are illustrated in Figure 17. Increase of phosphorus inputs increased the cyanobacteria dominance, because they became less limited by phosphorus and in Curonian Lagoon, they are almost not grazed by zooplankton therefore more advantageous than the other planktonic algae and diatoms in case of less nutrient limitation. The percentage of diatoms is not considerably different than the results of the basic simulation (Figure 12) indicating that the primary competition was between the other planktonic algae and cyanobacteria.

Decrease of phosphorus inputs for the same nitrogen inputs as in the basic simulation caused the other planktonic algae to increase considerably. Under these conditions, cyanobacteria were not dominant any more. Percentage of diatoms also increased, because they have a considerably higher growth rate than the other planktonic algae and cyanobacteria in the simulation during the cold season. Therefore, they were more advantageous by competition with the other two groups for phosphorus. Their percentage in the total phytoplankton biomass increased even more in the dry year that was colder. However, during the warmer season, the other planktonic algae advantage of faster nutrient uptake and growth became more

important and they became the dominant group when phosphorus inputs were decreased and nitrogen inputs were left the same as in the basic simulation.

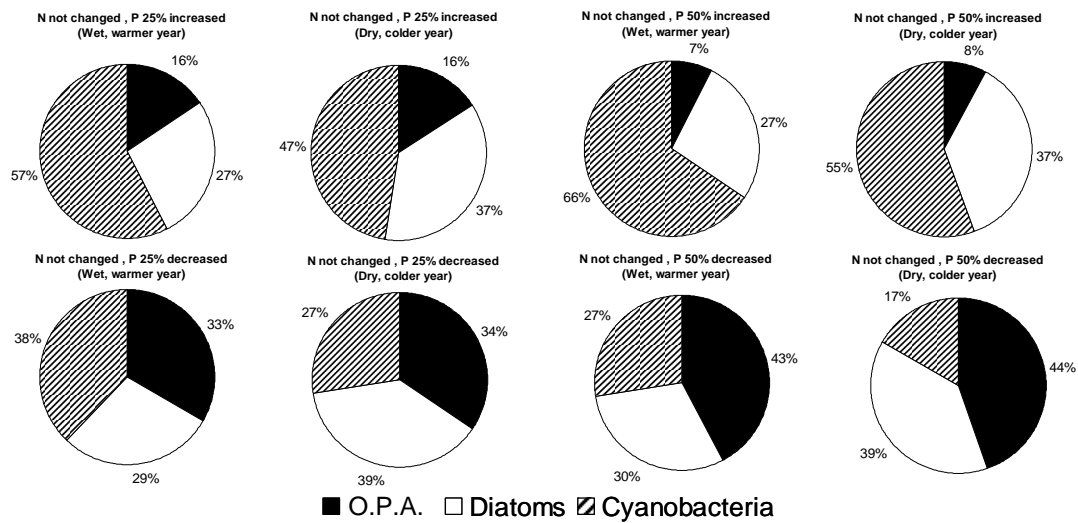


Figure 17. Yearly averaged compositions of phytoplankton according to three groups in case of change of phosphorus inputs only

Yearly averaged compositions of phytoplankton according to three groups in case of nitrogen and phosphorus inputs increase are illustrated in Figure 18. Cyanobacteria were the dominant group for any combination, where both of the nutrients were increased. The other planktonic algae were always less abundant than the other two groups. Diatoms were never dominating because of temperature limitation and grazing by zooplankton. In case of decrease of nitrogen and phosphorus inputs (Figure 19), the other planktonic algae were always more abundant than the diatoms and in cases of decrease of phosphorus inputs by 50% the most dominating phytoplankton group. Cyanobacteria were dominating group in two simulations, when nitrogen and phosphorus were decreased by 25% and when nitrogen inputs were decreased by 50% and phosphorus inputs were decreased by 25%.

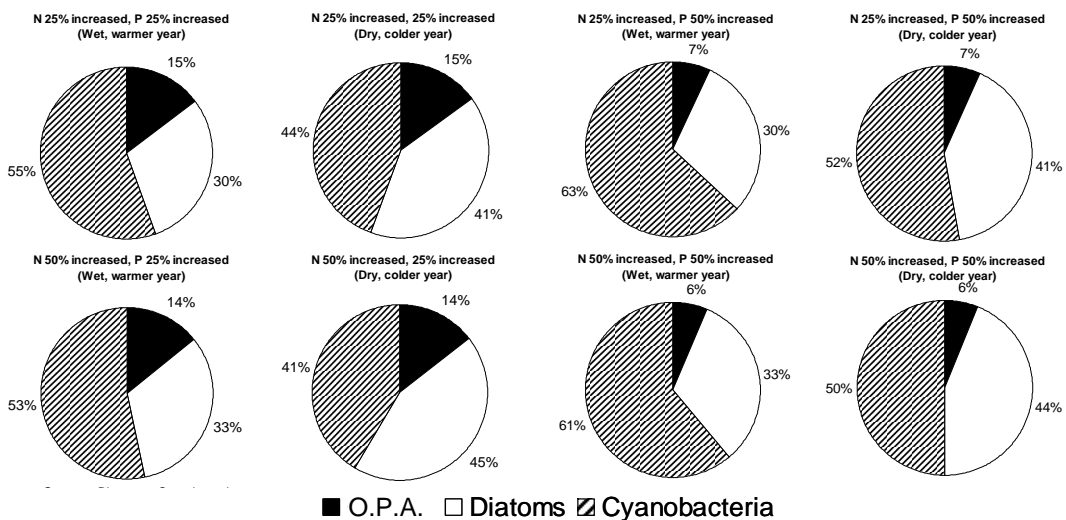


Figure 18. Yearly averaged compositions of phytoplankton according to three groups in case of nitrogen and phosphorus inputs increase

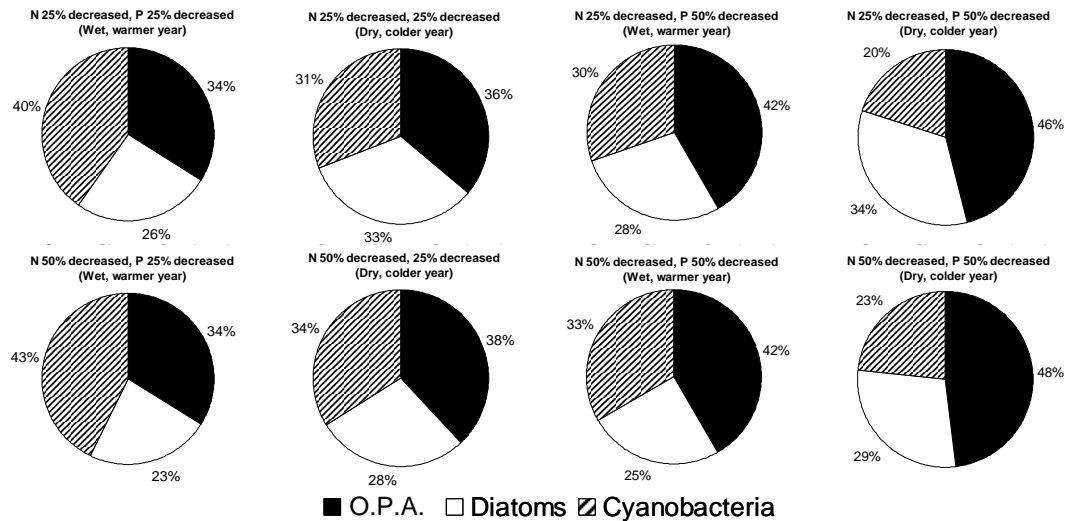
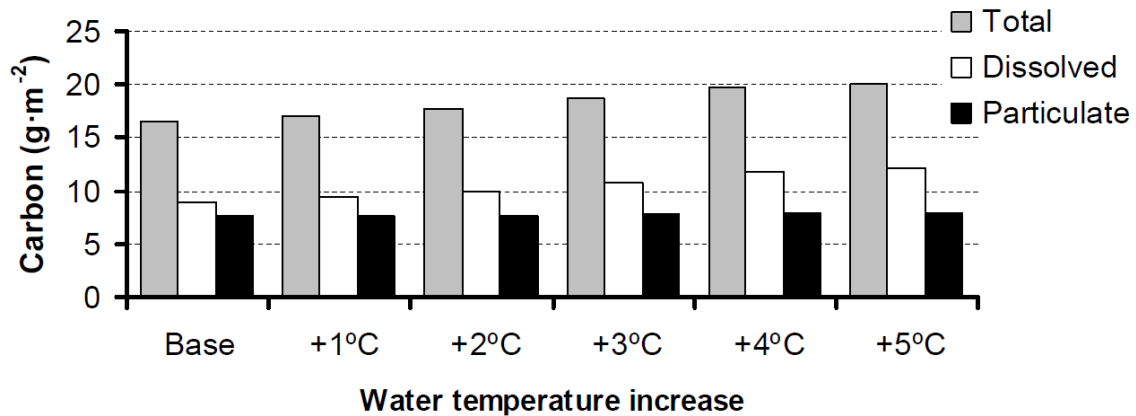


Figure 19. Yearly averaged compositions of phytoplankton according to three groups in case of nitrogen and phosphorus inputs decrease

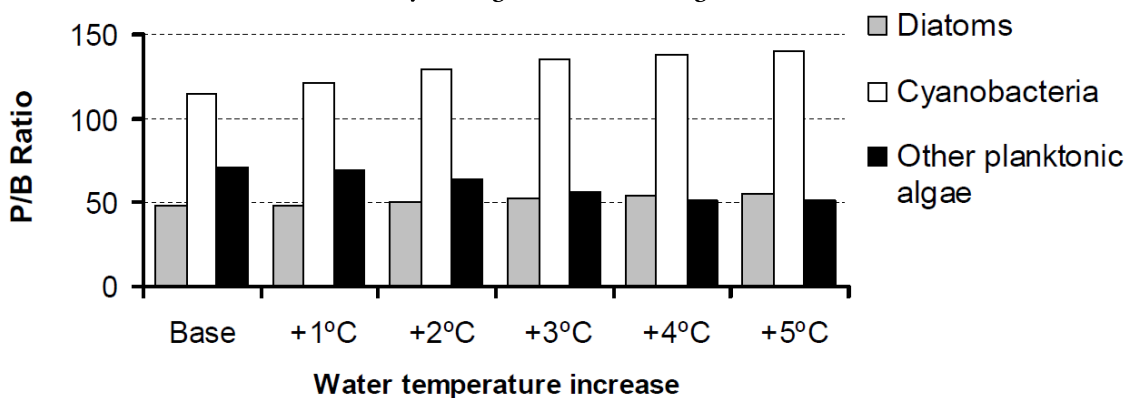
Taking into account all the discussions in the previous paragraphs together with Figure 15, where the differences of total phytoplankton biomass for nitrogen and phosphorus input changes from the basic simulation results are presented, it is clear that phosphorus is the limiting nutrient for primary production, if entire years are considered. However, different combinations of nitrogen and phosphorus inputs control the relative amounts of annual biomasses of three phytoplankton groups.

5.3 Estimating of the Impact of Climate Change on the Carbon Distribution in Lower Levels of the Curonian Lagoon Foodweb

The model was used to simulate the effects of possible warming of the Curonian Lagoon due to climate change. The scenarios here are fictive just to test the behaviour of the model at increased lagoon water temperature. Forcing factors except the temperatures were not changed. The spatially and temporally (yearly) averaged results are summarized in Figure 20 and Figure 21.



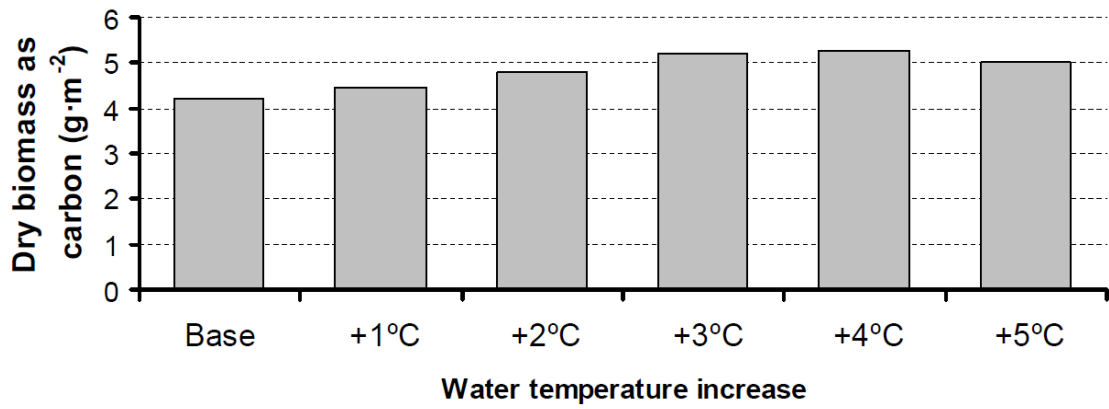
(a) Yearly Averaged Results for Organic Carbon



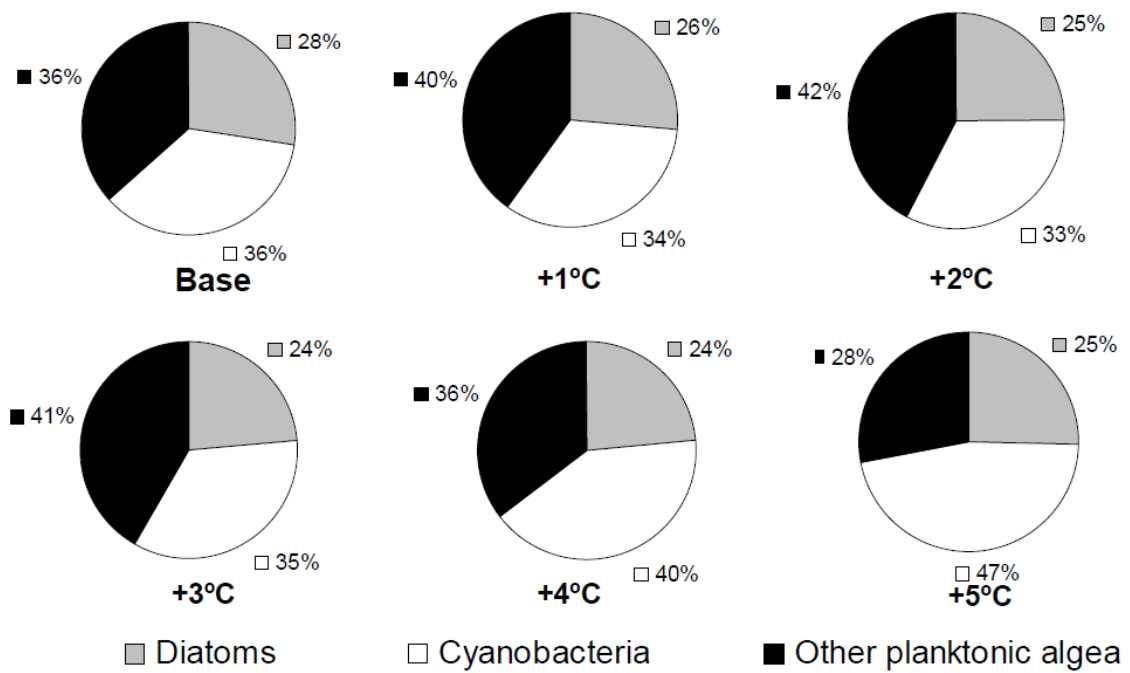
(b) Yearly Production over Biomass Results for Organic Carbon

Figure 20. Simulation results of organic matter and primary production with different increase of water temperature.

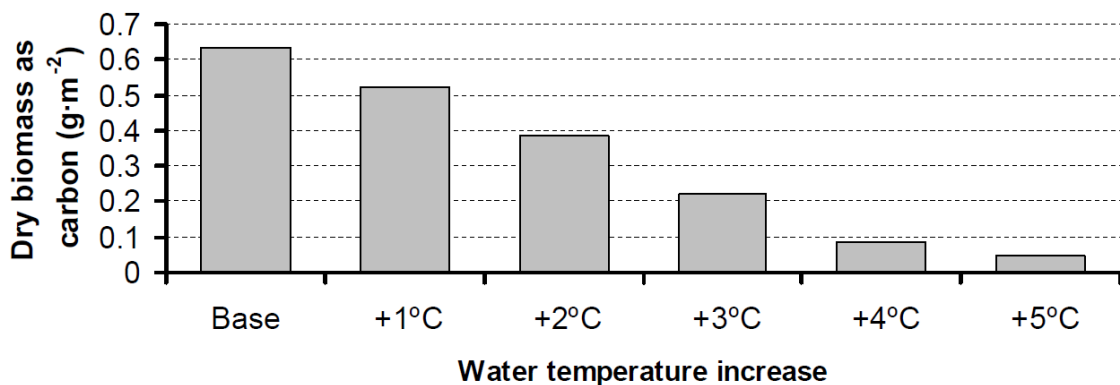
As seen from the figures, the total phytoplankton biomass increases first with temperature, but then decreases. This is because of the temperature stress effects considered by the model where the death rate constant is increasing with the temperature. Dead organic carbon is increasing with increasing temperature indicating that the total primary production is increasing, however with decreased net primary production so that dead organic matter is accumulating in the system even though the total phytoplankton concentration is decreasing after an increase of 4°C in water temperature. Figure 20b illustrates the response of production over biomass ratio to the increase in temperature. Basically, diatoms that prefer colder water are not affected by temperature increase since they dominate the phytoplankton community on the colder seasons and do not peak in warmer seasons. Therefore their yearly average biomass does not change considerably. Consequently, the main competition is between the cyanobacteria and the other planktonic algae. As seen in Figure 20b, production over biomass ratio is increasing by cyanobacteria and decreasing by other planktonic algae. Since cyanobacteria are less available as food source, the ecotrophic efficiency of the Curonian Lagoon can be expected to decrease if the temperature increases, because there would be less of available phytoplankton biomass to upper levels of the food web. This effect is reproduced by the model as well by the continually decrease of zooplankton when the temperature increases (Figure 21).



(a) Yearly Averaged Results for Total Phytoplankton Biomass



(b) Yearly Averaged Results for Phytoplankton Composition



(c) Yearly Averaged Results for Total Zooplankton Biomass

Figure 21. Simulation results of phyto and zooplankton for different increase of water temperature

6. Conclusions and recommendations

A box type ecological model, which is designed to run considerably faster than the spatially high resolution models, was developed for the Curonian Lagoon. The tests and simulations during this study have proven that the results of the model were accurate enough for representing the nutrient and phytoplankton dynamics in the Curonian Lagoon as well as spatial differences which are of ecological interest.

A trophic network model that was developed for the Curonian Lagoon in a previous study was extended, linked with NPZD model and used to test the consistency of an NPZD model with the Curonian Lagoons ecosystem. The NPZD model was found to be consistent.

The ecotrophic efficiencies calculated by linked trophic network and NPZD models were considerably lower than 1 as calculated by the trophic network model for three phytoplankton groups indicated that the primary production is relatively high in the Curonian Lagoon and is unlikely to be controlled by the organisms that are on the higher trophic levels of the food web. That was also confirmed by the experimental data (Pilkaitytė and Razinkovas, 2007).

Analysis of NPZD model scenarios with different nutrients inputs revealed that phosphorus is the main limiting nutrient for primary production in the Curonian Lagoon. However, different combinations of nitrogen and phosphorus inputs control the relative abundance of different phytoplankton groups.

NPZD model was also used for analysis of the ecosystem reaction to water temperature change. The results show that the temperature increase finally leads decrease of available phytoplankton biomass to upper levels of the food web.

This study was a first attempt to link an NPZD model and a high level trophic network model. The results have shown that such a type of linkage between two models dealing with different levels of the food web and producing results on different time scales can be considered as feasible. However, the trophic lagoon network model and the linkage could be considered as prototypes and further development is needed to have a better and more complete understanding of the Curonian Lagoon ecosystem.

First step to extend the trophic lagoon network model would be to add seasonality. Since Ecopath works on the assumption of mass balance of an arbitrary period it is possible to generate different trophic network models for different seasons within a year. Those models can be further extended by adding more accurate data (such as migration of fish and birds) related to the behaviour of several groups. Another extension could be to divide the Curonian Lagoon into different ecological zones or habitats and link them with the corresponding cells of the NPZD model. Extension of the linkage from Ecopath model to Ecosim and using that tool to investigate the dynamics of the Curonian Lagoon over different set of climatic conditions including “dry”, “wet”, “cold” and “hot” years could be considered as the final stage of this type of linkage. At this stage, the NPZD model should be further extended to write the information directly into the Ecosim model database file to prevent excessive efforts that is needed by the user by entering all the necessary link information manually, since Ecosim needs more detailed information than Ecopath when being linked with the NPZD model.

Acknowledgement

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ANGLIES-AZOTO-FOSFORO CIKLO IR MITYBININIO TINKLO MODELIŲ APJUNGIMAS ESTUARINEI LAGŪNAI

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Santrauka

Šioje studijoje buvo sukurti NPZD (Nutriens-Phytoplankton-Zooplankton-Detritus) modelis bei mitybinio tinklo modelis, aprašantis aukštesnių mitybos lygmenų organizmus ir šie abu modeliai buvo apjungti į vieną, remiantis “kontrolės iš apačios į viršų” principu. Toks apjungimas suteikia galimybę pasinaudoti abiejų tipų modelių privalumais; kiek įmanoma realistiškas sunkiai nuspėjamos planktono ir biogenų dinamikos aprašymas, tuo pačiu apimant sudėtingesnius organizmus, kurie į aplinkos poveikį reaguoja didesnėje laiko skalėje. Sukurti modeliai buvo pritaikyti Lietuvai svarbios estuarinės lagūnos, Kuršių marių, ekosistemai. Skaičiavimai ir modelio patikra parodė, kad NPZD modelis pakankamai gerai aprašo biogenų ir fitoplanktono dinamiką bei erdvinį pasiskirstymą. Apjungimas su mitybinio tinklo modeliu pademonstravo, kad NPZD modelio rezultatai gerai derinasi su Kuršių marių ekosistemos specifika. Modeliavimo rezultatai patvirtino, kad Kuršių marios pasižymi pakankamai aukšta pirmine produkcija ir kad nepanašu į tai, kad ji būtų kontroliuojama aukštesnių mitybos lygmenų organizmų. NPZD modelio scenarijų su skirtingais atnešamų biogenų lygiais analizė parodė, kad pagrindinis biogenas, limituojantis Kuršių marių pirminę produkciją, yra fosforas. Tačiau skirtingos azoto ir fosforo lygių kombinacijos nulemia skirtingų fitoplanktono grupių dominavimą. Ekosistemos reakcijos į vandens temperatūros kilimą analizė parodė, kad temperatūros kilimas galų gale pasireiškia fitoplanktono tinkamo aukštesnių mitybinio tinklo lygio organizmams sumažėjimu.

Pagrindiniai žodžiai: Ekologinis modeliavimas, NPZD modelis, Mitybinio tinklo modelis, Ecopath, SHYFEM, Kuršių marios.