LATVIJAS UNIVERSITĀTE
ĢEOGRĀFIJAS UN ZEMES ZINĀTŅU FAKULTĀTE
VIDES ZINĀTNES NODAĻA

Bärbel Müller-Karulis
Promocijas darbs

Modelling carbon and nutrient fluxes in Baltic Sea subsystems

Rīga, 2010

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Promocijas darbs izstrādāts doktora grāda iegūšani ģeogrāfijā, vides zinātnes nozarē, vides aizsardzības apakšnozarē

Darba zinātniskais vadītājs
Docents *Dr. ģeogr.* **Juris Aigars**

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1 Introduction

The Baltic Sea is one of the largest brackish water basins in the world (Leppäranta & Myrberg 2009). It is closely surrounded by land with a drainage basin approximately four times larger than its surface area. This catchment area supports a population of 85 million inhabitants with well developed agricultural and industrial sectors, in particular in the densely populated southern part (HELCOM 2009). The proximity to land makes the Baltic Sea vulnerable to eutrophication, defined as an increased supply of organic matter to the ecosystem (Nixon 1995). Inputs of dissolved inorganic nitrogen are presently approximately three times larger than in 1900; inorganic phosphorus exceeds the loads in 1900 even by four times (Schernewski & Neumann 2005, Savchuk et al. 2008). Eutrophication has, besides its primary symptom – the increase of phytoplankton biomass and primary production, far-reaching secondary impacts on the Baltic Sea ecosystem, leading to reduced water transparency, oxygen deficiency in coastal waters and loss of phytobenthos habitats and benthic macroinvertebrate communities (Elmgren 2001, Elmgren & Larsson 2001, Bonsdorff et al. 1997, Jansson & Dahlberg 1999). According to a recent HELCOM assessment eutrophication significantly affects the central parts of all Baltic basins except the Bothnian Bay and the northeastern tip of the Kattegat, as well as 150 out of the 161 coastal areas investigated (HELCOM 2009).

Restoring the Baltic Sea ecosystem to a state largely unaffected by eutrophication is the goal of major policy initiatives in the region, as for example the HELCOM Baltic Sea Action Plan (HELCOM 2007), the EU Water Framework Directive (2000/60/EC), and the EU Marine Strategy Framework Directive (2008/56/EC). However, nutrient load reductions are costly (Gren 2008), whereas their ecosystem effects are modulated by complex non-linear feedbacks (Vahtera et al. 2007, Conley et al. 2009) and dampened by long nutrient residence times (Elmgren 2001). Moreover, important components of the Baltic nutrient budget, as denitrification and nutrient burial in bottom sediments, cannot be adequately measured on basin-wide scales. Ecosystem models therefore provide a tool for integrating field observations to basin-wide nutrient budgets (Vichi et al. 2004, Savchuk 2002), as well as to predict ecosystem response to different nutrient load reduction scenarios (e.g. Wulff et al. 2007, Neumann et al. 2002). The oceanographic setting of the Baltic as a network of sub-basins with distinct ecosystem characteristics provides a number of test areas to exploit different modelling approaches. This thesis presents and compares five models developed to simulate the dynamics of nutrients and biota and to analyze the underlying carbon and nutrient fluxes, using the Kattegat, the Gulf of Riga, and several coastal ecosystems as study areas. In the following I will briefly introduce the oceanographic setting of the Baltic Sea and summarize how nutrients are transformed within its ecosystem, focusing on processes relevant to eutrophication effects, in order to provide a framework for presenting different modelling approaches.

The Baltic Sea basin was created during the last ice-age, when glaciers advancing from Scandinavia carved out a depression in the Fennoscandian bedrock. Corresponding to their shape and movement, several sub-basins where formed, which are separated from each other by sills of varying depth (Leppäranta & Myrberg 2009). These sills restrict the water exchange between the sub-basins, forming subsystems with distinct hydrological and biological characteristics. Shallow sills in Western part of the basin, within the Kattegat/Belt Sea area, restrict the water exchange with the North Sea. Major salt water inflows into the Central Baltic Sea, i.e. the area east of

Bornholm, occur infrequently during exceptional wind and pressure conditions (Matthäus & Franck 1992, Schinke & Matthäus 1998, Meier et al. 2006). Due to their high density, the inflowing water masses spread along the bottom of the Baltic Sea main basins, creating a permanent halocline which separates the brackish surface waters from saline bottom waters. Strength and depth of the halocline varies dependent on the frequency and intensity of salt water inflows, the distance of a sub-basin from the North Sea, and the effective sill depth by which it is separated from the inflowing salt water. Out of the subsystems represented in this thesis, only the Kattegat is stratified by a permanent halocline, while salinity stratification is negligible in the Gulf of Riga and the coastal areas modelled.

Eutrophication in the Baltic Sea came to attention in the 1960ies, when Fonselius (1969) reported extensive oxygen depletion in its deep basins. Fonselius' report triggered a scientific debate (Elmgren 2001) whether increased production and sedimentation of organic matter or natural fluctuations in hydrographic conditions were responsible for the decrease in oxygen concentrations. Because Baltic Sea nutrient and biota concentrations were poorly monitored and quantitative data on nutrient inputs were widely lacking, the first HELCOM assessment of the Baltic Sea ecosystem detected eutrophication effects in coastal areas, but was unable to distinguish changes in nutrient concentrations in its central basins from natural fluctuations (Melvassalo et al. 1981).

Since then a number of internal transformations have been identified, which determine, how the ecosystems in Baltic Sea sub-basins respond to increasing nutrient loads. Nutrient assimilation by phytoplankton and consequently primary production are determined by the supply of the limiting nutrient, i.e. the nutrient which is, compared to the phytoplankton elemental composition, in short supply (Granéli et al. 1990). Unassimilated nutrients partially accumulate in the water column or are exported with the water exchange between Baltic subbasins (Wulff & Stigebrandt 1989). Further, the structure of the pelagic ecosystem determines the magnitude of nutrient export to the bottom sediments (Heiskanen & Kononen 1994, Lignell et al. 1993, Wasmund et al. 2005). Subsystems with pronounced diatoms blooms in spring transport a large fraction of the nutrient inputs into the bottom sediments, while ecosystems with intensive pelagic remineralization of organic matter retain nutrients in the euphotic zone where they further increase primary production.

Sedimentation of organic matter and its subsequent decomposition coupled to oxygen consumption has far-reaching, non-linear effects on nutrient fluxes. Internal loading, i.e. the input of nutrients to the water column from organic matter remineralized in the bottom sediments consists a substantial flux in the nitrogen and phosphorus budgets of Baltic Sea subsystems (Conley et al. 2002, Vahtera et al. 2007). Phosphorus is released from bottom sediments under oxic and anoxic conditions (Karlson et al. 2007, Hille et al. 2005), but rates increase at low oxygen concentrations (Schneider et al. 2002, Gunnars & Blomqvist 1997, Mort et al. 2010). Also nitrogen transformations in the bottom sediments, in particular denitrification, depend in a complex, nonlinear way on bottom water oxygen conditions (see review by Conley et al. 2009), because despite being an anaerobic process, denitrification relies on a source of oxidized nitrogen. Further, stratification and intermittent bottom water renewal add to the complexity of nutrient fluxes from the bottom sediments. While oxygen contents in the deep basins of the Baltic Sea continuously decrease during stagnation periods, the resulting deepening of the halocline increases the area of well-oxygenated sediments and as a net effect, reduces the internal loading of phosphorus (Conley et al. 2002).

Phosphorus ultimately limits primary production in marine ecosystems, because phytoplankton communities can compensate nitrogen deficiency by nitrogen fixation (Tyrell 1999). On seasonal scales phytoplankton production in the Baltic is primarily nitrogen limited (Granéli et al. 1990), but salinity conditions in most parts of the Baltic are suitable for cyanobacteria growth (Wasmund 1997) and consequently also Baltic Sea phytoplankton communities partially compensate nitrogen deficiency by an increased proportion of nitrogen fixing cyanobacteria (Vahtera et al. 2007, Stal et al. 2003, Larsson et al. 2001). This creates a feedback loop between phosphorus inputs, enlarged algal growth, increased sedimentation and oxygen consumption, which in turn further intesifies the internal phosphorus loading (Vahtera et al. 2007).

Ultimately, the long-term response of Baltic Sea ecosystems to changes in nutrient loads is determined by the balance of nutrient sources and sinks (Wulff & Stigebrandt 1989) created by their major biogeochemical fluxes (Savchuk & Wulff 2009, Vichi et al. 2004). Because nitrogen can be transformed to gaseous N_2, the oceanic nitrogen cycle is generally more flexible than the phosphorus turnover (Toggweiler 1999) and also in the Baltic Sea, nitrogen removal by denitrification and anammox is an efficient nitrogen sink (Shaffer & Rönner 1984, Gran & Pitkänen 1999, Hietanen & Kuparinen 2008, Tuominen et al. 1998). Phosphorus is eliminated more slowly from Baltic ecosystems by burial in deep sediment layers (Hille et al. 2005) and export to adjacent basins (Artioli et al. 2008). As shown above, both nitrogen and phosphorus transformations are subject to complex, non-linear feedback mechanisms which make it difficult to predict the intensity of their removal, and therefore complicate forecasts of ecosystem response to changes in nutrient loads (Savchuk & Wulff 1999).

Eutrophication is also suggested to have caused substantial increases in higher trophic level productivity (Hansson & Rudstam 1990). Catches of herring and sprat have increased in the Baltic, but the relative importance of eutrophication, fishing effort, reduced predation by marine mammals and climate change are unclear (MacKenzie et al. 2002). However, even in the species poor central Baltic ecosystem interactions between eutrophication and fish communities are complex. While the planktivores herring and sprat seem to benefit from increased lower trophic level productivity, bottom water anoxia impacts recruitment of the main piscivore, cod (Hansson et al. 2007). Therefore successful management of the Baltic Sea ecosystem has to take on integrated approach, considering not only the effects of nutrient load reduction on the lower trophic levels, but also its impacts on marine resources.

The need for reliable predictions of ecosystem response to changes in nutrient loads is further amplified by the slow response of the Baltic Sea ecosystem to management actions and the high cost of nutrient load reductions. The long nutrient residence times effectively buffer the effect of load reductions (Elmgren 2001), putting pressure on managers and policy makers who need to see improvements in response to remedial actions. At the same time, cost of nutrient load reduction measures are substantial. For example, costs of reducing the nitrogen load to the Baltic Sea by 381 000 tons, about three times as much than proposed by the HELCOM Baltic Sea Action Plan (HELCOM 2007), are estimated at 360 Mio Euro if the reductions are allocated to the riparian countries in a cost-efficient manner; if each country were to reduce nitrogen emissions proportional to their present inputs, the associated costs would reach 1 Mill Euro (Gren 2008). In this context numerical models provide a basis for predicting ecosystem response to nutrient load reductions (Ducrotoy & Elliott 2008) and for designing a cost-efficient strategy in allocating nutrient load reductions. For example the MARE NEST model (Wulff et al. 2007), which forms the basis of the nutrient load reductions agreed upon in the Baltic Sea action plan, is based on a simple biogeochemical model of nitrogen and phosphorus fluxes (Savchuk & Wulff 2009) and represents a major success story in designing management actions based on quantitative model predictions.

Aim of the work

My thesis aims to compare different modelling approaches for simulating the dynamics of nutrients and biota in Baltic Sea subsystems in order to identify major carbon and nutrient fluxes within the ecosystem and to describe the driving factors shaping short-term and long-term ecosystem changes.

Tasks of the work

- Construct models of nutrient and phytoplankton dynamics in different Baltic Sea subsystems;
- Analyze how physical and biological process resolution in the models affects simulated nutrient and phytoplankton dynamics;
- Extract carbon and nutrient fluxes from the models constructed and compare their magnitude to field observations and experimental data;
- Identify the driving factors of nutrient and phytoplankton dynamics based on the model results;
- Test the ability of a biogeochemical model to hindcast the long-term dynamics of nutrients and biota in the Gulf of Riga;
- Exploit model approaches to simulate carbon fluxes to higher trophic levels

Scientific novelty

Ecosystem modelling in the Baltic Sea has progressed from qualitative descriptions of nutrient load effects on the ecosystem to hindcasts (Eilola et al. 2010, Savchuk & Wulff, 2009) of nutrient and oxygen dynamics on decadal scale. In this context, the long-term biogeochemical model for the Gulf of Riga (publication III) is the first model in the Baltic to include phytoplankton biomass and composition in the calibration data set and to my knowledge, is the only Baltic ecosystem model so far that is validated by an independent data set not applied during calibration.

Publications I, II, III, and IV systematically make use of marine monitoring data collected within the framework of HELCOM COMBINE and apply models to explain ecosystem properties as well as to support the interpretation of the monitoring data themselves (publication II). The models constructed demonstrate that basin-scale (publications I, III, IV) and station-scale (publication II) estimates of carbon and nutrient fluxes in the lower trophic levels can be derived from monitoring observations by means of ecosystem models.

Models presented in publications I - III apply optimization algorithms for parameter estimation. To my knowledge, numerical routines for parameter estimation have not been applied before in calibrating Baltic ecosystem models.

Finally, carbon transfers to higher trophic levels have so far mainly been analyzed for the central basins of the Baltic Sea. Publication V presents a first comparison of carbon flows in various coastal ecosystem.

Major achievements

Major achievements of this thesis are the successful modelling of phytoplankton and nutrient dynamics in the water column of the Gulf of Riga (publication II) and the calibration of a basin-scale biogeochemical model for the Gulf of Riga (publication III). The Gulf of Riga biogeochemical model can be directly applied to study the effect of nutrient load reduction scenarios, as proposed for example by the Baltic Sea Action Plan (HELCOM 2007) and is therefore highly relevant to marine environmental management in Latvia.

Analysis of carbon and nutrient fluxes simulated by the models highlight the importance of bottom water entrainment and land-based nutrient loads for phytoplankton dynamics in the Kattegat and the Gulf of Riga. The model constructed for the Southern Gulf of Riga (publication II) clearly indicated, that the current high-frequency monitoring station is not representative for the central Gulf of Riga and therefore contributes directly to data interpretation and design of the Latvian national marine monitoring programme.

Outcome of the work and approbation of the results

The results of the thesis are published in 4 scientific articles and an additional manuscript (publication III) is submitted to the Journal of Marine Systems. Further, the results of the thesis were presented at ten scientific conferences and gained a best poster award at the 2002 Baltic Sea Science Congress. In total the author has 14 publications.

Publications

The results of the thesis are published in 4 scientific articles (3 of them SCI publications) and one submitted manuscript.

Toompuu, A., Carstensen, J., Müller-Karulis, B. 2003. **Seasonal variation of average phytoplankton concentration in the Kattegat.** Journal of Sea Research, 49(4), 323-335 (publication I)

Müller-Karulis B. 2002. **Process simulation**. In: Carstensen, J., Conley, D., Lophaven, S., Danielsson Å., Rahm L., Toompuu A., Müller-Karulis B. 2002. **Statistical analysis and modelling of phytoplankton dynamics – exploitation of data in the Nordic and Baltic monitoring programs.** TemaNord 2002:532, 77-95 (publication II)

Müller-Karulis, B. Aigars, J. 2010. **Modelling the long-term dynamics of nutrients and phytoplankton in the Gulf of Riga.** Submitted to Journal of Marine Systems (publication III)

Carstensen, J., Conley, D., Müller-Karulis, B. 2003. **Spatial and temporal resolution of carbon fluxes in a shallow coastal ecosystem.** Marine Ecology Progress Series, 252, 35 – 50 (publication IV)

Tomczak, M., Müller-Karulis, B., Järv, L., Kotta, J., Martin, G., Minde, A., Põllumäe, Razinkovas, A., Strāķe, S., Bucas, M., Blenckner, T. 2009. **Analysis of trophic networks and carbon flows in South Eastern Baltic costal ecosystems**. Progress in Oceanography 81, 111-131 (publication V)

Other scientific publication

Conley, D., Bjorck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafson, B.G., Hietanen, S., Kortekaas, M., Kuosa, H., Meier, H.E., Muller-Karulis, B., Nordberg, K., Norkko, A., Nurnberg, G., Pitkanene, H., Rabalais, N., Rosenberg, R., Savchuk, O.P., Slomp, C., Voss, M., Wulff, F., Zillen, L. 2009. **Hypoxia-related processes in the Baltic Sea**. Environmental Science and Technology 43 (10), 3412-3420, DOI: 10.1021/es802762a

Mollmann, C., Diekmann, T., Muller-Karulis, B., Kornilovs, G., Plikshs, M., Axe, P. 2009. **Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea.** Global Change Biology 15, 1377–1393, doi: 10.1111/j.1365-2486.2008.01814.x

Möllmann, C., Müller-Karulis, B., Kornilovs, G., St. John, M.A. 2008. **Effects of climate and overfishing on zooplankton dynamics and ecosystem structure - regime shifts, trophic cascade and feedback loops in a simple ecosystem.** ICES Journal of Marine Science, 2008 65(3):302-310; doi:10.1093/icesjms/fsm197

Aigars, J., Müller-Karulis, B., Martin, G., Jermakovs,V. 2008. **Ecological quality boundary-setting procedures: the Gulf of Riga case study.** Environmental Monitoring and Assessment 138 (1-3), 313 – 326, DOI 10.1007/s10661-007-9800-5

Ustups D., Uzars D. and Müller–Karulis B. 2007. **Size structure and feeding ecology of fish communities in the surf zone of the Eastern Baltic**. Proceedings of the Latvian Academy of Sciences. Section B, Vol. 61, No. 3 (650), 20–30.

Nordic Council of Ministers. With contributions from Carstensen, J., Bjerkeng, B., Kauppila, P., Kubiliute, A., Müller-Karulis, B., Rolff, C. & Toompuu, A. 2006. **Ecological status classification of marine waters. Indicator development and monitoring requirements. Nordic Council of Ministers**. - TemaNord 2006:582: 150 pp.

Müller-Karulis, B., Poikāne, R., Segliņš, V. 2003. Heavy metals in the Ventspils harbour: identifying processes from a multi-parameter dataset. Environmental Geology 43: 445 – 456

Müller-Karulis, B. 1999. **Transformations of riverine nutrients in the Daugava river plume (Gulf of Riga).** ICES Journal of Marine Science 56 Supplement: 180 – 186

Conferences

Latvijas Universitātes 68. Zinātiskā Konference, Rīgā, 2010. gada februārī
Müller-Karulis, B., Sennikovs, J., Aigars, J. Klimata izmaiņu ietekme uz biogēnu vielu un fitoplanktona dinamiku Rīgas līcī – modeļa rezultāti, p. 66

Baltic Sea Science Congress 2009, Tallinn, Estonia, August 17 – 21
Müller-Karulis, B., Sennikovs, J., Aigars, J. Modelling the impact of climate change on nutrients and phytoplankton in the Gulf of Riga (p. 49)

Latvijas Universitātes 65. Konference, Rīga, 2007. gada februārī
B. Mueller-Karulis, C. Mollmann, M. Plikšs, G. Korņilovs Svarīgākie signāli Baltijas jūras un Rīgas līča vides monitoringa datu rindās: 1973–2004

Latvijas Universitātes 63. Konference, Rīga, 2005. gada februārī
Millere-Karulis, B., Strāķe, S., Ustups, D., Minde, A., Korņilovs, G. Oglekļa un biogēnu vielu aprite Rīgas līča atklātajā daļā, p. 207

Baltic Sea Science Congress 2003, Helsinki, Finland, August 24 – 28, 2003. Müller-Karulis, B., Timuhins, A., Bethers, U. A 1D coupled physical-biogeochemical model to assist marine monitoring data interpretation. p. 53

Baltic Sea Science Congress 2003, Helsinki, Finland, August 24 – 28
Müller-Karulis, B., Savchuk, O. Modelling the long-term dynamics of nutrients and phytoplankton in the Gulf of Riga. p. 194 (poster, best poster award)

BOOS Workshop on Ecosystem Monitoring and Modelling, May 13-15, 2002, St. Petersburg, Russia

ASLO International Meeting Copenhagen, Denmark June 5-9, 2000 (poster)
Müller-Karulis, B. Nutrient cycling in the pelagic system of the Gulf of Riga reconstructed from monitoring data

Young Scientists Conference on Marine Ecosystem Perspectives:
20-24 November 1999, Gilleleje, Denmark Müller-Karulis, B. A box model for phytoplankton dynamics at an intensive monitoring station, p. 27

Latvijas Universitātes 57. Konference, Rīga, 1999. gada februārī
Millere-Karulis, B. Rīgas līča barības vielu budžets un tā modelēšana

Contribution of the author

- **Kattegat new production model (publication I)**

For the Kattegat new production model, I have developed, programmed and calibrated the nutrient – phytoplankton dynamics in the upper layer of the Kattegat. I have also contributed the description of the biological part of the model and discussed its output for publication I (Toompuu et al. 2003).

- **Simulation model for phytoplankton and nutrient dynamics in the Southern Gulf of Riga (publication II)**

I have developed, programmed and calibrated the entire model as well as described its results in publication II (Müller-Karulis 2002).

- **Long-term biogeochemical model of nutrients and phytoplankton dynamics in the Gulf of Riga (publication III)**

The model is based on a biogeochemical model of the Gulf of Riga developed by Oleg Savchuk to simulate nutrient and phytoplankton dynamics in 1993 – 1995 (Savchuk 2002). Oleg Savchuk has provided a source code in FORTRAN, introduced me to its structure and helped to adapt the model code to long-term simulations. To overcome difficulties in describing e.g. phytoplankton species succession and to improve the response of geochemical reactions to reduced oxygen concentrations, I have later redesigned parts of the model. I have also changed the architecture of the code from procedural based FORTRAN to object oriented Visual Basic. Furthermore, I have introduced automated calibration routines not included in the original model, I have analyzed the outcome of the model simulations and described methods and results in publication III (Müller-Karulis & Aigars, submitted).

- **Kattegat lower trophic level carbon budget model (publication IV)**

The Kattegat lower trophic level carbon flux model was, together with the models presented in publications I and II, developed in the framework of the NorFA funded project “Statistical analysis and modelling of phytoplankton dynamics – exploitation of data in the Nordic and Baltic monitoring programs (STAMP)”. I participated in the developing the conceptual modelling approach, in interpretation of the results and writing of publication IV (Carstensen et al. 2003).

- **ECOPATH models of Southern Baltic coastal ecosystems (publication V)**

The development of carbon flow models in Southern Baltic coastal ecosystems started at a workshop I convened October 18 – 22 in Jūrmala, Latvia (Müller-Karulis 2004). The models were further refined at the 2004 meeting of the ICES Study Group on Baltic Sea Productivity Issues in Support of the BSRP (SGPROD, ICES 2005), which I chaired, and then presented at a theme session organized at the 2005 ICES Annual Science conference (Tomczak et al. 2005 in **Impact of External Forcing on Flows in Marine Trophic Networks,** Conveners: Bärbel Müller-Karulis, Villy Christensen, Arturas Razinkovas). I have participated in assembling and balancing the model of the Gulf of Riga coastal area and contributed at all stages of analyzing and summarizing the model results and writing of publication V (Tomczak et al. 2009).

2 Marine ecosystem model applications

Marine ecosystem modelling evolved by coupling simulation models of different marine ecosystem components. Typically marine ecosystem models focus as biogeochemical models on nutrient and phytoplankton dynamics, or, mainly for the support of fishery management, emphasize the representation of higher trophic levels. With respect to higher trophic levels, this introduction will be limited to models linking the dynamics of lower, i.e. phytoplankton and zooplankton, and upper trophic levels. Models solely simulating fish population dynamics, like surplus production models or age-structured virtual population models (for an overview see Haddon 2001) will not be discussed further. The following chapter will therefore give an overview of the representation of biological, geochemical, and physical processes in biogeochemical models, provide an introduction to models coupling lower and upper trophic levels, and briefly introduce ecosystem model applications in the Baltic Sea.

2.1 Biogeochemical models

Biogeochemical models are element-conserving simplifications of marine ecosystems (Tett & Wilson 2000), which describe the processes governing nutrient turnover, including nutrient regeneration in bottom sediments. Typically a biogeochemical model considers all nutrient sources (riverine input, atmospheric deposition, nitrogen fixation) and sinks (sediment burial, denitrification, export), together with all major pelagic nutrient transfer processes (phytoplankton uptake, pelagic regeneration, sedimentation) and geochemical reactions in the bottom sediments (remineralisation, adsorption, desorption, denitrification) within the system boundaries. Because they are capable of simulating the response of marine ecosystems to nutrient inputs, biogeochemical models are mainly applied for understanding and combating eutrophication of marine ecosystems (Lenhart 2001).

Early modelling approaches, for example the classical Vollenweider model for phosphorus retention in lakes (Vollenweider 1968) or the first nutrient budget model of the Baltic Sea (Wulff & Stigebrandt 1989) used empirical functions to describe the transfer of nutrients from the pelagic system to bottom sediments. Most biogeochemical models, however, now include a mechanistic representation of nutrient uptake by phytoplankton, zooplankton grazing, and sedimentation of particulate organic matter. The parameterization of these processes is often derived from NPZD (**n**utrient-**p**hytoplankton-**z**ooplankton-**d**etritus) models originally developed during the 1950ies and 1960ies to study the seasonal dynamics of phyto- and zooplankton (e.g. Riley 1946). In this context, Sverdrup (1953) simulated how seasonal stratification determines the onset of phytoplankton blooms via the average light intensity experienced by phytoplankton cells. His critical depth concept forms the basis of describing phytoplankton response to light in box models, which parameterize vertical mixing of water, dissolved and particulate matter by transfer fluxes between water layers considered as homogeneously mixed. With the development of more complex ecosystem simulations NPZD models have received fresh attention (Steele & Henderson 1992), providing simple formulations of phytoplankton growth and mortality in response to ambient light and nutrient concentrations as well as a basic description of zooplankton dynamics (e.g. Evans & Parslow 1985, Steele 1976, Steele & Henderson 1995).

Biogeochemical models also describe processes in bottom sediments, which in shallow marine ecosystems play an important role as nutrient sinks and temporal nutrient sources (e.g. Seitzinger, 1988, Conley et al. 2002, Conley et al. 2009, Savchuk 2005, Mort et al. 2010). However, the processes of particle settling, organic matter mineralization and early diagenesis of carbon, nitrogen and phosphorus compounds in the benthic boundary layer are highly complex (Boudreau & Jørgensen 2001). The biogeochemical reactions involved depend on the transport of solutes within the porewater to supply redox equivalents from the overlaying water column and to distribute reaction products within the sediment profile and through the sediment-water interface. Transport processes are limited by molecular diffusion, with bioturbation and bioirrigation in bottom sediments further adding to the complexity of transport and reaction processes. Reactive transport models that fully resolve the biogeochemical reactions as well as the advective and diffusive transports in sediments (e.g. Canavan et al. 2007, Regnier et al. 2003, Centler et al. 2010) require significant computation time during model execution. Therefore biogeochemical models of marine ecosystems mainly apply simplified parameterizations of geochemical reactions in bottom sediments (Kiirikki et al. 2006) that include the mineralization of organic matter, nitrification and denitrification, and the redox-dependent adsorption and desorption of phosphate.

The representation of physical processes within marine biogeochemical models describes the movement of water, dissolved substance and particulate matter fluxes within the model domain. Depending on model complexity, these range from exchange processes between homogeneous compartments in box-models (Anderson et al. 2000) to three dimensional oceanographic models, in which the transport of nutrients and biota is fully coupled to a solution of the Navier-Stokes equations of fluid motion (see for example Aksnes et al. 1995, Haupt et al. 1999 for the Norwegian Sea, Virtanen et al. 1993 for Finnish coastal areas, Crise et al. 1998 and Crispi et al. 1999 for the Mediterranean Sea, Søiland & Skogen 2000 for the North Sea, Tamsalu 1998 for the Gulf of Finland and Neumann 2000, Neumann et al. 2002 for the Baltic Sea). Because vertical gradients of nutrients and biota in marine ecosystems are more pronounced than horizontal differences, some biogeochemical models also resolve only vertical transports (e.g. Aksnes & Lie 1990, Burchard et al. 2006).

Three-dimensional (3-D) ecosystem models typically rely on well-tested oceanographic models to represent water, plankton and nutrient transports, e.g. the Princeton Ocean Model (Blumberg & Mellor 1987), the Modular Ocean Model (MOM 3, Pacanowski et al. 1990), or the Rossby Centre Ocean Model (RCO, Meier et al. 2003). Hybrids between box models and three-dimensional models use oceanographic models to simulate water exchange between model boxes which are treated as spatially homogeneous (e.g. ERSEM for the North Sea, Pätsch & Radach 1997, Baretta et al. 1995). The realistic description of transport processes provided by 3-D models allows simulating the spatial distribution of nutrients and biota, which is especially important for coastal areas and estuaries (Virtanen et al. 1993, Savchuk & Wulff 1999). A 3-D coupled ecosystem model (Neumann et al. 2002) for example indicated that coastal areas in the Baltic Sea will recover from eutrophication more quickly than its central region. 3-D models are also useful when local phenomena are of concern that are sensitive to oceanographic conditions, e.g. advection by currents and water column mixing. For example Roiha et al. (2010) used a 3-D model to produce forecasts of algal blooms in the Baltic Sea.

2.2 Models describing higher trophic levels

Using NPZD models as the core biological component of biogeochemical models limits their application to describing the dynamics of the lower trophic levels in marine ecosystems, since they mostly do not represent predation on zooplankton explicitly. Instead, a closure term is applied to simulate zooplankton mortality, allowing it to increase either linearly or quadratically with zooplankton biomass to mimic effects of intraspecific competition and predation. While the type of closure term affects the accuracy to which zooplankton dynamics and stage structure can be represented (Henderson & Steele 1995), the simple model cut-off at the zooplankton mortality level seems to have little impact on the skill of biogeochemical models to represent nutrient and phytoplankton concentrations (Fennel 2009).

Strong interactions between planktivorous fish, zooplankton and phytoplankton occur predominantly in lake ecosystems (Van de Bund et al. 2004). Limnic trophic cascades are especially pronounced in eutrophic (Jeppesen et al. 2003) and mesotrophic (Mehner et al. 2008) lakes, where they are even exploited to control phytoplankton biomass by biomanipulation (Shapiro & Wright 1984, Perrow et al. 2004). Estuarine and marine ecosystems seem to have weaker links between phytoplankton and zooplankton (Shurin et al. 2002). This is at least partially due to the absence of large cladoceran grazers in marine systems (Harris, 1999, Stibor et al. 2004). Trophic cascades in marine ecosystems are mainly evident when they involve large, mobile vertebrate predators with high food consumption rates and slow-growing, herbivore prey (Shurin et al. 2002, Reithaus et al. 2008). They are often detected along spatial gradients (Ware & Thomson 2005) or by analyzing time-series that cover also variations in fish populations. For the Baltic Proper, analysis of long-term data has demonstrated that planktivorous fish predation has a significant impact on zooplankton (Möllmann et al. 2008) that cascades further to summer phytoplankton biomass (Casini et al. 2008) and also influences the way zooplankton communities respond to climate forcing (Casini et al. 2009). Modelling approaches to integrate fish predation on zooplankton as well as fish production into biogeochemical models of the Baltic Sea are currently under development (Fennel 2008, Fennel 2009).

Ecosystem models represent higher trophic levels predominantly by individual- or population based approaches (Steele & Clark 1998). Population based models employ the number of individuals per unit volume as a state variable and characterize the members of the population by a statistical property, for example average weight, maturity, growth rate and mortality (Fennel & Neumann 2004). Individual based models in contrast construct a population from a discrete number of members with individual properties that cover the variability of traits in the population. Individual based models then describe the interaction of each individual with its resources, covering its full life cycle (Grimm & Railsback 2005). Both approaches have been used to include higher trophic levels, specifically fish, into ecosystem models.

An alternative to explicitly modelling the population dynamics of higher trophic levels is the analyses of fluxes between ecosystem components, expressed either in terms of energy, carbon or nutrients. ECOPATH (Christensen & Pauly 1992, Christensen et al. 2004) is a popular software tool originally developed for analyzing carbon flows in marine ecosystems at steady state, i.e. at constant biomass levels of all trophic groups. ECOPATH provides a number of network analysis tools to create equivalent flows in a linear trophic chain (Lindeman 1942), conduct input-output analyses (Leontief 1951) or investigate circular pathways (Finn 1976) in foodwebs. Together with ecosystem structure indices derived from information theory (Ulanowicz 1986) these tools offer a formalized approach for analyzing and comparing ecosystem structure (Baird & Ulanowicz 1993).

2.3 Ecosystem model applications in the Baltic Sea

Biogeochemical modelling of the Baltic Sea started in the late 1960ies with box models of phosphorus, phytoplankton, zooplankton and oxygen dynamics. Model development quickly led from steady state models (Bolin 1972, Fonselius 1972) to a dynamic simulation approach (Sjöberg et al. 1972). Already these early simulations showed the slow response of the Baltic Sea to nutrient load reductions (see review by Jansson & Wulff 1977). Presently, there are a number of biogeochemical models for the Baltic Sea or its subsystems available (see Table 1 for a list of current models of the entire Baltic Sea and the Gulf of Riga). Except CoastMab (Håkanson & Bryhn 2008, Håkanson 2009), all models are mechanistic biogeochemical models and include a representation of nutrient regeneration and early diagenesis in the bottom sediments. In particular, the models are capable of simulating the interactions between nitrogen and phosphorus turnover in Baltic ecosystems and its coupling to oxygen dynamics. GoR2002 (Savchuk 2002), GoR2010 (Müller-Karulis & Aigars 2010, publication III), BALTSEM (Gustafsson 2000), ERGOM (Neumann 2000, Neumann et al. 2002) and RCO-SCOBI (Eilola et al. 2009) are based on NPZD models of nutrient turnover in the pelagic system and simulate phytoplankton and nutrient dynamics on sub-seasonal, approximately daily, time-scales. SANBALTS (Savchuk & Wulff 2007, Savchuk & Wulff 2009) was constructed for web-based application within the Baltic NEST model, with model execution time as primary constraint (Savchuk & Wulff 2007). The model therefore uses an annual time-step without resolving the seasonal dynamics of nutrients and phytoplankton. Still, the model represents basin-scale differences and long-term (1970-2003) dynamics of nutrient and oxygen concentrations (Savchuk & Wulff 2009). The maximum allowable nutrient inputs to the Baltic Sea and the country wise load reductions agreed upon in the Baltic Sea Action Plan (HELCOM 2007) are based on simulations conducted with SANBALTS.

CoastMab (Håkanson & Bryhn 2008, Håkanson 2009) in contrast is limited to the phosphorus dynamics in the Baltic Sea. The model contains a detailed budget of phosphorus sources, including post-glacial land uplift, but does not include oxygen dynamics in its simulations and is not capable of describing the redox-dependent temporal storage of phosphorus in bottom sediments. Phytoplankton concentrations, primary production and nitrogen fixation are derived from empirical relationships using total phosphorus, total nitrogen and salinity as input functions.

Table 1: Biogeochemical models of the Gulf of Riga and the Baltic Sea

Model	**GoR 2002**[1]	**GoR 2010**[2]	**CoastMab**[3]	**SANBALTS**[4]	**BALTSEM**[5]	**ERGOM**[6]	**RCO-SCOBI**[7]
System	Gulf of Riga	Gulf of Riga	Gulf of Riga, Baltic	Baltic	Baltic	Baltic	Baltic
Physical resolution	3 boxes	2 boxes	2 boxes (GoR), 12 boxes (Baltic)	8 boxes	13 subbasins, density dependent, cm - m	3D, horizontal 3 – 9 nm, vertical 2 – 6 m	3D, horizontal 6 nm, vertical 3 – 12 m
Output temporal resolution (approximate)	daily	daily	annual	annual	daily	daily	daily
Nutrients	N, P, Si	N, P	P	N, P, Si	N, P, Si	N, P	N, P
Oxygen	x	x		x	x	x	x
Nutrient sources							
River input	x	x	x	x	x	x	x
Import (saline inflow)	x	x	x	x	x	x	x
Atmospheric deposition	x	x	x	x	x	x	x
Nitrogen fixation	x	x	empirical	x	x	x	x
Nutrient sinks							
Sediment burial	x	x	x	x	x	x	x
Denitrification	x	x		x	x	x	x
Export (outflow)	x	x	x	x	x	x	x
Internal processes							
Phytoplankton	three groups	three groups	empirical	nutrient uptake, basin specific maximum rates	three groups	three groups	three groups
Pelagic nutrient regeneration	x	x	x	x	x	x	x
Zooplankton	x	x			x	x	x
Sedimentation	x	x	x	x	x	x	x
Nutrient remineralization in bottom sediments	x	x	x	x	x	x	x
Redox-dependent phosphorus storage in sediments	x	x		x	x	x	x

1: Savchuk 2002, 2: Müller-Karulis & Aigars 2010, publication III, 3: Håkanson & Bryhn 2008, Håkanson 2009, 4: Savchuk & Wulff 2007, 2009, 5: Gustafsson 2003, 6: Neumann 2002, Neumann et al. 2002, Neumann & Schernewski 2005, 7: Eilola et al. 2009

After initial model applications to estimate the effects of nutrient load reductions (Wulff & Stigebrandt 1989, Savchuk & Wulff 1999, Neumann et al. 2002, Neumann & Schernewski 2005) and simulation runs to describe the pre-industrial state of the Baltic Sea (Schernewski & Neumann 2005, Savchuk et al. 2008) efforts have recently increased to demonstrate and improve the reliability of biogeochemical models, especially by conducting long-term hindcasts of nutrient and phytoplankton concentrations. For example, Schernewski & Neumann (2005) have validated the ERGOM model with hindcasts of DIN concentrations for 1990 – 2000; the output from RCO-SCOBI was compared to oxygen and phosphate concentrations in 1960 – 1999 (Eilola et al. 2009), and Savchuk & Wulff (2009) compared nutrient concentrations in nine Baltic subbasins simulated by SANBALTS to data from 1970 – 2003. Recently, Eilola et al. (2010) compared hindcasts by three coupled physical-biogeochemical models - BALTSEM, ERGOM and RCO-SCOBI - to nutrient and oxygen concentrations for 1970 - 2005. Largest differences in model results stemmed from uncertainties in the bioavailable fractions of nitrogen and phosphorus in the nutrient loading and from parameterizations in nitrogen and phosphorus fluxes from the bottom sediments (Eilola et al. 2010). As part of this thesis (publication III), Müller-Karulis & Aigars (2010) calibrated their model for the Gulf of Riga to nutrient, phytoplankton, zooplankton and oxygen concentrations from 1973 – 2000 and validated the simulation results with data from 2001 – 2008.

Also a number of carbon flux models to higher trophic levels have been constructed for Baltic Sea foodwebs. While most Baltic foodweb models describe foodwebs in the central part of its subbasins, Tomczak et al. (2009, publication V) present carbon flows in five coastal areas of the Southern Baltic. For non-coastal areas, Sandberg et al. (2000) analyzed carbon flows in the Baltic Proper, Bothnian Sea and Bothnian Bay, refining earlier carbon flow networks constructed by Elmgren (1984) and Wulff & Ulanowicz (1989). Their model, implemented in ECOPATH, included pelagic and benthic foodweb components. The pelagic components described carbon transfer from phytoplankton to mesozooplankton, invertebrate predators and pelagic fish, including a simplified microbial loop. Benthic fluxes were triggered by meio- and macrofauna consuming detritus and channelling carbon to demersal fish. Demersal fish, in the central Baltic Sea predominantly cod, are also the main piscivores in the system, linking pelagic and benthic foodweb components. Other models have specifically investigated the role of allochthonous carbon in the foodweb of the northern Baltic Sea (Sandberg et al. 2004, Sandberg 2007) or focused on the modelling of commercial fish species, their interactions with primary and secondary producers and the role of fisheries in the ecosystem (Jarre-Teichmann 1995, Harvey et al. 2003, Hansson et al. 2007). The models developed by Harvey et al. (2003) and Hansson et al. (2007) are implemented in the dynamic simulation module of ECOPATH, ECOSIM, and currently serve as fish module in the NEST (http://nest.su.se) decision support system for developing and testing strategies to reduce eutrophication in the Baltic Sea.

3 Study Methodology

The thesis presents five models, which were constructed to simulate different aspects of nutrient and phytoplankton dynamics in Baltic Sea subsystems. The models gradually expand the complexity of biological and geochemical processes included from a simple model of new production in the Kattegat (publication I), to a process model for phytoplankton and nutrient dynamics in the Southern Gulf of Riga (publication II) and finally a basin-scale biogeochemical model of nitrogen, phosphorus and phytoplankton in the Gulf of Riga (publication III). In particular, the processes modelled include phytoplankton response to inputs of new nutrients, the role of bottom water entrainment and freshwater advection for phytoplankton development, as well as nutrient regeneration in the water column and bottom sediments. Two models further focus on carbon turnover, both in the pelagic lower trophic levels of the Kattegat (publication IV) and, as a series of ECOPATH models, on carbon fluxes in coastal ecosystems of the Southern Baltic Sea (publication V).

Models included in publications I, II, and III therefore present a nutrient-based view of the ecosystem, simulating phytoplankton dynamics in response to ambient nutrient concentrations, while the models presented in publications IV and V are forced by measured carbon fluxes at the basis of the foodweb. The pelagic carbon budget model for the Kattegat (publication IV) uses the simulated carbon fluxes to describe the ecosystem response to changes in nutrient inputs, but the ECOPATH models for the southern Baltic coastal ecosystems (publication V) focus on the transfer of carbon to higher trophic levels.

3.1 Study areas

Models were applied to phytoplankton and nutrient dynamics in two open areas, the Kattegat and the Gulf of Riga, including a high frequency monitoring station in the Southern Gulf of Riga (Figure 1), and to five coastal areas along the South-eastern Baltic coast (Figure 2). Distinction between coastal and open areas roughly follows the definition of coastal waters in the EU Water Framework Directive (2000/60/EC), being located up to one nautical mile seaward of the baseline from which the national territorial waters are delimited. Open areas in the context of this thesis are waters outside coastal waters, and, in the case of the Gulf of Riga, also outside transitional waters, which are defined by significant fresh water influence according to the EU Water Framework Directive.

3.1.1 Open sea areas

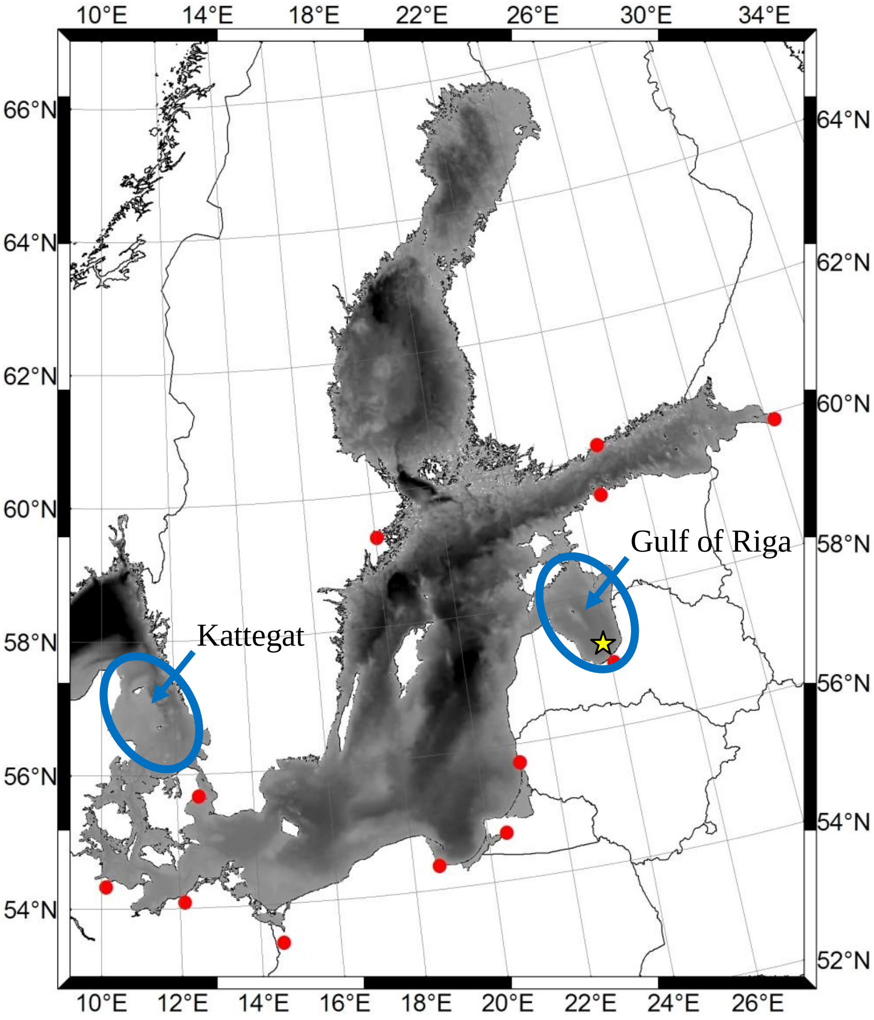

Figure 1: Open sea ecosystems modelled. ★denotes the location of the high-frequency monitoring station 119 in the Southern Gulf of Riga.

Publications I – IV present ecosystem models of two Baltic open sea areas, the Kattegat and the Gulf of Riga (Figure 1). Though similar in size and depth, hydrographic conditions differ greatly between both basins (Table 2). The Kattegat is a transition area between North Sea and Baltic Sea and while the bottom layer of the basin is filled by high saline North Sea water, the surface layer is occupied by the brackish outflow from the Baltic Sea. Typically, a pronounced permanent halocline located in approximately 15 m water depth separates both water layers (Leppäranta & Myrberg 2009). The Gulf of Riga is separated from the Baltic Proper by the Saaremaa and Hiumaa islands. The connecting Irbe Strait and Väinameri areas are shallow (sill depths 20 m and 5 m, respectively, Leppäranta & Myrberg 2009), restricting the water exchange with the Baltic Proper to water masses above the Eastern Gotland Basin halocline. The salinity difference to the Gulf of Riga water mass is not sufficient to generate a persistent halocline and therefore the water circulation is monomyctic, with a seasonal thermocline developing in the summer months.

While the Kattegat receives its nutrient load from a number of small rivers and coastal areas draining directly into the sea, the Gulf of Riga catchment includes the Daugava river, which, according to runoff, is the 4th largest river (HELCOM 2004) entering the Baltic Sea. Together with the close-by Lielupe and Gauja river mouths, the Daugava plume forms a transitional water body in the Southern Gulf of Riga. The extend of the freshwater plume depends on runoff (Müller-Karulis 1999), but during the spring flood the freshwater layer reaches far into the central Gulf, establishing a thin stratified layer before the onset of thermal stratification (Stipa et al. 1999, Stipa 2004). Representative for the open areas of the Southern Gulf of Riga, i.e. the region outside transitional waters but occasionally affected by freshwater during high runoff, publication II presents a model of phytoplankton and nutrient dynamics at a high-frequency monitoring station, station 119. Station 119 (Figure 1) is located at approximately 16 nm distance from the Daugava mouth and 5 nm from the seaward boundary of transitional waters in the Gulf of Riga.

Table 2: Characteristics of the Kattegat and the Gulf of Riga

		Kattegat	**Gulf of Riga**
Area[1]	km^2	22 287	17 913
Mean depth[1]	m	23	23
Stratification[1]		permanent halocline at 15 m depth	no halocline, seasonal thermocline
Salinity	PSU	Surface[1]: 18 – 26 Bottom[1]: 32 - 34	5.2 – 6.1[2]
Ice cover (annual probability) [1]		25 – 50 %	90 – 100 %
Residence time	years	Surface water[3]: 0.1 Bottom water[3]: 0.15	2.8[4]
Nutrient load (riverine + atmospheric)[5]	10^3 tons year^{-1}	N: 89 000 P: 1 900	N: 90 000 P: 2 500
Productive season		March - November	April - October
Primary production[5]	g C m^{-2} year^{-1}	150 – 200	200 – 260

1: Leppäranta & Myrberg 2009, 2: ICES 2009, 3: Gustafsson 2000, 4: Astok et al. 1999, 5: Savchuk & Wulff 2007

3.1.2 Coastal areas

Publication V presents a comparative foodweb analysis of five Southern Baltic coastal ecosystems, using ECOPATH to balance carbon flows. The five systems included (Figure 2) are Puck Bay, the Curonian Lagoon, the Lithuanian Baltic Proper coast, a coastal region in the Gulf of Riga stretching between Ainaži and Dzeņi, and Pärnu Bay. Puck Bay, the Curonian lagoon and Pärnu Bay are sheltered ecosystems with restricted water exchange, while the Lithuanian and Gulf of Riga coast represent open coastal stretches with high wave energy and continuous water exchange with adjacent open areas. Bottom substrate ranges from soft sediments in Puck Bay, the Curonian lagoon and Pärnu Bay to mixed sandy and rocky sediments in the glacial moraines at the Lithuanian and Gulf of Riga coasts. The study areas include only the marine part of the coastal ecosystems and their open sea boundary mostly corresponded to the delineation according to the EU Water Framework Directive.

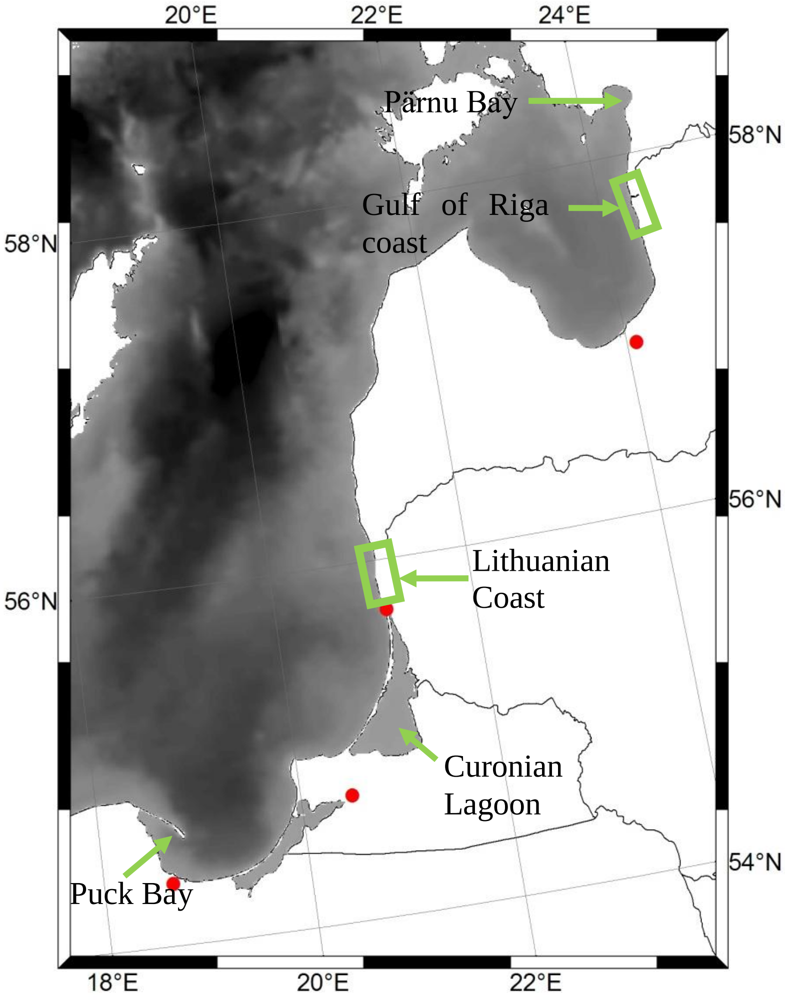

Figure 2: Coastal ecosystems modelled. Boxes exaggerate the extend of the coastal ecosystem for illustrative purposes, terrestrial part of coastal ecosystems was not included into the models

3.2 Models applied

3.2.1 Kattegat new production model (publication I)

Publication I presents a simple model simulating nutrient concentrations and phytoplankton biomass in the Kattegat. Phytoplankton P develops in the well-mixed water layer above the permanent halocline with specific growth rate g_r depending on solar radiation $I(t)$ and concentration of the limiting nutrient, dissolved inorganic nitrogen, $N(t)$. Phytoplankton loss from the upper layer is approximated by a first order loss rate l, resulting in

$$\frac{dP(t)}{dt} = g_r[I(t), N(t)] \cdot P(t) - lP(t)$$ Equation 1

The light and nutrient dependency of the specific phytoplankton growth rate g_r was modelled by Michaelis-Menten type relationships, where the minimum of nutrient and light dependencies limited the growth rate.

Phytoplankton growth was coupled to nitrogen uptake via constant cell nitrogen content *q*, leading to dissolved nitrogen loss by phytoplankton growth at rate $qg_r[I(t),N(t)]\cdot P(t)$. Simultaneously, input from land and atmosphere *L(t)* and entrainment of bottom water resupply nitrogen to the upper layer. The net entrainment of nitrogen is given by $\frac{w_e(t)}{H(t)}[N_c(t)-N(t)]$, where the ratio between entrainment velocity $w_e(t)$ and pycnocline depth *H(t)* describes the upward movement of water through the pycnocline. Because of the difference in nitrogen concentration $N_c(t)$ below and *N(t)* above the pycnocline the water movement leads to a nitrogen flux between both layers, which is usually directed upwards ($N_c(t) > N(t)$). The dissolved inorganic nitrogen dynamics in the upper layer of the Kattegat are therefore described as

$$\frac{dN(t)}{dt}=\frac{w_e(t)}{H(t)}[N_c(t)-N(t)]+L(t)-qg_r[I(t),N(t)]\cdot P(t) \qquad \text{Equation 2}$$

The model does not include regeneration of nitrogen in the water column and therefore simulates only new production. The physical process formulation, describing the entrainment velocity $w_e(t)$ and the dynamics of pycnocline depth *H(t)*, is derived from a model for the seasonal pycnocline by Stigebrandt (1985).

3.2.2 Simulation model for phytoplankton and nutrient dynamics in the Southern Gulf of Riga (publication II)

The simulation model for phytoplankton and nutrient dynamics in the Southern Gulf of Riga (publication II) extends the Kattegat new production model to include pelagic nutrient regeneration. Similar to the Kattegat model, nutrient and phytoplankton dynamics are modelled for the surface layer above the pycnocline only. Nutrient concentrations below the pycnocline are treated as external forcing. The entrainment of bottom water into the surface layer is not modelled explicitly, but estimated from observed changes in pycnocline depth.

Additionally, advection of freshwater in the surface layer was estimated by a simple salt budget of the surface layer. When the pycnocline deepens, surface salinity changes are linked to freshwater advection and entrainment by

$$\frac{dS^1}{dt}=\frac{1}{H}\left(-A\cdot S^1+w\cdot(S^2-S^1)\right),\ \text{if}\ w\geq 0 \qquad \text{Equation 3}$$

where *w* is the rate of pycnocline depth change, S^1 and S^2 denote salinity above and below the pycnocline, and *A* is the freshwater flow into the surface layer per unit surface area. The first term, $-A\cdot S^1$, states that the freshwater flow *A* generates an equal volume of saline water outflow, while the second term, $w\cdot(S^2-S^1)$, describes the flow of salt from the bottom layer into the surface layer as the pycnocline deepens. During pycnocline retreat the salt flow from below the pycnocline equals zero and the salt balance is determined by freshwater advection alone, giving

$$\frac{dS^1}{dt} = \frac{1}{H}\left(-A \cdot S^1\right), \text{ if } w \prec 0 \qquad \text{Equation 4}$$

Compared to the Kattegat new production model, biological processes are described in greater detail. The model incorporates two phytoplankton groups, diatoms and others, to simulate the seasonal succession of algal species in the Gulf of Riga. Because phytoplankton growth can be limited by nitrogen, phosphorus or silica during different periods of the growth season (Yurkovskis 2004, Maestrini et al. 1999, Maestrini et al. 1997, Põder et al. 2003, Tamminen & Seppälä 1999) all three nutrients were included into the model. Phytoplankton loss terms were expanded to include zooplankton grazing, but zooplankton concentrations themselves were interpolated from field observations.

The model also includes regeneration of nutrients via degradation of detritus and excretion by zooplankton. The actual processes involved in pelagic nutrient regeneration in marine ecosystems are far more complex and mainly connected to the microbial loop, which is a grazing chain involving bacteria, heterotroph nanoflagellates and ciliates (Azam et al. 1983). The microbial loop processes the majority of primary production in the open oceans (Steele 1998). While process formulations exist for incorporating the microbial loop in ecosystem models (Steele 1998, Baretta et al. 1995), the model developed for the Southern Gulf of Riga like many ecosystem models simplifies nutrient recycling in the pelagic ecosystem to a first-order degradation of detritus, reducing complexity to the level of an NPZD model.

3.2.3 Long-term biogeochemical model of nutrients and phytoplankton dynamics in the Gulf of Riga (publication III)

The long-term dynamics of nutrients and phytoplankton in the Gulf of Riga were modelled with a complex biogeochemical model (publication III), based on a box model (Savchuk 2002) developed for simulating ecosystem state during a three-year time period. The model represents the physical structure of the water column in the Gulf of Riga using a pelagic and a demersal box, separated by a fixed “thermocline” at 10 m water depth (Figure 3). Vertical mixing is parameterized depending on the water density difference between both boxes, i.e. high turnover and homogeneous conditions are generated during winter, when the observed density difference is small, in contrast to low mixing during summer, when the observed temperature difference between both water layers causes a large density gradient.

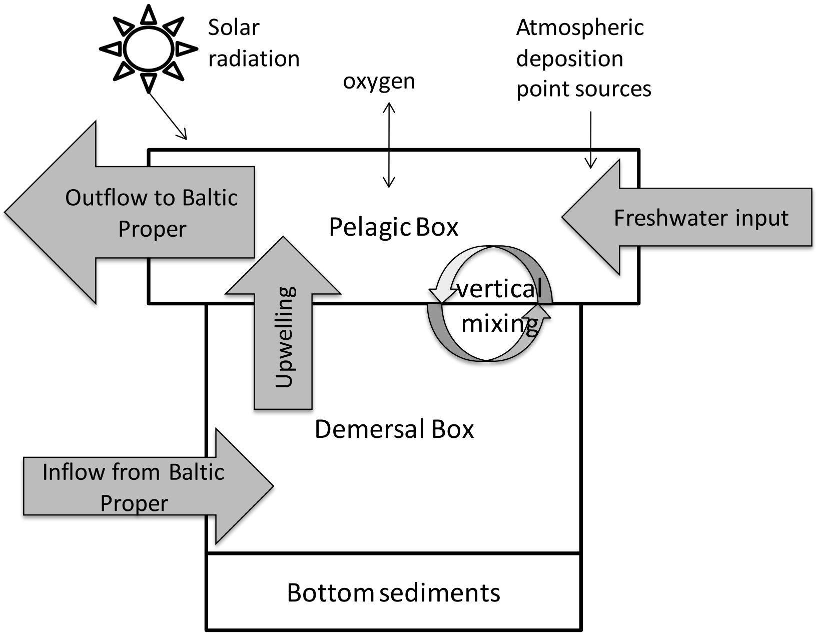

Figure 3: Physical process resolution of the long-term biogeochemical model of nutrient and phytoplankton dynamics in the Gulf of Riga

The biological part of the model is formed by an NPZD model with three phytoplankton and one zooplankton group. Phytoplankton growth and nutrient turnover in pelagic and demersal model boxes are parameterized in a similar way to the model presented in publication II for the Southern Gulf of Riga. A group of nitrogen fixing phytoplankton was added to simulate cyanobacteria growth. Since the number of state variables has a strong impact on model execution time, besides reducing the physical structure to two boxes compared to the original three boxes used by Savchuk (2002) also dissolved silica was removed from the model. Dissolved silica potentially limited diatom growth in spring during the first half of the 1990ies (Danielsson et al. 2008, Yurkovskis 2004) but contrary to most other subbasins of the Baltic, dissolved silica concentrations in the Gulf of Riga have been increasing recently (Papush & Danielsson 2006) and potential silicate limitation seems to have lessened (HELCOM 2009).

In contrast to the model developed for the Southern Gulf of Riga (publication II) the long-term biogeochemical model for the Gulf of Riga contains a sediment compartment which simulates the remineralisation of nitrogen and phosphorus, including their subsequent biogeochemical transformations via nitrification, denitrification, and redox-dependent adsorption and desorption of phosphorus (Figure 4). Therefore the model simulates all major pathways relevant to the biogeochemical cycling of nitrogen and phosphorus in the Gulf on decadal time scales. Because the transformations of nitrogen and phosphorus in the bottom sediments are redox-dependent, oxygen is included as a prognostic state variable by coupling all biogeochemical processes to their stochiometric oxygen consumption rates and by including a temperature and wind-speed dependent aeration resupply of dissolved oxygen at the surface of the pelagic box.

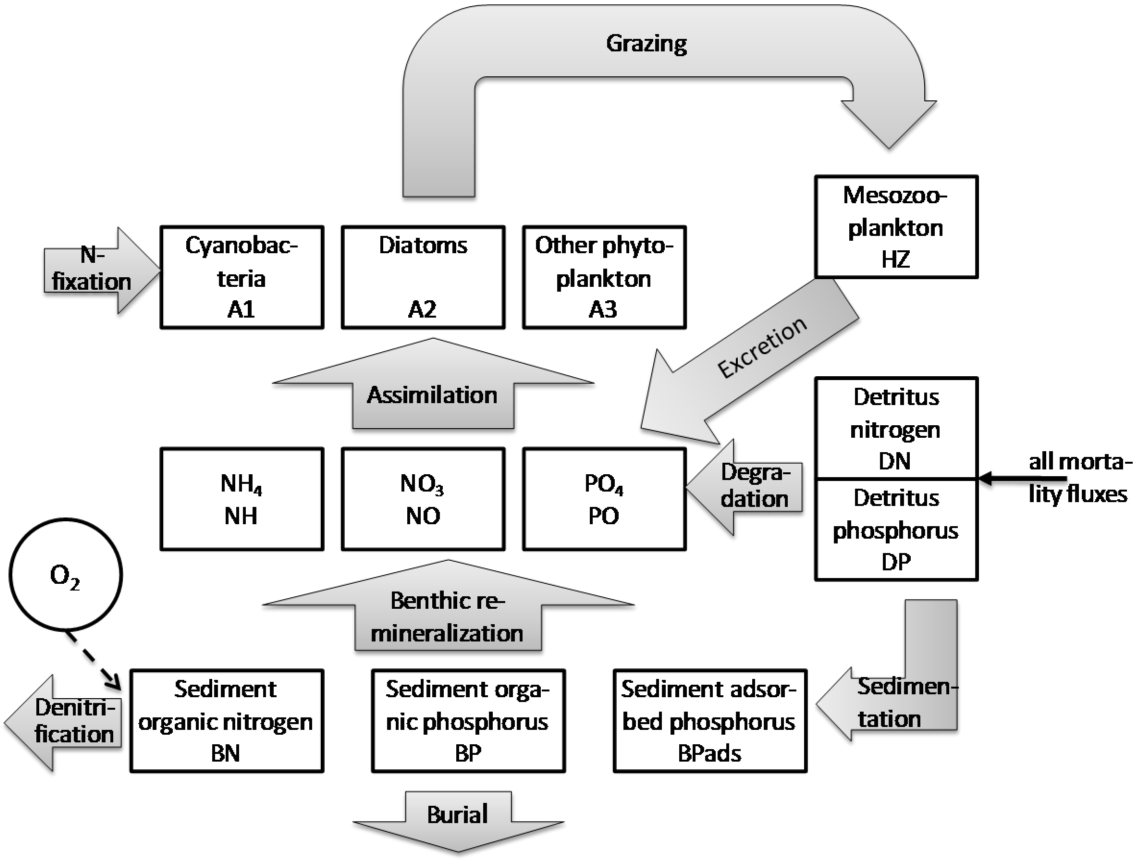

Figure 4: Nutrient transformation pathways in the long-term biogeochemical model of nutrients and phytoplankton dynamics in the Gulf of Riga

The model has been calibrated by simultaneously adjusting 37 parameters in the biogeochemical process equations, using a simulated annealing algorithm (Wah et al. 2007) to optimize the model fit to monitoring observations of dissolved nutrients, phytoplankton, zooplankton and dissolved oxygen for the time period 1973 – 2000. The model was subsequently validated by observations from 2001 - 2007.

3.2.4 Kattegat carbon budget model (publication IV)

The Kattegat carbon budget model (publication IV) describes the carbon budget of the lower trophic levels in the upper layer of the Kattegat. Unlike the Kattegat new production model and the models presented for the Gulf of Riga, it is driven by observed rates of primary production. Therefore, in contrast to the other simulation models presented, which follow a “bottom up” approach and simulate primary production based on nutrient fluxes, this model looks at the lower trophic levels from a “top-down” perspective and derives the uptake rate of new nutrients from a carbon budget of the productive surface layer.

The model estimates weekly carbon fluxes using a budget equation, where

Phytoplankton gross primary production = respiration + change in phytoplankton biomass + predation and mortality loss + sedimentation loss Equation 5

Phytoplankton gross primary production = respiration + new production + regenerated production Equation 6

In these equations, phytoplankton gross primary production and the change in phytoplankton biomass were available from observations at 13 stations in the Kattegat, after applying a general linear model to fill gaps in the observed time series. Respiration was estimated dependent on daylength by an empirical model. Further, the model assumes that phytoplankton losses by predation and natural mortality are temperature dependent and would increase in proportion to the mesozooplankton biomass. The model therefore applies a temperature-dependent grazing equation (Huntley & Lopez 1992) with an additional scaling parameter to describe the seasonal dynamics of phytoplankton losses by predation and natural mortality. Regenerated production was subsequently estimated at a constant fraction (33 %) of the grazing and mortality flux (Hansen et al. 1997) and the associated nutrients were regenerated.

This simple budget approach then allowed calculating sedimentation losses as well as the rate of new production from equations 5 and 6.

3.2.5 ECOPATH models of Southern Baltic coastal ecosystems (publication V)

Publication V presents an example of modelling carbon fluxes to higher trophic levels, using ECOAPTH software (Christensen & Pauly 1992, Christensen et al. 2004) to analyze the food web structure in five Southern Baltic coastal ecosystems. ECOPATH solves a mass-balance equation of carbon (or any other conservative unit, e.g. energy or nutrient content) for each ecosystem component in a system of n trophic species groups:

$$B_i \frac{P_i}{B_i} EE_i - \sum_{j=1}^{n} B_j \frac{Q_j}{B_j} DC_{ji} - EX_i = 0$$ Equation 7

where: B_i is the biomass of group *i*; P_i is its total production; DC_{ji} - the proportion of trophic group *j* in the diet of group *i* - is a diet matrix coefficient that describes the trophic relationship between groups; Q_i is the total food consumption of group *i*; the production/biomass ratio P_i/B_i and the consumption/biomass ratio Q_i/B_i are metabolic rates that express the productivity and consumption per unit of biomass, respectively. EE_i is the Ecotrophic efficiency, which is the fraction of production of group *i* that is utilized - i.e. consumed, exported or harvested - within the system, while EX_i is the net export.

For the five coastal ecosystems investigated – Puck Bay, the Curonian Lagoon, the Lithuanian Baltic Proper coast, a coastal section in the Gulf of Riga and Pärnu Bay – a common model structure (Figure 5) was chosen to facilitate comparing carbon fluxes between foodweb components. All fluxes were expressed in terms of carbon.

In the models, the five coastal ecosystems contained pelagic and benthic foodwebs. The basis of the pelagic foodweb was formed by phytoplankton, which is subsequently consumed by mesozooplankton. Mesozooplankton then provided the main food source of planktivorous fish. Planktivorous fish predate directly on mesozooplankton and/or feed on its planktonic predator, macrozooplankton. The bottom of the benthic foodweb was formed by benthic suspension and deposit feeders, which channel detritus into the food web, are at the bottom of the benthic foodweb. Sources of detritus are sedimenting phytoplankton, as well as annual and perennial macrophytes. The benthic foodweb is therefore indirectly linked to the pelagic pathways. Benthic suspension and deposit feeders are in turn consumed by a number of benthivorous fish species. Top predators in the Baltic coastal ecosystems modelled were birds and piscivorous fish. Piscivorous fish merged pelagic and benthic carbon pathways, as they prey both on benthivorous and planktivorous fish. Birds typically consumed planktivorous, in some systems also piscivorous fish, or benthic deposit feeders. All five coastal ECOPATH models also included coastal fisheries.

Monitoring data and measurements from research projects supplied the biomass data necessary to solve equation 7. Predator diet compositions were derived both from field observations and publications, while most production and consumption coefficients were taken from literature sources. The ecotrophic efficiency EE_i remained the only unknown parameter in equation 7 and initial model solutions were refined until the ecotrophic efficiency for each trophic group was less or equal to one, corresponding to a balanced solution, where the consumption of each predator group is fully accounted for by the production of its prey.

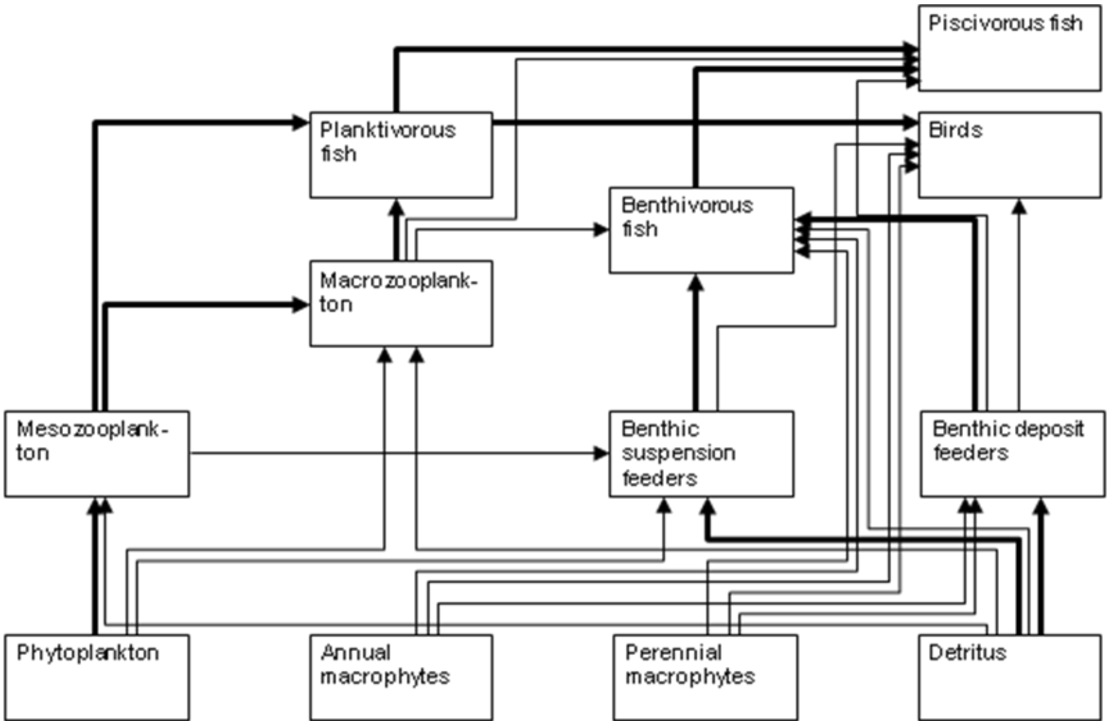

Figure 5: Carbon flow structure of the coastal ECOPATH models

4 Results

4.1 Simulated dynamics of nutrients and phytoplankton

Three of the models presented, the Kattegat new production model (publication I), the nutrient and phytoplankton model for the Southern Gulf of Riga (publication II) and the Gulf of Riga long-term biogeochemical model (publication III) simulate the dynamics of nutrients and phytoplankton from a “bottom-up” perspective, i.e. forced by nutrient inputs to the euphotic layer. All three models give a reasonable representation of observed nutrient and phytoplankton concentrations (see publications I-III). They use a similar box-model physical setup with a homogeneous pelagic box overlaying a demersal water layer, which delivers nutrients by vertical mixing into the upper layer. Moreover, the models use almost identical parameterizations of phytoplankton growth and its nutrient assimilation by first-order, Michaelis-Menten type kinetics with a minimum law formulation for growth limitation by light and nutrients.

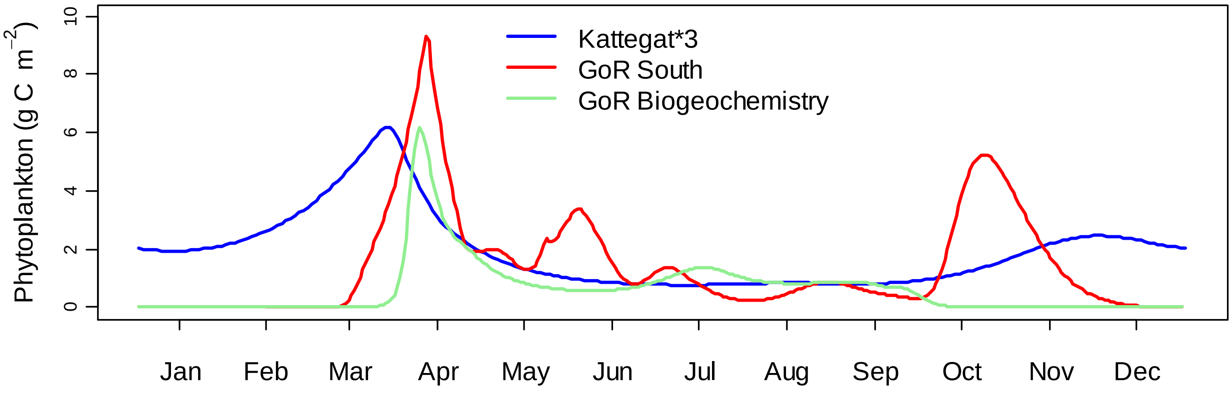

Figure 6: Dynamics of simulated phytoplankton biomass in the Kattegat new production model (blue), the nutrient and phytoplankton model of the Southern Gulf of Riga (red) and the Gulf of Riga biogeochemical model (green). Both Gulf of Riga models show output from 1998. Because of the difference in scale, simulated biomass in the Kattegat was multiplied by factor 3.

The three models (Figure 6, note different scale for Kattegat model) depict the typical phytoplankton biomass pattern in temperate latitudes of the Baltic (Hagström et al. 2001), with a spring bloom followed by low summer biomass and a second, smaller bloom in autumn. In the Kattegat the simulated spring bloom started more gradually and peaked about 2 weeks earlier than in the Gulf of Riga, whereas the autumn bloom reached its maximum about one month later, i.e. in early December compared to late October in the model of the Southern Gulf of Riga. The Kattegat new production model and the Gulf of Riga biogeochemical model produced smoother seasonal phytoplankton dynamics than the model for the Southern Gulf of Riga. In the Gulf of Riga biogeochemical model the only intermittent increase of phytoplankton biomass in the year presented occurred in July and was caused by a small bloom of cyanobacteria and other species. The model for the Southern Gulf of Riga however showed several secondary phytoplankton blooms during summer, in the beginning of June, beginning of July and beginning of September. Also the timing of the autumn bloom in the three models differed. While the Kattegat new production model predicted a slight autumn bloom in the end of November, the model of the Southern Gulf of Riga simulated pronounced phytoplankton growth in the second half of

October, and in the biogeochemical model of the Gulf of Riga no autumn bloom was generated during 1998. The Gulf of Riga biogeochemical model generally simulated weak autumn blooms, which started already in September (see Figure 9). Similar to the output for 1998, the autumn bloom was missing in 18 % of the simulation year.

Differences in phytoplankton dynamics between the models corresponded also to differences in nutrient fluxes in the upper layer of the three box models (Figure 7). The Kattegat new production model and the biogeochemical model for the Gulf of Riga produced smooth seasonal nutrient flux dynamics, while the model for the Southern Gulf of Riga showed several periods with increased entrainment, external nutrient input and higher nutrient regeneration. The temporal dynamics of phosphorus fluxes was similar to the DIN flux pattern. For a detailed presentation of phosphorus fluxes see publications II and III.

Because the Kattegat model did not include nutrient regeneration, the simulated nutrient assimilation into phytoplankton was by an order of magnitude lower than for the two Gulf of Riga models. In all three models nutrient assimilation during the spring bloom was not fully balanced by simultaneous fluxes into the upper layer, i.e. phytoplankton consumed also nutrients accumulated during the light-limited winter period. During summer, DIN assimilation and its fluxes into the pelagic box were at equilibrium, especially in the Kattegat new production model and the Gulf of Riga biogeochemical model. In the Kattegat new production model the simulated summer phytoplankton production was supported mainly by external nutrient inputs, i.e. by DIN supplied from land and atmosphere. In the Gulf of Riga biogeochemical model nutrient regeneration during summer by far exceeded the external inputs. Nutrient regeneration, together with entrainment of bottom water, consequently determined the magnitude of primary production during the equilibrium period. In contrast, simulated nutrient fluxes in the model for the Southern Gulf of Riga fluctuated strongly with periodic entrainment pulses and intermittent advection of freshwater. The model for the Southern Gulf of Riga interpolates pycnocline dynamics from field observations, which showed periods of pycnocline deepening and retreat (see publication II), equivalent to a loss of nutrients from the upper layer during retreat, while pycnocline deepening entrains additional nutrients from the bottom water into the surface layer. Responding to these fluxes, the onset of spring bloom in the Southern Gulf of Riga model was caused by pycnocline deepening to 22 m depth (see publication II), entraining nutrients into the surface layer, while pycnocline retreat initiated the decline of the bloom in the beginning of April. With the subsequent deepening of the pycnocline during summer its short-time depth fluctuations became weaker. Simultaneously bottom water nutrient concentrations decreased and consequently entrainment fluxes weakened. However, combined with freshwater advection pulses, which mostly coincided with periods of pycnocline deepening, both nutrient sources caused, with a short time-delay, peaks in phytoplankton assimilation and growth.

The relative importance of external nutrient sources, i.e. land and atmospheric inputs, and entrainment of bottom water, varied between the systems modelled (see Figure 7). In the strongly stratified Kattegat DIN external sources dominated the supply of new nutrients during summer, while in the Southern Gulf of Riga entrainment and external loads were of similar importance. In the Gulf of Riga biogeochemical model, which reflects average conditions in the central Gulf of Riga, entrainment by far exceeded external inputs. Both models for the Gulf of Riga also indicate that a large share of the nutrient flux to phytoplankton was provided by nutrient regeneration.

Since external inputs played only a minor role for the DIN dynamics of the central Gulf of Riga, nutrient regeneration essentially determined the amount of nitrogen available to phytoplankton in summer.

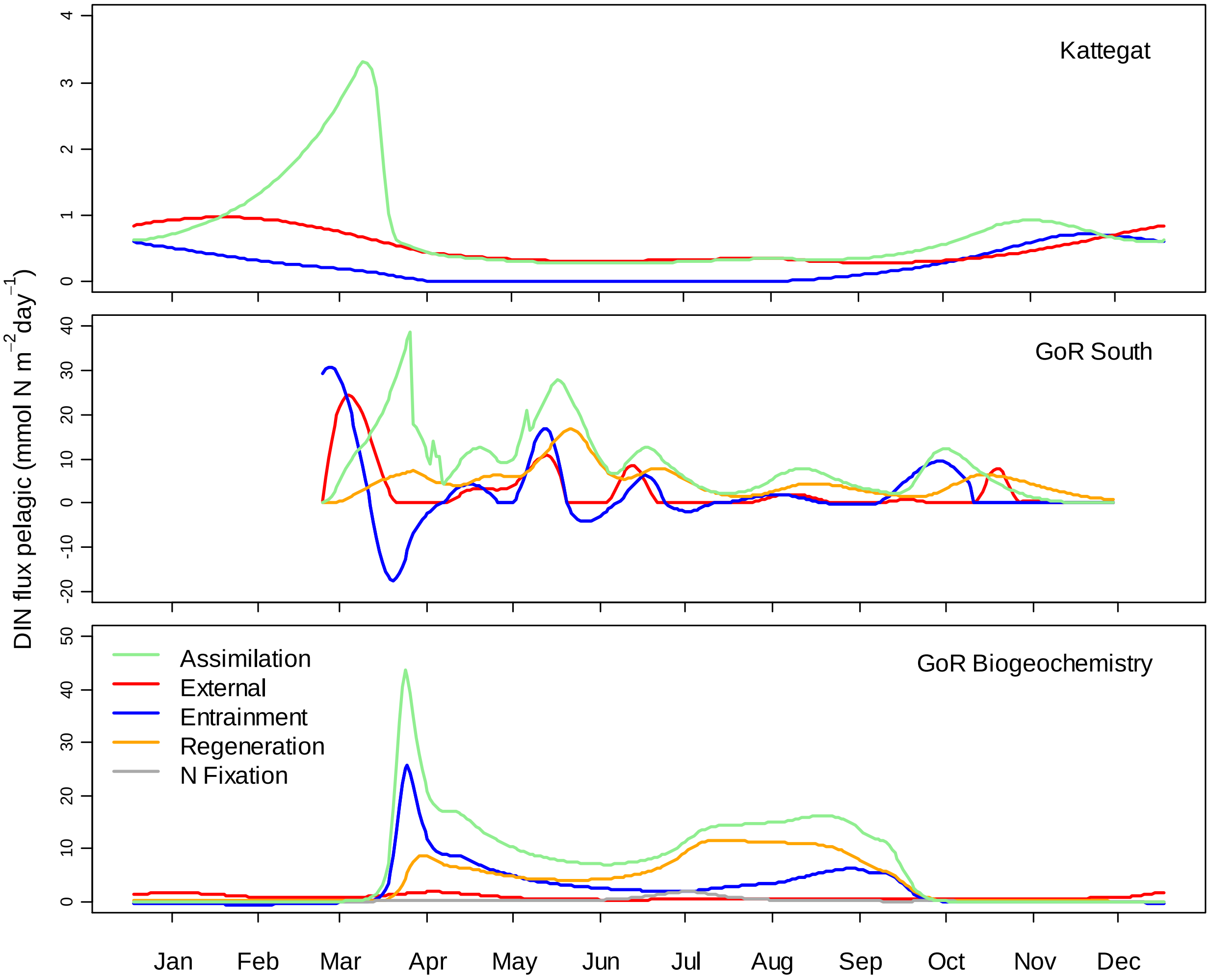

Figure 7: Simulated fluxes of dissolved inorganic nitrogen (DIN) into the pelagic box for the Kattegat new production model (top), the nutrient and phytoplankton model of the Southern Gulf of Riga (middle) and the Gulf of Riga biogeochemical model (bottom). For external (riverine and atmospheric) nutrient inputs (red), net entrainment from the demersal box (blue) and nutrient regeneration in the pelagic box (orange) positive fluxes are directed into the pelagic box; nutrient assimilation by phytoplankton (green) is shown in absolute values. Both Gulf of Riga models show output from 1998.

4.2 Lower trophic level carbon and nutrient fluxes

Table 3: Carbon fluxes (g C m^{-2} $year^{-1}$) in the lower trophic levels estimated by the model for the Southern Gulf of Riga, the Gulf of Riga biogeochemical model for 1998 and as averages for 1973 – 2000, the Kattegat new production model and the Kattegat carbon budget model

Flux	**Southern Gulf of Riga**	**Gulf of Riga, 1998**	**Gulf of Riga, 1973-2000**	**Kattegat new production model**	**Kattegat carbon budget**
Net primary production	194	201	202	n.a.	127
Grazing[1]	46	17	17	n.a.	60
Secondary production	15	5.9	5.3	n.a.	20
Sedimentation	43	48	49	n.a.	66
Regenerated production	107	107	109	n.a.	41
New production	100	94	93	23	86
Entrainment	50	73	73	7	74[2]
External inputs	62	24	24	16	21[3]

Blue background: Fluxes derived from model forcing, green background: Literature data on fluxes not included in the models for comparison. 1: zooplankton grazing on phytoplankton and detritus in the upper model box, 2: based on the input of total nitrogen from the bottom layer estimated by a hydrodynamical model (Gustafsson, unpubl. data, see publication IV), 3: based on total nitrogen (Carstensen et al. 2003, see publication IV).

All models presented for open areas in this thesis (publications I – IV) provide estimates of carbon fluxes to phytoplankton and zooplankton and give information on the nutrient source from which primary production is derived. For the nutrient driven models, i.e. the Gulf of Riga models and the Kattegat new production model, carbon dynamics can be described by converting simulated nutrient fluxes into carbon units based on Redfield ratios (Redfield 1958, Redfield et al. 1963) for phytoplankton biomass (C:N:P = 106:16:1 based on molar units), whereas the Kattegat carbon budget model addresses carbon fluxes directly. Accordingly, Table 3 gives an overview of the carbon fluxes derived from both Gulf of Riga models, the Kattegat new production model and the Kattegat carbon budget model.

All models except the Kattegat new production model provide an estimate of net primary production. Despite the significant impact of freshwater advection in the Southern Gulf of Riga, which triggered production bursts in the model, simulated primary production was not larger than in the Gulf of Riga biogeochemical model. In all systems, a moderate fraction of the primary production was further grazed by mesozooplankton, ranging from 5 % in the 1973 – 2000 average of the Gulf of Riga biogeochemical model to 47 % in the Kattegat carbon budget model. All models parameterize pelagic secondary production, approximated by the assimilation of carbon into zooplankton biomass, as 33 % of grazing based on growth yields determined by (Hansen et al. 1997). Therefore secondary production equals three times the grazing flux in all models and the Kattegat carbon budget transfers the largest share (16 %) of primary production to mesozooplankton. In contrast to the large differences in primary and secondary production, sedimentation estimates were similar in all models, ranging from 43 – 66 g C m^{-2} $year^{-1}$.

All models except the Kattegat new production model also allow splitting the nutrient and carbon turnover into new and regenerated production. Regenerated production is based on nutrient remineralisation in the upper mixed layer, whereas new production consumes nutrients supplied from sources outside the planktonic ecosystem (Dugdale & Goering 1967), in this case entrained from the bottom layer and supplied by riverine and atmospheric sources. In the models, regeneration covered 32 - 55 % and new nutrient inputs 46 – 68 % of net primary production. The Kattegat new production model estimated much smaller new production than the Kattegat carbon budget model (23 vs. 86 g C m^{-2} $year^{-1}$), provided largely (70 %) by external inputs.

4.3 Long-term dynamics of nutrients and phytoplankton in the Gulf of Riga

Among the modelling approaches in this thesis, only the biogeochemical model of the Gulf of Riga includes nutrient transformation processes in the bottom sediments and describes the entire nutrient turnover in a Baltic Sea subbasin on decadal time scales. Model performance, seasonal turnover of nutrients in the water column as well as simulated nitrogen and phosphorus budgets are presented in publication III. In the following, I will highlight indicators of model performance, present simulated shifts in phytoplankton composition and nutrient limitation and describe the long-term nutrient budget of the Gulf of Riga for the model calibration period 1973 – 2000. For this time-period nutrient inputs to the Gulf of Riga had fluctuated widely, increasing in generally between 1973 – 1990, and decreasing afterwards. Maximum nitrogen and phosphorus inputs within this period occurred in 1990 and were 2.8 and 2.2 times larger than their minimum in 1996. Therefore the biogeochemical model simulations also represent a time-period of increasing eutrophication pressure and subsequent recovery of the ecosystem. However, even the minimum annual nutrient inputs were about twice as large as pre-industrial nutrient inputs (Savchuk et al. 2008 based on load estimates from Schernewski & Neumann 2005) to the Gulf of Riga.

4.3.1 Gulf of Riga biogeochemical model performance

The Gulf of Riga biogeochemical model was calibrated by optimizing the model-data fit to observations nutrient concentrations, dissolved oxygen, as well as phytoplankton and zooplankton biomass during 1973 - 2000. Further, the model was validated by hindcasting the same state variables for the time-period 2001 - 2007, i.e. by an independent dataset not used in model calibration. Correlation coefficients (Spearman r, Table 4) between model output and observations for the calibration period were largest for pelagic and demersal oxygen concentrations (0.92 and 0.91), ranged from 0.59 - 0.75 for all nutrient concentrations except NH_4, and between 0.33 - 0.53 for biotic state variables. A bootstrapping test (Håkansson 1999) showed that due to the large variability in the observational data the model data fit was close to the maximum achievable correlation coefficients (0.53 – 0.90 for nutrients, 0.41 - 0.86 for biotic state variables). Therefore the model was thought to give a reasonable fit for the simulated state variables. For phosphate, dissolved oxygen concentrations, chlorophyll *a* and biomass of other phytoplankton the model performed equally well during the validation and the calibration period. For all other parameters, correlation coefficients decreased by 0.2 – 0.3 units. Only for diatoms the model data correlation dropped drastically in the validation period.

Biota	**Spearman r**	**rmax**		
Chlorophyll *a*	0.53 (0.45)	0.86		
Cyanobacteria	0.48 (0.21)	0.42		
Diatoms	0.38 (-0.04)	0.48		
Other phytoplankton	0.33 (0.37)	0.41		
Mesozooplankton	0.48 (0.29)			
Winter nutrient concentrations				
NO_3	0.75 (0.54)	0.70		
PO_4	0.23 (0.38)	0.53		
Nutrients and oxygen	***Pelagic box***		***Demersal box***	
	Spearman r	**rmax**	**Spearman r**	**rmax**
NH_4	0.00 (-0.10)	0.54	-0.09 (-0.08)	0.61
NO_3	0.70 (0.55)	0.75	0.59 (0.30)	0.74
PO_4	0.75 (0.77)	0.90	0.66 (0.63)	0.64
O_2	0.92 (0.91)	0.90	0.90 (0.92)	0.84

Table 4: Model data correlations (Spearman r) for calibration period and validation period (in brackets), compared to the empirical maximum correlation coefficient rmax. For winter nutrient correlations, 2002 data were omitted

Despite the low correlation coefficient for winter phosphate, the model gives a good description of winter nutrient concentrations in the Gulf of Riga (Figure 8). Winter nutrient concentrations, measured when biological uptake is negligible, are a widely accepted indicator of nutrient status in Baltic Sea subbasins (HELCOM 2009, Fleming-Lehtinen et al. 2008a, Fleming-Lehtinen et al. 2008b, HELCOM 2007, ICES 2009). In the Gulf of Riga, winter nitrate concentrations in surface waters have increased up to 1991, declined afterwards and only after 2000 have started to increase again. In contrast, winter phosphate concentrations have increased steadily during the model calibration and validation periods. These features were well represented in the model simulations, but the model does not represent the exceptionally high winter nitrate concentrations observed in 2002. These observations were made at two stations in the Southern Gulf of Riga and significant freshwater influence is evident by the low salinity (5.1 PSU) in the surface layer. Surveys taken at the end of January and in mid March both observed significantly lower nitrate concentrations (11.5 and 14.5 mmol m^{-3}). The high winter nitrate concentrations measured in the February survey are therefore believed to be an outlier caused by freshwater advection and were not used for assessing the model-data fit.

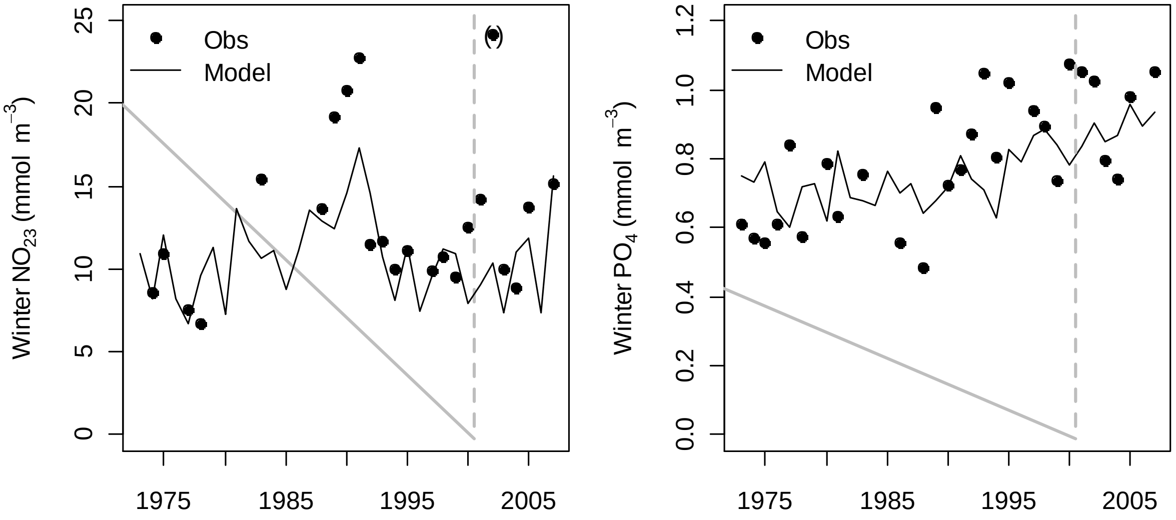

Figure 8: Observed (dots) and simulated (line) winter nutrient concentrations in the surface layer (0 – 10 m) of the central Gulf of Riga (left panel: nitrate, right panel: phosphate), high observed NO_{23} in 2002 were considered an outlier. The stippled grey line marks the begin of the model validation period 2001-2007.

4.3.2 Simulated shifts in phytoplankton composition and nutrient limitation

Corresponding to the changes in Gulf of Riga nutrient pools, the model predicted shifts in phytoplankton biomass and species composition (Figure 9). The simulated seasonal succession mostly started with a spring bloom composed of the other species and diatom model groups. Diatoms then dominated the modelled phytoplankton community during summer and autumn. The proportion of diatoms reached a maximum in the late 1980ies, when the diatom group contributed 95 % of the simulated phytoplankton biomass in 1988, compared to 70 % in the 1970ies and only 34 % in 1996 – 2000. Simultaneously, the share of other species dropped from 25 % in the 1970ies to 5 % in 1988 and subsequently increased to 58 % in the second half of the 1990ies. Significant development of cyanobacteria (> 5 % of annual phytoplankton biomass) was simulated at the beginning of the modelled period, in 1974, 1976 and 1977, and starting from 1996, when blooms were modelled for all years except 1999 (calibration period) and 2005 and 2007 (validation period).

For the diatom and other species group, the calibrated maximum growth rates strongly exceed their specific mortality (Δ 3.6 day^{-1} for other species and 3.2 day^{-1} for diatoms). Therefore both groups are capable of rapid growth under high ambient nutrient concentrations and consequently jointly form the spring bloom. However, the other phytoplankton group in the model has a higher half saturation constant for phosphate than the diatom group (1.3 mmol m^{-3} compared to 0.23 mmol m^{-3}). The higher phosphate affinity gives the diatom group a competitive advantage towards the end of the modelled spring bloom, when phosphate concentrations have already declined. Low winter phosphate concentrations therefore trigger spring blooms in the model that are dominated by diatoms, whereas the other species group remains in the phytoplankton community longer and reaches higher biomasses at high winter phosphate pools. In particular, the model generated larger biomass of the other phytoplankton species group during the second half of the 1990ies (see Figure 9), in accordance with the rising winter phosphate concentrations.

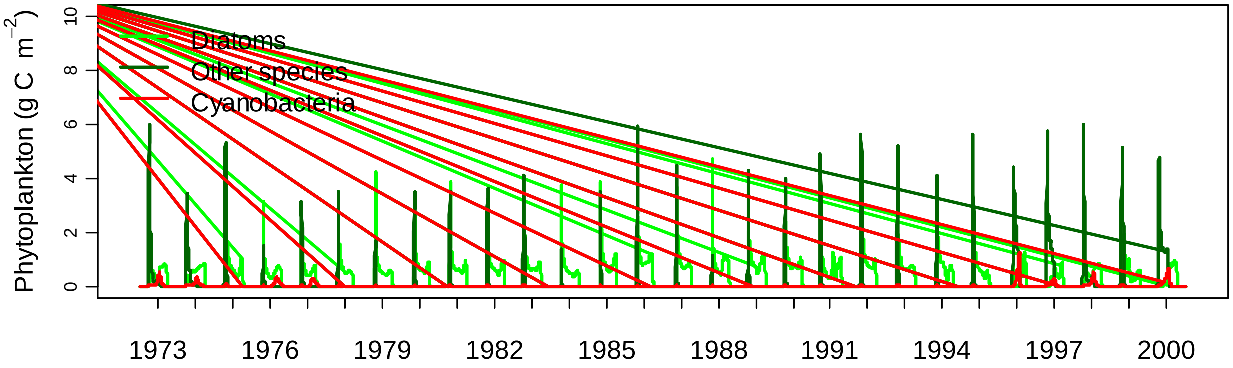

Figure 9: Simulated long-term dynamics of phytoplankton species groups in the Gulf of Riga biogeochemical model

4.3.3 Modelled Gulf of Riga nitrogen and phosphorus budget

The nitrogen and phosphorus budgets of the Gulf of Riga are formed by the balance of external inputs, nutrient sinks and exports. According to the modelled fluxes (Figure 10), river loads were the largest source of bioavailable nitrogen and phosphorus to the Gulf, providing 73 % of the nitrogen and 51 % of the phosphorus input in the model calibration period 1973 – 2000. Direct point sources and inflow from the Baltic Proper each contributed only 4 % of the nitrogen budget, while 14 % stemmed from atmospheric deposition and 6 % from nitrogen fixation by cyanobacteria. Import from the Baltic Proper and direct point sources were more important for the phosphorus budget, contributing 27 % and 14 % of the phosphorus inputs, while only 9 % originated from atmospheric deposition.

The biogeochemical model showed substantial differences in the nitrogen and phosphorus sinks. On average, 81 % of the bioavailable nitrogen input to the Gulf of Riga were removed by denitrification, 19 % were exported to the Baltic Proper and only 3 % were permanently buried in the bottom sediments. For phosphorus, burial removed 23 % of bioavailable phosphorus inputs while 76 % were exported to the Baltic Proper, making phosphorus export the dominating loss process. During the calibration period, the modelled nutrient budgets were not completely balanced. In total, the Gulf of Riga lost 77 200 tons of nitrogen and gained 9 880 tons of phosphorus. Almost half of the nitrogen loss occurred during the first year of the simulation, presumably as a model spin-up effect. Altogether, the nitrogen loss, which occurred predominantly from the sediment pool, equalled approximately the average annual nitrogen input of 2.6 years, whereas the phosphorus gain was slightly less than the yearly phosphorus inputs.

In contrast to the gradually changing phosphorus budget, the nitrogen budget of the Gulf showed large interannual variability with net gains and losses following each other (see Figure 10, bottom). During 1973 – 1990 more nitrogen was received than lost and, disregarding the spin-up year 1974, the Gulf accumulated 2 800 tons of nitrogen annually. Later nitrogen losses mostly exceeded inputs and on average 8 920 tons of nitrogen were removed from the Gulf each year. In contrast to nitrogen, the phosphorus pool changed steadily, with increasing gains until 1990. After 1990, phosphorus accumulation slowed and, starting from 1994, turned into net loss. Both nitrogen and phosphorus pool changes occurred predominantly in the bottom sediments, accounting for 71 % of the modelled nitrogen loss and 76 % of the phosphorus gain.

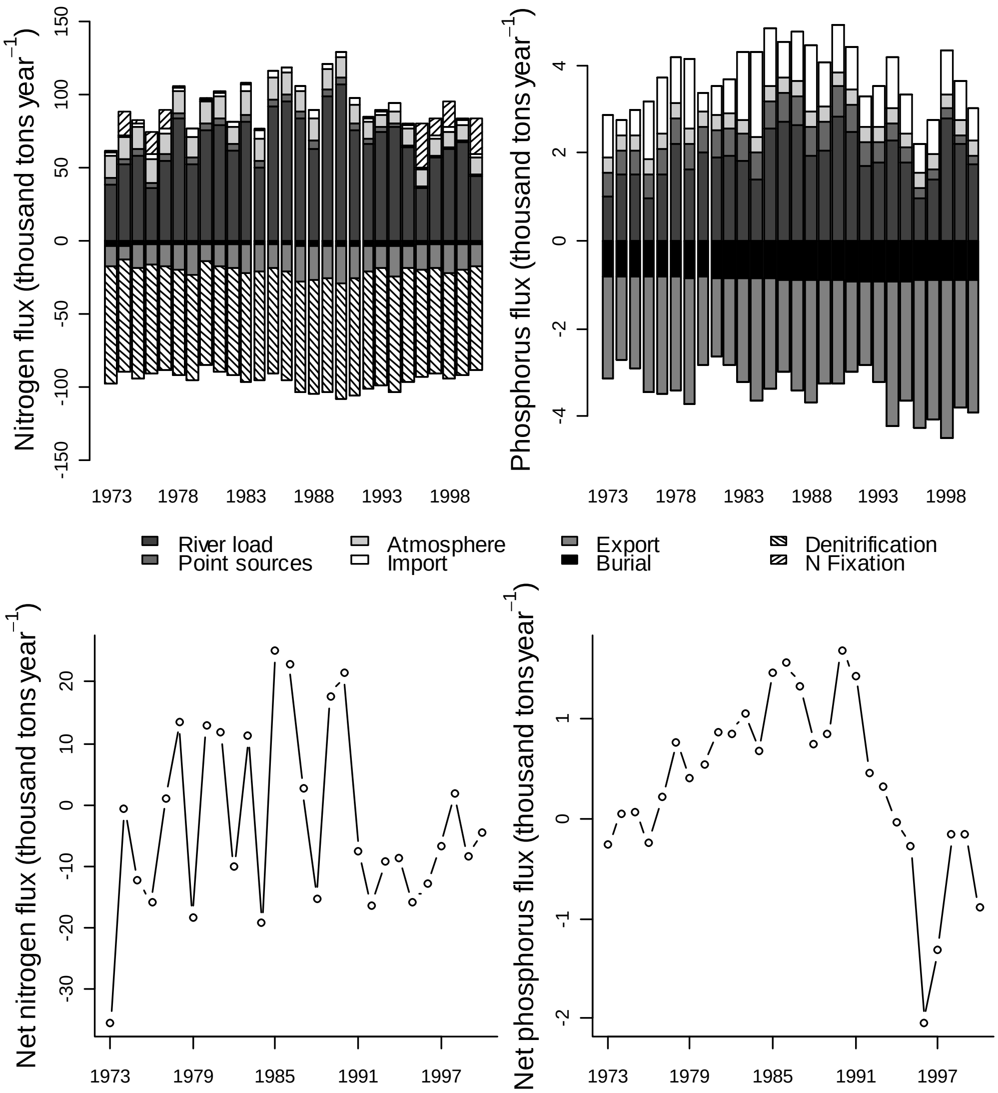

Figure 10: Budget of bioavailable nitrogen (left column) and phosphorus (right column) in the Gulf of Riga. Top row shows individual fluxes, bottom row summarizes net gains and losses

Compared to the water column and sediment pools, the annual inputs of bioavailable nutrients to the Gulf of Riga were relatively small (Table 5). Annually, only 19 % of the nitrogen and 2.6 % of the phosphorus pool were renewed, equivalent to residence times of 5.4 years for nitrogen and 38 years for phosphorus. For both nutrients, bottom sediments stored more than 90 % of the total pool.

	Nitrogen	Phosphorus
Pelagic pool	18 200 tons (3.6 %)	2 610 tons (1.8 %)
Demersal pool	32 900 tons (6.6 %)	4 820 (3.4 %)
Sediment pool	449 800 tons (90 %)	135 000 (95 %)
Input	92 700 tons year^{-1} (19 % year^{-1})	3 755 (2.6 % year^{-1})
Residence time	5.4 years	38 years

Table 5: Pools, inputs and residence time of bioavailable nitrogen and phosphorus in the Gulf of Riga as averages for the model calibration period 1973 – 2000. Numbers in brackets are fractions of the total nitrogen and phosphorus pool.

4.4 Modelling carbon flows to higher trophic levels – examples form coastal ecosystems

In contrast to the Kattegat new production model and the models presented for the Gulf of Riga, which derive carbon and nutrient fluxes from dynamic simulations of nutrients and phytoplankton, the ECOPATH models of coastal ecosystems (publication V) estimate carbon fluxes from standing stocks of producers and consumers using a priori knowledge of their production/consumption rates and diet composition. Further, the models of the Kattegat and the Gulf of Riga described open waters, where phytoplankton were the only primary producers, whereas the five ECOPATH models depict shallower areas, with significant macrophyte growth in Puck Bay and the Gulf of Riga coastal area.

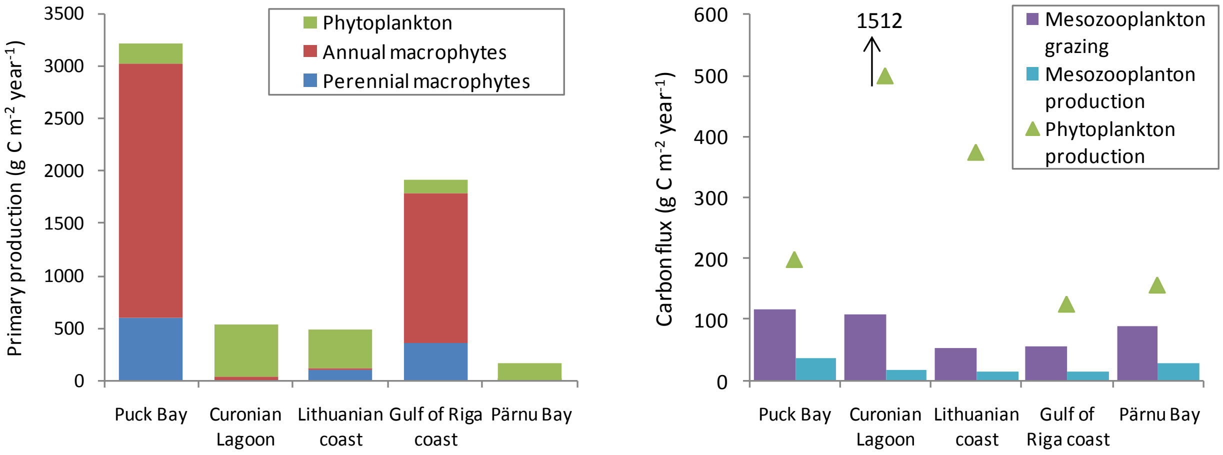

Figure 11: Primary production (left) and carbon flux to mesozooplankton in the five coastal ecosystems investigated

In these systems macrophyte carbon fixation by far exceeded phytoplankton production (Figure 11) and especially annual macroalgae produced large quantities of organic carbon. However, macrophyte production was channelled very inefficiently into the coastal foodwebs. Their ecotrophic efficiency (Table 6), i.e. the fraction of production consumed by the next trophic level, ranged from 0 to 1.6 % for all systems except Pärnu Bay. Nevertheless, also in Pärnu Bay macrophytes did not provide a large direct source of organic carbon to the foodweb, because macrophyte biomass on the predominantly soft bottom of the bay was low. Despite the small direct carbon transfers into the coastal foodwebs, macrophytes supported indirect carbon fluxes in the ECOPATH models by generating detritus which is further utilized by benthic primary consumers, i.e. benthic deposit and suspension feeders.

According to the foodweb structure of the coastal ecosystems (Figure 5), the pelagic part of the foodweb was supported solely by phytoplankton primary production, which ranged between 125 – 370 g C m^{-2} year^{-1} in all systems except the hypertrophic Curonian lagoon (1 500 g C m^{-2} year^{-1}). According to the models, 23 – 85 % of phytoplankton production was grazed by mesozooplankton (56 – 116 g C m^{-2} year^{-1}), with the exception of the Curonian lagoon, where despite a high grazing flux (107 g C m^{-2} year^{-1}), grazing reached only 6 % of the extremely high primary production. Following carbon flows further up the foodweb, carbon fluxes from planktonic and benthic primary consumers to higher trophic levels showed, with the exception of the Curonian lagoon, a consistent pattern. Carbon flows from planktonic consumers were correlated to planktivorous fish biomass, while carbon flows from benthic consumers, resembled the biomass of benthivorous fish (for details see publication V, figures 4 and 5). Lindeman spines (Lindeman 1942, Ulanowicz 1986) constructed for the five systems showed that 5.3 - 20.7 % of organic carbon consumed at trophic level III, i.e. mainly by planktivorous and benthivorous fish, were transferred further up the foodweb to piscivorous fish and birds, or were removed by fisheries. Carbon consumption at trophic level IV (piscivorous fish, birds) was small and ranged between 0.4 – 7.3 g C m^{-2} year^{-1} (for details see publication V, figure 7).

	Puck Bay	**Curonian Lagoon**	**Lithuanian coast**	**Gulf of Riga coast**	**Pärnu Bay**
Birds	0.002	0	0	0.008	0
Piscivorous fish	0.747	0.75	0.589	0.059	1
Planktivorous fish	0.335	0.239	0.893	0.982	1
Benthivorous fish	0.87	0.913	0.045	0.940	0.948
Benthic deposit feeders	0.877	0.508	0.015	0.919	0.478
Benthic suspension feeders	0.327	0.236	0.037	0.827	0
Macrozooplankton	0.727	0.493	0.69	0.978	0.991
Mesozooplankton	0.81	0.647	0.172	1.000	0.754
Perennial Macrophytes	0.011	0	0	0.001	0.211
Annual Macrophytes	0.016	0	0	0.001	0.63
Phytoplankton	0.845	0.062	0.232	0.109	0.606
Detritus	0.854	0.039	0.192	0.140	0.963

Table 6: Ecotrophic efficiencies of the individual foodweb components in the investigated coastal ecosystems

Ecotrophic efficiencies (Table 6), the fraction of biomass produced that is consumed within the ecosystem, give a rough indication of predation pressure for the different foodweb components. High ecotrophic efficiencies were found for meso- and macrozooplankton in Puck Bay and the coastal area in the Gulf of Riga. In most systems benthivorous and piscivorous fish were intensely consumed, which was either predominantly caused by fishing (Puck Bay), or was a combined effect of fishing and predation by piscivores (Gulf of Riga coast), birds and piscivores

(Curonian Lagoon) or even mainly attributable to predation by birds (benthivorous fish in Pärnu Bay). At the Lithuanian and Gulf of Riga coastal areas, where herring was intensely fished, fisheries together with predation by piscivores caused high ecotrophic efficiency of planktivorous fish.

While the ecotrophic efficiencies depict direct predator-prey interactions between foodweb components, indirect interactions were studied by mixed trophic impact analysis (Leontief 1951, Majkowski 1982). The mixed trophic impact routine in ECOPATH applies a small disturbance to each carbon flux and evaluates its impact on all other ecosystem components. Mixed trophic impact analysis revealed cascading effects (see publication V, Figure 9) in the coastal foodwebs, which were not obvious from the direct carbon flow patterns. For example, in Pärnu Bay, where the large cormorant colonies were debated as competitors for coastal fisheries, birds actually had a positive effect on total catches. While the coastal fishery mainly targeted herring, birds predominantly fed on piscivorous fish and therefore released herring from predation pressure. At the Gulf of Riga coast mixed trophic impact analysis suggested that increasing the fishing pressure would only slightly reduce the biomass of herring, the main target species, but cascading impacts on the foodweb would lead to lower mesozooplankton biomass and larger phytoplankton biomass.

5 Discussion

5.1 Modelling total versus new production

The three nutrient driven simulation models presented, the biochemical model for the Southern Gulf of Riga, the Gulf of Riga biogeochemical model and the Kattegat new production model, all give a reasonable representation of nutrient and phytoplankton dynamics. This is surprising, because the Kattegat new production model disregards nutrient regeneration and reflects only production based on new nutrients. Substantial regenerated production characterizes marine ecosystems (see review by Wassmann 1998) and for the Kattegat Carstensen et al. (2003, publication IV) estimated that regenerated production supports approximately 32 % of net primary production. Even higher proportions of regenerated production were found in process studies of primary production and sedimentation in the Southern Kattegat (86 %, Richardson 1996) as well as by nitrogen uptake measurements (75 %, Sahlsten et al. 1988).

Despite disregarding a large part of the nutrient flux in the ecosystem, the Kattegat new production model corresponds well to observations, because its nutrient – phytoplankton parameterization applies phytoplankton growth and loss rate constants (maximum growth rate 0.14 d^{-1}/0.09 d^{-1}, loss coefficient 0.11 d^{-1}/0.8 d^{-1}) that are distinctly lower than maximum growth rates reported from marine ecosystems (Eppley 1972, Banse 1982) and values applied in models resolving also regenerated production (for example models by Savchuk 2002, Eilola et al. 2009, Neumann et al. 2002). Firstly, this indicates, that NPZD models fitting nutrient and phytoplankton data well do not necessarily give a correct description of the rates of nutrient turnover and primary production. Nevertheless, a new production model, like the one presented for the Kattegat, provides valuable insights into the dynamics of the ecosystem, because new production corresponds to the load of carbon that will ultimately leave the euphotic zone (Wassmann 2004), either by sedimentation or by transfer to higher trophic levels, while nutrient regeneration represents a closed loop in the ecosystem. Consequently, a new production model still describes key carbon fluxes, especially the export to bottom sediments, where the additional carbon supply aggravates secondary eutrophication effects as for example bottom water oxygen deficiency.

Further, the Kattegat new production model also showed that new production models can indicate the significance of different nutrient sources for phytoplankton during its seasonal succession. According to the model, new production in summer was almost exclusively derived from land and atmospheric nitrogen inputs, indicating that anthropogenic loading is especially important during the summer period, when nutrient entrainment from bottom water is low.

5.2 Influence of physical process resolution on model results

The three nutrient driven models all apply a box-modelling approach to phytoplankton and nutrient dynamics in the euphotic zone. In the Kattegat new production model smooth Fourier approximations of physical forcing functions drive the entrainment fluxes (see publication I), which consequently produce gradual changes in pycnocline depth and nutrient inputs to the surface layer. Similarly, gradual changes in entrainment are a characteristics of the biogeochemical model of the Gulf of Riga, which forces mixing between pelagic and demersal model boxes dependent on density gradients interpolated between monthly observation means. Especially during summer, the smooth delivery of new nutrients to the upper layer leads to a stable equilibrium between phytoplankton production and loss in these models and consequently to little change in phytoplankton biomass. In contrast, the model for the Southern Gulf of Riga, which estimates nutrient entrainment from observed changes in pycnocline depth (see publication II), depicts also corresponding short-term fluctuations in phytoplankton biomass.

Hydrological conditions, together with variations in nutrient pools, affect the composition of summer phytoplankton communities in the Baltic (Suikkanen et al. 2007, Jaanus et al. 2009). In particular the role of nutrient entrainment was extensively studied to explain the formation of cyanobacteria blooms, which develop in calm, phosphate rich water columns (Kanoshina et al. 2003), often preconditioned by nutrient entrainment (Laanemets et al. 2006, Kononen et al. 1996). Pulses of nutrient rich water also seem to increase productivity in general, as was shown along a salinity front in the Eastern Gotland Basin (Kahru et al. 1984). Also during spring physical processes significantly influence Baltic phytoplankton communities, as the offset of light limitations with beginning water column stratification determines spring bloom timing (Fleming & Kaitala 2006, Fennel, 1999) and mixing depth affects its species composition (Wasmund & Uhlig 2003, Wasmund et al. 1998).

In the Gulf of Riga Babichenko et al. (1999) showed that variations in hydrophysical conditions are reflected in the horizontal phytoplankton distribution. Moreover, in particular during summer vertical mixing has a profound impact on the light regime and nutrient limitation patter experienced by phytoplankton (Tamminen & Seppälä 1999) in the Gulf, leading to fluctuations in primary production (Olesen et al. 1999) and sedimentation (Olli & Heiskanen 1999). Contrary to the central areas of the Gulf, stratification in the Southern Gulf of Riga is initiated when spring flood freshwater spreads across the surface (Stipa et al. 1999). This implies that models designed to describe phytoplankton and nutrient conditions on a fine spatial and temporal scale have to take into account the short-term variations in vertical mixing of the water column and the influence of area specific factors like freshwater advection. The short-term fluctuations observed in the model of the Southern Gulf of Riga therefore seem to be a closer approximation to the true dynamics of nutrients and phytoplankton at a specific monitoring station, whereas the Gulf of Riga biogeochemical model and the Kattegat new production model due to their forcing with highly averaged, smooth entrainment rather represent conditions averaged over the entire model domain.

As indicated in the model simulations for 1998 (Figure 6), the Gulf of Riga biogeochemical produces no or only very small autumn phytoplankton blooms. This is caused by the parameterization of water column mixing in the model, which increases the water exchange between pelagic and demersal model box quickly starting from mid-September, leading to light limitation of the phytoplankton community. The observed magnitude of the autumn bloom in the Gulf of Riga is highly variable (Yurkovskis et al. 1999), ranging from small to distinct increases in phytoplankton biomass. Its species composition is mostly dominated by *Coscinodiscus granii*, a diatom species that does not form a major part of the phytoplankton community during other seasons (see Yurkovskis et al. 1999, Kalveka 1996). Allowing different growth and mortality rates for diatoms in autumn, Savchuk (2002) successfully generated regular autumn blooms in his model of the Gulf of Riga, indicating that a unified parameterization might not be able to capture the physiological characteristics of the diatom community during the entire growth season. Moreover, field measurements (Wasmund et al. 2001) indicate, that the autumn bloom contributes only 9 % of annual phytoplankton primary production. Consequently it has little impact on annual nutrient fluxes, making the biogeochemical model rather insensitive to autumn phytoplankton development.

5.3 Simulated lower trophic level nutrient and carbon fluxes

Both models constructed for the Gulf of Riga gave similar estimates of its net primary production. The simulated net primary production agrees reasonably well with field observations at various locations in the Southern Gulf of Riga, which resulted in an estimated annual gross primary production of 255 g C m^{-2} $year^{-1}$ (Wasmund et al. 2001) during 1991 - 1997. Following carbon fluxes in the pelagic foodweb, the models transferred different proportions of net primary production to mesozooplankton. In the models of the Gulf of Riga, zooplankton grazed a moderate share (biogeochemical model 8 %, Southern Gulf of Riga model 23 %) of phytoplankton primary production annually, whereas the Kattegat carbon budget model estimated that 47 % of the primary production were consumed by mesozooplankton. Grazing estimates from the coastal ecosystems investigated by ECOPATH models ranged, except in the Curonian lagoon, between 23 – 85 % of primary production. The comparison of the different grazing rates suggests, that mesozooplankton grazing in the Gulf of Riga biogeochemical model might be underestimated. Also estimates of foodweb fluxes in the Southern Gulf of Riga based on field measurements gave higher grazing rates than in the biogeochemical model (9 % of gross primary production in spring, 25 % during a summer cyanobacteria bloom, and 42 % in autumn, Donali et al. 1999). However, the zooplankton biomass simulated by the biogeochemical model agreed well with the available data and the calibrated specific maximum ingestion rates (1.2 d^{-1} at 20 ºC) were in a realistic range, being slightly lower than rates typically reported for small copepods (Hansen et al. 1997), but larger than rates characteristic for large copepods (Sommer et al. 2005). This agrees well with the mesozooplankton composition in the Gulf of Riga, which is dominated by comparatively small species (*Acartia* spp., *Eurytemora affinis*, ICES 2009, Yurkovskis et al. 1999). Still, compared to the fluxes estimated for the Southern Gulf of Riga (Donali et al. 1999) and to grazing rates assumed in food web models of the adjacent Baltic Proper (45 g C m^{-2} $year^{-1}$, Sandberg 2000), the Gulf of Riga biogeochemical model seems to underestimates mesozooplankton grazing.

On subseasonal scale, grazing control in the Gulf of Riga models reached at maximum 40 % of simulated daily primary production in the Gulf of Riga biogeochemical model, but up to 98 % in the model of the Southern Gulf of Riga. In both models maximum grazing control is simulated in summer. Peak values in the Southern Gulf of Riga model occur during a short period of pycnocline retreat, nutrient loss and consequently decreased primary production. This implies that models that capture short-term fluctuations in primary production, which are harvested by a slowly changing zooplankton population, will create larger variability and higher maximum values for grazing control of the summer phytoplankton community. Generally, grazing control of phytoplankton production in marine ecosystems is variable and depends also on the size and growth rates of available phytoplankton. Studies in the Kattegat have found grazers to control large phytoplankton, while only 10 – 20 % of the production of small phytoplankton cells was harvested (Kiørboe & Nielsen 1994). Grazing fluxes derived from the Kattegat carbon budget model are tuned to create an equilibrium between phytoplankton production and grazing during summer (see publication IV) and therefore present a maximum estimate of mesozooplankton impact on the pelagic ecosystem. Strictly speaking, the grazing flux in the carbon budget model rather resembles the combined effect of zooplankton predation and all other phytoplankton loss processes, which further contributes to the high grazing control estimate.

Modelled nutrient fluxes into the pelagic model boxes indicate that varying proportions of entrainment and external inputs support the primary producers (Table 3). Comparing both Gulf of Riga models, despite the high impact of entrainment on pelagic nutrient fluxes in the model of the Southern Gulf of Riga, which created pulses of phytoplankton production (Figure 6, Figure 7), the biogeochemical model created higher entrainment fluxes. However, both models differ significantly in the way they describe nutrient fluxes through the halocline. The model for the Southern Gulf of Riga is forced with nutrient concentrations observed immediately below the pycnocline, while the Gulf of Riga biogeochemical model uses average nutrient concentrations in the demersal box as nutrient source for the entrainment flux, disregarding the typical nutrient gradient between sediment surface and thermocline in the Gulf. Also the entrained water flux into the pelagic box during the time period covered by both models was larger in the Gulf of Riga biogeochemical model, in particular during pycnocline formation in spring and its breakup in autumn, resulting in a total volume of water exchanged between pelagic and demersal box of 220 m^3 m^{-2} compared to 118 m^3 m^{-2} in the model for the Southern Gulf of Riga. In the Southern Gulf of Riga salinity stratification has been indicated to reduce vertical mixing (Wassmann & Tamminen 1999), but without a physical model of vertical mixing and water column stratification in the Gulf of Riga both entrainment estimates are difficult to validate.

5.4 Long-term dynamics of nutrients and phytoplankton in the Gulf of Riga

5.4.1 Shifts in phytoplankton composition and nutrient limitation

The Gulf of Riga biogeochemical model does not represent all features of phytoplankton community composition in the Gulf of Riga. While it captures the spring bloom to consist of diatoms with varying proportions of other species, which often follow the primary diatom spring bloom peak (Yurkovskis et al. 1999, Kalveka 1996), the model underestimates the share of the other species group during summer. In part this is caused by the structure of the calibration dataset, where diatoms were covered by more observations than other species and cyanobacteria, giving them a higher weight during the model calibration. Because diatoms are little affected by different sample fixatives (Klein Breteler 1985), all available diatom observations have been included into the calibration dataset, resulting in a time-series starting in 1976. Non-diatoms, where small cells might be lost by formalin preservation, have been included into the calibration dataset only starting from the end of 1993, when the Latvian marine monitoring programme replaced formalin fixation by acid Lugol's solution.

According to the calibrated growth parameters, the diatom group in the model corresponded to phytoplankton species with high affinity for phosphate. Therefore the modelled shifts in phytoplankton composition track changes in nutrient availability and limitation. Nutrient limitation in the Gulf of Riga varies both in space, with areas close to the river mouths in the Southern Gulf of Riga being more phosphorus limited (Tamminen & Seppälä 1999, Seppälä et al. 1999), as well as in time. Prior to 1990 phytoplankton growth was mainly P-limited (Yurkovskis 2004, Yurkovskis et al. 1993) and switched to nitrogen or N/P co-limitation afterwards (Yurkovskis 2004), which was also confirmed later by bioassays for 1996-1997 (Maestrini et al. 1999, Maestrini et al. 1997). This agrees well with the increasing importance of the other phytoplankton group in the modelled spring blooms during the late 1990ies.

The peak share of the diatom group in the simulated phytoplankton biomass in the late 1980ies coincides with highest nutrient loads to the Gulf of Riga (Figure 10), i.e. a period when the high N/P ration in the external input increased the availability of nitrogen and therefore made the basin more phosphorus limited. With declining loads in the 1990ies, nitrogen was quickly removed from the ecosystem, whereas the still increasing winter phosphate concentrations (Figure 8) suggested, that phosphorus was efficiently retained in the Gulf of Riga. Similar to the Baltic Proper, where high availability of DIP at simultaneous nitrogen shortage leads to the development of cyanobacteria blooms (Nausch et al. 2008, Vahtera et al. 2007, Stal et al. 2003), the biogeochemical model also depicted an increase in nitrogen fixing phytoplankton in the Gulf of Riga between 1993 – 2000. Varying proportions of cyanobacteria are a characteristic feature of summer phytoplankton communities in the Gulf of Riga (Kalveka 1996, Yurkovskis et al. 1999), but the modelled increase in cyanobacteria growth during the 1990ies agrees well with satellite observations (Kahru et al. 1994, Kahru et al. 2007), which found virtually no cyanobacteria surface blooms in the Gulf of Riga before 1992, while later blooms occurred regularly.

5.4.2 Processes driving the long-term dynamics of nitrogen and phosphorus

The long-term dynamics of nutrients and phytoplankton in the Gulf of Riga are driven by the balance between inputs and major nutrient sinks. Denitrification removed on average 80 % of the bioavailable nitrogen inputs to the Gulf, while export to the Baltic Proper was the dominating phosphorus loss process (Figure 10, see also publication III), covering 76 % of the phosphorus inputs. The simulated denitrification rates, on average 4.6 g N m^{-2} $year^{-1}$ in 1973 - 2000, were within the range of rates observed in the Eastern Gotland Basin (2.7 – 11 g N m^{-2} $year^{-1}$, Schneider et al. 2002). However, they were larger than observations in the Northern Baltic Proper and the Gulf of Finland (0.08 – 1.54 g N m^{-2} $year^{-1}$, Tuominen et al. 1998 and 0.5 – 3.32 g N m^{-2} $year^{-1}$, Gran & Pitkänen 1999). This is surprising, because field measurements mostly cover fine-grained, organic rich accumulation sediments (Hietanen & Kuparinen 2008), which make up only 28 % of the Gulf of Riga bottom area (Carman et al. 1996), but denitrification rates outside accumulation areas are potentially significantly smaller (Stockenberg & Johnstone 1997). However, the denitrification flux estimated by the Gulf of Riga biogeochemical model, on average 75 000 tons $year^{-1}$ during 1973 – 2000, ranges between the Gulf of Riga denitrification flux calculated in the SANBALTS steady state budget (55 000 tons $year^{-1}$ in 1997-2003, Savchuk & Wulff 2007) and the SANBALTS transient simulation (84 000 tons $year^{-1}$ for 1970 – 2003, Savchuk & Wulff, 2009). It also agrees well with the denitrification estimate derived from short-term simulations (74 100 tons $year^{-1}$ in 1993 - 1995, Savchuk, 2002) and budget calculations for 1991 – 1999 (84 000 tons $year^{-1}$ including burial, Savchuk, 2005).

Because of the estuarine nature of the Baltic Sea, which transports nitrogen rich riverine inputs towards a, in relative terms, nitrogen poor North Sea, all subbasins of the Baltic are net exporters of nitrogen (see for example flows between basins in Savchuk & Wulff 2007 and Savchuk 2005). The nutrient exchange between the Gulf of Riga and the Baltic Proper cannot be measured directly on long time-scales, but models and budget calculations give a range of estimates of the net nitrogen export from the Gulf of Riga with lowest values calculated by the Gulf of Riga biogeochemical model (publication III), 17 500 tons year^{-1} in comparison to 19 200 tons year^{-1} estimated by Savchuk (2002), 20 700 tons year^{-1} for DIN in Yurkovskis et al. (1993) and 44 000 tons year^{-1} according to Savchuk (2005). The Gulf of Riga biogeochemical model suggests that nitrogen export to the Baltic Proper follows the riverine input signal (see Figure 10). Therefore part of the variation in net nitrogen export between the models might also be attributable to the different time periods covered.

Published budget models also give a range of estimates for the net phosphorus export from the Gulf of Riga, ranging from 800 tons year^{-1} (Savchuk 2005) to 2 530 tons year^{-1} in the Gulf of Riga biogeochemical model (publication III). Export simulatd by the Gulf of Riga biogeochemical model agrees well with short-term biogeochemical model simulations (2 200 tons year^{-1}, Savchuk 2002) and the long-term SANBALTS simulations (2 000 tons year^{-1}, Savchuk & Wulff 2009). The phosphorus mass balance model constructed by Håkanson (2009) gave a significantly larger export flux (6 160 tons year^{-1}) because phosphorus sources in this model also include a large input from land uplift.

Sediment burial is the smallest phosphorus sink in the Gulf of Riga biogeochemical model, removing 870 tons year^{-1} of phosphorus, or 23 % of the annual phosphorus inputs (publication III). The magnitude of the burial flux is within the range of recent budget model estimates (0 – 1 500 tons year^{-1}, Savchuk 2002, Savchuk 2005, Savchuk & Wulff 2007) and only slightly lower than the phosphorus storage of 1 100 tons year^{-1} estimated based on measurements of phosphorus content in bottom sediments (Carman et al. 1996). Compared to the magnitude of phosphorus budget components (see Figure 10) the differences between the model estimates are considerable, indicating large uncertainty in both net phosphorus export and the phosphorus burial flux. In particular the phosphorus export can be expected to be sensitive to changes in N/P ratios and phytoplankton community structure in the Gulf, but also to DIP concentrations in the surface layer of the Baltic Proper, since the net phosphorus flux depends on the phosphate concentration gradient between both basins.

Winter nutrient concentrations (Figure 8) indicated that nitrogen pools in the Gulf of Riga respond quickly to changes in nutrient loads, while phosphate concentrations continued to increase also after decreasing inputs in the 1990ies. The slow response of the phosphorus pool is caused by its long residence time (see Table 5) and large internal loading. Simulated internal loading, i.e. modelled phosphate outflows from the bottom sediments reached on average 4.7 times the annual riverine, point source and atmospheric input in the biogeochemical model. In contrast, nitrogen concentrations quickly followed the changes in riverine inputs, with internal loading equivalent to only 34 % of the annual nitrogen input. Similar differences in internal loading and nitrogen and phosphorus residence time, caused by the magnitude of their biogeochemical sinks, have been found in earlier nutrient budgets of the Gulf of Riga (Savchuk 2002) and nutrient budgets for the entire Baltic Sea (Wulff & Stigebrandt 1989, Savchuk, 2005). In the Gulf of Riga biogeochemical model, the difference in residence time and response to nutrient load changes ultimately led to the simulated shifts in nutrient availability, phytoplankton growth limitation and species composition.

5.5 Simulating carbon fluxes to higher trophic levels

The coastal ECOPATH models depict carbon fluxes to higher trophic levels as a fraction of food consumption, determined by the biomass and physiological characteristics assumed for predators. Assembling the five coastal models showed, that the consumption and production rates of many groups were difficult to obtain and only in some cases, for example Pärnu Bay, were measured in the system modelled (see Table A1 in publication V). Further, data on the biomass of producer and consumer groups were often measured at different spatial scale than the model area. This led to upscaling and downscaling problems. For example, macrophyte density was known only for individual transects at the Latvian coastal area, which were extrapolated to the entire study area and probably contributed to the high macroalgae biomass applied in the model. Biomass estimates of mobile predators like fish, birds, but also catches from fishing fleets on the other hand were mostly available for larger regions and biomasses had to be downscaled to the model area and, in the case of temporal residents in the coastal zone, for example spawning schools of herring, adjusted to the fraction of time spent in the model area. Further, error propagation is an inherent problem of models that use a stepwise procedure for prediction (Håkanson, 1999). With respect to the carbon flux models constructed this implies, that uncertainty in estimated carbon transfers increases with trophic level.

Because NPZD models truncate the foodweb at the level of primary consumers and do not include higher predators, they inherently depict zooplankton dynamics as driven by phytoplankton productivity. For example, in the Gulf of Riga biogeochemical model variations in secondary productivity are controlled by fluctuations in summer phytoplankton biomass. In the coastal ECOPATH models the ecotrophic efficiency of the individual producer and consumer group indicated varying degrees of trophic control (Table 6), with highest ecotrophic efficiencies observed for fluxes received by fish, birds and fishing fleets. Their large impact on the ecosystem is consistent with the efficiency hypothesis, claiming that large and efficient predators increase the strength of trophic cascades (Borer et al. 2005, Strong 1992, Polis 1999). For the Baltic Proper, sprat as a mobile predator seem to cause predation control of zooplankton that further cascades to higher phytoplankton summer blooms (Casini et al. 2008). High phytoplankton resource availability on the other hand, which is discussed to increase the strength of trophic cascades by boosting carbon turnover also at consumer level (Borer et al. 2005, Polis 1999, Leibold 1989) does not necessarily lead to higher ecotrophic efficiencies. Among the five coastal systems investigated, the hypertrophic Curonian lagoon is a prime example of low carbon transfer efficiency because the cyanobacteria dominated phytoplankton community is not grazed efficiently (Razinkovas & Gasiunaite, 1999, see publication V).

6 Conclusions

Marine ecosystem models can provide a reasonable representation of phytoplankton and nutrient dynamics in Baltic Sea subsystems. The success of the Kattegat new production model shows, that simulated phytoplankton and nutrient concentrations primarily depend on the supply of new nutrients to the euphotic zone, with little sensitivity to the magnitude of regenerated production. This is due to the structure of NPZD models, where underestimated phytoplankton growth and loss processes can compensate each other.

Marine ecosystem models allow estimating the magnitude of nutrient fluxes in the pelagic system and to study the nutrient sources fuelling primary production. The magnitude of the estimated fluxes is sensitive to the underlying model assumptions and to the type of processes included into the model. For example, the Kattegat carbon budget model estimated higher grazing pressure on phytoplankton than the models constructed for the Gulf of Riga, because the carbon budget was based on the assumption that mesozooplankton grazing was the dominant phytoplankton loss processes during summer. Further, being mechanistic ecosystem models that are based on a mass balance of nutrients or carbon in the ecosystem, the models will explain all gain and loss processes of nutrients, phytoplankton or zooplankton in terms of the processes included into the model and simulated fluxes have to interpreted taking into account the process resolution of the model. For example omitting nutrient regeneration from the Kattegat new production model still provides valuable insight into the nutrient sources sustaining phytoplankton production, but the magnitude of the simulated nutrient fluxes reflect only the turnover of new nutrients.

Resolution of physical processes in the models affects the simulated temporal dynamics of nutrients and phytoplankton. To capture short-term fluctuations, models have to represent variations in vertical mixing and horizontal advection on a similar time scale. The model for the Southern Gulf of Riga showed that variations in entrainment cause nutrient pulses into the upper layer, which lead to peaks in phytoplankton biomass. Observed nutrient and phytoplankton dynamics at individual monitoring station have therefore to be interpreted taking into account concurrent hydrographic conditions. Further, the importance of freshwater advection for stratification and nutrient fluxes in the model of the Southern Gulf of Riga clearly showed, that the high-frequency station 119, for which the model was constructed is not representative of phytoplankton and nutrient turnover in the central Gulf of Riga.

The long-term dynamics of nutrients and primary producers in Baltic Sea subsystems depend on geochemical processes in the bottom sediments and, in particular in the case of phosphorus, on the nutrient fluxes between Baltic subbasins. Biogeochemical models are capable of simulating the magnitude of nutrient sources and sinks, but verification of sediment fluxes by observations is difficult due to the large variability in field measurements and the point nature of observations compared to the basin-wide spatial scale of the models. Differing nutrient sinks for nitrogen and phosphorus lead to longer phosphorus residence time and consequently to shifts in nutrient availability and limitation when nutrient loads decrease.

In contrast to the truncated NPZD models used as the core of biogeochemical models, ECOPATH models of carbon fluxes in marine ecosystems are capable of indicating trophic cascades. However, biomass and ecophysiological data are not always available for study areas of interest and often need to be upscaled or downscaled, increasing the uncertainty of the model results. Hindcasting biomass dynamics using ECOSIM might be a valuable approach to validate ECOPATH models in areas where long-term data are available.

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