

Modelling nitrogen and phosphorus limitation on phytoplankton growth in Narva Bay, south-eastern Gulf of Finland*

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Abstract

The relative roles of nitrogen and phosphorus in the limitation of phytoplankton growth in Narva Bay, south-eastern Gulf of Finland, were studied by combining the results of numerical modelling and nutrient enrichment experiments. Modelled biomass-based intracellular nutrient concentrations (nutrient functions) were used to estimate the limiting nutrient in Narva Bay. Nutrient functions – $NF \in [0; 1]$ for nitrogen and $PF \in [0; 1]$ for phosphorus – define the dependence of the phytoplankton growth rate on nutrients: $NF = PF = 1$ corresponds to non-limitation of phytoplankton growth by nutrients, whereas $NF = 0$ or $PF = 0$ to zero growth. The biotests indicated the response of phytoplankton growth to an increase in nutrient concentration in the surrounding water. Three locations were selected for detailed analyses of temporal variations in the nutrient functions: the offshore station N12, station N8 at the mouth of the River Narva, and coastal station 38. The biotests were performed at the same stations. NF and PF reached values of 0.9 prior to the spring bloom. With the onset of the spring bloom, NF

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decreased rapidly and remained below 0.1 in the open part of Narva Bay for the rest of that period. In the coastal zone, NF was in excess of 0.1, with a local maximum in the river mouth area. PF decreased to 0.3–0.4 in the open bay after the spring bloom. In the coastal zone PF remained above 0.4, with a certain increase from the midsummer minimum towards the end of summer. The numerical modelling results clearly show that nitrogen limits phytoplankton growth in Narva Bay. Phosphorus limitation may occur only for a limited period and over a limited area at the Narva River mouth and other coastal locations. In general, the biotests backed up the modelling results, the main exception being in the open bay during summer. The model does not account for nitrogen fixation, however. Since N-fixing cyanobacteria were prevalent in the offshore area, the addition of phosphorus led to enhanced phytoplankton growth at station N12.

1. Introduction

Understanding the roles of nutrients essential to phytoplankton growth is crucial for the successful control of eutrophication in coastal areas. The limiting nutrient can be detected using different methods, e.g., by inorganic nitrogen to phosphorus ratios (Neill 2005), enrichment experiments (e.g., Ryther & Dunstan 1971, Graneli 1987), or measuring intracellular concentrations of nutrients (Hecky & Kilham 1988).

Nutrient limitation in the Baltic Sea has been studied widely by the use of both experimental (e.g., Tamminen et al. 1985, Graneli 1987, Graneli et al. 1990, Seppälä et al. 1999, Wasmund et al. 2001) and modelling (e.g., Savchuk & Wulff 1999, Savchuk 2000) approaches. Large areas of the Baltic are nitrogen-limited, but sporadic phosphorus limitation is detectable during several phases of phytoplankton succession (e.g., immediately after the spring bloom). Phosphorus limitation also occurs in estuaries and river plumes. Studies in the Gulf of Finland (Kivi et al. 1993; Pitkänen & Tamminen 1995, Kuusisto et al. 1998, Kiirikki et al. 1998) generally report phosphorus limitation in some parts of the Neva estuary, whereas the central and western parts of the gulf are nitrogen-limited for much of the growing season. According to Kivi et al. (1993), phytoplankton production in the north-western Gulf of Finland was limited by nitrogen only during the spring bloom and late summer, but by both nitrogen and phosphorus in the early summer.

The aim of this work was to investigate the relative roles of nitrogen and phosphorus limitation on phytoplankton growth in Narva Bay, in the south-eastern Gulf of Finland, by combining the results of numerical modelling with those of nutrient enrichment experiments. Narva Bay is bound by the coastline in the south and in the east; its northern and western boundaries

fall within the respective coordinates of $59^{\circ}55'N$ and $26^{\circ}35'E$ (Pirsoo et al. 1992). The south-eastern part of Narva Bay receives the outflow of the River Narva, one of the largest in the catchment area (Fig. 1). Annual time-averaged loads carried to sea by the Narva are estimated at 4010 t of nitrate nitrogen and 290 t of phosphate phosphorus (Stålnacke et al. 1999). A detailed model description and mathematical formulation will be found in Lessin & Raudsepp (2006).

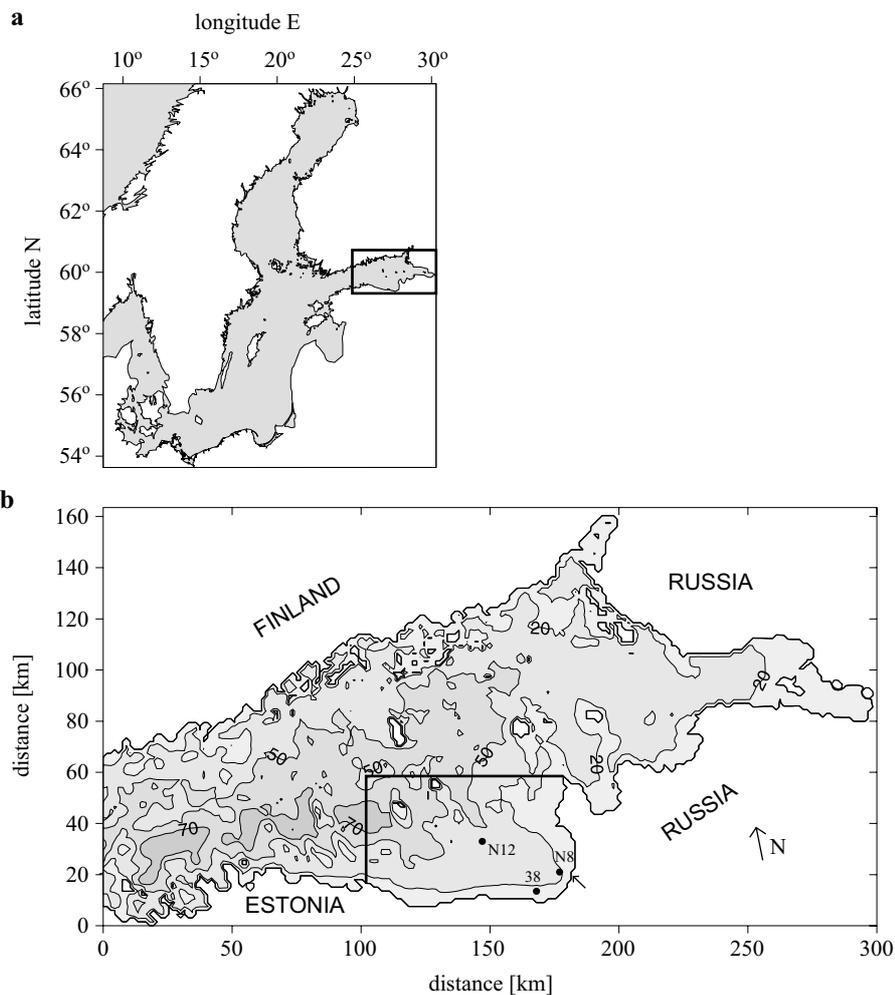


Fig. 1. The Baltic Sea (a) and the model domain covering the central and eastern parts of the Gulf of Finland (b). The limits of Narva Bay and the location of monitoring stations N8, N12 and 38 are shown. The small arrow points to the mouth of the River Narva

2. Methods

2.1. Model

The MIKE 3 ecohydrodynamic 3-dimensional model developed by the Danish Hydraulics Institute (DHI Water and Environment 2001) was applied to the central and eastern parts of the Gulf of Finland. The simulation time covered the biologically active period from 1 April to 30 September 2001. The spatial resolution of the model was 1500 m in the horizontal and 2 m in the vertical, except for the upper layer, which was 3 m thick. Model results were stored at 6-hour intervals. In the basic setup, the conservation equation for a compressible fluid, non-linear momentum equations in the three main directions, the conservation equation for salinity and temperature, and the equation of state of sea water (Rasmussen 1993) were solved in the hydrodynamic model. In particular cases, the simulations were performed using a hydrostatic model version with the Smagorinsky formulation applied to horizontal eddy viscosity and the $k-\varepsilon$ formulation to the vertical turbulent closure model (Burchard et al. 1998, Rasmussen et al. 1999). The main forcing factors were wind stress and heat exchange at the surface, the prescribed sea level, temperature and salinity at the open boundary and river inflow (Lessin & Raudsepp 2006).

The ecological processes of the model describe the interrelations between phytoplankton carbon P_C , nitrogen and phosphorus, chlorophyll a , zooplankton, detritus carbon, nitrogen and phosphorus, inorganic nitrogen, inorganic phosphorus and dissolved oxygen (DHI Water and Environment 2001, Erichsen & Rasch 2001, Lessin & Raudsepp 2006). Nutrients are supplied by rivers and transported into the area across the model's open boundary. The prescribed distribution of state variables is applied at the open boundary of the model (Lessin & Raudsepp 2006). Phytoplankton growth in the MIKE 3 model depends on internal nutrient pools, and nutrient limitation for growth is calculated from the relative saturation of phytoplankton cells by nutrients.

The phytoplankton carbon balance is calculated as

$$\frac{dP_C}{dt} = prP_C - grP_C - seP_C + seP_C^{n-1} - deP_C, \quad (1)$$

where P_C – phytoplankton concentration, prP_C – production, grP_C – zooplankton grazing, seP_C – sedimentation, seP_C^{n-1} – sedimentation from the layer above, and deP_C – death of phytoplankton.

Phytoplankton production is expressed as

$$prP_C = \mu f(I) f(T) f(N, P) F_C rd, \quad (2)$$

where μ – maximum growth rate of phytoplankton, $f(I)$ – dependence on light availability, $f(T)$ – temperature dependence, $f(N, P)$ – nutrient function, F_C – correction factor for dark reaction, rd – relative day length.

The nutrient function is calculated as

$$f(N, P) = \frac{2}{\frac{1}{NF} + \frac{1}{PF}}, \quad (3)$$

where $f(N, P)$ – nutrient function, NF – nitrogen function, and PF – phosphorus function.

The nitrogen and phosphorus functions describe phytoplankton cell saturation with nitrogen or phosphorus: this saturation is calculated with respect to the maximum and minimum nutrient-to-carbon ratio in phytoplankton. The phosphorus function is further dependent on the half-saturation constant.

The nitrogen function is formulated as

$$NF = \frac{P_N/P_C - P_{N \min}}{P_{N \max} - P_{N \min}}, \quad (4)$$

where P_N – intracellular phytoplankton nitrogen content, P_C – phytoplankton carbon concentration, $P_{N \min}$ – the minimum and $P_{N \max}$ – the maximum nitrogen-to-carbon ratio in phytoplankton.

The phosphorus function is calculated as

$$PF = \frac{(P_P/P_C - P_{P \min})}{(K_C + P_P/P_C - P_{P \min})} \bigg/ \frac{(P_{P \max} - P_{P \min})}{(K_C + P_{P \max} - P_{P \min})}, \quad (5)$$

where P_P – intracellular phytoplankton phosphorus content, $P_{P \min}$ – the minimum and $P_{P \max}$ – the maximum phosphorus-to-carbon ratio in phytoplankton, and K_C – half-saturation constant for phosphorus in phytoplankton.

The mass balance of phytoplankton nitrogen is formulated as

$$\frac{dP_N}{dt} = unP_N - grP_N - seP_N + seP_N^{n-1} - deP_N, \quad (6)$$

where unP_N – uptake of inorganic nitrogen, grP_N – zooplankton grazing, seP_N – sedimentation, seP_N^{n-1} – sedimentation from the layer above, and deP_N – death of phytoplankton nitrogen.

The uptake of inorganic nitrogen under limiting conditions is calculated as

$$unP_N = \min \left[\max \left[\begin{array}{l} V_{kn} I_N P_C \\ Mineralization + external \ load \\ prP_C P_{N \max} \end{array} \right. \right. \quad (7)$$

and under non-limiting conditions as

$$unP_N = \min \left[\begin{array}{l} V_{kn} I_N P_C \\ prP_C P_{N \max} \end{array} \right], \quad (8)$$

where V_{kn} – uptake rate constant for nitrogen and I_N – inorganic nitrogen concentration.

The mass balance of phytoplankton phosphorus is calculated as

$$\frac{dP_P}{dt} = unP_P - grP_P - seP_P + seP_P^{n-1} - deP_P, \quad (9)$$

where unP_P – uptake of inorganic phosphorus, grP_P – zooplankton grazing, seP_P – sedimentation, seP_P^{n-1} – sedimentation from the layer above, and deP_P – death of phytoplankton phosphorus.

The uptake of inorganic phosphorus under limiting conditions is calculated as

$$unP_P = \min \left[\begin{array}{l} \max \left[\begin{array}{l} V_{kp} I_P P_C \\ Mineralization + external \ load \end{array} \\ prP_C P_{P \max} \end{array} \right] \end{array} \right] \quad (10)$$

and under non-limiting conditions as

$$unP_P = \min \left[\begin{array}{l} V_{kp} I_P P_C \\ prP_C P_{P \max} \end{array} \right], \quad (11)$$

where V_{kp} – uptake rate constant for phosphorus and I_P – inorganic phosphorus concentration.

Table 1 lists the values of these parameters. Further mathematical formulation of the ecological model is given in Lessin & Raudsepp (2006).

2.2. Nutrient addition experiments

The measurements and biotests were carried out in the Narva Bay area in 2001. Measurements and water sampling for the biotests at two coastal stations (N8 – near the river mouth, and 38 – in the south-eastern bay) and at one offshore station (N12) were carried out once in May and September and every week from 27 June to 27 August. For the biotests 25 dm³ of surface water from every station were taken to the laboratory, where nutrient treatment experiments were set up. Subsamples (1.5 dm³) of seawater were transferred into acid-rinsed 1.5 dm³ polycarbonate bottles; 10 cm³ inorganic nitrogen (33 μmol dm⁻³ as NaNO₃) or 10 cm³ inorganic phosphorus (2 μmol dm⁻³ as K₂HPO₄) were then added alone or in combination (+N, +P, +NP and control). All treatments were performed in triplicate for

Table 1. Values and description of parameters required for calculation of nutrient limitation

Parameter	Description	Unit	Value
μ	maximum growth coefficient at 20°C	d ⁻¹	0.8 (diatoms) 1.4 (green algae)
F_C	correction factor for dark reaction	n.u.	1.3
$P_{N \min}$	minimum internal nitrogen content in algae	gN gC ⁻¹	0.07
$P_{N \max}$	maximum internal nitrogen content in algae	gN gC ⁻¹	0.17
$P_{P \min}$	minimum internal phosphorus content in algae	gP gC ⁻¹	0.002
$P_{P \max}$	maximum internal phosphorus content in algae	gP gC ⁻¹	0.03
K_C	half saturation constant for phosphorus in phytoplankton	gP gC ⁻¹	0.2
V_{kn}	the uptake rate constant for nitrogen	gN gC ⁻¹ d ⁻¹	1
V_{kp}	the uptake rate constant for phosphorus	gP gC ⁻¹ d ⁻¹	0.5

a total of 12 bottles per station. The bottles were placed in an incubator (a large plastic box filled with water at the same temperature as the in situ surface temperature in the sea on each sampling date – the temperature was monitored) at a light intensity of 350 $\mu\text{E m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR). Chlorophyll *a* from each replicate following the 40 h incubation period was measured.

3. Results

A detailed validation of the ecological model for Narva Bay is given in Lessin & Raudsepp (2006) and Lessin & Raudsepp (2007). For better clarity of the model's behaviour, comparisons of modelled and measured phytoplankton and inorganic nitrogen concentrations are reproduced in Fig. 2a–c (Lessin & Raudsepp 2006, 2007). In general, the model results compared reasonably well with the available measurement data. Additionally, the modelled surface inorganic phosphorus concentrations at station N8 were validated to ensure the accuracy of the *PF* calculations. Inorganic phosphorus was strongly variable in the summer period in both the measured and the modelled data, which is evidence for river discharge (Fig. 2d). The modelled spring values match the measurement data rather well.

Three sites – one offshore station N12 (Fig. 3) and two coastal stations N8 (Fig. 4) and 38 (Fig. 5) – were selected for detailed analysis of the

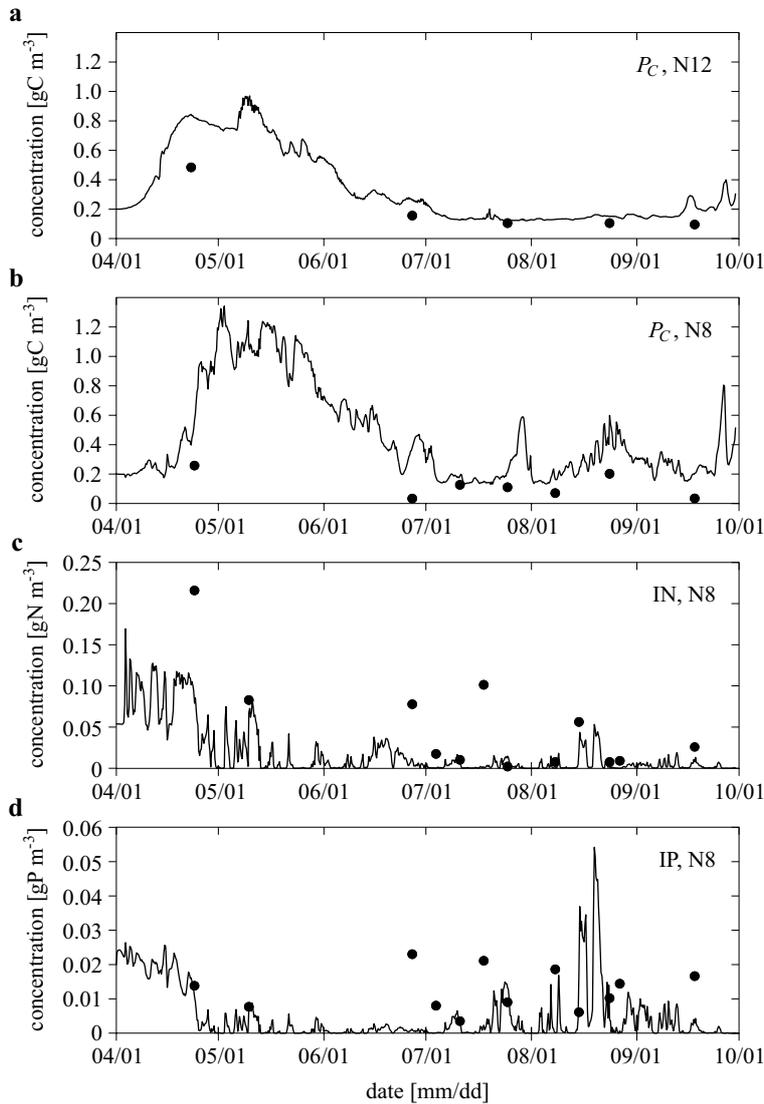


Fig. 2. Model validation results for Narva Bay in 2001: a) P_C at N12 (redrawn from Lessin & Raudsepp 2006, Fig. 5a, with permission from Springer Science and Business Media), b) P_C at N8 (redrawn from Lessin & Raudsepp 2007, Fig. 2c, with permission from Elsevier), c) surface inorganic nitrogen at N8 (redrawn from Lessin & Raudsepp 2007, Fig. 2a, with permission from Elsevier), and d) inorganic phosphorus at N8. Lines – model results, dots – observed data

temporal variations in nutrient functions and their ratios. The NF/PF ratio estimates the relative roles of limiting nutrients. An NF/PF ratio close to 1 ± 0.2 can mean either weak or no nutrient limitation (both nutrients are

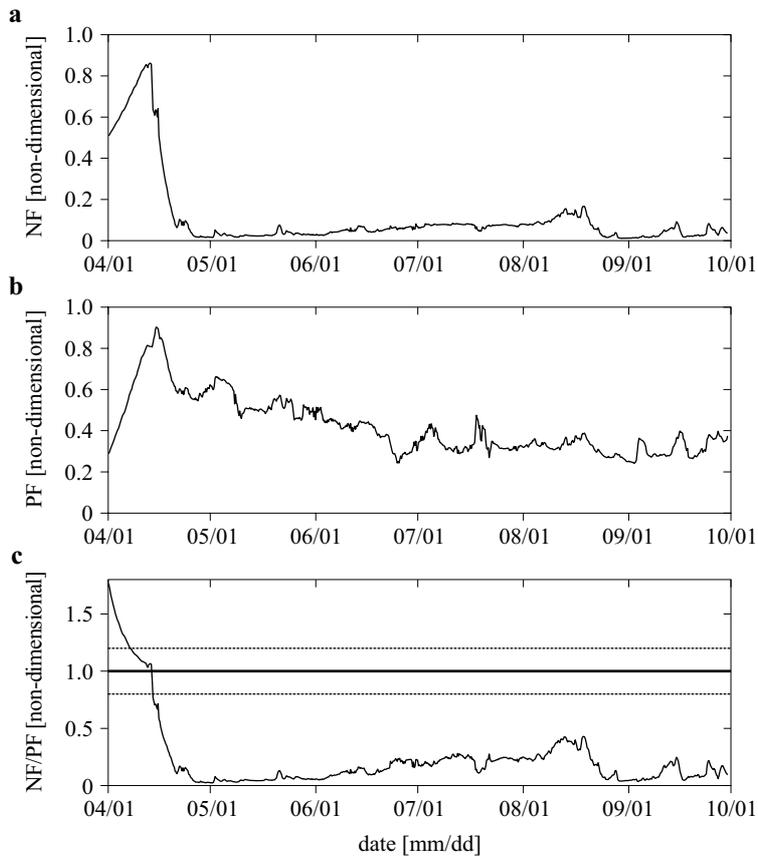


Fig. 3. Modelled time-series of nitrogen (a) and phosphorus (b) functions and their ratio (c) at station N12 in Narva Bay in 2001

high), or co-limitation (both nutrients are low). Station N12 was located in the open bay, where nutrient functions were generally lower than in the coastal area. Station N8 was close to the Narva River mouth. Although station 38 was outside the area immediately affected by outflow from the Narva, there was a local outlet on the coast adjacent to this station. The biotests were performed at the same sites.

The model results showed relatively high nitrogen and phosphorus contents in the phytoplankton during April, when NF and PF reached maximum values of ~ 0.8 – 0.9 at all three stations. The function values at the near-shore stations 38 and N8 remained high until the end of April, but dropped rapidly in the middle of the month at the offshore station N12. The very rapid increase in NF and PF and the corresponding phosphorus limitation (NF/PF ratio up to 1.8) during the first week of April could

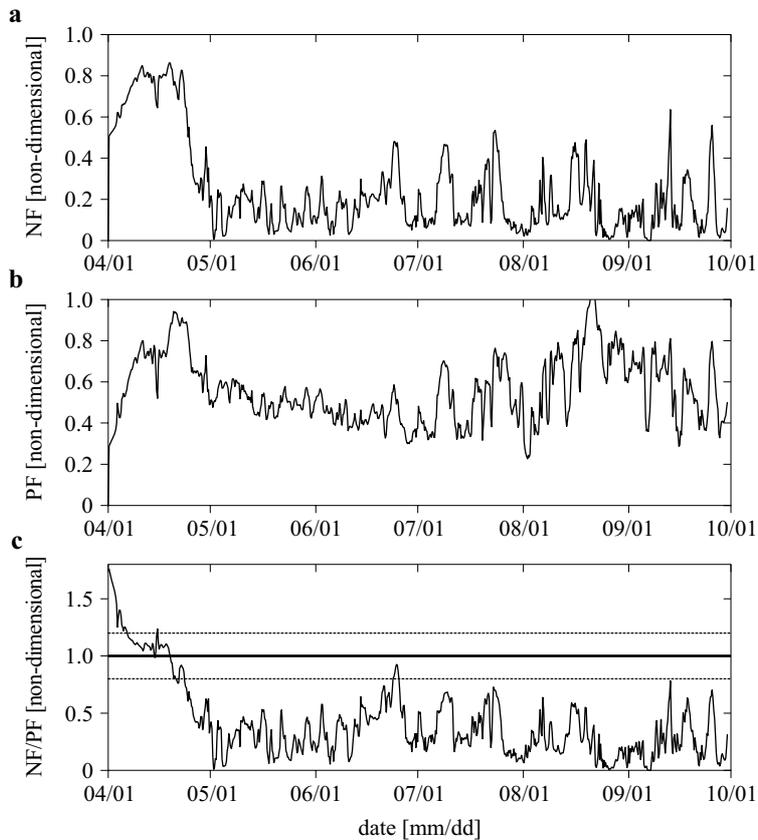


Fig. 4. Modelled time-series of nitrogen (a) and phosphorus (b) functions and their ratio (c) at station N8 in Narva Bay in 2001

be attributed to the short-term adjustment of initial fields to the model dynamics.

After the spring bloom, the nutrient dynamic at the offshore station differed somewhat from that at the coastal stations. At station N12, NF values remained low compared to the stations near the coast; they did not display any strong fluctuations, which was the case at the coastal stations. NF increased steadily from late April until the middle of August, after which its values dropped. At station 38 this steady increase was less pronounced, however, and at station N8 was scarcely detectable. Generally speaking, NF values at station N8 were slightly higher and more variable than at station 38, except for two distinct peaks at the latter station – one at the end of June and another in the middle of September. In contrast, the values of PF declined steadily from the beginning of May until mid-June. At the offshore station N12 this function stabilised at values of 0.3–0.4. There was

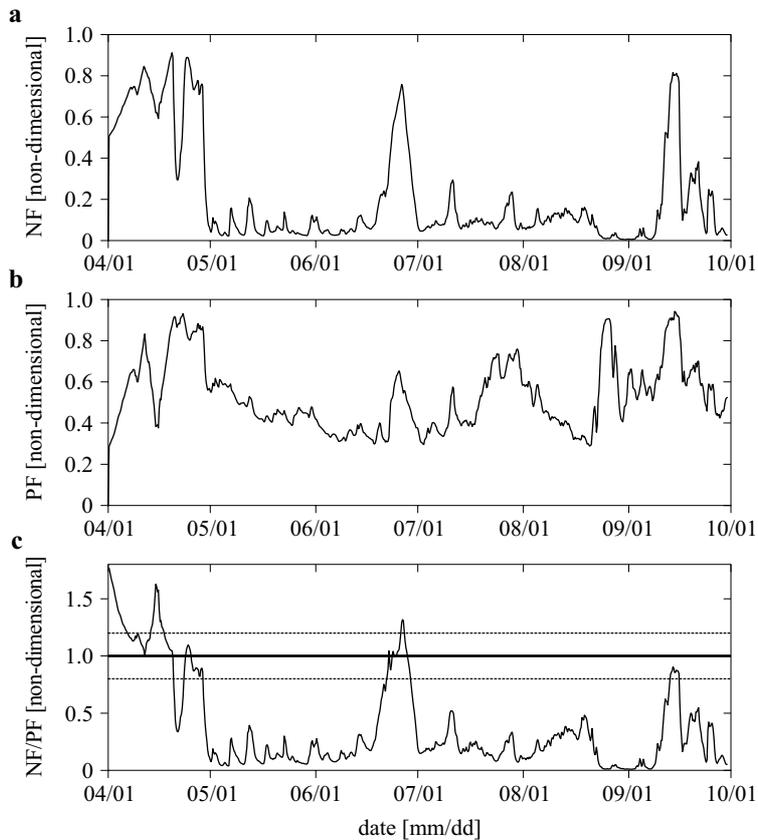


Fig. 5. Modelled time-series of nitrogen (a) and phosphorus (b) functions and their ratio (c) at station 38 in Narva Bay in 2001

considerable variability at station N8, but the general trend was a rising one until the third week of August, when PF reached the maximum value of 1; thereafter, until the end of the modelled period, the function diminished in value. At station 38 fluctuations in PF were less frequent but more variable, values reaching ~ 0.9 in late August and ~ 0.94 in mid-September.

In general, the NF/PF ratio was < 1 at all stations after the spring bloom, which indicates nitrogen limitation of phytoplankton growth. At station N12 the ratio was mostly < 0.4 . At station 38 the average NF/PF ratio was the same, except for two short events at the end of June and in mid-September. In the first of these, NF/PF was > 1.2 , indicating a sporadic shift to phosphorus limitation: NF increased to 0.75, and PF increased to 0.65. During the second event, the NF/PF ratio rose to 0.9 as a result of an increase in NF to 0.8 and in PF to > 0.9 . The probable interpretation of this situation is that neither nutrient limited phytoplankton growth.

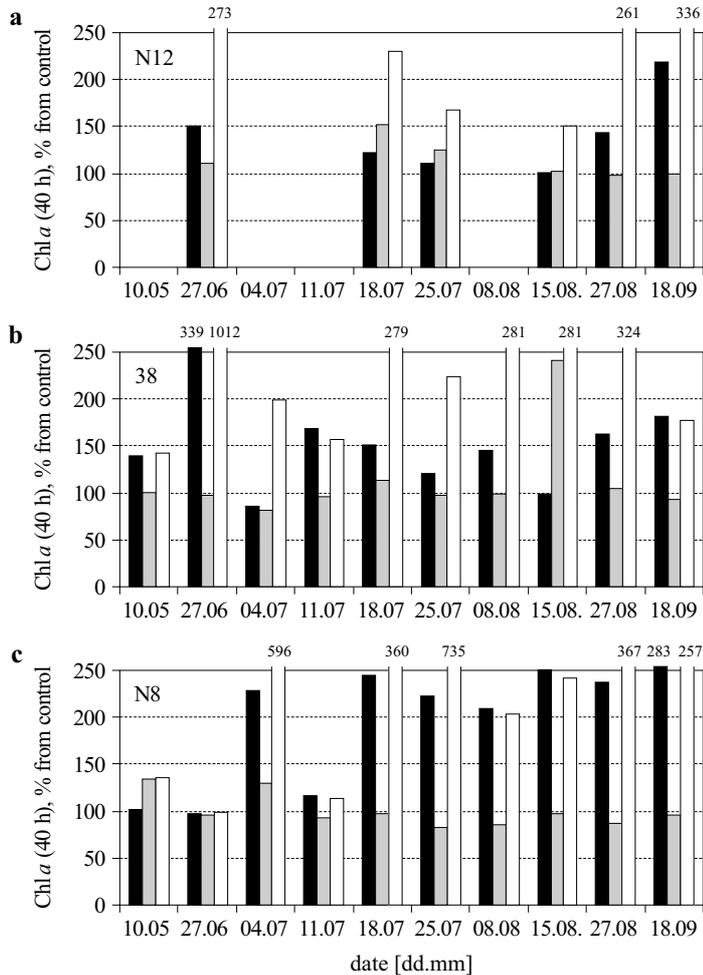


Fig. 6. Results of nutrient enrichment experiments in 2001 at monitoring stations N12 (a), 38 (b) and N8 (c): nitrogen (black bars), phosphorus (grey bars), combined additions (white bars)

The experiments showed that at the offshore station N12 (Fig. 6a) and at station 38 (Fig. 6b) phytoplankton always responded with enhanced growth during the combined addition of nitrates and phosphates. Also, growth was usually rapid following the addition of nitrates only. The rapid growth of phytoplankton in response to the combined addition of nitrates and phosphates on 27 June, 27 August and 18 September at station N12 is consistent with the modelling results, which indicate a low level of both nutrient functions. There were two exceptions that are inconsistent with the modelling results. At station N12, separate treatment

experiments showed a faster phytoplankton growth response to phosphate addition than to nitrate addition on 18 and 25 July. On 15 August the phytoplankton response to both separate treatments was nearly equal. The second exception was at station 38 on 15 August when in the separate treatments the phytoplankton responded to the addition of phosphorus with rapid growth.

At station N8 the average NF/PF ratio was higher (~ 0.4) and the temporal variability stronger than at the other stations after the spring bloom. It is noticeable that nitrogen limitation was the strongest at station N8 in late August-early September, when NF was low and PF very high (a consequence of inorganic phosphorus inflow). Until mid-July (except 4 July) the biotests showed a slow response to nutrient addition (Fig. 6c). After the second half of July, phytoplankton growth was faster following the combined addition of nutrients. In a separate treatment, nitrogen addition resulted in rapid phytoplankton growth, whereas the addition of phosphorus even retarded growth: this clearly indicates nitrogen limitation at the mouth of the Narva. The results of the biotests are consistent with the modelling results, which show a high level of phosphorus in the phytoplankton cells.

4. Discussion

In the present study both the modelling results and the nutrient enrichment experiments have shown that nitrogen is in general the main limiting nutrient in Narva Bay; this is in agreement with previous studies in the Gulf of Finland (Kivi 1993, Pitkänen & Tamminen 1995). Phosphorus limitation was expected in the Narva River plume area, as had been reported from Neva Bay (Pitkänen & Tamminen 1995) and the Daugava River plume (Seppälä et al. 1999, Tamminen & Seppälä 1999). However, the relatively low freshwater discharge ($14.3 \text{ km}^3 \text{ yr}^{-1}$) and nitrate load (4010 t yr^{-1}) in the River Narva compared to the Neva (discharge – $81.7 \text{ km}^3 \text{ yr}^{-1}$; nitrate load – $21\,260 \text{ t yr}^{-1}$) and the Daugava (discharge – $23.3 \text{ km}^3 \text{ yr}^{-1}$; nitrate load – $28\,680 \text{ t yr}^{-1}$) (Stålnacke et al. 1999) explains why phosphorus limitation was not recorded even in close proximity to the Narva mouth, i.e., at station N8. Moreover, the Neva's influence is prevented from reaching as far as Narva Bay by the cyclonic general circulation in the eastern Gulf of Finland (Andrejev et al. 2004).

Nonetheless, distinct features of nutrient limitation and their influence on the relevant phytoplankton biomass in the open part of the bay and the coastal area are discernible. The phytoplankton nutrient content and biomass (Fig. 7) were higher in the coastal zone than in the open bay. But the pre-bloom period in the southern part of Narva Bay was an exception: this period was much influenced by the initial fields of the model state

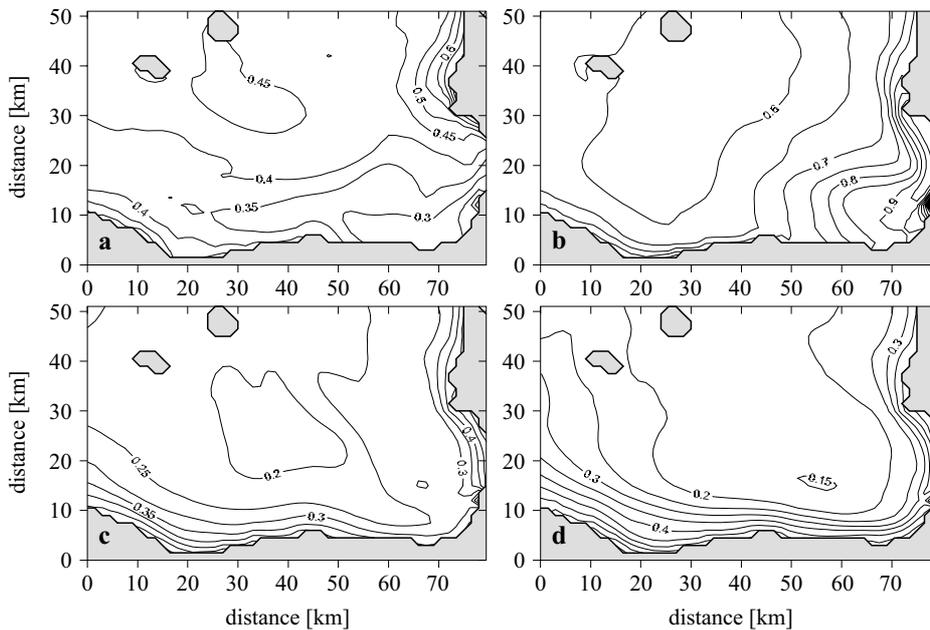


Fig. 7. Modelled average distribution of phytoplankton carbon [g m^{-3}] in Narva Bay in 2001 during a) pre-bloom (1.04–20.04), b) spring bloom (21.04–15.06), c) bloom termination (16.06–15.07) and d) summer-autumn minimum (16.07–1.10) periods. The contour interval is 0.05 g m^{-3}

variables, which had been defined on the basis of a very limited amount of data (Lessin & Raudsepp 2006). No biotests were performed during that period either.

P_C concentrations reached their highest values during the spring bloom. From the spatial point of view, these values were higher in the south-eastern bay and along the coasts (Lessin & Raudsepp 2007). On average, NF dropped significantly in comparison to the pre-bloom period, both offshore and near the coast. The biotest results show that there were sufficient inorganic nutrients in the water to support phytoplankton growth, and that the maximum growth capacity of phytoplankton was reached (Kiirikki et al. 1998). In the model, the spring bloom started earlier than the measurements showed (see Lessin & Raudsepp 2006).

After mid-June, P_C , NF and PF remained low until the end of the modelled period in the open bay, which showed that nitrogen- and co-limitation were taking place. The biotests support this conclusion at the end of June and after the end of August. During the summer, the addition of nitrogen resulted in only minor growth of phytoplankton. Experimental results showed that N-fixing cyanobacteria prevailed at the

offshore station N12 during summer. The other phytoplankton groups were of little importance. The species composition explains the fact that at the offshore station in July, phytoplankton growth was quicker after the addition of phosphates than after the addition of nitrates. The response to nutrient addition was somewhat slower than expected because the incubation bottles were closed. In late August the community structure became more heterogeneous, which also led to a faster growth response in the nutrient addition experiments. Atmospheric nitrogen fixation is not simulated by the model. Therefore model results showed strong nitrogen limitation during this period. Taking into account the higher value of PF relative to NF in the model, conditions favouring N-fixing cyanobacteria growth were established in the open bay (Kahru et al. 2000, Stal et al. 2003).

The experiments showed that at the river mouth station N8 the growth of the phytoplankton community was clearly N-limited. During the spring bloom, nutrient additions led to a weak response from phytoplankton, which had probably reached its maximum growth capacity. On 27 June there were sufficient inorganic nutrients in the water to support phytoplankton growth. The model results showed a pulsed nutrient discharge from the River Narva in summer.

Both the nutrient addition experiments and the model results demonstrated that the growth of the phytoplankton community was limited mainly by nitrogen at coastal station 38. Nevertheless, the addition of nitrates in July–August did not elicit a very quick response in phytoplankton growth: clearly, both nutrients were needed during this period. The rapid response to the addition of phosphorus in mid-August could have been due to nitrogen leakage from a local outlet in the vicinity of the station. The model results showed that upwelling events along the southern coast of the bay were able to bring considerable amounts of inorganic nitrogen to the surface layers (Lessin & Raudsepp 2007). This led to several distinct NF peaks shifting to sporadic P- or co-limitation at that station. Shifts in nutrient limitation due to physical processes had previously been reported in the Gulf of Riga, where thin or moderately mixed layers favoured nitrogen limitation and deep mixing favoured phosphorus limitation of phytoplankton growth (Tamminen & Seppälä 1999).

5. Conclusions

Nitrogen and phosphorus limitation of phytoplankton growth in Narva Bay, in the south-eastern Gulf of Finland, was investigated by combining the results of numerical modelling with those of nutrient addition experiments. The model involved the study of normalised intracellular concentrations

(nutrient functions) of nutrients in order to determine the limiting roles of the nutrients taken up by the cells. The results of the biotests indicate the response of phytoplankton growth to the addition of nutrients.

The current study showed that, in general, nitrogen is the main limiting nutrient in Narva Bay. This is in accordance with previous studies on nutrient limitation in the Gulf of Finland (Kivi 1993, Pitkänen & Tamminen 1995) and in the Gulf of Riga (Seppälä et al. 1999, Tamminen & Seppälä 1999). The high nutrient content in spring supports an intensive phytoplankton bloom in spring. *NF* drops to a minimum in advance of the bloom peaks, while the average level of *PF* and a high phytoplankton concentration are maintained. The decrease in *NF* is faster over the open bay than in the coastal zone. Phosphorus levels continue to remain high, thus preconditioning the open bay area for the growth of N-fixing cyanobacteria during summer. The N-fixing cyanobacteria were not simulated in the model, but according to the experimental data they are dominant in the phytoplankton composition. Phosphorus limitation can occur sporadically near the Narva mouth and elsewhere in the coastal zone. Except for the pre-bloom period, the nitrogen function was relatively greater in the coastal zone than in the open bay. This is consistent with the higher concentration of inorganic nitrogen in the coastal zone (Lessin & Raudsepp 2007).

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