

Review article

## Nitrogen Fixation of Cyanobacteria (Blue-Green Algae) and the Nitrogen Cycle of the Baltic Sea

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### Abstract

The stable stratification of the water and the slow and irregular exchange of bottom waters enhance the build up of stagnant conditions in the deep basins of the Baltic Proper and the Gulf of Finland. This causes oxygen depletion, a decrease in inorganic nitrogen reserves through denitrification, the trapping of inorganic phosphorus in the bottom water, and a phosphorus flux from the sediment resulting in a decrease in the nitrogen:phosphorus ratio. During the summer, when the nutrient concentrations are low in the euphotic layer, heavy blooms of nitrogen-fixing cyanobacteria are common in the Baltic Proper, the Gulf of Finland and the southern parts of the Bothnian Sea. They are favoured by the warm stable surface water and by the upwelling water with a low N:P ratio. The total amount of nitrogen fixation is estimated to correspond to ca. 10% of the total nitrogen input to the Baltic Proper. During the blooms, however, nitrogen fixation seems to represent only a minor contribution to the nitrogen requirements of the phytoplankton. No photosynthetic plankton group has been found to be formed immediately after the degradation of the cyanobacterial bloom that would have gained benefit from the input of nitrogen through nitrogen fixation.

## 1. Introduction

There has been debate about the extent to which the mass occurrence of nitrogen-fixing cytotobacteria in the Baltic Sea is connected to the eutrophication of the sea, and about how essential is nitrogen fixation for the functioning of the ecosystem (e.g. Öström, 1976; Rinne et al., 1978; Niemi, 1979; Lindahl et al., 1980; Melvasalo et al., 1983; Rönner 1983, 1985; Larsson et al., 1985; Niemistö et al., 1988). In addition, some strains of bloom-forming cyanobacteria have been observed to be toxic and caused death of animals (Persson et al., 1984 and literature cited therein). The dynamics of the cyanobacterial blooms and nitrogen fixation have been studied since the 1970s in Swedish coastal areas (Lindahl et al., 1978; Lindahl et al., 1980; Lindahl and Wallström, 1985) and in the open sea areas by the "MERININNI" group at the Finnish Institute of Marine Research (Rinne et al., 1978, 1979, 1980, 1981; Melvasalo et al., 1982, 1983; Melvasalo and Niemi, 1985; Niemi, 1979, 1982; Niemistö et al., 1988). This paper is mostly based on the results obtained by the "MERININNI" group.

The semistagnant conditions of the Baltic Sea have a profound effect on the nutrient balance in the different water layers, on the cycling of organic matter in the ecosystem, and on the biological features. A short description of the general hydrographical, chemical and biological features of the Baltic Sea is therefore included in this paper.

## 2. The Baltic Sea

The brackish Baltic Sea, situated between 54° and 66°N (Fig. 1), is a cold sea with great differences between the temperate summer and the long, cold winter. The surface area of the Baltic Sea is 374000 km<sup>2</sup>, and it contains ca. 22000 km<sup>3</sup> water (Ehlin, 1981). The mean depth is only 60 m. It is connected to the North Sea through the Kattegat and extends to the east and north as a series of basins (Fig. 2). The shallow Danish Sounds limit the direct water exchange between the Baltic Sea and the Kattegat. The inflowing saline water from the North Sea is injected to the Baltic Proper at depths corresponding to its density, maintaining a deep water salinity of > 10‰ and a stable pycnocline, the permanent halocline occurring at a depth of 60–80 m (Fig. 2). The mean salinity of the outward flowing surface layer, a mixture of river and saline water, ranges from 1–4‰ in the northernmost parts of the Gulf of Bothnia and the easternmost parts of the Gulf of Finland, to about 7‰ in most of the Baltic Proper (Kullenberg, 1981). The stable stratification of the water and the slow and irregular exchange of



Figure 1. The Baltic Sea.

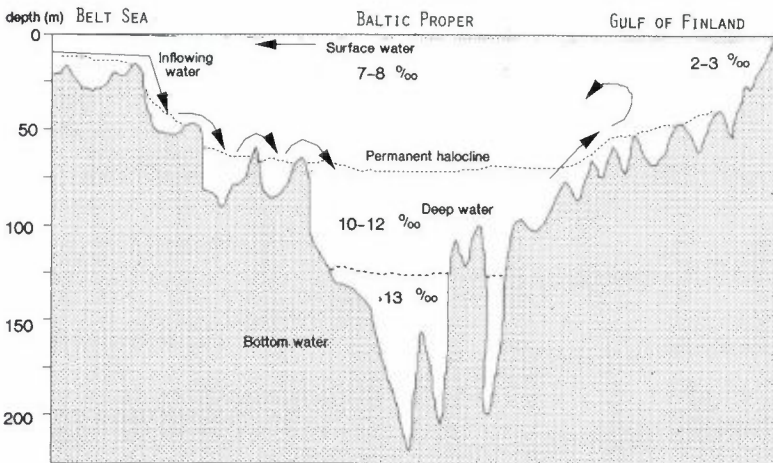


Figure 2. Transect of the Baltic Sea from the Danish Sounds to the Gulf of Finland.

bottom waters enhance the build up of stagnant conditions in the deep basins of the Baltic Proper and the Gulf of Finland. This causes oxygen depletion, a decrease in inorganic nitrogen reserves through denitrification, the trapping of inorganic phosphorus in the bottom water, and a phosphorus flux from the sediment resulting in a decrease in the nitrogen:phosphorus ratio (Fonselius, 1969, 1976, 1978). The episodic, intensive injections of very dense Kattegat water flush out the basins, causing a switch between anoxic and oxic conditions. The sills south of the Åland Sea and in the Archipelago Sea prevent the direct inflow of anoxic Baltic deep-water, rich in phosphorus, into the Gulf of Bothnia. To date, no permanent salinity stratification, resulting in stagnant periods with hydrogen sulphide formation and phosphorus increase, has been recorded there. The phosphorus level decreases markedly and the inorganic N:P ratio increases when moving northward in the Gulf of Bothnia (Lassig et al., 1978; Niemi, 1979).

The accumulation of phosphorus below the permanent halocline increases the biological significance of the vertical water transport mechanism. The most intensive transport takes place along the coasts through the processes of turbulent mixing and advection (Wallin, 1972; Svansson, 1975). Since upwelling and downwelling regimes probably play an important role for a large part of the Baltic coast (Jansson, 1980), most of the nutrient flux through the halocline takes place along the coasts. However, the nutrients probably spread rapidly through the interior of the Baltic (Shaffer, 1979). Even though the Baltic is a cold sea, the open surface temperature may reach values of 18–20°C in summer. Under such conditions the thermocline is situated at a depth of ca. 15–20 m.

### 3. The Seasonal Pattern of the Pelagic Ecosystem

In the open Baltic Sea the reserves of inorganic nutrients, accumulated during the winter, are consumed by phytoplankton down to a depth of at least 40 m during the spring bloom in April-May (Niemi, 1973; Lahdes and Leppänen, 1988). The spring bloom ends when inorganic nutrients, especially nitrogen, are exhausted from the surface layer and the extensive mass sedimentation of algal material takes place (e.g. Niemi, 1975; Forsskåhl et al., 1982; Leppänen, 1988).

The primary production during the early summer is mainly based on the recycling of nutrients in the euphotic layer (e.g. Kuparinen et al., 1984). When the maximum temperature and thermal stability in the euphotic layer is reached in July-August, the filamentous, nitrogen-fixing cyanobacteria start

blooming. Such blooms have been observed still in October. Autumnal diatom blooms have been observed only when the weather conditions are exceptionally favourable (Hällfors et al., 1981). The winter, with low solar radiation and prominent mixing of the surface waters during periods without ice, is characterized by low decomposition rates (Jansson, 1980).

#### 4. Blue-Green Algal Blooms

In the open areas of the Baltic Proper, the Gulf of Finland and the southern parts of the Bothnian sea, the mass occurrence and blooms of the heterocystic, nitrogen-fixing cyanobacteria *Nodularia spumigena* Martens, *Aphanizomenon flos-aquae* (L.) Ralfs, and to a lesser degree *Anabaena lemmermannii* P. Richter and *A. baltica* Schmidt, are an annual phenomenon in late summer (Niemi, 1979). However, the intensity of the blooms is characterized by great year-to-year variation, due to the annual fluctuation in environmental conditions. Satellite pictures have revealed that the blooms extend over wide areas (Öström, 1976; Horstmann et al., 1986). Blooms of the nitrogen-fixing cyanobacteria have not been observed in the open waters of the Bothnian Bay (Alasaarela, 1979). Mass occurrences of the cyanobacteria, *Oscillatoria agardhii* Gomont and the subdominant *Anabaenopsis elenkinii* V. Miller, which are capable of fixing molecular nitrogen, are common in the eutrophied coastal waters around pollution centres (Niemi, 1979 and literature cited therein). The eutrophied river waters have caused autumnal blooms of *Microcystis* sp. in the eastern parts of the Gulf of Finland in 1987.

Vigorous blooms of cyanobacteria have been considered to be indications of increasing eutrophication. Such blooms, however, were observed in the open sea already during the 19th century (cf. Pouchet and de Guerne, 1885; Hensen, 1887), and in unpolluted coastal waters early in the 20th century (e.g. Häyrén, 1921, 1940; Purasjoki, 1947), when the nutrient load on the Baltic Sea was much lower than it is today. Such blooms are typical of natural waters with an excess of phosphorus and a low N:P ratio. The cyanobacterial blooms must be regarded as a natural phenomenon of the Baltic ecosystem (Niemi, 1979). However, the increased load of phosphorus on the Baltic Sea has probably favoured the development of vigorous blooms.

The nitrogen-fixing cyanobacteria are considered to be independent of inorganic nitrogenous compounds, but are favoured by the addition of  $PO_4$  phosphorus (cf. Melin and Lindahl, 1973; Horstmann, 1975; Rinne and Tarkiainen, 1978; Lindahl et al., 1980). Thus the phosphorous-rich, upwelling water is important in initiating the blooms. The yellowish surface streams

Table 1. Total amount of nitrogen fixed by the cyanobacteria, the land-based load and atmospheric input of nitrogen in the different parts of the Baltic Sea as metric ton/sea area-year. The figures for nitrogen fixation are based on the estimations by Rinne et al. (1981) and Niemistö et al. (1988), and for the land-based and atmospheric load by Baltic Marine Environmental Protection Commission (1987).

	Nitrogen fixation	Land based load	Atmospheric input
Bothnian Sea	1500-5000	56360	67000
Gulf of Finland	5000	74000	24000
Northern Baltic Proper	20000	} 166570	} 230000
Central Baltic Proper	40000		
Southern Baltic Proper	40000		

dominated by *Nodularia* are typical of the upwelling areas. The N:P ratio in the Bothnian Bay, where the blooms do not develop, is clearly higher than that in other parts of the Baltic Sea, and inorganic nitrogen is not supposed to be the growth-limiting nutrient for the phytoplankton (Niemi, 1979).

## 5. Nitrogen Fixation

Measurement of the acetylene reduction rate in the different Baltic Sea sub-areas revealed that efficient nitrogen fixation is limited to a period of 1-2 months a year. The calculated amount of nitrogen fixed varies markedly from year to year. The vertical and diurnal variation in the nitrogen fixation rate is clearly light dependent. About 80% of the nitrogen fixation by cyanobacteria takes place in the uppermost 10 m layer (Niemistö et al., 1988). The heterocystic activity is dependent on the development stage of the bloom. The highest heterocystic activities have been recorded during the initial development stage of the heterocysts (Vuorio et al., 1978; Lindahl et al., 1980). The most intensive levels of nitrogen fixation have been observed in the Baltic Proper, and at the entrance to the Gulf of Finland. In the Gulf of Bothnia the values decrease on moving northward. The total amount of nitrogen fixed by the cyanobacteria in the open sea areas is presented in Table 1. The Finnish measurements made in the southern Baltic Sea are few, and may underestimate the total nitrogen fixation in that area. For instance, Hübel and Hübel (1987) have measured clearly higher nitrogen fixation rates than those used for the estimation of total nitrogen fixation in Table 1.

## 6. Nitrogen Cycle

Nitrogen is considered to be a limiting factor for primary production in most areas of the Baltic Sea. The flow of nitrogen within the organic matter cycle is controlled by a large number of environmental factors and interactions between the biological components of the system (cf. Rönner, 1983).

The main pathways of the nitrogen cycle in the Baltic Proper are presented in Fig. 3. River runoff, water transport between the sea areas and atmospheric fallout are the external inputs of nitrogen into the system. In addition, an input of nitrogen is also mediated by nitrogen fixation. Water transport out from the Baltic Sea, burial in the bottom sediment and bacterial denitrification are the processes through which nitrogen is lost from the system.

The most important factors regulating the nitrogen cycle are light and the redox conditions. Phytoplankton is mainly responsible for the assimilation of inorganic compounds in the euphotic zone and bacteria in the layers below it. Bacterial nitrification is an aerobic process and denitrification is an anaerobic one. This means that different nitrogen transformation processes take place in different water layers (Fig. 3).

Rönner (1985) has compiled an annual budget for nitrogen in the Baltic Proper (Fig. 3). His quantification of nitrogen fixation is based on the measurements of Lindahl et al. (1978), which is in good accordance with the Finnish quantification (Rinne et al., 1978; Niemistö et al., 1988, Table 1). Nitrogen fixation by cyanobacteria contributes only ca. 13% to the total annual input of nitrogen into the system. The opposite reaction, bacterial denitrification, removes over three times more nitrogen from the system than the input through nitrogen fixation. However, these annual figures may underestimate the ecological significance of nitrogen fixation. Nitrogen fixation is most important in the open sea areas where the direct effect of river runoff is small. Nitrogen fixation takes place during the season when the dissolved inorganic nitrogen compounds are at minimum levels in the euphotic zone, and thus forms the major external input. The degradation and disappearance of the cyanobacterial clusters in the surface is a fast process during the final stage of the bloom. There is evidence that the nutrients, including nitrogen, are rapidly released into the surface water (e.g. Gabrielson and Hamel, 1985) and the sinking of particulate nitrogen from the euphotic layer is small (Forsskåhl et al., 1982; Kuparinen et al., 1984). However, no photosynthetic plankton group has been found to develop immediately after the degradation of the cyanobacterial bloom that apparently would have gained

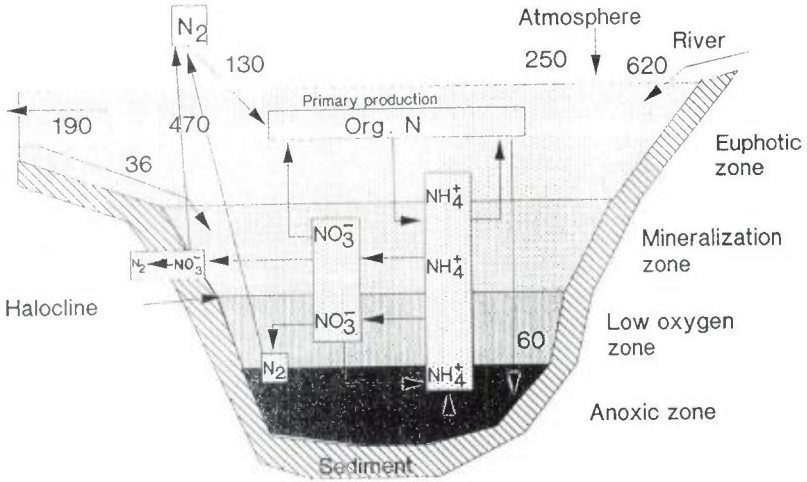


Figure 3. The main pathways of the nitrogen cycle in the ecosystem of the Baltic Proper and the annual nitrogen budget (modified from Rönner, 1985). All the fluxes are given in  $10^3$  metric tons  $N \cdot a^{-1}$ .

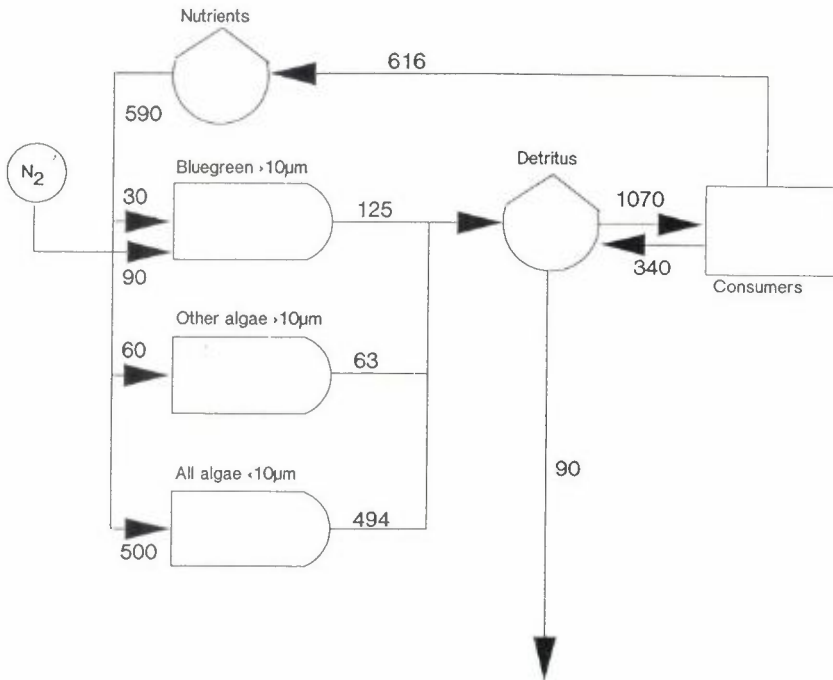


Figure 4. Nitrogen budget for the pelagic system during a blue-green algal bloom in the northern Baltic Proper. All the rates are expressed in  $nmol N l^{-1} \cdot d^{-1}$  (simplified from Cederwall and Wulff, 1984).



benefit from the input of nitrogen through nitrogen fixation. There is, however, evidence that heavy autumnal blooms of *Aphanizomenon* in the Gulf of Finland were followed by a marked increase in the level of  $\text{NO}_3$ -nitrogen in the winter, thus indicating an input of nitrogen into the biological cycle (Niemi, 1975). The SEM analysis carried out by Smarda et al. (1986) shows that the colonies of *Nodularia* represent a characteristic micro-niche which is intensely colonized by various algae, cyanophytes, epiphytic bacteria and Actinomycetes-like hyphae, and thus present a special community of micro-organisms. The function of this system in the food chain has not, however, so far been studied.

Wulff and Cederwall (1984) have presented the results of an intensive, interdisciplinary field study on the dynamics of a *Nodularia* bloom in the northern Baltic Proper. The results (Fig. 4) indicate that most of the nitrogen uptake through primary production was connected to phytoplankton groups other than cyanobacteria. Nitrogen fixation was a very small nutrient source compared to ammonia and urea recycled within the system through the decomposition of available organic matter. Nitrogen fixation contributed 13% to the total nitrogen uptake during the study period. Nitrogen fixation corresponded to the amount lost through sedimentation. The results of Gunvor Lindahl (pers. comm., 1987) show that there was a significant phosphatase activity, predominantly associated with non-nitrogen-fixing phytoplankton. This indicates that the system was also phosphorus limited. The 6-day study period most probably occurred in the end phase of the bloom, and Wulff and Cederwall (1984) are doubtful if the nitrogen fixation could have been of greater importance in earlier phases of the bloom, i.e. building up a store of nitrogen that was then efficiently used and recycled during later stages. This is, in our opinion, evidenced by the high concentrations of  $\text{NH}_3$ -nitrogen in the euphotic layer. Lindahl and Wallström (1985) have estimated that nitrogen fixation contributes 8% and 1% of the requirements of primary production in the coastal area of the Baltic Proper and the Bothnian Sea, respectively.

In conclusion, during the summer, when the nutrient concentrations are low in the euphotic layer, heavy blooms of nitrogen-fixing cyanobacteria are common in the Baltic Proper, the Gulf of Finland and the southern parts of the Bothnian Sea. They are favoured by the warm stable surface water and by the upwelling water with a low N:P ratio. The total amount of nitrogen fixation is estimated to correspond to ca. 10% of the total nitrogen input to the Baltic Proper. During the blooms, nitrogen fixation represents only a

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