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Marine Eutrophication: A Growing International Problem

Almost a century has passed since Brandt, Raben, and others associated with the Kiel Commission for the Scientific Study of the German seas first identified the importance of nutrients in enhancing the primary productivity and fisheries yields of marine coastal waters. Now we have come full circle. This special issue and a recently released report from GESAMP identify eutrophication or excessive nutrient enrichment as a major pollution problem in the coastal waters of the Baltic Sea, the Kattegat, the Skagerrak, and the North Sea. All the areas that served as the first natural laboratories in which the Scientific Community studied the positive contributors of nitrogen and phosphorus to the economy of the sea have now become case studies in marine eutrophication.

But the recent awareness of marine eutrophication as a serious coastal issue is not confined to northern Europe and Scandinavia. From around the rim of the Mediterranean, and from increasing numbers of bays and estuaries along the coastlines of North and South America, Africa, India, southeast Asia, Australia, China, and Japan have come increasing reports of noxious (and sometimes toxic) algal blooms, anoxic bottom waters, and fish kills. While our understanding of the factors required to produce many types of algal blooms is still too primitive to allow predictions, it seems that any coastal area receiving significant drainage from land but little tidal mixing energy from the sea is at risk for developing low oxygen problems.

Many estuaries and bays are already among the most intensively fertilized environments on earth, and there are good reasons to believe that the fluxes of nutrients, especially nitrogen, into coastal waters will continue to increase. The dramatic growth of human population along the coasts, the pressure to increase agricultural production through fertilization, the conversion of forest and wetlands into fields and urban areas, and the release of nitrogen oxides into the atmosphere, will all contribute to the problem. Nutrients, especially nitrogen, are among the most difficult and expensive materials to remove from wastewaters.

Because estuaries receive the accumulated runoff from a much larger drainage basin, they are particularly sensitive to land-use practices and to deposition from the atmosphere. Small changes in the storage of nutrients in terrestrial systems can appear as large changes in the loadings of nutrients to estuaries downstream. An important question for the future of our coastal waters may be how changes in global climate will affect nutrient retention on land.

As the papers in this special issue illustrate, much has been learned about marine eutrophication since Karl Brandt first applied Liebig's "Law of the Minimum" to the sea in 1899. But much is still not understood with sufficient clarity to enable us to predict the changes that will occur in any particular coastal area with a qualitative or quantitative change in nutrient input. The experimental and comparative studies of whole lake ecosystems by the limnologists have placed them well ahead of marine ecologists in dealing with this problem.

In recent years we have begun to develop some reasonably reliable nutrient budgets for coastal systems, including, in a few places, exchanges with the atmosphere, and there is now a widespread appreciation for the speed and importance of nutrient regeneration in supporting much of the primary production in coastal areas. But it is still not clear if, or how, nutrient enrichment might lead (or could be managed to lead) to increases in secondary production of desirable species. While it is common to apply agricultural terms to marine waters, it is unlikely that complex natural systems with large amounts of internal nutrient cycling will respond to fertilization in as straightforward a manner as fodder crops and farm animals.

Most of our knowledge about marine ecology is derived from expeditions or cruises that obtain increasingly reliable quantitative information about certain things (abundances of organisms, concentrations of chemicals, etc.) at particular places and times. Descriptive information of this kind is then interpreted in combination with reductionist data on the physiology, behavior, etc. of individual parts of the system studied under controlled laboratory conditions. This combination has proven to be a powerful tool for analyzing nature, but it can not move marine ecology into the next stage of development as a predictive science. For that, we need to expand and improve our ability to do experimental work with natural systems, or at least with complex parts of nature set off in the field or in laboratory mesocosms. Experimental manipulations and perturbations, including nutrient enrichments, are not meant to replace cruises or culture studies, but must be used in combination with them. This is much more difficult in the marine environment than in freshwater or on land, but that is no reason for us to shrink from the task.

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EDITORIAL

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Article

Rutger Rosenberg, Ragnar Elmgren, Siegfried Fleischer,
Per Jonsson, Gunnar Persson and Hans Dahlin

Marine Eutrophication Case Studies in Sweden

This article summarizes the eutrophication of two sea areas: 1) the Baltic Sea and in particular a coastal area which is affected primarily by effluents from a tertiary sewage plant; and 2) the Kattegat and in particular the Laholm Bay, which is affected primarily by nutrient inputs from agriculture and forest land. During this decade, inputs of N and P to these larger sea areas have increased by factors of approximately 4 to 6 and >8, respectively. Internal nutrient transport and atmospheric deposition is discussed. It is concluded that N availablility generally limits primary production, except in the Bothnian Bay, where P has this role. P is, however, the limiting factor at times in some coastal areas, and in the Baltic for N-fixing blue-green-algae, which bloom in warm summers when low N/P ratios prevail. Noted eutrophication effects are localized elevated primary production, decreased depth distribution and species richness of macroalgae. Eutrophication is most likely a stimulus to high benthic infaunal biomass and fish biomass in well ventilated sea areas. Other areas suffer today from almost permanent (the Baltic proper) or seasonal (the Kattegat) hypoxia with devastating effects on benthos and demersal fish. The N cycle and future possible consequences in relation to nutrient input are discussed. It is concluded that a reduction by at least half of external N and P inputs to the Baltic sea, and of N inputs to the Kattegat is needed to mitigate the negative effects of eutrophication

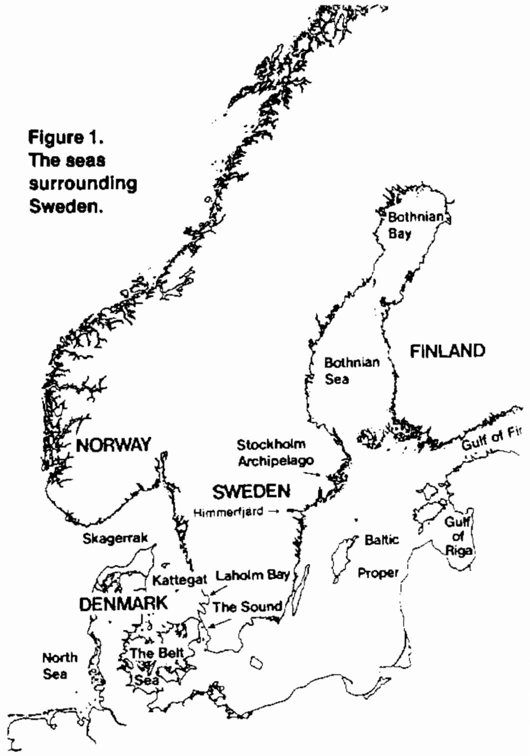


Figure 1. The seas surrounding Sweden.

INTRODUCTION

Sweden has a long coastline extending from the Gulf of Bothnia in the northern Baltic Sea to the Skagerrak on the Swedish west coast (Fig. 1). Salinity in the regions varies greatly—Gulf of Bothnia 2–4‰, the central Baltic proper 7–13‰, the Kattegat 15–30‰ in the surface water and 32–34‰ in the bottom water, the Skagerrak 20–30‰ in the surface water and 32–35‰ in the bottom water. The water is stratified by a halocline at 60–80 meters depth in the Baltic proper, and at 10–20 meters in the Kattegat and eastern Skagerrak, in summer coinciding with the thermocline.

The salinity gradient structures marine life both horizontally and vertically, with few species occurring in the Baltic and increasing numbers of species occurring towards the Skagerrak. Different organism communities are found above and below the halocline.

Disturbances in the marine environment became apparent in the Baltic Sea in the 1960s, when significant decreasing long-term trends in oxygen concentrations were demonstrated at 150–400 meters in several deep basins (1). An increasing concentration of phosphate had already been observed in the deep water. Since then, further signs of eutrophication have appeared. Assessments of the state of the Baltic Sea marine environment (including contaminants and oil, which are not dealt with here) have already been published (2–4).

The first obvious signs of eutrophication in the Kattegat were noted in the mid-1970s when filamentous algae were washed ashore in large quantities. In 1980 and 1981, fish mortality due to oxygen deficiency was reported by fishermen.

In 1980–1981, the Swedish Environmental Protection Agency launched a comprehensive research project called *Eutrophication in the Marine Environment, Research Proposal*, to start in July 1983 (5, 6).

The objectives of this project were "to support and initiate research that may be expected to provide the basis for decisions on: 1) Swedish national policy for the conservation of the coastal areas of Sweden, primarily those areas influenced by discharges of substances that cause eutrophication; and 2) Swedish international policy for the protection of the marine environment." The six-year project had an average annual budget of SEK 5 million (USD 800 000).

The project focused on (a) the effects of discharges of tertiary treated municipal wastewater; and (b) the effects of leakage of nutrients from agricultural land. Studies within the project centered on two areas. The Himmerfjärd area (Fig. 1) is an enclosed bay in the southern Stockholm archipelago. Since 1977, this area has received 20% of the municipal wastewater from urban centers (210 000 inhabitants) south of Stockholm. The Kattegat including Laholm Bay (Fig. 1) receives nutrients mainly from forest and farmland. In addition, the project modelled the Baltic Sea and advised the Swedish Governmental Action Plan on means to prevent and reduce pollution of the sea (7).

PAST AND PRESENT NUTRIENT SUPPLY

The Baltic Basin

A recent estimate of external supplies of nitrogen (N) and phosphorus (P) to the Baltic (including the Danish straits) from rivers, point sources, and atmospheric deposition, indicates levels of $980 \cdot 10^3$ tonnes N and $50 \cdot 10^3$ tonnes P (Table 1). An earlier estimate indicated $1190 \cdot 10^3$ tonnes N and $78 \cdot 10^3$ tonnes P (8, 9).

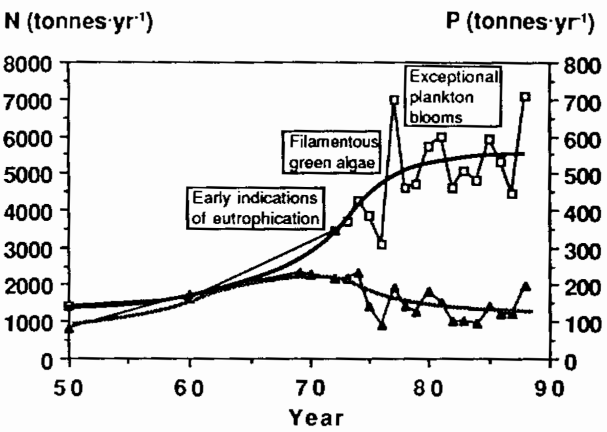
About 50% of the present N supply is from atmospheric input, including nitrogen fixation, whereas P input is strongly dominated (about 90%) by the supply from land areas, including point sources. The contributions of N and P from different land-based sources have been discussed elsewhere (2, 8).

Nutrient inputs to the Baltic at the turn of the century were much lower both from the atmosphere and from land sources and have been estimated by Larsson et al. (8), to have been about $300 \cdot 10^3$ tonnes N and $10 \cdot 10^3$ tonnes P. The present day supply

Table 1. External supply of nitrogen and phosphorus to different subbasins within the Baltic area (68). Mean inputs for one or several years during the period 1982–1987 have been compiled from data supplied to the Helsinki Commission for the first periodic assessment and from later Swedish monitoring data.

	Tot-N tonnes · yr^{-1}	%	Tot-P tonnes · yr^{-1}	%
Bothnian Bay				
Sweden	19 000	28	1000	29
Finland	32 000	47	2000	57
Deposition	17 000	25	500	14
Subtotal	68 000	100	3500	100
Bothnian Sea				
Sweden	35 500	30	1600	37
Finland	22 100	19	1660	38
Deposition	60 000	51	1100	25
Subtotal	117 600	100	4360	100
Gulf of Finland				
Finland	16 300	21	860	16
USSR	57 700	76	3990	76
Deposition	2100	3	410	8
Subtotal	76 100	100	5260	100
Baltic Sea proper incl. Gulf of Riga, The Sound and the Belt Sea				
Sweden	44 300	6	1780	5
USSR	72 600	10	1890	5
Poland	109 900	15	19 100	52
GDR	3600	1	380	1
FRG	16 400	2	2370	6
Denmark	51 000	7	7860	22
Deposition	289 900	41	3420	9
N_2-fixation	130 000	18	–	–
Subtotal	717 700	100	36 800	100
Kattegat				
Sweden	37 000	46	900	29
Denmark	18 000	22	1900	61
Deposition	26 000	32	300	10
Subtotal	81 000	100	3100	100

Figure 2. Transport of nutrients to the Laholm Bay from the drainage basin. Periods of significant changes in the marine biota are also indicated.



to the same area was estimated by the same authors to be higher by factors of about 4 and 8 for N and P, respectively.

In the Baltic, most of the increase in input of nutrients is likely to have taken place since 1950. The inorganic fractions of these nutrients are likely to have increased most since these generally constitute a higher proportion of the supply derived from anthropogenic sources.

The Himmerfjärd area receives 60% and 30% of external N and P input, respectively, from one large sewage-treatment plant. The remaining part is derived from adjacent land and from Lake Mälaren (10).

The nutrient supply to the Himmerfjärd area has also undergone change. From 1974 onwards, sewage from the southern Stockholm region was successively diverted to a new central treatment plant with chemical precipitation and with outfall into the inner Himmerfjärd. This new efficient treatment plant (≈95% P reduction) actually meant a slight reduction of P input to the Bay, whereas N supply increased about fivefold. The treatment plant has recently (1988/89) been modified to facilitate N reduction (≈50% to 70%).

The Kattegat

The nitrogen supply to the Sound and the Kattegat has increased fourfold from 1930 to 1980 (11) and doubled in the period 1950–1980 (12). A review of the data (13) shows that this doubling took place mainly after 1970 and that P supply was constant or decreased slightly during this latter period.

The external supply to the Laholm Bay is dominated by river runoff (≈90%) for both N and P. Deposition and direct sewage input is about 5% for N and 5% for P. The river input is dominated by drainage from forests and mires (41% of N input) and agricultural land (38% of N input) (14).

The total N supply to the Laholm Bay has increased between 3.5 and 4 times since 1960 (Fig. 2). After an increase from around 1950 and a peak during the 1960s the P supply was cut to half its previous level by the introduction of chemical precipitation in the sewage works in the 1970s. Thus, in the areas of special study increases in the supply of N have been larger than of P in recent times, and the P input has in fact declined. For both areas, a reduction in N input from agriculture and sewage is forecast.

MASS BALANCE OF NUTRIENTS

The Baltic Basin

Wulff and Stigebrandt (15) used estimated nutrient inputs from 1950 onwards in a dynamic mass-balance model for the Baltic. A tight coupling between supply and estimated nutrient concentration in the Baltic has emerged from these simulations. Winter concentrations of N and P increase by 2.2 (N) and 3.7 times (P), when the corresponding loading increase is 2.1 and 3.9 times normal concentrations, respectively. Measured concentrations, when available, are in agreement with simulated concentrations. The time lag between loading increase and concentration increase is well described by the two modifications of the model presented. The model thus contributes significantly to an understanding of the impact of nutrient supply on nutrient concentrations and eutrophication in the Baltic and is a strong argument against the scenario of climatic change as the ultimate cause of nutrient increments.

Jonsson et al. (16) emphasize the erosion of old sediments, due to land uplift, as an additional source of input of carbon and nutrients to the Baltic. This input has, however, occurred for thousands of years and it is unlikely that it has influenced the eutrophication process. Moreover, most nutrients from this source are firmly bound to the minerogenic and highly degraded organic matter and are thus not available for production.

The Kattegat

The Kattegat research partly concentrated on an equilibrium description of mass-balance for the spring bloom and summer

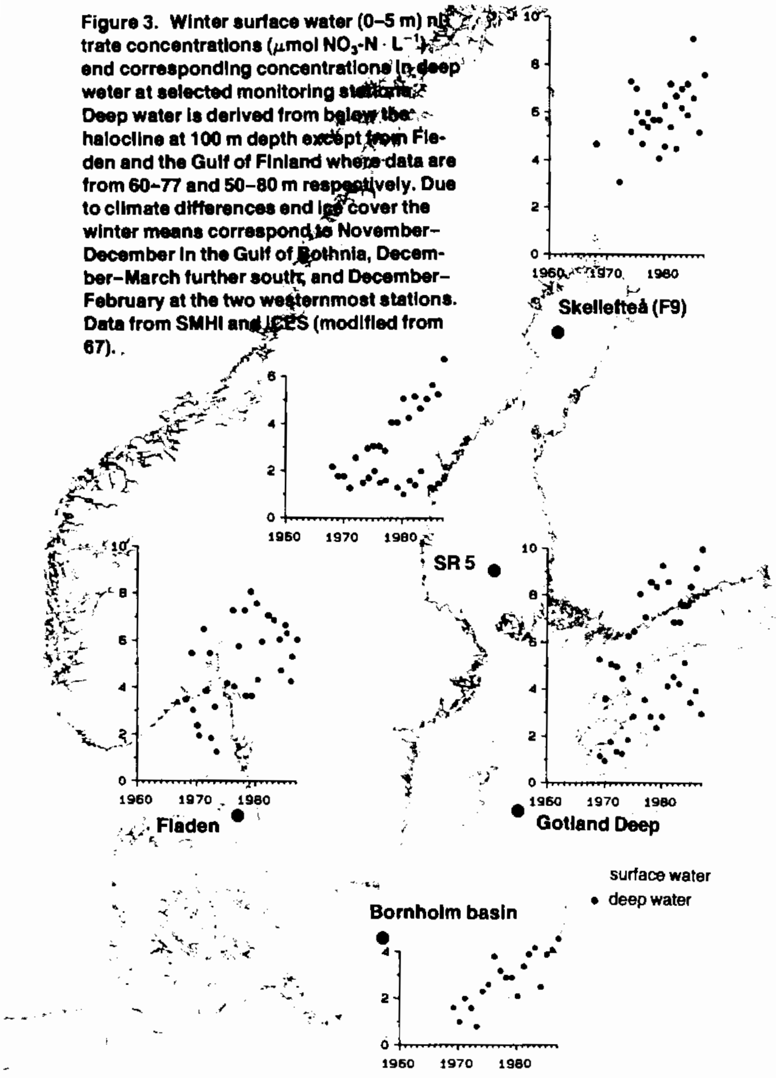


Figure 3. Winter surface water (0–5 m) nitrate concentrations (μmol NO_3-N · L^{-1}) and corresponding concentrations in deep water at selected monitoring stations. Deep water is derived from below the halocline at 100 m depth except from Fladen and the Gulf of Finland where data are from 60–77 and 50–80 m respectively. Due to climate differences and ice cover the winter means correspond to November–December in the Gulf of Bothnia, December–March further south, and December–February at the two westernmost stations. Data from SMHI and ICES (modified from 67).

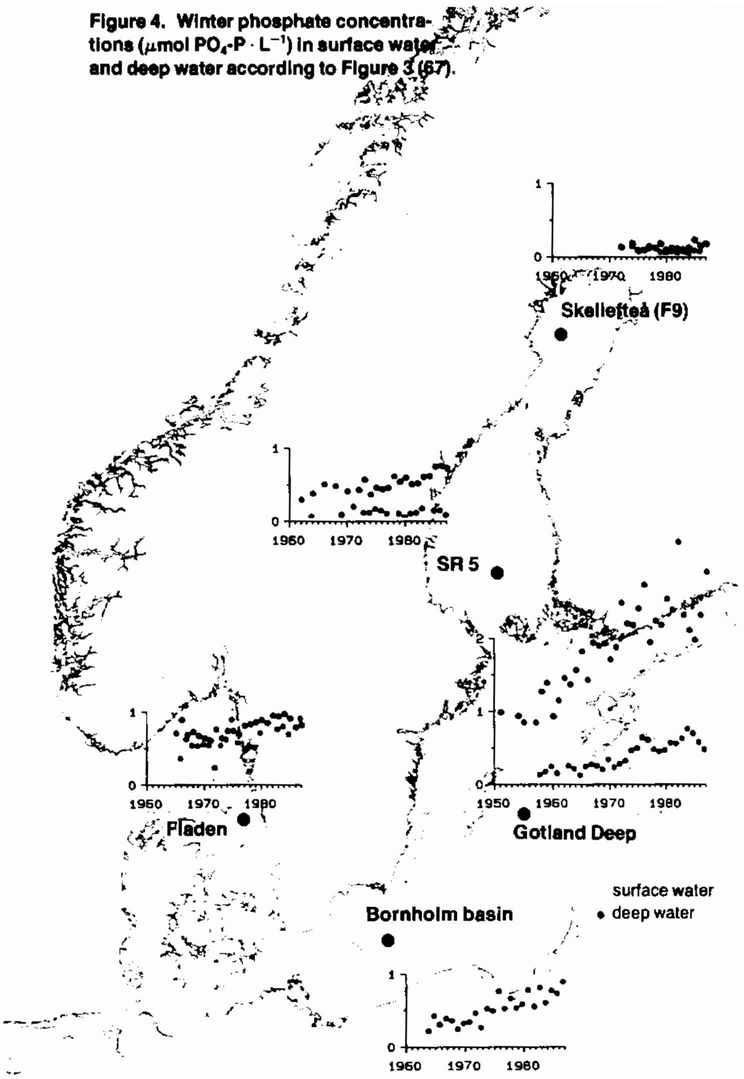


Figure 4. Winter phosphate concentrations (μmol PO_4-P · L^{-1}) in surface water and deep water according to Figure 3 (67).

periods (17). Nutrient input to the Kattegat surface water is dominated by entrainment of more saline bottom water, emanating from the Skagerrak. The Rydberg et al. (17) mass-balance study for the surface-water productive season indicates that about 30% of the supply of inorganic N from surrounding areas is directly derived from rivers and atmospheric input and ca. 10% is derived from the Baltic (18). The rest is derived from the deep water. The corresponding inorganic P input is derived to a lesser degree from local sources (10%), and to a larger degree from the Baltic (20%) and the deep water (70%). Rydberg et al. (18) point out that this water originally has a constant nutrient concentration and that increased inorganic nutrient concentrations found in deeper Kattegat water during summer are due to regeneration of sedimenting organic nutrients. The rapid water renewal (about 1 month) and the approximately constant supply of nutrients from the Skagerrak make the inputs from the surrounding areas and atmosphere obvious and immediate regulators of surface-water nutrient concentrations.

NUTRIENT CONCENTRATIONS

Accurate measurements of nutrients in the different sea areas are available for the past 20 years (Figs 3, 4). The potential for plant production at different sites is described by the data on inorganic nutrients accumulated during winter. The regional concentration pattern represents the net result of input from external sources (Table 1); exchange between the different basins; and retention in the basins (15, 18). The highest winter surface-water nitrate concentrations are found in the peripheral sea areas, i.e. the Gulf of Finland, the Skagerrak, and the Bothnian Bay. The highest winter phosphate concentrations are found in the Gulf of Finland, followed by the Kattegat and the Baltic proper. The corresponding winter N/P ratios (by atoms) are in the range 6–8 in all areas except in the Bothnian Bay where these ratios are one order of magnitude higher. Since algae utilize nutrients in an approximate N/P ratio of 16/1, these data indicate a relative N deficiency in all offshore regions of the total area, except in the Bothnian Bay (discussed in detail below). In some coastal areas, intermediate N/P ratios that are optimal for algal growth will appear.

The relative excess of N in land-drainage supply to some localized bay areas increases N/P ratios, for example, in the Himmerfjärd and the Laholm Bay, whereas in other coastal zones N/P ratios can be lower than in the open sea.

Mean winter surface concentrations of 16 and 11 μmol $NO_3 \cdot L^{-1}$ in the Himmerfjärd area and the Laholm Bay, respectively, indicate N enrichment compared to the corresponding sea areas (Fig. 3), whereas concentrations of about 0.7 μmol $PO_4 \cdot L^{-1}$ in both areas are at the same level as those in the open sea. The N/P ratios at the onset of spring production (21 and 15, respectively) are thus similar to those of algal demand. These data refer to means for the periods 1982 to 1984 for the Laholm Bay (19) and between 1985 to 1988 for the central Himmerfjärd basin (20).

LIMITING NUTRIENTS

The question of which nutrient is most limiting for the primary producers is of central importance when investigating means to counteract the negative effects of eutrophication. In the following, we consider only major plant nutrients, not the less well-known trace elements. Since carbon is abundant in the sea, it is not likely to limit phytoplankton development. Silicon has not yet been a limiting nutrient in the Baltic Sea, which is naturally rich in silicate. Silicate concentrations in the surface water have, however, decreased in recent years (21). Most discussions of limiting nutrients have centered on the two major plant nutrients, nitrogen and phosphorus.

Nitrogen limitation of primary producers in coastal areas of the sea was first reported off the NE Atlantic coast of the USA (22). Shortly thereafter, it was pointed out that offshore Baltic waters in the spring, and following up-welling events, had an excess of mineralized phosphorus, relative to mineralized nitrogen (23). Other researchers in the Baltic (24) demonstrated that the availability of nitrogen limited the production of *Oscillatoria agardhii* in the open Baltic area, but not of the nitrogen-fixing *Aphanizomenon flos-aquae*, which was limited by phosphorus.

In the inner part of the Stockholm archipelago phosphorus removal from sewage effluent has had positive effects. The previously large blooms of nitrogen-fixing cyanobacteria disappeared as the inner zone changed from an excess of phosphorus to an excess of inorganic nitrogen (25). But, as has been pointed out (23), the phosphorus discharged from the Stockholm sewage works had functioned as a trap for nitrogen, through assimilation in phytoplankton. After reduction of the phosphorus discharges, more of this nitrogen now reaches the outer archipelago, where a tendency towards increased chlorophyll concentrations has been recorded (25).

A situation analogous to that in the Stockholm archipelago has developed in the Himmerfjärd area, as a result of more efficient P removal in the new treatment plant. Heterocystous cyanobacteria are less prevalent in the Himmerfjärd area, where nutrients with high N/P ratio are discharged, than in the outer coastal area where N/P ratios are lower (26).

In the Laholm Bay area, nitrogen is the most limiting nutrient virtually year-round, except in an area at the mouth of the rivers. This area is small in the summer, when phytoplankton nutrient uptake and transformation is active, but somewhat larger during the other seasons (27, 28).

Only in the Bothnian Bay is phosphorus the most limiting nutrient for plant production. The Bothnian Sea is a transition area where either nitrogen or phosphorus may be limiting, depending on time and place, whereas the Baltic proper, the Danish Sounds and the Kattegat are clearly nitrogen-limited (28, 29). Within the generally nitrogen-limited area, nitrogen-fixing cyanobacteria are an exception, since they are limited by phosphorus (24). Blooms of cyanobacteria (Fig. 5) are frequent and characteristic summer features of the Baltic proper, but less common in the Bothnian Sea and the Danish Sounds, and rare in the Kattegat. In areas such as the inner Himmerfjärd where nitrogen limitation is less pronounced, nitrogen-fixing cyanobacteria do not bloom (26). Indications are that nitrogen is the most limiting nutrient in the open Skagerrak.

In coastal areas with excessive local nutrient discharges and with a limited exchange of water with the sea, the nutrient limiting primary production may be different. Studies of Danish fjords and inlets have demonstrated primary phosphorus limitation in some restricted areas and nitrogen limitation in others (30). Likewise, phosphorus limitation has been recorded at stations in the inner Stockholm archipelago after phosphorus removal from sewage was implemented (25); in the inner Himmerfjärd area in spring-early summer (31); and in spring in the Darss-Zingster Bodden chain in the southwestern Baltic (32).

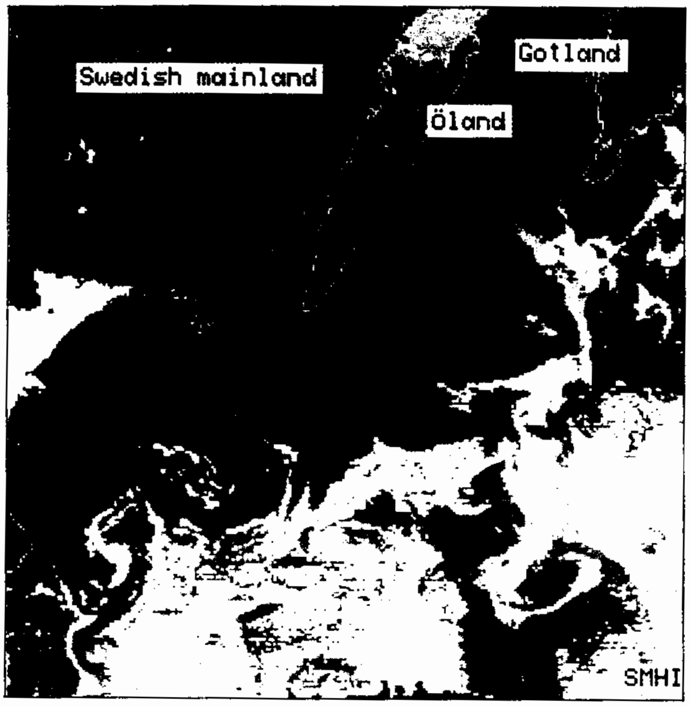


Figure 5. The image shows the surface distribution of floating blue-green algae in the southern Baltic proper during August 22, 1984. This type of algae was observed by M. Karhu (pers. comm.) from the Institute of Physics in Tallinn two weeks befora they whare remotely sensed by the NOAA weather satellite. The floating algae are shown in green-yellow-white indicating increasing concentrations of the algae, whereas water masses almost absent of algae are shown in blue-grey colours.

BIOLOGICAL EFFECTS

The Baltic Basin

In the Himmerfjärd phytoplankton primary production can be 70% higher than at a reference station close to the sea. The increase was mainly due to higher production by diatoms in spring and autumn (33). In summer, blue-green algae (cyanobacteria) blooms can constitute a real nuisance in the Baltic Sea (Fig. 5), but it is not clear whether such blooms have increased or decreased recently.

An increased dominance by filamentous benthic algae has been reported from the Swedish Baltic coasts, and as a consequence, local negative effects on the hatching of herring eggs have been documented (34). North of Stockholm depth distribution of bladderwrack, *Fucus vesiculosus* has decreased since the 1940s, probably as a result of decreased transparency caused by eutrophication (35).

Since the 1950s, hypoxia (<2 ml · L^{-1}, ca. 20% saturation) has occurred most of the time below about 70 meters in the Baltic proper. Also from the 1950s onwards, deep-bottom fauna have been severely affected and nowadays over a bottom area of approximately 100 000 km^2 fauna are strongly reduced (36). A drastic change has also occurred in the sediments of deposition areas in the Baltic deeper than 75 m (16). Several centimeters of laminated sediments overlay a homogenous blue-green-greyish clay (Fig. 6). The total area of laminated sediments in the late 1980s has, as a crude estimate, increased about three-fold since 1960 (37).

In bottoms shallower than 70 meters, on the other hand, the faunal biomass has increased significantly in the central Baltic proper, most likely as a result of eutrophication (38). Similar benthic fauna changes have also been noted in the Bothnian Sea (39) and in the southern Baltic Sea (40).

Fish catches in the Baltic Sea have increased severalfold during this century, probably as a combined result of higher fishing efficiency, eutrophication (more food), and reduced seal stocks (4, 41). The reproduction of cod (*Gadus morhua*) is, however, endangered in years when hypoxia or anoxia occurs at the water depths (80–100 meters) to which the cod eggs sink before becoming buoyant (i.e. at salinities of about 10–12‰).

The Kattegat

There are indications of recent increases in primary production in the southern Kattegat and the Belt Sea (42, 43).

Blue-green algal blooms have rarely been reported from the Swedish west coast. However, many other toxic algal blooms have been observed in this area in the last decade and most recently the devastatingly toxic flagellate *Chrysochromulina polylepis* (44).

In the Laholm Bay, long-term trends in macroalgal succession have been documented since the 1950s, as increased dominance of filamentous algae (45). As in the Baltic Sea, the vertical distribution of macroalgae in the Gullmarsfjord on the Swedish west coast declined during the 1970s (46) and the 1980s (47) compared to the 1920s. Although methodological differences may contribute to the discrepancies, the results fit the idea of a general eutrophication impact.

The mass occurrence of filamentous algae in the nearshore areas of the SE Kattegat was followed by a mass mortality of bivalves in shallow waters in 1980 and by reports of fish kills in southeastern Kattegat (48). Since that time, bottom hypoxia has been observed over increasingly large areas and volumes, and has affected

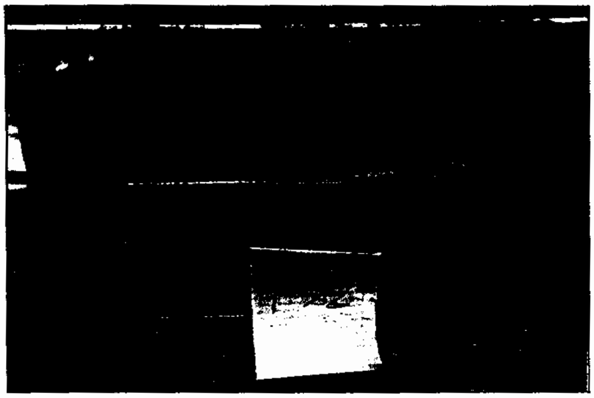


Figure 6. A typical sediment core from the deep part of the Baltic proper showing a laminated layer of some 5 cm overlaying a homogenous blue-greyish clay. Photo: P. Jonsson.

benthic faunal communities (49, 50). Eutrophication-induced effects have also recently been reported from the Swedish and Norwegian coasts of Skagerrak (51, 52).

Fish mortality has been noted several times over the last few decades in the Kattegat. In the autumn of 1988, few fish and Norway lobster (*Nephrops norvegicus*), but many dying benthic invertebrates, were caught in trawls in SE Kattegat (53).

We suspect that effects relating to eutrophication are more far-reaching and extensive than presented here. However, in the absence of long-term data series this cannot be documented. It is likely that significant structural changes in the phytoplankton communities, induced by eutrophication, will affect the rest of the pelagic system directly and the benthic system indirectly. Detailed long-term investigations are however scarce, although one monitoring station in the German Bight of the North Sea shows significant structural changes in phytoplankton (54).

FUTURE PERSPECTIVES

The resilience of the Baltic ecosystem to eutrophication has probably undergone change during the last three decades due to the increase in areas with anoxic bottoms. Budget calculations indicate denitrification as the major sink for the nitrogen discharged into the Baltic Sea (8, 55, 56). Most of this denitrification seems to take place in the upper sediment layers (55). Increasing anoxia of deep Baltic sediments is likely to slow the rate of denitrification in two ways. The pumping of water through the sediment by bioturbating macrofauna enhances denitrification rates (57) by supporting the microbial community, but anoxia eliminates this fauna. In the event of total anoxia, ammonia regenerated through mineralization of organic matter cannot be oxidized to nitrate and the potential for denitrification in the sediments will decrease and move to the redoxcline in the water column. As azooic and anoxic bottoms spread, the capacity of the Baltic for neutralizing the nitrogen inputs will probably be reduced and eutrophication intensified. Conversely, if nitrogen inputs can be reduced to the point where anoxia declines, this may help recovery by improving conditions for denitrification in the deep bottom areas of the Baltic proper.

Recent results suggest that the present concentrations of H_2S reducible phosphorus in the anoxic offshore sediments in the Baltic proper is only one tenth of that in the oxidized archipelago sediments (58), indicating a lower sink of phosphorus in the deep offshore sediments. This might have contributed to higher phosphorus concentrations in the water mass and/or a higher degree of sequestering of phosphorus in the oxidized bottoms above the halocline.

In the Kattegat, the strong vertical stratification prevents immediate contact between the surface water and the potential denitrification region at greater depths. Denitrification (and nitrogen fixation) in the surface water is insignificant. Not until planktonic nutrient uptake has occurred, followed by sedimentation, can mineralization, nitrification and denitrification occur, mainly at the sediment/water interface. These processes depend thus on specific conditions regulated through the microbial food web.

In the open oceans phosphorus and nitrogen cycling gradually develop balanced systems. A biogeochemical time scale is the prerequisite for attaining these "mature" conditions. For coastal areas in the Kattegat the residence time is short (59). In the Kattegat, in areas without processes for counteracting the direct effects of nitrogen supply (denitrification in the surface water), and with no possible compensation for nitrogen fixation, reducing the nitrogen supply appears to be the best measure to reverse eutrophication.

Occasionally, it has been suggested that increased nitrogen supply to the coast would be compensated for by increased denitrification. Although the special hydrography makes it difficult for denitrification to counteract eutrophication in the Kattegat, it is of interest to examine this reasoning for other waterbodies. Data from 50 lakes and freshwater wetlands indicate a relationship between nitrogen loading and nitrogen retention (65). Increased nitrogen loading implied increased retention (indicating increased denitrification), but also increased residual nitrogen (not denitrified). Increased nitrogen supply is apparently directed to both denitrification and increased surplus nitrogen. For marine systems it has been shown that increased additions of inorganic nitrogen may enhance denitrification, but not to the extent that all the nitrogen will be removed (61).

FUTURE NUTRIENT REDUCTION GOALS AND MEASURES

The Baltic

Efforts at controlling eutrophication effects must primarily be based on existing ecological conditions. In many Baltic areas that receive effluents that result in eutrophication it is necessary to reduce the input of both nitrogen, in order to lower the general level of nutrient production, and phosphorus, to prevent nuisance blooms of potentially toxic cyanobacteria.

When such local programs are implemented the resulting effects on the surrounding sea area, even though small, should be taken into account. Today, for the Baltic Sea as a whole, only reductions in nitrogen discharges are likely to result in measurable reductions in primary production. But, concentrations of nitrogen have increased faster than those of phosphorus in recent years (21, 28) and if this increase is not halted, phosphorus may gradually become the limiting nutrient, also for primary producers other than cyanobacteria.

The work by Wulff et al. (62) does not indicate the degree of nutrient reduction that would be necessary to create the desirable ecological conditions in the Baltic. To quantify the needed measures we have to define periods of acceptable conditions and to estimate the actual nutrient load during such periods. The mid-1950s may be such a period, since the first reports of bottoms totally devoid of macrobenthic fauna were published during this period (63) and the extension of the azooic bottoms increased drastically during the periods of the 1960s and 1970s.

The residence times for nitrogen and phosphorus in the Baltic were calculated to be 6 and 13 years, respectively (62). From this it is reasonable to assume that the effects recorded in the mid-1950s reflect the nutrient load some five years earlier. Thus, if we desire to achieve conditions without severe effects on the bottom ecosystem, we have to reduce the input of nitrogen and phosphorus to the load figures for the late 1940s. However, the effects of eutrophication are not all negative. Since the beginning of the 1950s there has been a remarkable increase in fish catches in the Baltic, which may partly be an effect of eutrophication.

If we wish to balance a high fish catch in the Baltic with fairly good conditions at the Baltic bottoms, we should strive for a load of nutrients representative of the mid-1950s. There is no accurate estimate of the load at that time, but it is likely to have been less than half of today's load. Therefore, to achieve this goal, at least a 50% reduction in nitrogen is probably necessary. A commensurate decrease of the phosphorus load will also be necessary to prevent increased summer blooms of toxic blue-green algae.

The Kattegat

In the Laholm Bay, more than 40% of the nitrogen load before the spring bloom is due to local sources. Before the autumn blooms these sources amount to about 70% (14). The coastal nitrogen gradient formed indicates that significant measures to counteract eutrophication in the Kattegat can be carried out in the drainage basin. Reduced nitrogen supply to the Baltic will also influence the Kattegat. Eutrophication in the Baltic and the Kattegat can, however, largely be counteracted within the respective drainage basins of these waterbodies.

Biological changes over time and changes in nutrient loading are indicated in Figure 2. In the 1950s anthropogenic input was still not much higher than the estimated background level (64, 65). For the period before 1970 few transport data are available, but subsequent to this time the drainage basin was monitored continuously.

During the period 1960–1980 nitrogen transport has more than doubled. This estimate is in good agreement with the increased use of commercial fertilizers in the coastal regions (14), and also with increased surplus nitrogen in agriculture in the region (65).

The river-transported nitrogen increased most rapidly around 1970. Since the first indications of eutrophication appeared in the 1960s, nitrogen transport from the drainage basin to the Laholm Bay has increased about threefold. However, the transport of phosphorus from the drainage basin (including coastal municipal outlets) has decreased by about half over the last twenty years.

This change in loading pattern—increased total nitrogen and decreased total phosphorus supply from local sources—agrees with measurements of nutrient concentrations in the open Kattegat and the Belt Sea (13).

A 50% reduction of river transported nitrogen to the Laholm Bay has been estimated to result in about 35% reduction of the net primary production during summer and early autumn. For the Kattegat as a whole, a 50% reduction of local sources (in Sweden and Denmark) would result in 15–25% reduction in spring-bloom production (66). Thus, a nitrogen reduction of at least 50% is the minimum requirement to substantially improve the biological conditions in that area.

Sources of river transported nitrogen, and measures to decrease this transport, were studied in the drainage basin of the Laholm Bay (65). Agriculture is responsible for about half the anthropogenic nitrogen transport to the Bay, and decreasing the area of annual spring-sown crops was one of the most efficient measures to decrease nitrogen. It is also necessary to increase areas of grassland or other perennial crops (e.g. energy crops). Use of catch crops on the rest of the spring-sown crop area is a cost-efficient measure that leads to significant decreases in nitrogen leaching (65) (Table 2).

However, if measures to attain the nitrogen reduction goal (50%) are restricted to reducing leaching and point sources, very radical measures are needed. This would in fact require afforestation of all agricultural land, introduction of 80% nitrogen reduction in all sewage-treatment plants, decreased discharges from industries, and reduced leaching from the forests by 50%. The leaching from forest areas is now increasing (60) and there seems to be no realistic way of reversing this trend before the year 2000. The reasons for this leaching is increased atmospheric deposition coupled with modern forest production and harvesting methods. Thus, for this area, measures to reduce nitrogen loading on coastal waters cannot be restricted to reducing point and non-point sources.

Table 2. Comparison of different marginal costs for nitrogen reduction (65).

Action	USD per kg N reduced in the coastal water
Wetland restoration in the coastal zone	0.6
Remedial measures in agriculture	1.9–53.4
75% reduction in municipal wastewater	15.6–31.2

A cheap and effective way to obtain the reduction goal may be to restore wetlands (65) (Table 2). There is a strong relationship between nitrogen load and nitrogen retention per unit area wetland. This relationship could be used for planning wetland and estimating the costs. This measure is also beneficial to other interests (e.g. nature conservation, wildlife). In conclusion, the needed 50% reduction of nitrogen transport to the coastal water from the drainage area of Laholm Bay is possible only if reduced point sources and reduced leaching are combined with extensive restoration of wetlands.

CONCLUSIONS

The Swedish eutrophication research program concentrated on nutrient input from a sewage-treatment plant in the Baltic and from forest and farmland in the Kattegat. In both, the discharge of nitrogen clearly dominated over that of phosphorus, when compared to the demands of phytoplankton. Despite this, phosphorus was found to limit primary production only locally close to discharge points, and in the oligotrophic Bothnian Bay. Otherwise, nitrogen is the most limiting nutrient for phytoplankton growth both in coastal and offshore waters in the Baltic and in the Kattegat. Summer blooms of blue-green algae in the Baltic are, however, an exception and their growth is limited by phosphorus.

That excess nitrogen input in relation to phosphorus can lead to nitrogen limitation seems a paradox, but denitrification reduces the nitrogen concentration in the marine system, whereas no such process exists for phosphorus. The increased bottom areas, with low or no oxygen, both in the Baltic and in the Kattegat, are likely to reduce the sites for the successive processes of nitrification (aerobic) and denitrifiction (anaerobic), due to decreasing volumes of bioturbated sediments. At the same time anoxic sediments release more phosphorus than oxidized sediments. Thus, eutrophication can, based on this simplified argument, be a self-generating process, i.e. the effects may spread with the present nutrient input to the systems.

The ecological effects are extensive and have occurred rapidly, mainly due to the enclosure (Baltic) and stratification of these waters. Recent results strongly suggest that primary production has increased and that the occurrence and negative effects of toxic algal blooms have gone up during the last decade(s). The disorder of the ecosystem is now obvious to Man, e.g. from periodic failures and unpredictability in fish and Norway Lobster catches (Kattegat). As a consequence, fishermen are faced with major socioeconomic problems.

Obviously, we must restore the marine ecosystem. How can this be done and what kind of balanced ecosystem do we want? From the above it can be seen that the function and structure of the marine waters surrounding Sweden seem to have been in a satisfactory condition in the 1950s (Baltic) and 1960s (Kattegat) without prolonged periods of oxygen deficiency. To return to a similar condition we suggest that the input of nitrogen must be reduced by at least 50%. It has also been stressed that the eutrophication problem in the Baltic can be alleviated and that the same is true for the Kattegat.

Coastal marine eutrophication is a ubiquitous problem. Many urban coastal areas worldwide are affected and/or threatened by eutrophication. The future risk for eutrophication-related effects is greatest in those coastal regions where human settlement is increasing and where nutrients enter the sea from forests, agricultural land, and the atmosphere. Stratified water bodies are particularly sensitive. To arrive at a balance for a combination of all these systems, we need both holistic ecological knowledge and a management approach.

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Article

Hans Cederwall and Ragnar Elmgren

Biological Effects of Eutrophication in the Baltic Sea, Particularly the Coastal Zone

The reported biological effects of the increased nutrient load on the Baltic Sea are summarized, with some comparisons with the Kattegat and Skagerrak. Interest is focused on the coastal zone, where effects are more obvious than in offshore areas, but from which results have not often been published internationally. Reports demonstrate environmental degradation over extensive coastal areas of the Baltic Sea. Recorded effects include increased nutrient levels; increased algal blooms, chlorophyll *a* concentrations, and primary productivity; decreased water transparency and decreased depth penetration of *Fucus vesiculosus*; increased deposition of organic matter on the bottom and increased frequency and severity of oxygen deficiency in bottom waters; and reduction of bottom fauna. It is concluded that for most Baltic countries efforts to reduce local eutrophication are likely to have important positive effects, even when reductions in discharges of nutrients are relatively insignificant in comparison to the total nutrient load on the Baltic Sea.

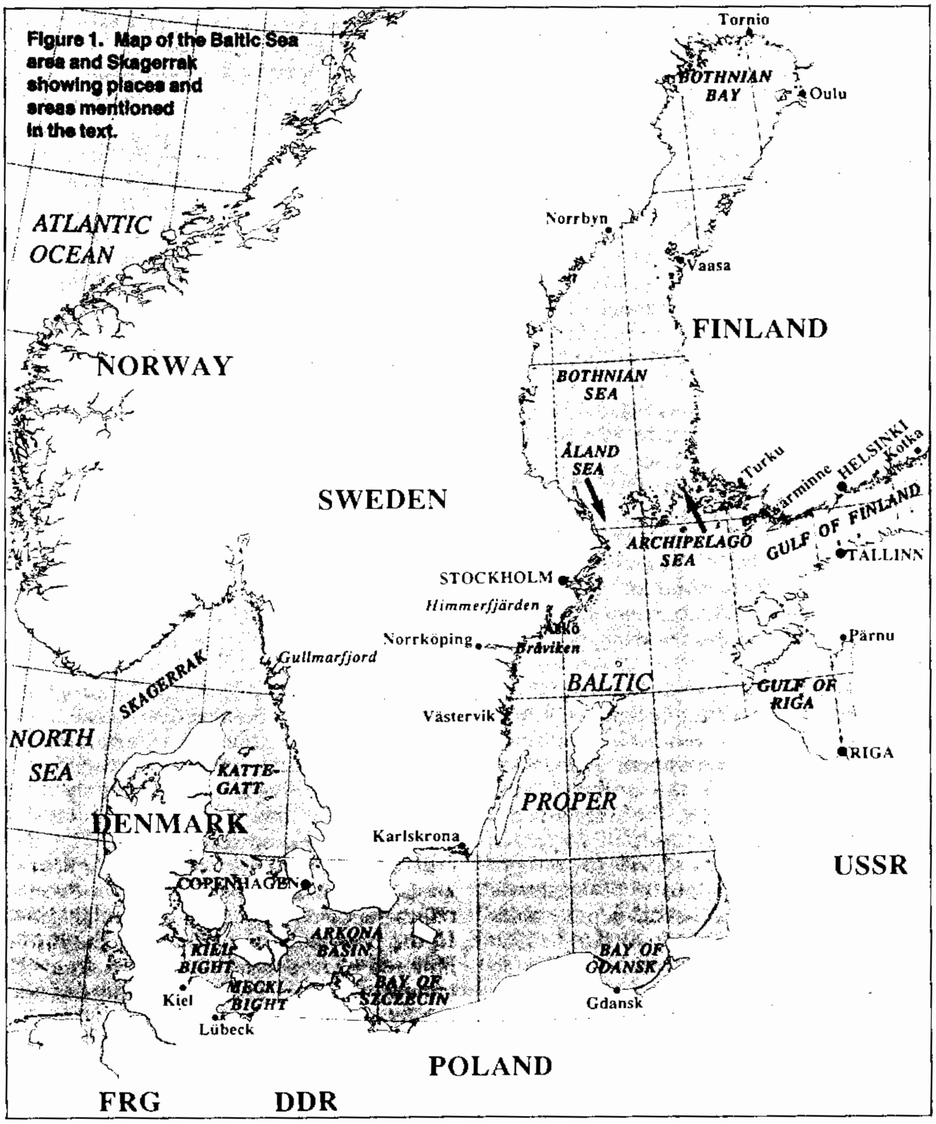

Figure 1. Map of the Baltic Sea area and Skagerrak showing places and areas mentioned in the text.

INTRODUCTION

In the following we summarize the discussion on the biological effects of eutrophication in the Baltic Sea and make some comparisons with the Kattegat and Skagerrak. We focus on inshore waters, since several reviews have already dealt with the open Baltic Sea (1–4). Effects on fish and fisheries are discussed elsewhere in this issue (5). The locations and areas mentioned in the text are shown in Figure 1.

In the open Baltic Sea, concentrations of the major plant nutrients, nitrogen and phosphorous, have increased significantly. The winter pool of nitrate as well as the sum of all inorganic nitrogen compounds has increased in the surface waters of all basins of the Baltic Sea since measurements started in the late 1960s. The winter pool of phosphate has increased since the late 1950s or mid-1960s in all basins, except the Gulf of Riga and the Bothnian Bay (6).

At the same time, concentrations of nitrate and phosphate have increased in the deep waters of all basins except the Gulfs of Riga and Finland and the Bothnian Bay, where only nitrate has increased (6).

Since most of the nutrient load derives directly from land (approximately 60% of the nitrogen and 90% of the phosphorus; 7), it is not surprising that nutrient concentrations are higher in the coastal waters than in the open sea. This has been shown by Pitkänen et al. (8) for Finnish waters and by Cederwall and Larsson (9) for Swedish waters. Accordingly, biological effects may be expected to be more pronounced and visible in the coastal zone than in the open sea. Conversely, where decreases in pollution load have been achieved, clearer biological responses can be expected in the coastal zone.

In winter, inorganic nutrient concentrations in offshore, surface waters are distinctly higher (about 25% for phosphate and 50% for nitrate + nitrite, Figs 2 and 3) in the Kattegat-Skagerrak area than in the Baltic Sea, except for nitrate concentrations in the Bothnian Bay, which approach those of the Kattegat and Skagerrak. This is true in spite of a longer winter period with insignificant primary production in the Baltic Sea, and in particular its northern parts. In contrast, winter concentrations of nitrate + nitrite in inshore waters tend to be higher in the Baltic Sea (Fig. 2), while corresponding phosphate concentrations seem to be roughly the same in both areas (Fig. 3).

meters) concentrations of nitrate + nitrite in the Baltic Proper, the Kattegat and the Skegerrak (Each column unit = 100 μg N · L^{-1}).

Figure 3. Winter surface water (0–20 meters) concentrations of phosphate in the Baltic proper, the Kattegat and the Skegerrak (Each column unit = 10 μg P · L^{-1}).

Figure 4. Summer Secchi-depth values in the Baltic Proper, the Kattegat and the Skagerrak (Each column unit = 1 m).

Figure 2.

BIOLOGICAL EFFECTS

Pelagic Zone

Few long-term biological changes in the pelagic zone of the open Baltic Sea have been convincingly linked to eutrophication. Primary production in summer has approximately doubled in the southern Baltic proper since the 1970s, and chlorophyll *a* concentrations have also increased (by about half) during this period (10, 11). Polish data show an increase in zooplankton biomass between 1951 and 1969 in the southern Baltic proper. After 1969, analytical methods were changed twice, so nothing can be said of the time trend (10).

At the entrance to the Gulf of Finland, phytoplankton biomass increased during the period 1968–1981 (12). The increase is considered to be caused, at least partly, by increased nutrient availability. The increase of nitrogen-fixing cyanobacteria during the period is considered to be connected with the increase in phosphate concentration and the low N:P ratio. Similar, statistically significant increases in phytoplankton biomass have also been reported off two Finnish coastal nuclear-power plants (13, 14).

In the open Gulf of Bothnia, there has been no alteration in the summer values of chlorophyll *a* for the period 1969–1983 (15), but in the southern part of the Bothnian Sea the May–June figures for phytoplankton biomass increased strongly during the period 1979–1983. In the open northern Bothnian Sea the phytoplankton biomass and chlorophyll *a* increased slightly from the early 1970s to 1979–1981 (16).

Launiainen et al. (17) have reported the mean Secchi-depth in the northern Baltic Sea to have decreased from 9.3 meters in the period 1914–1939 to 6.5 meters in 1969–1986, i.e. the present Secchi-depth is estimated to be between 2.5 and 3 meters less than in the early century.

The reason for this scarcity of demonstrated biological effects of eutrophication in the open Baltic Sea is hardly that they are nonexistent, but rather the lack of time series of biological measurements with an adequate time span and sampling frequency (4).

From the coastal zone, there are innumerable reports on the biological effects of increased discharges of nutrients. Compared to the 1960s there has been an increase in primary production in the Archipelago Sea (18). An increase was recorded for several places along the Finnish coast to the Gulf of Finland as early as in the 1970s (19). In the 1980s the increase has also continued at the outer stations off the coast of Helsinki (20), while no increase is seen for the stations closer to Helsinki. This could be due to improved wastewater treatment for the area. Also in the Kotka and Vasa regions, primary production levels have increased since the 1970s (8).

In the few coastal areas where local pollution is low, and where primary production has been studied (Askö area, Norrbyn area) no increase has been demonstrated (21, 22). Primary production is about three times higher in the Askö area than at Norrbyn, while in the Gullmarfjord in the Skagerrak it is about 60% higher than at Askö (23). In the eutrophied Himmerfjärd, primary production is nearly twice as high as that at the reference station in the Askö area (21).

An increased amount of chlorophyll *a* has been reported from several locally polluted areas around the Baltic Sea, e.g. Helsinki archipelago (24), Bay of Tallinn (25), the Himmerfjärd area (21), Norrköping archipelago (9), Bay of Gdansk and Bay of Sczecin (26). In the archipelago of Turku, the phytoplankton biomass increased considerably between 1966–1970 and 1979–1982 (27). In the areas outside Oulu and Tornio (Bothnian Bay) there was an increase in chlorophyll *a* during the 1970s (28), but this increase could not be connected to increased wastewater load.

From many locally polluted areas, improved sewage-water treatment has led to decreased chlorophyll *a* concentrations and/or phytoplankton biomass, e.g. Stockholm archipelago in the 1970s (29) and Turku archipelago in the 1980s (18).

Very few increases in chlorophyll *a* and/or phytoplankton biomass have been reported from coastal areas with no local pollution sources. In the outer Archipelago Sea, Kippo-Edlund and Niemi (27) found that biomass had increased between 1966–1970 and 1979–1982. This increase was partly caused by increased salinity, affecting the species composition. Data from Tvärminne area (Gulf of Finland) indicate an increase in chlorophyll during the 1970s (30, 31) and the 1980s (32). In spite of the differences in primary production, the summer level of chlorophyll in the Askö area (9) is about the same as that in the Gullmarfjord in the Skagerrak (23).

The Secchi-depth has been routinely measured in monitoring programs around the Baltic Sea for a relatively long time, but practically no assessment of the data has been published. In the nutrient loaded Stockholm archipelago, the Secchi-depth nearly doubled as a result of improved wastewater treatment (29). In a non-loaded coastal area north of Västervik (Baltic proper), the Secchi-depth values decreased by about 40 m from 1965 to 1989 (33). This decrease was probably due to regional eutrophication, since the archipelago north of this area, up to Norrköping, shows signs of eutrophication such as high nutrient and chlorophyll *a* concentrations, oxygen depletion, and bottoms without macrofauna (34, 9).

In general, Secchi-depths are one third shallower in the Baltic Sea than in the Kattegat-Skagerrak area, in both the open sea and the coastal zone (Fig. 4). This is probably due to higher concentrations of river-derived humic substances in the Baltic.

Phytal Effects

Changes in the amount and species composition of macrophytes have been reported from several coastal areas, of the Baltic proper. Decreases or disappearances of *Fucus vesiculosus* have been reported from several locally polluted areas, e.g. the inner Stockholm archipelago (35), Bråviken and the archipelago south thereof (34), Tallinn Bay (36, 37), Gulf of Gdansk (38), Helsinki archipelago, Bay of Pärnu, Gulf of Riga, and Mecklenburg Bight (39). In most areas increased amounts of filamentous algae have also been recorded (39) as well as increases in the growth of epiphytes (34, 37).

As a result of improved sewage-water treatment a recovery of the macrophyte community has been reported from the Helsinki area (40).

A decrease or disappearance of *Fucus vesiculosus* has also been reported from areas with little local pollution on the south coast of Finland (41, 34), but since a spontaneous recovery seems to have started (34), it is not clear whether this particular decrease was related to eutrophication. Other pollution sources may also influence *Fucus*. On the Swedish coast of the Bothnian Sea, *Fucus vesiculosus* is often lacking or rare in the vicinity of paper mills (42), and both decreased light penetration and toxic pollutants have been suggested as causes.

In an area relatively far from local pollution sources, e.g. the Swedish coastal zone of the Åland Sea, the lower limit of *Fucus vesiculosus* has risen from 11.5 to 8.5 meters since the 1940s (43), probably as a result of the increased water turbidity associated with eutrophication. The decrease in the penetration depth of *Fucus* is about the same as the decrease in Secchi-depth reported by Launiainen et al. (17). In the polluted Bay of Gdansk, the lower limit of phytobenthos has risen from 25 meters to 6 meters since the turn of the century (38).

Benthal Effects

Increased concentrations of nutrients in the water during winter lead to a larger

Figure 3.

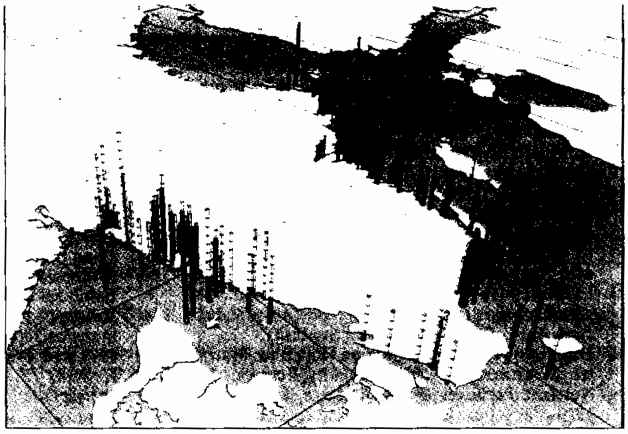

Figure 4.

spring bloom, most of which sinks to the bottom (44). This input of organic matter provides most of the annual energy supply for the benthic fauna below the summer thermocline. Increased organic enrichment leads to increased zoobenthos production, but also to increased oxygen consumption. If the sedimentation of organic matter increases excessively, oxygen depletion may occur, drastically changing the bottom fauna (45, 46). The risk of oxygen deficiency is particularly high in stagnant water masses, such as under a pycnocline. The benthic biomass increase in areas not influenced by oxygen deficiency and the decrease in areas with low oxygen are thus two sides of the same coin.

Rumohr (47) has reviewed historical reports of events in the Kiel Bight area that, if they occurred today, would easily be interpreted as indicating anthropogenic eutrophication. Even if clearly less prevalent than today, the existence of such reports suggests that caution should be taken in interpreting isolated instances, e.g. of benthic oxygen deficiency, as strong evidence of pollution. Particularly in the southwestern Baltic, the Danish Sounds and the Kattegat the coincidence of thermo- and haloclines in summer leads to strong density stratification, and a natural risk for the development of oxygen deficiency, when the water layer between pycnocline and bottom is thin and stagnant.

Nevertheless, there is an abundance of reports documenting instances where local pollution has greatly impoverished or even annihilated the soft-bottom macrofauna. Such places are the innermost areas of the Stockholm archipelago, inner Bråviken and several bays south of Bråviken (9), some areas in the Helsinki archipelago (48) and Turku archipelago (49, 50), as well as in some places of the Tallinn Bay (51) and in Lübeck Bay (52). In many other areas the species composition and dominance has been changed as a result of eutrophication, e.g. the Gulf of Riga (53), the archipelago of Karlskrona (54), Gdansk Bay (55) and Kiel Fjord (56–59).

In areas of the Baltic proper, not influenced by local pollution, there has been an increase in zoobenthic biomass above the halocline, compared to studies carried out from the 1920s up to the 1960s. Such increases have been reported for the central Baltic (60) as well as for the Northern Baltic proper (61), the Arkona Basin (62, 63) and Kiel Bight (64). On the other hand, decreased biomass has been reported from the Polish fishery zone (55).

Beneath the halocline in the Baltic proper the amount of macrofauna has decreased drastically as a consequence of oxygen depletion (60, 65, 66).

Increases in benthic biomass have also been reported for the Åland Sea and the Bothnian Sea (67–69). Here the increase is not restricted to the region above the weak halocline, since oxygen conditions are good throughout the water column.

Where biomass increases have been recorded, they have mainly been due to an increase in molluscs, and since there has either been an increase also in most other species or at least no significant decrease, it seems safe to assume that benthic production also has increased (4). Indeed, increased production has been calculated for the Tvärminne Sea area (Gulf of Finland) for the period 1926 to 1970 (70).

In comparison, Rosenberg et al. (71) have reported that benthic macrofaunal biomass in the eastern Skagerrak has also increased since the beginning of the century. In that area biomass was estimated to have increased by a factor of 1.8, while the corresponding figure for the central Baltic proper is 4–5 (60). Since the communities have changed in different ways, these ratios are a poor indication of the magnitude of the inferred causative change in organic matter input (cf. 4).

CONCLUSIONS

Published reports of increased nutrient concentrations, oxygen deficiency in water above the halocline, undesirable changes in phytoplankton, algal vegetation and macrobenthos demonstrate severe environmental degradation in large areas of the coastal zone of the Baltic Sea, primarily in the vicinity of local pollution sources. Furthermore, even areas of the coastal zone free from major local pollution sources show nutrient concentrations, and often negative environmental changes, greater than those reported for the open Baltic Sea. This appears to indicate that the changes derive primarily from local, diffuse pollution sources. It then follows that in most Baltic countries, particularly those with large archipelago zones which restrict water exchange, efforts to reduce local discharges of substances that cause eutrophication are likely to have positive environmental effects in the coastal zone, even if the discharge reductions may seem insignificant compared to the total nutrient load on the Baltic Sea.

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Article

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Effects of Eutrophication on Benthic Communities Including Fish: Swedish West Coast

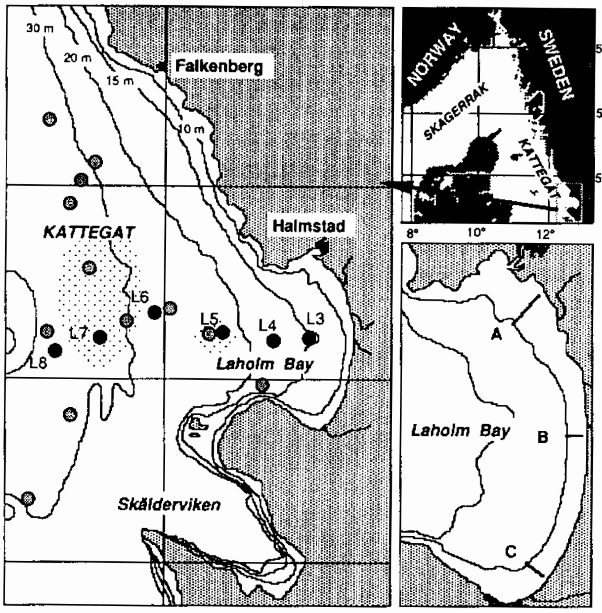


Figure 1. The SE Kattegat including Laholm Bay. Black circles are benthic infauna stations and the gray circles are trawling stations for *Nephrops norvegicus* and fish. The trawling profiles for juvenile flatfish are indicated with A, B and C. Oxygen measurements were taken within the dotted areas. (The small dotted area is Area 1 and the large is Area 2.)

The southern Kattegat is susceptible to eutrophication due to shallow mean depth (23 m) and a strong halocline which reduces intrusion of oxygen to bottom waters. The effects of eutrophication were first observed in the area in the autumn of 1980. Since then investigations on primary producers, fish, lobsters, and benthic infauna have been conducted to document the effects of eutrophication. Above the halocline in the Laholm Bay a change in the macrophyte species from *Fucus* spp. to filamentous green algae has been observed. Mortality of benthic macrofauna, mainly bivalves, has been observed in most years and seasons. The recruitment of flatfish has not been negatively affected. Around the halocline the benthic infauna were seriously affected by oxygen deficiency. Below the halocline, fish disappeared and lobsters emerged from burrows when oxygen saturation declined below 40%. When oxygen saturation decreased below 15% Norway lobsters were immobilized and their blood-pigment concentration decreased. Benthic infaunal species emerged from the sediment. Lobsters died when saturation dropped to 10%, while many infauna species tolerated levels of 7–5% for some weeks. Analysis of stomach content indicated that neither fish nor lobsters died from lack of food, but from hypoxia. Subsequent to the reoxygenation of the bottom water during winter, flatfish and benthic infauna recovered whereas cod and lobster populations did not.

INTRODUCTION

In most coastal marine areas where there is a high level of residential and industrial development the effects of eutrophication have been obvious for many years. Over the last decade, it has become increasingly apparent that the resulting ecological effects of eutrophication are not minor and localized, but have large-scale implications and are spreading rapidly (1–3). This paper reports on the effects of eutrophication in the SE Kattegat on the west coast of Sweden (Fig. 1).

The Kattegat is a shallow sea (mean depth 23 m) with a strong vertical water stratification. The Kattegat is influenced by incoming salinity (15 to 20‰) surface water from the Baltic and high salinity (32 to 34‰) bottom water from the Skagerrak. The halocline is normally located at a depth of around 15 m and mixing between the surface and bottom water is greatly reduced during the productive season (March to November). The temperature in the bottom water varies between 4°C and 11°C, being at its highest in the autumn.

During the past decades the Kattegat has received increasing amounts of nutrients, particularly nitrogen and phosphorus, and the coastal areas are now considered to be eutrophic (1). Today, about 5000 tonnes of nitrogen and 150 tonnes of phosphorus are transported annually to the Laholm Bay by five rivers (4). In coastal areas, such as the Laholm Bay (Fig. 1), primary production has increased and a change in the species composition of micro- and macro-algae has also been observed (5, 6). Another effect of eutrophication is decreased oxygen concentration in the bottom water (4, 7). Low oxygen concentration (hypoxia) $<2\ \text{ml} \cdot \text{L}^{-1}$ ($<30\%$ saturation) has been registered in the SE Kattegat in the late summer and autumn of every year during the 1980s. Discharges of organic substances from the cities in the area have declined during the 1970s due to the installation of water-treatment plants.

In the Kiel Bay and in the SE North Sea, hypoxia recently caused reduction of demersal fish and the death of benthic fauna (8, 9). Similar effects caused by low oxygen concentrations have also been reported from the coast of Brittany (10), the Adriatic Sea (11), the coast of Alabama (12) and the New York Bight (13). A feature which all these areas have in common with the SE Kattegat is that freshwater outflow creates a salinity stratification which reduces the mixing capacity between surface and bottom water. These areas are sensitive to eutrophication-enhanced primary production and subsequent sedimentation of organic matter which, in turn, leads to oxygen deficiency in the bottom water.

In 1984, the Swedish Environmental Protection Agency initiated a multidisciplinary research program to study the processes causing eutrophication in the SE Kattegat and to evaluate the effects. The aim of this paper is to report on the effects on benthic algae, benthos (including Norway lobster *Nephrops norvegicus*) and demersal fish. Most of these studies were carried out in the Laholm Bay and in the SE Kattegat during the 1980s and the re-

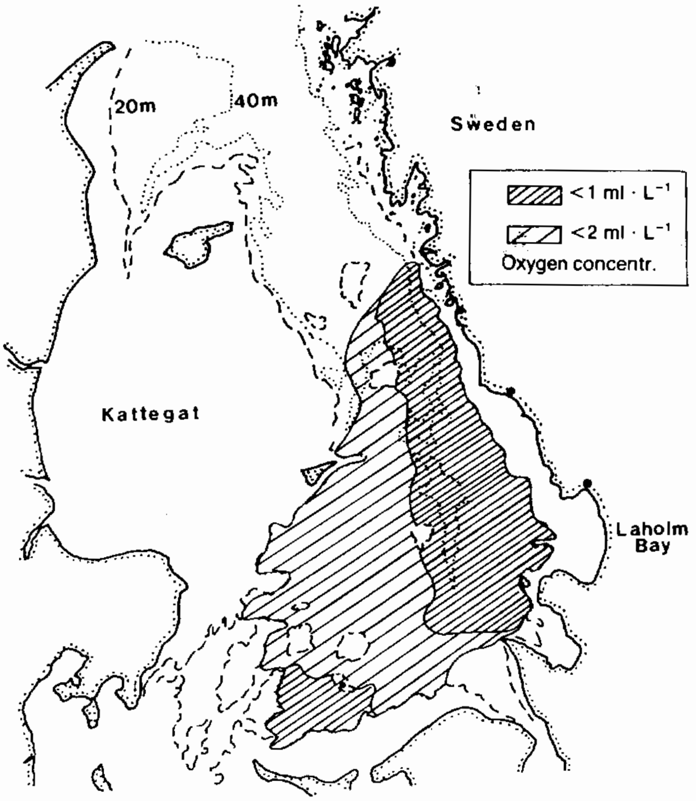
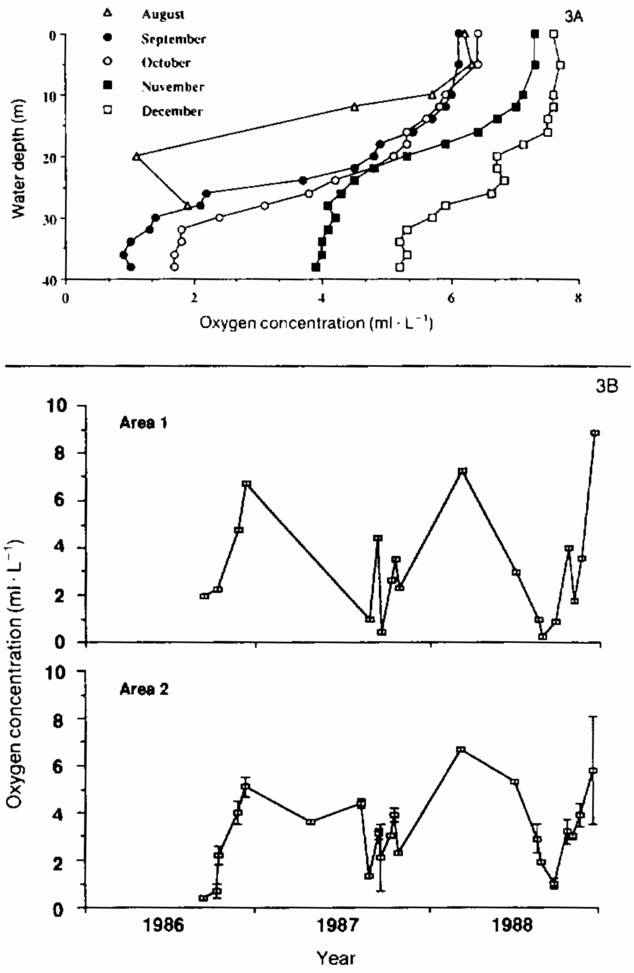


Figure 2. The spatial distribution of low oxygen concentration in the southern Kattegat, September 1988. Samples of oxygen are taken < 0.5 m (eastern Kattegat) or 1.0 m (southern Kattegat) above the sediment surface at 20 to 60-m water depth.

Figure 3. A: Monthly oxygen profiles in Laholm Bay Area 2 (see Fig. 1) from August to December 1988. The samples were taken from the surface down to the bottom. B: The oxygen concentration in Areas 1 and 2 just above (< 50 cm) the bottom, from 1986 to 1988. Mean values with standard deviations are indicated.



sults are compared with previous investigations in the area. Sampling locations for benthic fauna, *Nephrops norvegicus*, and fish are given in Figure 1.

THE SPATIAL AND TEMPORAL DEVELOPMENT OF OXYGEN DEFICIENCY IN THE KATTEGAT

Measurements of oxygen concentrations in the SE Kattegat were started in 1981. Samples collected during the period 1981 to 1985 (14) were taken 1 meter above the bottom and samples from 1986 to 1988 (this study) less than 50 cm above the bottom (Figs 2 and 3).

The extent of the area affected by oxygen deficiency in the SE Kattegat has varied during the 1980s. In 1981, 1982 and 1983, large areas (7) with oxygen levels <1 ml · L^{-1} were recorded, but in 1986 and 1988 low oxygen conditions were more extensive. In 1988, oxygen concentrations down to 0.2 ml · L^{-1} were recorded.

The depth of the oxygen-deficient water above the seabed was about 10 meters during the autumn of 1988 (Fig. 3), whereas in previous years it had been <1 m (7). In August, the oxygen concentration was at minimum at 20-m depth. Lowest oxygen concentrations were recorded in September with levels gradually increasing to normal in December.

Seasonal variations in deep-water oxygen concentrations in 1986 to 1988 are shown for two areas (Figs 1 and 3). Minimum O_2 levels occurred for all years recorded, during the period August to October. In both areas, the autumn values differed between years depending on hydrography. In 1987, low oxygen tensions occurred in pulses over an extended time period. In 1988, one period of oxygen tension down to 0.2 ml · L^{-1} occurred in September in Area 1 and down to 0.4 ml · L^{-1} in Area 2. In 1987, a decline in oxygen tension was noted in Area 2 also after the spring bloom.

EFFECTS ON MACROALGAE

A long-term study conducted from 1952 to 1985 (6) has shown that the species composition of benthic macroalgae in Laholm Bay, at a jetty in Båstad in the southernmost part of the bay, has undergone drastic changes since the 1970s. An increase in filamentous and other green algae (*Cladophora* spp. and *Enteromorpha* spp.) during the mid 1970s was followed by a decline and finally an elimination of *Fucus* species (Fig. 4).

From the mid-1970s onwards filamentous green algae and large red algae(e.g. *Furcellaria lumbricalis* and *Phycodrys rubens*) have often been washed ashore during the summer in the eastern parts of Laholm Bay. Since 1980, this has also been observed regularly in the bay south of Laholm Bay, Skälderviken (Fig. 5). In both areas, these events cause a serious nuisance for fishing, boating, and bathing activities, and may be precursors to mass die-off events initiated by eutrophic-driven production. Similar changes in macro-algal composition have been observed elsewhere, especially in semi-enclosed areas such as the Swedish fjords in the Skagerrak.

EFFECTS ON SOFT-BOTTOM BENTHOS. MACROFAUNA

The position of the halocline (at about 15 m) and water-column oxygen concentrations have a strong effect on benthic faunal composition (15). Above the halocline (down to about 10 m) the bottom is a well-oxygenated sandy habitat. Around the halocline (13–20 m) salinity, temperature, and oxygen concentrations vary, and below the halocline the sediment is muddy with stable environmental conditions except for occasional oxygen deficiencies (7).

The sampling program was, therefore, set up in relation to the halocline, i.e. between 1983 and 1988 samples of macrofauna (> 1 mm) were taken above the halocline (0–10 m), around the halocline (stations L3, L4; 16 and 18 m) and in deeper parts of the Kattegat (stations L5–L8; 22 to 56 m) using a 0.1 m^2 van Veen grab (16).

Above-halocline

In the exposed sandy Laholm Bay in the southeastern Kattegat the benthic faunal biomass was dominated by the suspension feeding bivalves *Cardium (Cerastoderma) edule* and *Mya arenaria*. Residence time of water in the bay (0–10 m, area 60 km^2) is approximately 7 days (17) and these bivalves could theoretically filter the bay volume in 3 days (estimated for the autumn of 1985). Bivalve ingestion is, however, limited to about half of its potential capacity, possibly as a consequence of environmental disturbance (wave action, hypoxia) or because a proportion of the food (phytoplankton) does not come in close enough contact with the bivalves. Overall, bivalve suspension feeders consume approximately 25% of new production in the bay and reduce some of the immediate eutrophication effects (18). In shallow areas with long residence times for the water, such reductions could be more important due to tighter benthic-pelagic couplings (19–21).

Extensive to moderate mortality of *C.edule*, *M. arenaria* and the starfish *Asterias rubens* have been noted for several seasons during the 1980s, probably as a result of hypoxia. Different theories as to how oxygen can occur above the halocline are discussed by Dyer et al. (7).

Without the reduction of suspension feeding animals, by hypoxia and by the predation of juvenile flatfish species (see below), the phytoplankton biomass might have been reduced even further.

Around- and Below-halocline

Benthic communities at two stations around the halocline (L3, L4) at 16 and 18 m water depth have shown great temporal variations which seem to coincide with varying oxygen concentrations. Macrofaunal abundance has been as low as <400 ind. · m^2, and the mean number of species was 16 per 0.3 m^2 (n=12) (7). These figures are low compared to other areas with the same depth (15), but are consistent with faunal reductions observed in other oxygen-stressed environments (28). Dominant species at station L3 and L4 were the bivalves *Arctica islandica* and *Abra alba*. Temporal variations in total faunal abundance were due to variations in *Abra alba*, which is sensitive to hypoxia (7).

Station L5 at 22 m depth is, with few exceptions, situated below the halocline. Low oxygen concentrations (<2 ml · L^{-1}, 30% O_2 saturation) recorded during the period 1983 to 1986 had devastating effects on the fauna (7) (Table 1). The numerically dominant species at station L5 in August

Figure 4. Temporal changes in species composition of macroalgae in the southernmost part of Laholm Bay at Båstad during 1965 to 1985. Thick line: very common, medium thick line: common, thin line: sparse to rare (6).

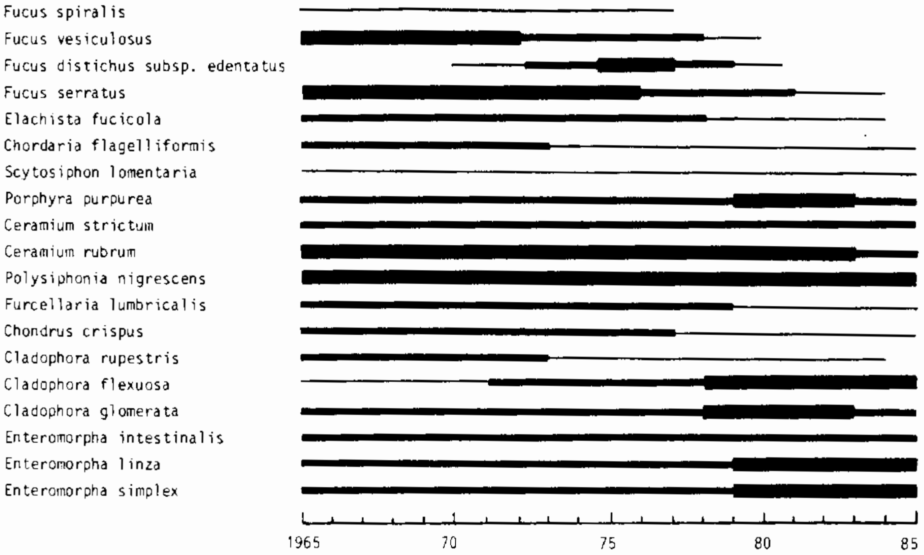


Figure 5. Mats of green filamentous macroalgae (mainly *Cladophora* spp. and *Enteromorpha* spp.) washed ashore and floating in a bay south of Laholm Bay (Skälderviken) in August 1983. This has been a common event at many places since 1976. Photo: Rutger Rosenberg.

Table 1. Abundance per m^2 of some of the dominant species at station L5 (22 m depth) in 1986–1988 during autumn 1986, 1987, and 1988. The total abundance per m^2 and the total number of species per 0.3 m^2 are also given.

Species	1986 Oct.	1967 Aug.	1987 Sep.	1987 Oct.	1988 Nov.
Diastylis rathkei	277	153	460	140	0
Amphiura filiformis	80	160	67	77	0
Ophiura albida	47	43	67	77	0
Abra alba	3663	2630	1657	477	0
Eucone papillosa	43	77	190	53	0
Scoloplos armiger	33	50	57	130	0
Terebellides stroemi	7	27	93	13	0
Arctica islandica	113	97	100	110	70
Corbula gibba	123	150	130	37	60
Total number of species per 0.3 m^2	41	36	41	46	26
Total abundance per m^2	5337	4237	3690	2397	1380

1987 was the bivalve *Abra alba*. Its size frequency distribution in August was unimodal and the bivalves were probably of the 1987-year class (Fig. 6), as individuals collected in June 1988 had one clear winter-ring and growth-zone. Thus, the *A. alba* grow faster here than in the southeastern Baltic (22), and are more similar to the populations on the west coast of France (23).

In September 1987, station L5 was scanned by a video camera operated from a remote-controlled submersible vehicle (24). Dead *A. alba* were observed on the sediment surface. In October, thousands of dead *A. alba* were noted at L5, most of them with flesh (Fig. 7). Higher oxygen concentrations recorded in October 1987 suggest that the oxygen concentration was rising at that time and that the mass mortality must have occurred during the preceding week(s). *A. alba* is a conspicuous food item for the dominant flatfish (dab, plaice, flounder) (26), yet the number of predatory invertebrates and fish was apparently low, as clam flesh remained unconsumed. These mass mortalities, of organisms leaving the sediment, have been observed in other oxygen deficient areas (25). Large numbers of benthic invertebrates captured in trawls for demersal fish throughout the Kattegat during September 1988 suggest that this phenomenom was widespread.

The results strongly suggest that the mass mortality of *A. alba* was caused by hypoxia. No recruitment occurred in 1988 and it seemed evident that the great variations in oxygen concentrations had a strong impact on the benthic ecosystem. No such reductions have been recorded from other areas in the vicinity, on the contrary Arntz et al. (27) stated that "*Abra alba* is the most persistent species in the Kiel Bay Channel System being present in 90% of all samples."

Not only *A. alba* suffered from this high mortality. Other dominants of the benthic community that survived the autumns of 1986 and 1987 are presented in Table 1. Most of these species were absent in November 1988, except *A. islandica* and *Corbula gibba*, which were numerically reduced. These two species are known to tolerate hypoxia (28). Greater losses in 1988, relative to 1986 and 1987, were most probably a consequence of lower oxygen concentrations in 1988 (Fig. 3: Area 1). The total abundance and total number of species dropped during the period.

During the examination of the seabed at station L5 in September 1987 with the remotely operated submersible vehicle we observed thousands of brittle stars (*Ophiura albida*) standing on their arm tips and with central discs elevated as high as possible from the sediment surface (Fig. 8). The seabed contained ripples and all brittle stars were standing immobile at the top of these. The oxygen concentration at the sediment surface was at that time 0.5–0.6 ml $\cdot$ L^{-1} (7–10% O_2 saturation). Nearby, at a depth of 26 m, the measured oxygen concentration was 1.4 ml $\cdot$ L^{-1} and here the brittle stars were mobile and close to the bottom. Similar behavior for *Ophiura albida* during low oxygen conditions has been observed in the North Sea (29) and for other brittle stars in the Adriatic Sea (30).

Temporal variations in stations L6, L7 and L8 are presently under evaluation. No dramatic changes can be observed for the period 1983 to 1988 in total abundance, biomass, and species numbers. Numerical variation for one of the dominants, the brittle star *Amphiura filiformis* has been presented by Rosenberg and Loo (7). They also demonstrated that *A. filiformis* was significantly reduced both in number and biomass by more than 90% over a one-month period in October to November 1985, due to hypoxia (7). No significant reduction was recorded during the same period at that station for *Amphiura chiajei*, and the difference in response was suggested to be the 5 times higher respiration of *A. filiformis* compared to *A. chiajei* (31).

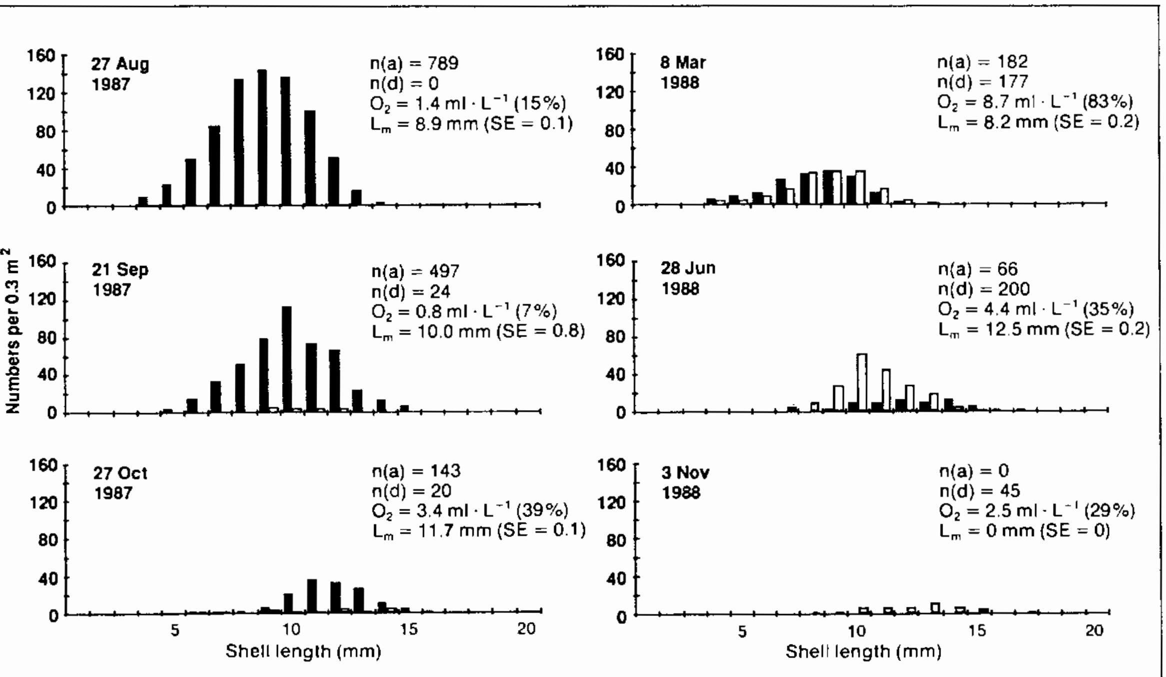
In 1984, twenty-four historical benthic stations, originally sampled during 1911 and 1912 in the open Kattegat, were revisited (32). The total biomass of the benthic macrofauna present in 1984 was significantly reduced in the western and northern Kattegat at depths between 12 and 25 m. The majority of species in the whole area were smaller in individual size in 1984, and a comparison of similarity showed that the community composition had changed markedly over the area. It was concluded that the most likely cause for the changes was eutrophication, although the influence of other factors may also have been partially responsible.

MEGAFAUNA—*Nephrops norvegicus*

Norway lobster, *Nephrops norvegicus*, is a commercially important decapod in the Kattegat and Skagerrak, ranking third in importance after herring and cod. In this area, the lobsters live in burrows on accumulating silt-clay bottoms at depths between 25 and 75 m. Burried females and juveniles spend more time in their burrows than males. Foraging activity on the bottom occurs mainly in twilight.

The effects of low oxygen concentrations on the behavior of lobsters were first observed in 1975, when the catch per unit effort (CPUE) more than doubled in the southern Kattegat as the O_2-saturation decreased to about 40% in the bottom water (33). In the burrow, the oxygen consumption of the lobster, and other microbial processes can lead to hypoxic conditions, especially when the O_2-saturation of the overlying water decreases (34). Lobsters kept in the laboratory emerged from the burrows when O_2-saturation fell below 25% (35). The high CPUE was thus a

Figure 6. Size-frequency diagram for the bivalve *Abra alba* at station L5 in the SE Kattegat between August 1987 and November 1988. Numbers of living (n[a]) and dead (n[d]) bivalves and their mean lengths (mm) are given together with the oxygen concentration (and saturation) about 10 cm above the sediment.



result of the lobsters emerging from burrows when oxygen levels were low. In laboratory experiments with oxygen saturation levels below 20%, the lobsters stretched their legs (supported by claws and telson), to reach water with somewhat higher oxygen levels, and stopped feeding (36).

Changes in the Lobster Fishery in the Kattegat

The SE Kattegat was an important area for lobster fishing from the late 1970s, when the fishery became economically attractive, until 1986. During the autumn of 1985 dead and dying lobsters (up to 50% of the total catch) were reported for the first time in the northern part of the investigated area (Fig. 1). In 1986, this occurred at many places over the whole SE Kattegat (Fig. 9). The average catch of lobsters declined from about 100 kg to about 40 kg per boat each night, making the fishery unprofitable (37). The catch statistics show that the CPUE peaked at 30 kg $\cdot$ h^{-1} in 1982, probably due to hypoxia that induced the lobsters to leave their burrows, and decreased to 10–15 kg $\cdot$ h^{-1} in 1984. From 1985 onwards the CPUE did not exceed 5 kg $\cdot$ h^{-1}, and in 1988 the *Nephrops* stock collapsed. In 1988, the mean CPUE was 3.5 kg $\cdot$ h^{-1}, and from October 1988 to the last investigation in September 1989 no lobsters were caught in an area south of Falkenberg and east of station L8 (Fig. 1) (36).

As oxygen levels decreased, the ratio of female/male lobsters in the catch increased (33). The sex ratio of lobsters in the Kattegat was between 7 and 38% females in the period 1984 to 1988. In September 1988, however, a reverse in the sex ratio was observed in the center and southern part of the investigated area where females represented between 74 and 77% of the total numbers. At this time extremely low (<1 ml $\cdot$ L^{-1}; <15% saturation) oxygen

Figure 7. Dead *Abra alba* photographed *in situ* at station L5 (see Fig. 1) on 27 October 1987. Note that the mantle edge is visible on most of the bivalves indicating that the bivalves died recently. Oxygen concentrations in the area are given in Figure 3A Photo: Lars-Ove Loo.

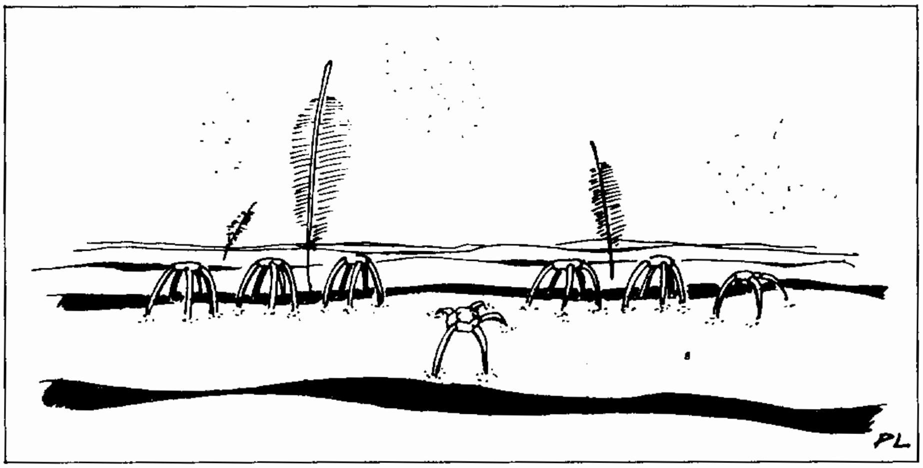


Figure 8. Sketch from video-recording of *Ophiura albida* standing immobile and with the central disc elevated at the tops of the ripples at station L5 (see Fig. 1) on 25 September 1987. The featherlike anthozoan *Virgularia mirabilis* is also shown. The oxygen concentration was 0.8 ml $\cdot$ L^{-1} corresponding to a saturation of 7%. Drawing: Per Lager.

Figure 9. The catch of 11 dead and 2 live *Nephrops* after trawling for a half hour, in the SE Kattegat, October 1986. Photo: S. P. Baden.

concentrations were recorded, which may have forced the females to leave their burrows. In the northern part of the area no living lobsters were caught on this sampling occasion.

Blood Pigment Concentration

The blood pigment of lobsters is hemocyanin, which is blue when oxygenated. It consists of large protein molecules (825 000 mol.wt) with Cu atoms binding the oxygen (38). To compensate for moderate hypoxia (oxygen concentration between 40 and 15% sat.) in seawater, the lobsters can increase the blood pigment concentration. However, when exposed to hypoxia (< 15% saturation in the bottom water) the blood pigment concentration will decrease (35, 36, 39). Lobsters can not escape from areas with low oxygen concentrations to the same extent as fish. Therefore, the blood pigment concentration is an indicator of the oxygen conditions in which lobsters have spent the weeks prior to testing. Lobsters are almost immobile in O_2 saturations < 15% (35, 36).

In 1985 and 1986, when dead and dying lobsters were reported by fishermen for the first time in the SE Kattegat, blood-pigment concentrations of lobsters caught in the area were < 0.11 mmol $\cdot$ L^{-1}, i.e. < 20% of what is regarded as a normal level (39). This indicates that the blood protein had been metabolized and was being used as an energy source, without any regeneration, suggesting a probable mechanism for surviving during shorter periods of hypoxia without feeding.

Blood analyses of lobsters from the Kattegat were carried out during 1986–1988. Low blood-pigment concentrations were found during autumn over the whole area, coinciding with low oxygen (< 20% O_2 saturation) measurements in the bottom water. At some stations, mainly in the southern Kattegat, recovery of the blood pigment concentrations was observed when normoxia (70–100% oxygen saturation) returned to the bottom water. No quick recovery occurred in the rest of the study area. Each year the whole investigated area seemed to be equally affected, although there were differences in the recovery rates of hemocyanin levels in lobsters from different areas.

Blood hemocyanin levels were investigated in lobsters from different areas along the coast of the Skagerrak during the autumn of 1987 and 1988. In one locality, monthly variations were recovered and related to O_2-measurements taken at the same place (40). Moderate hypoxia in the bottom water of 35–43% induced an increase in hemocyanin to a mean of 1.1 mmol $\cdot$ L^{-1} with maximum values of 1.5 mmol $\cdot$ L^{-1}. The blood of these animals was highly viscous due to the large amounts of protein, and the color was so blue that it was visible through the ventral abdomen. Other localities in the Skagerrak showed very low hemocyanin concentrations, and it is possible that these areas had been affected by hypoxia. Experiments have shown that oxygen saturation of less than 15% is the level below which hemocyanin concentrations rapidly decrease, in some cases to half the original level within one week (36).

Food Selection During Oxygen Deficiency

A possible reason for slow recovery of blood hemocyanin in lobsters from the Kattegat could be a decline in food availability. To investigate this possibility, stomach analyses were carried out on the same specimens from which blood was analyzed, and from a couple of stations in the NE Kattegat (36). In total, 30 different species belonging to four major groups (crustaceans, echinoderms, molluscs, and polychaetes) were found in the lobster stomachs. Animals from each of the four groups in the SE Kattegat occurred in an average of 50–60% of the stomachs, except in September 1988, when most of the stomachs were empty. When compared to lobster stomachs from the NE Kattegat and the west coast of Scotland (36, 41, 42), the lobsters from the SE Kattegat contained a larger proportion of echinoderms (*Amphiura/Ophiura*) and hermit crabs (*Pagurus bernhardus*), but a smaller proportion of total amount of crustaceans than in the NE Kattegat. This could be a result of *Amphiura/Ophiura* emerging from the sediment at low oxygen tensions and the lobsters being able to eat them. The hermit crabs are probably eaten when dead from oxygen deficiency, as they are otherwise well-protected. Even though a certain change in food selection has occurred, lobsters from the southern Kattegat do not seem to starve or lack any important category of food, when they are able to eat.

EFFECTS ON FISH

Changes in the Fishery

The SE Kattegat is a traditional fishing area for Swedish and Danish fishermen. Among the demersal fish species, cod and plaice dominate and are caught in all seasons, but mainly in autumn and winter. During the last decade the total catch of cod and plaice in the Kattegat has decreased compared to the 1960s and 1970s by approximately 40 and 70%, respectively (43, 44). Data from Swedish catch statistics revealed a considerable decrease in catch efficiency (CPUE, kg $\cdot$ h^{-1}) of cod in demersal fish trawls in the SE Kattegat during the 1980s. CPUE in cod and lobster trawls was reduced by 80 to 90% in the autumns (September–December) of 1978 to 1988 (Fig. 10). This was probably due to migration from the area when bottom water oxygen was depleted. The SE Kattegat is the most important spawning area for cod in the Kattegat (44). Cod used to spawn close to the shore, but after 1981 the spawning stock spread in the southern Kattegat. A reduction of the spawning biomass has also been noted during the 1980s (44).

Fish Requirement in the Laholm Bay

The Laholm Bay is one of the major nursery areas for juvenile flatfish in the Kattegat. 0- and 1-group fish mainly occur in the shallow parts (0 to 10 m) of the bay (45, 46). Changes in the structure of sediment and macro-vegetation at these depths have been observed during the last decade in the western part of the Kattegat (Danish coast), and a decline in recruitment of flatfish has been recorded in these areas (47). Changes in macroalgae composition and increased bivalve mortality could have lowered the value of the Laholm Bay as a nursery for flatfish. To study this possibility, surveys of young fish were carried out monthly by beam-trawling at different depths (1.5, 3.0, 5.0, 8.0 and 11.0 m) at three stations, during the recruitment season (May to October) from 1984 to 1986 (46).

Juveniles of six flatfish species (plaice-*Pleuronectes platessa*, sole-*Solea solea*, dab-*Limanda limanda*, turbot-*Scophthalmus maximus*, brill-*Scophthalmus rhombus* and flounder-*Platichthys flesus*) were found in the Laholm Bay. Plaice was the dominant species and represented 75 to 91% of all individuals in 1984 to 1986. On average, plaice has represented > 90% of the flatfish abundance during each of the last three decades (46), and species composition has not changed (46–48). The species found in the Laholm Bay are the most abundant flatfish species also found in other nursery areas around northwestern Europe (49–55).

The total mean abundance of 0-group flatfish in the study area ranged from 1.5 to 25 ind. $\cdot$ 100 m^{-2} during the period 1984 to 1986. 1-group total mean abundance ranged from 3 to 11 ind. $\cdot$ 100 m^{-2}. Total mean biomass for 0- and 1-group flatfish ranged from 0.2 to 10.2 and 1.9 to 51.4 g ash-free dry weight (AFDW) $\cdot$ 100 m^{-2}, respectively. Previous investigations on flatfish abundance carried out in the area since the 1930s showed an increase in density of the dominant species, plaice (Fig. 11). The abundance of juvenile flatfish in the Laholm Bay was high compared to that found in shallow areas in the western Kattegat (47).

Abundance and biomass of plaice, sole, turbot, brill and flounder showed a general decrease with increasing depth, whereas the mean length of each year-class increased. For dab, the highest abundance and biomass and the lowest mean length were found in the deeper parts (5 to 11 m) of the study area. A similar distribution with depth has been found for these species in other nursery areas in Great Britain and in the continental Wadden Sea (50, 51, 53, 57, 58).

The total annual production (measured from May to May) was estimated for 0-group and 1-group of the three dominant species: plaice, sole and dab. As depth distribution varied for the three species, production was estimated in two different depth strata within the study area (1.5 to 5 and 5 to 11 m) in Laholm Bay. The total annual production of 0- and 1-groups of the three dominants together, in the shallow part of the area, was estimated to be 101, 24 and 88 g AFDW $\cdot$ 100 m^{-2} during the periods 1984–1985, 1985–1986 and 1986–1987, respectively. The corresponding figures for the depth range 5 to 11 m were 12, 13 and 54 g AFDW $\cdot$ 100 m^{-2}, i.e. a production 50 to 75% lower than in the shallow part.

The results show that Laholm Bay, despite increased eutrophication in the

Kattegat, is still a highly productive nursery area for juvenile flatfish. No significant change in species composition has occurred during the last four decades, and the abundance of the dominant plaice has been high in some recent years. As a deterioration in quality in nursery areas in the western Kattegat has occurred during the last decade, probably due to eutrophication, the importance of Laholm Bay on the eastern side, as one of the main nurseries for flatfish in the Kattegat, has increased.

Effects of Oxygen Depletion on Demersal Fish

Avoidance reactions to hypoxia by fish have been observed in coastal areas of the SE Kattegat at depths of 10 to 20 m (i.e. where the halocline is normally situated) in the autumn of each year during the 1980s (59). These avoidance reactions have been manifested by the fact that unusually large numbers of fish, mainly adult flatfish, have been caught in gillnets and found to be dead despite the fact that the nets have been fishing for less than a day. The increased catches were due to the increased mobility of the fish when avoiding areas of low oxygen. When caught in the nets the fish will die from stress caused by low oxygen concentration. Fish avoidance reactions to hypoxia were first observed in the mouth of the Laholm Bay in the autumn of 1959. Avoidance reactions were also reported from the area in 1961, 1966, 1975, and 1979, but the geographical extension of these events was limited. During the 1980s, however, avoidance behavior by fish has taken place over vast areas and during periods of weeks to months each year.

The effects of oxygen depletion on demersal fish in the SE Kattegat have been studied in this project during the period 1984 to 1988. Demersal trawling has been carried out during spring and autumn each year in several areas below the halocline (20 to 50 m depth) (60). On each occasion 8 to 12 trawl samples were taken. Abundance, biomass, species composition, and food selection were investigated and related to oxygen concentrations in the bottom water.

During spring, when oxygen concentrations are normal, the demersal fish species were evenly distributed in the area and the total biomass was similar between the years 1984 to 1988 (Fig. 12). In autumn, low oxygen levels were noted during September and October for most years (Figs 3 and 12). A reduction in the total biomass of demersal fish from between 200 to 250 $kg \cdot h^{-1}$, when the oxygen concentration was high, to approximately 50 $kg \cdot h^{-1}$, in 1985, 1986, and 1987, and to 5 $kg \cdot h^{-1}$, in 1988, was recorded in the area when the oxygen in the bottom water was reduced (<2 $ml \cdot L^{-1}$, about 30% saturation) (Fig. 12). During the autumn of 1986, the total biomass of demersal fish in each trawl sample was compared with the oxygen concentration at the site, and a significant ($p < 0.01$) positive correlation was found (60).

Cod and whiting, together, represented about 50% of the total biomass during

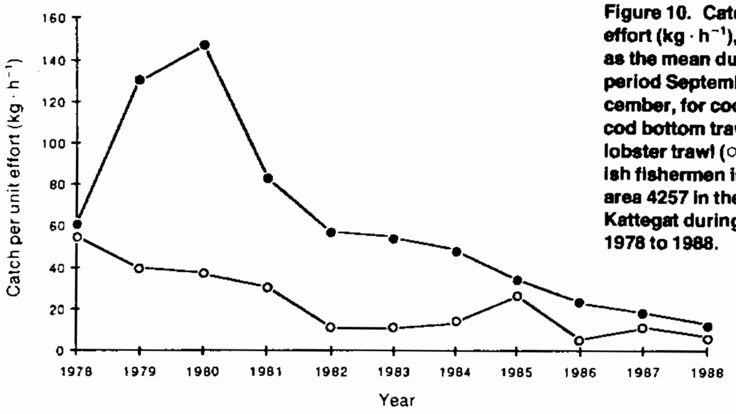


Figure 10. Catch per unit effort ($kg \cdot h^{-1}$), estimated as the mean during the period September to December, for cod taken in a cod bottom trawl (•) and lobster trawl (○) by Swedish fishermen in the ICES-area 4257 in the SE Kattegat during the period 1978 to 1988.

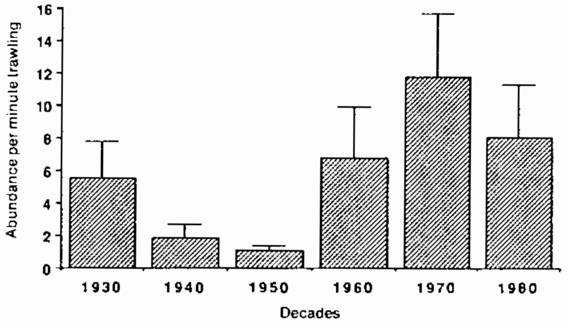


Figure 11. Mean abundance (ind. per minute of trawling) and standard deviation (SD) of 0-group plaice (*Pleuronectes platessa*) during the last six decades in Laholm Bay. Samples taken in August (1980 to 1983 in July) at 1.5 to 2.0 m depth. (46).

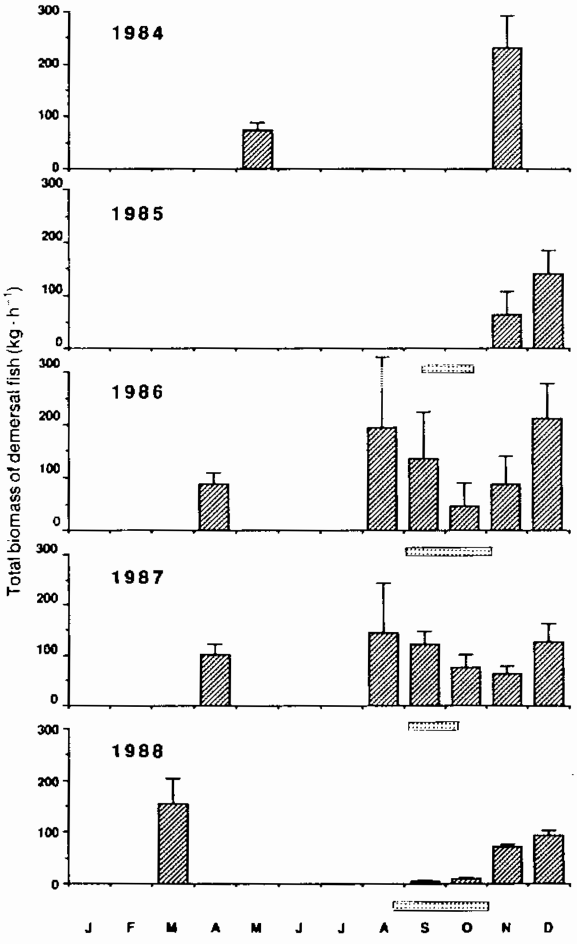


Figure 12. Total biomass (mean and 95% confidence limits, $kg \cdot h^{-1}$ wet weight) of demersal fish on all sampling occasions in the area investigated in SE Kattegat from 1984 to 1988. Periods of low (<2 $ml \cdot L^{-1}$) oxygen concentrations in the bottom water (measured <0.5 m above the sediment) are indicated below the x-axis (shaded bar). On each occasion 8 to 12 samples were taken, except in August 1985 and 1986 when 5 and 3 samples were taken. Samples were taken with a lobster trawl with a mesh size of 60 mm in the cod end.

periods of the autumn when oxygen concentrations were high (> 3 ml · L^{-1}). As oxygen decreased in the bottom water, these two species were the first to disappear from the area, mainly to shallow areas, and as a consequence a change in the species composition of the dominants was observed. In October 1986, when the mean oxygen concentration in the bottom water was 1 ml · L^{-1}, cod and whiting represented only 15% of the fish biomass, whereas the long rough dab *Hippoglossoides platessoides* alone made up 49% of the total biomass (60).

In September 1988, the oxygen concentration in the bottom water was approximately 1 ml · L^{-1} (15% saturation) or less in the whole area investigated, and the mean biomass of demersal fish was reduced to approximately 2% of normal values (Fig. 12). In most of the trawl samples some dead fish were found and in half of the 12 samples no live fish were caught. The scavenger hagfish, *Myxine glutinosa* (Agnatha), which is normally rare in the trawl samples, occurred in high densities (100–1000 ind · h^{-1}). They were found both dead and alive. Instead of fish, 200 to 400 kg · h^{-1} of benthic invertebrates were caught (Fig. 13). Conspicuous species were the Echinoderms *Echinocardium cordatum, Brissopsis lyrifera, Cucumaria elongata, Asterias rubens, Ophiura* spp., *Amphiura chiajei, A. filiformis* the Polychaetes *Polyphysia crassa, Aphrodite aculeata, Nephtys* spp., the Crustaceans *Macropipus* spp., *Eupagurus* spp. and *Priapulus caudatus*. In one sample the biomass of benthic animals amounted to 1.6 tonnes. Under normal conditions, when the bottom water is well oxygenated, the catch of benthic fauna is between 10 and 20 kg · h^{-1} trawling. The benthic animals emerged from the sediment when the oxygen decreased to critical concentrations. A similar response by benthic fauna to low oxygen concentrations was observed in the eastern North Sea September 1981, where the biomass increased 18-fold in sledge samples when compared to previous studies (8).

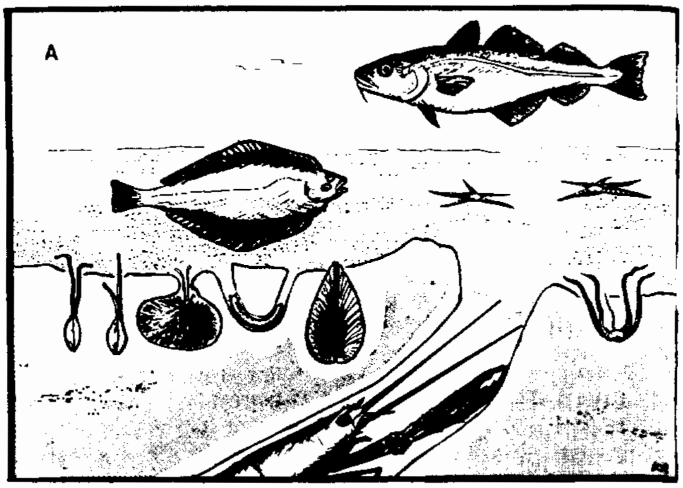
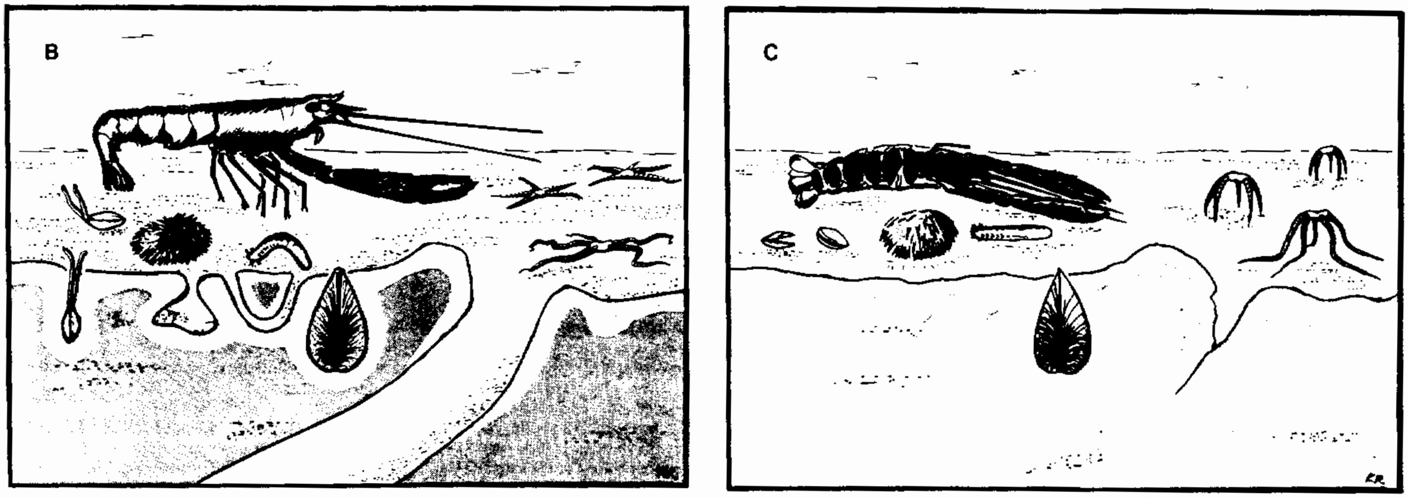


Figure 14. Some dominant benthic macrofaunal species and fish in the Kattegat in normoxia (A), in an oxygen saturation of 15% (B), and in an oxygen saturation of 5 to 10% (C). Dark grey sediment indicates anoxic conditions and light grey sediment oxic conditions. Drawing: K. Rosenberg.

GENERAL DISCUSSION

Over, approximately, the last 15 years, drastic changes have been observed in the species composition of macroalgae in the Laholm Bay and adjacent areas. This is partly a response to the increased use of commercial nitrogen fertilizers on agricultural land close to these areas and of increased nitrogen leakage from forest land. From 1960 to 1975, the supply of fertilizers on farmland more than doubled, from 40 to approximately 90 kg^{-1} ha (61). The changed algal composition is likely to have altered the fauna, which were associated

Figure 13. Benthic invertebrates (*Echinocardium cordatum, Brissopsis lyrifere, Cucumaria elongata, Asterias rubens, Ophiura* spp., *Amphiura chiajei, A. filiformis, Polyphysia crassa, Aphrodite aculeata, Nephtys* spp., *Macropipus* spp., *Pagurus* spp. and *Priapulus caudatus*) caught during demersal fish trawling in September 1988 in the SE Kattegat. About 150 kg benthic fauna were caught in a 30-minute sample, whereas the demersal fish amounted to 2.5 kg. Oxygen concentration in the bottom water was measured to be 1 ml · L^{-1} (15% saturation) at this station. Photo: Leif Pihl.



with the earlier dominants, *Fucus* spp. However, the role of the Laholm Bay as an important nursery area for flatfish does not seem to have been reduced so far. On the comparatively more protected Danish side of the Kattegat, however, negative effects are obvious (47, 62).

The mortality of suspension-feeding bivalves, which in some seasons was high and widespread in Laholm Bay (7), has not been proved to be linked to hypoxia, although this is the most likely explanation. Better environmental conditions for the suspension feeders could have resulted in higher population densities and higher total assimilation of the phytoplankton biomass. This would have reduced the effects of eutrophication more than the suspension feeders do today.

Primary production in the outer Laholm Bay was 25 to 30% higher in the 1980s compared to production measurements made in the Kattegat in the 1970s (5). The annual primary production in the outer Laholm Bay (approximately 135 g $C \cdot m^{-2}$) is not high, however, compared to other nutrient-rich areas. The strong biological effects observed in the Kattegat are due to the fact that organic material, including phytoplankton biomass, will be deposited and decomposed below the strong halocline where ventilation is poor.

The first observation of hypoxia in autumn was made in 1980, although sporadic reports by fishermen of dead fish in catches suggest that minor effects of hypoxia occurred earlier. In 1988, the area affected by oxygen deficiency was larger than ever and fish and Norway lobster were either absent or found in low quantities over approximately 5600 km^2. This has had large negative socioeconomic effects for Danish and Swedish fishermen.

During at least 4 months in 1988 no fishing was carried out in the area mentioned above and the future economic feasibility of fishing is uncertain. The local fishermen have moved north to the Skagerrak or east to the Baltic. The environmental effects obvious in the Kattegat must be considered strong warning signals of the rapid spread of eutrophication, and that the first areas to be affected are coasts and stratified waterbodies (1).

Eutrophication-induced organic enrichment and effects of hypoxia on the benthic environment including demersal fish are depicted in Figure 14 and are described in four phases, although deoxygenation is a continuous process. We have selected some of the conspicuous species in the Kattegat as actors. The effects of hypoxia on marine life is dependent both on concentration and duration of exposure. Here, each phase of hypoxia is thought to last 1 to 2 weeks, i.e. oxygen concentrations decrease slowly.

The first phase is normoxia (normal oxygen concentration) (70–100%) (Fig. 14A a dab, a cod, and a Norway lobster in his burrow). Other animals are, from the left to right, 2 *Abra alba, Echinocardium cordatum, Polyphysia crassa, Arctica islandica*, 2 *Ophiura albida* and *Amphiura filiformis*. The light-dark structure of the sediment indicates oxygenation.

In phase 2 (Fig. 14B), the oxygen concentration has dropped to 15% saturation. Here the fish have left the area and the lobster has emerged from its burrow. The lobster is immobile, has stopped feeding and stretches its body upwards to reach water with a slightly higher oxygen content. Some of the infaunal species have left their protected positions in the sediment and lie exposed on the seabed. No active predators are in evidence. The oxygenated parts of the sediment have decreased.

In phase 3 (Fig. 14C) the oxygen concentration has decreased further to 5 to 10% saturation. The lobster, *Abra alba* and *Echinocardium cordatum* are dead and *Polyphysia crassa, Ophiura albida* and *Amphiura filiformis* are dying. The ophiuroids are immobile and elevating their central disk from the sediment surface. *Arctica islandica* is still in the sediment with open valves. The oxygenation of the sediment has decreased even further.

Phase 4 (not depicted) occurs when the oxygen concentration is below 5%, or if this level of saturation continues for some weeks. Most, or perhaps all macrofauna have died. Some meiofaunal species will still be present (63).

As both fish and lobster disappear or die at higher oxygen concentrations than many of the tolerant infauna species, a temporary steady state in abundance of these species can be expected, due to less predation and less bulldozing by the lobsters disturbing the sediment (64). In a longer perspective, and if no reduction of nutrients to the sea occurs, even the tolerant infauna will most probably be affected. With a reduction of the benthic fauna, a decrease in the amount of nitrogen that could leave the marine system by denitrification will follow, as the presence of macrofauna increases the denitrification process severalfold (65, 66). Thus, eutrophication might be a self-accelerating process and could spread to other areas with restricted ventilation of the bottom, even if the input of nitrogen is kept at the present level.

We have described changes in the marine benthic ecosystem, i.e. of the macroalgae communities, the benthic fauna communities and of the demersal fish density. Although some signs of eutrophication effects were observed about 15 years ago, it was not until 1980 that scientists realized that these first signals could constitute a warning, indicating aggravated ecological effects. However, at that time no one anticipated that the effects could be so drastic and rapid and affect fisheries to such a large degree.

Can the clock be turned back? Marine ecosystems are extremely resilient, but when the effects are caused by anthropogenic inputs, those have to be reduced before recovery can occur. Looking back to the long-term changes shown in Figure 4 and to the discharge figures for nitrogen to the Laholm Bay (61), it has been suggested by the scientists in this multidisciplinary research project that the input of nitrogen to the Kattegat must be reduced by approximately 50% before recovery can be initiated (67).

Based on scientific experience from the Kattegat, we anticipated that eutrophication in the near future will cause far-reaching and unexpected effects in coastal areas near urban conglomerations. This is likely to happen particularly in stratified coastal waters where the water flushing rate is too low to allow rapid dilution of nutrients in the surface and/or continuous oxygenation of the bottom water. In view of the experience from the Kattegat study, we hope that immediate measures will be taken to reduce the input of nutrients to all marine areas, and especially to those susceptible to eutrophication.

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Article

Sture Hansson and
Lars G. Rudstam

Eutrophication and Baltic Fish Communities

The total fish catch in the Baltic has increased tenfold in the past fifty years. During the past 20 years catches have doubled. Quantitatively, herring is the dominant species. Photo: G. Aneer.

The discharge of nutrients to the Baltic Sea has increased considerably during the 20th century. There are several indications that this eutrophication has affected the fish community. Changes in species composition have been reported from coastal areas, e.g. local increases in the abundance of pikeperch and decreases in whitefish. Total fish catches, dominated by herring, sprat, and cod, have increased tenfold in the past fifty years and doubled in the last twenty-five years. This increase is mainly due to intensified fishing, but possibly also to eutrophication and decreased fish predation by seals.

INTRODUCTION

Our knowledge of the effects of eutrophication on fish communities is based primarily on observations in lakes. A limited increase in nutrient loading of oligotrophic lakes often increases food production and favors most fish species. Continuous fertilization has negative effects on salmonids, while percids and especially cyprinids benefit (e.g. 1–5). The negative effects on salmonids have been explained mainly by eutrophication induced decreases in the oxygen concentration in the deeper, colder waters preferred by these species (6). There is no similar generalization of the effects of eutrophication on marine fish communities. Comparisons between upwelling zones, coastal areas and open sea areas, however, show a positive correlation between primary production and fish production (7–10).

Discharges of nutrients to the Baltic Sea have increased considerably, from a calculated 10 000 tons of phosphorus and 300 000 tons of nitrogen annually at the end of the 19th century to around 80 000 and 1 200 000 tons, respectively, today (11). The effects of these discharges are increased nutrient concentrations and probably increased phytoplankton production, indicated by changes in the vertical distribution of macrophytes, increased biomasses of benthic macrofauna above the halocline and, frequently, low oxygen levels and decreased deep benthos. These effects on organisms other than fish are discussed in other articles in this issue of Ambio and our contribution is to briefly review observed and suggested effects of eutrophication on Baltic fish communities.

In the brackish Baltic Sea, the fish fauna is a mixture of marine and freshwater species. In offshore areas, marine species such as herring, sprat, and cod (*Clupea harengus* L., *Sprattus sprattus* (L.), and *Gadus morhua* L.) dominate, while a mixture of marine and freshwater species inhabit coastal areas (12). Effects of eutrophication on these fish populations could be of great economic and social significance, since the Baltic Sea supports both an intensive commercial fishery, with annual catches of almost one million tons, and a large recreational and household fishery.

GENERAL EFFECTS ON THE BALTIC FISH COMMUNITY

The total fish catch in the Baltic has increased tenfold in the past fifty years (Fig. 1). During the last twenty-five years catches have doubled, to almost one million tons. Three marine species, cod, sprat, and herring constitute 80–90% of the total catch (13–14). The most important reasons for the increased catches are intensified fishing and new, more effective, techniques. Another contributing factor could be decreased predation by seals. At the turn of the century, seals were abundant and their annual fish consumption has been estimated at 300 000 tons, i.e. 30–40% of today's human catches. Since then, hunting and pollutants have reduced the populations drastically, and today their annual consumption is only about 10 000 tons (15). Increased fish production can also be due to natural (16) or anthropogenic (17–18) eutrophication. Recently, Nehring et al. (19) estimated that the fish biomass had increased by 5% during the period 1973–1984. The effects of eutrophication on fish may, however, also be negative. Oxygen depletion, caused by degradation of organic substances, may force the fish to abandon large areas and kill their prey organisms (20–21).

The effects of eutrophication are reviewed separately for commercially dominant species (cod, herring, and sprat), followed by observations on freshwater species in coastal areas. It must, however, be recalled that fish populations normally fluctuate considerably, that fishery technology has changed drastically during the second part of the 20th century, and that quantitative data on Baltic fish stocks are available only since the beginning of the 1970s. In addition to this, the Baltic Sea is an open system, with exchange of both fish and fishing fleets with neighboring areas. The Rügen herring, for example, spawn in the southern Baltic but are caught also in Kattegat, Skagerrak, and the North Sea (22) and its abundance and catches in the Baltic are thus influenced by environmental conditions and fishing outside the Baltic. Catches in the Baltic are also indirectly influenced by the fish abundance in Kattegat, Skagerrak, and the North Sea. If catches are small in these areas, fishing activity may increase in the Baltic. Thus, the changes discussed below must not be used as evidence of eutrophication, but only as possible effects of eutrophication.

COD

A possible result of the eutrophication of the Baltic Sea is that primary production has increased, as has oxygen depletion in deep waters (23). This aspect of eutrophication could be particularly negative to cod, since their reproduction in the Baltic is restricted to areas with salinities above 10‰, which are found mainly in five deep basins (12). Decreased reproductive success and a decline in the cod stock is thus an anticipated result of eutrophication. Using regression analysis and data from 1969–1983, Berner et al. (24)

supported this by showing statistically significant positive effects of oxygen concentration in deep waters, but weak effects of temperature and salinity on the recruitment of cod.

Oxygen levels can also influence the occurrence of adult cod. Low abundances of cod have been reported from polluted coastal areas where oxygen levels were low (25–26).

Negative effects on cod are particularly problematic for commercial fishery, since cod is more valuable than herring and sprat. Also, there are no other piscivore species that could replace cod as a top predator in the open Baltic.

HERRING

In contrast to cod, herring reproduces along the coast of the entire Baltic and spawns on littoral vegetation. In this zone, longer periods of oxygen deficiency are unlikely, but if vegetation is dense short periods with low concentrations can develop during the night. Aneer (27) concluded that such an oxygen deficiency has only limited effects on the survival of herring eggs, but that filamentous brown algae may produce exudates that are toxic to the eggs. Increased distribution and biomass of these algae, as a result of eutrophication (23), could thus affect the herring populations by increasing the mortality of their eggs.

Eutrophication may also influence the distribution of herring. Berner et al. (24, 25) explained changes in the occurrence of adult herring in parts of the southern Baltic by low oxygen levels induced by pollution, and in the most polluted areas outside the city of Helsinki, Finland, herring has disappeared (28–30). However, hydroacoustic data from a eutrophied bay and a nearby reference area in the northern Baltic proper, showed higher abundance of pelagic fish, mainly herring, in the eutrophied area (Fig. 2).

As already mentioned, catches of herring have increased considerably, and fishing is now considered one of the limiting factors for the population (14, 31–32). That this increase has been at least partly possible because of eutrophication has been suggested by several authors (e.g. 16, 33–34).

In some areas, the growth rate and condition (weight/length relationship) of herring has increased during the last 20 years (12, 35–38). A considerable increase in growth was, however, observed already in the 1940s (33, 39), when anthropogenic nutrient discharges were much smaller than today, and decreased growth has also been recently reported (40, 41). The effects of eutrophication on the growth of herring are probably complex because of ontogenetic shifts in diet. Young herring feed mainly on zooplankton while older fish, to a large extent, feed on benthic and epibenthic crustaceans. Thus, the growth of small fish may be stimulated by increased zooplankton production, while larger herring may grow more slowly if oxygen deficiency in bottom waters decreases the abundance of amphipods and mysids (42). It is, therefore, difficult to state definitely whether the recently observed growth changes result from eutrophication.

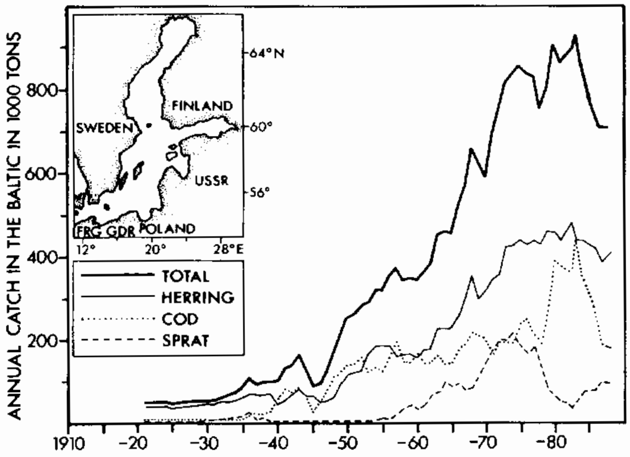

Figure 1. Catches of herring, sprat, and cod in the Baltic Sea. (Subdivisions 22–32 according to the International Council for the Exploration of the Sea ICES). Data from the Swedish National Board of Fisheries.

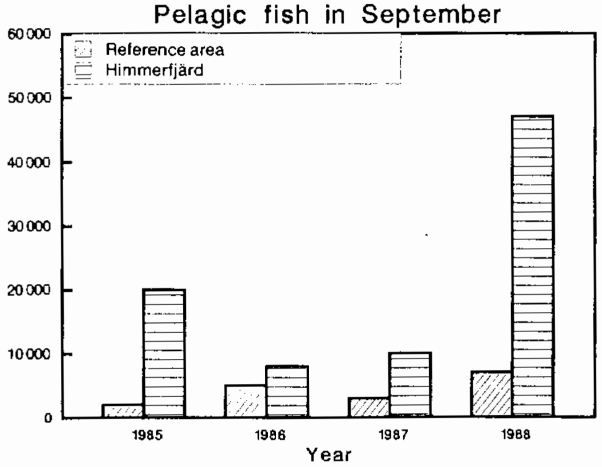

Figure 2. Hydroacoustic abundances of pelagic fish in the eutrophied Himmerfjärd and a nearby reference area in the northern Baltic proper. The late summer (September) abundances presented are dominated by young-of-the-year and one-year-old herring (54).

SPRAT

There was a drastic increase in the catches of sprat from the mid-1950s to the mid-1970s (Fig. 1). It has been suggested that this increase was made possible, at least partly, as a result of eutrophication (16, 43, 44). Since the mid-1970s however, catches have decreased significantly, probably due to a combination of fishing and heavy predation by an unusually large stock of cod (14).

Compared to herring, sprat is a more specialized zooplankton feeder. As a consequence, eutrophication-induced increase in zooplankton production is more likely to have increased the growth of sprat than herring (see above). Increases in sprat growth have also been observed (6, 45), as has a rise in fat content (46).

FRESHWATER SPECIES

The most detailed information with regard to effects of eutrophication on archipelago fish communities comes from the area off Helsinki, Finland. There, the changes in species composition in the eutrophied area are similar to those observed in lakes. Trout, whitefish, burbot, ide, and pike have decreased in abundance, while roach, white bream, and ruffe have increased (*Salmo trutta* L., *Coregonus* spp., *Lota lota* (L.), *Leuciscus idus* (L.), *Esox lucius* L. and *Rutilus rutilus* (L.), *Blicca bjoerkna* (L.), *Gymnocephalus cernua* (L.) respectively) (28, 30).

Pikeperch (*Stizostedion lucioperca* (L.) has frequently been reported to be favored by eutrophication in lakes. Since the 1950s catches of pikeperch have increased significantly along the Finnish coast (47–49) and in regions off the coast of the German Democratic Republic (50). According to local Swedish fishermen, the species has also become more abundant in the Stockholm archipelago and in the bays of Himmerfjärden and Bråviken south of Stockholm. In the early 19th century, pikeperch was rare in the Himmerfjärd bay and generally small in size (51), while today at least 10 tons are caught annually (52). In all these cases, the increases have been associated with eutrophication.

In contrast to pikeperch, whitefish has been reported to be negatively affected by eutrophication in lakes, and catches of whitefish have decreased in the eutrophied area off Helsinki. According to Lehtonen (49, 53) catches have decreased even in other regions along the Finnish coast as a result of eutrophication. Swedish fishery statistics show that whitefish catches in the Stockholm region have decreased steadily since the middle of the 1950s. In less eutrophied regions no such tendency has been noted (6).

CONCLUSIONS

From comparisons with lakes, it is clear that eutrophication of the magnitude of that in the Baltic is likely to have influenced the fish populations. Changes in species composition similar to the ones associated with eutrophication in lakes have also been observed in some coastal areas. However, lack of long time series that study the size of the fish stocks, their age composition, and individual growth rates prevents definite conclusions being reached about large-scale eutrophication effects on Baltic fish stocks. Changes in temperature and salinity may also have influenced the fish, as discussed in a more extensive review on effects of eutrophication on Baltic fish communities (6). There are some indications of more basin-wide effects, e.g. changes in species composition, increases in some fish stocks, and enhanced growth.

Of the most commercially important species, cod is probably the species most negatively affected by eutrophication. For successful reproduction in Baltic deep waters cod needs relatively high oxygen concentrations. With increased eutrophication the frequency of low concentrations of oxygen, or anoxia, increases in these areas. For herring, the effects of continued eutrophication could be both positive and negative. Increased densities of filamentous brown algae may have negative effects on reproductive success. If the production of zooplankton is increased, this could increase growth and survival of larvae and young fish, but impaired oxygen conditions in bottom waters could decrease the production of benthic and epibenthic crustaceans, which are important prey for larger herring. Sprat would probably increase in response to increased eutrophication, since it has pelagic eggs and feeds mainly on zooplankton. In addition, its natural mortality rate is likely to decrease if the abundance of cod decreases.

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Since 1984, both authors of this paper have been working together on the effects of eutrophication on pelagic fish communities in the Himmerfjärd Bay in the northern Baltic proper. Both obtained their doctoral degrees at the Department of Zoology, University of Stockholm. Their present addresses: Sture Hansson, Askö Laboratory, University of Stockholm, S-106 91 Stockholm, Sweden and Lars G. Rudstam, Center for Limnology, University of Wisconsin, Madison, WI 537 06, USA.

Article

Fredrik Wulff, Anders Stigebrandt and Lars Rahm

Nutrient Dynamics of the Baltic Sea

A prerequisite for understanding the large-scale eutrophication of the Baltic Sea is an understanding of the factors responsible for regional and long-term variations of nutrients. This article summarizes recent studies on the changes in overall total amounts and the distribution pattern of nutrients. The total amounts of phosphorus and nitrogen have increased over the last few decades. On the other hand, silicate levels have been decreasing, indicating a higher net primary production and sedimentation of diatoms. A series of models has been used to test our present understanding of the critical processes controlling nutrient and oxygen conditions. It is shown that a few morphometric factors are essential, like shallow sill depth at the entrance of the estuarine-like sea and shallow mean depth. It is also shown that phosphorus, nitrogen and silicate differ in terms of residence times and their response to external loading. Some of the critical processes controlling the fate of these nutrients take place in the sediments. A model showing the long-term behavior of this system in response to external loading illustrates the importance of these processes.

INTRODUCTION

The Baltic Sea is surrounded by seven highly industrialized countries, inhabited by over 70-million people. It lies close to the main centers of air pollution in central Europe. The drainage area is about four times as large as the surface area of 373 000 km^2. During the present century the Baltic has been subject to an increased nutrient load and signs of large-scale eutrophication are now obvious (1). Inherent properties, including a relatively small mean depth and narrow, shallow connections to the sea, seem to make the Baltic Sea particularly vulnerable to anthropogenic influences.

The purpose of the present paper is to present those features of the Baltic Sea which we now understand to be of major importance for nutrient dynamics. Since topography, vertical circulation including water exchange with the external areas and density stratification as well as biogeochemical transformations between different organic and inorganic nutrient forms are all factors of importance, the paper will cover a broad scientific field. It should be stressed that we do not review the vast literature on the Baltic Sea. For broader reviews the reader is referred to Voipio (2), Melvasalo et al. (3), and Lassig (4).

After a description of the large-scale distribution, and the seasonal and long-term variations of different important state variables, we will focus upon physical and biogeochemical processes which are recognized to be important for nutrient dynamics. We will try to illustrate the principal behavior of the nutrient distributions with regard to internal dynamics and external loading. We will also discuss the internal sinks of nutrients which actually regulate the equilibrium concentrations in different parts of the system for a given load. A discussion of how changes in the concentration of one nutrient may affect the concentrations of other nutrients is also presented.

In addition, two different models for the nutrient dynamics, which have been developed recently, are described. The main use of these models has been to synthesize our present knowledge and to suggest and design new research projects. The models are of quite different types. One is a highly simplified, explorative box model that concentrates on describing sources and sinks of nitrogen, phosphorus, silicate, and humic substances for the three subareas of the Baltic Sea. The other model describes the biogeochemical and hydrographic processes controlling the nitrogen cycle in a detailed mechanistic, horizontally integrated model of the Baltic proper, which has a high vertical and temporal resolution. We conclude with a discussion of how the actual type of large-scale vertical circulation of estuaries, as induced by buoyancy fluxes to the system and modified by the topography at the entrance, affects overall nutrient budgets.

PHYSICAL CIRCULATION OF THE BALTIC SEA

The Baltic Sea features three major basins, the Bothnian Bay, the Bothnian Sea and the Baltic proper (Figs 1, 6). The water exchange of this large brackish estuarine-like sea with Kattegat and the North Sea takes place through the narrow and shallow Danish Sounds. The two northerly basins are characterized by low salinities (1–3 and 3–7 PSU, Practical Salinity Unit, respectively) and rather weak vertical salinity stratifications, although strong thermoclines usually develop during the summer. The subarctic climate in these regions leads to extensive ice coverage, frequently for almost half the year. The Baltic proper, on the other hand, is normally only partially ice-covered. It has a strong permanent halocline at about 60-meters depth separating the surface water (salinity 7–8 PSU) from the deep water (salinity 9–20 PSU). The latter is formed by salty water entering through the Danish Sounds under substantial entrainment of water from the surface layer of the Baltic Sea. Depending on the supplies of organic matter and oxygen, anoxic conditions can develop even rather high up in the deep water with consequences for both biota and nutrient recycling.

To a large degree, the salinity distribution in the Baltic Sea is determined by the topography of the mouth and by the large net freshwater supply (on the average about 15 000 $m^3 \cdot s^{-1}$). The water exchange through the Danish Sounds is mainly driven by the sea-level difference between the southern Kattegat and the southwestern Baltic Sea. Thus, barocline pressure effects, due to the presence of waters of different densities, are of minor importance for the magnitude of the water exchange. Due to the small ratio between the vertical surface area of the Danish Sounds and the horizontal surface area of the Baltic Sea, high frequency sea-level fluctuations in the Kattegat are strongly dampened by the Sounds. For this reason, co-oscillating tides of high frequencies are rare in the Baltic Sea (5, 6).

The inflow of dense water through the Danish Sounds is intermittent (5, 7). The greatest flow events occur in autumn and winter when the low-frequency sea-level variability in Kattegat that is related to the weather is at its maximum (6). As a result, the depth to the halocline in the shallow (about 45 meters) Arkona Basin, near the entrance, is variable (20–40 meters), as is the salinity below the halocline (10–20 PSU). The dense water is believed to form a hydraulically controlled (in the rotational sense) "pool" in the Arkona Basin (37). the statistics of the outflow of dense water from the Arkona pool, and further into the Baltic Sea, are shown in Figure 2. Measurements of the actual flow of dense water in the Bornholm Channel have been carried out by Walin (8).

The large-scale vertical circulation in the Baltic Sea is illustrated in Figure 3. During

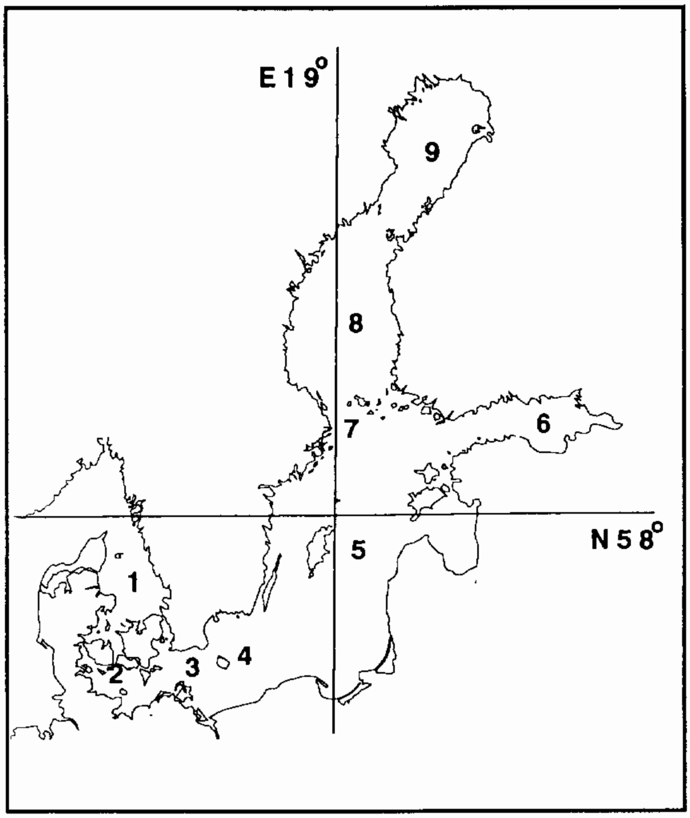


Figure 1. Map of the Baltic Sea showing the different areas: 1-Kattegat, 2-Belt Sea, 3-Arkona Basin, 4-Bornholm Basin, 5-Eastern Gotland Basin, 6-Gulf of Finland, 7-Åland Sea, 8-Bothnian Sea and 9-Bothnian Bay. The area between the Åland Sea and the Belt Sea constitutes the Baltic proper.

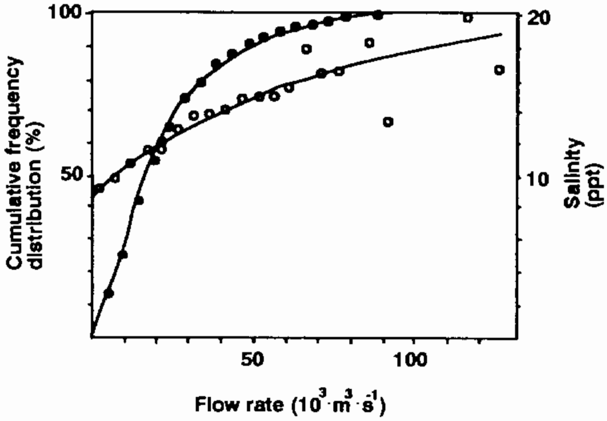
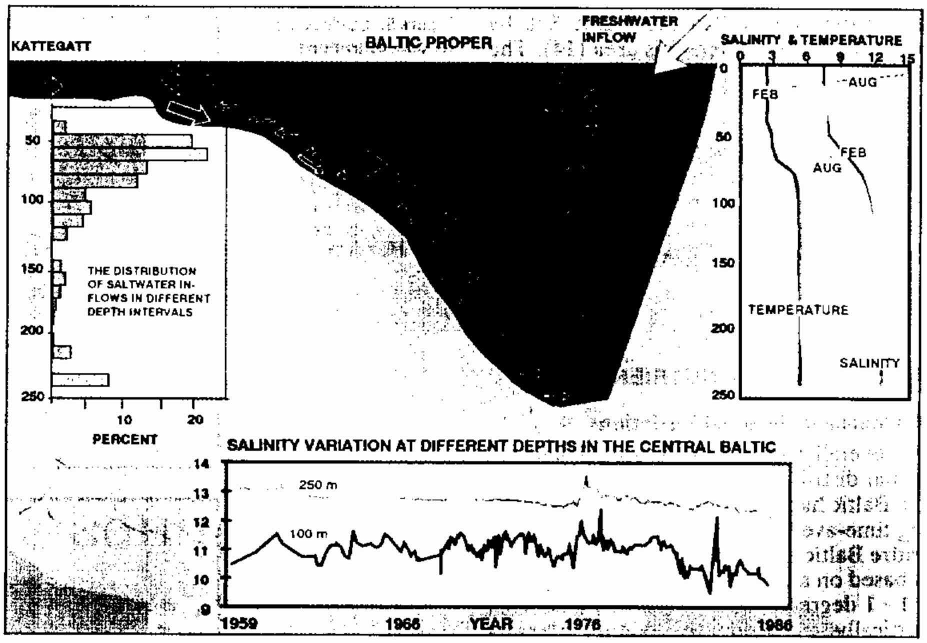


Figure 2. Inflow statistics determined from historical hydrographical data from the Arkona Basin (37). Cumulative frequency distribution (solid dots) of volume flows and observed mean salinity of inflows (open circles) for different classes of volume flows.

Figure 3. Sketch of the large-scale vertical circulation of the Baltic proper (central panel). The right panel illustrates typical vertical summer and winter profiles of salinity (S) and temperature (T) in the central Eastern Gotland Basin. The computed distribution of interlaying of "new" deepwater as a function of depth in the Baltic proper (9) is shown in the left panel. The bottom panel shows long-term variations at 100 and 250 meters in the Eastern Gotland Basin.



the descent of the dense water from the Kattegat into the different basins, ambient water is entrained. The dense current thus becomes lighter and, subsequently, attains the same density as the ambient water. The inflowing water is interlayed with the basin water at the depth where this occurs. The calculated distribution of the depth of interlaying (9), shows that most of the inflowing water is interlaying in and just below the halocline. Inflows to depths greater than about 130 meters seem to be quite intermittent, as illustrated by the less variable salinity at 250 meters compared to 100 meters in the long-term records from the central Gotland basin (Fig. 3). Since most of the oxygen supplied to the deep water comes with the dense bottom current, it is understandable that the lower deep water may become anoxic while the upper deep water and the halocline are always well flushed and therefore well oxygenated. It is important to realize that even dramatic changes in concentrations of salt and nutrients in the deep basins do not necessarily mean a significant change in overall budgets, since these basins constitute less than 5% of the total volume of the Baltic proper (10). Calculations of the total oxygen consumption below the halocline by Rahm (11) show that the input of oxygen with new saltwater would be sufficient to keep the deep basins well oxygenated if the water was mixed well. The average calculated oxygen consumption corresponds to earlier sedimentation estimates of organic matter (12).

Figure 3 also shows typical summer (August) and winter (February) vertical profiles of salinity and temperature in the Baltic proper. The summer temperature is at maximum in the well-mixed surface layer, typically some 10 m thick, above the seasonal thermocline. In the depth interval from about 30 meters and down to the main halocline, one finds old "winter water" with a temperature close to the temperature of maximum density (≈2.5°C). The properties of this water mass are formed during the winter cooling and are retained until the following autumn when the seasonal thermocline deepens due to cooling and wind-driven erosion of the underlying water. Below the main halocline, in deep water, the temperature is typically about 5–6°C. Salinity is almost homogeneous above the main halocline, with a weak minimum in the surface-mixed layer in the summer due to the supply of

Article

Fredrik Wulff, Anders Stigebrandt and Lars Rahm

Nutrient Dynamics of the Baltic Sea

A prerequisite for understanding the large-scale eutrophication of the Baltic Sea is an understanding of the factors responsible for regional and long-term variations of nutrients. This article summarizes recent studies on the changes in overall total amounts and the distribution pattern of nutrients. The total amounts of phosphorus and nitrogen have increased over the last few decades. On the other hand, silicate levels have been decreasing, indicating a higher net primary production and sedimentation of diatoms. A series of models has been used to test our present understanding of the critical processes controlling nutrient and oxygen conditions. It is shown that a few morphometric factors are essential, like shallow sill depth at the entrance of the estuarine-like sea and shallow mean depth. It is also shown that phosphorus, nitrogen and silicate differ in terms of residence times and their response to external loading. Some of the critical processes controlling the fate of these nutrients take place in the sediments. A model showing the long-term behavior of this system in response to external loading illustrates the importance of these processes.

INTRODUCTION

The Baltic Sea is surrounded by seven highly industrialized countries, inhabited by over 70-million people. It lies close to the main centers of air pollution in central Europe. The drainage area is about four times as large as the surface area of 373 000 km^2. During the present century the Baltic has been subject to an increased nutrient load and signs of large-scale eutrophication are now obvious (1). Inherent properties, including a relatively small mean depth and narrow, shallow connections to the sea, seem to make the Baltic Sea particularly vulnerable to anthropogenic influences.

The purpose of the present paper is to present those features of the Baltic Sea which we now understand to be of major importance for nutrient dynamics. Since topography, vertical circulation including water exchange with the external areas and density stratification as well as biogeochemical transformations between different organic and inorganic nutrient forms are all factors of importance, the paper will cover a broad scientific field. It should be stressed that we do not review the vast literature on the Baltic Sea. For broader reviews the reader is referred to Voipio (2), Melvasalo et al. (3), and Lassig (4).

After a description of the large-scale distribution, and the seasonal and long-term variations of different important state variables, we will focus upon physical and biogeochemical processes which are recognized to be important for nutrient dynamics. We will try to illustrate the principal behavior of the nutrient distributions with regard to internal dynamics and external loading. We will also discuss the internal sinks of nutrients which actually regulate the equilibrium concentrations in different parts of the system for a given load. A discussion of how changes in the concentration of one nutrient may affect the concentrations of other nutrients is also presented.

In addition, two different models for the nutrient dynamics, which have been developed recently, are described. The main use of these models has been to synthesize our present knowledge and to suggest and design new research projects. The models are of quite different types. One is a highly simplified, explorative box model that concentrates on describing sources and sinks of nitrogen, phosphorus, silicate, and humic substances for the three subareas of the Baltic Sea. The other model describes the biogeochemical and hydrographic processes controlling the nitrogen cycle in a detailed mechanistic, horizontally integrated model of the Baltic proper, which has a high vertical and temporal resolution. We conclude with a discussion of how the actual type of large-scale vertical circulation of estuaries, as induced by buoyancy fluxes to the system and modified by the topography at the entrance, affects overall nutrient budgets.

PHYSICAL CIRCULATION OF THE BALTIC SEA

The Baltic Sea features three major basins, the Bothnian Bay, the Bothnian Sea and the Baltic proper (Figs 1, 6). The water exchange of this large brackish estuarine-like sea with Kattegat and the North Sea takes place through the narrow and shallow Danish Sounds. The two northerly basins are characterized by low salinities (1–3 and 3–7 PSU, Practical Salinity Unit, respectively) and rather weak vertical salinity stratifications, although strong thermoclines usually develop during the summer. The subarctic climate in these regions leads to extensive ice coverage, frequently for almost half the year. The Baltic proper, on the other hand, is normally only partially ice-covered. It has a strong permanent halocline at about 60-meters depth separating the surface water (salinity 7–8 PSU) from the deep water (salinity 9–20 PSU). The latter is formed by salty water entering through the Danish Sounds under substantial entrainment of water from the surface layer of the Baltic Sea. Depending on the supplies of organic matter and oxygen, anoxic conditions can develop even rather high up in the deep water with consequences for both biota and nutrient recycling.

To a large degree, the salinity distribution in the Baltic Sea is determined by the topography of the mouth and by the large net freshwater supply (on the average about 15 000 m$^3 \cdot$ s^{-1}). The water exchange through the Danish Sounds is mainly driven by the sea-level difference between the southern Kattegat and the southwestern Baltic Sea. Thus, baroclinc pressure effects, due to the presence of waters of different densities, are of minor importance for the magnitude of the water exchange. Due to the small ratio between the vertical surface area of the Danish Sounds and the horizontal surface area of the Baltic Sea, high frequency sea-level fluctuations in the Kattegat are strongly dampened by the Sounds. For this reason, co-oscillating tides of high frequencies are rare in the Baltic Sea (5, 6).

The inflow of dense water through the Danish Sounds is intermittent (5, 7). The greatest flow events occur in autumn and winter when the low-frequency sea-level variability in Kattegat that is related to the weather is at its maximum (6). As a result, the depth to the halocline in the shallow (about 45 meters) Arkona Basin, near the entrance, is variable (20–40 meters), as is the salinity below the halocline (10–20 PSU). The dense water is believed to form a hydraulically controlled (in the rotational sense) "pool" in the Arkona Basin (37). the statistics of the outflow of dense water from the Arkona pool, and further into the Baltic Sea, are shown in Figure 2. Measurements of the actual flow of dense water in the Bornholm Channel have been carried out by Walin (8).

The large-scale vertical circulation in the Baltic Sea is illustrated in Figure 3. During

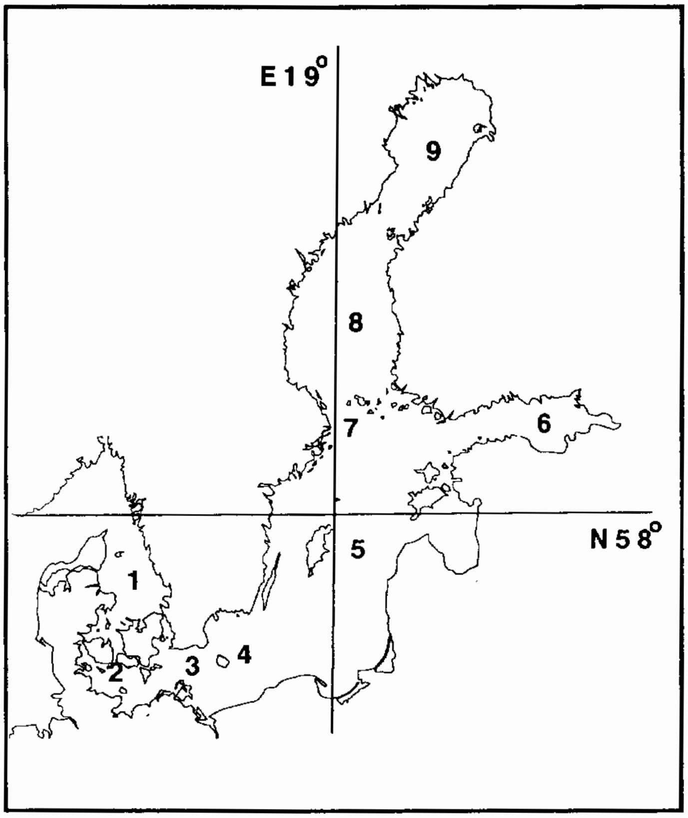


Figure 1. Map of the Baltic Sea showing the different areas: 1-Kattegat, 2-Belt Sea, 3-Arkona Basin, 4-Bornholm Basin, 5-Eastern Gotland Basin, 6-Gulf of Finland, 7-Åland Sea, 8-Bothnian Sea and 9-Bothnian Bay. The area between the Åland Sea and the Belt Sea constitutes the Baltic proper.

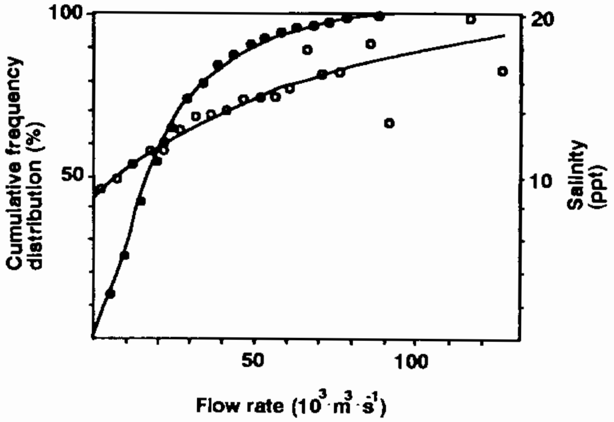
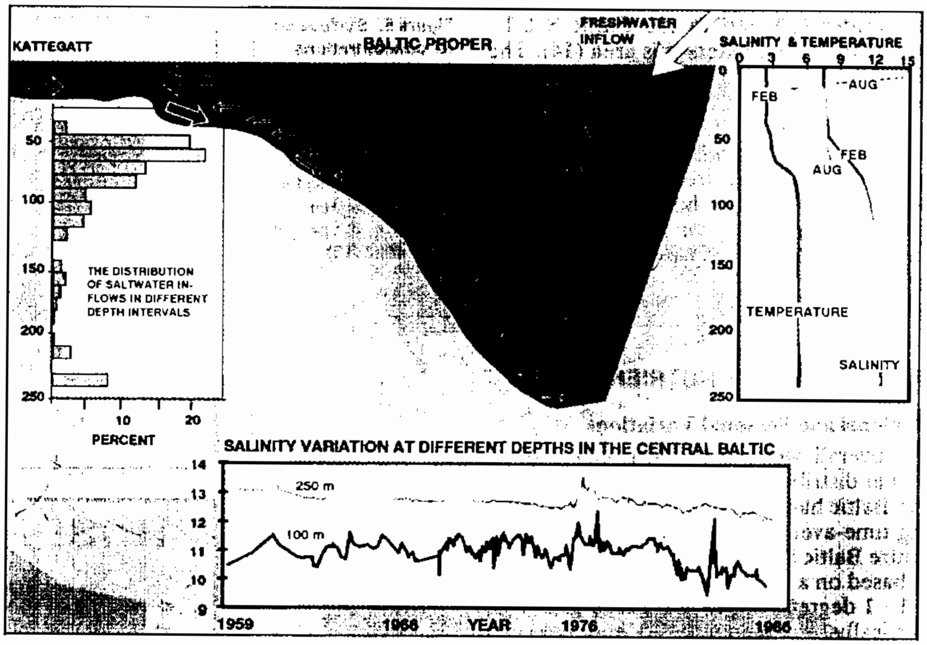


Figure 2. Inflow statistics determined from historical hydrographical data from the Arkona Basin (37). Cumulative frequency distribution (solid dots) of volume flows and observed mean salinity of inflows (open circles) for different classes of volume flows.

Figure 3. Sketch of the large-scale vertical circulation of the Baltic proper (central panel). The right panel illustrates typical vertical summer and winter profiles of salinity (S) and temperature (T) in the central Eastern Gotland Basin. The computed distribution of interlaying of "new" deepwater as a function of depth in the Baltic proper (9) is shown in the left panel. The bottom panel shows long-term variations at 100 and 250 meters in the Eastern Gotland Basin.



the descent of the dense water from the Kattegat into the different basins, ambient water is entrained. The dense current thus becomes lighter and, subsequently, attains the same density as the ambient water. The inflowing water is interlayed with the basin water at the depth where this occurs. The calculated distribution of the depth of interlaying (9), shows that most of the inflowing water is interlaying in and just below the halocline. Inflows to depths greater than about 130 meters seem to be quite intermittent, as illustrated by the less variable salinity at 250 meters compared to 100 meters in the long-term records from the central Gotland basin (Fig. 3). Since most of the oxygen supplied to the deep water comes with the dense bottom current, it is understandable that the lower deep water may become anoxic while the upper deep water and the halocline are always well flushed and therefore well oxygenated. It is important to realize that even dramatic changes in concentrations of salt and nutrients in the deep basins do not necessarily mean a significant change in overall budgets, since these basins constitute less than 5% of the total volume of the Baltic proper (10). Calculations of the total oxygen consumption below the halocline by Rahm (11) show that the input of oxygen with new saltwater would be sufficient to keep the deep basins well oxygenated if the water was mixed well. The average calculated oxygen consumption corresponds to earlier sedimentation estimates of organic matter (12).

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The annual cycles of temperature and salinity above the permanent halocline in the Baltic proper, in response to wind and buoyancy fluxes through the sea surface, were computed by Stigebrandt (13). He showed that the buoyancy fluxes are dominated by heating/cooling for about 10 months of the year. Salinity plays a major role only during the remaining 2 months. Above the main halocline the Baltic proper behaves like an inland lake for the greater part of the year. There is an appreciable flow of salt into the upper layer during some short periods in winter, when the seasonal thermocline reaches the permanent halocline. The latter, which marks the maximum depth of the surface mixed layer, seems to deepen about 10 meters each winter due to wind-driven erosion. It has been found that the seasonal thermocline formed early in the spring may be destroyed during episodes of cold and windy weather (10). The temporary breakdown of the virgin seasonal thermocline explains why phytoplankton may utilize the nutrients down to the main halocline during the spring bloom, although this is deeper than the 20 meters thick photic zone.

The salinity of the deeper parts of the Bothnian Sea is about the same as that in the surface water of the Baltic proper (6–7 PSU). The surface layer is less saline due to the large freshwater supply to the Bothnian Sea and Bay. About 40% of the freshwater supplied to the Baltic Sea by runoff from land enters this area (14). The Bothnian Bay has a salinity in the deeper parts which is about the same as that in the surface waters of the northern Bothnian Sea (about 3 PSU), while surface salinity is still lower due to the freshwater input. The large-scale water exchange between the different basins and with the Kattegat is shown in Figure 4 (15).

DISTRIBUTION OF NUTRIENTS

Regional and Seasonal Variations

An overall view of the seasonal and regional distribution patterns of nutrients in the Baltic has been obtained by interpolating time-averaged concentrations over the entire Baltic Sea. The averaging procedure is based on a partitioning of the Baltic into a 1 · 1 degree longitude-latitude grid. It is vertically separated into 22 depth intervals with a resolution that decreases with increasing depth, corresponding to standard observational depths. Monthly mean values are calculated for those cells which have observations for a specific month. the data used are obtained from the ICES databank in Copenhagen and span the time periods 1972–1976 and 1977–1981.

The beginning of the first time period roughly coincides with the introduction of new and more reliable analytical methods. especially for nitrogen (Stig Fonselius, pers comm.). The choice of 1976–1977 as the pivot for the time series is motivated by the large inflow of deep water during 1976 (see also the salinity variations at 200 meters in Fig. 3), which started a period characterized by higher stability and more stagnant conditions than in the previous period. The interpolation routine applied to the whole Baltic is founded on a partitioning of the Baltic into subareas, following the major basins. The hydrographic conditions inside each subbasin are thus assumed to vary less than between different basins, an assumption supported by a study of the eastern Gotland Basin (16). These subareas, which are further divided by a halocline, are treated separately in the calculations to minimize interpolation errors (see Wulff et al., 17). Therefore, no interpolations over the subarea boundaries are carried out, which can lead to a lack of calculated total amounts for an entire basin during certain months.

Concentrations of total phosphorus, soluble reactive phosphate, total nitrogen, nitrate and silicate have been calculated for each period and month by Wulff and Rahm (18). These variations follow the biological production cycle. The spring bloom and the successive summer blooms reduce the concentrations in the trophogenic layer while the recovery phase becomes discernible in late autumn. Results from two different months, March and

Figure 4. The water exchange (km³ · yr⁻¹) between the Bothnian Sea and the Baltic proper and the Bothnian Bay, respectively and between the Baltic Sea and Kattegat. Also shown is the net freshwater supply to the different subbases (15). The numbers within the boxes represent the volumes of the respective basins (km³).

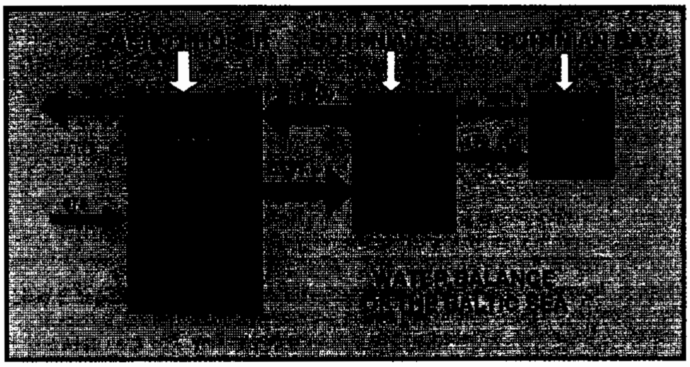
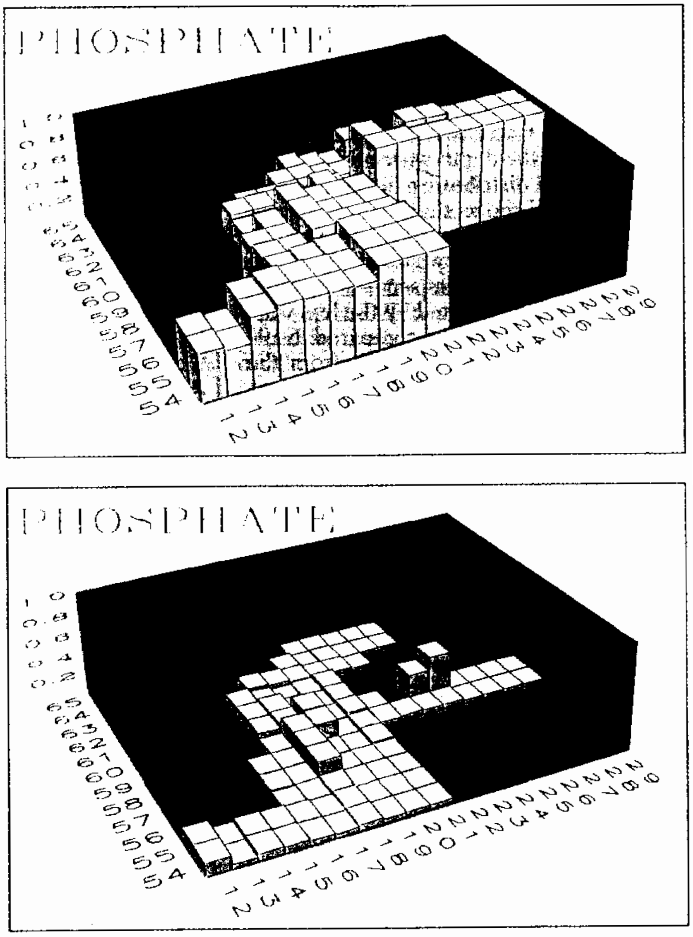


Figure 5. Surface water concentrations (µmol · L⁻¹) of phosphate, nitrate and silicate, averaged for March (upper diagrams) and August (lower diagrams) for each 1 · 1 degree square for the period 1977–1981 (18).



August, for the period 1977–1981, are shown in Figure 5. Only data from offshore stations are used, but the large-scale regional and seasonal variations are evident. In March, which reflects winter conditions prior to the spring diatom bloom, high concentrations of phosphorus are found everywhere except in the Bothnian Bay. In August almost the whole pool has been depleted, only the heavily nutrient-loaded Gulf of Finland has substantial concentrations left. The lack of observations from the inner parts of this region makes the interpolated distribution patterns quite uncertain. It is likely that concentrations will increase further towards Leningrad. Nitrate shows a similar large-scale distribution in time, though high levels are sustained during the whole year in the Bothnian Bay. The concentrations are decreased during the spring by a factor of two in the Bothnian Bay, but are reduced by a factor of about forty in the rest of the Baltic Sea. The gulf of Finland has the highest winter concentration levels but the stored nitrate is consumed during the spring and summer seasons. The oligotrophic, phosphorus-limited Bothnian Bay thus stands in sharp contrast to the more eutrophic Baltic proper. The Bothnian Sea becomes a transition zone between these two extremes. This is reflected in the very high N:P ratio of the Bothnian Bay (compared to the Redfield ratio of 16:1) and the very low ratios of the Baltic proper (18).

Silicate reveals a predominantly north-south gradient due to its main sources in the northern parts of the Baltic drainage area. It shows the same seasonal variation as the other nutrients except in the Bothnian Bay, where low primary production and large inputs via freshwater, cannot alter the high concentration levels over the year. In the southern parts of the Baltic proper, the situation is the opposite. Here, the spring bloom can consume the whole winter period silicate pool.

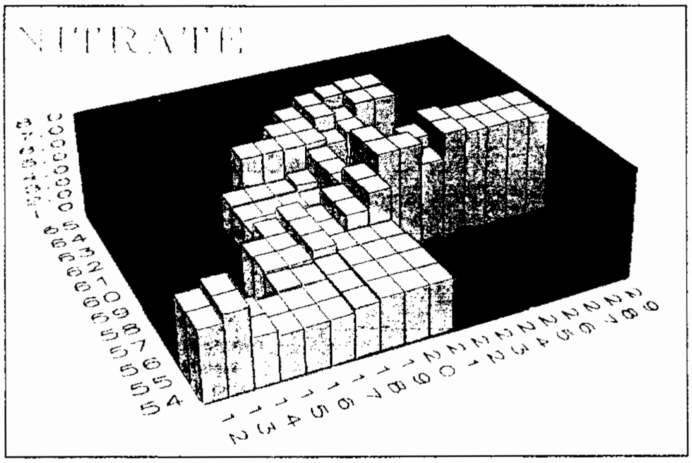
Total Amount of Nutrients

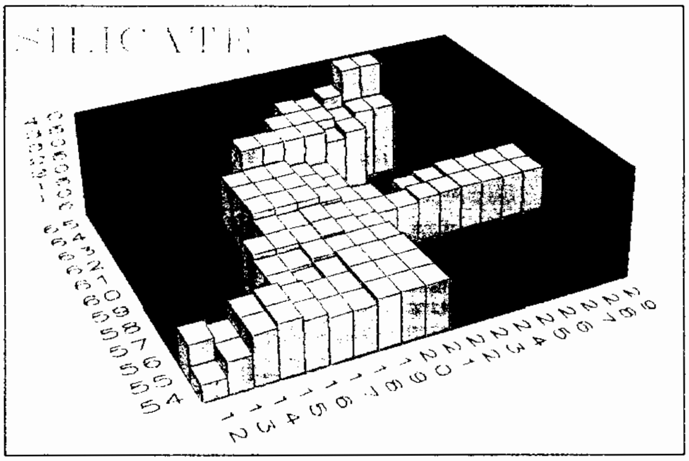
The nutrient matrices discussed above have been coupled to a similarly structured matrix with volumes for each cell. The volume calculations are based on a bathymetric database (10) for the Baltic Sea with a resolution of 5' · 5' (Fig. 6). It is then easy to calculate the total amounts of the different nutrients in the different subareas and to determine the changes in the pool of nutrients over the year and between the different periods. Unfortunately, the lack of observations, especially for the northern parts of the system, due to ice cover, prevents a complete description of the monthly variations. However, it has been shown by Wulff and Rahm (19) that these estimates are dominated by only a few hydrographic stations. The estimates are then rather reliable because of the size (volume) distribution of the different basins.

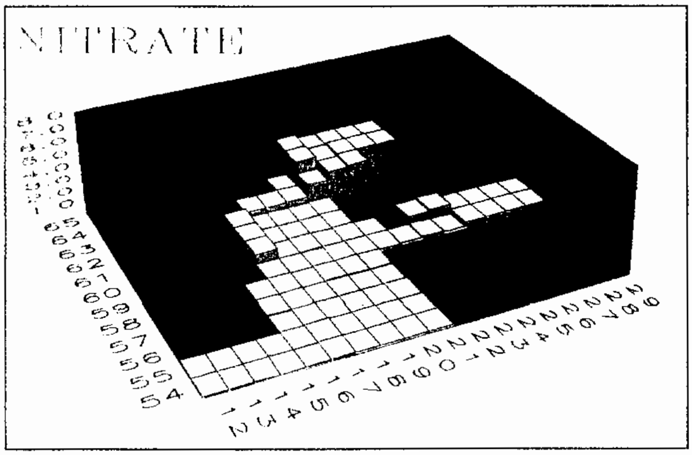
A comparison between the two five-year periods for the total Baltic Sea (18) shows a slight increase in the total amount of phosphorus during the spring season, but otherwise no trends are evident. A corresponding analysis comparing the different basins reveals no substantial differences. A similar comparison for nitrogen shows a drastic increase in total amounts for all basins and seasons during the latter period. Silicate, on the other hand, shows a decreasing trend throughout the entire Baltic.

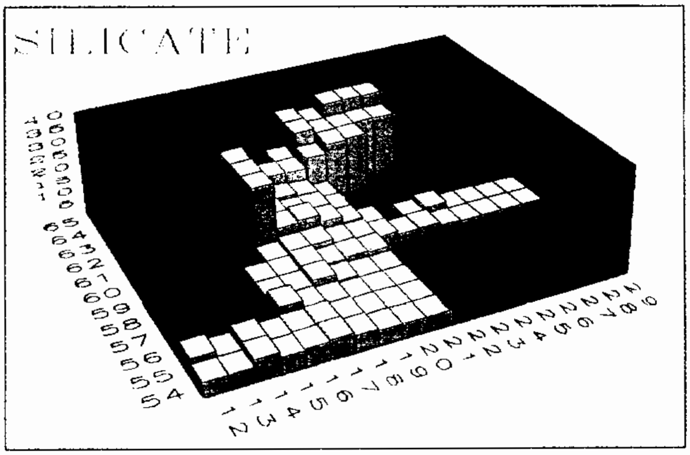
The increase in total amounts of nitrogen and, to a lesser degree, phosphorus corresponds to the increased loading reported by Larsson et al. (1). An increased supply of nutrients, leading to higher concentrations in the system, should lead to an increase in net primary production, but this has been difficult to prove from available measurements, except for the southern parts of the Baltic proper (20). However, the prevailing anoxic conditions in the deep basins during the last decades and changes in biomass and food-web structure (21) indicate increased organic production.

The decreasing amount of silicate is a further indication of increased net primary production analogous to the trend described for Lake Michigan (22, 23), which is attributed to eutrophication. The silicate load from Swedish rivers shows an almost 50% increase during the last two decades









(T. Ahl, pers. comm.). Increasing concentrations of nitrogen (and phosphorus) will result in a larger spring bloom and a larger part of the silicate will be used by the diatoms and eventually be deposited in the sediments. As demonstrated by Elmgren (21), increased phytoplankton primary production can be shown for the spring bloom period in response to higher concentrations of inorganic nitrogen. This should lead to a decrease in the dissolved silicate pool if the major part of the missing amount of silicate in the trophogenic layer is deposited in the sediments.

PROCESSES OF IMPORTANCE FOR THE NUTRIENT DISTRIBUTION

The detailed knowledge of the Baltic that exists today makes this system ideal for developing and verifying hypotheses about the relative importance of different processes which may control the development of this ecosystem. Although we now have a fair understanding about the overall structure and food webs, in terms of energy flows through the Baltic ecological communities (12, 24) and tools to analyze these (25), the first priority in our approach has been to understand which factors are primarily responsible for controlling the overall productivity, oxygen, and nutrient levels. Since the nitrogen-limited Baltic proper has undergone the most dramatic changes during the last decades, we chose to develop a model describing the nitrogen cycles of this basin first (10).

The Nitrogen Model

This model does not take into account horizontal variations but has a high vertical resolution in describing the distribution of water, dissolved and suspended matter, and sediments. A seasonal pycnocline model computes the hydrodynamics of the mixed surface layer, coupled to an advective-diffusive model for the water column below this layer and to a description of the dense water inflows.

Primary production of suspended organic nitrogen in the model is controlled by light, temperature, nitrate, ammonia, and density stratification (critical depth). Remineralization, nitrification, and sedimentation are described using general simple functions, scaled to conditions in the Baltic. Denitrification in the water and sediment is controlled by temperature and concentrations of oxygen, nitrate, and organic substrate. Sulfate reduction to hydrogen sulfide occurs during anaerobic conditions when nitrate has been depleted. The model is driven by nitrogen inputs typical for the last decades, and by statistical distributions of weather and saltwater inflows.

When the model was run for a 20-year period, the simulated seasonal and long-term distributions of salt, temperatures nutrients, and oxygen appeared realistic when compared to field data. The model also demonstrates that denitrification at the sediment redoxcline is quantitatively much more important than denitrification in the water column. Since the deep parts of the basins contain only a very small fraction of the total volume, their influence on the overall nutrient budget is insignificant, in spite of the often dramatic changes in nutrient and oxygen concentrations.

We concluded from this analysis that is not necessary to use detailed ecosystem models to understand and explain the large-scale distribution of nitrogen and oxygen in the Baltic Sea. In addition to the physical circulation, only some general biogeochemical processes need be invoked.

We could have continued to develop this model, adding more spatial resolution or biological realism, but since we wanted to understand the evolution of the Baltic up to the present and to anticipate future changes, another approach was chosen. Although the current primary production of the Baltic proper is nitrogen limited (24), this has not necessarily always been the case. Recent studies (1, 30) indicate that the contemporary nitrogen and phosphorus loads are to large degree counteracted by denitrification (of N) and by sediment accumulation (of P). The loading of nitrogen has increased fourfold and of phosphorus eightfold during the last century. At present we don't know what the future overall scenario of N and P loadings will look like. If we want to include a dynamic description of the role of nitrogen fixation in relation to loading, we must also include descriptions of phosphorus concentrations. This is also necessary if the northern basins are to be included, particularly the phosphorus limited Bothnian Bay.

Box Model

The common paradigm that nitrogen usually limits primary productivity in the marine environment has been challenged, principally with scale arguments (27). Ecosystem-level organic production is not necessarily nitrogen-limited because algal growth is (38). From the analysis presented earlier, we have seen that the silicate concentration is decreasing and has

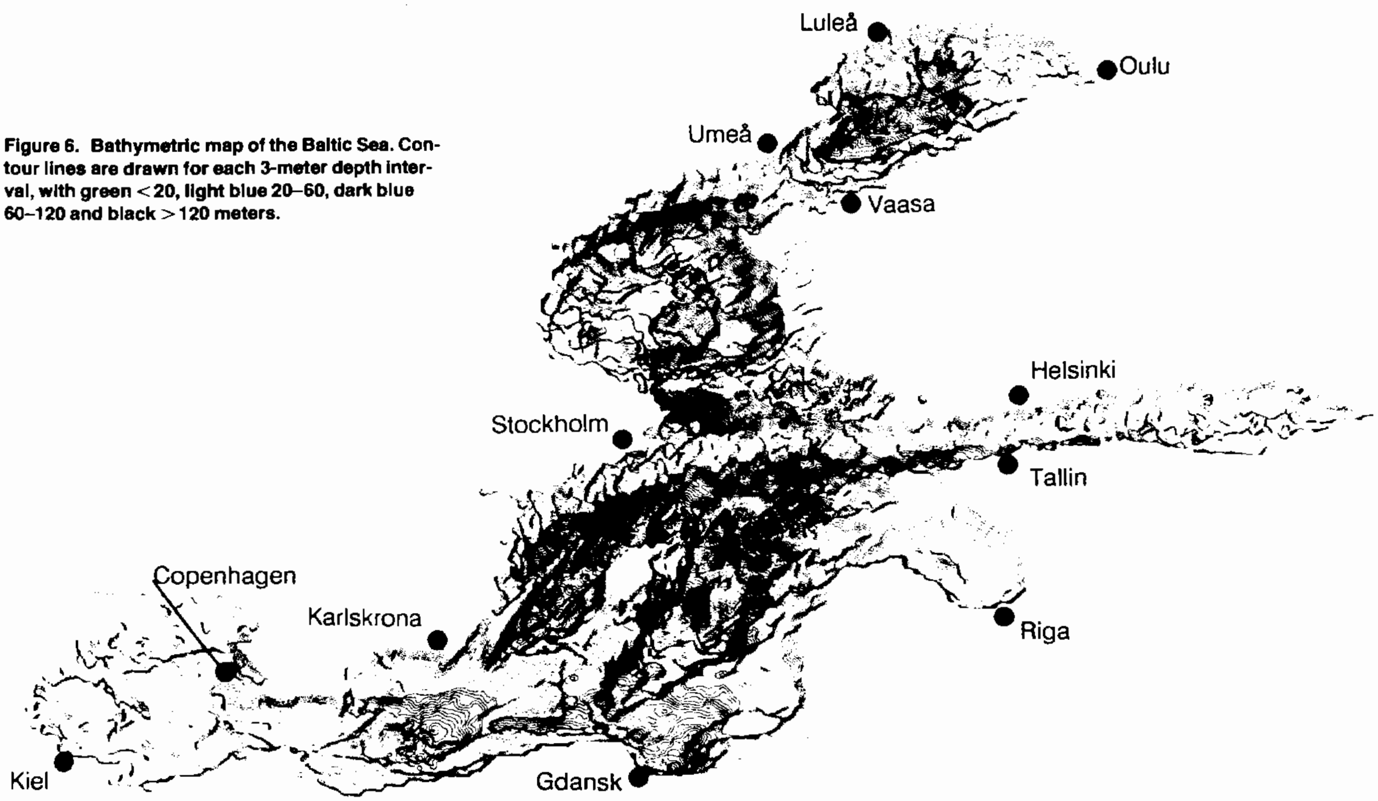


Figure 6. Bathymetric map of the Baltic Sea. Contour lines are drawn for each 3-meter depth interval, with green <20, light blue 20–60, dark blue 60–120 and black >120 meters.

now decreased to a level in the southern Baltic where it may limit the development of the diatom spring bloom. This may affect the food-web structure directly, but also the vertical transports (via sedimentation) of organic matter and nutrients (28). Thus, we need a better understanding of the factors controlling the biogeochemical cycles of nitrogen, phosphorus, as well as of silicate, and how these cycles are interconnected, before management strategies relevant for the entire Baltic can be formulated.

As a step toward this goal, we have utilized the information about total amounts and changes (18), inputs (1), volume flows between the basins (Fig. 4) and concentration gradients to establish budgets for nitrogen, phosphorus, and silicate for the three sub-basins of the Baltic Sea (15). The inputs of silicate were estimated using data from Ahl (29). The results of these calculations are summarized in Figure 7 for the period 1977–1981.

For nitrogen, the internal sink (loss), due either to denitrification or accumulation in the sediments is about 880 000 t · yr^{-1}. In fact, the previously mentioned estimates of oxygen consumption below the halocline (11) correspond to a nitrate production of about 450 000 t · yr^{-1}, based on a C:N weight ratio of 9.1, this ratio was used by Stigebrandt and Wulff (10) and is close to that advocated by Shaffer (39) for the Baltic. Assuming a quasi-steady state, this nitrate will disappear from the deep water either by denitrification, accumulation in sediments or recycling to the surface waters.

Earlier calculations (30) show a denitrification loss of 470 000 t · yr^{-1} in the deep water. The Bothnian Sea has a larger sink (127 000 t · yr^{-1}) than the annual load (85 100 t · yr^{-1}), due to inputs from both the Baltic proper and the Bothnian Bay. Its import of phosphorus from the Baltic proper is of the same magnitude as the local input (3900). Almost 90% of the total Baltic load of both nitrogen and phosphorus enters the Baltic proper, whereas the figure for silicate is only 50%, reflecting the different origins of these substances. Silicate is derived mainly from freshwater discharges to the northern parts of the drainage basin. The loads of nitrogen and phosphorus are delivered primarily to the southern parts which are surrounded by the highest concentrations of populations, agriculture, and industry.

In this crude analysis, we cannot distinguish between the biologically active fraction of N, P and Si, and there are certainly large regional variations. For instance, most of the total nitrogen brought into the Baltic proper is inorganic which can be easily incorporated into the biogeochemical cycles, whereas the major part of the input to the Bothnian Bay is organic nitrogen, some contained in less degradable humic substances. Different fractions will thus have highly different cycling rates in the system, depending on their biogeochemical activity. A crude estimate of recycling rates can be obtained by comparing molar ratios of N:P:Si for the sinks (44:1:26) and the uptake of nutrients in organic production, assuming Redfield ratios (16:1:16). Such calculations show that the sink for nitrogen is more effective than the sinks for phosphorous and silicate. This implies that both phosphorous and silicate are more efficiently recirculated to the water column than nitrogen (15). These budgets may have direct management implications. For instance, efforts to reduce concentrations of phosphorus in the Bothnian Sea by reducing local inputs will have a limited effect, due to the large additional inputs from the Baltic proper (Fig. 7).

The estimates of sinks, although calculated as averages for the entire basins, agree surprisingly well (within 25%) with other recent estimates, based on direct measurements of processes in the sediments (see Carman & Wulff (31); and Koop et al. (32) for a detailed discussion).

The budgets can also be used to illustrate how the efficiencies of the sinks, in relation to load and concentrations, vary between the three basins. Knowing the total amount and the advective and internal (biogeochemical) loss terms and assuming steady state, it is possible to calculate the average residence time of substance. As shown in Figure 8, phosphorus and silicate have residence times of about 13 and 11 years in the Baltic Sea, which is about half of the residence time for a conservative, stable tracer (e.g sea salt). The denitrification process in the Baltic Sea is, on the other hand, very efficient and the residence time for nitrogen is only about 5 years. These calculations also show that the residence times are almost entirely (90%) due to internal biogeochemical sinks, which means that advective transports between the Baltic and the Kattegat have very little influence on the nutrient conditions.

An often useful parameterization in studies of the phosphorus dynamics of lakes is to relate the sink to winter concentrations of nutrients. We have calculated the "apparent removal rate" of total and inorganic phosphorus, nitrogen and

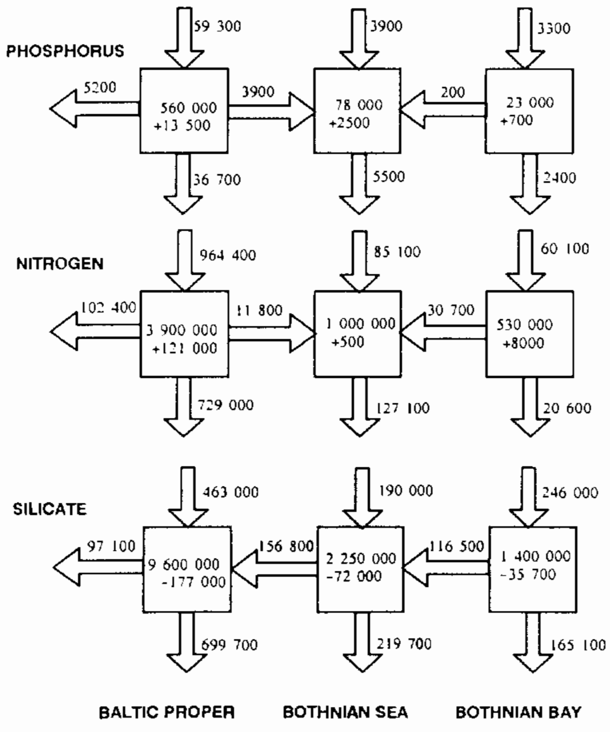


Figure 7. Nutrient budgets of phosphorus, nitrogen and silicate calculated for the sub-basins of the Baltic Sea for the period 1971–1981. Storages (tons) and annual changes (t · yr^{-1}) for the basins are shown in each box. Net flows between basins, inputs from the drainage basins and the atmosphere and internal sinks are shown as arrows between, above and below boxes (t · yr^{-1}) (15).

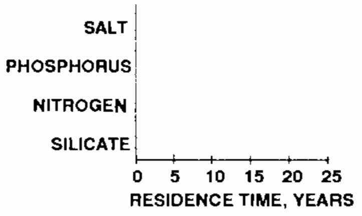


Figure 8. Residence times of a conservative substance (salt) compared to phosphorus, nitrogen, and silicate in the Baltic Sea.

silicate for the three sub-basins of the Baltic (15). The results show inverse relationships for phosphorus and nitrogen. The efficiency of the phosphorus sink decreases going from the Bothnian Bay to the Bothnian Sea and, finally to the Baltic proper. However, a larger fraction of the nitrogen is lost going south while the primary production increases from about 28 to 110 and 160 g C · m^{-2} · yr^{-1} (12) for the different basins. The trend for silicate is less clear. The fraction of phosphorus deposited on the bottom (the phosphorus sink) appears to decrease with an increased loading of the bottom with organic matter. The reason for this could be that the sediments in the northern basins are well oxidized, whereas in the Baltic proper more than a third of the sediments are now anoxic and large additional areas have a very thin oxidized sediment layer with greatly reduced capacity for adsorption of phosphorus. On the other hand, an increased organic load, a redoxcline close to the sediment surface, and high nitrate concentrations, are conditions that will favor higher denitrification rates in the Baltic proper compared to the northern basins. This behavior of the N and P sinks tends to decrease the N:P ratio with increasing eutrophication.

Modelling Long-Term Changes, Past and Future

The overall nutrient budgets and the parameterizations of the nutrient sinks described above make it possible to develop a model describing the changes in nutrient concentrations of the Baltic Sea in relation to loading (15). The model was run both for phosphorus and nitrogen and was forced with estimated nutrient inputs for the period 1950–2000. Some results are shown in Figure 9. Data for model verification are sparse, but the computed concentrations and total N:P ratios agree well with available observations for the last decades. The model indicates that phosphorus concentrations will continue to increase almost to the end of this century, even if the loading is kept constant from 1975. The nitrogen concentrations on the other hand, will decrease after the load is assumed constant, i.e. from 1980. The basic behavior of this model reflects the characteristics of the nutrient budgets and the sinks described earlier. The decreasing N:P ratios agree well with the extensive analysis of nutrient data from lakes (33), suggesting a shift from phosphorus to nitrogen limitation with increasing eutrophication. The model also suggests that, while there has always been a net export of nitrogen, the oligothropic Baltic imported phosphorus from the Kattegat in the 1950s whereas the more eutrophic system of today exports phosphorus. It is clear, however, from this study that using the estimates of the net transports between basins might be misleading in an analysis of the causes of eutrophication. For instance, nutrients leaving the Baltic might cause extensive organic production in the surface waters of the Kattegat and the Baltic Sea. The net export may be small, since a large proportion of the organic matter sinks to the bottom, is mineralized and returned to the Baltic with the inflowing denser bottom water. Before returning, the nutrients may have contributed to anoxic conditions in the adjacent area, in spite of a small net contribution to the nutrient balance of the Kattegat and the Belt Sea.

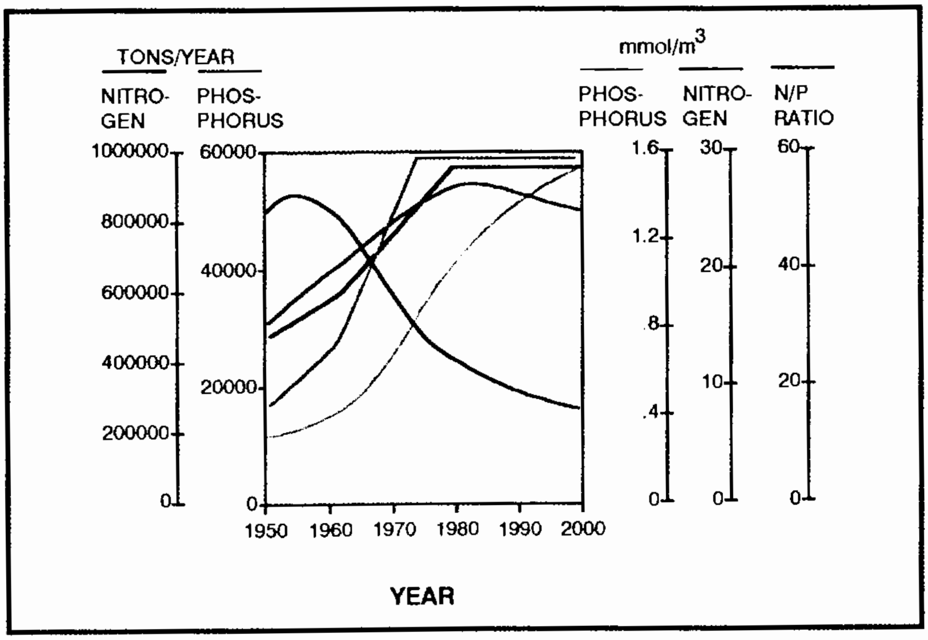


Figure 9. Long-term variations in nitrogen and phosphorus concentrations in the Baltic proper, compared with hypothesized nutrient input, computed with the model by Wulff and Stigebrandt (15).

Although simplistic, the model is in reasonably good agreement with the observation data available today. In addition, it has also highlighted some basic weaknesses in our present understanding of the Baltic Sea. In order to verify the model, a better description of the long-term changes in external supplies of nutrients and of the pools of stored nutrients in the sediments must be developed. This is especially important in order to understand coastal-offshore transports between different bottoms due to erosion and resuspension (34). Also, a better understanding of the couplings between different nutrients and organic matter is needed as well as of the coupling between the different subbasins and the Kattegat and the Belt Sea.

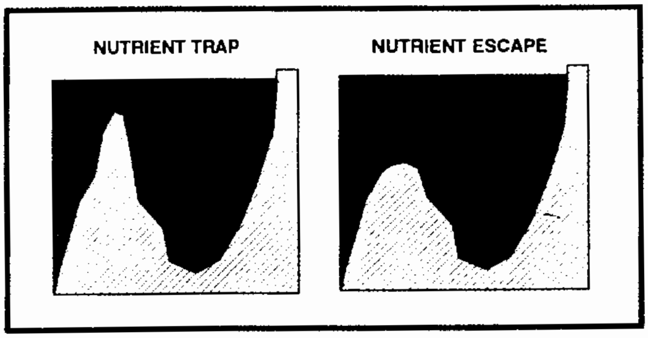


Figure 10. Schematic illustration of conditions for nutrient trap (left) and nutrient escape (right). The basin functions as a nutrient trap if the nutrients in the deep water re-enter the trophogenic surface layer (due to a shallow sill) and contribute to the formation of organic matter sinking down into the deep water.

CONCLUDING REMARKS

It has become more and more obvious that in order to understand, model, and manage the effects of marine eutrophication, a better understanding of the factors controlling the overall biogeochemical cycles is needed (27). In addition to an integration of biogeochemical studies, we must incorporate hydrodynamic aspects into the models. It has been suggested that the nutrient dynamics of large semi-enclosed basins like the Baltic and the Mediterranean seas depends on whether the vertical circulation is of the estuarine type (where the basin water below the sill level is imported from outside) or of the Mediterranean type (35) (where the basin water is formed by thermocline convention within the sea itself).

The flushing of a sill basin with the Mediterranean type of circulation means that basin water need not reach much higher than the sill to escape the sea. For a sea with estuarine circulation the "old" deep water may have to reach high above the sill level to be able to leave the system. Nutrients regenerated in the basin water may thus escape the Mediterranean-type of sea without entering the surface layer while, for the same sill level, for estuarine type of sea regenerated nutrients may reach the trophogenic surface layer within the sea. In the latter case, the nutrients may contribute to new biological production and may, through sinking organic matter, again be released to the lower deep water.

In this way the nutrients are believed to be more easily trapped in the estuarine-type of system. However, as pointed out by Aure and Stigebrandt (36), the question of possible trapping of nutrients is mainly a question of sill depth. If, for instance, the sill depth is sufficiently small in a Mediterranean type of sea, the nutrients may not escape the sea without first entering the photic zone within the sea. On the other hand, nutrients should be able to escape a sea with an estuarine-type of circulation without contributing to the primary production if the sill depth is sufficiently great (Fig. 10). Thus, it appears that the sill depth is the primary variable determining the degree of nutrient trapping. The kind of vertical circulation appears to be only a second-order effect.

Contrary to the situation in the Mediterranean sea, which has a relatively deep sill at Gibraltar, the nutrient enriched deep water in the Baltic Sea may not leave the system without entering the surface layer and the photic zone. Instead of being transported out of the system much of the nutrient load returns to the deep water through sinking organic matter. Thus, a large shallow-silled sea may acquire high nutrient concentrations in the deep water. Primary productivity is to a high degree maintained by recycling. This means that nutrients originally released in the deep basins may be relocated to shallow sediments next time it is used in primary production and settles out as organic matter. In the shallow Baltic, the likelihood that a particle will enter a zone where the conditions to be withdrawn from the biogeochemical cycles of the water column (through denitrification or accumulation in sediments) is therefore high. Accordingly, other nutrient sinks besides advective export to external areas may be important for this kind of system. It was found (15) that only about 10% of the nutrients supplied to the Baltic Sea were exported to external areas. In a very deep system like the Mediterranean, a larger proportion of organic matter is mineralized within the water column, and due to a relatively deep sill, nutrients accumulated in deep water are exported to the Atlantic without reentering the trophogenic surface layer again. The response of such a system to changes in load might be quite different from what we have described here for the Baltic Sea and, in fact, Sarmiento et al. (35) concluded from their analysis that the internal sink for phosphorus will be more efficient at higher nutrient loads in such a system.

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Report

Lars Rydberg, Lars Edler, Sören Floderus and Wilhem Granéli

Interaction Between Supply of Nutrients, Primary Production, Sedimentation and Oxygen Consumption in SE Kattegat

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Intensive measurements of nutrient fluxes, carbon and nitrogen assimilation, sedimentation and oxygen consumption within the SE Kattegat are used in an effort to follow the coupling between increasing nutrient supply and decreasing deep-water oxygen concentrations. The investigated area is a part of the strongly stratified Baltic estuary, with a hampered deep-water exchange and a large supply of nitrogen from nearby anthropogenic sources. Measurements were undertaken during 1981–1988. The results are discussed, mainly in terms of annual or seasonal mean values. The average primary production, 11.4 mol $C \cdot m^{-2}$ (corresponding to 45 mmol $C \cdot m^{-2} \cdot d^{-1}$ during the "productive season"; from March to October), was surprisingly well correlated with the uptake of inorganic nitrogen, which averaged 1.68 mol N m^{-2} (11.1 mol $C \cdot m^{-2}$, using the Redfield ratio). The oxygen consumption (deep water and benthic) which averaged 20 mol O_2 $m^{-2} \cdot d^{-1}$, was well correlated both with the measured nitrate uptake and with the external supply of nitrate to the surface water. The consumption was twice as high as that in the open Kattegat.

INTRODUCTION

During the past decades, oxygen deficit and subsequent benthic mortality have become frequent phenomena in the seas surrounding Sweden, particularly in the deep water of the Baltic, but also in more shallow waters like the Kattegat and the Great Belt (1, 2). These areas, which form the narrow entrance to the Baltic Sea (Fig. 1a), are characterized by very strong salinity stratification and restricted vertical mixing.

Like many other coastal waters, the Baltic Sea has experienced a rapidly increasing anthropogenic nutrient load. Larsson et al. (3) estimated that the supply of nitrogen has increased by a factor of 4 and phosphorus by a factor of 8 since the beginning of this century. A corresponding development seems probable also for the

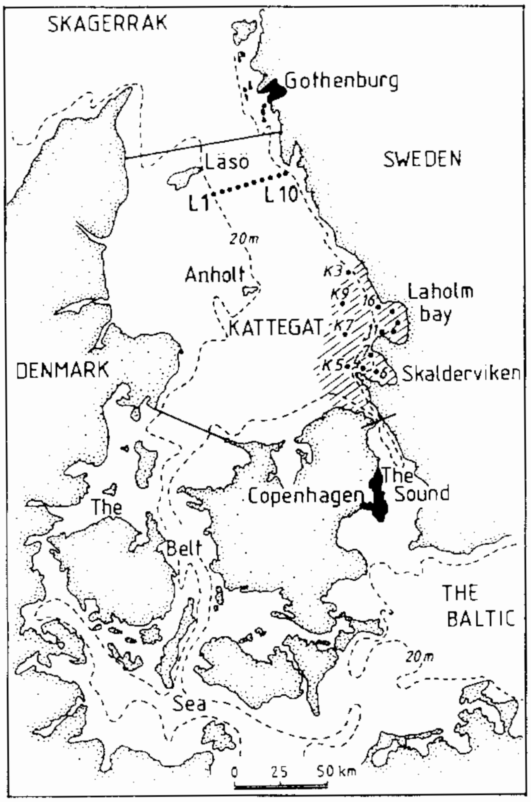


Figure 1a. Map of the Kattegat and adjacent areas. Stations used in the hydrographic programs in SE Kattegat and in the section at Läsö are indicated with an (•). The borders of the Kattegat are marked with thick lines, while the SE Kattegat area is shaded. Broken line shows 20-m isobath.

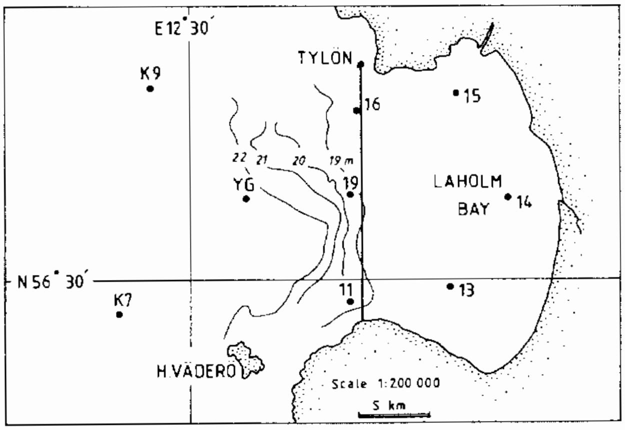


Figure 1b. Map of Laholm Bay showing the sampling stations. The outer border indicating the Laholm Bay area is marked by a thick line.

Kattegat area. Undoubtedly, these strongly increased loads must have had an effect on phytoplankton production and oxygen consumption. For a specific area, like the SE Kattegat, it is far from obvious whether local or large-scale nutrient input dominates the local effects.

In the Kattegat, marine monitoring was initiated at the end of the 1960s. Since then, there has been a direct response to the increased load in the form of increasing nutrient concentrations in the deep waters, but also in the surface waters during the winter when primary production is low (4, 5). The increase was much more pronounced for nitrogen, as phosphate supply to the Kattegat is dominated by inflow of oceanic water (5). Primary production, on the other hand, seems to be only slightly affected, except in Danish coastal areas (1, 6). On the other hand, long-term data on primary production from the open waters are far from complete.

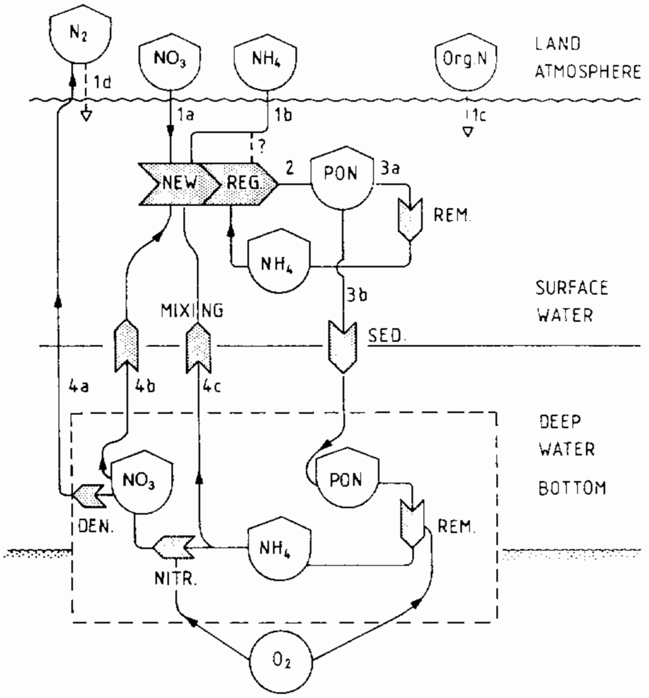
Immediately after a period of severe oxygen deficit in the SE Kattegat during the fall of 1980, an intensive research activity was commenced in that region. The primary purpose of the study was to describe the coupling between nutrient supply to the surface water and oxygen consumption in the deep water. This purpose, in turn, was related to the question of whether it would be possible, by decreasing the anthropogenic load of nutrients, to improve the deep-water oxygen conditions (7). The region receives a large nitrogen load from some smaller rivers that enter Laholm Bay and Skälderviken. In addition, the outflow of Baltic water through the Sound adds considerable amounts of nitrogen and phosphorus to SE Kattegat. Thus, an urgent task was to determine the amount of nutrients added from land (including atmospheric deposition) to SE Kattegat and to compare these quantities to the supply of nutrients from the Baltic and from the Kattegat deep water, respectively.

In this paper we address a number of topics influencing the coupling between nutrient supply and oxygen consumption. Some of the results discussed here have been presented elsewhere; e.g. hydrography, including nutrient and oxygen conditions (8); primary production (9); sedimentation, including resuspension and burial (22); and oxygen consumption (11). Parallel studies of nitrogen uptake, using the ^{15}N technique are presented separately in this issue. Most measurements were undertaken in the Laholm Bay and SE Kattegat (see Figs 1a and 1b) during 1981–1985. Some investigations continued until 1988, and were extended into the open Kattegat. Figure 2 is a flow scheme indicating the main processes discussed.

Although the conclusions are mainly based on our own studies in SE Kattegat, it must be emphasized that the national monitoring programs (1, 4) as well as lightship observations (13) and modelling (14, 15) within the Kattegat have contributed extensively. In fact, box modelling and calculations on nutrient fluxes would have been impossible without these data.

Figure 2. A flow scheme, showing nitrogen circulation, where the processes studied in SE Kattegat are numbered 1 to 4. The main feature is the external supply of nitrogen to the surface water; 1a, b as local land-based sources of nitrogen (which include atmospheric deposition) and 4b, c as deep-water supply. External loading from adjacent seas occurs occasionally in concert with outflow of Baltic Sea water (see Fig. 3). Loading of nitrogen from Skagerrak is treated as a source term only when the whole Kattegat is discussed, but enters the deep-water supply (mixing) through the deep-water nitrogen pools. The only process within deep water and benthic areas which is calculated here is oxygen consumption.

DEN = denitrification
REM = remineralization
REG = regeneration
NITR = nitrification
PON = particulate organic nitrogen



Hydrography

Circulation is dominated by a two-layer, estuarine flow (Fig. 3), driven by the outflow of low salinity water from the Baltic. The surface-water salinity varies from 15 to 30‰, with a significant north-south gradient. Deep water enters from the north as Skagerrak water with salinities between 32 and 34‰. The halocline lies at about 15 meters deep, but the depth varies due to the fluctuating flow from the Baltic and due to local winds. Mixing across the halocline is dominated by upward wind entrainment. A mean entrainment velocity of 0.25 m · d^{-1} was calculated by Stigebrandt (14) from a combination of entrainment theory and lightship data. Due to the variability in wind stress and stratification, this mean value features strong seasonal variations, with a minimum of <0.1 m · d^{-1} during summer (16).

Primary Production

Primary production and surface-water nutrient concentrations follow an annual cycle typical of temperate waters. The production is low from the end of October until the spring bloom in March. Typical nutrient concentrations within Kattegat and surrounding waters are shown in Table 1. In February, before the Kattegat spring bloom, the surface water dissolved inorganic nitrogen (DIN) concentrations are normally 8.4 ± 3 μmol · L^{-1} and the dissolved inorganic phosphorus (DIP) con-

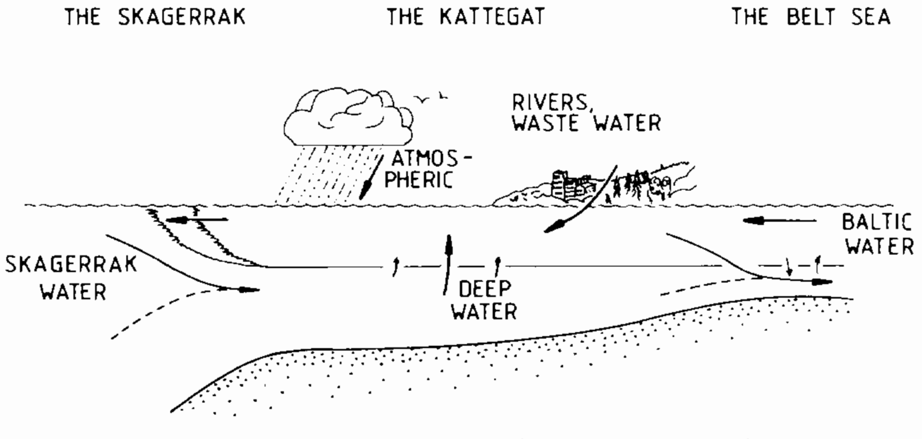


Figure 3. A cross-section through the Kattegat indicating the circulation of water and nutrients entering the surface water nutrient budget. (Mean salinities and nutrient concentrations are shown in Table 1.)

Figure 4a, b. Annual primary production (pp) (bars) and daily mean summer production (C-prod. circles) at Anholt in the Kattegat and at Halskov Rev in the Belt Sea during 1955–1984 (6).

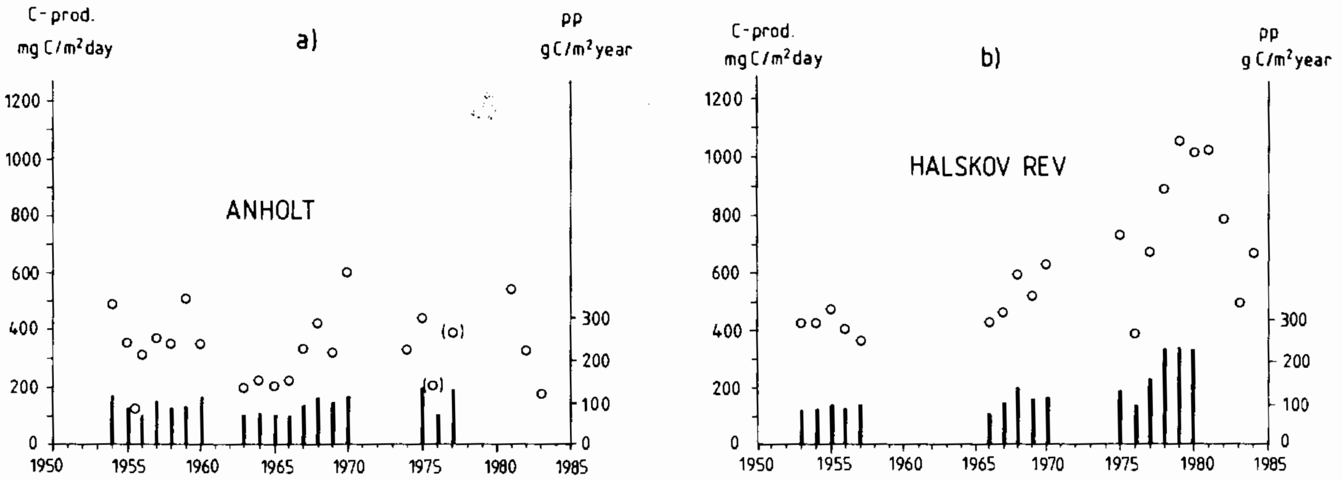


Table 1. Mean salinity concentrations (‰), DIN (dissolved inorganic nitrogen) and DIP (dissolved inorganic phosphorus) (μmol L^{-1}) in Kattegat and surrounding waters (mean values for the years 1974 and 1978–82).

	January–February			April–September	
	Salinity	DIN	DIP	DIN	DIP
Skagerrak water	33.6	7.9	0.69	4.9	0.39
Kattegat deep water	33.3	8.5	0.74	8.2	0.70
Baltic water	8.5	4.3	0.51	0	0
Kattegat surface water	22.2	8.4	0.71	0	0

centrations 0.74 ± 0.1 μmol · L^{-1}. Thereafter, concentrations are low (near the detection limit) until the end of the productive season. In the deep water, DIN and DIP are high and nearly constant during all seasons. The concentrations in Baltic water are lower; 4.3 (DIN) and 0.51 (DIP) μmol · L^{-1}, respectively, indicating a dilution when Baltic water enters the Kattegat. The inflowing Skagerrak water, on the other hand, which forms the Kattegat deep water has concentrations which are nearly equal to those of the Kattegat during winter. During summer, however, the concentrations are much lower than in the Kattegat deep water, indicating a considerable mineralization within the Kattegat.

Primary production has been measured at Anholt in the central Kattegat and at Halsskov Rev in the Great Belt since the mid-1950s. These measurements were initiated by Steemann Nielsen (20) and continued by the Danish authorities (1, 6). The annual primary production at these stations during 1955–1984 are shown in Figure 4. At Anholt, there is a weak increase over time, with an annual mean value of about 105 g C · m^{-2} (8.75 mmol C · m^{-2}). At Halsskov Rev, on the other hand, production increased from 100 g C · m^{-2} during the 1950s to about 185 g C · m^{-2} during 1975–1979. The high levels continued during the 1980s (6). During 1975–1979, Ærtebjerg et al. (1) also studied the spatial variability and found that the primary production was highest in the southwestern part of the Kattegat (122 g C m^{-2}) compared to 81 g C · m^{-2} in the NE and 101 gC · m^{-2} in the SE Kattegat.

Oxygen Levels

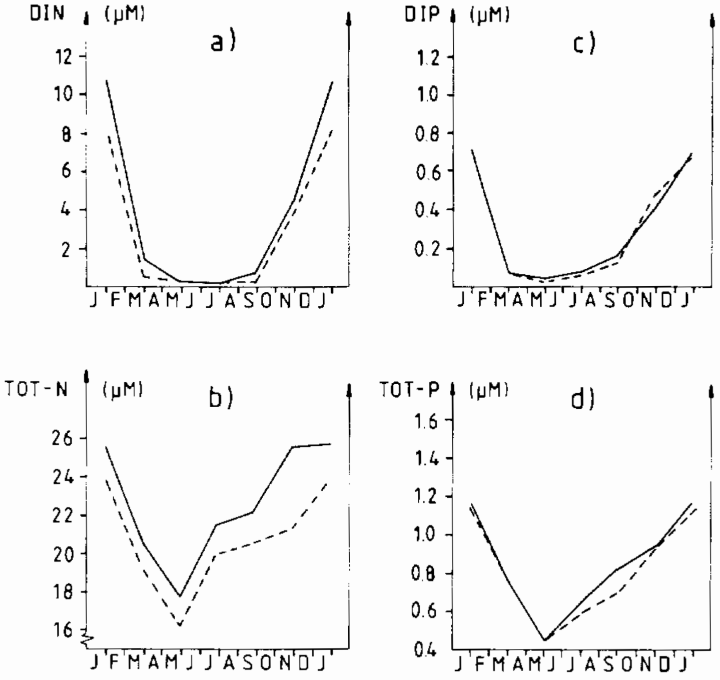
Although different signs of oxygen deficit have been reported from the Belt Sea and the Kattegat for over 20 years, the first measurements of oxygen deficit were made in the southern Great Belt deep holes during the 1970s. In 1980 and 1981, hydrogen sulfide was found both in the northern Great Belt and in Laholm Bay (25), mainly in shallow areas just below the halocline. Still later, it was shown (5) that the summer mean oxygen concentrations in the Kattegat deep water had decreased by about 10% between 1971 and 1982, a decrease which corresponded to an increase in oxygen consumption of 50%. The change was discussed in the light of an increased nutrient supply from land and atmosphere of almost 100% during the same period. In the end, we shall make a similar approach for the SE Kattegat, linking nutrient supply to deep-water oxygen concentrations, with the ultimate purpose of calculating which change in deep-water oxygen concentration can be obtained for a given decrease in the land-based nitrogen supply as nitrogen is considered to be a limiting nutrient.

MATERIALS AND METHODS

The hydrographic field program in SE Kattegat continued from 1982 to 1985, and comprised almost monthly measurements of salinity and temperature, oxygen, Tot-N, NO_3^-, NO_2^-, NH_4^+, Tot-P and PO_4^{3-} at the 12 different stations shown in Figures 1a and 1b. Methods, measurements and a summary of raw data and results are given in Sundberg and Rydberg (17). Parallel, monthly measurements on nutrient input from rivers and wastewater were made by local authorities (7).

Another, parallel field program was carried through in a cross-section east of Laesö (Fig. 1a) in the northern Kattegat. This study included measurements of nutrients, oxygen, salinity and simultaneous current measurements with gelatine pendulums (18). These measurements were made repeatedly during 1984–1988. In this way we obtained estimates of the flux of deep water ($S > 30$‰), oxygen and nutrients from the Skagerrak into the Kattegat, which supplemented the entrainment-based flow estimate used previously (8, 16) (Fig. 3).

Phytoplankton studies were started in November 1980 and continued until 1988. For details concerning methodology and results, see Edler (9). An important part of the program comprised repeated measurements of primary production at several depths at Stn 19, in the outer part of Laholm Bay. More than 100 observations of daily production were made during 1981–1985. Occasionally, production studies were made for the innermost part of the bay, in the Nissan estuary (Fig. 6) out into the open Kattegat, mainly to evaluate horizontal variability. Studies on dominat-



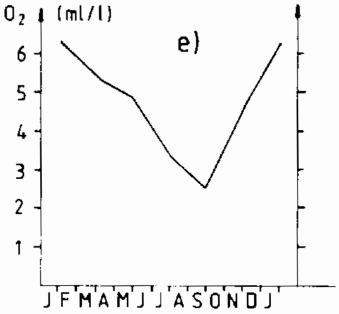


Figure 5a–d. Bimonthly mean concentrations of DIN, DIP, Tot-N and Tot-P within the surface water of Laholm Bay (——) and SE Kattegat (- - - - -), respectively. Averages for the years 1982–1985 (8).

Figure 5e. Bimonthly mean oxygen concentration in the SE Kattegat deep water (1-m above the bottom). Averages for the years 1982–1985 (8).

ing phytoplankton species were carried out parallel to the production studies.

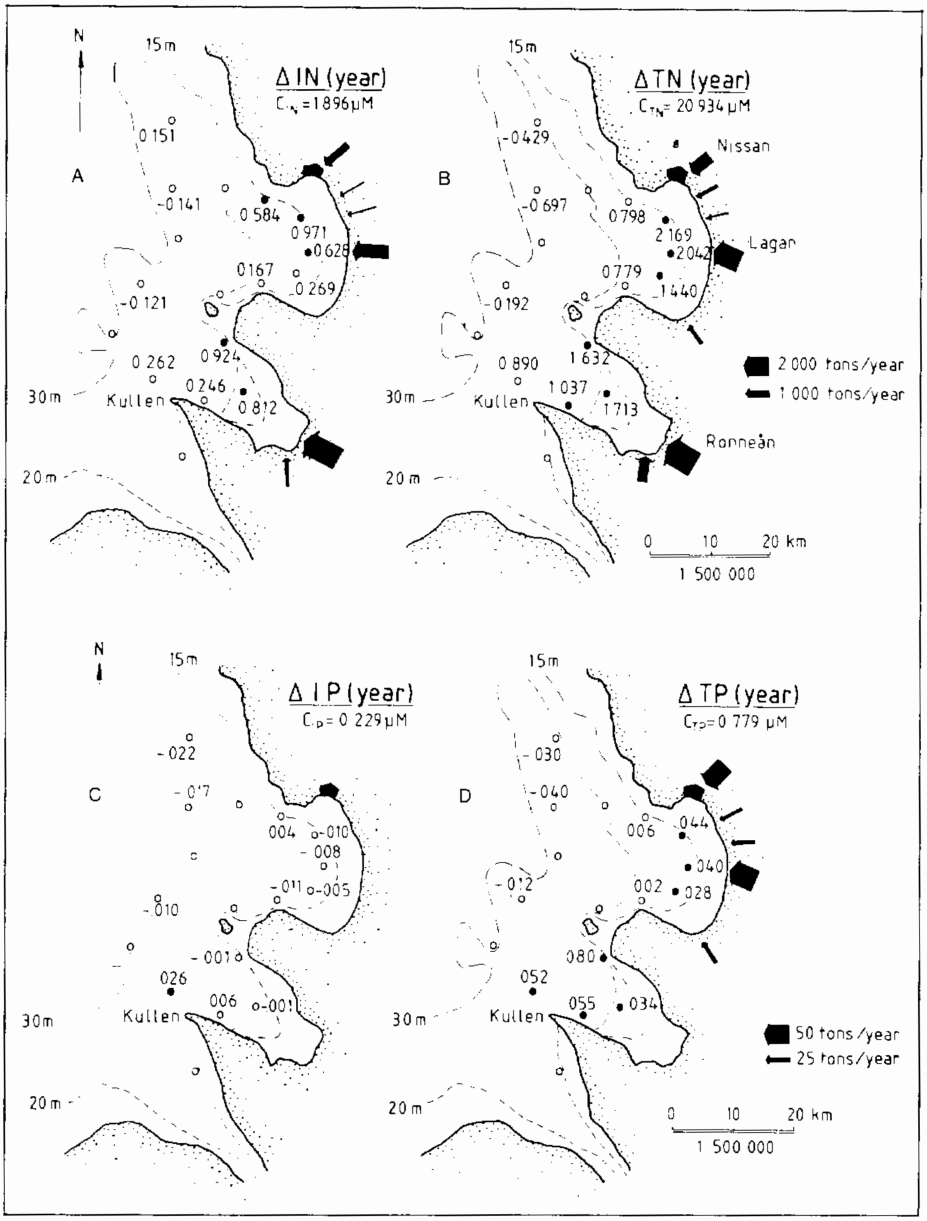
Sedimentation of particulate organic carbon and nitrogen was studied by using sediment traps, deployed at different positions and depths (mainly below the halocline) in SE Kattegat. Relevant results were obtained during shorter periods in connection with the spring bloom in March 1984 and 1988 (10, 21). As an alternative means of estimating sedimentation and resuspension, the extension of "ephemeral mud blankets", including their content of carbon and nitrogen, was studied within the Laholm Bay area. These observations were made repeatedly over a period of 2 months after the spring bloom in 1984 and 1985 (10).

Benthic and deep-water oxygen consumption was studied in three different ways. Laboratory studies on incubated sediment samples were used to determine benthic oxygen uptake (11). Measurements of oxygen concentrations in dark Winkler bottles were used to determine deep-water consumption (24) and full-scale experiments, based on intensive mapping of currents, salinity and oxygen within a confined deep-water volume were used to make indirect calculations of deep-water and benthic consumption (23). Bottom and deep-water samples were taken in the outer, deeper part of Laholm Bay during all seasons in 1984 and in 1987–1988. The full-scale experiments were undertaken on three occasions during spring and autumn 1983–1984, covering an area of 100 km^2 (centered around Stn YG, Fig. 1b) and a period of 48 hours.

RESULTS

Bimonthly mean values, from the hydrographic program, of DIN, Tot-N, DIP, and Tot-P within the surface water and oxygen within the deep water are shown in Figure 5. DIN and DIP varies strongly, starting with a rapid decrease during the

Figure 6a–d. Stationwise annual deviations, △IN, △TN, △IP and △TP (surface water) from the overall mean value, which is given in the figure (as C in µmol · L^{-1}). The data are based on measurements during 1982–1985. Land-based loading from rivers and wastewater are indicated by arrows. (About 50% of the Tot-P is inorganic.)



spring bloom. Tot-N and Tot-P follow with only a minor phase lag. Significant gradients appear between the Laholm Bay water and SE Kattegat surface water. These gradients are even more clear from Figure 6, which shows horizontal deviations from an overall mean value. High values of DIN and Tot-N within the Laholm Bay and Skälderviken (Figs 6a–b) reflect the concentrated land-based nitrogen supply (8), while the surplus in Tot-P (Fig. 6d) is surprising. This surplus may be caused by the land-based supply (compare the land-based supply of Tot-N and Tot-P indicated in Fig. 6), but may also be due to a comparatively large biomass. High DIP concentrations north of Kullen (Fig. 6c) probably indicate DIP input from The Sound.

Bimonthly mean values of Tot-N and DIN (Figs 5a–b), including the observations of nitrogen supply from rivers and wastewater, the atmospheric nitrogen supply, and the deep-water supply according to Rydberg and Sundberg (16) were used to model the exchange of water and nitrogen between the SE Kattegat and the Laholm Bay surface water (8); Tot-N was used as a tracer by which the water exchange was determined, while DIN and DIP were used to calculate the fluxes and net uptake of inorganic nitrogen and phosphorus within Laholm Bay.

Table 2. External nutrient loading to the surface waters (0–15 m) of the Kattegat, SE Kattegat and Laholm Bay from March to October (horizontal borders are shown in Fig. 1 a, b). The load "winter nutrient pool" represents the sum of nutrient concentrations in Table 1 (Jan–Feb) and a (relatively small) spring-bloom loading between 1–15 March.

LOADING SOURCE	DIN	DIP	DIN	DIP	N/P ratio
	tonnes		mmol · m^{-2} · day^{-1}		(atoms)
KATTEGAT (18 000 km^2)					
WINTER NUTRIENT POOL	26 400	4900	7.5	0.63	11.9
Deep water	13 200	2700	3.7	0.35	10.6
Local (45% from atm)^1	7400	500^2	2.1	0.06	35
Baltic water	5800	1700	1.6	0.22	7.3
16 MARCH–31 OCTOBER	73 000	10 900	1.26	0.085	14.8
Deep water	47 500	8900	0.82	0.070	11.7
Local (45% atm)	22 000	900^2	0.38	0.007	54
Baltic water	3500^3	1100^3	0.06	0.008	7.5
SE KATTEGAT (2000 km^2)					
WINTER NUTRIENT POOL	3000	610	7.7	0.70	11.0
Deep water	935	200	2.4	0.23	11.7
Local (25% atm)	650	10^2	1.6	0.01	130
Baltic water	1400	400	3.6	0.46	7.8
16 MARCH–31 OCTOBER	9750	1230	1.51	0.086	17.6
Deep water	4400	800	0.68	0.056	12.1
Local (30% atm)	4400	50^2	0.68	0.004	190
Baltic water	950^3	380^3	0.14	0.027	5.2
LAHOLM BAY (300 km^2)					
WINTER NUTRIENT POOL	475	63	8.1	0.49	16.5
Deep water	85	18	1.4	0.14	10.0
Local (10% atm)	240	5^2	4.1	0.04	100
Baltic water	150	40	2.6	0.31	8.4
Export to Kattegat	−75^5	0			
16 MARCH–31 OCTOBER	1900	145	1.88	0.065	28.9
Deep water	400	75	0.40	0.034	11.7
Local (13% atm)	1400	20^2	1.39	0.009	154
Baltic water	$<$100^4	50^4	$<$0.1	0.022	5
Export to Kattegat	−350^5	0			

[1] Local loading includes land-based sources (river input and sewage) and atmospheric deposition over the sea surface (the proportion is given within parentheses).

[2] May be underestimated. The sewage effluent is occasionally higher and DIP measurements have been made after filtering the samples.

[3] The loading occurs mainly during March–April, before the Baltic spring bloom.

[4] Uncertain value, due to an unpredictable uptake of DIP north of The Sound.

[5] Due to higher concentrations of DIN in the Laholm Bay surface water than in Kattegat, there is a diffusive export of DIN from Laholm Bay to Kattegat, mainly in March–April and October.

Table 3. Oxygen consumption within the SE Kattegat deep water (>32‰ salinity) and benthic zones during the full-scale experiments. Salinity, oxygen concentrations and deep-water height, above sea bottom (h), (at >32‰ salinity).

	s (ppt)	O$_2$ (ml · L^{-1} · d^{-1})	h (m)	O$_2$ Consumption (ml · L^{-1} · d^{-1})	(L · m^{-2} · d^{-1})
September 1983	32.0–32.7	1.2–3.6	2.5	0.54	1.35
March 1984	32.0–34.0	5.1–5.8	3.0	0.09	0.27
September 1984	32.0–33.1	1.2–3.3	2.5	0.19	0.48

Similar calculations were made for the exchange of water and nutrients between SE Kattegat and the open Kattegat, and between the open Kattegat and the surrounding waters, i.e. the Skagerrak and the Baltic (8, 16). These calculations were partly based on salinity and nutrient data from the national monitoring programs. The results, concerning fluxes and uptake of inorganic nutrients for all three areas; Laholm Bay, SE Kattegat and Kattegat, are compiled in Table 2, in which the deep-water fluxes are recalculated using results from the measurements at the Laesö-section (18). Here, we have distinguished between nutrient supply from local sources, i.e. the sum of atmospheric, wastewater, and river input to the area considered, input from the deep water and input from the Baltic. The low-productive winter period, from November to February, is not considered, but a division in time is made between the spring-bloom period (first half of March) and the rest of the productive season (from 16 March to 31 October). Thus, nutrient supply during winter affects the results in Table 2 through the "winter nutrient pool", which is assumed to be assimilated during the spring-bloom period.

The horizontal (inorganic) nutrient transport between different parts of the Kattegat surface water is normally negligible during the productive season because the concentrations of DIN and DIP are low (Table 1). In Laholm Bay, however, about 25% of the DIN supply is exported to SE Kattegat (19). This export occurs mainly in March and October due to a large input of freshwater, which rapidly leaves the bay. With this exception, however; disregarding denitrification in the surface water, the only sink through which the inorganic nutrient concentrations can be kept at a low level is by nutrient assimilation.

Table 2 shows that the total external supply of nutrients to the surface water per unit area, before the spring bloom is almost the same in all parts of the Kattegat, indicating an evenly distributed spring-bloom production. The origin of the nutrients differs, however; local DIN supply, land-based plus atmospheric, dominates in Laholm Bay, Baltic water supply dominates in SE Kattegat and deep-water supply dominates in the open Kattegat. For DIP, the Baltic water is of considerable importance in all regions. The N/P ratio indicates a smaller surplus of P during this period.

About 25% of the annual external DIN supply (disregarding the part of the annual supply that is exported from Kattegat through horizontal advection from November to February) is assimilated during the spring bloom, 75% from 16 March to 31 October. After the spring bloom, the local supply of DIN is generally more important compared to the deep-water supply, particularly in Laholm Bay, where at least 2/3 is of local origin, mainly as river input. During this period there is also a larger supply of external nitrogen to Laholm Bay and SE Kattegat compared to

Figure 7a. Observations of daily primary production at Stn 19 in the outer Laholm Bay during 1981–1985 (9).

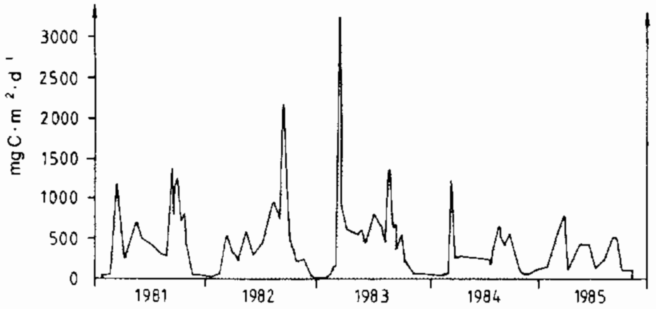
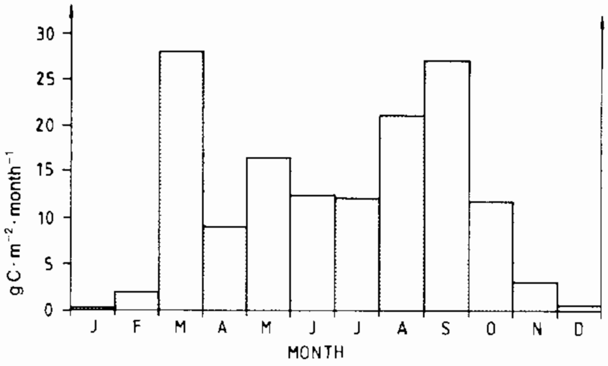


Figure 7b. Monthly mean primary production at Stn 19 for the years 1981–1985 (9).



the open Kattegat. In Laholm Bay, the supply is 45% higher, in SE Kattegat 25% higher. The supply of DIP, on the other hand, is strongly dominated by the deep-water in all parts. The imbalance between supply of DIN and DIP is large in Laholm Bay, compared to the Redfield ratio (N/P = 28.9), and from this point of view, phosphorus might locally limit "new" production.

Primary Production

Results from measurements on primary production in the outer Laholm Bay (Stn 19) are summarized in Figure 7. All observations on daily primary production during 1981–1985 are shown in Figure 7a, the monthly mean primary production from these measurements in Figure 7b. The mean annual production was 144 g C · m^{-2} (12 mol C m^{-2}) considerably higher than the preliminary averages. The winter production was very low, usually below 0.05 g C · m^{-2} · d^{-1}. The spring bloom took place at the beginning of March, and was dominated by diatoms. A few peaks higher than 3 g C · m^{-2} · d^{-1} were found, but 1 g C · m^{-2} · d^{-1} was a normal value during the bloom. Variable hydrographic conditions, due to rapid changes in outflow of Baltic water made it difficult to "hit" the peak from observations at Stn 19 only, and the large interannual variations in integrated spring-bloom production (10–35 g C · m^{-2}) probably reflect this feature. On average, however, the bloom added 19 g C · m^{-2} (Fig. 7b), corresponding to 13% of the annual production.

From mid-March until mid-August mean daily production was below 0.5 g C · m^{-2} · d^{-1}. This period added 65 g C · m^{-2}, or 45% to the annual production. From mid-August through September, a second bloom developed which occasionally reached daily rates as high as during the spring bloom. This autumn bloom was dominated by dinoflagellates. The average production during this period was 0.88 g C · m^{-2} · d^{-1}, adding another 45 g C · m^{-2} (30%) to the annual production. The horizontal variations were generally small (<10%), except for the area just outside the estuary of Nissan (Fig. 6) where primary production was more than twice as high.

Sedimentation

The sinking of non-resuspended organic matter through the halocline was measured daily during the spring bloom in 1984 and 1988. In 1984, the measurements at Stn YG indicated a maximum sinking rate of 407 mg C · m^{-2} · d^{-1} over a two-day period and a mean rate of 216 mg C · m^{-2} · d^{-1} over two weeks (21). The daily mean primary production during these days was 750 mg C · m^{-2}. In 1988, sedimentation was measured over a period of 3 days at 5 different positions in SE Kattegat giving between 200 and 300 mg C · m^{-2} · d^{-1} (10). At this time however there were no parallel measurements on primary production, but chlorophyll concentrations were high, indicating an ongoing spring bloom.

Floderus and Håkanson (22) also estimated the sinking of particulate matter by looking at sea-floor deposits of newly settled organic matter. The amounts of organic carbon found in ephemeral mud blankets after the spring bloom in 1984 and 1985 were between 25 and 50 g C · m^{-2}, averaged over the bottoms of Laholm Bay. These levels are nearly an order of magnitude above what would be expected from the measured sedimentation rates during the bloom, but are still not unreasonable compared to the mean spring-bloom production (19 g C · m^{-2}) if one assumes that the main part of the bloom within the bay reaches the deep-water bottoms. Studying the fate of these deposits indicated a successive export to the deeper bottoms of the Kattegat (22), and thus that resuspension and successive burial are important factors in the coupling between production rates and sedimentation.

Oxygen Consumption

The full-scale experiments on oxygen consumption were carried out and presented by Rydberg and Sundberg (23). The results are summarized in Table 3. Oxygen consumption, which in these cases includes deep water as well as benthic consumption, amounted to 0.09, 0.19 and 0.54 ml · L^{-1} · d^{-1} (4.0, 8.5, and 24 mmol O$_2$ · m^{-3} · d^{-1}). The lowest value occurred in March, before the spring bloom was over. The very high rate in September 1984 was obtained soon after an intensive autumn bloom (28) which might have influenced the results considerably. The deep-water layer was thin during all three experiments, 2.5–3 m only, and the observed values correspond to a consumption per unit area of 0.27–1.35 L · m^{-2} · d^{-1} (12–60 mmol O$_2$ · m^{-2} · d^{-1}), which seems high compared to the Kattegat mean value of 9 mmol O$_2$ · m^{-2} · d^{-1}, indirectly calculated by Rydberg (8).

While the full-scale experiments seemed to indicate that the oxygen consumption was dominated by benthic processes, measurements on sediment samples and dark Winkler bottles produced another result. The sediment samples taken during March–October 1985 in the outer Laholm Bay and SE Kattegat indicated a sediment oxygen uptake which varied between 0.8 and 0.19 L · m^{-2} · d^{-1} (3.7 and 8.5 mmol O$_2$ · m^{-2} · d^{-1}) with a mean value of 0.14 L · m^{-2} · d^{-1} (6.1 mmol O$_2$ · m^{-2} · d^{-1}) (Fig. 8). A few samples from shallow waters above 15 m, indicated similar results, 0.12–0.24 L · m^{-2} · d^{-1} (5.4–10.7 mmol O$_2$ · m^{-2} · d^{-1}), on more sandy substrate. The seasonal variations were relatively small. The deep-water oxygen consumption, on the other hand, showed stronger seasonal variations (Fig. 8). Minima occurred during summer. The mean value was 0.09 L · m^{-3} · d^{-1} (3.8 mmol O$_2$ · m^{-3} · d^{-1}) which for a deep-water depth of 2.5–3 m corresponds to 10.7 mmol O$_2$ · m^{-2} · d^{-1}. These measurements were repeated in 1987 and 1988. In this period, however, the seasonal variations were small. The annual mean consumption in the deep water amounted to 6.2 mmol O$_2$ · m^{-2} · d^{-1} in a 10-m layer (deeper stations, more shallow halocline), while the mean sediment oxygen uptake amounted to 8.0 mmol O$_2$ · m^{-2} · d^{-1}.

Thus, the full-scale experiments indicate twice as high oxygen consumption as the other studies. The annual mean for the

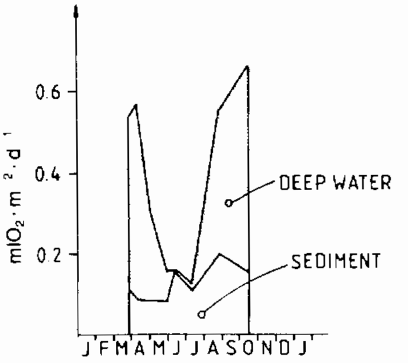


Figure 8. Deep water and sediment oxygen uptake on incubated samples from 1985 (24).

Table 4. Carbon and dissolved inorganic nitrogen (DIN) budgets based on primary production and ^{15}N-nitrogen uptake in the surface water of SE Kattegat, external loading of DIN to the surface water, sedimentation through the halocline and oxygen consumption in deep-water and benthic areas (numbers within parentheses are recalculated from observed DIN values using Redfield ratios).

	Spring bloom (1–15 March)		16 March–31 October		Total	
	carbon	DIN	carbon	DIN	carbon	DIN
	($mmol \cdot m^{-2}$)		($mmol \cdot m^{-2}$)		($mmol \cdot m^{-2}$)	
Primary production	1580	–	9830	–	11 420	–
Nitrogen uptake						
$NO_3 + NH_4$ + urea	(2390)	360	(13 590)	2050	(15 980)	2410
$NO_3 + NH_4$	(1330)	220	(9680)	1460	(11 140)	1680
NO_3	(780)	120	(3090)	470	(3890)	590
DIN external load	(770)	116	(2300)	350	(3070)	460
Sedimentation	300	–	–	–	–	–
Oxygen consumption	–	–	–	–	(4300)	–

[1] 85–90% is NO_3^-, the rest mainly NH_4^+.

full-scale experiments was 30.3 mmol $O_2 \cdot m^{-2} \cdot d^{-1}$ (1983–1984) and for the sum of the incubation studies 14.2 (1987–1988) and 16.8 (1985) mmol $O_2 \cdot m^{-2} \cdot d^{-1}$, divided approximately equally between deep-water and benthic consumption. The results may be compared to experimental investigations on Belt Sea sediments which gave values of 10.6 mmol $O_2 \cdot m^{-2} \cdot d^{-1}$ (26, bell-jar experiment) and 26.8 mmol $O_2 \cdot m^{-2} \cdot d^{-1}$ (27, oxygen electrode), respectively. However, none of these five studies were comparable. The variation in time and space in our measurements was also considerable, but the mean value (March–October), based on equal weight for each study, of 20 mmol $O_2 \cdot m^{-2} \cdot d^{-1}$ might still be a useful estimate in future discussions.

DISCUSSION

We may now try to put the results, including those from the studies on nitrogen uptake (12) together. First, however, let us make two general statements: 1) as mentioned nitrogen is considered to be the limiting nutrient in SE Kattegat (and Kattegat), this conclusion is based on different approaches, where both ambient nutrient concentrations, mass balance equations and laboratory incubations have been used (8, 29, 30); 2) in SE Kattegat, where there are other important sources of "new" nutrients than from the deep-water supply (Table 2), we use the terminology suggested in Wassmann (31), implying that new production (determined from "new" nitrogen) is made up of the sum of all external sources of DIN which enter the surface water.

In Table 4, we have summarized our results from SE Kattegat on primary production, nitrogen uptake (12, 32, 33), supply of inorganic nutrients to the surface water, sedimentation and oxygen consumption (benthic and deep water). A distinction is made, as previously, between the spring-bloom period and the rest of the productive season until the end of October. In presenting these averages we must be aware of the scattering in sampling strategy. Primary production and nutrient fluxes were determined monthly during 1981–1985 and 1982–1985, respectively. Measurements on nitrogen uptake are mainly from 1985, while oxygen uptake was determined on several occasions over a number of years. Results on sedimentation through the halocline were obtained only during the spring blooms of 1984 and 1988.

According to Table 4, the spring bloom represents about 15% of the primary production from March to October. This relation holds also for the nitrogen uptake, both when urea is included and when it is not. For nitrate uptake only, the corresponding proportion is 20%, and for the external supply of DIN to the surface water about 25%. These results correspond to our initial hypothesis; a larger proportion of new production during the spring bloom seems realistic, as there is a considerable amount of nitrate available in the winter nutrient pool, showing up also in the ^{15}N measurements.

A comparison between measured primary production and carbon uptake, determined from nitrogen uptake (using Redfield ratios), indicates that the latter, if urea is included, overestimates the carbon uptake by about 25%. On the other hand, carbon uptake determined from the sum of nitrate and ammonia uptake only, is almost exactly equal to the measured primary production, both during the bloom and for the whole season. The overestimate may be due to different factors. One is that ^{15}N-uptake may be enhanced in nitrogen depleted waters as suggested by McCarthy and Goldman (34). Another reason could be that measurements were not made simultaneously, but on the other hand, most ^{15}N measurements were made during 1985, when the primary production was 30% below the mean annual production, corroborating the overestimate.

Nitrate uptake in relation to primary production indicates 50% new production during spring bloom and 30% thereafter. The corresponding numbers using a definition (32), where nitrate uptake is compared to the total nitrogen uptake, including urea, are considerably lower (30 and 23%, respectively). The nitrate uptake is also nearly equal to the external supply of DIN to the surface water.

Sedimentation through the halocline during the spring bloom is far below the corresponding nitrogen uptake and the external DIN supply, and only 20% of the primary production. The value is in the same range, however, as observations by Smetacek (35) and by Smetacek et al. (36) in the southern Belt Sea (12–40%), but lower than seasonal mean values found by Wassman (37) in a Norwegian fjord. The large amounts of ephemeral mud blankets in the outer Laholm Bay, reported by Floderus and Håkanson (22), however, indicate that the sedimentation flux is underestimated.

The average oxygen consumption (benthic and deep water), finally, exceeds, if recalculated to carbon uptake (using Redfield ratios) both the external DIN supply and the nitrate uptake, with between 10 and 25% (one abnormally high value, obtained during September 1984, raised that value from 3800 to 4300 mmol $O_2 \cdot m^{-2}$). There is no reason to exclude this value (as discussed earlier) but according to the results shown in Table 4 there seems to be at least a 1:1 relationship between oxygen consumption and external DIN supply. In fact, it is not surprising that the ratio exceeds 1:1, as sinking organic matter from the inner part of Laholm Bay and other areas may be exported to the deep-water bottoms of SE Kattegat.

We can now also make an estimate of how a decreased nitrogen supply from land would affect oxygen consumption. Rydberg and Sundberg (38) first approached this problem by suggesting a 1:1 relationship between oxygen consumption and external DIN. Thus, a 50% decrease of the land-based nitrogen load to Laholm Bay, Skälderviken and the northern Sound would decrease the external DIN supply by slightly less than 20% (Table 2; assuming unchanged supply from other sources including the deep water), decrease oxygen consumption by as much (1:1 relationship), and increase the mean deep-water oxygen concentrations during late summer by about 7% for an unchanged water exchange (38).

Summarizing results for the SE Kattegat, the mean annual primary production was 144 g C · m^{-2}, about 15% of which was produced during the spring bloom. These figures are almost a perfect match with the corresponding uptake of inorganic nitrogen (not including urea) observed using the ^{15}N technique. The nitrate uptake in relation to primary production indicated 50% new production during the spring bloom and 30% thereafter. The measured nitrate uptake exceeded slightly ($\approx$10%) the external supply of DIN to the surface water, of which 50% was of local origin and 50% from the deep water. There seems to be an almost 1:1 ratio between oxygen consumption and nitrate uptake:DIN supply. In relation to the Kattegat as a whole and the Laholm Bay, the supply of nutrients according to Table 2 indicated that the spring-bloom production is evenly distributed while the external nutrient supply during the rest of the productive season indicates higher production rates in SE Kattegat and Laholm Bay compared to the open Kattegat waters. The primary production in SE Kattegat (144 g C · m^{-2}, Stn 19) also exceeded the Kattegat mean value which was about 105 g C · m^{-2} (1). The measurements were from different periods, however, but from the few measurements of summer production at Anholt during the 1980s (Fig. 4) it would appear that the changes are small. The oxygen consumption, finally, was about twice as high in SE Kattegat compared to the open Kattegat (20 mmol $\text{O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and 9 mmol $\text{O}_2 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (8), respectively). This difference is greater than motivated by the difference in nitrogen supply and primary production.

As much as 50% of the land-based nitrogen supply is organic (Fig. 6), of which a large proportion seems strongly bound to humic substances. However, organic supply from land-based sources could increase the external nutrient supply by about 10–20%. For phosphorus the organic part is small in wastewater, but high in river water. Compared to the deep-water supply, however, these levels are negligible (Table 2). This is not true, however, when considering the fluxes of organic nutrients across the horizontal and vertical borders which were also excluded in our budgets (Table 2). Particularly interesting is the contribution from the Baltic. One article (39) gives a very rough estimate; 25% of the outflowing Tot-N can be made available for the Kattegat primary production, which would correspond to a supply of about 12000 tons nitrogen to the Kattegat from March–October. One can imagine from the flux estimates in Table 2, that this is not negligible, but also that it is not indispensible for the conclusions drawn here. Obviously, this is a problem which must be solved in the future.

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Article

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Nutrient Limitation of Primary Production in the Baltic Sea Area

In the Baltic Sea area, including the Kattegat, the external N/P loading ratios are generally well above the 16:1 Redfield ratio for all subareas (the Bothnian Bay, the Bothnian Sea, the Baltic proper and the Kattegat). During winter, the inorganic N/P ratio in surface waters varies. Appreciably higher values than the loading ratio are found for the northernmost basin, the low-saline Bothnian Bay, while lower values than the loading ratio are found for the Baltic proper and the Kattegat. Nutrient enrichment tests indicate general N limitation in the Baltic proper and the Kattegat, although stimulation of algal growth after P enrichment has been found in the Baltic proper during summer blooms of blue-green algae. Blooms of blue-green algae are common in the Baltic proper but hardly ever occur in the Bothnian Bay and the Kattegat. This has been the case for the last century, indicating natural summer N limitation. Full-scale experimental manipulation of the external N/P loading ratio has been carried out in the Himmerfjärd basin, south of Stockholm. Results suggest nitrogen as the most limiting nutrient in coastal areas of the Baltic proper, uninfluenced by direct nutrient discharges. The knowledge of the effects of altered external nutrient supplies for nutrient limitation in the Baltic Sea system as a whole is too limited to allow for reliable predictions. However, the Baltic Sea may have developed towards a more pronounced N limitation due to a twofold historic increase in P supply relative to N supply. At present, the situation may be reversed as N supply is probably increasing more rapidly than P supply. Management of the Baltic Sea area cannot be based on removal of either N or P in sewage, but must take both elements into consideration, as well as differences between sub-basins and between polluted coastal and offshore areas.

INTRODUCTION

The Baltic Sea area comprises several more or less distinct basins or subareas in a large-scale salinity gradient, ranging from a few ‰ in the Bothnian Bay to more than 20‰ in the northern Kattegat (Fig. 1). Although the Kattegat surface water is strongly influenced by the north-going low-salinity Baltic current, there are fundamental differences between the hydrography of the Baltic proper and the Kattegat. In the latter a thin (10–20 m) surface layer of low salinity water (15–25‰) is underlain by water of almost full oceanic salinity (>30‰, (1). Water exchange in the Kattegat is measured in months. The Baltic proper has a deep (60–80 m) halocline separating two brackish water masses of salinities approximately 6 and 10‰ for surface and deep water. Water renewal is slow, 20–30 years is the mean residence time for a conservative element in the Baltic Sea.

There is strong, albeit largely indirect, evidence that in the last decades primary production and sedimentation have increased in the Baltic including the Kattegat (2–4). As a consequence, oxygen deficiency has become more widespread in these strongly stratified brackish waters due to the greatly increased external nutrient loading from rivers, direct sewage discharges, and atmospheric deposition (1, 5).

Since it is generally believed that total primary production can not be simultaneously limited by several nutrients (6), the question arises as to which nutrient should be controlled in order to stop or reverse eutrophication. A debate resembling the limiting-nutrient controversy in North America in the beginning of the 1970s (7) has been raging for the last few years (6–17). While the earlier controversy dealt with lakes and involved phosphorus versus carbon as limiting nutrients, the new controversy focuses on marine and brackish coastal waters and involves phosphorus versus nitrogen. Following the paper by Ryther and Dunstan (18), marine scientists have generally favored nitrogen limitation (6), and the study of nitrogen in marine ecosystems has proliferated (19). However, phosphorus limitation has been inferred in several studies (14, 20–23). For the Baltic Sea, N limitation of phytoplankton production was proposed already in the early 1970s (24–29).

Extrapolations from geographically limited investigations to all coastal (or even all marine) ecosystems may be one reason for the N-P controversy. Theoretically, the interplay between external nutrient supply (through N/P-balanced oceanic deep-water, P-deficient unpolluted freshwater, P-enriched domestic sewage or N-enriched agricultural runoff) and internal ecosystem processes (excretion, microbial immobilization or mineralization, nitrogen fixation, sedimentation, denitrification, P-adsorption, burial) could lead to any type of limitation on the N-P scale. Seasonal shifts in nutrient limitation have been observed (30–32) as have shifts within salinity gradients (33, 34), which are of relevance for the Baltic Sea, a vast estuarine-like area. Differences in opinion on nutrient limitation may also be due to the methodology used (6, 14, 16).

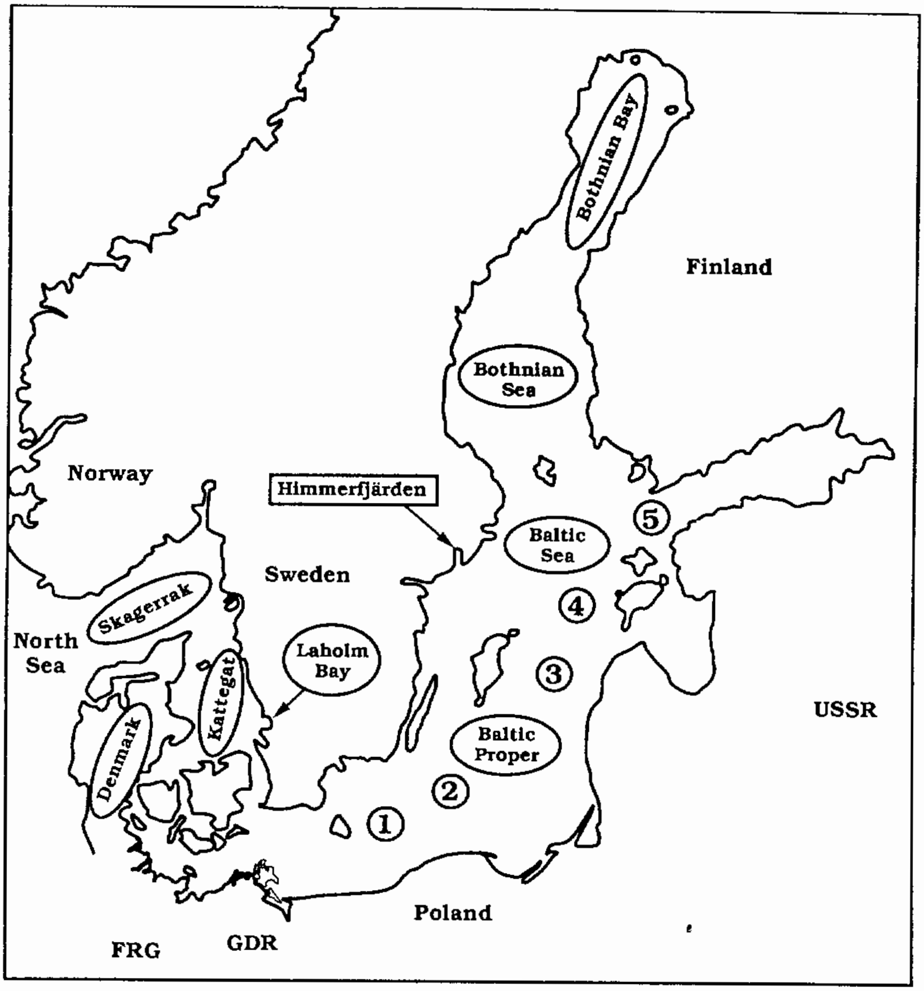
When discussing eutrophication one must treat the question of nutrient limitation in a long-term perspective; what was limiting in the pristine condition, what is limiting at present, what can be made limiting through nutrient-control efforts and what effects will different nutrient management strategies have on the Baltic Sea ecosystem?

The N-P controversy has great practical implications since phosphorus and nitrogen have different biogeochemical cycles, different man-made sources, and for their control require different approaches. Contrary to nitrogen, control of phosphorus in sewage is technically rather simple and has been adopted on a large scale in Sweden for the last two decades (35). Because there are other input sources, often larger than sewage (5, 36), nitrogen control is more costly and requires profound changes in, e.g. agricultural practice, and transportation routes (37). If, as has been argued by some scientists (13, 14), nitrogen does not limit net primary production or net ecosystem production, nitrogen reduction measures to control marine eutrophication would be an enormous waste of money.

We will try to show that there is sound scientific evidence in favor of both nitrogen and phosphorus control, but that management policies must consider local as well as regional differences in the Baltic Sea system.

We discuss nutrient limitation in the various sub-basins of the Baltic with main emphasis on the Baltic proper and the Kattegat, where most research has been

Figure 1. Map of the Baltic Sea with intensively studied areas (Laholm Bay and Himmerfjärden) and stations for nutrient enrichment tests in the open Baltic proper.



conducted, partly in connection with the Marine Eutrophication Project of the National Swedish Environmental Protection Agency (38). We will try to separate nutrient limitation in inshore waters, that are directly influenced by river discharge or sewage, from limitation in open waters.

THE CONCEPT OF NUTRIENT LIMITATION

There are three main types of nutrient limitation of primary producers: limitation of the growth rate of the individual algal population; limitation of net primary production or net biomass accumulation; and limitation of net ecosystem production (6, 14, 15).

The supply rate of nutrients and the ratio between these supply rates has a decisive influence on the species composition of the plankton community (39). Because different algae have different nutrient requirements some species may be phosphorus limited, while others are simultaneously nitrogen limited. From a practical point of view the species composition of the algal community is important because, e.g. blue-green algae, dinoflagellates and green macroalgae are noxious due to toxicity, scum formation, accumulation on shores, etc., while other species, e.g. diatoms, are regarded as positive due to a high nutritive value for zooplankton.

The definition most often applied to nutrient limitation in aquatic ecosystems is the limitation of net primary production or biomass accumulation (6). Nutrient limitation of net ecosystem production is most relevant when discussing production of harvestable products (e.g. fish), net sedimentation and deep-water and benthic oxygen uptake. Net sedimentation sets an upper limit on deep-water and benthic oxygen consumption and is therefore of special interest in strongly stratified waters such as the Baltic Sea area (40).

For the Baltic Sea area, export of inorganic nitrogen and phosphorus is small compared to external supply or internal biological turnover (5, 41 42). This is a strong indication that total primary production is nutrient limited, but does not suggest which nutrient is limiting.

METHODOLOGICAL APPROACHES

Nutrient limitation of marine phytoplankton growth has been inferred, e.g. through nutrient supply ratios (14), N/P ratios in surface water (43) and physiological indices (21, 44). Experimental approaches are common, e.g. nutrient enrichment tests (45), but investigations of whole ecosystems are rare. In this respect, marine research on limiting nutrients lag behind limnological research where many "whole-lake" experiments have been made (e.g. 46–48). Much of the methodology on phytoplankton nutrient-limitation research is open to criticism (14, 16, 49), but we believe that through a combination of approaches (50) a coherent picture of nutrient limitation can be gained for the Baltic Sea area. However, as has been pointed out by, e.g. Howarth (6) there is a strong need for full-scale and mesoscale experiments involving manipulation of the external nutrient supply. A full-scale experiment on marine (brackish-water) nutrient limitation involving variation of the external N/P supply ratio is currently being performed in the Himmerfjärd basin of the Baltic proper (51, 52). Although this experiment has not yet terminated we believe its provisional results merit presentation here.

EXTERNAL NUTRIENT LOADING

Net ecosystem production is directly proportional to the external supply of the limiting nutrient under steady-state conditions. Theoretically, the ratio between the different nutrients in the external supply should determine what element ultimately limits net ecosystem production, unless there are internal sinks and sources. The external supply for the different subareas of the Baltic must, beside river and direct sewage inputs, also include net advective transports between the areas and atmospheric deposition directly on the sea surface. While a large fraction of the nitrogen input is in organic (partly humic) form of limited direct availability, much of the organic phosphorus may be bioavailable (53, 54), e.g. after enzymatic splitting of organic compounds (23, 55). To what extent organic nitrogen is directly or indirectly (e.g. after bacterial breakdown) available to phytoplankton is still largely unknown. Another problem with external nutrient supplies is that reliable data are difficult to obtain. For the Baltic Sea area nutrient loading has only recently been estimated with an acceptable accuracy, and historic trends in the supply are uncertain (5).

The molar tot-N/tot-P external supply ratio (excluding N_2 fixation and net advection) on the Baltic Sea area (including the Sound and the Belt Sea) is 30, i.e. double the Redfield value (5), and ranges from 16 for the Sound and Belt Sea (including the Kattegat) to 46 in the Bothnian Sea (Fig. 2a). Only the Sound and Belt Sea area have external N/P supply ratios close to the Redfield value. This is due to large municipal and industrial phosphorus discharges in the Sound area. According to Larsson et al. (5), the external loading ratio before the 20th century on the Baltic Sea area was over 50, thus, even more towards relative excess of N than at present. All these loading ratios, with the possible exception of the ratios for the Sound and the Belt Sea area, presently indicate a phosphorus limited potential primary or net ecosystem production. Roughly half of the external nitrogen load is in organic form (56). If we make the assumption that all externally supplied P is available to algae on a short-term basis (weeks), but only half the N, the present overall N/P supply ratio (excluding N_2-fixation and net advection) decreases to 15, i.e. a rather balanced situation with respect to the mean demand of the phytoplankton.

For the more intensely studied areas, the Himmerfjärden and the Laholm Bay, external loading ratios are somewhat more complicated to compute because a large part of the "external" loading is in the form of horizontal advection and vertical entrainment of deep water (1, 15). For the Laholm Bay, land-based supply had a N/P ratio of 77–142 (inorganic fractions for both N and P), while deep-water supply ratios varied between 8.9 and 12.2, giving a total inorganic nutrient supply ratio of 22–49 (15).

In summary, external nutrient loading ratios imply phosphorus limitation of net primary or ecosystem production in the Baltic Sea (including the Kattegat with Laholm Bay). However, inorganic nutrient ratios in surface water as well as phytoplankton species composition and enrichment experiments usually indicate nitrogen limitation.

NUTRIENT CONCENTRATIONS AND N/P RATIOS IN SURFACE AND DEEP WATER

A general criticism when discussing nutrient limitation utilizing concentrations of potentially limiting elements is that it is not the amount present in the water at any given moment, but the supply rate to the algae which is of importance (13, 57). During summer only small amounts of available nutrients can be found in surface waters. Supply of nutrients under these conditions is mainly through regeneration and vertical transport, which may bear no proportionality to concentrations of inorganic nutrients in the surface water. More relevant to a discussion of limitation of net ecosystem production in such a situation would be to use nutrient ratios in the external supply, e.g. deep water and river input. In spring, however, algal growth is based on nutrients accumulated during the winter. Since the nutrient pool at this time of the year is more important to algal growth than the external supply and regeneration, the concentration ratios in the winter surface water may be used to indicate which nutrient is most limiting for the spring bloom.

While the external loading ratios are mostly well above the Redfield value in all Baltic Sea subareas, inorganic N/P ratios in the water during winter are usually substantially below. There is a marked gradient in this ratio (Fig. 2a). The Bothnian Bay stands out as different from the other subareas, with a relatively high inorganic N/P ratio, which resembles freshwater conditions. This is due to a combination of low phosphate and high inorganic nitrogen levels. The Bothnian Sea is a transition area, where the ratio decreases rapidly to below the Redfield value. In the Baltic proper, the Sound and the Kattegat the inorganic N/P ratio in the surface layer is well below 16 during winter. However, there seems at present to be a trend towards an increase in the N/P ratio (Fig. 2b), possibly due to an increase in the external nitrogen supply, but no further increase in the phosphorus supply.

In the Laholm Bay, the mean winter ratio was for January-February 1982–1984, 15, while in the open southeastern Kattegat the mean ratio was 12; the difference being caused by large amounts of river water with a high N/P ratio entering the Bay (15). If total fractions are used the ratios increase substantially, <20, due to organic nitrogen contributing some 60% of total N, but organic P contributing less than 40% of total P.

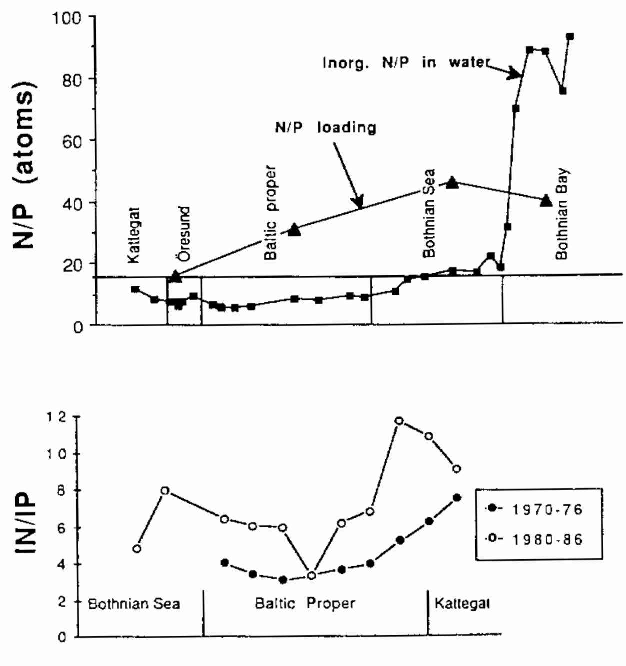


Figure 2. Winter (November–December, before the onset of the spring bloom) inorganic N/P-ratios (atoms) in surface water (0–10 m) from the Kattegat-Baltic proper-Bothnian Sea-Bothnian Bay section (data for the period 1974–1978 [108]). External total N/P loading ratios (not including nitrogen fixation or advection from adjacent basins) also shown (5). Lower figure shows inorganic N/P-ratios from 1970–1976 and 1980–1986 for the Baltic Sea (based on ICES data F. Wulff, Askö Laboratory, Sweden).

A comparison of external N/P supply ratios and ratios in the winter surface water (when primary production is low) reveals the importance of internal processes for the regulation of nutrient concentrations. Low N/P ratios in surface water may arise due to preferential regeneration of P from organic matter in surface water of the open sea (58) or due to benthic denitrification in shallow waters or in near anoxic deep waters. In the Bothnian Bay, the external tot-N/tot-P loading ratio is approximately 40, while the winter layer may show a ratio approximately double the level for inorganic N/P and even higher for total fractions. It seems then that phosphorus is preferentially retained in the Bothnian Bay and nitrogen in the rest of the Baltic Sea. Judging from these figures the spring bloom should be nitrogen limited in the Baltic Sea, except for the Bothnian Bay, where P limitation should be found.

As deep-water supplies a large fraction of nutrients for open water new primary production after the spring bloom, the N/P ratio of this water should determine which element becomes limiting. Deep-water N/P ratios in the Baltic are very low, indicating N limitation. The low N/P ratio of Kattegat below-halocline water has been mentioned above, driving production towards N limitation (45). The low N/P ratio in these deep waters is no doubt due to (benthic) denitrification (59–61).

COMPOSITION OF THE ALGAL COMMUNITY

Different algal species have different nutrient requirements. This means that the supply ratio of the nutrients is one potential factor that structures phytoplankton communities, through the process of resource competition (62). However, nutrient supply is not the only structuring force, loss factors, e.g. sinking, grazing, and parasitism, as well as light conditions and temperature may gain equal importance. Loss factors are likely to be species-specific. Grazers may avoid larger blue-green algae and dinoflagellates but select for diatoms (63–65). The optimal nutrient requirements of most algal species are not sufficiently known to permit a detailed discussion of the influence of nutrient ratios on species composition. However, diatoms as a group have an obligate requirement for silica and many blue-green algae can fix molecular nitrogen, making them potentially superior competitors under low nitrogen conditions. The prevalence of blue-green algae and a high heterocyst activity (N_2-fixation) may thus indicate nitrogen limitation (48). A low N/P supply ratio and a high P availability are thought to favor N_2-fixing blue-greens (6, 48, 66–69), although Cole et al. (70) have proposed that N_2-fixation is depressed by an unfavorable sulfate/molybdate ratio in saline waters and Paerl et al. (71) by lack of organic substrates. The occurrence of blue-green algae may also be strongly dependent on water temperature (69, 72).

The substitution of diatoms by, e.g. dinoflagellates or other algae may indicate silica shortage (73). As silica supply is influenced relatively little by human activity, eutrophication (due to increased external input of nitrogen and phosphorus) may deplete silica if net primary production is increased, especially since silica is not as efficiently regenerated from sedimenting algae as is nitrogen and phosphorus (74). This indirect effect of eutrophication on phytoplankton-community structure deserves attention since diatoms are regarded as more desirable than dinoflagellates and blue-green algae.

In the Baltic proper, large summer blooms of nitrogen-fixing blue-green algae are common (75). In lakes, dominance of blue-green algae has been correlated to low N/P ratios (67), which obviously is also valid for the Baltic proper (75). However, equally low N/P ratios can be found in the Kattegat, where blooms of blue-green algae occur only exceptionally (76, 77). The reason is probably related to salinity, as the N_2-fixing species dominating the blue-green algal blooms in the Baltic, *Aphanizomenon flos-aquae* and *Nodularia spumigena*, tolerate salinities ranging from freshwater to 20‰ (78). Blooms of *Nodularia spumigena* are also found in some other brackish water areas, e.g. the Peel-Harvey estuary in Australia, but only when river discharge is high and salinity low (79).

As the external phosphorus supply to the Baltic has increased more than the external nitrogen supply over the present century (5) leading, thus, to a decreased N/P supply ratio, it may be hypothesized that blue-green algal blooms are novel phenomena, or at least that such blooms have increased in frequency, size, and biomass (68). However, blooms of *Nodularia spumigena* seem to be natural phenomena in the Baltic and were recorded as far back as the middle of the 19th century (80, 81). If there was an environment favoring blue-green algae in the Baltic before man had any appreciable influence on the external nutrient supply, then there must be naturally occurring processes leading to nitrogen limitation.

On an annual basis, pelagic nitrogen fixation seems to contribute little (approximately 15%) to the external nitrogen supply to the Baltic proper (5). Denitrification is several times higher than nitrogen fixation (5, 60). This means that a large nitrogen excess in the external loading is necessary to balance the nitrogen budget. One of the main arguments of Smith's (14) hypothesis that phosphorus supply controls net-ecosystem production is that nitrogen fixation will match any nitrogen deficiency, especially in systems with a long water-residence time, such as the Baltic. There is no indication that this occurs in the Baltic Sea.

PHYSIOLOGICAL INDICATORS

There is often no physiological indication of nutrient limitation in oligotrophic oceanic water. Such indications may show up at the end of algal blooms in eutrophic coastal waters (82). For the Baltic Sea area physiological signs of nutrient limitation should be most easy to detect in connection with the spring diatom bloom or during the summer dinoflagellate or blue-green algal blooms.

A common test for P-deficiency is the analysis of alkaline phosphatase activity (APA) (21, 23, 55, 83–85). Alkaline phosphatases are inducible enzymes, used to split off phosphate from organic phosphorus compounds. Their presence may indicate P-shortage. The interpretation of APA values is difficult since both bacteria and zooplankton produce these enzymes and internal phosphatases may be leaked to the water upon injury or autolysis (55). However, together with other nutrient limitation indicators APA may provide valuable information.

In the Kattegat and the Laholm Bay APA was investigated by Nyman and Granéli (83). They found low activity before, during, and after the spring-bloom period as well as in the autumn, both in absolute terms and when normalized to chlorophyll *a*. High APA could, however, be induced if Laholm Bay water was mixed with river water with high N/P ratios, indicating that the spring bloom in the Kattegat is not P starved, but that river water could, potentially, induce P limitation. Zero APA was observed in the open Kattegat in the summer of 1988 (Granéli unpublished data). In all cases N/P ratios were low and enrichment tests indicated N as potentially biomass limiting. Results from the Kattegat differ from measurements of APA in the North Sea, where high activity has been observed in connection with blooms of *Phaeocystis pouchetii* (23), or in the Adriatic Sea (21). Wallström (86) measured occasional increases of SAPA (chlorophyll-specific APA) at the control (outer) station in the Askö archipelago after the spring bloom and in connection with high blue-green algal or diatom biomass in summer. However, high SAPA was not always correlated with low phosphate concentrations. During a bloom of nitrogen fixing algae in the open Baltic proper high APA was mainly associated to monads and picoplankton (87). The simultaneous occurrence of nitrogen fixing algae and high APA (87), suggests that the N and P supplies are well balanced for phytoplankton during blue-green algal blooms in summer. This may partly be an effect of nitrogen fixation successively increasing the nitrogen pool in the trophogenic layer.

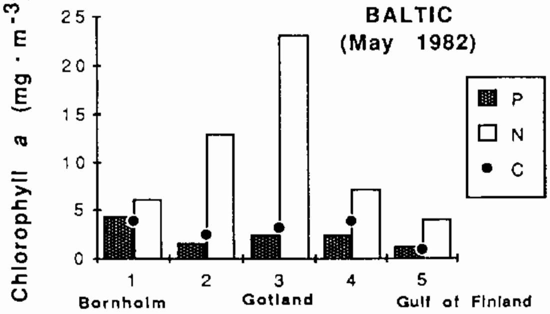


Figure 3. Enrichment tests with water from various parts of the open Baltic proper (stations according to Fig. 1). To filtered surface water samples an inoculum of a test algae was added (*Phaeodactylum tricornutum*) along with various single nutrient spikes. Bottles were laboratory incubated and the maximum concentration of chlorophyll *a* produced was recorded for each bottle. C = control, no additions; N = nitrate addition; P = phosphate addition.

ALGAL GROWTH POTENTIAL AND NUTRIENT ENRICHMENT TESTS

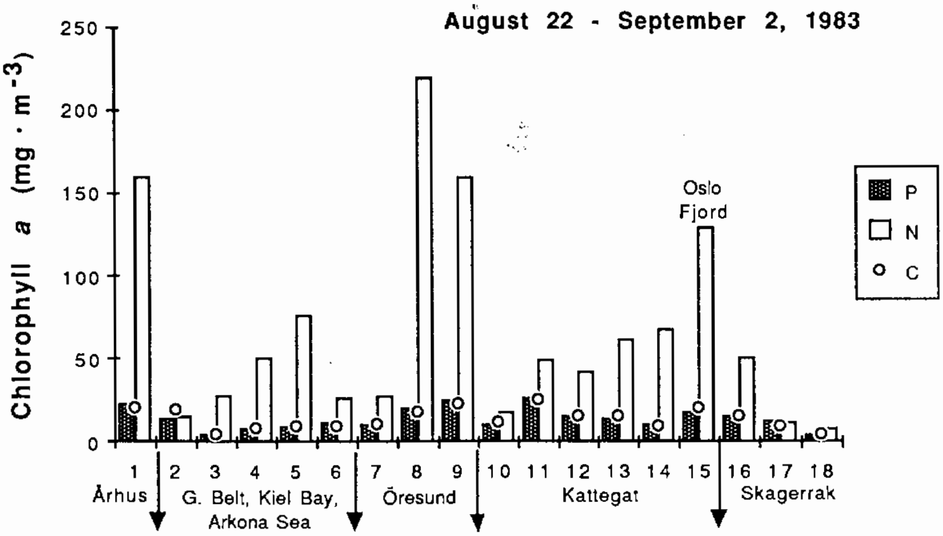
Algal growth potential (AGP) is a measure of the capacity of biomass formation, and AGP is often measured by adding an innoculum of a test algae to a filtered water sample which is incubated in a flask under laboratory light and temperature conditions for up to a week. Instead of test algae the natural plankton community can be used. In combination with differential nutrient enrichments such tests (enrichment tests, algal bioassays) can indicate the possibility for further algal growth and what nutrient potentially limits growth. The same principle can be applied in situ, using larger systems, e.g. plastic bags.

Traditional enrichment experiments can be criticized on the ground that nutrient supply from deep water, etc. is blocked and that the test is usually of such short duration that feedback mechanisms are not operational. However, in combination with nutrient supply data, nutrient ratios in surface water, and absolute nutrient concentrations, enrichment experiments give an idea of which nutrient momentarily limits further algal biomass production.

A large number of enrichment experiments have been performed in the various subareas of the Baltic Sea (15, 27–29, 45, 88–96), although a majority of these tests have been concerned with nearshore waters (92). Few results are available from the open Baltic and none from the open Bothnian Sea and Bothnian Bay. Enrichment tests have been made using either unialgal cultures, both blue-greens and diatoms (88, 94), natural plankton communities in laboratory bottle experiments (45, 90), bags, or larger plastic enclosures *in situ* (89, 91, 96).

Strong algal growth stimulation after nitrogen addition was observed for surface water from the Baltic proper during a cruise in May 1982, i.e. after the spring bloom, but before the onset of blue-green algal blooms (Fig. 3) (97). Enrichment bioassays from transects in the open Kattegat, the Belt Sea, including the Sound and the Skagerrak, during the summer period also indicate marked nitrogen

Figure 4. Enrichment tests for stations in the Skegerrak–Kattegat–Öresund (The Sound)–Belt Sea section. The diagram shows the maximum amount of chlorophyll *a* produced in bottles with the natural phytoplankton assemblages from surface waters, incubated under laboratory conditions without additions (C) with nitrate (N) and phosphate (P) additions.



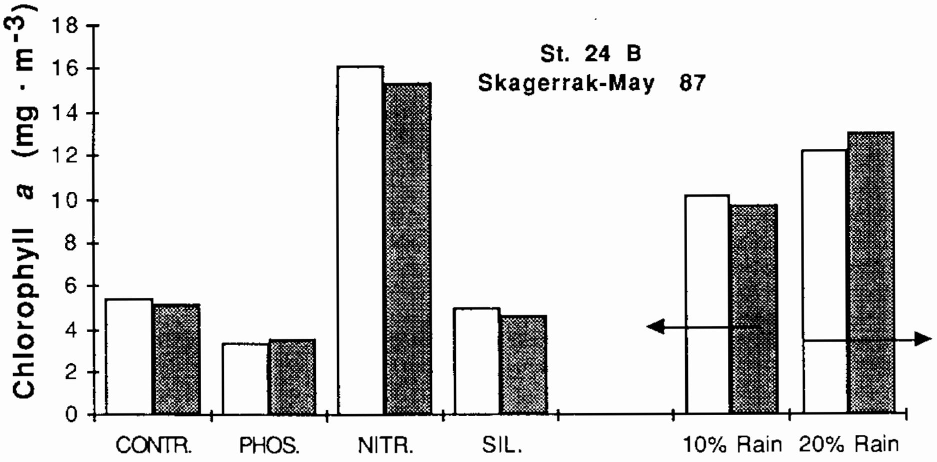


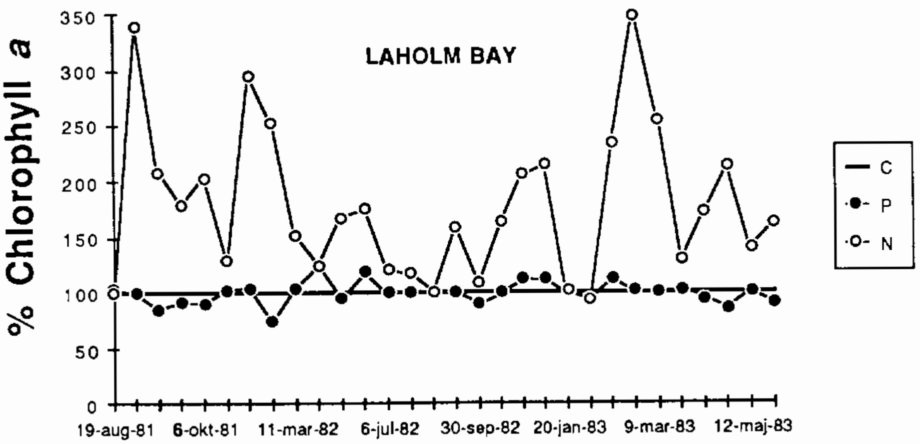
Figure 5. The effects on biomass production (maximum chlorophyll *a* values) of laboratory-incubated surface water with the indigenous phytoplankton assemblage from a station in the open Skagerrak, incubated without additions (contr.), and with additions of phosphate (phos.), nitrate (nitr.), silicate (sil.) and 10 and 20 % rainwater, collected at Lund, south Sweden. Arrows show chlorophyll *a* values for samples diluted with 10 and 20 % distilled water. The open and stippled columns represent replicate trials.

stimulation, but no effects from P enrichment (Fig. 4). These results are entirely consistent with low N/P ratios, low APA (in the Kattegat and Skagerrak) and the occurrence of N_2-fixing blue-green algae (in the Baltic proper). Unfortunately, similar experiments have not been performed in the open Bothnian Bay, where P limitation should be the rule, judging from high N/P ratios in surface water.

Beside tests with nitrogen (mainly nitrate) additions, the effects of rainwater on Kattegat and Skagerrak phytoplankton communities have also been investigated. Precipitation over southern Scandinavia is acidic and the content of inorganic nitrogen has increased markedly, as is the case in other industrialized areas (98). Rainwater, which is low in P, should thus have a growth stimulating effect on N-limited phytoplankton (98, 99). Rainfall containing 0.8–1.2 mM inorganic N-stimulated phytoplankton growth in the Skagerrak (Fig. 5), stressing the importance of direct atmospheric nitrogen deposition on the Baltic Sea area (5).

Coastal studies on the effects of nutrient enrichment using laboratory tests have been conducted over the whole year, e.g. in the Sound (90), the Laholm Bay (15, 45) and the Askö area. These studies show that nitrogen addition, almost universally, stimulates phytoplankton growth and that phosphorus addition has no effect (Fig. 6), except during blue-green algal blooms in the Baltic proper. There are, with respect to the transition area from the Baltic proper to the Skagerrak, no indications of a seasonal switch between potential N and P limitation, as has been observed, e.g. in Chesapeake Bay (30) and the Oslo fjord (32). Such seasonal effects in open waters are less likely due to the slow water turnover time of the Baltic and the great dominance of Baltic water in Kattegat surface water. However, in coastal areas, and

Figure 6. Relative increase in chlorophyll *a* produced in laboratory-incubated bottles with water containing the indigenous phytoplankton assemblage from a central station in Laholm Bay, southeast Kattegat. C = control, no additions; P = phosphate addition; N = nitrate addition. (45).



especially in bays receiving high amounts of river or sewage-transported nutrients, relative to the magnitude of mixing with the open sea, there may be marked switching in potential nutrient limitation. This has, e.g. been observed in the inner part of the Laholm Bay (15) and the Himmerfjärd, where potential P limitation may be found during spring floods in the rivers, while during the rest of the year N limitation prevails even quite close to the river mouths. Enrichment tests using river water instead of single nutrient additions verify the strong growth stimulating effect of water originating in agriculturally dominated areas, and the induction of APA due to high N/P ratios of such water (83).

Enrichment tests have also been made with chelators and mixed trace metals. Except in combination with N such additions do not generally increase phytoplankton biomass in the Kattegat (Fig. 7) (45). Multiple additions usually indicate phosphorus as the secondary limiting nutrient (45, 88).

FULL-SCALE NUTRIENT MANIPULATION

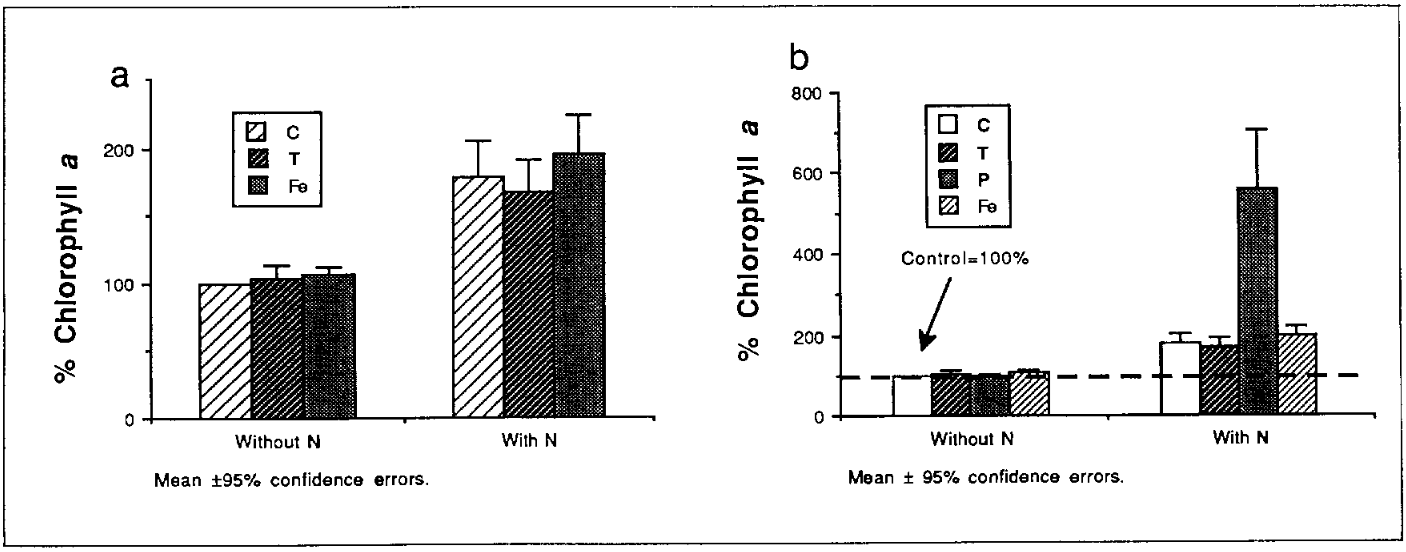
As a final test of the hypothesis that a specific nutrient limits net ecosystem production, experiments at the ecosystem level must be carried out (14, 16). The most unobjectionable test would be to decrease or increase nutrient supply to the whole ecosystem and measure effects on nutrient concentrations, phytoplankton community structure, pelagic primary production, sedimentation, and benthic metabolism. Experiments must be of an ecologically realistic duration to detect effects on time scales that are pertinent to environmental management. Such experiments have frequently been carried out on whole lakes and have mostly indicated phosphorus limitation (47), although for a substantial increase in production a simultaneous addition of nitrogen has sometimes been necessary (100). Whole-lake experiments finally terminated the phosphorus versus carbon limiting-nutrient controversy (7) by showing that given enough time a shortage in inorganic carbon or nitrogen caused by an increase in the external phosphorus loading will be overcome by invasion from the atmosphere and nitrogen fixation. Such experiments have been made on small lakes only and there are statistical problems due to the lack of replication and difficulties in finding suitable control lakes or control years. However, compared to the problems involved in similar marine experiments the limnologists have an easy task. Marine ecosystems are not confined as lakes are and careful attention has to be directed towards advective transport through water exchange with adjacent systems, e.g. the open sea. Time becomes a potentially large problem. Even a relatively small marine system such as the Baltic Sea most likely needs decades to fully adjust to changes in external nutrient loading (41). For smaller systems, e.g. the Laholm Bay and the Himmerfjärd basin, adjustment time may on the other hand be from a few months to a few years, which makes ecosystem experimentation potentially possible in such bays. One advantage of marine systems compared to lakes is that the former probably are not as buffered by nutrient stores in sediments as are lakes (74).

To our knowledge, beside "natural" experiments through eutrophication (usually poorly investigated) only one full-scale nutrient-addition experiment involving manipulation of N/P ratios has been performed in a marine or brackish-water area: the Himmerfjärd experiment in the archipelago south of Stockholm. Although this project is not yet finished results from the first years are discussed below.

The experiments in the Himmerfjärd inlet aimed at testing the full-scale effects of alternative management options regarding P and N removal in Baltic coastal areas. At the time of planning, effective P removal had been implemented in all major Swedish sewage-treatment plants, but some concern remained about the necessity of N removal. Thus, one object of these experiments was to test if predictions of a general nitrogen limitation could be validated in full-scale experiments. In the Baltic proper, N/P relations in the external load are particularly important in determining water quality. Excess phosphorus may cause nuisance blooms of nitrogen fixing blue-green algae, and thus counteract efforts to reduce the nitrogen load.

The Himmerfjärd area is a brackish (6‰ salinity) coastal inlet of 195 km^2 now receiving the effluent from a sewage-treatment plant serving 240 000 people, i.e. 50% (870 ton N · yr^{-1}) and 43% (17 ton P · yr^{-1}) of the external nitrogen and phosphorus loads. Water exchange is limited, particularly below the summer thermocline and during periods of ice cover. The tertiary sewage-treatment plant started operation in 1974, serving 90 000 people, and replaced the release of secondary-treated sewage from some 30 000 people further up the system. The number of people served increased gradually to 160 000 in 1983. In October 1983, phosphorus removal in the plant was deliberately reduced leading to a 3–4-fold increase in total phosphorus and 10-fold increase in phosphate phosphorus release which continued for one year. In 1985, the release of total nitrogen increased by 30–40% as a consequence of sewage from an additional 70 000 people being diverted to the plant. In 1988, nitrogen removal through denitrification started in the treatment plant, but the results from this manipulation are not included here.

Figure 7. Enrichment tests with Laholm Bay (southeast Kattegat) surface water containing the indigenous phytoplankton assemblages. Maximum chlorophyll *a* concentrations relative to a control without additions (C) in laboratory-incubated bottles supplied either with a trace-metal mixture (T), iron (Fe) or phosphate (P, only in experiment b), with and without nitrate (N).

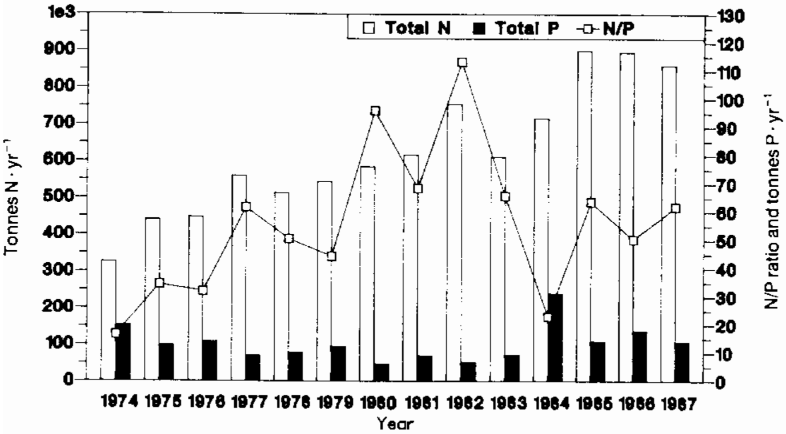


The high N/P ratio in the external sewage load to the Himmerfjärd inlet (Fig. 8) creates a pronounced inorganic nitrogen gradient, with concentration values in the area of the sewage outlet exceeding those at the reference station by a factor of 3 to 4 during winter.

Enrichment studies show that nitrogen was the most limiting nutrient in the reference area (Station B1), except on two occasions, in July/August 1982 and 1986, and during the 1988 spring bloom (Fig. 9a). Phosphorus limitation in July/August coincided with the occurrence of nitrogen-fixing blue-green algae. In 1985 and 1988, high inorganic nitrogen concentrations caused an almost balanced relation between nitrogen and phosphorus before the onset of the spring bloom. This was reflected in phosphorus being the most limiting nutrient on two occasions at the end of the 1988 spring bloom (no data available for 1985). Measurements of alkaline phosphatase activity (APA) also indicated phosphorus deficiency at the end of the 1985 spring bloom (Fig. 10). Otherwise, APA was generally low or undetectable, except during August 1984, again coinciding with the occurrence of nitrogen-fixing blue-green algae.

Contrary to the situation in the reference area there was an excess of nitrogen relative to phosphorus during the winter in the Himmerfjärden inlet (Fig. 9b). Consequently, phosphorus is the most limiting nutrient during spring and early summer, but when the inorganic nitrogen pool is exhausted, nitrogen becomes limiting (Fig. 9b). In 1984, decreased P removal in the sewage-treatment plant resulted in a higher P availability and thus P limitation occurred for only a short time at the end of the spring bloom as indicated by low APA values (Fig. 10). An increased nitrogen load 1985–1988 on the other hand resulted in a prolonged period of phosphorus limitation and increased alkaline phosphatase activities.

Figure 8. Annual total nitrogen and total phosphorus load from the sewage treatment plant to the Himmerfjärd inlet 1974 to 1987. Annual N/P weight ratios connected by solid line. Data from SYVAB (sewage-treatment plant).



Measurements of the number of heterocysts of *Aphanizomenon flos-aquae* showed very low values in 1983 and 1985, but a clear increase in 1984 (69), most likely as a consequence of higher inorganic phosphorus availability. The corresponding increase in nitrogen fixation has been estimated to be 6 to 8 tons per year (Wallström unpublished data), a small amount compared to the total discharged to the area of 1700 ton N per year.

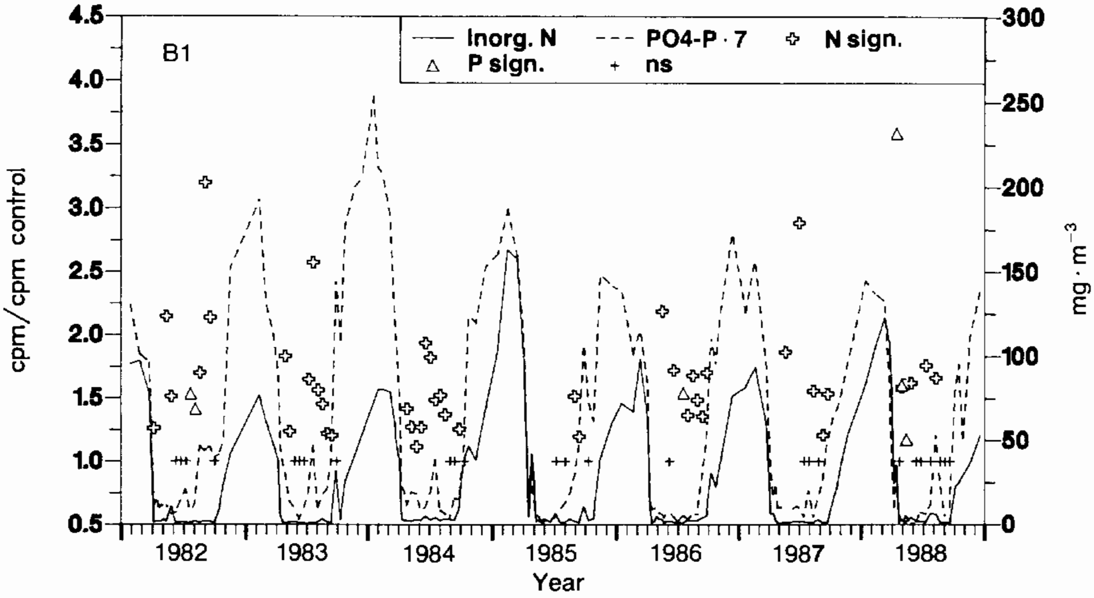
The results from the full-scale experiments support the observations presented above of nitrogen being the most limiting nutrient in coastal areas of the Baltic proper uninfluenced by direct nutrient discharges. In areas receiving external nutrient load, the N/P ratio of that load will determine whether nitrogen or phosphorus will be the most limiting nutrient. In the case of the Himmerfjärd inlet a substantial reduction of the present nitrogen load (70%) will probably not cause more than a minor increase in nitrogen fixation. The alternative approach, to improve the present 95% P reduction, will have only marginal effects in improving water quality close to the outlet, and result in increasing nitrogen export to the open Baltic.

OUTLOOK FOR THE FUTURE

The Baltic Sea ecosystem is most likely far from steady state and marked changes in the external nutrient supply, surface and deep-water nutrient concentrations, and nutrient ratios as well as in the biota have been seen during the last decades (3, 41, 42, 101, 102). This means that the most limiting nutrient today, may not have been most limiting 100-years ago and may not be so in the future.

Silica depletion has been reported from the Laurentian Great Lakes, (similar size to the Baltic Sea) due to increased external N and P supply (103). If less silica is avail-

Figure 9. Average inorganic nitrogen and phosphorus (multiplied by 7) concentrations (mg · m⁻³) in the top 5 m of the water column at stations B1 (reference area) and H4. Results of nutrient addition experiments are expressed as cpm (counts per minute) of fixed inorganic carbon-14 compared to the controls. Nitrogen additions yielding significant increases compared to controls are indicated by an open cross and significant increases due to phosphorus addition by a triangle. No significant increase is indicated by a plus sign.



able diatoms may ultimately become outcompeted. Indications of such a process have been found in the North Sea, which is heavily affected by eutrophication along the Dutch and Belgian coasts due to sewage and nutrients from the Rhine (73). There is a trend towards lower silica concentrations in the open Baltic (41), although there is still no indication that this has affected diatom growth, e.g. during the spring bloom. As eutrophication of the Baltic will most likely increase for several years, silica depletion and its effect on the balance between different groups of phytoplankton deserves further attention.

Silica enrichment experiments with Kattegat and Skagerrak water showed no effect on total biomass produced, and there were no indications of a reduction in diatom growth (45). The Kattegat may be less vulnerable to silica depletion compared to the Baltic proper due to a much shorter water residence time and larger admixture with Atlantic water. Silica depletion in the Baltic proper will, however, also influence silica concentrations in the Kattegat, especially in connection with the spring bloom, due to the transport of nutrient-rich Baltic "winter" water into the Kattegat surface water.

IMPLICATIONS FOR MANAGEMENT

In this paper, we have summarized our present knowledge of nutrient limitation of phytoplankton growth in the Baltic Sea including the Kattegat. Although substantial insight has been gained over the last decades, conclusions on proper management actions must still be based on a number of assumptions. Fundamental to a proper management of these enclosed sea areas is a knowledge of what nutrient was limiting in the pristine stage and how the rather different biogeochemistry of both nitrogen and phosphorus are affected when nutrient-load changes. The latter is closely connected to our possibilities to predict how relations between and absolute amounts of available nutrients will change with or in the absence of management actions.

The question of what nutrient limited algal growth in the pristine stage can, at present, only be dealt with through inference. The observations of blue-green algal blooms in the Baltic proper some 100 years ago, when anthropogenic contributions to the nutrient load were much less than today, is a strong indication that nitrogen was limiting algal growth at that time, at least during summer. This conclusion is also consistent with recent observations of nutrient limitation in the Baltic proper. If, however, we accept the estimate of Larsson et al. (5) of a twofold increase in phosphorus relative to nitrogen load since the pristine stage, the Baltic Sea may have developed towards a more pronounced nitrogen limitation.

A return to a pristine Baltic Sea is probably not feasible within decades. The question is whether nitrogen management can cause a reduction in primary production or whether internal regulatory mechanisms in the nitrogen cycle will offset all such management efforts (13, 104) and whether phosphorus management is meaningless in a seemingly nitrogen- limited system. All discussions about the Baltic Sea as a whole will by necessity be speculative. Thus, it is perhaps more relevant to start with local receivers when discussing nutrient management.

The "natural fertilization experiment" in the Stockholm archipelago shows that a strong reduction in phosphorus has improved water-quality conditions markedly in the inner archipelago (105), while the reduced uptake of nitrogen (the supply of which has not diminished proportionally) in the inner archipelago due to P limitation may even have aggravated conditions in the outer N-limited archipelago. In any case, blue-green algal blooms and nitrogen fixation have been markedly reduced in the inner archipelago due to P management (105, 106).

The Himmerfjärd experimental nutrient manipulation showed that increased P supply caused an increase in *Aphanizomenon flos-aquae* biomass and number of heterocysts in the inner part of the basin (69), analogous to the situation in the Stockholm archipelago. Even a reduction in the N load, without an increased P supply, may promote growth of blue-green algae

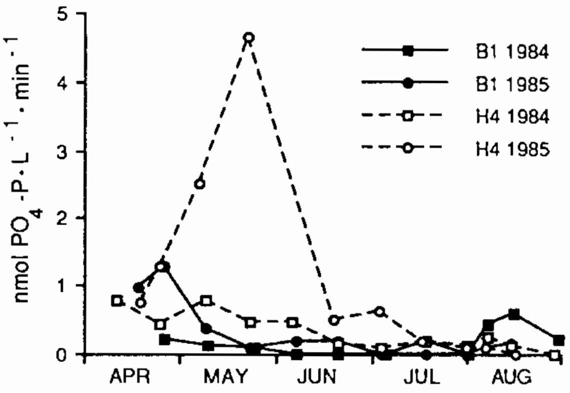
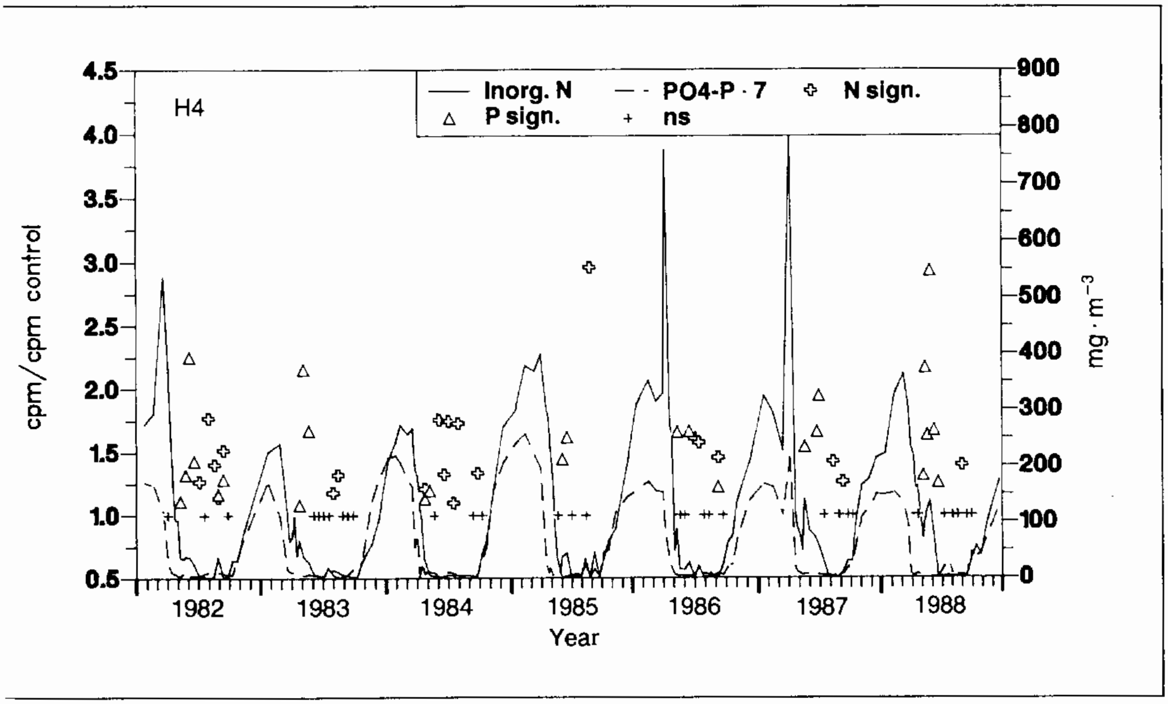


Figure 10. Alkaline phosphatase activity (APA, M 0–15 m) at stations B1 and H4 1984 and 1985 (K. Wallström, unpublished data).



through their competitive advantage at low N/P supply ratios (69). On the other hand, the Himmerfjärd experiment indicates that increased N supply, at least during spring, leads to increased primary production and sedimentation (4, 51). This is analogous to the situation in the Kattegat, where a clear correlation has been found between nitrogen supply and primary production (107).

For the Baltic proper both P and N management may be essential, although the behavior of the Baltic Sea as a whole is not understood in sufficient detail to permit reliable predictions of the quantitative effects of altered nutrient loadings.

In the Kattegat there does not seem to be a potential for blue-green algal blooms

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or pelagic nitrogen fixation (Leonardson and Granéli, unpublished data). This situation suggests that N management may be more straightforward than for the Baltic proper. For the Laholm Bay and the southeastern Kattegat, it has been estimated that a 50% reduction in the external nitrogen supply will markedly improve oxygen conditions in the deep water (11, 40).

Unfortunately, conditions in the Baltic Sea area may at present be deteriorating at such a speed that large-scale nutrient management cannot wait for full scientific proof of what nutrient(s) should be controlled. This situation is all too familiar when discussing corrective measures for environmental problems.

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Article Per Jonsson, Rolf Carman and Fredrik Wulff

Laminated Sediments in the Baltic—A Tool for Evaluating Nutrient Mass Balances

This paper describes the large-scale distribution of laminated sediments and the deposition of nutrients in the Baltic offshore accumulation region. The area of laminated surficial sediments in the Baltic proper, excluding the Gulf of Finland and the Gulf of Riga, has been estimated to cover approximately one third of the total area. Accumulation of autochthonous and allochthonous material accounts for only a minor part of the total amount of nutrients sequestered in these deep offshore accumulation bottoms; most of the nutrients may originate from shallow sediments that are eroded as a result of the isostatic land uplift.

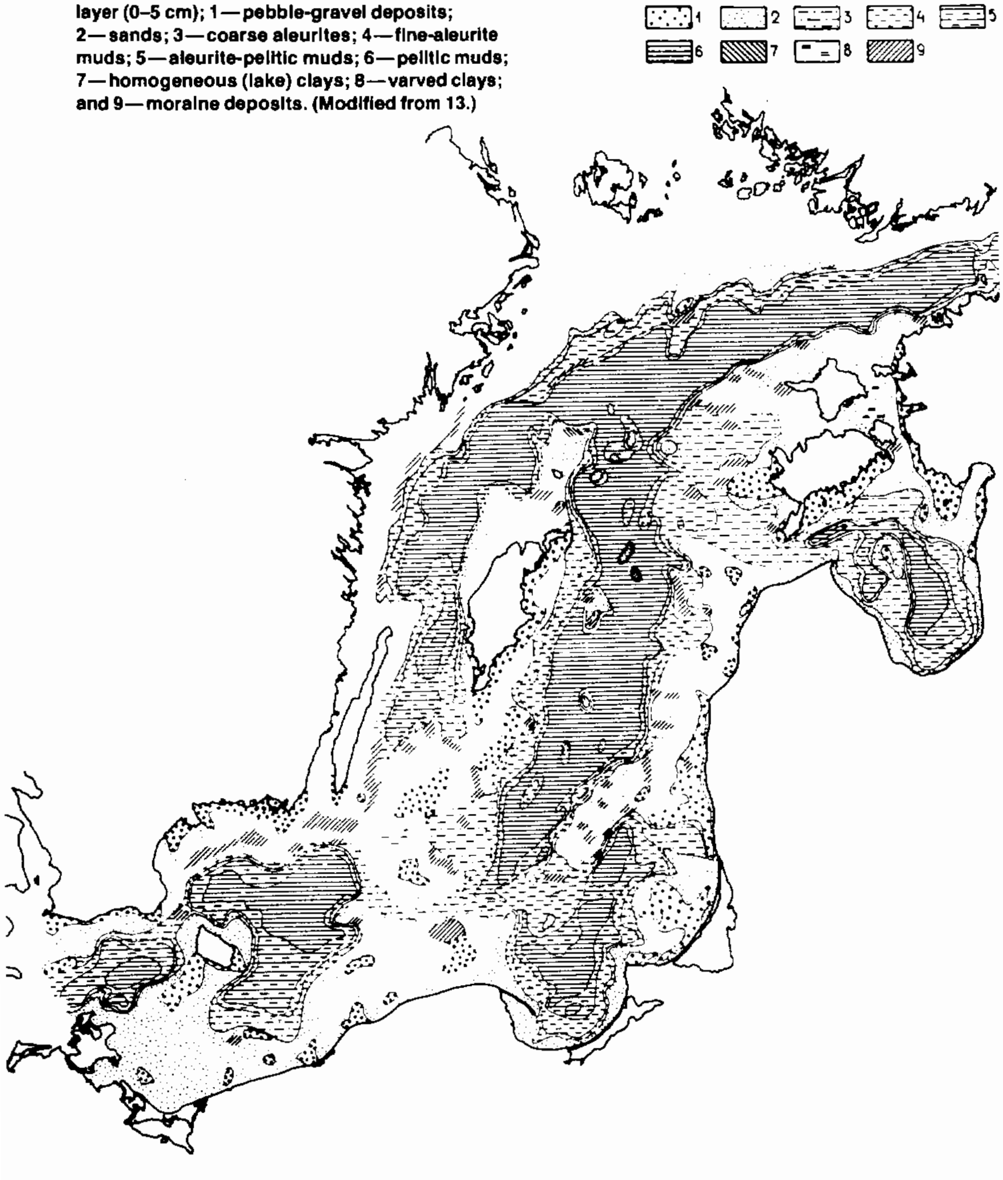


Figure 1. Types of bottom sediment in the upper layer (0–5 cm); 1—pebble-gravel deposits; 2—sands; 3—coarse aleurites; 4—fine-aleurite muds; 5—aleurite-pelitic muds; 6—pelitic muds; 7—homogeneous (lake) clays; 8—varved clays; and 9—moraine deposits. (Modified from 13.)

INTRODUCTION

This work was carried out within the framework of a comprehensive Swedish research project, "Marine Eutrophication" (1).

The occurrence of laminated surficial sediments is a well-known phenomenon in lakes (2, 3), in coastal areas of the Bothnian Bay (4) and the Bothnian Sea (5, 6), in coastal (7) as well as in open parts of the Baltic proper (8–10). Ignatius (11), argues that recent Baltic deep-bottom sediments generally consist of "homogeneous clay or clay gyttja, which is sometimes characterized by a distinct, exceedingly thin lamination, possibly an annual varve microstructure with 0.1–2-mm layers".

Climatic variations throughout the year form the basic condition for the formation of annually laminated sediments in Swedish lakes (12). Normally, differences in sedimentation rate and in the composition of sedimenting material, in combination with alterations in diagenetic processes, are the most important factors leading to the creation of annually laminated sediments. If macroscopic benthic fauna are present the sediment will be mixed due to bioturbation, and a sediment without lamination will be formed. During the post-glacial period, deposition of this type of homogeneous clay or clay gyttja predominated in all the different basins of the Baltic. In the deepest parts of the Baltic proper, laminated sediments have been formed periodically during the post-glacial period (11). The present large-scale distribution of different sediment types in the Baltic proper is shown in Figure 1 (13).

There are many indications that the prerequisites for lamination of sediments are now favorable for large areas. Several studies have shown that the macrobenthic fauna has become almost extinct in the periodically anoxic basins below the halocline; an area of almost 100 000 km^2 in the Baltic proper (14, 15).

The aims of this paper are to:

- describe the large-scale appearance of laminated sediments in the Baltic proper and the concentrations of nutrients in these sediments.
- estimate the annual deposition of nutrients in the open-sea accumulation bottoms for the entire Baltic proper.
- relate these results to recent mass-balance studies of nutrients in the water column (16, 17).

A Ponar sediment sampler. The upper five cms of sediment are generally very soft, and the laminae form slices resembling slate if the sampler is inclined. Photo: G. Renman.

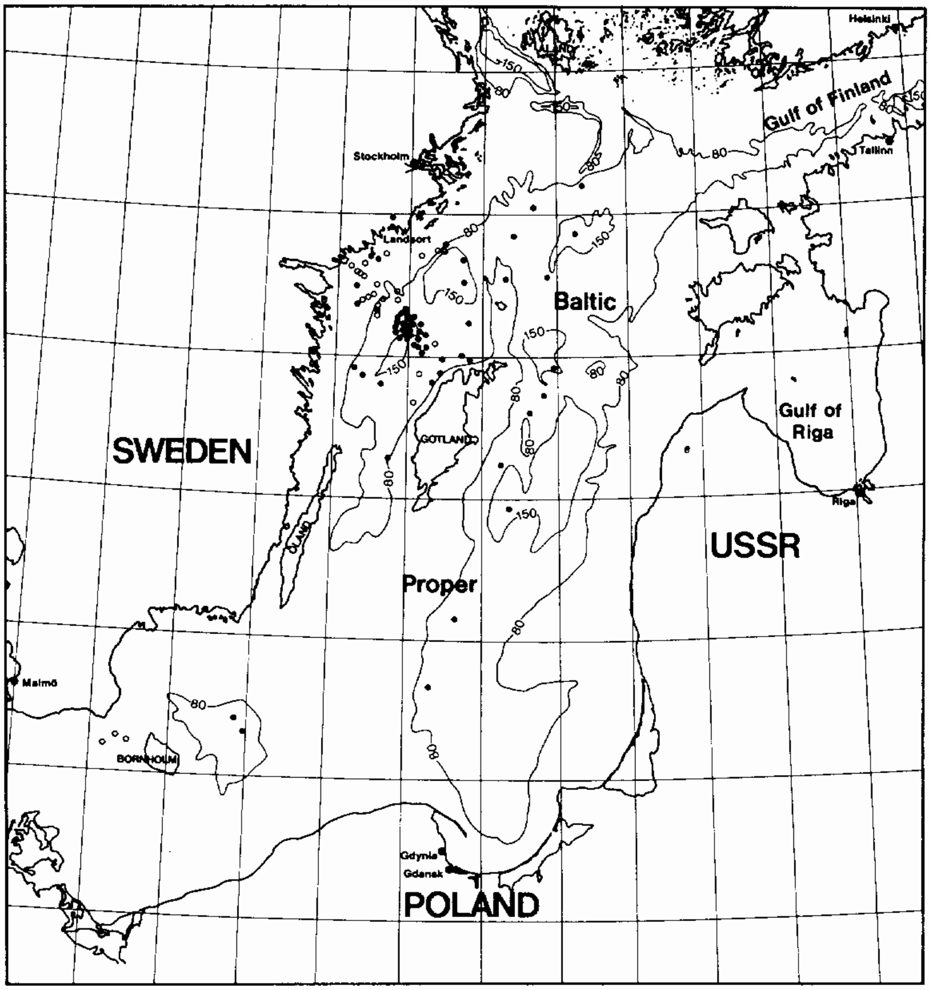


Figure 2. Map showing the location of the sampling sites. Open circles denote stations where no surficial lamination was found, filled circles where lamination occurred. Contours for 80 and 150-m depths are also shown.

AREAS AND OBJECTS STUDIED

During expeditions in 1986–1989, a total of 69 sediment samples were collected in the open Baltic proper and 28 in coastal and archipelago areas (Fig. 2).

The sediments were sampled with a modified Ponar grab sampler (18), which allows free water passage through the sampler during descent and sediment penetration. Great care was taken to ensure that the sediment surface was intact, e.g. with a bacterial film of *Beggiatoa* and/or clear supernatant water. At 23 stations we used a Niemistö gravity corer (19) in addition to the Ponar sampler, and at 8 stations a box corer (20) in order to describe the sediment down to 35–70 centimeters below the surface. The sediments in the Ponar sampler and box corer were immediately subsampled by slowly pressing plastic tubes into the sediment. All samples were stored at between 4°C and 6°C until preparation in the laboratory.

After splitting the cores in two halves, the cores were described, photographs were taken, the lamination was examined and subsamples were taken for determination of loss on ignition (IG), water content (W), and total nutrient amounts. The analyses were made for 1-cm sections, evenly distributed in the upper part of the laminated layer, down to a maximum of 5 cm. In the homogeneous layer, evenly distributed 1-cm sections were taken for analysis between 5 and 13-cm depth.

The water content was determined after drying the sediment at 105°C overnight (>6 hours) (18). The loss on ignition was determined after heating the dried sediments at 500°C for 6 hours (21). The organic carbon content was calculated by multiplying the loss on ignition by 0.5, a good approximation for organic rich sediments, and the bulk density was calculated according to Håkansson and Jansson (18).

The total phosphorus content in the sediments, after wet-acid oxidation (22), was measured spectrophotometrically in aliquots at 880 nm using the molybdenum-blue complex method (23). Total nitrogen was determined as Kjeldahl-nitrogen (24). All wet chemical determinations were made in duplicate.

The core descriptions, in combination with the analyses of water content and loss on ignition, formed the basis for separating the material into cores taken from accumulation (A) bottoms, from cores sampled at erosion (E), and transportation (T) bottoms. This separation was made according to specific criteria (18); i.e. at A-bottoms fine material (< medium silt) is continuously deposited, at T-bottoms fine material is discontinuously deposited and at E-bottoms there is no deposition of fine material. If any of the following criteria were applicable to a sediment core, we considered it to be an E- or T-bottom: rapid change in water content from more than 75% in the laminated layer to substantially less than 75% in the homogeneous part; a similar rapid change in loss on ignition from more than 10% to less than 6%; drastic changes in bulk density; occurrence of coarser material (sand or stones) at the border between the laminated and the homogeneous layers. If there were any doubts about whether a core was from an A-bottom, or an E- or T-bottom, it was considered to be an E/T-bottom (erosion or transportation bottom). In all sediment cores from accumulation bottoms the number of lamina was determined.

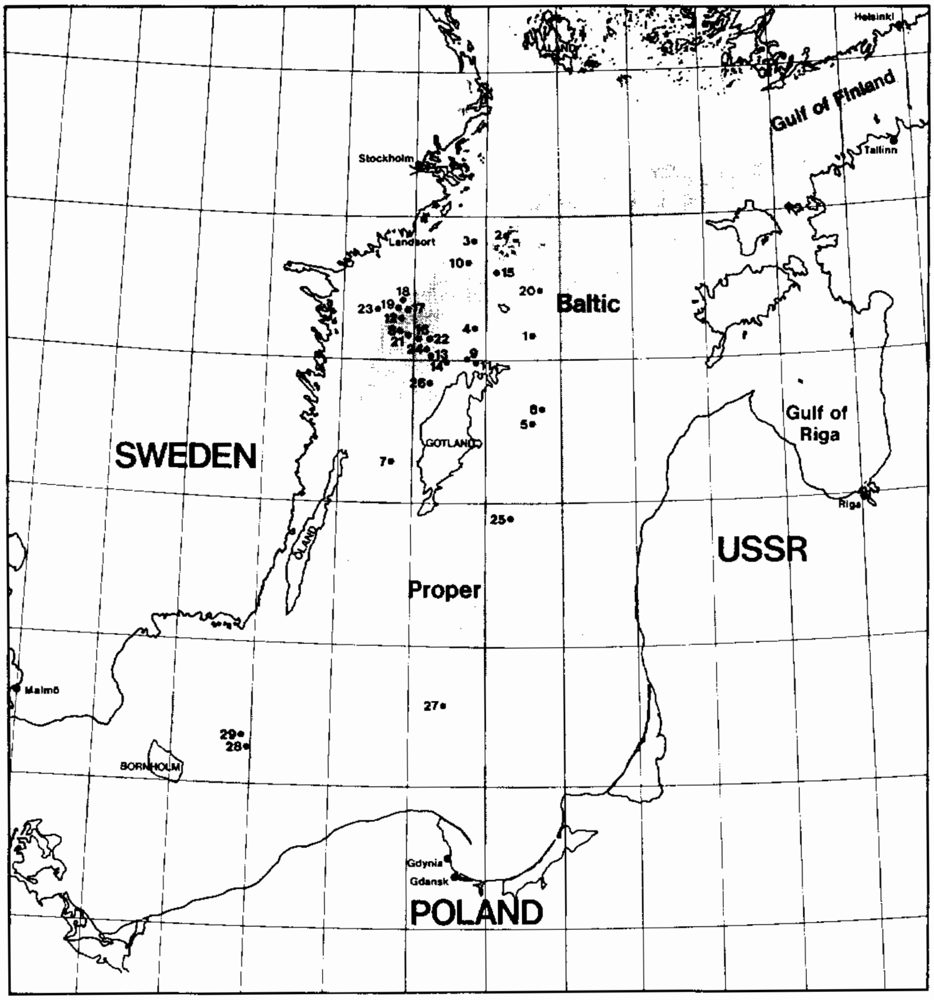


Figure 3. Positions of the stations (1–35) where cores were taken for physical and chemical analyses (results in Tables 1A, B). The probable extent of laminated surficial sediments in the Baltic proper is shown by the colored area.

RESULTS

Distribution of Laminated Sediments in the Baltic proper

Of the total 69 stations visited in the open Baltic proper, 50 were characterized as accumulation bottoms for fine material (i.e. < medium silt); 48 of these showed clearly visible lamination in the surficial sediments. Because of the consistency in the area extension of the laminated sediments, the probable extension of laminated sediments in the open parts of the Baltic proper, excluding the Gulf of Finland and the Gulf of Riga can be outlined (Fig. 3). This map was drawn by compiling the bottom dynamic map of Emelyanov (13) (Fig. 1) and our own results. The area of laminated sediments covers 70000 km^2.

The physical and chemical properties have been studied in 29 and 8 cores, respectively (Table 1 A, see also Fig. 3 for locations). The average thickness of the recently laminated layer (stations 1–21, Table 1 A) was 4.5 cm with an average thickness of 2.5 mm (Table 2) for each lamina. At stations 22–29, the entire cores were laminated with more than 100 laminae. The primary results of varve counting are given in Table 1 A. As an average for the 21 examined cores, the level 4.5-cm below the sediment surface is 19-years old, i.e. deposited 1968–1969 (Table 2), if each lamina represents one year.

The physical and chemical properties in the homogeneous layer were analyzed for the same A-bottom cores as for the laminated layer (Table 1B, locations in Fig. 3).

Table 1A. Results from the laminated layer in Baltic proper accumulation bottom cores. The results on dry substance (ds), loss on ignition (IG), bulk density, total-N and total-P are mean values from three analyses from three different levels within the upper 5 cms of the laminated layer.

Stn	Depth (m)	Lamin. layer (cm)	No. of lamina	ds (% ws)	IG (% ds)	Bulk dens.	Amount N	Amount P	Deposition ds	Deposition N	Deposition P
							($\mu g \cdot g^{-1}$) dry substance		(ton $\cdot$ km^{-2} $\cdot$ yr^{-1})		
1	125	0.5	3	–	–	–	–	–	–	–	–
2	102	2.0	5	–	–	–	–	–	–	–	–
3	86	2.5	6	–	–	–	–	–	–	–	–
4	112	2.5	10	–	–	–	–	–	–	–	–
5	94	2.5	10	13	17	1.07	6.7	0.8	348	2.4	0.8
6	105	2.5	10	–	–	–	–	–	–	–	–
7	97	3.5	15	12	19	1.06	6.5	1.1	296	1.9	0.2
8	128	7.0	17	–	–	–	–	–	–	–	–
9	107	5.0	18	17	16	1.10	4.5	0.9	519	2.6	0.5
10	130	4.0	20	–	–	–	–	–	–	–	–
11	117	4.0	20	–	–	–	–	–	–	–	–
12	103	4.0	20	18	19	1.10	3.5	1.0	396	1.0	0.4
13	119	4.5	20	18	14	1.11	6.1	0.8	450	2.8	0.4
14	100	7.0	23	–	–	–	–	–	–	–	–
15	137	4.0	25	–	–	–	–	–	–	–	–
16	146	8.0	25	–	–	–	–	–	–	–	–
17	124	4.0	26	–	–	–	–	–	–	–	–
18	128	6.0	27	–	–	–	–	–	–	–	–
19	92	9.0	27	21	13	1.13	4.6	1.0	791	3.6	0.8
20	162	5.0	30	–	–	–	–	–	–	–	–
21	136	7.0	40	–	–	–	–	–	–	–	–
22	135	>13	>100	–	–	–	–	–	–	–	–
23	73	>15	>100	–	–	–	–	–	–	–	–
24	130	>40	>200	6	26	1.03	13	1.2	143^1	1.9^1	0.2^1
25	168	>40	>200	–	–	–	–	–	–	–	–
26	112	>40	>200	–	–	–	–	–	–	–	–
27	92	>40	>200	–	–	–	–	–	–	–	–
28	92	>40	>200	–	–	–	–	–	–	–	–
29	88	>35	>200	20	14	1.12	7.5	0.7	597^2	4.5^2	0.4^2

[1] Calculated from 29 lamina in the upper 8 cm
[2] Calculated from 15 lamina in the upper 4 cm
ws = wet substance

The average contents of dry matter, loss on ignition, total carbon, total nitrogen and total phosphorus for the laminated as well as for the homogeneous layer, are shown in Table 3, together with deposition rates. These annual deposition rates, calculated per km^2 for the entire laminated area (70 000 km^2) were estimated using a mean lamina thickness of 0.25 cm (Table 2), multiplied by a mean dry-matter content of 15.6% (Table 3), and a mean bulk density of 1.09 g · cm^{-3} (calculated from Table 1A). For the homogeneous layer, we assumed a deposition rate of 1 mm consolidated sediment per year (Table 4), a mean dry-matter content of 34%, (Table 3), and a bulk density of 1.24 g · cm^{-3} (from Table 1B). Based on these figures, the annual depositions average 433 tons of dry matter, and 16, 1.1, 0.21 tons of C, N, P km^{-2} · yr^{-1}, respectively. Compare this with the average for the upper five cm of the laminated layer, i.e. 443, 39, 2.6 and, 0.4 ton km^{-2} yr^{-1}, respectively.

DISCUSSION

Sedimentation Rates

In Table 4 we have summarized information about the sedimentation rates of accumulation bottoms for fine material in different parts of the Baltic proper. Ignatius (11) found by counting varves in old postglacial sediments that the sedimentation rate over a period of about one-thousand years was approximately 1 mm per year. Other studies (25) suggest an average deposition rate of approximately 1 mm consolidated sediment per year in the Gotland Deep basin for the last 7000 years. Chemical dating of recent sediments from the beginning of the 1970s showed that, during the decades preceding the sampling, the sedimentation rate in this area was only slightly higher, 1.0–1.3 mm · yr^{-1}, (26). Other authors (27–31) have found higher sedimentation rates in the surficial unconsolidated sediment, most of these in the interval 1.2–2.2 mm · yr^{-1}.

We have calculated an annual deposition rate of dry matter in the laminated layer, based on the assumption that the laminae are annual. For the homogeneous layer, we used an annual deposition rate of 1 mm. The deposition of dry matter calculated for the two types of layers (Table 3) are in good agreement. This indicates that the deposition of dry matter in the Baltic during the last two decades is similar to the mean deposition for at least the last two centuries, supporting the conclusion by Ignatius et al. (32) that "the rate of sedimentation has been surprisingly uniform for several thousand years".

Nutrient Ratios

The mean C:N:P ratio (by atoms) in living marine organisms is 106:16:1 (33). The organic C:N:P ratio is often used to characterize the organic matter with respect to quality, origin and degree of decomposition. However, most sediments consist of a mixture of more or less refractory organic material with completely different C:N:P ratios which to some extent baffles the interpretation of registered ratios.

Microbial decomposition of the particulate organic matter during settling in the

Table 1 B. Results from the homogeneous layer in Baltic proper accumulation bottom cores. The results on dry substance (ds), loss on ignition (IG), bulk density, total-N and total-P are mean values from 2–3 analyses within the homogenous layer at 5–13 cm below the sediment surface.

Stn	Depth (m)	ds (% ws)	IG (% ds)	Bulk dens.	Amount (μg · g^{-1} ds)		Deposition (ton · km^{-2} · yr^{-1})		
					N	P	ds	N	P
5	94	32	7.0	1.23	3.3	0.47	390	1.3	0.2
7	97	37	6.5	1.28	3.1	0.49	470	1.5	0.2
9	107	55	3.4	1.51	0.3	0.29	830	0.2	0.2
12	103	33	6.5	1.24	3.7	0.50	410	1.5	0.3
13	119	32	6.6	1.23	1.3	0.46	390	0.5	0.2
19	92	32	7.1	1.22	1.9	0.49	390	0.7	0.2
29[3]	88	22	13	1.13	6.2	0.77	250	1.6	0.2

[3] Sampled in a homogenous layer 49 cm below surface

Table 2. Characteristics for recently occurring laminated surficial sediments in the open parts of the Baltic proper.

	Mean	S.D.	Range	No. of samples
Thickness of the laminated layer (cm)	4.5	2.2	0.5–9	21
Number of lamina	19	9	3–40	21
Lamina thickness—average for the upper 5 cm of the laminated layer (mm)	2.5	0.8	1.5–4.2	21

Table 3. Annual deposition and annual sink of dry matter, organic matter (IG), nitrogen and phosphorus. For the laminated layer calculated from Table 1 A, and for the homogenous layer from Table 1 B.

Parameter	Amount (mg · g^{-1} ws)	Amount (mg · g^{-1} ds)	Annual deposition (ton · km^{-2})	Sink in Baltic laminated sediments (ton · yr^{-1})
LAMINATED LAYER				
Dry matter				
– Mean	156	–	443	31 · 10^6
– S.D.	50			
IG				
– Mean	–	173	77	5.4 · 10^6
– S.D.		59		
Carbon		–	39*	2.7 · 10^6*
Tot-N				
– Mean		6.6	2.6	182 · 10^3
– S.D.		2.9		
Tot-P				
– Mean		0.94	0.4	28 · 10^3
– S.D.		0.17		
HOMOGENOUS LAYER				
Dry matter				
– Mean	339	–	443*	3.0 · 10^6
– S.D.	10			
IG				
– Mean	–	75	32	2.2 · 10^6
– S.D.		28		
Carbon		–	16*	1.1 · 10^6*
Tot-N				
– Mean		3.3	1.1	77 · 10^3
– S.D.		2.0		
Tot-P				
– Mean		0.50	0.21	15 · 10^3
– S.D.		0.17		

* The deposition of carbon has been estimated by multiplying the figure for loss on ignition (IG) by 0.5.
ws = wet substance.
ds = dry substance.

Table 4. Sedimentation rates in Baltic proper accumulation sediments.

Area	Dating method	Sed. rate (mm · yr^{-1})	Reference
Gotland Deep	Varve-counting in postglacial sediments	1.0	(11)
Gotland Deep	Depth of ds during the last 7000 years in correlation with recent redox conditions	1.0	(24)
Gotland Deep	Pb^{210}	1.6 mm in the upper unconsolidated 18 cm (age 1857–1971)	(25)
N Baltic proper	Pb^{210}	2.2 mm in the upper unconsolidated sediment	(26)
Gotland Deep	Pb^{210}	1.2 mm in the upper unconsolidated sediment	(26)
S Baltic proper	Various	0.5–2.0 mm	(27) (28) (29) (30)
Baltic proper	Varve-counting	1.5–4.2 mm in the upper 5 cm of the laminated layer	(this work)

ds = dry substance

water column normally increases the organic C:N, N:P as well as the C:P ratios (e.g. 34–36). The same preferential stripping pattern of nutrients from the organic matter occurs during benthic degradation. However, observed ratios in sediments are sometimes far below ratios measured in the water column (36, 37). A decreasing organic C:N ratio often occurs in sediments containing high amounts of aluminum silicates, such as montmorillonite, due to its capability to incorporate and protect organic nitrogen compounds against microbial attack (38). The organic C:N ratio shows the opposite pattern in sediments with a low percentage of clay (34, 36, 39).

The organic C:P ratio has a more complex pattern. The general behavior during decomposition of organic matter in the water column as well as in the sediment, is a very rapid autolytic phosphorus remineralization (35, 40, 41). Hendrikson (42), however, found that the organic C:P ratio decreased during settling and Balzer (39) found a slight decrease with sediment depth. When only less-degradable phosphorus remains, organic carbon is preferentially decomposed and the organic C:P ratio might decrease.

The organic N:P ratio also tends to increase during decomposition in the water column whereas the pattern in sediments is complex even though it seems that the ratio in some sediments decreases due to preferential nitrogen decomposition (39).

Changes in the inorganic C:N:P ratio in the sediment depends on the origin, supply and decomposition of detritus and inorganic components, as well as on authigenic mineral formation and interactions with sedimentary solids. Organic matter decomposition, authigenic precipitation and interaction with sedimentary solids in turn depends, either indirectly or directly, on a variety of biogeochemical factors such as redox potential, pH, surface properties, and mineralogy.

The amount of inorganic phosphorus in the sediment is altered during redox shifts. This is mainly due to the fact that phosphorus adsorbs to the positively charged iron (III) oxyhydroxides (43, 44) in oxidized sediments whereas it is liberated under reduced conditions. However, the amount of phosphorus linked to iron oxyhydroxides represents only a fraction of the total inorganic phosphorus in the sediment (45, 46). Biogenic and inorganic calcium carbonates, clays and aluminum hydroxides, may also affect the amount of inorganic phosphorus in the sediment. The stability of carbonates mainly depends on pH and redox milieu. Anoxic environments may preserve and produce carbonates through the authigenic formation of carbonate minerals (10). The inorganic nitrogen accounts for almost half of the total amount of nitrogen in some sediments (36). High inorganic nitrogen content in the sediment is normally attributed to ion exchange (ammonium-potassium) with some clay minerals, preferably to illite under reduced conditions.

Hence, the mechanisms behind alteration of C:N:P ratios during diagenesis are very complex. Therefore, interpretations, based only on changes in total C:N:P ratios, can be misleading. However, with these complexities in mind, Koop et al. (46) found a preferential loss of nitrogen relative to carbon along a depth gradient in the Baltic proper. They suggest that this is an indication of a depletion of organic nitrogen relative to carbon along the depth gradient. One explanation for this could be that material, originally deposited in shallow water, is frequently resuspended and that a more rapid loss of nitrogen occurs during transport to its final settling on a "true" accumulation bottom. The same pattern can be seen in the laminated sediment examined in this study; the mean C:N ratio is even higher (17.5 by atoms, even though the carbon determined is only measured as IG). Koop et al. (46) found that the C:P and N:P ratios increased with decreasing redox potential, from 18 and 2 to 134 and 13, indicating inorganic phosphorus enrichment relative to C and N at oxidized conditions, although the total phosphorus content of deeper sediments are about twice those in the shallower sediment. The mean C:P ratio from the laminated sediments in this study is even higher; 252.

The Role of Erosion in Overall Nutrient Budgets

How do the accumulation rates of carbon, nitrogen and phosphorus in laminated sediments (Table 3) compare to overall budgets of these compounds for the Baltic? It has been estimated that $0.32 \cdot 10^6$ tons of organic carbon are sequestered annually in the sediments of the Baltic proper, excluding the Gulfs of Finland and Riga (17). This figure is based on estimates of net primary production and of inputs from the atmosphere, rivers and coastal point sources. With a C:N:P ratio (by weight) of 98:6.5:1, observed in the laminated sediments (Table 3), this amount of carbon would imply that $21 \cdot 10^3$ tons of nitrogen and $3.3 \cdot 10^3$ tons of phosphorus may also be sequestered. We have calculated that $2.7 \cdot 10^6$, $0.18 \cdot 10^6$, and $28 \cdot 10^3$ tons of carbon, nitrogen, and phosphorus, respectively, are sequestered annually in the laminated offshore areas, comprising only about 33% of the total area of the Baltic proper (Table 3). These figures are not plausible as a result of sedimentation of "primary" production from the water column and external inputs only. They are, in fact, too high, even if we assume that all material originally deposited on shallower E/T-bottoms is finally sequestered in the laminated A-bottoms. Assuming that our calculations are reasonable, an additional major source is needed to explain the differences.

In a geological perspective, the Baltic Sea basin is a very dynamic area. The crustal rebound, ranging from nil in the southern part of the Baltic proper to 80–90 cm per 100 years in the northern Bothnian Bay, is the result of a glacial retreat (47).

Table 5. Carbon, nitrogen and phosphorus sources in relation to carbon, nitrogen and phosphorus sequestered in laminated sediments (tons per year for the Baltic proper in a 70 000 km² area).

	Carbon (10^6)	Nitrogen (10^3)	Phosphorus (10^3)
From erosion	2.17	220*	50*
From primary production and external sources	0.32**	21***	3.3***
TOTAL	2.49	241	53.3
Sequestered in laminated sediments	2.7****	182****	28****
DIFFERENCE	+0.21	−59	−25.3

* The C/P ratio 40:1 is a mean (n = 10) from E- and T-bottoms presented in (48). C/N ratio 10:1 origins from (49) for highly degraded organic matter

** From (17)

*** Using C:N:P ratios in Table 3

**** From Table 3

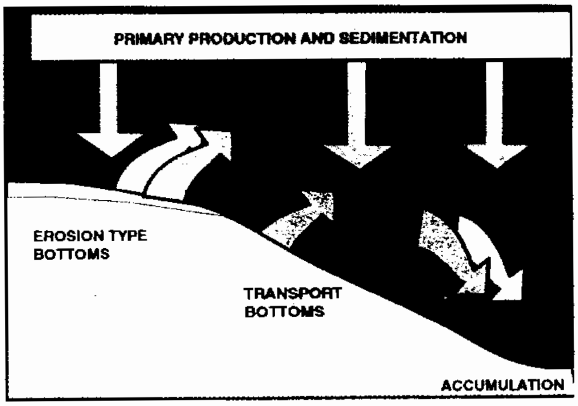


Figure 4. Schematic illustration of physical transport between the water column and different bottom types.

The present uplift of the land can be estimated to about 4 mm per year for the northern Baltic proper.

Due to this postglacial land uplift of the Baltic region, schematically illustrated in Figure 4, postglacial and glacial clays deposited hundreds to thousands of years ago are eroded from shallow areas (<80 m). This eroded material is likely to accumulate on the laminated A-bottoms.

A conservative estimate of the importance of erosion for the entire Baltic proper, indicates that 1.5 mm of shallow soft bottoms are eroded per year. We assume that these types of bottoms constitute 50% of the total area for E- and T-bottoms. The remaining 50% are supposed to consist of coarser material where erosion is negligible in this context. If the eroded 1.5 mm layer has a water content of 50%, a bulk density of 1.4, and a carbon content of 3% (calculated from data in 47), 1050 g dry sediment per m^2, corresponding to 31 g C $\cdot$ m^{-2}, is eroded per year (from 70 000 km^2). If we assume that all this material is not further decomposed, $2.17 \cdot 10^6$, $0.22 \cdot 10^6$ and $50 \cdot 10^3$ tons of carbon, nitrogen and phosphorus, respectively, are finally deposited on the A-bottoms. Thus, if erosion is considered, a reasonable agreement can be found between the estimates of the input to the system and what is sequestered in laminated sediments (Table 5). These speculative calculations suggest that erosion of post-glacial deposits from the water column contributes more than 85% of the total accumulation of organic matter and nutrients found in the deep laminated sediments.

However, we have yet no firm evidence that erosion is as important as the results suggest. If we had used other assumptions on the C:N:P ratios, for instance those of Wulff and Stigebrandt (16), direct deposition and resuspension might account for a larger fraction of the sequestered material.

Based on our calculated annual deposition rates for recent laminated layer versus the deeper homogeneous layer (Table 3), it is tempting to speculate that these rates have at least doubled during the last few decades. However, the number of cores studied so far are few, especially from the homogeneous layer.

CONCLUDING REMARKS

Is the Area of Laminated Sediments in the Baltic Proper Expanding?

If the occurrence of laminated sediments only depends on the rising redoxcline in the Baltic during the 20th century (15), a correlation between water depth and number of laminas in the cores is to be expected. However, there is no such evident correlation (Fig. 5). The correlation does not increase even if the material is treated separately for the different main basins. We therefore suggest that due to the variable bottom topography and hydrography of the Baltic, a mosaic of more or less separated small basins exists with different oxygen conditions close to the bottom.

There are many indications that the area covered by laminated sediment has increased substantially during the last decades. In the deepest parts of the major basins of the open Baltic proper, laminated sediments have been deposited for more than a hundred years, indicating natural oxygen deficiency in these areas. At 7 sites out of 29 (Fig. 3, Table 1A), laminated sediments are found throughout the investigated cores down to 13–70 cm below the sediment surface, which is the maximum depth investigated.

We also know that laminated sediments are currently being deposited on all accumulation bottoms for fine material, deeper than 75 m, in the open Baltic proper. We found no cores with between 40 and 100 varves (Table 1A), which indicates that the recent expansion of the area of laminated sediments started in the late 1940s. This conclusion is supported by several reports from the 1950s concerning decreasing abundance of benthic macrofauna and oxygen concentrations below the halocline (15).

In Figure 6 we attempt to visualize the expansion of the laminated bottoms in the Baltic proper, assuming that each laminated core represents equal fractions of the total A-bottom area. We are aware that this is an uncertain assumption and that the number of cores is small. However, there is strong evidence that the major expansion took place between the end of the 1940s and the end of the 1980s. Therefore, we conclude that the expansion shown in Figure 6 is at least a qualitative estimate. Expansion will, however, probably be halted, because the lamination has now reached the level of the halocline.

The Importance of Erosion and Resuspension

A fine-grained particle that finally settles out in the A-bottoms may have its origin in organic matter produced during the spring bloom a few weeks earlier. On the other hand, its origin might be thousands of years before, when it was originally deposited in glacial or post-glacial sediments. Together with other particles, deposited on T-bottoms just recently or several years ago, it has been resuspended, transported and deposited several times before reaching its final destination—the true A-bottoms for fine material. Thus, the accumulation bottoms consist of material of a highly variable age, even within the same strata.

How important is the relocation of carbon and nutrients for the overall biogeochemical cycles of the Baltic? In magnitude, these flows of nutrients are large but the crucial point is whether these nutrients, stored in various inorganic and organic compounds, are available for biological production or consumption. If they only represent very stable compounds, their role may be insignificant. The scenario sketched here emphasizes the view (16) that a better understanding of the chemical characteristics of Baltic

Figure 5. The relationship between water depth and number of sediment laminae.

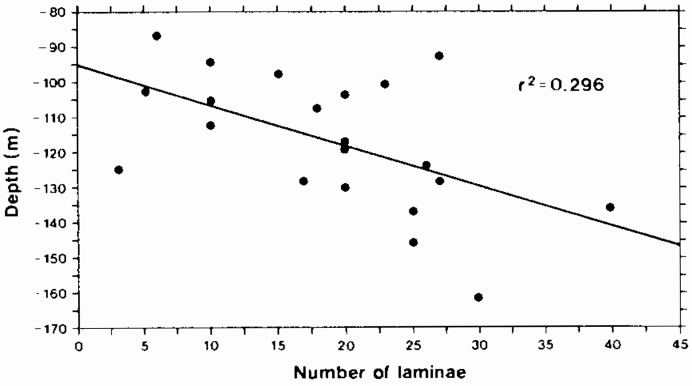
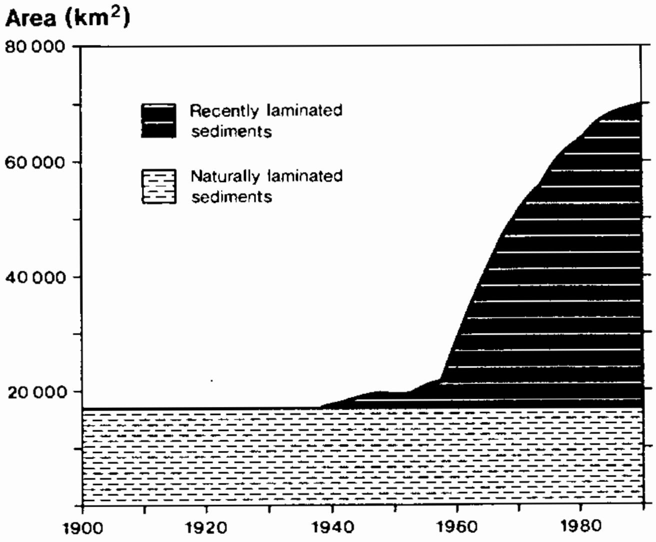


Figure 6. Schematic illustration of the probable expansion of laminated surficial sediments during the 20th century in the Baltic proper.



sediments is essential in order to understand the overall biogeochemical cycles.

Laminated Sediments and Mass Balances

In estimating future mass balances and budgets for the Baltic, we consider it to be of major importance to discover methods that discriminate between the natural and the anthropogenic inputs of carbon, nutrients and contaminants. Sediments are excellent tools to help us estimate the final output, including the sum of the natural relocation of substances and the anthropogenic load, from the pelagic Baltic ecosystem to the sediments. However, we must focus on studies aimed at gaining a better understanding of the E/T-bottom systems in the shallow and coastal areas of the Baltic, where large relocations occur in the resuspension/transport/sedimentation zone above the halocline. We must try to determine to what extent these pools of nutrients are available for biological production.

Thanks to the ease of datings of the laminated sediment cores, analyses of contaminants in these sediments may be valuable in estimating the total load of different contaminants to the Baltic. Lamination offers possibilities to determine changes in the load over time, with a better resolution than is possible in a bioturbated sediment. However, if the load to a large extent is due to erosion of post-glacial sediments, as we have proposed is the case for nutrients, the temporal variations will be obscured by a high "background". Use of tracer substances, like radionuclides, are other important tools to determine the time scales for the transport and relocation processes in the coastal areas, until the time when particles reach the true A-bottoms for fine material and finally leave the recent Baltic ecosystem for the long-term geological system.

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Article

Viveka Enoksson, Fred Sörensson and Wilhelm Granéli

Nitrogen Transformations in the Kattegat

Strong indications that eutrophication is a self-accelerating process in shallow, stratified coastal waters were obtained from studies of internal nitrogen dynamics in E Kattegat, western Sweden. Rate determinations included ^{15}N-isotope methods for phytoplankton uptake, remineralization and nitrification, intact sediment-core incubations for denitrification with acetylene blockage technique and net sediment-water exchange measurements for O_2, inorganic nitrogen (IN) and phosphate. Spring and autumn blooms were 50 and 30%, respectively, based on nitrate and consisted of large, rapidly sedimenting algal cells, whereas summer phytoplankton was dominated by algal cells <10 μm which utilized mainly regenerated nitrogen, ammonium and urea. Nitrification did not take place in the upper mixed layers during the productive season. There was a strong inverse correlation between sediment release of IN and deep-water concentration of O_2 below approximately 200 μmol · L^{-1}. An empirically obtained relation between sediment release of CO_2 and sediment oxygen consumption (SOC) was used for recalculating SOC, IN-flux out of the sediment and sediment C/N ratio in order to obtain sediment IN production and IN-loss in the sediment (mainly denitrification). The results strongly indicate that denitrification will not increase in proportion to eutrophication-induced increases in sedimentation and that there is no evidence of denitrification in the deep water and sediment during low oxygen conditions. Therefore, such conditions may result in accumulation of large amounts of nitrogen in the system

INTRODUCTION

Kattegat is a rather shallow (average depth 23 m), permanently stratified sea which receives low saline surface water from the Baltic and deep water with nearly oceanic salinities from the Skagerrak. Hydrographical properties are described in more detail by Svansson (1) and, with respect to nutrients, by Rydberg (2). The phytoplankton primary production in the open Kattegat is in the order 100 g C · m^{-2} · yr^{-1} (3, 4). Of 35 estuarine and coastal areas listed by Nixon (5), only 7 areas are less productive than the Kattegat. Nevertheless, during the last decade many symptoms of eutrophication have been observed in this area, e.g. altered compositions of both macroalgae and benthic macrofauna as well as oxygen depletion in the deep water (6). A major cause of this eutrophication is considered to be increased nitrogen loads (7). According to Andersson and Rydberg (8) the local (riverborne and atmospheric) supply of total nitrogen to the Kattegat is 47 000–67 000 tons · yr^{-1} (0.19–0.27 mol N · m^{-2} · yr^{-1}). Budget calculations show, however, that the total amount of nitrogen which enters the area from the south (the Baltic Sea and the Belt Sea) is approximately equal to the amount which is transported out of Kattegat with the northbound Baltic current (8). Therefore, an amount of total nitrogen equivalent to the local supply disappears from the water body within the Kattegat.

Being part of a joint issue from an interdisciplinary research program (9) on eutrophication of Swedish coastal waters, the present report emphasizes biological nitrogen transformations. We attempt to describe the transformation rates in waters and sediments and their regulating factors. Important questions to investigate were 1) whether a decreased local anthropogenic supply of nitrogen to these waters would significantly decrease the net phytoplankton carbon (10) and nitrogen production (11); 2) whether denitrification or burial dominates the disappearance of nitrogen; 3) to what extent denitrification in the coastal zone may counteract eutrophication; and 4) to what extent the degree of eutrophication may affect the amount of nitrogen removed by denitrification.

INTERNAL NITROGEN CIRCULATION IN THE SOUTHEASTERN KATTEGAT SURFACE WATER

The major mechanisms of nitrogen transformations in the surface waters are nitrogen uptake into phytoplankton and mineralization of detrital material back to inorganic nitrogen (IN), which can again be taken up. Nitrification, the oxidation of ammonium to nitrite and nitrate, has not been found to take place at any significant rate in the upper mixed-water layer of the areas investigated so far (e.g. 12, 13). Light is probably the ultimate cause of this phenomenon (14), but whether or not it is a direct effect of light is still not known. In order to see whether this was true also for the Kattegat, the nitrification potential was measured twice in the spring and twice in the autumn with the ^{15}N-ammonium oxidation method described by Enoksson (12). Nitrification was not detected in upper mixed layers of the E Kattegat, and generally no nitrification occurred above 20-m depth. On one sampling occasion water layers with virtually no nitrifying potential and layers with high nitrifying activity were only 2 m or less apart.

Extensive measurements of nitrogen uptake and regeneration have only been carried out in the southeastern Kattegat. The uptake of nitrogen shows strong seasonal variations (11). During winter, the uptake rates are very low, permitting a gradual increase in concentrations of nitrate and phosphate. The primary production and thus nitrogen uptake usually starts at the beginning of March, and increases rapidly during the build up of the spring bloom. During the bloom the nitrate uptake is about half of the measured nitrogen (ammonium + nitrate + urea) uptake (11). The spring bloom consists of many larger species, mainly diatoms. These can sediment rapidly to the bottom water (15), thus causing an export of nitrogen to deeper water and sediment.

The spring bloom lasts for a few weeks and after this, the nutrient concentrations are depleted to low levels throughout the rest of the productive season, March–November. This reduces the phytoplankton standing stock during summer, and also causes a shift towards smaller algal forms that are degraded in the surface water, rather than sedimenting out. The plankton size fraction smaller than 10 μm totally dominated the nitrogen uptake during summer. The nitrate uptake was 18–23% of the total nitrogen uptake. The total daily uptake was about 30% of the spring-bloom average. During the autumn, increased supply of nitrogen to the surface water caused the average daily nitrogen uptake to increase to 50% of the spring-bloom average. The proportion of larger species, mainly consisting of dinoflagellates, also increased again. As in the spring the size fraction smaller than 10 μm accounted for only 30–35% of the total autumn uptake (11). These findings suggest that the main sedimentation occurs in spring, and that there is also an elevated sedimentation in the autumn. The dominance of larger forms during higher nutrient inputs in the spring and autumn, and the change to dominance of small forms during stable low-nutrient conditions seems to be a general finding that is valid in many other areas (16, 17).

The C/N atomic ratio of the particulate material was about 8 during most of the year (11). During the spring bloom, the ratio decreased towards the Redfield ratio 6.6. This suggests that the phytoplankton population in the Kattegat does not have any significant superfluous store of nitrogen. Combined with the fact that nitrogen supplied to the surface waters during the productive season is used up entirely, this makes it likely that an increased nitrogen supply would cause an increase in the primary production and phytoplankton standing crop (7).

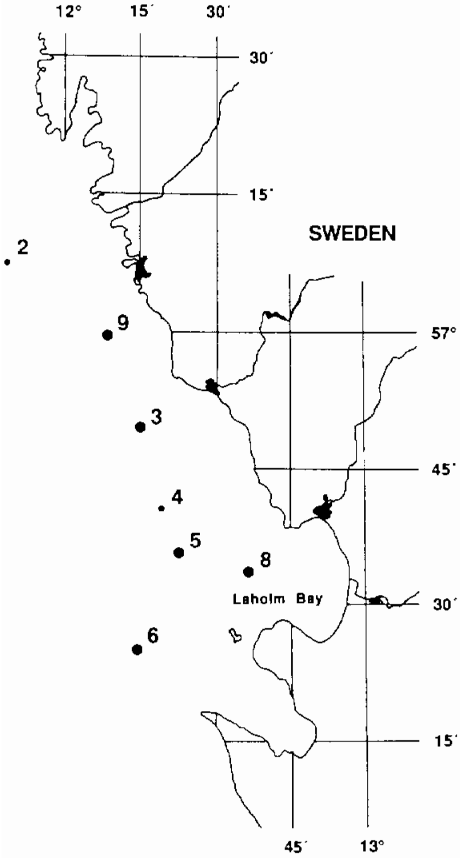


Figure 1. Map of E Kattegat showing stations where sediment-water flux studies were carried out. Averages (Table 1) are calculated for stations indicated by large dots.

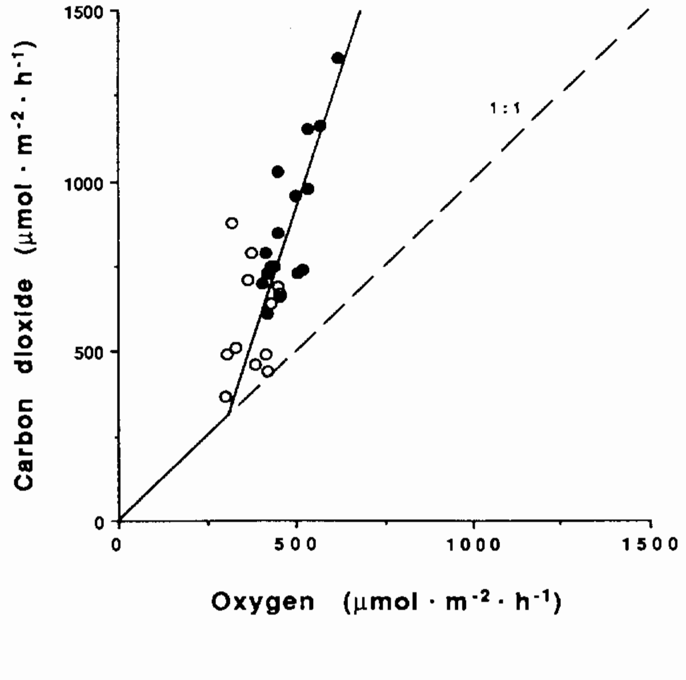


Figure 2. Sediment oxygen consumption vs release of CO_2, obtained during core-flow incubations of 7 intact sediment cores from SE Kattegat. Four measurements for each core over a 6-day period. Closed and open circles represent samples with oxygen concentrations of around 100 and 200 μmol · L^{-1}, respectively, in headspace water.

Both the river water and, for most of the time, the deep-water nitrogen supply is mainly in the form of nitrate, and as there is virtually no nitrification in the surface water, new production is essentially equal to phytoplankton nitrate uptake even in the shallow Laholm Bay (Fig. 1). The fraction of the primary production supported by new nitrogen sources (nitrate) is 25% as an annual average (11). The average annual primary production in the central bay has been estimated to be 135g C · m^{-2} · yr^{-1} from ^{14}C measurements (3) and 180 g C · m^{-2} · yr^{-1} from ^{15}N uptake measurements, using the Redfield ratio (11). If the new production equals the sedimentation to deeper waters (18), this would then correspond to 34–45 g C · m^{-2} · yr^{-1}.

A large part of the nitrogen bound in plankton biomass and detritus is mineralized in the water column. The rates of mineralization seem to be relatively evenly distributed in the area and are virtually the same in the middle of the bay as in the outlet of the river Nissan (19). Higher mineralization rates were observed at the peak of the spring bloom and during the autumn. During the spring, the rates increased with depth, suggesting that the substrate for mineralization was sedimenting diatoms. This was contrary to the autumn, when the rates were higher in the surface waters, probably reflecting either a slower sedimentation velocity or a higher surface-water temperature.

The particulate material in the water reflects typical marine C/N ratios. Only close to the mouth of river Nissan are the elevated C/N ratios typical of terrestrial particulate matter encountered. It is therefore probably safe to assume that the sedimenting material is mainly of marine origin, and that the contribution of terrestrial particles to the oxygen consumption in the bottom waters is negligible.

BENTHIC MINERALIZATION AND SEDIMENT-WATER EXCHANGE OF NUTRIENTS IN EASTERN KATTEGAT

Regulatory Factors

The exchange of nitrogen between sediment and water depends on several biological transformations that are regulated by biotic as well as abiotic factors. The benthic nitrogen cycle with its most important biological processes, mineralization, nitrification and denitrification, has been described by Blackburn (20). The major regulatory factors for sediment transformation of organic material are the quantity (5, 21, 22) and quality of deposited material (23–25), and the physical environment (temperature, currents, water stratification, etc.). If the sedimentation rate changes it will also induce changes in a number of other regulatory factors, such as the oxygen availability (26), the sediment composition (27–29), the biomass (30, 31) and the composition and abundance of the fauna (32) and thereby the bioturbation (33–35). We carried out direct studies of sediment-water exchange in order to 1) show the temporal and spatial variation; 2) clarify its regulation; and 3) be able to predict the effects of a changed supply of detritus to the sediment.

Approaches to Measuring Mineralization

Mineralization of organic carbon compounds in aerobic environments may be fairly accurately determined as oxygen consumption. This carbon mineralization can subsequently be converted to IN production by using the substrate C/N ratio (atomic ratios are used throughout the text). For the complete mineralization of an algal cell with the C/N ratio of 106:16 (36), 8.6 molecules of O_2 will be used per nitrogen atom if the formed ammonium is also nitrified (37). The use of oxygen uptake and substrate C/N ratios has two great advantages: 1) oxygen consumption is easily measured; 2) it includes the activity of organisms at the sediment-water interface and of the macro infauna. One weak point is that microbial biomass may accumulate and that the C/N ratios of the specific substances being mineralized are not known and may vary with time, as discussed by Blackburn (38). In many coastal sediments such as those in the Kiel Bight, most of the sedimented organic material is expected to be mineralized within one year, however (21, 39–41), and intermittent accumulation of bacterial biomass and substrate composition will be of little consequence for annual averages.

Because the sediments are anoxic except for the upper few mm at the sediment-water interface (42), a more serious error is due to different kinds of respiratory and fermentative metabolic pathways, with other electron acceptors than oxygen (43). Graf et al. (40) demonstrated that fermentation became more important during periods of rapid sedimentation. A better alternative than sediment oxygen conumption (SOC) is therefore the estimaon of total CO_2 release. This should be a irect measure of the organic carbon nineralization in the sediment, if care is aken not to change the solubility of caronates. Blackburn (38) found that CO_2 roduction rates correlated well with elecron acceptor reduction rates in the North ering and Chukchi Sea sediments. We sed 7 intact sediment cores sampled in eptember in SE Kattegat for comparing he release of total CO_2 (coulometric analsis) with SOC. The oxygen content of the eadspace water was kept at approximatey 100 and 200 $\mu mol \cdot L^{-1}$, respectively. At igher SOC rates there was a deviation rom the 1:1 relation between SOC and O_2 release from the sediment (Fig. 2), howing that oxygen was not the only terninal electron acceptor. Therefore, organic carbon mineralization in E Kattegat vas estimated by use of the SOC rate and he obtained relation to total CO_2 release hown in Figure 2; i.e. estimated carbon nineralization (ECM).

The rate at which organic nitrogen was nineralized was estimated by dividing the ECM rate by the sediment organic C/total N ratio, averaging 10.4 (Table 4) for the ipper 0.5-cm layer (Table 1). The ratio vas virtually the same at 0–0.5 and 0.5–1.5 m for all stations. The estimated formaion of IN (nitrogen mineralization) and he measured release of IN by the sedinent were subsequently used to calculate he "IN-loss rate" by difference. The loss f IN as such is due to ammonium adsorpion to the sediment and to denitrification n the sediment. The organic substances hat are buried permanently or that leave he sediment are not monitored by this nethod.

Rates of SOC and nutrient flux rates vere measured from the same samples, at he stations shown in Figure 1, on 7 occaions in the E Kattegat during the period August 1987 to October 1988. Intact seditnent cores, 4-cm diameter, 4–8 replicates, vere incubated at *in situ* temperature for –24 hours, depending on the season. The eadspace water was sampled at the same ite as the sediment and was stirred gently luring the incubation. In order to minimize the effect of disturbance from sampling, the cores were kept a few hours in the temperature controlled water bath before the measurements started. In addition, laboratory experiments were performed using intact sediment cores, incubated in a flow-through system (26). After a period of stable conditions the environment was changed experimentally and the effects monitored.

Temporal Variations

Sediment-water flux rates and relevant ambient parameters are given in Table 1 (means of 5 stations, Fig. 1). The oxygen concentrations in the bottom water were extremely low in September of both 1987 and 1988, of which the latter period was studied. During that autumn, a large number of benthic macrofauna, including sea urchins, Norway lobsters, holoturians, and even hagfish *Myxine glutinosa* died of hypoxia (6).

The SOC rates in E Kattegat, based on station means, varied between 270 (March) and 570 $\mu mol \cdot m^{-2} \cdot h^{-1}$ (October) which indicates a fourfold variability in benthic mineralization (ECM). Single stations revealed an order of magnitude variability in ECM, however. A sevenfold increase in ECM at one single site (Stn 5), from March to April, was the only recorded benthic effect of the spring bloom. With the less than 3 weeks needed for mineralizing the bloom in the sediment as demonstrated by Graf et al. (39), it is possible that we missed the peak in benthic activity. Otherwise, high rates were only recorded in August 1987 and October 1988 with the latter being the highest. During September 1988, the SOC rates were low, probably due to oxygen deficiency (18–49 $\mu mol \cdot L^{-1}$ *in situ*) (44). A large potential for SOC might therefore have been created in the form of reduced substances from dead animals and anaerobic metabolism. This may have enhanced SOC during the cruise five weeks later. Such stimulation of the benthic activity was reported from the Kiel Bight where the heat production increased by a factor 3 subsequent to a period with low oxygen concentrations (40).

The net rates of IN exchange between sediment and water (Table 1) were mostly low, but ammonium entered the deep water more rapidly (on average 16–30 $\mu mol \cdot m^{-2} \cdot h^{-1}$) during two autumn studies with prevailing low oxygen concentrations. Nitrate exchange was small and mostly directed out of the sediment, but in April all sediments consumed nitrate and all, except at Stn 5, consumed ammonium as well. A similar seasonal pattern, high SOC/IN release ratio in May and a low ratio in August, was observed in Chesapeake Bay, although actual rates were several times higher than in the Kattegat (45).

Because of the large IN uptake by the sediments in April the IN-loss rates were high (25–143 $\mu mol \cdot m^{-2} \cdot h^{-1}$). Equally high IN-loss rates were found in August 1987, but in contrast to April, IN was released by the sediment. According to Jensen at al. (46), the most rapid denitrification was recorded in April in the SW Kattegat sediments subsequent to the settling of the spring bloom. During the severe oxygen deficiency of September 1988, the maximum estimate of IN-loss rate was 26 $\mu mol \cdot m^{-2} \cdot h^{-1}$ and the average only 4 $\mu mol \cdot m^{-2} \cdot h^{-1}$ (13% of the estimated IN-production). At Stn 8 there was even faster release of IN than would be expected from ECM values. Later (October 1988) the release of IN from the sediment decreased somewhat and the IN-loss was estimated to be 95 $\mu mol \cdot m^{-2} \cdot h^{-1}$ for E Kattegat.

Spatial Variations

The SOC rates based on averages for all sampling occasions ranged between 280 (Stn 6) and 400 $\mu mol \cdot m^{-2} \cdot h^{-1}$ (Stn 5) in E Kattegat, but far greater spatial variability was revealed when examining the distribution of SOC and ECM on each occasion. With respect to the sediment-water exchange of IN the spatial differences were large, averages ranging from 3 $\mu mol \cdot m^{-2} \cdot h^{-1}$ at the far north station to 24 $\mu mol \cdot m^{-2} \cdot h^{-1}$ at Stn 8 at the border of the Laholm Bay. Station 8 and the two sites further to the northwest and west (Stn 4 and 5, respectively) often showed the

Table 1. Spatial (means of 7 occasions) and temporal (means of 5 stations) variation in sediments in E Kattegat (Fig. 1). Sediment properties, sediment oxygen consumption (SOC), nutrient flux rates (positive values for flux out of sediment), estimated production and estimated loss of inorganic nitrogen (IN) and concentrations of oxygen, ammonium and nitrate in bottom water.

	Station	Depth m	Temp. °C	Water content %	Org. C mmol · gdw^{-1}	OrgC/totN	O_2 *in situ* $\mu mol \cdot L^{-1}$	SOC flux	PO_4^{-3} flux	NO_3^- flux	IN flux	IN prod.	IN loss	NH_4^+ *in situ* $\mu mol \cdot L^{-1}$	$NO_3^- + NO_2^-$ *in situ* $\mu mol \cdot L^{-1}$
								$\mu mol \cdot m^{-2} \cdot h^{-1}$							
	9	45	8.3	74	1.4	10.4	211	379	1.6	3.8	2.7	58	56	–	–
	3	35	9.1	81	1.9	10.3	160	375	1.3	0.9	5.3	53	48	–	–
	5	32	8.6	81	1.7	10.0	140	396	1.4	−2.2	8.0	70	62	2.6	8.0
	6	34	7.8	81	1.7	9.9	145	283	1.3	0.8	5.4	32	26	2.0	7.8
	8	21	9.6	67[1]	1.4[2]	11.3	101	370	0.8	1.9	25.7	52	27	3.5	5.7
Year	Week No.														
1987	35		6.9	85	1.9	10.8	123	431	1.2	−2.9	12.8	64	51	0.3	11.6
1987	42		11.0	–	–	–	143	275	1.1	3.1	5.3	31	25	–	–
1988	12		6.2	71	1.6	10.5	270	268	1.3	0.5	1.9	27	25	0.1	13.8
1988	16		5.9	71	1.2	10.6	215	359	0.8	−4.6	−6.7	52	59	1.3	8.6
1988	33		7.1	–	–	–	126	319	0.8	2.0	5.7	41	35	1.2	5.6
1988	38		11.1	84	2.1	9.7	38	298	1.0	1.9	32.4	36	4	4.9	0.6
1988	43		12.5	–	–	–	93	566	2.7	6.1	22.5	117	95	6.5	2.1

[1] Range: 51–89; [2] range 0.4–3.3

highest SOC-rates. Furthermore, they often released IN at high rates but Stn 4 and 5 did so only during periods with low oxygen concentrations in the deep water. It is reasonable to assume that these three sites are influenced by the elevated primary productivity in the bay (see above). The sediment which supposedly was most influenced by water from the Baltic and Öresund (Stn 6) was the least active site according to SOC and always released IN at moderate rates.

Sediments in shallow areas, close to the depth of the halocline, are especially important in the nutrient circulation because nutrients leaving the sediment are likely to enter the photic zone. A thin sub-halocline layer (average 6 m) also makes these sediments sensitive to oxygen deficiency (6) due to a small oxygen store compared with the SOC-rates. Such areas in the Laholm Bay (Stn 8) were mainly responsible for the build up of high ammonium concentrations in the deep water during the low-oxygen period in autumn 1988 (Table 1). This station also showed a relatively low average IN-loss for all the sampling occasions of 27 μmol · m^{-2} · h^{-1} (56% of the assumed IN production). In contrast to the shallow Stn 8 sediment, high IN-loss rates were obtained to the west of the bay at Stn 5 (average 62 μmol · m^{-2} · h^{-1}) and at Stn 9 further to the north (average 56 μmol · m^{-2} · h^{-1}).

Annual Mineralization and IN-loss

Most often SOC and IN release from E Kattegat sediment amounted to only a few percent of what was utilized for primary production. Even during low oxygen periods the nitrogen release was low when compared to other coastal areas (5, 47, 48).

As a mean for five stations and seven sampling occasions in E Kattegat, we have estimated an ECM rate of 538 μmol · m^{-2} · h^{-1}, which should correspond to an IN-production (mineralization) rate of 52 μmol · m^{-2} · h^{-1}. The IN leakage from the sediments was far smaller, indicating that 43 μmol · m^{-2} · h^{-1} (82%) were lost in the sediments, denitrification probably comprising the main sink for IN. These averages were used for the productive period (8 months) and the average rates for March 1988 and October 1987 were assumed to be representative of the dark months, in order to obtain annual estimates. ECM was 47 g C · m^{-2} · yr^{-1} which may be compared with the annual primary production of 100 g C · m^{-2} (3, 4). Using the Redfield C/N ratio of algae and a sediment C/N ratio of 10.4, the calculated IN-formation in the sediments is 0.38 mol · m^{-2} · yr^{-1} which equals 30% of the nitrogen used by primary producers, i.e. a smaller fraction than for carbon but still high.

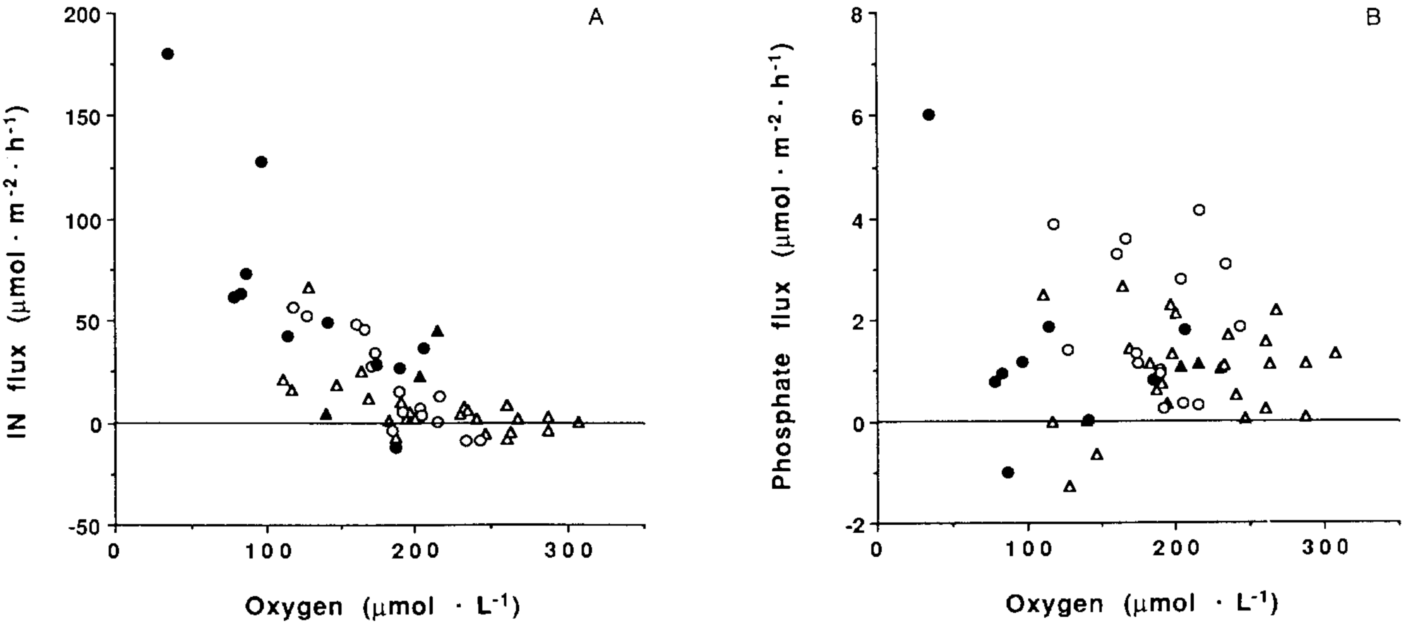
Most of the sediment cores were obtained from accumulation bottoms which may result in an overestimation of the mineralization rate compared to the Kattegat as a whole. In order to estimate the fraction of primary production that reaches the sediment both the mineralization and the burial of organic nitrogen must, however, be considered. Permanent burial is highly variable, especially in the NE Kattegat and the burial on typical accumulation bottoms in SE Kattegat may range between 2 and 5 mm · yr^{-1} (49). In shallower areas like at Stn 8 in the Laholm Bay there is virtually no permanent accumulation of sediment (50). The annual benthic ECM was the same in the bay as in Kattegat as a whole, in spite of a higher primary production in the bay (144 g · m^{-2} · yr^{-1} (10), and 180 g C · m^{-2} · yr^{-1} from ^{15}N-uptake rates (11)). Therefore, both the ECM fraction (26–33%) and the nitrogen fraction (15–19%) of the primary production that was mineralized in the sediment were smaller in the bay and comparable with the estimated new production of 25% (see above).

Denitrification

Denitrification is one of the key processes in environments where nitrogen is a limiting nutrient. It is likely that denitrification is the major component of the estimated IN loss. All methods for determining denitrification have shortcomings. By far the most common direct method is to use acetylene to inhibit reduction of nitrous oxide and then determine the formation of this intermediate (51). Both at low nitrate levels (52, 53) and in the presence of sulfide (54), it has been shown, however, that the inhibition of the nitrous-oxide reductase can be incomplete, leading to a loss of some nitrogen as nitrogen gas. The inhibition of nitrifying bacteria by acetylene, leading to a depletion of nitrate during the incubation, has been reported (55), but we have failed to observe this effect in nitrification studies. Another approach is to estimate the denitrification as IN-loss from mass balances as described above. This has no obvious methodological source of error, but includes both a number of assumptions and the summed errors from several measurements.

A comparison between individual parallel measurements of estimated IN-loss and the denitrification measured with the acetylene inhibition technique (AIT) showed a considerable scatter and deviations from the 1:1 relationship expected if the IN-loss was due entirely to denitrification. Most of the stations showed lower rates of denitrification than of IN loss. The agreement was best at measured denitrification (AIT) rates above 25 μmol · m^{-2} · h^{-1}. In spite of

Figure 3. Sediment-water exchange of nutrients vs oxygen concentration in headspace water for intact sediment cores sampled in E Kattegat. Triangles and circles indicate samples with sediment oxygen consumption lower and higher than 400 μmol · m^{-2} · h^{-1}, respectively. Open symbols indicate simulated *in situ* conditions on 7 occasions in 1987–1988 at stations shown in Figure 2 and closed symbols indicate experiments (26) using core-flow incubations: Before and after additions of *Skeletonema costatum* before and after asphyxiation of macrofauna, and at varied oxygen conditions. Exchange of inorganic nitrogen (IN) (Fig. A) and phosphate (Fig. B).



he scatter, the average for the measurements in 1987 and 1988 from 7 stations in he autumn and 4 stations in the spring was 36 μmol · m^{-2} · h^{-1}. This compares well with the average of 42 μmol · m^{-2} · h^{-1} for he total IN-loss determinations described above.

Earlier measurements have shown that the shallower areas (less than 20 m depth) n the Laholm Bay (east of station 8 in Fig. 1) generally had low denitrification rates as measured by AIT. The rates were less than 28 μmol · m^{-2} · h^{-1} in the spring and less than 12 μmol · m^{-2} · h^{-1} in the autumn. In April 1986, AIT measurements were also carried out on sediments from a few stations in the southwestern Kattegat. These showed relatively high rates, 89–105 μmol · m^{-2} · h^{-1}, compared to the Laholm Bay stations.

To investigate whether there was a further potential for denitrification, nitrate was injected into sediment cores to a final enrichment of 10 nmol · cm^{-3} of sediment. This was done in September 1987 and in April 1988. The denitrification rates as measured with AIT, were 2–10 times higher in the nitrate enriched cores as compared to the unenriched cores from the same occasions, indicating that the denitrification could increase with an increased nitrate supply, and that the denitrification rate probably was nitrate limited as has been found in many other studies (56).

We have now three independent measurements of the nitrogen disappearance within the Kattegat, 0.19–0.27 mol · m^{-2} · yr^{-1} from large-scale budget calculations (8), 0.32 mol · m^{-2} · yr^{-1} from sediment-water flux measurements and 0.32 mol · m^{-2} · yr^{-1} from denitrification measurements (AIT). One would not expect these three approaches to give the same result because 1) the large-scale budget calculations are valid for the whole Kattegat, whereas the two methods using sediment cores mainly represent the deeper sediments of E Kattegat; 2) many processes in the sediment may be responsible for temporary IN-loss, whereas the AIT method specifically measures denitrification; 3) only a limited number of measurements were carried out with the two sediment incubation methods; 4) the use of ECM for estimating IN-loss (see above) is not very precise; 5) the large-scale measurements and the sediment incubations were not carried out during the same period. In this perspective, the good agreement between the two sediment incubation methods is striking and the somewhat lower full-scale estimate must be regarded as quite reasonable.

Regulation of Sediment Nitrogen Transformations

Oxygen: Oxygen availability strongly regulates the sediment-water exchange of IN (57). The influence of oxygen on benthic organisms, of which all act as nitrogen transformers, is complex and both direct and indirect effects are important (58). Only at oxygen concentrations below 200 μmol · L^{-1} (4.5 ml · L^{-1}) in the headspace water, was there a significant release of IN by the sediments and sediment release of ammonium was increased both by a lowered oxygen concentration and an increased SOC-rate (Fig. 3a). In a laboratory experiment a concentration of approximately 100 μmol · L^{-1} of oxygen in the headspace water gave an efflux of as much as 80 μmol · m^{-2} · h^{-1} of ammonium as compared to 40 μmol · m^{-2} · h^{-1} where 200 μmol · L^{-1} of O_2 was present (26). Nitrification stops or moves entirely from the sediment to the deep water when the oxygen concentrations decrease and SOC-rates increase. As a consequence, the nitrate-reduction zone in the sediment moves upwards to the layer where nitrate is still available. Denitrification will, however, not take place in the deep water unless the oxygen concentration falls to around 10 μmol · L^{-1} (0.2 ml · L^{-1}) (59), 11 μmol · L^{-1} (60) or a few μmol · L^{-1} (61). Our data (Fig. 3a) agree with previous reports (62) on efficiently linked nitrification-denitrification in sediments, provided that oxic conditions prevail in the upper sediment layer. In fact, we may have overestimated the IN-loss during the low oxygen periods in the autumn because the oxygen concentration in the water used above the sediment cores was about 60 μmol · L^{-1} higher than the *in situ* concentration in the deep water.

Mineralization: A model that describes the interrelation between benthic mineralization and IN-loss should be a valuable tool in understanding the role of the sediments in the ecosystem response to external nitrogen loading. ECM is our best available parameter for mineralization. From a practical point of view the question is if the change in nitrogen mineralization or the change in IN-loss is the most sensitive to a change in ECM. This depends on whether oxygen availability for nitrifiers or organic carbon for denitrifiers is the strongest regulating factor.

One experiment (26), using sediment cores from SE Kattegat was carried out in order to show the effect of a sedimentation event on benthic mineralization. Portions of an old culture of *Skeletonema costatum* were added to the sediment surface. The effect was a prompt and persistent (>3 weeks) increase in SOC rate by a factor of 1.6 (ECM by a factor of 2.8). As the water-renewal rate for the headspace water was not changed, the oxygen concentration was lowered. The addition of algae was followed by even larger increases in the release of IN, DON and phosphate by the sediment and the IN-loss rate was lowered. These results indicate a strong correlation between sedimentation and SOC (ECM) and that an increase in deposition of easily utilized algal material will not be followed by a corresponding increase in IN-loss.

In order to obtain a clear picture of the regulating factors for IN-loss, the sedimentation effects have to be analyzed independently. This was done by plotting the IN-loss rate vs ECM for narrow ranges of oxygen concentrations (Fig. 4). There is a linear correlation between the IN-loss and ECM for each of three ranges of oxygen concentration. At oxygen concentrations higher than 150 μmol · L^{-1} the ratio between ECM and IN-loss was rather constant (Fig. 4). However, supposing that a decreased external nitrogen load to E Kattegat will result in a decreased mineralization and SOC rate at the bottom, it is more likely that the IN-loss rate will remain high because of improved oxygen conditions when the external loads are lowered. The important conclusion is therefore that the reduction of the external nitrogen load to E Kattegat would result in a proportionally larger reduction of the release of IN from the sediment. This agrees with the finding of Seitzinger and Nixon (63) that a smaller nitrogen load to a mesocosm resulted in proportionally larger denitrification. Seit-

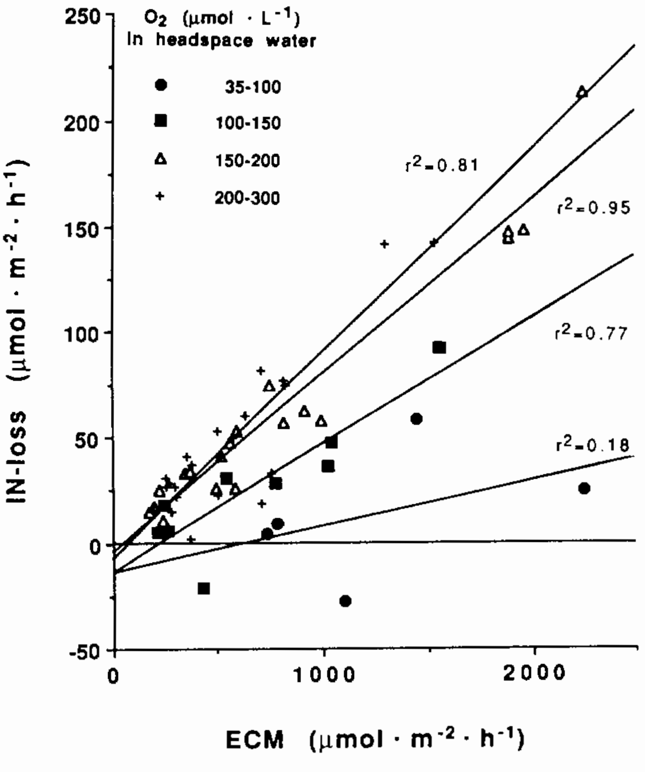


Figure 4. IN (inorganic nitrogen) loss rate in sediments vs estimated mineralization of organic carbon (ECM) for the same samples as in Figure 3.

zinger (56) compared ecosystems ranging from shallow estuarine sediments in highly eutrophicated areas to the deep ($>$60 m) water-sediment system of the relatively low productive, permanently stratified Baltic proper and found that most of these systems had the capacity to denitrify 50% of the external nitrogen load on the system. The latter ecosystem may not be representative, however. If the deep water is only removing 50% of the added nitrogen, there must be other, very actively denitrifying sites in the Baltic Sea as a whole because it accumulates or exports only a small portion of the external nitrogen load (64). A plot of denitrification vs nitrogen load for stratified systems, where the oxygen store in the deep water is a critical factor, would be expected to deviate sharply from the relation for-well mixed systems.

"Ephemeral mud blankets" of a few centimeters thickness and with extremely high contents of water and organic material (65) may, however, release virtually all the mineralized nitrogen to the water, even at relatively high oxygen concentrations. IN-release rates of around 130 µmol · m^{-2} · h^{-1} were observed for such sediments that were sampled at 15 m depth in the Laholm Bay in August (66).

Fauna: So far we have ignored the important bioturbation which will be influenced by both oxygen conditions and the food supply. Numerous papers (33, 34, 67, 68) have shown the multiple role of the benthic fauna as stimulators of benthic metabolism and sediment-water transport. Kristensen and Blackburn (69) found almost no difference in sediment mineralization when comparing nonbioturbated sediments that were incubated with oxic and anoxic headspace water. They found a clear stimulatory effect of burrowing polychaetes *Nereis virens*, however, on the mineralization rate. Especially important is the stimulation of nitrification by the fauna as reviewed by Henriksen and Kemp (58). Here, we will emphasize the role of the brittlestars *Amphiura* spp. which increase in biomass during the periods with high sedimentation rates (31). One experiment was carried out with sediment cores with various numbers of *Amphiura* spp. and the result exemplified the dual action of these animals: increasing the SOC-rate and decreasing sediment release of IN (70). At the highest SOC-rate, IN was actually taken up by the sediment. These animals counteract eutrophication as long as there is a plentiful supply of oxygen, but they will also speed up the oxygen consumption, even after they die. That the presence of recently killed macrofauna can influence SOC profoundly was shown in two experiments. Even though oxygen was continuously added to the headspace water, the oxygen depletion lasted for three days (max 1100 µmol O_2 · m^{-2} · h^{-1} added, (26)) or two weeks (500 µmol O_2 · m^{-2} · h^{-1} added; (66)) respectively, after the asphyxiation of the fauna.

Regulation of Sediment-Water Phosphate Flux

Phosphate is transported to the Kattegat surface layer mainly from the deep water (71). Sediment-water phosphate flux data show that there was a net addition of phosphate from the sediment to the deep water, at higher rates in the autumn (Table 1). Sediment-water phosphate flux did not correlate with oxygen concentrations in the headspace water (Fig. 3b). In laboratory experiments only concentrations of oxygen close to or at zero caused an increased phosphate leakage (72). The phosphate flux instead appeared to be closely linked to ECM, even though less phosphate was released by the sediment (Fig. 4) than postulated from ECM and an assumed substrate C/P ratio of 106 (36). Additional factors seem to regulate phosphate flux, because the Laholm Bay sediment (Stn 8) released phosphate at a relatively slow rate (Table 1). In SE Kattegat (Stn 6), near to the phosphate rich effluent from Öresund, the sediment phosphate release agreed better with the expected release. All sediments released 1–14 µmol · m^{-2} · h^{-1} less than expected from ECM rates, however, during the two periods with high rates of ECM in August 1987 and October 1988.

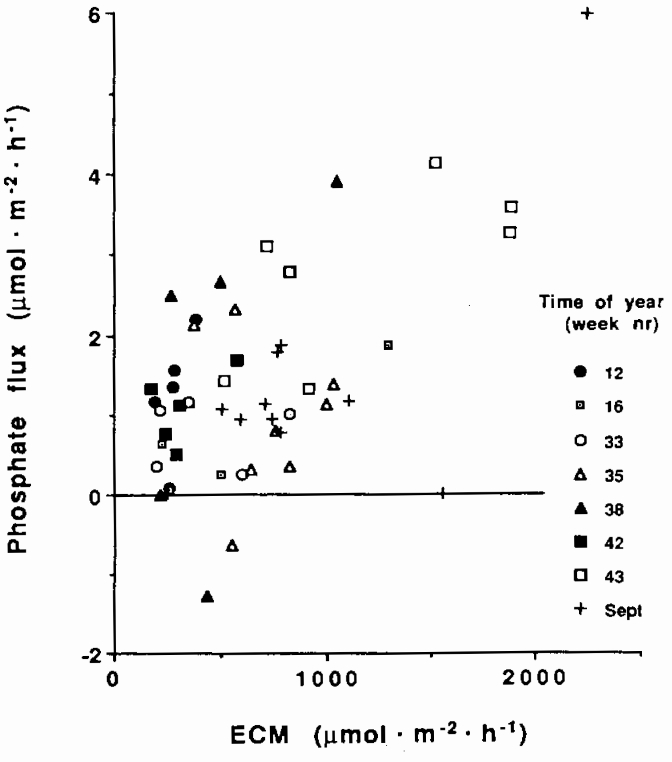


Figure 5. Sediment-water exchange of phosphate vs estimated mineralization of organic carbon (ECM) for the same samples as in Figure 3. Symbols show time of year. The three experimental studies were carried out in September (+).

IN/IP ratios of the nutrients released by the sediments were close to the expected Redfield ratio of 16 for low oxygen concentrations, but ratios were very low at high oxygen concentrations due to an approximately zero net IN flux (compare Figs 3a and 3b). Low IN/IP release ratios were also found in the Narragansett Bay (73).

NITRIFICATION IN DEEP WATERS

Kattegat deep water is formed when surface- or intermediate water from Skagerrak sinks below the less saline surface layer of the Kattegat. In summer, the water entering the deep layer of Kattegat is therefore more or less devoid of IN but local nutrient formation will increase the concentrations (71). Measurements of potential nitrification (see above) were carried out in order to determine whether nitrification could account for the large nitrate pool (Table 1) normally found in Kattegat deep water. In the deep water, nitrifying activity was detected at all sites. The activity always increased towards the bottom and was always highest in the samples taken with the bottom-water sampler ($\approx$0.5 m above the sediment).

Spatial variations in potential nitrification were small compared to the temporal variations. The highest rates, 110–220 nmol · l^{-1} · d^{-1} at the bottom, were measured in August 1987. The large nitrate pool, as much as 12–14 µmol · L^{-1} (Table 1), might thus have been formed by nitrification in the Kattegat deep water during its approximate turnover time of 75 days in the summer. In September 1988, nitrate concentrations were extremely low, less than 0.9 µmol · L^{-1}, at all stations. The highest concentrations were still found close to the bottom, in the samples with the lowest oxygen concentrations, in the range 27–49 µmol · L^{-1} (0.6 to 1.1 ml · L^{-1}). Ammonium was rapidly released from the sediment and ammonium concentrations were 3–7 µmol · L^{-1} in the deepest samples. These conditions should favor nitrifying bacteria, which grow well even at low oxygen concentrations (74). The average nitrification rate at the bottom was, however, only 12 nmol · L^{-1} · d^{-1}. The potential nitrification rates in March and April 1988 were intermediate, one half and one fourth, respectively, of the rates measured in August 1987. Neither the distribution of ammonium nor oxygen could explain the observed distribution of nitrification. The deep water was, however, abnormally warm (8.5–14.7°C) in September 1988 as compared to August 1987 (5.7–8.5°C), indicating a recent transport from a much shallower layer where it was warmed by the sun.

The minimum time needed to nitrify the ammonium in the deep water in September 1988 would be 5 months (2.7 μmol · L^{-1} at a rate of 18 nmol · L^{-1} · d^{-1} at Stn 6). With the average turnover time of the deep water being only 2 months, one may assume that most of the ammonium will reach the productive layer as such. During relatively dark periods this addition would stimulate phytoplankton production more than if the same amount of nitrate was added, the reason being that the algae can avoid the energy-consuming nitrate reduction to the level of amino acids. The addition of ammonium may therefore extend the productive period. Also the productive layer may be extended downwards. In April 1988, as much as 27% on average of the IN just below the halocline was ammonium (0.9–1.8 μmol · L^{-1}). Because there was no nitrification at that depth it is expected that this ammonium would stimulate algal growth, either at the halocline or after being mixed into the surface layer.

DENITRIFICATION IN DEEP WATER

Nitrate is often absent in anoxic waters and this is clearly an effect of denitrification, like in the Baltic Sea (59). Permanently anoxic waters are unimportant, however, with respect to denitrification, since the supply of nitrate from external sources is very limited. Even in the Baltic deep water, where large volumes of anoxic waters occur, about 80–90% of the denitrification is expected to take place in the oxygenated sediments (75) and not in the anoxic waters. Nitrate concentrations are low also in the Kattegat deep water during periods with low oxygen concentrations, when instead the ammonium concentrations are high due to inefficient denitrification in the sediment as discussed above (Table 1). In order to better understand the effect of low oxygen concentrations on the total pool size of combined nitrogen in the ecosystem we need to know the reason why there was no nitrate in the deep water during such periods. There are two plausible explanations: 1) denitrification, which would mean a significant loss of nitrogen from the ecosystem; and 2) a combination of transport of nitrate-poor water from the Skagerrak and low nitrification activity.

In September 1988 (week 38), the lowest observed oxygen concentration in the E Kattegat deep water was 18 μmol · L^{-1} (0.4 ml · L^{-1}) and the highest observed nitrate concentration was less than 1 μmol · L^{-1}. Such circumstances will not favor denitrification (61). Our incubations at in situ concentration of oxygen showed that the net change in nitrate + nitrite corresponded well with the nitrification determined using ^{15}N tracer. Therefore, no significant consumption of nitrate occurred either through assimilation or denitrification. Our data indicated that at most 50 nmol · L^{-1} · d^{-1} might have been denitrified in the bottom water at two stations in September 1988. A significant loss of IN was, however, indicated when comparing the IN-concentrations with the very high apparent oxygen utilization (AOU = oxygen concentration at saturation minus observed oxygen) according to Richards (37). There was also an apparent loss of phosphate, corresponding to about half of the amount estimated from AOU. The apparent loss of IN and phosphate was most pronounced for thin bottom-water layers like at Stn 8 and for most stations in September 1988. On this occasion the bottom-water layer was in the range 1–10 m thick compared to the average thickness of 6–20 m. Therefore, the oxygen, nitrogen and phosphate concentrations in a thin deep-water layer are expected to be highly influenced by the presence of the sediment, and SOC might have caused the high AOU during an earlier period when higher oxygen concentrations favored IN and phosphate loss in the sediment (see above). High AOU values and relatively low IN concentrations would also result from degradation of dinoflagellates because of their high content of carbohydrates. We suggest that the absence of nitrate was due to 1) the lack of nitrification; 2) absence or low concentrations of nitrate in the in-flowing surface or intermediate Skagerrak water during summer (71) and 3) sediment uptake of any nitrate initially present. The fact that there was very little nitrate in the Kattegat deep water in September 1988 is therefore no evidence of

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extensive deep-water denitrification due to low oxygen concentrations as it might at first appear. It is therefore feasible that periods of low oxygen conditions in Kattegat deep water may be followed by excessive accumulation of nitrogen in the ecosystem as compared with periods with high oxygen concentrations in the water overlying the sediments.

CONCLUSIONS

In the Kattegat, nitrate is the major nitrogen source for phytoplankton during the spring bloom and is also important during the autumn bloom. The nitrate is supplied from land or deep water, and nitrification does not occur in the photic zone. During periods with a high nitrate uptake in the photic zone, larger phytoplankton species dominate. These algae sediment out of the photic layer and thus remove a large fraction of the external nitrogen supply.

Oxygen conditions at the sediment-water interface, which depend on the amount of sedimenting algae, strongly influence the fate of mineralized nitrogen. When the water above the sediment is well oxygenated, a major part of the nitrogen is lost within the sediment, mainly through coupled nitrification-denitrification. However, if an increase in primary production and sedimentation—due to an increase in the external nitrogen supply—causes a decrease in sub-halocline oxygen concentrations, our data indicate that proportionally less nitrogen will be nitrified-denitrified and more nitrogen will leave the sediment surface in the form of ammonium, and that this effect will be strengthened during the degradation of asphyxiated fauna. Most likely the nitrogen will then be returned to the Kattegat surface waters by entrainment. Thus, since sedimentation of organic material from primary production seems to be nitrogen limited, eutrophication of the Kattegat may be a self-accelerating process.

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Report **Jan Risberg**

Siliceous Microfossil Stratigraphy in a Superficial Sediment Core From the Northwestern Part of the Baltic Proper

The siliceous microfossil composition has been determined in a superficial sediment core (0–34 cm) from the northwestern part of the Baltic proper. The results are shown in three diagrams. Four stratigraphical zones have been established and described. The lithostratigraphy shows a sequence with laminated clay-gyttja (2.5–5 cm) containing high abundancies of the ebridian *Ebria tripartita* (Schumann) Lemmermann and the diatoms *Actinocyclus ehrenbergi* v. *crassa* (W. Smith) Hustedt and *Coscinodiscus asteromphalus* (Ehrenberg). In the uppermost layers of sediment there is a mass occurrence of *Chaetoceros* spp. resting spores and *Achnanthes taeniata* Grunow. Other diatoms, together with Chrysophyceae stomatocysts and ebridians, show trends of decreasing relative abundance. In general, the autochthonous planktonic taxa have played a more important role during the last 100 years with a peak about 20-years ago. The changes in the siliceous microfossil composition have been nterpreted as mainly reflecting an increased input of nutrients into the Baltic basin. However, other parameters such as current pattern variations, both temporal and spatial, and erosional changes in the littoral zone and on coastal land areas can affect the composition of siliceous microfossils within the sediments.

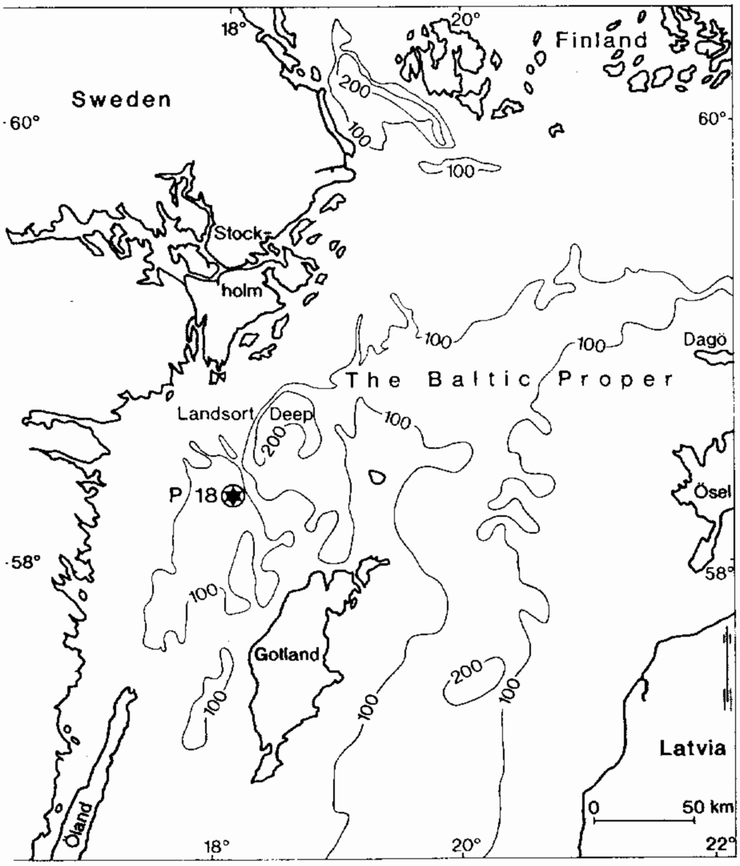

Figure 1. Location map, showing the sampling site north-west of Gotland.

INTRODUCTION

The Swedish Environmental Protection Agency has initiated a project called "Eutrophication in Marine Environments" (1, 2). Within the framework of the project laminated top sediments have been found covering a large area in the northwestern part of the Baltic proper (3). These are possibly the result of an increased input of nutrients from the surrounding land areas, i.e. eutrophication. This paper presents the results of analyses of diatoms, with *Chaetoceros* spp. resting as two separate groups, Chrysophyceae stomatocysts, ebridians and phytoliths, in a superficial sediment core 0–34 cm (called P 18) sampled in January 1988 northwest of Gotland (Fig. 1). Sampling position was 58°10′16″N, 18°11′24″E. The bottom topography in the area is relatively flat and the water depth about 135 m. Salinity at the sampling site is 6–7 per mille (1).

The purpose of the study was to determine the possibilities of using analyses of siliceous microfossils in order to detect changes in the recent and sub-recent sedimentary conditions in the Baltic basin.

Living diatom assemblages are sensitive to changes in the environmental parameters at a given site. Shifts in, e.g. salt content, nutrient content, water depth, temperature (in marine conditions) result in changes in species composition. However, after death of the diatom cell, the frustules are affected by other parameters, e.g. currents, re-suspension which will determine the fallout from the water column onto the sediment surface. The physical and chemical status of the sediment, invertebrate grazing, the ruggedness of the frustules and sediment compacting processes will then affect the preservation of the frustules.

For lake sediments, analyses of diatoms within the sedimentary strata have been extensively used relating to eutrophication problems (4–9). It has been possible to detect changes in the species composition, changes in the C/P ratio (Centrales/Pennales) (10) and in the A/C ratio (Araphidineae/Centrales) (6). The latter ratio is, however, valid only within certain limitations (4) and is not used here.

In brackish water environments, diatom and/or siliceous microfossil analyses in connection with eutrophication problems are rare and few data are available. The most complete investigation has been carried out from a position about 24 km south of the Landsort Depth in the north-

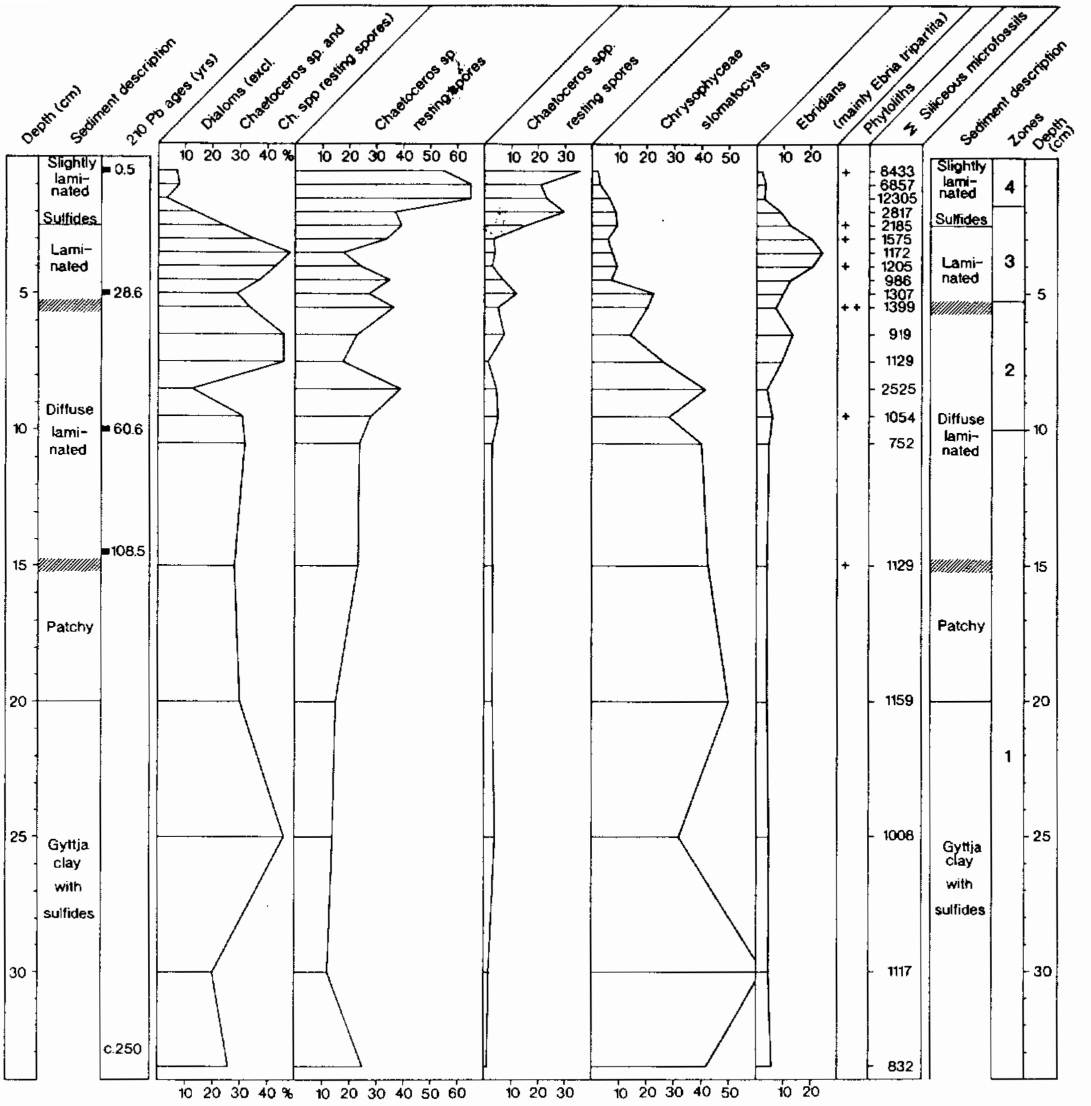

Figure 2.
Total siliceous microfossil diagram.
(+ = single finds of phytoliths).

ern Baltic proper, where the uppermost 42 cm have been investigated by Miller (11). It was concluded that the changes observed (increasing biogenic silica upwards, changes in species composition and a decrease of the number of diatom taxa upwards) could be interpreted as the result of an increased outwash of nutrients into the Baltic basin.

From the western part of the Baltic a sediment core, excluding the uppermost 20 cm, has been investigated (12). It was concluded that the mesohalobous taxa and the ratio plankton/nonplankton decreased towards the top of the core. There was a slight trend towards less salinity towards the upper sediment layers.

From the northern part of the Gulf of Finland three sediment cores have been investigated (13). It was concluded that the most recent clay was absent due to shallow water depth. The diatom taxa *Coscinodiscus lacustris* v. *septentrionalis* Grunow and *Thalassiosira baltica* (Grunow) Ostenfelt increased towards the sediment surface.

MATERIAL AND METHODS

The analyzed sediment core is described below (Per Jonsson, pers. comm.). The uppermost 20 cm is considered as clay-gyttja, followed in downward direction by gyttja-clay.

0–2.5 cm	Black, loose sediment with diffuse lamination about 25% loss on ignition.
2.5–5 cm	Laminated sediment.
5–15 cm	Light, diffuse laminated sediment.
15–20 cm	Darker, patchy, diffuse laminated sediment.
20–33+ cm	Dark gyttja clay with sulfides. 3–6% loss ignition.

Twenty-one samples were analyzed of the sediment core. About 0.25 cm^3 of material was sub-sampled from each analyzed level and approximately 0.02 ml was spread out on the slide. The analyzed part of the slide varied between about 20 and 60 mm^2, depending on the frequency of siliceous microfossils. Sampling intervals were 0.5 cm between 0 and 5.5 cm, 1 cm between 5.5 and 10.5 cm and 5 cm between 10.5 and 33.5 cm. The slides were mainly prepared according to Battarbee (14) and mounted in Naphrax (refraction-index = 1.7).

The literature was studied as an aid to identification and for ecological information (15–19). The taxa were named according to the literature cited although new taxonomic nomenclature has already been established for some of the species used in this paper. As an example *Coscinodiscus lacustris* v. *septentrionalis* Grunow has been renamed as *Thalassiosira hy-*

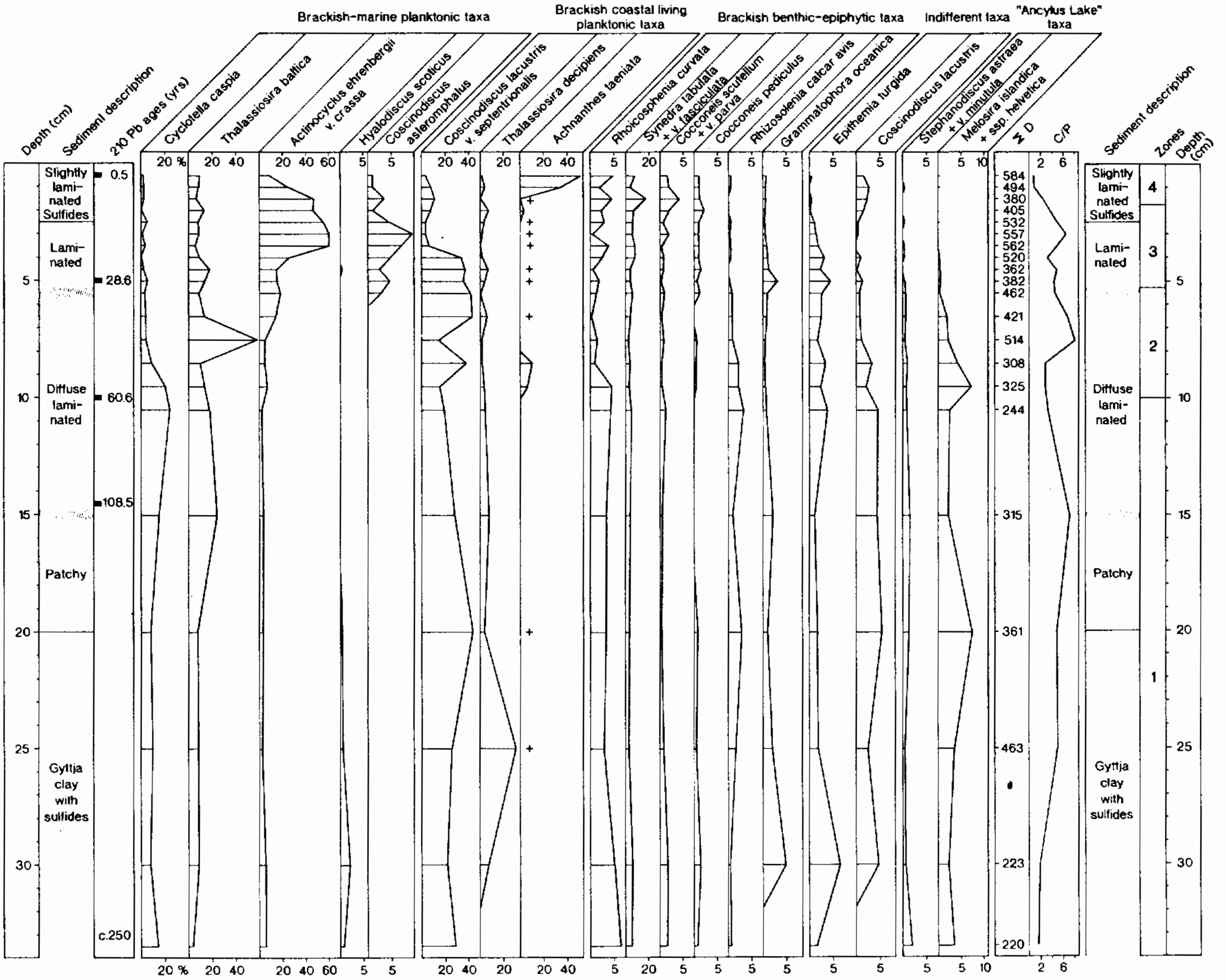

Figure 3. Selected diatom diagram showing taxa with an abundance of more than 1.5% in any sample analyzed. The grouping of planktonic taxa living in open sea (autochthonous) and coastal areas (allochthonous) should be considered as tentative.

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perborea v. *lacunosa* (Berg) Hasle (20).

The number of diatom frustules counted (diatom sum) varies between 220 and 548. Fragments containing at least one pole were counted as halves, complete valves as one. Centric diatoms larger than halves, but not complete, were counted as halves. The analyses were carried out under X1000, using oil immersion and phase contrast.

RESULTS

A total number of 108 diatom taxa, from 33 genera, were identified. A total siliceous microfossil diagram (Fig. 2), a selected diatom diagram showing taxa with an abundance of more than 1.5% in any sample analyzed (Fig. 3) and a diagram showing a salt-ecological grouping of diatom taxa according to different life forms (Fig. 4) were constructed.

Because of mass occurrence of *Chaetoceros* spp. resting spores at 0.5 cm and 1.5 cm (Figure 2) the basic sums for siliceous microfossils have been estimated mathematically (by counting the number of *Chaetoceros* spp. in relation to 100 other diatoms and then applying extrapolation). Single finds of phytoliths have been indicated with "+".

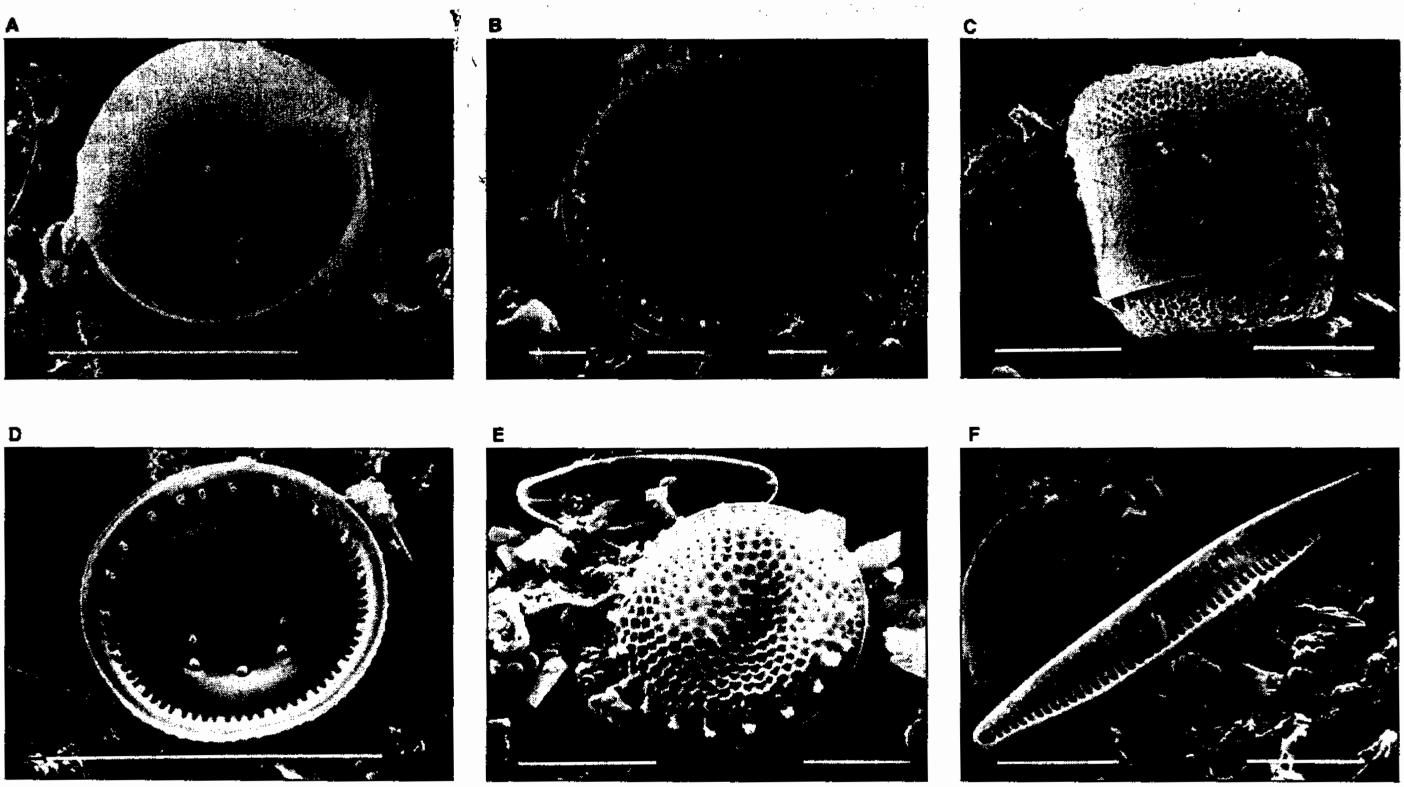
In Figure 3 the total diatom sum (ΣD) excludes *Chaetoceros* spp. resting spores. The diatom taxa tentatively have been grouped into different life forms and combined with salt-ecological requirements. Here, the brackish-marine planktonic taxa can be considered as autochthonous, i.e living as plankton in the Baltic Sea. The other groups are mainly redeposited allochthonous taxa, emanating from the coastal areas and from river outwash. Due to the water depth (135 m) no benthic diatoms are expected to grow at the sampling site (21). The C/P ratio has been calculated from the number of specimens (diatom valves) counted.

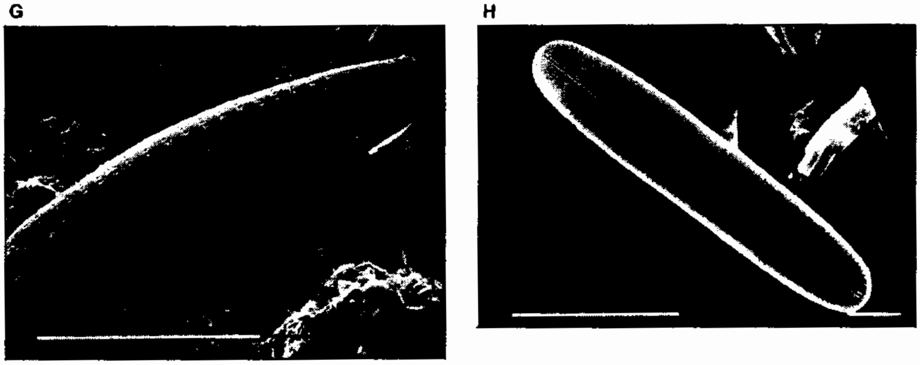
In Figure 4 all diatom taxa found during the analyses have been grouped into different life forms combined with salt-ecological requirements. The brackish-marine planktonic living taxa, contribute about 22% (20–25 cm below the sediment surface) and up to about 80% (3 cm below the sediment surface) of the total diatom flora. The mainly allochthonous brackish-marine taxa contribute 18–60% and freshwater, river transported taxa 1–10% of the total diatom flora.

Dr. Farid El-Daoushy, Institute of Physics, University of Uppsala carried out the Pb^{210} (CRS) dating. The age of the oldest sediments, about 250 years B.P., was estimated from the mean sedimentation rate in the uppermost 15 cm.

Some of the characteristic diatom taxa

Plate 1. Micrographs showing the autochthonous diatom taxa *Coscinodiscus asteromphalus* Ehrenberg (A), *Thalassiosira baltica* (Grunow) Ostenfelt (B), *Actinocyclus ehrenbergi* v. *crassa* (W. Smith) Hustedt (C), *Cyclotella caspia* Grunow (D) together with the more or less allochthonous taxa *Coscinodiscus lacustris* v. *septentrionalis* Grunow (E), *Synedra tabulata* v. *fasciculata* (Kützing) Grunow (F), *Rhoicosphenia curvata* (Kützing) Grunow (G) and *Achnanthes taeniata* Grunow (H). Scale bar 100 microns (A), 10 microns (B, C, E, F, G, H) and 5 microns (D).





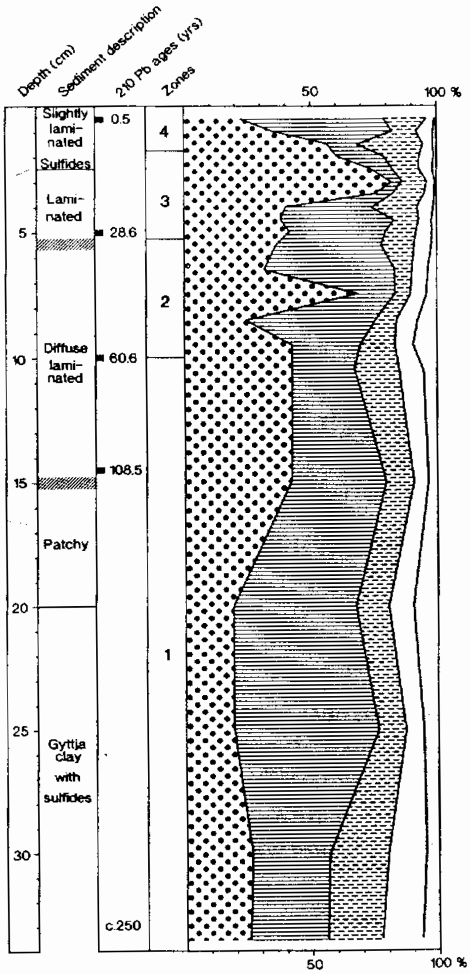
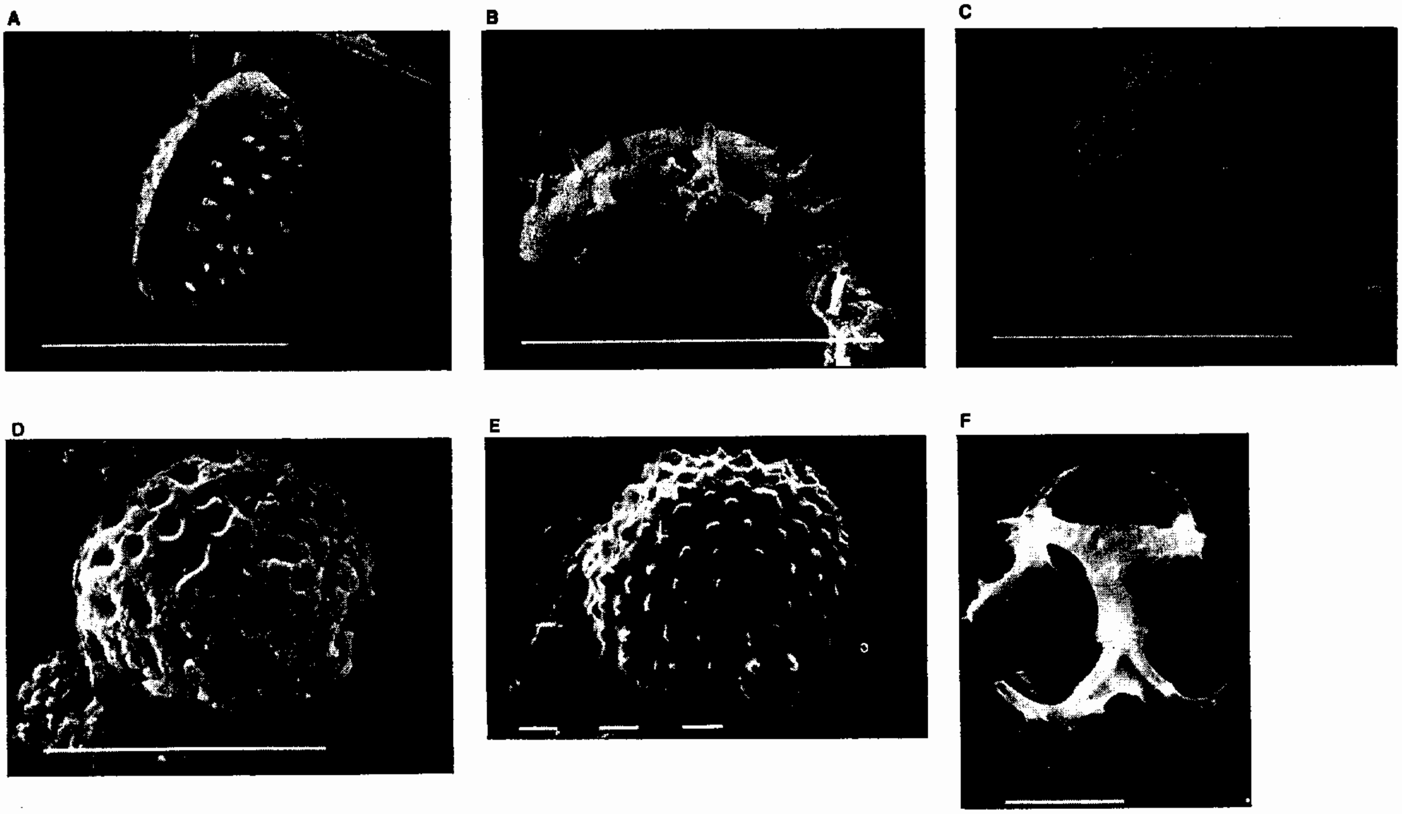


Figure 4. Tentative grouping of diatoms according to different life forms combined with salt and ecological requirements.

found in the sediments are shown in Plate 1. *Chaetoceros*. spp. resting spores have been divided into two groups. The first group, *Chaetoceros* sp. resting spores, frequently occurring throughout the analyzed interval, is shown in Plate 2 (A). One example of the other types, *Chaetoceros* spp. resting spores, is shown in Plate 2 (B). Some of the Chrysophyceae stomatocysts found are also shown in Plate 2 (C–E) (22) together with the ebridian, *Ebria tripartita* (Schumann) Lemmermann. The micrographs were taken by the author at the Department of Quaternary Research, University of Stockholm, using a Philips SEM 515.

The diagrams (Figs 2–4) have been divided into four stratigraphical zones. They are described below with the oldest zone first:

Plate 2. Micrographs showing *Chaetoceros* sp. resting spore (A) and an example of a *Chaetoceros* spp. resting spore (B). Also examples of Chrysophyceae stomatocysts (C–E) and the ebridian *Ebria tripartita* (Schumann) Lemmermann (F) are shown. Scale bar 5 microns.



Zone 1 is characterized by a more or less constant relationship between different types of siliceous microfossils. Chrysophyceae stomatocysts dominate. Among diatoms the brackish coastal living plankton *Coscinodiscus lacustris* v. *septentrionalis* Grunow dominates. Autochthonous taxa vary between 20 and 43% and the C/P ratio between 1.8 and 7.0. Age ≈250–60 Pb^{210} years.

Zone 2 is a transition zone with increasing abundances of the ebridians (mainly *Ebria tripartia* (Schumann) Lemmermann), diatoms and *Chaetoceros* spp. resting spores. At 7.5 cm there is a peak (≈50%) in the abundance of the brackish-marine plankton *Thalassiosira baltica* (Grunow) Ostenfeld. Taxa typical for the Ancylus Lake, a former freshwater stage of the Baltic, (*Stephanodiscus astraea* (Ehrenberg) Grunow + v. *minutula* (Kützing) Grunow, *Melosira islandica* Müller and *Melosira islandica* spp. *helvetica* Müller) decrease. Autochthonous taxa increase between 25 and 70%. Also the C/P ratio increases to between 3.0 and 8.0. Age ≈60–30 Pb^{210} years.

Zone 3 comprises the laminated sedimentary sequence and is characterized by peaks of ebridians, the centric diatoms *Coscinodiscus asteromphalus* Ehrenberg and *Actinocyclus ehrenbergi* v. *crassa* (W. Smith) Hustedt while *Coscinodiscus lacustris* v. *septentrionalis* Grunow decreases. Autochthonous taxa continue to increase (up to 40–80%) The C/P ratio varies between 3.0 and 6.2. Age ≈30–10 Pb^{210} years.

Zone 4 is characterized by the marked increase of *Chaetoceros* spp. resting spores. In the uppermost sample, the brackish pennate planktonic taxon *Achnanthes taeniata* Grunow (Plate 1 (H)) is relatively abundant (≈50%). The amount of autochthonous taxa decreases to between 22 and 60%. The C/P ratio decreases to between 1.0 and 3.0. Age ≈10–0 Pb^{210} years.

DISCUSSION

The relative abundance of *Chaetoceros* spp. resting spores clearly increases towards the upper layers of sediment and shows mass occurrence in the topmost sediment (Fig. 2). This could be caused by an increased access of nutrients, stimulating the production of *Chaetoceros* vegetative cells, which in its turn will produce more resting spores. However, another possible explanation could be that the living conditions for this genus have become unfavorable, making the production of resting spores increase. The vegetative cells of *Chaetoceros* are thin and are easily dissolved during the sedimentation processes (23), therefore, they were not observed during the analyses.

The decreasing trends for diatoms, ebridians (from zone 3 upwards) and Chrysophyceae stomatocysts (from zone 2 upwards) are probably caused by the high frequencies of *Chaetoceros* spp. resting spores. The Chrysophyceae stomatocysts are here considered as redeposited. The ecology of the cysts is poorly known (22) but most of them seem to occur in freshwater environments (5, 24).

Among diatoms *Actinocyclus ehrenbergi* v. *crassa* (W. Smith) Hustedt and *Coscinodiscus asteromphalus* Ehrenberg, taxa living as plankton in the open sea, and *Achnanthes taeniata* Grunow, taxon mainly living as plankton near the coast, seem to be favored by the increased input of nutrients (Fig. 3). The relatively low number of frustules from *Achnanthes taeniata* Grunow in the buried sediments may partly be explained by breakdown and/or dissolution of frustules during sediment-compacting processes.

The C/P ratio varies between 0.5 and 8.0 (Fig. 3). The higher ratio values reflect the higher frequencies of the autochthonous centric diatoms *Thalassiosira baltica* (Grunow) Ostenfelt, *Actinocyclus ehrenbergi* v. *crassa* (W. Smith) Hustedt and *Coscinodiscus asteromphalus* Ehrenberg and the more or less allochthonous *Coscinodiscus lacustris* v. *septentrionalis*. No obvious trends, related to litho- and/or diatom stratigraphy, can be seen. The diatom flora, recorded from an offshore sediment core is, for natural reasons, dominated by autochthonous centric taxa. Therefore, the C/P ratio does not seem to be useful in this context.

In general, there has been a trend over the last 100 years or so towards more autochthonous planktonic taxa within the sediment, culminating about 20 years ago (zone 3), perhaps at a time when the input of nutrients was largest (Fig. 4). Also *Ebria tripartita* (Schumann) Lemmermann, which thrives in nutrient-rich, cool water (25), shows a contemporary peak during zone 3. This interpretation is supported by the laminated sequence which indicates sedimentary conditions with oxygen deficit. The decrease of indifferent, freshwater and Ancylus Lake taxa may be the result of less erosion and sediment transport from coastal areas and rivers into the Baltic basin. The Ancylus Lake taxa *Melosira islandica* Müller + ssp. *helvetica* Müller probably originate as river outwash from Lake Mälaren where the species occurs frequently (26).

However, caution has to be taken when interpreting the results as being mainly dependent on eutrophication. Concerning diatoms, it is known that changed nutrient conditions may benefit the growth of some species and cause others to disappear. The changes can also be explained on the basis of biological interaction (6, 7, 9). From analyses of the sediment in Lake Ontario it was concluded that the floristic modifications observed could be attributed to eutrophication (8). In Lake Mälaren, Sweden, it was concluded that a reversal in eutrophication caused by reduced phosphorus in sewage, has led to a decrease in diatom biomasses (26). There is also a possibility that an increase in phosphorus could lead to a depletion of silica and thus a decrease in diatom frequency and abundance (8, 27). In general, for freshwater basins, it is thought that phosphorus is the limiting factor for growth of algae (28, 29). Since the oceans are always undersaturated with silica (23), this element might become the limiting factor for the Baltic Sea also (30). It is clear, however, that consideration has to be taken to the large ecological differences between lacustrine small-lake conditions and brackish large-basin conditions. The usual indicators of eutrophication in freshwater basins might not be adequate for the Baltic basin.

Another parameter to reconsider is changes in the current pattern, both temporal and spatial, within the Baltic basin (31, 32). This could result in algae assemblages emanating from a variety of sources and could possibly be the explanation for minor changes in the diatom stratigraphy, e.g. the peak of *Thalassiosira baltica* (Grunow) Ostenfelt during zone 2.

Achnanthes taeniata Grunow, which shows mass occurrence in the uppermost sediment, is recorded as an Arctic species living in sea ice (33–35). This may indicate that even the ice-cover conditions within the Baltic basin affect the diatom flora recorded in the sediments.

SUMMARY

There are changes in both the total siliceous microfossil stratigraphy (Fig. 2) and in the diatom stratigraphy (Figs 3 and 4). These changes may reflect (in order of significance from most to least important):

- an increased input of nutrients into the Baltic basin;
- changes in current patterns within the Baltic Sea resulting in algal assemblages from a variety of sources;
- changes in the erosion and transport of minerogenic matter from the surrounding littoral zones and streams flowing into the Baltic basin.

It is obvious that analyses of siliceous microfossils is a useful method when studying eutrophication problems in the Baltic basin. However, the trophic conditions are not the only parameters affecting the microfossil composition at a specific site. Parameters such as current patterns causing deposition of reworked taxa or erosion of the top-most sediments, water column fall-out processes, sediment-compacting processes and different sampling equipment will also affect the results.

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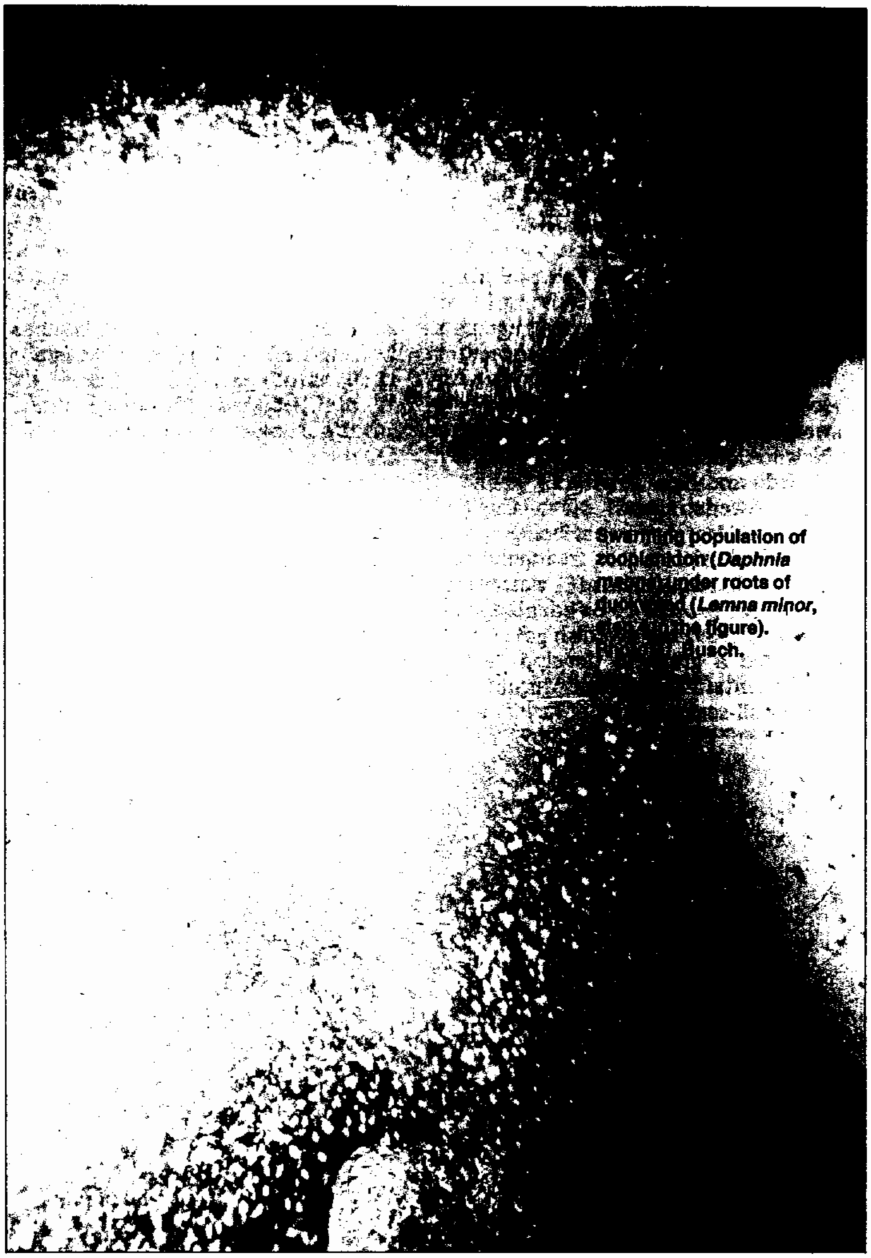
Synopsis

Ecological Engineering for Wastewater Treatment and its Application in New England and Sweden

Conventional wastewater-treatment technologies do not provide the level of treatment necessary for industrial societies. They are technologically inadequate for at least four reasons:

1. They produce a byproduct called sludge. This sludge is often contaminated and toxic and is disposed of by ocean dumping, land filling, spreading on agricultural land, incinerating, or by composting.
2. Environmentally-damaging chemicals are employed in the waste-treatment processes. For example, aluminum salts are used to precipitate out solids and phosphorus. Chlorine is widely used in ammonia control and in fecal coliform reduction. Chlorine, in the presence of organic compounds, can create chloramines, known carcinogens.
3. They fail to remove metals and synthetic organic chemicals produced and discarded by industrial societies from the waste streams. In Sweden, some 20 000–70 000 manufactured chemical substances contaminate the environment (1). The volume of waste material is also large. For example, in the United States thirteen thousand coastal industries dump 19-billion cubic meters of wastewater annually into coastal waters.
4. They are too costly. In the past conventional waste-treatment facilities have required heavy government subsidization. Reasonable user fees have not been adequate to support efficient wastewater treatment.

An alternative approach to wastewater treatment is urgently needed. An environmentally responsible technology would produce little or no sludge, generate useful byproducts, use no hazardous chemicals in the process chain, and remove synthetic chemicals from the water. The technology should also be cost effective.

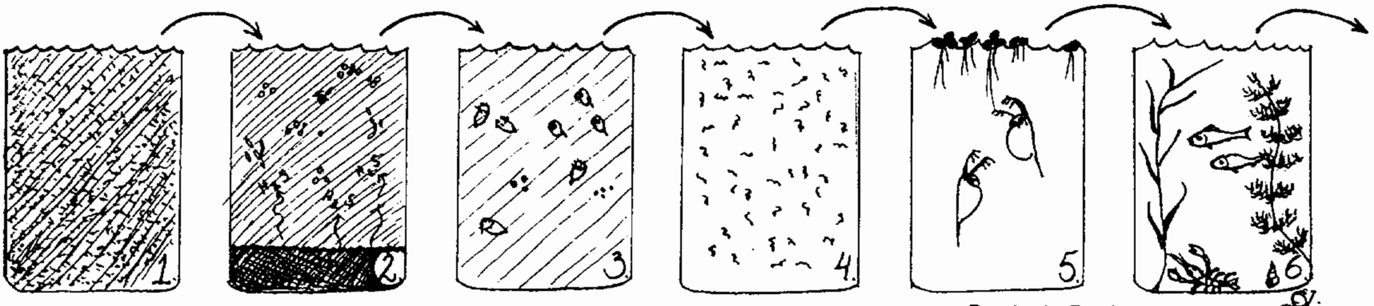


Swarming population of zooplankton (*Daphnia magna*) under roots of duckweed (*Lemna minor*, top of the figure). [illegible] Busch.

Principal steps of the wastewater treatment at the Stensund Aquaculture:

1. **Raw sewage**
2. **Anaerobic treatment**
3. **Aerobic treatment**
4. **Phytoplankton-bacteria basin**
5. **Zooplankton basin**
6. **Polyculture (fish, crayfish, plants)**

2–3 are steps of mineralization and detoxification
4–6 are steps of aquaculture



Drawing by Eva Jansson

A technology which fits the above criteria is currently being developed. It encompasses systems based upon ecosystem strategies that are derived from natural systems and applied in engineered environments for waste transformation and purification. In 1971, Howard T. Odum (2) defined the management of natural living systems for human use or environmental repair as ecological engineering.

By the mid-1970s ecological engineering had been applied to wastewater treatment in the southern United States (3, 4) and to the aquatic culture of fish and vegetables in New England, and Maritime Canada (5). These were developed as complex ecosystems with assemblies of bacteria, algae, zooplankton, crustaceans, fish, and higher plants for nutrient recovery and toxin removal. Internal biotic self regulation is central to the ecological engineering models. Light is the primary energy source. Light-capturing technologies were created for the facilities at the New Alchemy Institute in eastern Canada and New England (5).

In Sweden and New England, ecological engineering is being applied to cold-climate water treatment. The Stensund aquaculture wastewater-treatment project in Sweden began in 1983. In 1989, the Swedish government provided a grant to develop "an environmental protection technology" and a full-scale treatment facility was in operation by October 1989. In the United States, development of solar aquatic facilities for treating diverse waste streams began in the early 1980s (6) and the first prototype facility was established in Vermont in 1987.

The Stensund (Sweden) and New England facilities employ the same basic overall biological design principles. However, the elements of the ecological engineering are distinct for the two projects as a result of the climatic restraints in Sweden which are more severe than in New England.

Stensund

The Stensund facility located at a boarding school with 130 residents treats approximately 25 m^3 per day. Treatment takes place in an energy-efficient greenhouse. Detention time is one week, compared to between 8 and 48 hours (depending on degree of treatment) for conventional waste-treatment plants.

The first phase of treatment is anaerobic to promote the production of sulfides by sulfur bacteria in order to precipitate most metal ions as metal sulfides. In the pilot study the bulk of the copper in the sludge was removed by this means. The second step in the treatment chain involves oxidation of sulfides with aeration. This step includes microbial detoxification and mineralization. Step three involves the culture of algae for nutrient and food-chain diversification. A combination of artificial and natural sunlight is employed for 16–18 hours per day to facilitate growth. Step four involves the culture of zooplankton which graze upon bacteria, protozoa and algae cultured during the proceeding stage. Water plants cover the surface. They provide habitat for zooplankton, additional nutrient uptake, and algae-growth inhibition. Temperate and tropical plants are most effective for this purpose. The next step (5) involves the polyculture of fish and crayfish in order to remove detritus, sludge, and plankton from the system prior to discharge. The final step involves nutrient polishing with hydroponically grown plants including willows (*Salix* spp.) and water-cress (*Lepidum* spp.). The results from the pilot study, upon which the full-scale design was based, are encouraging. Between September 1987 and April 1988, 99.999% of the coliform bacteria were removed; 97% of the suspended solids, 96% of the BODs; 85% of the total nitrogen; and 62% of total phosphorus. With a one- to two-week retention time the pilot study produced good quality waste water.

New England

To date, five solar aquatic facilities have been built in New England. The first three were built with town, state, federal, corporate, and private support from the Center for the Protection and Restoration of Waters at Ocean Arks International. The fourth is a joint project between the Center and the Ecological Engineering Associates, Inc. The fifth is a commercial venture undertaken by Ecological Engineering Associates.

The first facility was established in Vermont in 1987 to treat 15 m^3 of sewage per day from a mountain resort. The sewage-treatment study was carried out for a period of two years in a state with the nation's strictest water-quality standards. The second was a sewage-treatment demonstration facility built in 1988 in Harwich, Massachusetts. It treated up to 4.6 cubic meters per day of concentrated and toxic wastes pumped from septic and holding tanks. The third in Providence, Rhode Island, was a permanent research facility for the treatment of industrial sewage and sludge from conventional facilities. It treats up to 76 m^3 per day to advanced standards. The fourth is a demonstration and research plant in Marion, Massachusetts installed to protect a neighboring estuary. By spring 1990, this plant will treat pump-out wastes from boat-holding facilities. The fifth is a newly completed commercial facility built to treat sewage on a year-round basis for the town of Harwich, Massachusetts. Ecological Engineering Associates has financed, built, and is operating the facility on a contract basis for the town, providing a unique "clear water" service. The Center is currently building research and demonstration facilities in Muncie, Indiana, and in Santa Fe, New Mexico. Both are collaborative projects together with local universities and engineering groups.

Facilities

The solar aquatic facilities are housed within greenhouse structures that are built with advanced light-gathering and heat-retaining materials. All of them use clear-sided silo-like containers for heat storage and light transmission. Each facility has multiple-treatment lines for backup, redundancy, and research capabilities. Internal recycling is employed to maintain ecological diversity and to speed up system recovery after toxic shocks. Aerated and photosynthetic environments are continuous throughout. Providence and Harwich are pulsed with engineered marshes at midstream which function as alternating pairs of wet-dry "tidal" marshes. Animals including fish, snails, clams, and crayfish remove sludge after microbial treatment. Water polishing and final nutrient removal is completed by higher plants including flowers, shrubs, and trees that in themselves are of commercial value. Retention times vary from four days for sewage to up to eleven days for concentrated wastes such as septage and sludges. During the winters of 1987–1988 and 1988–1989 the Vermont sewage facility produced high-quality water and achieved excellent ammonia removal. Even when the input of aluminum salts and bromine made the facility toxic it continued to function to secondary-treatment standards (7).

The Harwich septage pilot facility was situated outdoors without a greenhouse facility. It was operated during the summer and fall. BOD removal was more than 99%, suspended solids more than 98%. Nitrogen removal varied from 85% to 98% of the nitrogen mass and phosphorus removal from 43% to 95%. The lower figures occurred during a two-week period when the oxygen supply was disrupted in the early autumn. Fourteen of the fifteen volatile organic compounds on the EPA primary list were found in the influent but not in the effluent. 1,1,2 trichloroethane (*purgeable halocarbon*), toluene and 1,4 dichlorobenzene (*purgeable aromatic*) were detected in the influent but not in the effluent. Fecal coliforms were dramatically reduced. At peak performance coliform levels were reduced from above $2 \cdot 10^6$ per 100 ml in the influent to <10 per 100 ml in the effluent.

Metals, including copper, silver, mercury, and chromium were present in the sediments at the upper part of the system. But, fish kept further downstream showed very low levels in their flesh and livers. Uptake took place primarily in the midway engineered marsh.

Results from the other facilities have yet to be compiled. In its first six months of operation nitrogen, coliform, BODs, and suspended-solid removal were excellent at the Providence facility.

Ecology as the basis for wastewater treatment is still in its infancy. Ecological engineering as an idea will celebrate it 20th anniversary in 1990. By the turn of the century, it may well take its place as a major contestant in the race to protect and restore the waters of our planet Earth.

Summing up we conclude: 1) Ecological approaches to wastewater treatment permit wastes to be used as a resource for producing biomass, including plants and fish; 2) Pathways can be established to remove toxic substances from the wastewater. At the Stensund facility metals are precipiated as metal sulfides before nutrient reuse. In the Solar Aquatics facilities plants on the water surface and within engineered marshed take up metals. Toxic organic compounds in both types of systems are degraded by micro-organisms or utilized by higher plants; 3) Sludge, instead of being a waste product, can be incorporated into beneficial food chains; 4) In northern climates solar energy can be utilized within the greenhouses for heating and photosynthesis.

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8. We gratefully thank the following organizations for financial support for the Stensund Pilot Study: Magn Bergvall Foundation. Nyköping Community, and the Swedish Council for Forestry and Agricultural Research.
9. Readers who are interested in this subject are recommended to contact the secretariat for the "International Conference on Ecological Engineering for Wastewater Treatment" to be held at Stensunds Folk High School, Trosa, Sweden on March 25–28, 1991. The conference is co-sponsored by the Center for Protection and Restoration of Waters at Ocean Arks International (OAI), the World Wide Fund for Nature (WWF), and Apple Computer AB. Address: Conference Secretariat, Stensunds Folkhögskola, S619 00 Trosa, Sweden.

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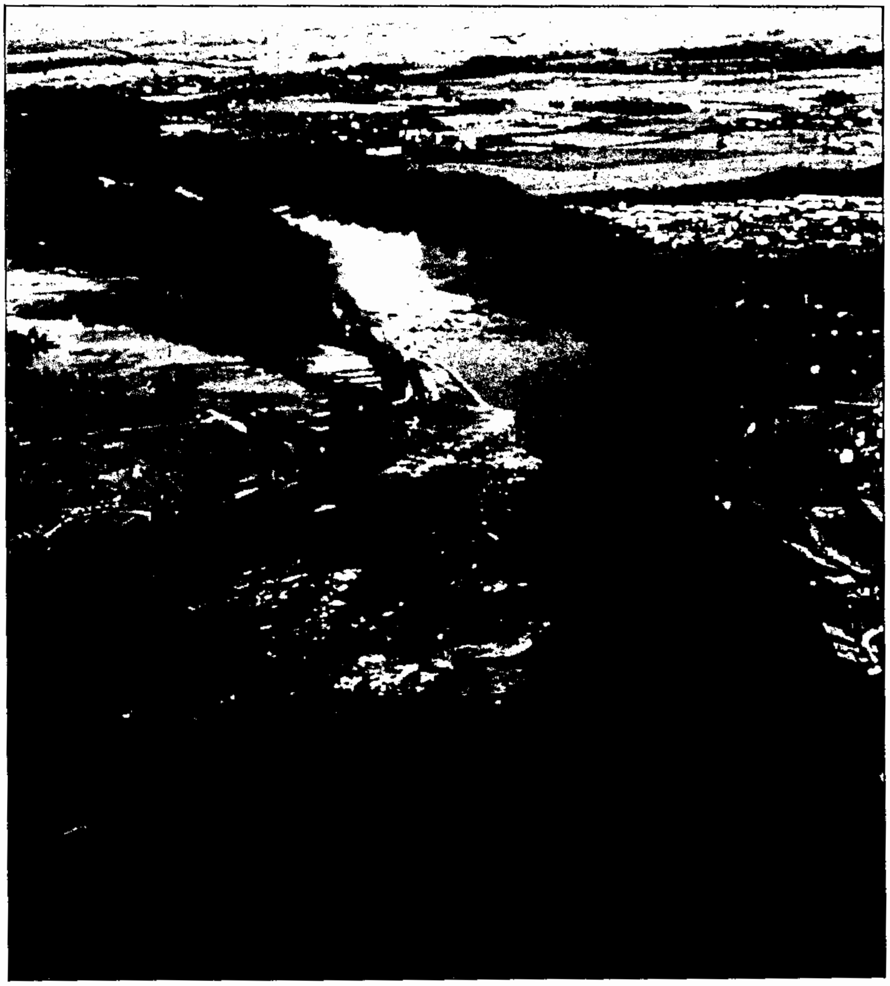
Synopsis

An International Research Effort on Land/Inland Water Ecotones in Landscape Management and Restoration 1990–1996

In April 1986, a meeting was held in Toulouse, France on "Land Use Impacts on Aquatic Ecosystems; the Use of Scientific Information". The conference was jointly supported by Unesco (within the framework of MAB Project Area 5) and the Centre National de la Recherche Scientifique (CNRS). One of the outcomes of this meeting was the realization of the role that ecotones play in regulating biochemical processes and determining the character of the landscape (1). It was proposed, and accepted by the assembly, that the focus of the informal working group on MAB (Man and the Biosphere) Project Area 5 would be reoriented towards the role of international meetings on the concept of ecotones, a technical consultation within SCOPE (Scientific Committee on Problems of the Environment) -MAB resulted in a special issue of Biology International (2).

Subsequently, an international workshop was organized as a joint undertaking of Unesco, The International Institute of Applied Systems Analysis (IIASA) and the Hungarian Academy of Sciences, Hungary, in May 1988, and resulted in a proposal for collaborative research (3) and in a state-of-the-art synthesis (4).

The riparian ecotone of the Garonne River near Toulouse, provides a buffer between the river and agricultural land of the catchment. Photo: H. Décamps.



The overall aim of the collaborative research is to determine the management options for the conservation and restoration of land/inland water ecotones through increased understanding of ecological processes. Special emphasis is being given to ecotones occurring at the terrestrial/aquatic interface because of their importance in regulating the flow of water, materials and information across the landscape. Such ecotones include riparian forests of both lakes and rivers, wetlands, littoral zones of lakes, and areas where groundwater-surface-water exchanges are substantial.

Objectives of the Unesco/MAB Ecotone Program

The specific objectives of the program are:

1) to identify the gaps in our present knowledge and understanding;
2) to understand the role of ecological processes within ecotones in determining landscape patterns;
3) to develop management plans to conserve ecotones and to address detrimental environmental practices;
4) to develop a collaborative research project on the theme of recovery and restoration of degraded ecotones occurring at the terrestrial-aquatic interface.

The main research activity of the collaborative effort will be concentrated on testing 19 related hypotheses grouped into three categories: 1) ecotone function, 2) relations between ecotones and adjacent systems, and 3) management and human investment.

Ecotone Functions

1. Land/inland water ecotones are often characterized by higher biological diversity than adjacent patches, consequently the frequency of ecotones across a landscape directly affects biodiversity in a predictable manner. The edge effect, the tendency for communities to be more dense and diverse in transition zones, is a common observation in ecological studies.

2. The reciprocal relationships between hydrology and vegetation are maximized in land-water ecotones. In contrast to upland, lentic ecosystems, the hydrology of ecotones tends to change with and determine changes in vegetative succession.

3. Regular interactions between seasonal phenomena and ecotones contribute to the broader regeneration of both terrestrial and aquatic ecosystems.

4. Community composition and structure in the ecotone are more sensitive to changes in hydrology than changes in nutrient availability.

5. Within a given hydrologic regime, rates of nutrient recycling and availability through decomposition are strongly influenced by the chemical quality of particulate and dissolved organic matter and their mass balance throughout the ecotone.

6. Spatial and temporal variations in oxidation-reduction (redox) conditions characteristic of ecotones enhance rates of certain microbial and physical processes (e.g. denitrification, methane production, phosphorus precipitation with sesquioxides). These processes proceed more slowly in adjacent ecosystems with stable (less fluctuating) redox conditions.

7a. In riverine landscapes, nutrient and sediment retention efficiency is positively related to the percentage of the landscape that is composed of land/inland water ecotones. This is the case in small streams and also in large rivers. Water-level fluctuations are also important in riverine landscapes because retention is most efficient when the riparian wetlands are flooded and water comes into contact with the superficial ecotones of the wetlands.

7b. For smaller scale ecotones, nutrient and sediment retention efficiency is greatest when surface and subsurface flows are evenly distributed across the entire length of the ecotone between two patches. Retention efficiency would be less when the flow of materials is concentrated in corridors such as gullies, drainage lines, and man-made ditches.

8. The structure and function of the land/inland ecotones are related to the frequency of disturbance by extreme hydrological events.

Relationships Between Ecotones and Adjacent Systems

9. Sequence of flooding events affects the coupling of ecotones to adjacent systems.

10. The influence of the ecotone on adjacent systems is proportional to the length and shape of the contact zones.

11. The quantity and direction of water flow through ecotones directly affects the rate of exchange of dissolved and suspended solids between ecotones and adjacent systems.

12. Rates of exchange of dissolved and suspended solids between ecotones and adjacent systems are functions of internal processes such as residence time of water, response time of seedlings and vegetation, and the rate of production.

13. Material retention is greatest in ecotones where there is a sharp decrease in the kinetic energy of wind or water. These ecotones frequently occur at breaks in topography (e.g. the juncture of upland and wetland patches).

14. There are components of land/inland water ecotones that are more sensitive to disturbance or changes in the global environment than the aquatic and upland ecosystems with which they interact.

15. Human interventions between upland and lowland or estuarine coastal segments of land/inland water ecotones affect their longitudinal dynamics.

16. In most types freshwater ecosystems, fish diversity, recruitment and productivity is dependent to a great extent on land/inland water ecotones.

Management and Human Investment

17. The restoration and creation of land/inland water ecotones will promote the recovery of their ecological functions, including; soil-bank stability, nutrient and sediment trapping, habitat for species conservation and regeneration, and will re-establish the processes of floodplain formation and maintenance.

18. The maintenance, restoration and creation of ecotones are efficient management tools: 1) for regulating water quality and runoff; 2) for water conservation; and 3) for enhancing amenity and recreational opportunities.

19. The restoration and creation of land/inland water ecotones will provide for and enhance the economic and social values of landscapes including landscape quality, recreational use (including tourism), production of resources (such as fish and fiber), wastewater management from urban, industrial and agricultural sources, and flood control.

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