

COOPERATIVE RESEARCH REPORT
RAPPORT DES RECHERCHES COLLECTIVES
NO. 175

THE CHRYSOCHROMULINA POLYLEPIS BLOOM IN
THE SKAGERRAK AND THE KATTEGAT IN MAY-JUNE 1988:
ENVIRONMENTAL CONDITIONS, POSSIBLE CAUSES, AND EFFECTS

Report of the ICES Workshop on the Chrysochromulina polylepis bloom
in the Skagerrak and Kattegat in May-June 1988
Bergen, 28 February - 2 March 1989

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ISSN 2707-7144
ISBN 978-87-7482-478-7

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Palægade 2-4, DK-1261 Copenhagen K
Denmark

April 1991

<https://doi.org/10.17895/ices.pub.5524>

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1. INTRODUCTION

1.1 Background

In response to the bloom of Chrysochromulina polylepis which occurred in Scandinavian waters during May and June 1988, two Council Resolutions were adopted at the 76th Statutory Meeting of ICES. They are as follows:

C.Res.1988/2:38:

A Workshop on the Chrysochromulina polylepis bloom (Chairman: Prof. I. Dundas) will be held in Bergen from 28 February - 2 March 1989 to:

- a) Amalgamate relevant observations on taxonomy, physiology and toxicity of C. polylepis;
- b) describe the environmental background associated with the bloom;
- c) evaluate the effects of the bloom on the aquaculture industry as well as the marine ecosystem;
- d) prepare the papers for rapid publication as a Cooperative Research Report; and
- e) report to ACMP at its June 1989 meeting on the results of the Workshop.

C.Res.1988/1:10:

Subject to clearance by the Chairman of the Consultative Committee, the proceedings of the Workshop on the Chrysochromulina polylepis bloom, edited by I. Dundas and H.R. Skjoldal, will be published in the Cooperative Research Report series. The estimated number of pages is 100.

1.2 Participation and Organization of the Workshop

The venue for the Chrysochromulina Workshop was the Institute of Marine Research, Nordnesparken 2, Bergen, Norway.

Forty-two participants from nine ICES member countries attended the Workshop. A list of the participants is attached as Annex 1. A detailed outline of the schedule and the organization of the workshop is attached as Annex 2. Sub-groups on environmental conditions, properties of Chrysochromulina polylepis, effects of the bloom, and ameliorating actions, were formed. The chairmen, rapporteurs and participants in these sub-groups are listed in Annex 3.

The present report is based on contributions from the sub-groups. The editors have felt it their liberty to amend these contributions for the sake of completeness of documentation and uniformity of presentation. A draft version of the report was circulated to all participants for their comments and approval of the text.

The editors wish to extend thanks to the Workshop participants for their contributions to the Workshop and this report.

1.3 The Kattegat-Skagerrak Area

The Kattegat and inner Skagerrak form a transition area between the North Sea and the Baltic Sea. The water circulation in this area is part of the general counter-clockwise circulation pattern of the North Sea. Water from the southern

or the central North Sea flows into the Skagerrak along the northwestern coast of Denmark (Figure 1.1; see also section 3.1). This water dives under the outflowing Baltic water, causing highly stratified hydrographic conditions in the Kattegat and inner Skagerrak. The deep water is entrained into the outflowing Baltic water in the Kattegat and the mixed water flows northward and westward in the Skagerrak as the Norwegian Coastal Current.

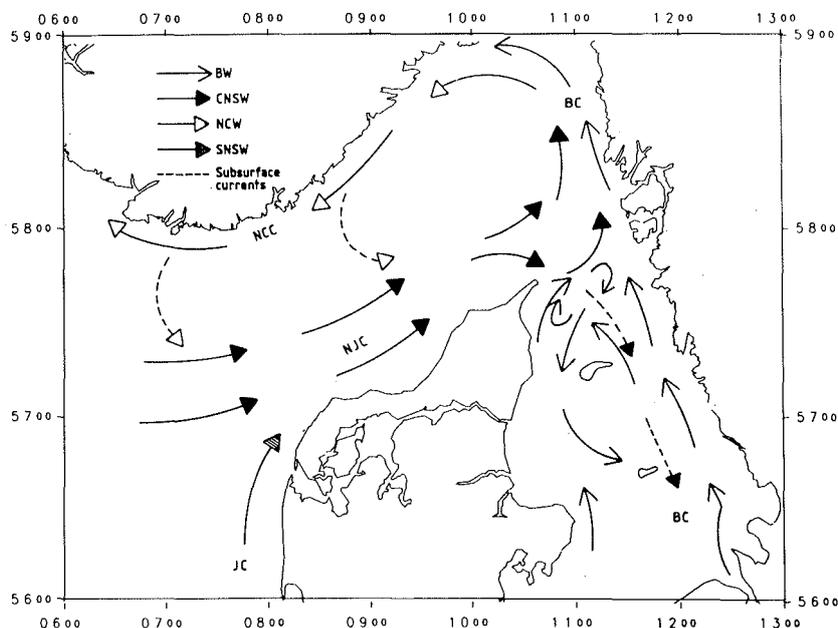


Figure 1.1 Surface currents and water masses of the Skagerrak and the Kattegat. JC = Jutland Current, NJC = North Jutland Current, NCC = Norwegian Coastal Current, BC = Baltic Current. Water masses: BW = Baltic Water, CNSW = Central North Sea Water, NCW = Norwegian Coastal Water, SNSW = Southern North Sea Water.

The Kattegat and inner Skagerrak are marine areas which are strongly influenced by freshwater runoff. The freshwater discharge to the southern North Sea is about $150 \text{ km}^3 \text{ year}^{-1}$ and most of this is transported into the Kattegat and Skagerrak. The direct freshwater runoff to the Skagerrak and Kattegat is $106 \text{ km}^3 \text{ year}^{-1}$. The major freshwater source, however, is the brackish Baltic Sea outflow, which carries a surplus of 440 km^3 of fresh water per year (Svansson, 1975). In comparison, the inflow of oceanic water along the southern slope of the Norwegian Trench is $35,000 \text{ km}^3 \text{ year}^{-1}$ (Dooley, 1974). The counter-clockwise circulation causes doming in the central Skagerrak, which brings nutrient-rich Atlantic water up to the euphotic zone (Pingree et al., 1982).

The environmental conditions in the Kattegat and the Skagerrak were recently assessed by ICES (1987). This assessment concluded that there was little or no anthropogenic effect on the nutrients and primary production in the open waters of the Skagerrak. In contrast, there is clear evidence of eutrophication in the Kattegat. The input of nutrients to the area has increased many-fold in the last decades and this has led to an increasing trend in nutrient concentrations (Ærtebjerg, 1987; Anderson and Rydberg, 1988). There is also evidence for increased primary production in the Belt Sea and the southern part of the Kattegat.

1.4 Outline of the Bloom Development

The bloom of Chrysochromulina polylepis was first noticed on 9 May 1988, when fish in fishfarms near Lysekil on the Swedish west coast were affected. The first sign of the bloom on the Norwegian Skagerrak coast was noted in a fishfarm on 13 May 1988. The bloom developed rapidly and spread with the Norwegian Coastal Current westward in the Skagerrak. The toxicity of the algae was high and the bloom caused extensive damage to both farmed fish and natural biota, including a range of organisms such as fish, various invertebrates, and even some macroalgae.

The bloom was characterized by some people as an ecological catastrophe and received great attention by the media and the public. A large effort was spent by various institutions to carry out monitoring and research on the bloom and its ecological effects. There was, thus, a large amount of information collected during the bloom. However, since the research and monitoring had to be done on an ad hoc basis, there were obvious limitations in terms of planning and coordination. As a result of this, there are some unfortunate gaps in the available information which make interpretation of the bloom event difficult. We have in this report attempted to arrive at a plausible scenario which is consistent with observations and which may be regarded as the most likely explanation for the development of the toxic bloom of Chrysochromulina polylepis.

2. PHYSICAL ENVIRONMENTAL CONDITIONS

2.1 Meteorology

2.1.1 Wind conditions

Wind and atmospheric pressure are among the most important factors affecting circulation and stratification in a shelf sea like the North Sea and the Skagerrak (Aure and Sætre, 1981; Furnes, 1980; Dooley and Furnes, 1981; Davies and Heaps, 1980). The structure of the vertical stratification, in turn, has a strong influence on biological processes.

Mean values for wind speed and direction over the North Sea and the Skagerrak have been obtained from the Norwegian Meteorological Institute's hindcast archive (Aksnes *et al.*, 1989). The average values are based upon wind field data taken every 6 hours, covering the months between November 1987 and May 1988. The velocity fields during the months of January and February show the strongest mean winds over the southern North Sea, with speeds slightly above the normal. The directions in January were between westerly and southerly, a quite normal situation, while in February the average winds were more from westerly to north-westerly directions. Over the Skagerrak, the winds were southerly. The wind fields for November and March resemble each other, with northwesterly winds in the western regions of the North Sea and southerly winds over the Skagerrak. The December wind field was rather uniform with respect to magnitude. The directions were southwesterly, except for the area over the Skagerrak, where the winds were from the northwest. The wind fields in April and May deviate considerably from the winter circulation, particularly during May. In April, the winds over the eastern North Sea and the Skagerrak were predominantly from a northwesterly direction, whereas in May they were of more or less the opposite direction.

In order to give an impression of the variability of the winds over the Kattegat during April and May, time series of wind speed and direction have been plotted for a position at the northern entrance to the Kattegat (57° 10' N, 11° 15' E) (see Figures 2.1 and 2.2). These time series show strong variability, with some pronounced events including strong winds. The strongest winds occurred around 10 April, reaching nearly 20 m s⁻¹ from a northwesterly direction. Between the

strong wind events, there were longer periods of calm wind conditions, e.g., in mid-May.

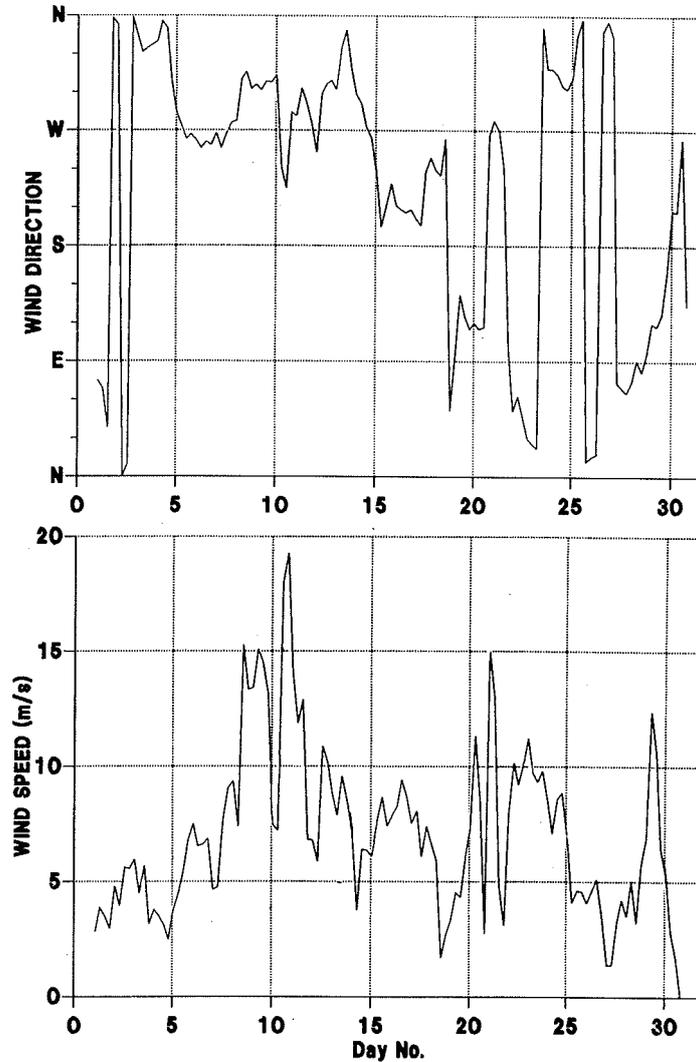


Figure 2.1 Wind direction and speed during April 1988 at a station in the northern Kattegat. From Aksnes *et al.*, (1989).

The wind speed cubed is a measure of the wind energy available for vertical mixing across the pycnocline. Mixing is a two-way entrainment process in which the entrainment is proportional to the amount of energy produced in each of the layers. The wind activity determines the vertical stability of the water column for a given freshwater runoff. If no wind action were present, one would expect that the lower layer would be saltier and the surface layer fresher because of reduced mixing. Furthermore, the net horizontal flow of water in both layers would be smaller. When the water column stabilizes as a consequence of low wind activity, the difference in density, which is primarily a function of salinity and temperature, increases. This, in turn, leads to an increase in the amount of energy required to destabilize the water column. Hence the intensity of vertical mixing is a sensitive function of the available wind energy (Barth and Nielsen, 1989).

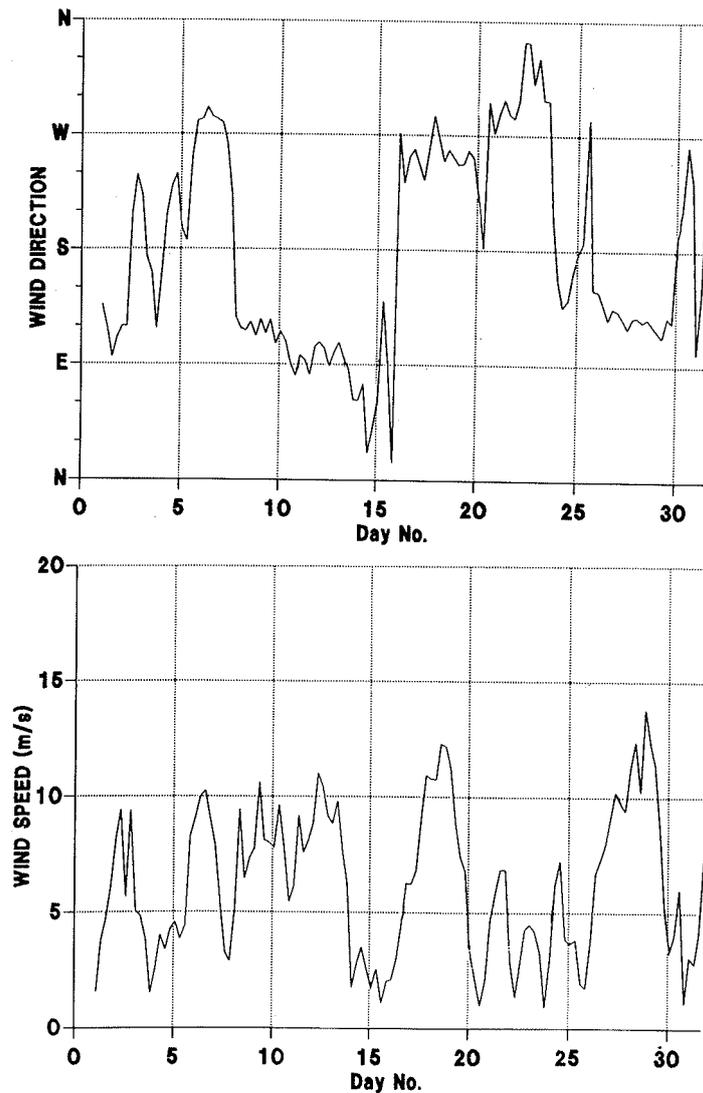


Figure 2.2 Wind direction and speed during May 1988 at a station in the northern Kattegat. From Aksnes *et al.* (1989).

In January and especially February 1988, the wind energy was record high, while the bloom months May and June, in contrast, had very low wind energy (see Figure 2.3). This indicates an intense vertical mixing of the winter nutrient runoff from land during the beginning of 1988. At the onset of the algal bloom, the water column was stabilized owing to both the low input of wind energy and the high freshwater runoff. The physical indications of the stabilization are the decreasing salinity and the heating of the surface layer (see Section 2.2).

2.1.2 Precipitation and freshwater runoff

The winter 1987/1988 was mild and rainy in northwestern Europe. Precipitation in the Kattegat region was close to normal until the middle of December. From week 51 until the end of March, the precipitation was approximately 50% above normal. This coincided with a positive temperature anomaly and a dominating south-southwesterly air flow. April, May and June were generally more dry and sunny than normal.

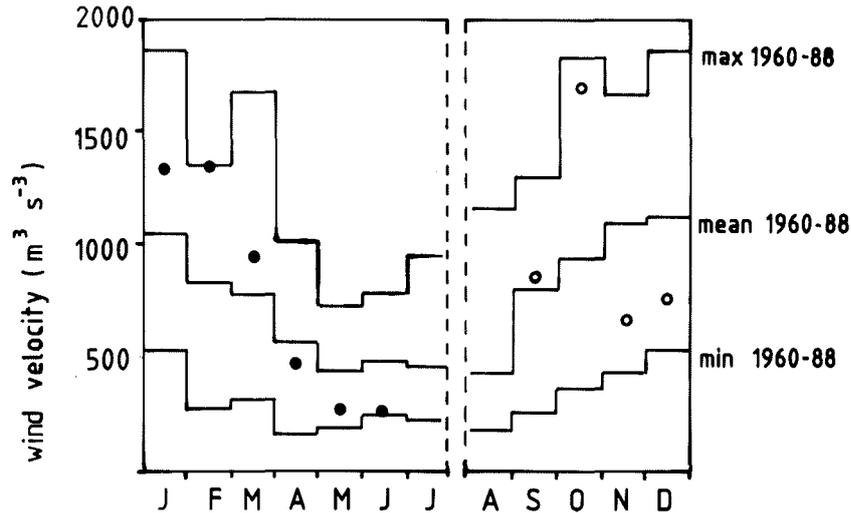


Figure 2.3 Monthly mean wind speed cubed at Skagen, Denmark, from September 1987 (right part of the figure) to June 1988 (left part). From Barth and Nielsen (1989).

Precipitation in Denmark was 55% above normal for the period September 1987 through March 1988. Precipitation in western Jutland is shown as monthly sums and compared to the normal in Figure 2.4. During autumn (September through November), precipitation was approximately 50% above normal in western Jutland. An even larger positive anomaly occurred during January, February and March 1988, when precipitation was on average 140% above normal in Western Jutland (Barth and Nielsen, 1989).

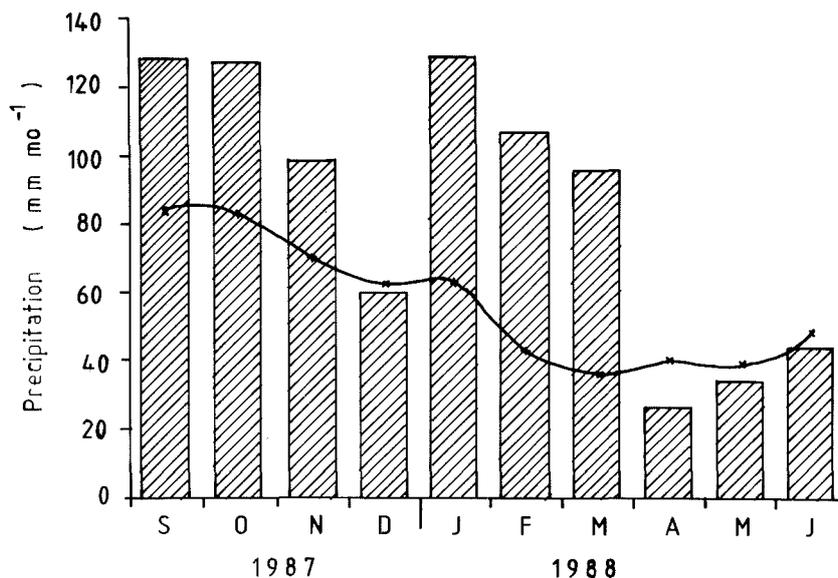


Figure 2.4 Monthly precipitation in western Jutland from September 1987 to June 1988. From Barth and Nielsen (1989).

Precipitation was also very high in southwestern Sweden in January-March 1988, with values typically 150-250% above normal (see Figure 2.5). In April, precipitation was generally less than normal. The high precipitation during the winter was reflected in high riverine discharge to the Kattegat-Skagerrak area. The Swedish river Örekilsälven had the highest mean February discharge on record (Lindahl and Rosenberg, 1989).

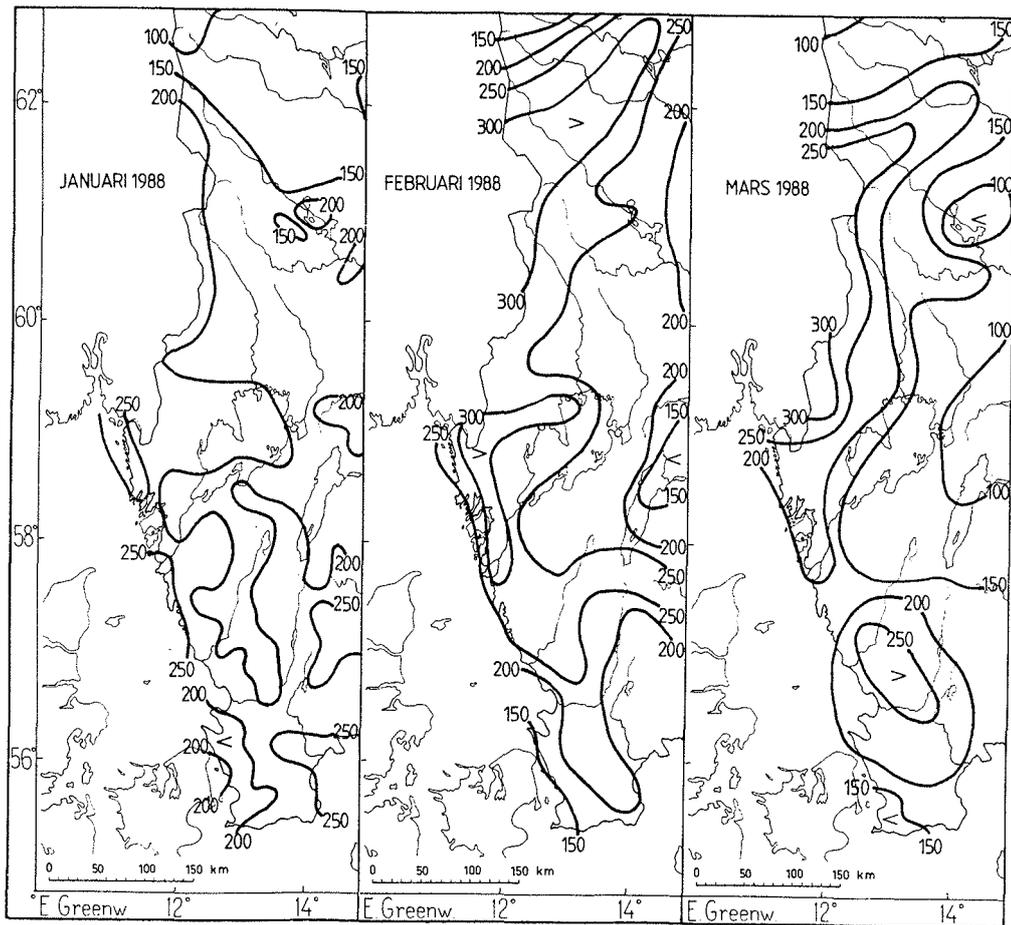


Figure 2.5 Precipitation (mm) during January, February and March over western Sweden. From Lindahl and Rosenberg (1989).

The amount of accumulated precipitation (largely in the form of snow) in southern Norway for the winter season 1987-1988 was more than 50% above average for a large part of the region. The effect of this can be seen on the discharge from the river Glomma, which was 45% above average in May (see Figure 2.6). The Glomma discharge was above average for almost the whole period September 1987-May 1988, particularly for the second half of October (nearly 3 times the average) and the first half of February (70% above average) (Aksnes *et al.*, 1989).

The discharge into the German Bight from the River Elbe is shown in Figure 2.7. The Elbe outflow was somewhat greater than normal from the end of December 1987 until the end of April 1988, with an extreme discharge of three times the normal and severe flooding in Germany in early April 1988 (Aksnes *et al.*, 1989; Backhaus *et al.*, 1988).

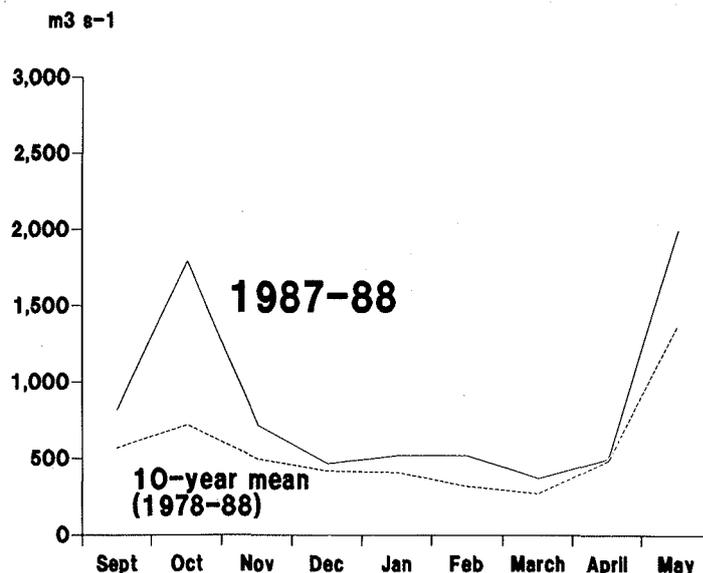


Figure 2.6 Freshwater discharge from the river Glomma in Norway from September 1987 to May 1988. From Aksnes *et al.* (1989).

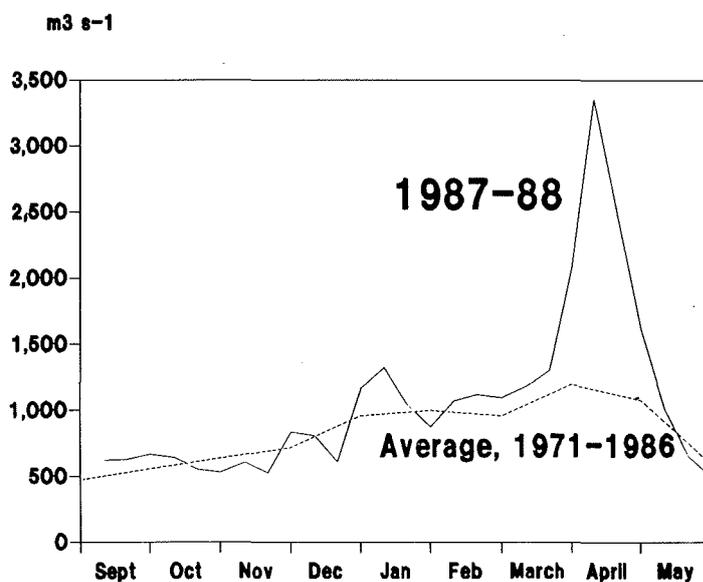


Figure 2.7 Freshwater discharge from the river Elbe from September 1987 to May 1988. From Aksnes *et al.* (1989).

2.1.3 Air temperature

The air temperatures in four regions of the Kattegat and Skagerrak are shown in Figure 2.8. The air temperature in the Kattegat-Skagerrak region was normal for the season until the middle of December. After a cold spell, the temperature was approximately 3°C above normal for 8 consecutive weeks. This coincided with an anomaly in water temperature in inner the Skagerrak and Kattegat. From the last week of February through March and April, temperatures were close to normal. May and June had temperatures slightly above normal (Barth and Nielsen, 1989).

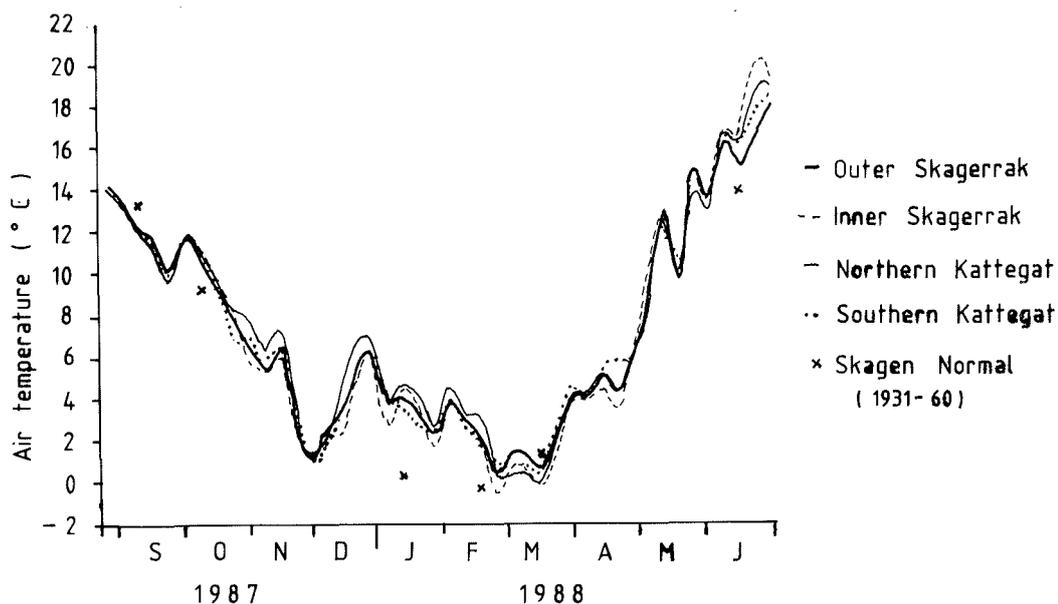


Figure 2.8 Air temperatures in four regions of the Skagerrak/Kattegat area from September 1987 to June 1988, compared to a 30-year normal at Skagen. From Barth and Nielsen (1989).

2.1.4 Irradiance

The light conditions during spring and early summer are illustrated as weekly hours of sunshine in the Kattegat in Figure 2.9. The number of hours of bright sunshine was far below average in the latter half of March. This could have contributed to a delay in the spring bloom of diatoms. During April and May, the sunshine was generally above normal. The largest positive anomaly occurred in week 19, which coincided with the first registration of the *C. polylepis* bloom in the beginning of May (Barth and Nielsen, 1989).

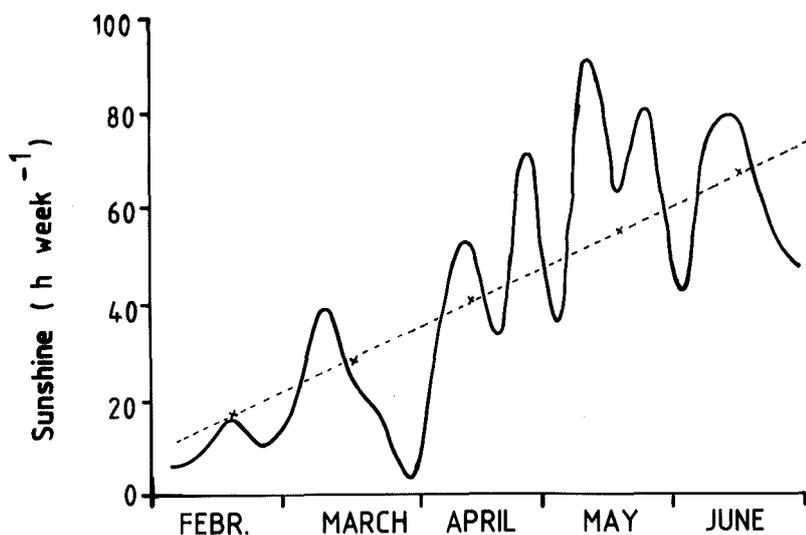


Figure 2.9 Weekly hours of bright sunshine in the Kattegat from February to June 1988. From Barth and Nielsen (1989).

2.2 Hydrographic Conditions

2.2.1 Temperature

The mild winter of 1987/1988 was reflected in relatively high water temperatures. The temperature of the surface water layer at Frederikshavn was 3-4°C higher than normal in February (see Figure 2.10). In addition to high air temperature, increased mixing with the warmer underlying water may have contributed to this elevated temperature level. During March, the temperature at Frederikshavn was 1-2°C higher than normal, whereas it was closer to normal during April and May (Barth and Nielsen, 1989).

The surface temperature at Arendal on the Norwegian Skagerrak coast showed the same general pattern, being about 3°C above normal in January and February (see Figure 2.11). The temperature was close to normal in April, while being higher than normal in May (Aksnes *et al.*, 1989).

2.2.2 Salinity

The winter period from January to March was characterized by lower salinity than normal at the Norwegian Skagerrak coast (see Figure 2.11), while the salinity at Frederikshavn was approximately normal (see Figure 2.10). From mid-April there was a marked decrease in surface salinity both at Arendal and at Frederikshavn. These low values were related to increased outflow from the Baltic in mid-April (Aksnes *et al.*, 1989; Barth and Nielsen, 1989).

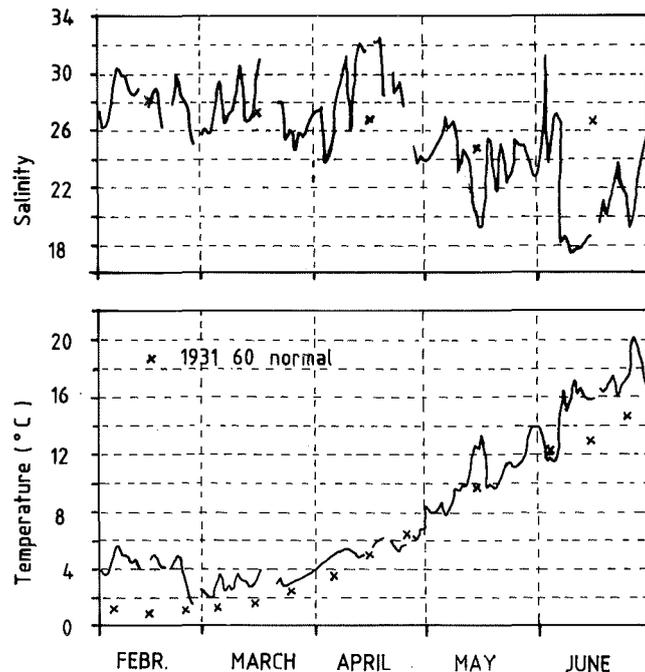


Figure 2.10 Daily recordings of temperature and salinity at Frederikshavn in Denmark from February to June 1988, compared to 30-year normals. From Barth and Nielsen (1989).

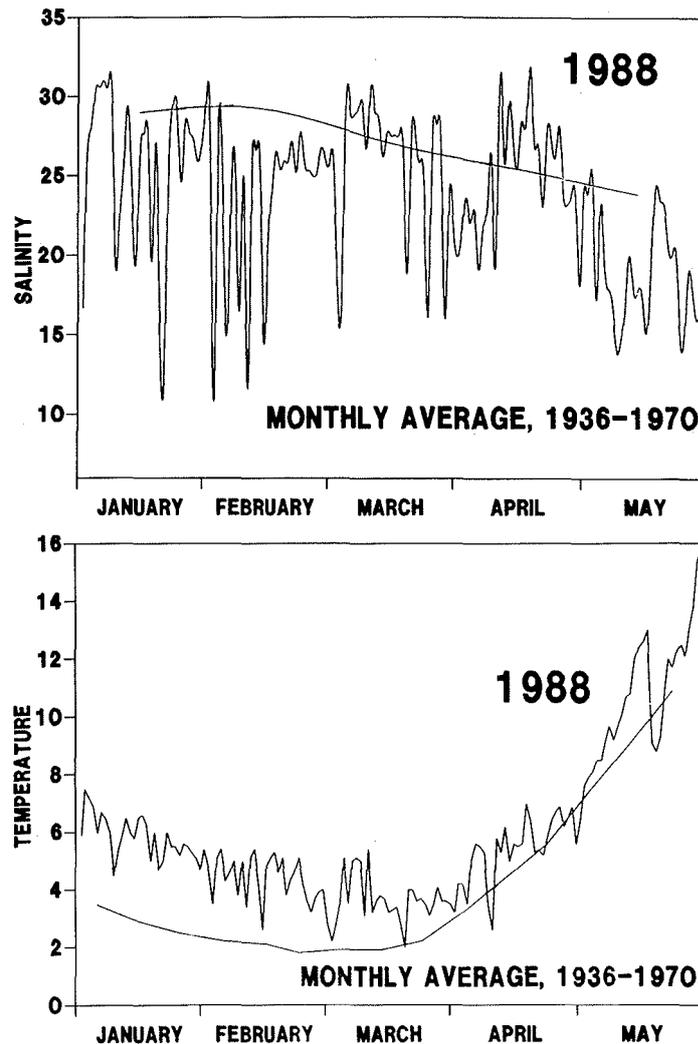


Figure 2.11 Recordings of salinity and temperature at 1 m depth at Arendal in Norway from January to May 1988, compared to 25-year monthly averages. From Aksnes *et al.* (1989).

2.2.3 Stratification

The increased freshwater outflow during spring, which resulted in low surface salinity, had no apparent effect at 20 m depth on the Norwegian Skagerrak coast at Lista during the last part of April and May. The low surface salinity and the high surface temperature indicate that during this period the upper layer was more strongly stratified than normal and that the depth to the pycnocline was less than normal (Aksnes *et al.*, 1989). This appeared also to be the situation in the Kattegat due to high freshwater runoff and reduced vertical mixing (Barth and Nielsen, 1989).

3. CURRENTS AND CIRCULATION PATTERN

3.1 General Circulation Pattern

The general current pattern in the Kattegat and Skagerrak is shown in Figure 1.1. There is generally a counter-clockwise circulation in the Skagerrak, with water entering from the southwest along the northern coast of Denmark and leaving as the Norwegian Coastal Current. The water entering the Skagerrak originates either from the southern North Sea and the German Bight or from the central North Sea. These water masses have different properties and are distinguished as the Jutland Current and the North Jutland Current, respectively (see Figure 1.1). There appears to be an alternation and pulsation of these two currents, with frequent blocking of the Jutland Current at the west coast of Denmark.

As the Jutland and North Jutland Currents pass the northern tip of Denmark, these denser water masses dive under the lighter, brackish outflowing Baltic water forming deep or intermediate water layers. Details of the flow patterns of these water layers are not well known. The deep water in the Kattegat is entrained into the surface layer of outflowing Baltic water. The surface water flows northwards along the Swedish Skagerrak coast and continues along the Norwegian coast as the Norwegian Coastal Current.

3.2 Circulation Pattern in Winter and Spring 1988

The circulation pattern in the North Sea and Kattegat and Skagerrak for the period prior to and during the bloom of Chrysochromulina polylepis has been analyzed by several groups of researchers using both circulation models and hydrographical and meteorological observations (Aksnes *et al.*, 1989; Backhaus *et al.*, 1988; Barth and Nielsen, 1989; Lindahl and Rosenberg, 1989). These analyses have revealed some peculiarities in the circulation pattern during that period. The total circulation of the North Sea appeared, however, not to be atypical, being within the normal range of variation (Backhaus *et al.*, 1988).

3.2.1 Transport in the Jutland and North Jutland Currents

Westerly winds above 10 m s^{-1} will produce inflow to the Skagerrak (Dietrich, 1951) resulting in increased salinity at Frederikshavn. It is reasonable to assume that this inflow is coupled to a strengthening of the North Jutland Current. To what extent water from the German Bight contributed to increased flow in the Jutland Current during winter and spring 1988 is unclear. Inflow of water from the southern North Sea to the Kattegat is a normal feature. Indirect observations such as wind pattern and freshwater runoff indicate, however, that this transport may have been large (Barth and Nielsen, 1989).

Results from numerical model simulations (Aksnes *et al.*, 1989) support this supposition. Figure 3.1 shows calculated volume fluxes in an east-west section across the Jutland Current at 55°N . The figure shows considerable short-term variability on a time scale of days, in addition to more long-term changes. During January, February and March there was a considerable northward net flux of water masses through the Jutland section. The simulations indicate that the strongest outflow from the German Bight occurred in the first half of February (see Figure 3.1). The simulated mean surface current pattern for the week of 8 to 14 February is shown in Figure 3.2. This indicates strong surface flow in a counter-clockwise direction over the southern and central North Sea. The flow along the north Jutland coast and into the Skagerrak was particularly pronounced, with a mean current strength of 0.3 m s^{-1} .

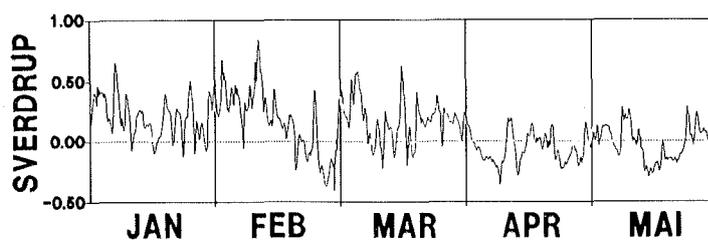


Figure 3.1 Simulated volume fluxes through the Jutland section from January to May 1988. From Aksnes *et al.* (1989).

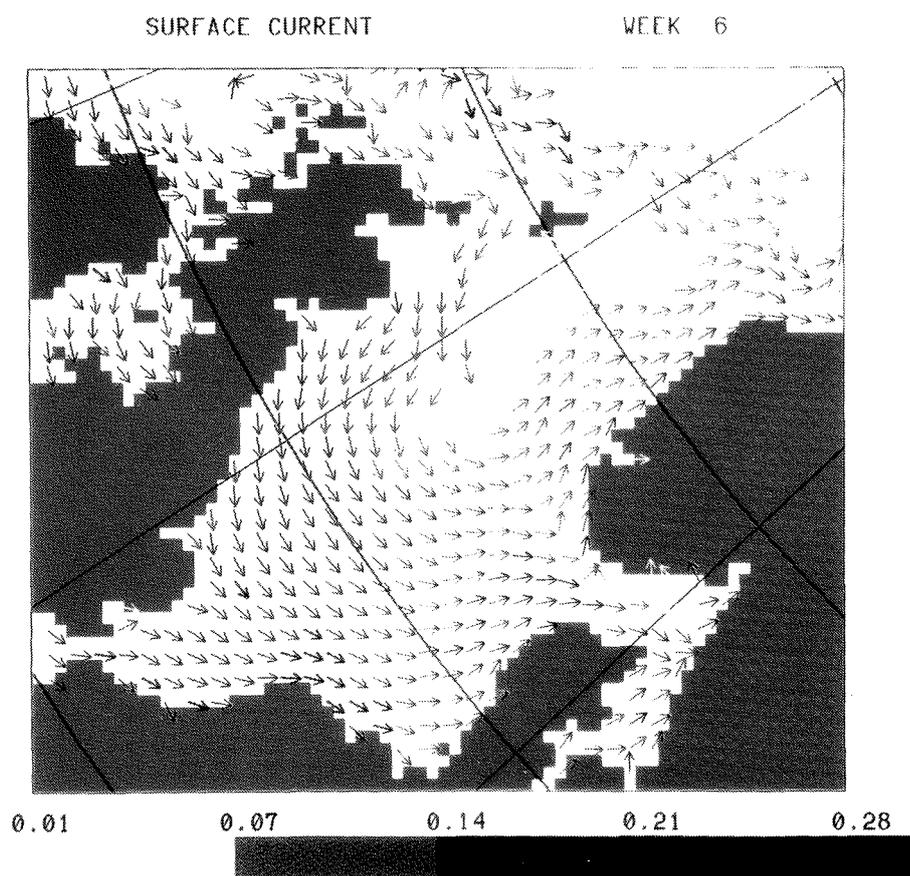


Figure 3.2 Simulated mean current pattern for the week 8-14 February 1988. From Aksnes *et al.* (1989).

The flow through the Jutland section was much reduced in April and May and the mean monthly flow was reversed to a southerly direction (see Figure 3.1). Hence, the general counter-clockwise circulation of the North Sea seems to have been strongly hampered during the spring months (Backhaus *et al.*, 1988; Aksnes *et al.*, 1989). The simulated mean surface current pattern for the week of 11 to 17 April is shown in Figure 3.3. This figure shows a reversal of the Jutland Current. The model indicates, however, a significant flow of water from the central North Sea towards northern Jutland and into the Skagerrak.

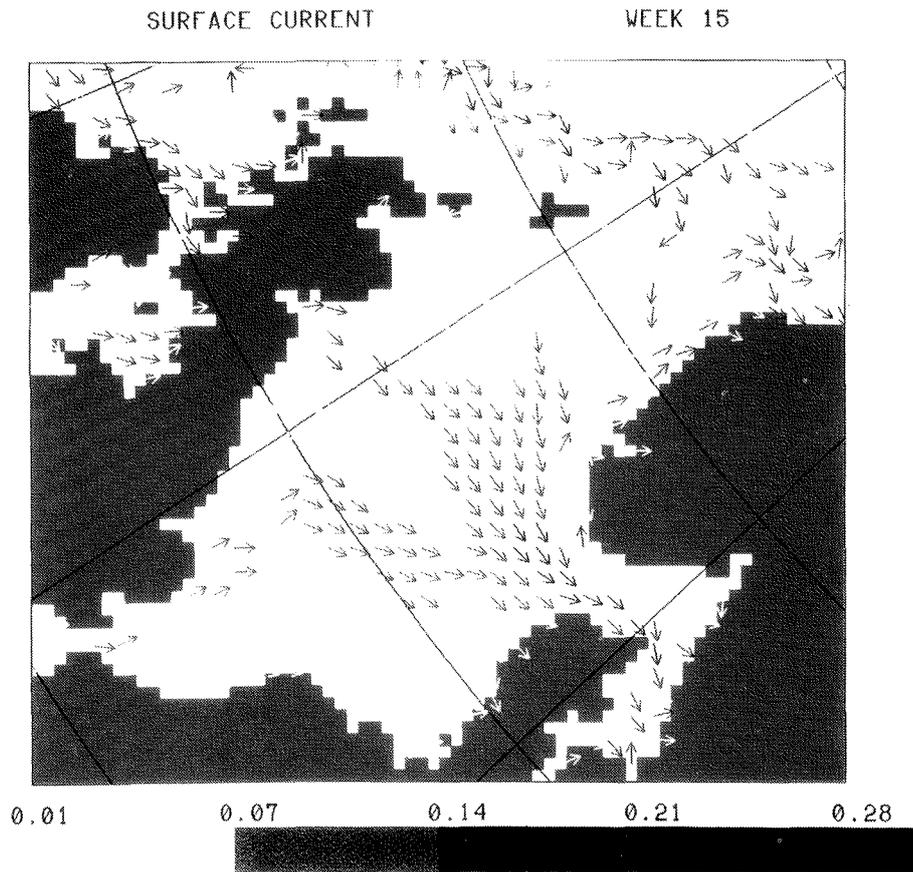


Figure 3.3 Simulated mean current pattern for the week 11-17 April 1988. From Aksnes *et al.* (1989).

3.2.2 Outflow from the Baltic Sea and the Skagerrak

The outflow from the Skagerrak along the Norwegian coast is variable, with alternations between blocking and outflowing regimes controlled by the prevailing winds (Aure and Sætre, 1981; Sætre *et al.*, 1988). There is a direct relationship between the outflow from the Skagerrak, the Baltic outflow and the sea level variations in the Baltic Sea. This relationship may be demonstrated by looking more closely at two situations. The first one is the westerly/north-westerly gale during 8-12 April, when the wind speed reached up to 20 m s^{-1} (see Figure 2.1). The second is the westerly wind event of 17-20 May (see Figure 2.2). At the Norwegian Skagerrak coast, the effect of these wind events was seen as a sudden increase in surface salinity (see Figure 2.11). This is caused by upwelling at the coast when the wind displaces the Skagerrak outflow seawards and eventually blocks it. The blocking effect and its relation to the Baltic outflow is seen by the rising sea level in the Baltic Sea during the same periods. Between these blocking periods both the Skagerrak and the Baltic outflows were high (see Figure 3.4; Aksnes *et al.*, 1989; Barth and Nielsen, 1989).

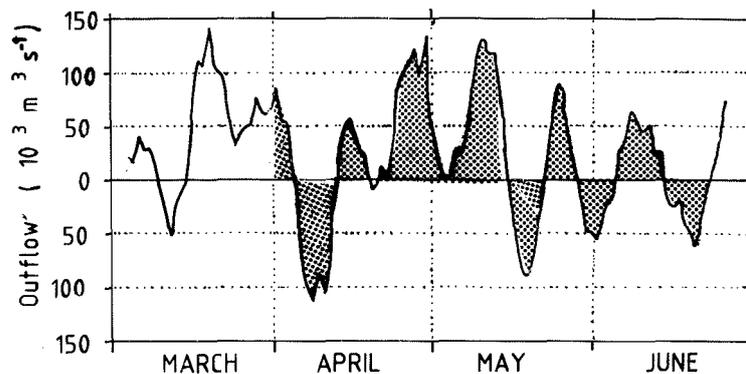


Figure 3.4 Outflow from the Baltic Sea to the Kattegat computed from water level variations at Marviken in the Baltic Sea. From Barth and Nielsen (1989).

4. CHEMICAL ENVIRONMENTAL CONDITIONS

4.1 Distribution and Transport of Nutrients

4.1.1 Distribution of nutrients prior to the bloom

Data on nutrient concentrations during the winter and spring period prior to the bloom of *Chrysochromulina polylepis* exist from Danish, Swedish and Norwegian investigations in the Kattegat-Skagerrak area (Barth and Nielsen, 1989; Lindahl and Rosenberg, 1989; Aksnes *et al.*, 1989). During a Norwegian cruise from 11 to 23 April, the distributions of nitrate, phosphate and silicate were mapped over most of the Kattegat and Skagerrak area (Aksnes *et al.*, 1989; L. Føyn, unpubl. results).

The horizontal distribution of nitrate in the surface layer (5 m) and at 25-30 m depth is shown in Figure 4.1, together with the distribution of salinity at the same depths. The distribution of water masses is reflected by salinity. High nitrate concentrations, exceeding the winter levels in Atlantic water, were found in the deeper layer over an extensive part of the Kattegat and the eastern part of the Skagerrak (see Figure 4.1A). Nitrate concentrations higher than 15 μM were found in the northeastern part of the Kattegat. High concentrations were also found along the west coast of Denmark. These high concentrations of nitrate were associated with water of a salinity around 33 (Fig. 4.1B). The higher salinity (>34) water in the central and western Skagerrak had lower nitrate concentrations (<10 μM).

High concentrations of nitrate in the surface layer (5 m) were found near the western and northwestern coasts of Denmark, again associated with water with a salinity of about 33 (Fig. 4.1C, D). Moderately high concentrations of nitrate (2-5 μM) were observed in the northern Kattegat and along the Swedish coast in the eastern Skagerrak at salinities of 30 or less. Moderately high nitrate concentrations (2-6 μM) were also found along the Norwegian Skagerrak coast associated with upwelling of 30-33 salinity water. Low nitrate concentrations (<1 μM) occurred in the low salinity water of the central and southern Kattegat and in the relatively low salinity (32 or less) surface water of the central Skagerrak (see Figures 4.1C, D).

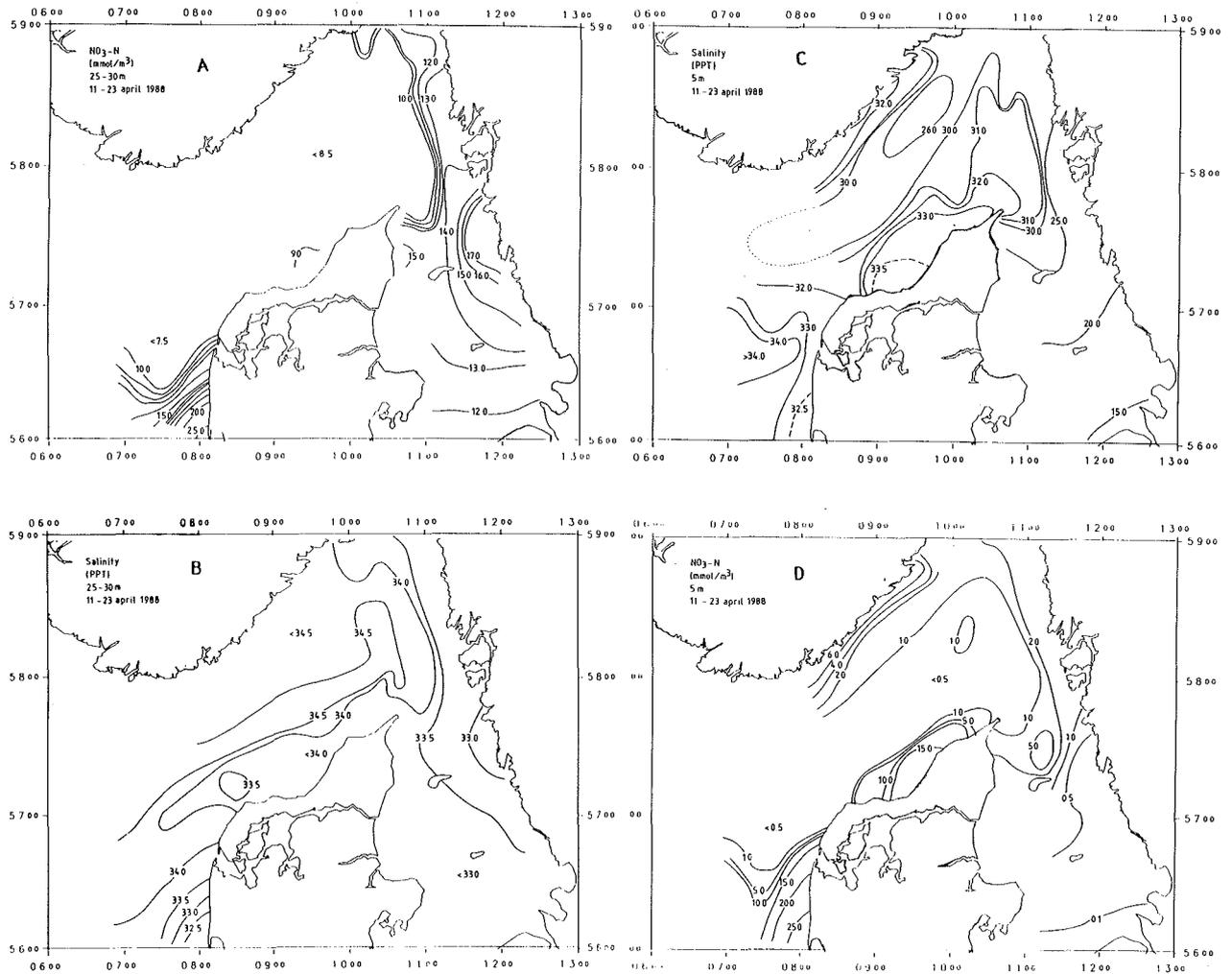


Figure 4.1 Horizontal distributions of nitrate and salinity at 25-30 m depth (A, B) and at 5 m depth (C, D) in the Skagerrak and the Kattegat in April 1988. From Aksnes *et al.* (1989).

The average concentrations of nitrate, silicate and phosphate in the upper 30 m in the Kattegat and Skagerrak in mid-April are shown in Figure 4.2. The silicate concentrations were generally low and showed little correspondence to those of nitrate (see Figures 4.2A, B). The areas of high nitrate concentrations along the west coast of Denmark, in the northern Kattegat, and along the eastern coast of the Skagerrak had low concentrations of silicate ($<1 \mu\text{M}$). The distribution of phosphate (see Figure 4.2C), on the other hand, showed a general correlation to that of nitrate.

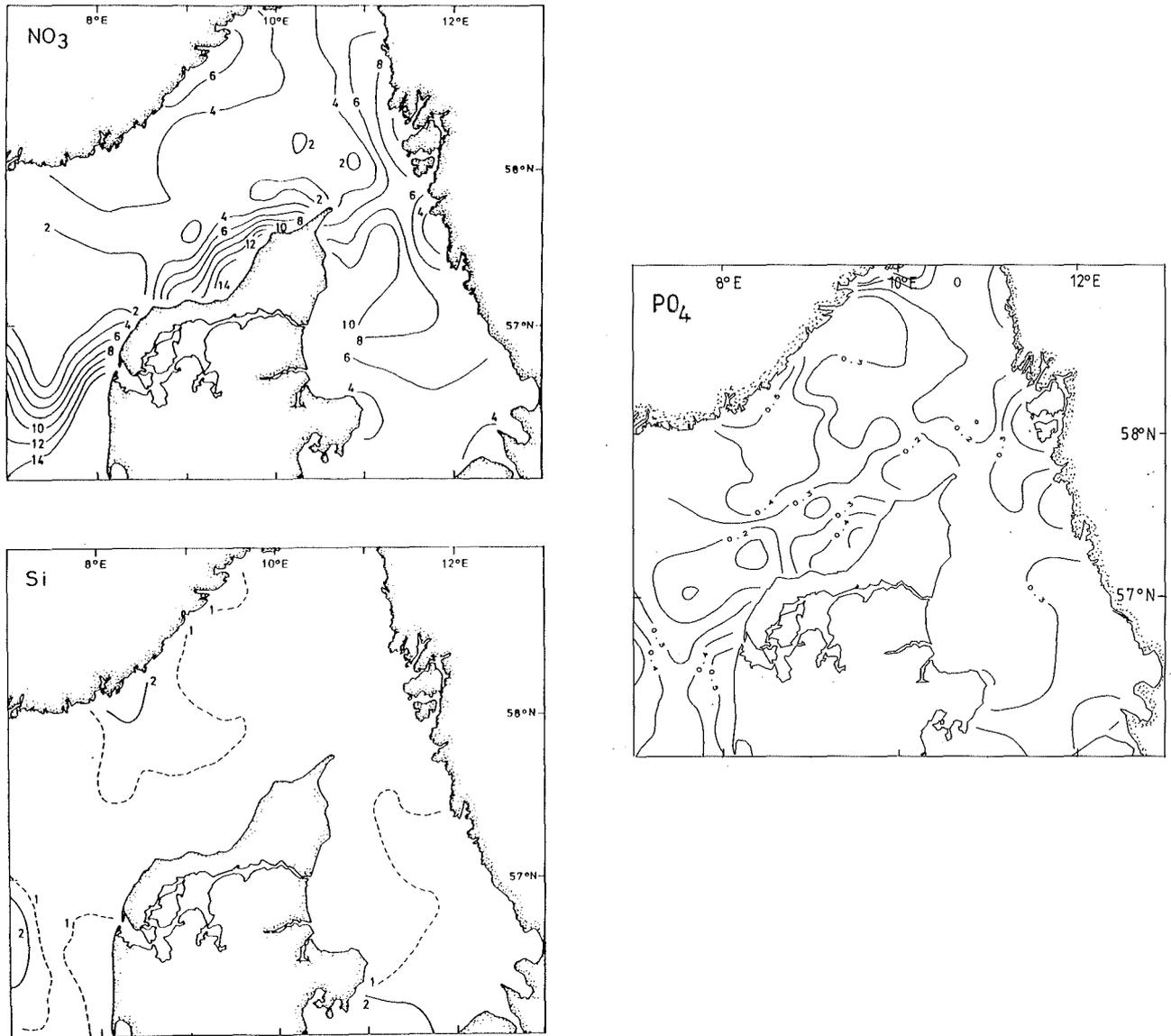


Figure 4.2 Average concentrations (μM) of nitrate, silicate, and inorganic phosphate in the upper 30 m in the period 11-23 April 1988. From Aksnes *et al.* (1989).

The temporal distribution of nutrients near Fladen in the northern Kattegat is shown in Figure 4.3, based on data from Danish, Norwegian and Swedish investigations. High nitrate concentrations in the intermediate water layer were observed from early February to early March and again in late April (see Figure 4.3B). The surface layer was depleted of nitrate by early April, with a deepening of the nitracline from about 10 m in April to about 25 m in June. While the nitracline was associated with the halocline in April, it became progressively more deeply positioned relative to the halocline during May and June (see Figures 4.3A,B).

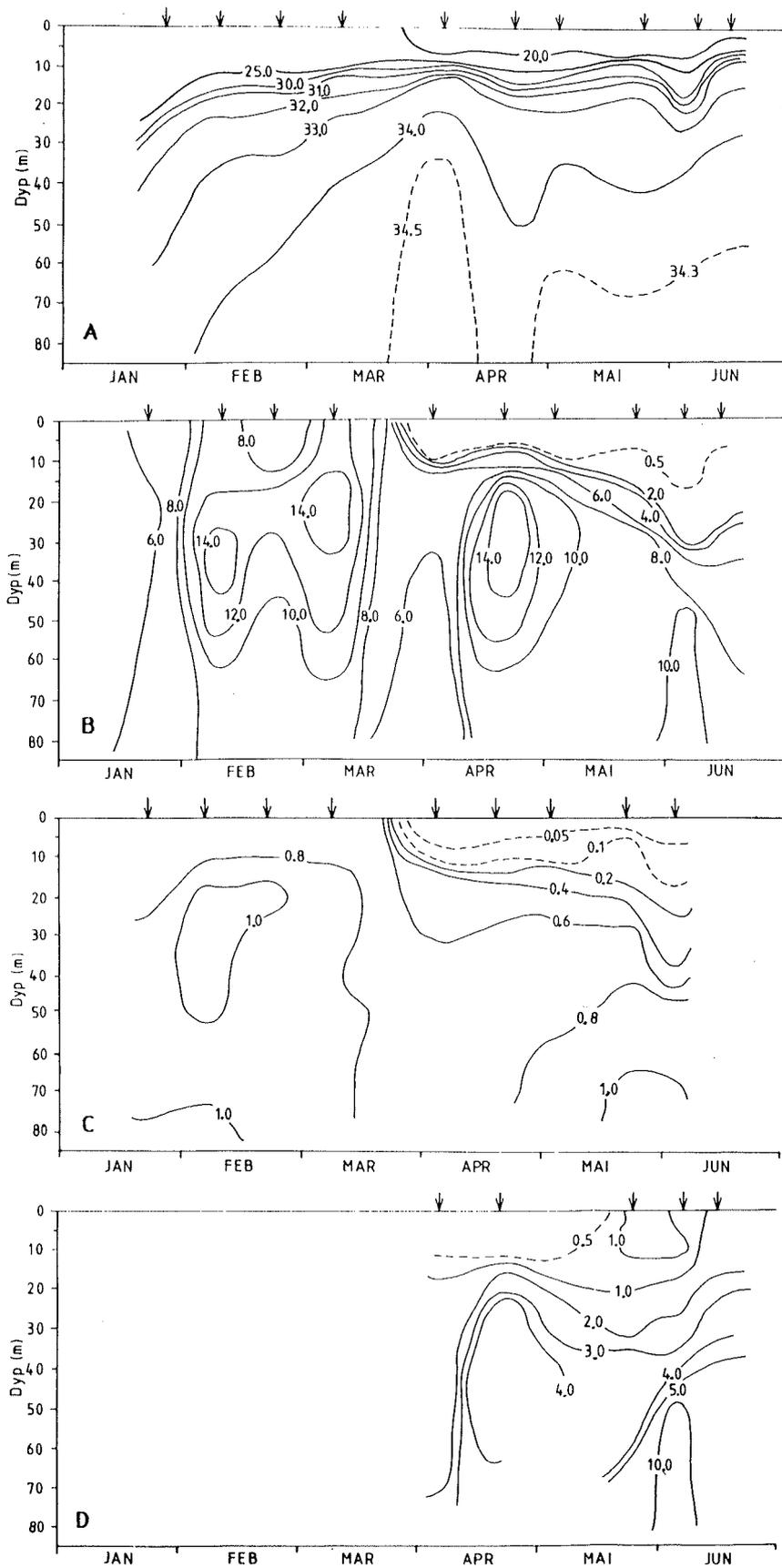


Figure 4.3 Vertical distributions of salinity (A), nitrate (B), phosphate (C), and silicic acid (D) at Fladen in the northern Kattegat from January to June 1988. From Aksnes *et al.* (1989). Arrows indicate sampling times.

4.1.2 Distribution of nutrients during the bloom

There are few observations available for the early period of the bloom development. The observations made at Fladen in the northern Kattegat in early May showed a low content of nutrients in the surface layer (see Figure 4.3). The concentration of nitrate was $1.8 \mu\text{M}$ at a station close to Nidingen on 2 May, which may indicate somewhat elevated concentrations along the Swedish west coast (Lindahl and Rosenberg, 1989).

Due to the monitoring and research activities, there are many data available on nutrients in the late part of the bloom development. These data show that the surface layer in the Kattegat and Skagerrak in general had a low nutrient content. In parts of the Kattegat and Skagerrak affected by the Chrysochromulina bloom, however, there were somewhat elevated concentrations of nitrate ($0.1\text{--}0.8 \mu\text{M}$) (Institute of Marine Research, Bergen, unpubl. results). Along the coast of southern Norway, unusual nutrient patterns were seen following the culmination of the bloom. Figure 4.4 shows vertical profiles of temperature, salinity and nutrient concentrations at a station outside Egersund. Nitrate had a maximum at 30–50 m, which coincided with salinities around 34. In contrast to nitrate, phosphate was depleted above this maximum and occurred in relatively low concentrations also in the nitrate maximum. It is likely that the nitrate-rich water mass was a remnant of the water from the southern North Sea which was transported into the Kattegat-Skagerrak area during the preceding winter.

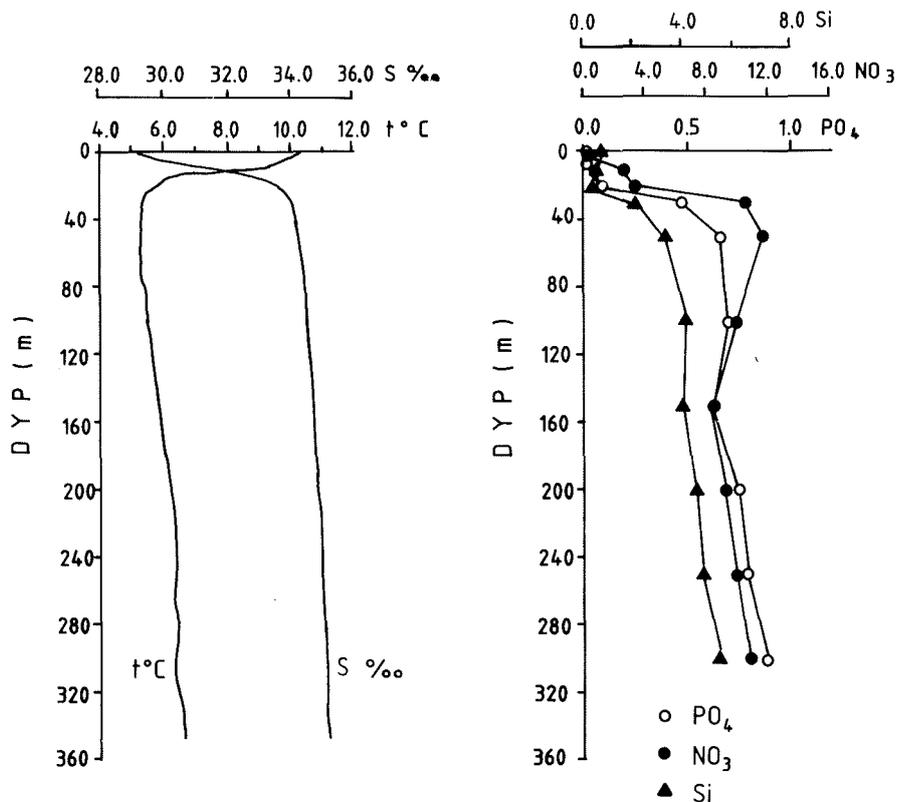


Figure 4.4 Vertical profiles of temperature, salinity and nutrient concentrations off Egersund on the southwestern coast of Norway, 5 June 1988. Data from the Institute of Marine Research, Bergen.

4.1.3 Transport of nutrients by the Jutland Current

The southern North Sea receives an annual riverine input of 150 km^3 of freshwater (Gerlach, 1988). When mixed with Atlantic water to a salinity of 33, this freshwater inflow represents a flow of $0.08 \cdot 10^6 \text{ m}^3 \text{ s}^{-1}$, or approximately 0.1 Sverdrup. This gives a rough indication of the typical volume transport of coastal water from the southern North Sea in the Jutland Current.

Winter nutrient concentrations in the coastal waters of the southern North Sea indicate average concentrations in the freshwater source of about $320 \mu\text{M}$ nitrogen (nitrate plus ammonium) and $7.6 \mu\text{M}$ phosphate (Lancelot *et al.*, 1989; see also Dickson *et al.*, 1988; and Gerlach, 1988). The corresponding N:P atomic ratio is 42, which is considerably higher than the Redfield ratio of 16 which is typical for marine waters.

When diluted with oceanic water to a salinity of 33, the anthropogenic input of nitrogen from the river discharge represents an increase of $18 \mu\text{M}$ above the normal winter level of about $10 \mu\text{M}$ in water of Atlantic origin. Combined with an average flow of 0.10-0.15 Sv in the Jutland Current, as estimated by the model simulations (see Figure 3.1), this represents a transport of anthropogenic nitrogen of 70,000-100,000 tonnes per month during the period from January to March 1988. Although part of this nitrogen was probably consumed by phytoplankton growth, the calculation suggests a considerable input of nitrogen to the Kattegat and Skagerrak during the winter months prior to the bloom of *Chrysochromulina polylepis*.

The deep or intermediate water layer with high nitrate concentrations in the Kattegat and Skagerrak can be identified from its salinity characteristics as originating from the southern North Sea. This water mass was present in the Kattegat from early February onwards (see Figure 4.3). In April it covered most of the Kattegat and the eastern part of Skagerrak (see Figure 4.1). Mixing diagrams based on nitrate and salinity further corroborate the identity of the water mass. The water at 30 m at Fladen in April had characteristics intermediate between those of surface waters in the southern North Sea (SNSW) and in the central North Sea (CNSW) (see Figure 4.5A). The surface water at Fladen in February and March had characteristics intermediate between those of Baltic Sea water (BSW) and the nitrate-rich deeper water (see Figure 4.5B).

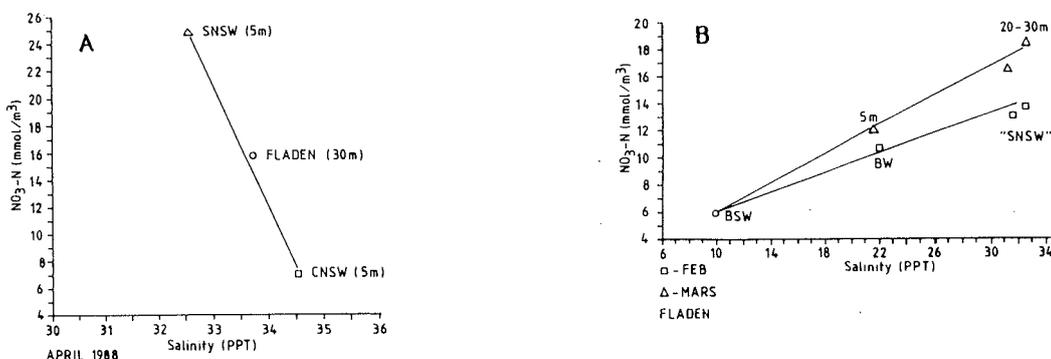


Figure 4.5 Nitrate versus salinity diagrams showing (A) the mixture of Southern North Sea Water (SNSW) and Central North Sea Water (CNSW) at 30 m depth at Fladen on 19 April 1988, and (B) the mixture of Baltic Sea Water (BSW) and water at 20-30 m depth at Fladen ("SNSW") at 5 m depth in the outflowing Baltic water (BW) at Fladen in February (squares) and March (triangles), 1988. From Aksnes *et al.* (1989).

4.1.4 Transport of nutrients by the Baltic outflow

The events of outflow of water from the Baltic Sea were probably more important in terms of their influence on the physical oceanographic processes in the Kattegat than in terms of the bulk transport of nutrients. The winter levels of inorganic nutrients are not higher in the Baltic surface water than in the Kattegat surface water (Anderson and Rydberg, 1988). Therefore, increased transport of water does not necessarily represent an increased availability of nutrients for phytoplankton growth. Following the spring bloom in the Kattegat in late March, the nutrient levels in the surface layer were generally low (see Figure 4.3). Swedish data from measurements done by the Swedish Meteorological and Hydrological Institute (SMHI) on 6 April showed somewhat elevated concentrations of nitrate and phosphate in the upper surface layer in the northern Øresund. This may reflect some transport of nutrients into the Kattegat at this time.

The outflowing water from the Baltic Sea contributes an estimated annual input of nitrogen to the Kattegat of about 250,000-300,000 tonnes (Anderson and Rydberg, 1988; Barth and Nielsen, 1989). The outflow of Baltic water was strong during the winter and spring of 1988. There were massive outflows during January and the latter half of March. There were also major outflow events in late April and during the second week of May (see Figure 3.4).

4.1.5 Supply of nutrients by local runoff

The direct supply of nitrogen to the Kattegat and the Belt Sea is about 200,000 tonnes annually (Anderson and Rydberg, 1988; Barth and Nielsen 1989). It is estimated that the total load of nitrogen has increased by a factor of 2.5 from 1950 to 1980, reflecting increased use of mineral fertilizers in agriculture (Barth and Nielsen, 1989). The local supply of nitrogen to the Skagerrak is about 50,000 tonnes per year from Sweden and about 30,000 tonnes per year from Norway (ICES, 1987).

The high precipitation and river runoff to the Kattegat and Skagerrak in the winter 1987/1988 contributed high inputs of nutrients. For example, for Odense River in Denmark it has been established that precipitation and nitrogen runoff have an exponential relationship. Thus, a 50% increase in precipitation caused a 90% increase in nitrogen runoff (Barth and Nielsen, 1989). For Swedish rivers, the concentrations of nitrate, phosphate and silicate have been found to be fairly constant over a 15-year period. It is, therefore, assumed that the nutrient transport is proportional to the water flow in these rivers (Lindahl and Rosenberg, 1989).

The precipitation over Denmark and southwestern Sweden was exceptionally high during January, February and March (see Section 2.1.2, above). During April, however, the precipitation in the Kattegat area was less than normal. Much of the extra input of nutrients, therefore, came during the winter months preceding or coinciding with the normal spring phytoplankton bloom. Most of the surface water from the winter months was probably flushed out from the Kattegat before the bloom of Chrysochromulina polylepis occurred. The remaining nutrients in the surface layer were consumed by the spring bloom, which started in the latter part of March (see Figure 4.3).

The river runoff lagged behind the pattern in precipitation. Thus, Swedish rivers had about a 50% higher runoff in April compared to the normal (Lindahl and Rosenberg, 1989). It is, therefore, possible that they contributed additional supplies of nutrients at the time the growth of Chrysochromulina polylepis was initiated. The effect of these extra supplies is likely, however, to have been very local, as the waters influenced by the river runoff were confined to narrow regions along the coast (Backhaus *et al.*, 1988). The nutrient

contents of the Swedish rivers are elevated, but still relatively low. Thus, the Göta River, which is by far the largest freshwater source in the area, has a nitrate content in February of about 45 μM (Lindhahl and Rosenberg, 1989). This is about 1/10 of the concentration in the dominant freshwater sources to the southern North Sea (Dickson *et al.*, 1988; Lancelot *et al.*, 1989).

It is considered unlikely that the local supply of nutrients to the surface water of the Kattegat and Skagerrak played a decisive role in the development of the Chrysochromulina polylepis bloom (Nielsen and Richardson, 1988; Aksnes *et al.*, 1989). It remains a possibility, however, that the bloom started in the coastal areas nourished by the input of nutrients from the river outflow. The freshwater runoff may also have contributed micronutrients and other agents which influenced the growth and species composition of the bloom, although there is no evidence available to support this possibility.

4.1.6 Vertical transport of nutrients by entrainment

The Kattegat and inner Skagerrak constitute a transition area between the North Sea and the Baltic Sea. This transition area is characterized by pronounced stratification. The outflowing Baltic Sea water has a salinity of about 8 as it enters the Belt Sea. The surface salinity at the transition between the Kattegat and the Skagerrak is on average about 27 (Barth and Nielsen, 1989). The increase in salinity en route from the Belt Sea until the water leaves the Kattegat represents admixture of deep Kattegat water by mixing and entrainment processes. Applying the classical Knudsen relations, the volume fluxes through the Kattegat and the associated fluxes of bound nitrogen have been calculated (Barth and Nielsen, 1989). It was estimated that there was a net upwards transport through the pycnocline of 600,000 tonnes of bound nitrogen annually, or close to 2,000 tonnes per day on average. A large fraction of this nitrogen is of anthropogenic origin, being transported from the southern North Sea by the Jutland Current.

In the stratified waters of the Kattegat and Skagerrak, vertical mixing is primarily determined by the wind conditions. Mixing by entrainment processes depends on the wind energy, which is proportional to the wind speed cubed. The wind energy was very high in January and February (see Figure 2.3), and this is likely to have resulted in intense vertical mixing of the nutrient runoff from land at this time of the year (Barth and Nielsen, 1989). The wind energy progressively decreased during spring to very low levels in May and June. This would act to reduce the vertical entrainment during the period of the Chrysochromulina polylepis bloom. Vertical entrainment might still have been high, however, due to the strong outflow of Baltic Sea water for parts of this period (see Figure 3.4). The normal salinity off Frederikshavn in the northern Kattegat in June is 26, which indicates a mixture of 1 part Baltic Sea water with 2 parts of North Sea water entrained into it. In June 1988, the salinity at Frederikshavn was only about 20, indicating a 1:1 mixture of Baltic Sea and North Sea waters (Barth and Nielsen, 1989).

In April preceding the outbreak of the Chrysochromulina polylepis bloom, the wind energy at Skagen was close to normal (see Figure 2.3). This suggests close to normal rates of upwards entrainment during this period. The salinity at Frederikshavn was above normal in April (see Figure 2.10), but apart from entrainment this reflected also a major inflow of water from the Jutland Current and the Skagerrak during the first half of April (Barth and Nielsen, 1989; Aksnes *et al.*, 1989).

The vertical transport of nutrients depends on their concentrations as well as on volume fluxes of water. The nitrogen concentrations in the Kattegat deep water were elevated (see Figure 4.1), and this would contribute to increased upwards transport of nitrogen by entrainment into the upper layer. A rough calculation indicates that this transport was of the order of 2,000 tonnes of nitrogen per day.

4.1.7 Vertical transport of nutrients by upwelling

Upwelling along the Skagerrak coast is a common phenomenon occurring in response to prevailing wind conditions (Aure and Sætre, 1981). Upwelling was also documented on several occasions in the spring of 1988. In the period 8-12 April there were strong westerly and northwesterly winds (see Figure 2.1), which resulted in upwelling along the Norwegian Skagerrak coast. This is evident from the marked increase in salinity at Flødevigen, Arendal (see Figure 2.11) and resulted in a high nitrate content and high salinity in the surface water along the coast (see Figure 4.1).

Just prior to and during the outbreak of the Chrysochromulina polylepis bloom along the Swedish Skagerrak coast, the wind was easterly and moderately strong ($6-11 \text{ m s}^{-1}$) (see Figure 2.2). This is a condition which would be expected to result in upwelling along the Swedish west coast. The available data did not show such a situation. The salinity of the Gullmar Fjord decreased during this period (Lindahl and Rosenberg, 1989), which is opposite to what one would expect to be associated with upwelling. However, there was a large outflow of water from the Baltic Sea during the same period (see Figure 3.4). It is likely that the change from westerly to easterly winds and the associated change from inflow to outflow from the Baltic Sea resulted in a general uplifting of the pycnocline and nutricline in the Kattegat and the inner Skagerrak. If so, this may have improved the light conditions for phytoplankton growth.

From 16 May the wind direction changed to westerly and increased in intensity to more than 10 m s^{-1} on 18 and 19 May (see Figure 2.2). This resulted in a blocking of the Skagerrak outflow, and surface water was transported away from the Norwegian Skagerrak coast (Aksnes et al., 1989; Dahl et al., 1989; Dundas et al., 1989). This caused upwelling along the coast and increased transport of nutrients into the upper layer.

4.2 Nutrient Ratios

4.2.1 Silicic acid to nitrate ratio

Silicic acid is a nutrient required by diatoms. The anthropogenic nutrient load to the southern North Sea has caused increases in nitrogen and phosphorus but not in silicic acid. Following the spring growth of diatoms, which is limited by the relatively low content of silicic acid, the surplus N and P are used by massive blooms of the colony-forming flagellate Phaeocystis (Lancelot et al., 1989).

The intermediate or deep water in the Kattegat and inner Skagerrak, which originated from the southern North Sea, had a low content of silicic acid relative to nitrate (see Figure 4.2). This is further exemplified by vertical profiles from April. Figure 4.6A shows profiles from the non-stratified shallow water column off the west coast of Denmark, where the content of silicate was about $1 \mu\text{M}$ at a nitrate content of about $18 \mu\text{M}$. Profiles from the stratified water of the northern Kattegat showed high nitrate and low silicic acid contents below the surface layer (see Figure 4.6B). In contrast, profiles from deeper water off northwestern Denmark showed more typical nutrient concentrations and normal ratios of silicic acid to nitrate (see Figure 4.6C).

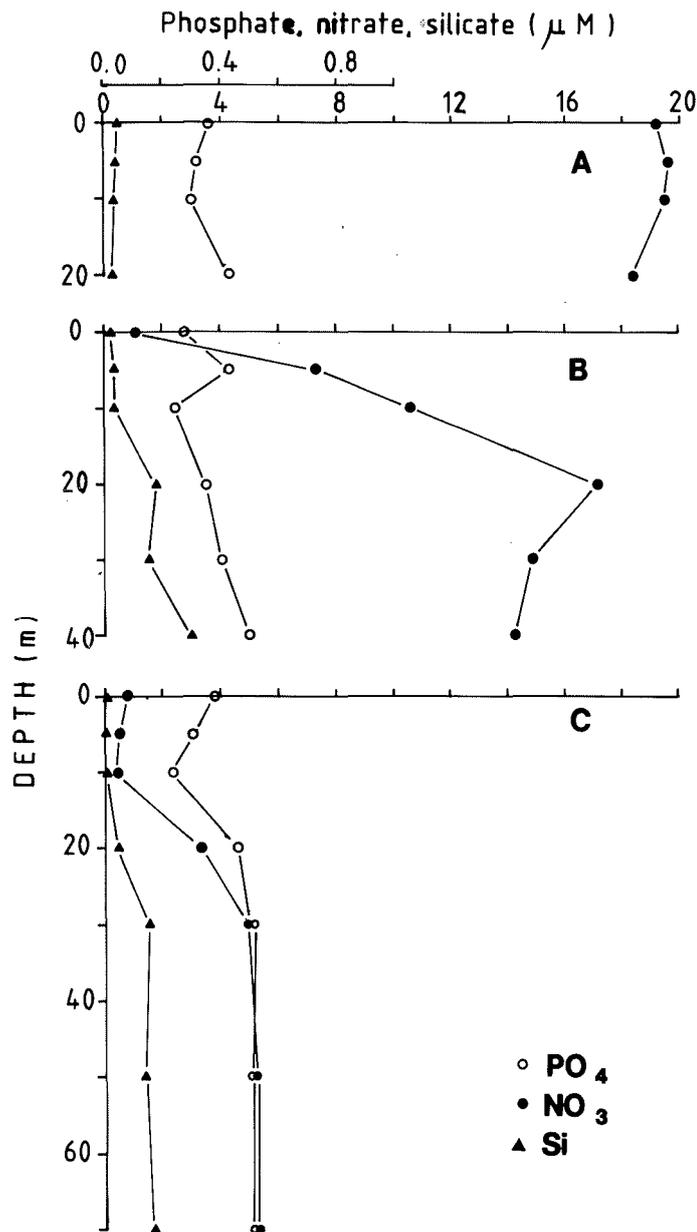


Figure 4.6 Vertical profiles of phosphate (upper scale), nitrate and silicate (lower scale) off the west coast of Denmark (A), in the northern Kattegat (B), and in the southern Skagerrak northwest of Denmark (C). Stations No. 60, 109 and 40 during a cruise with R/V "G. M. Dannevik" in April 1988. Data from the Institute of Marine Research, Bergen.

Figure 4.7 shows a scatter plot of silicic acid *versus* nitrate for different water masses in April. The group of stations from offshore waters in the eastern North Sea and the Skagerrak had Si:N ratios that fell at or slightly below the line corresponding to a typical atomic ratio of 1:2. The stations west of Denmark and in the Kattegat and inner Skagerrak, with water that originated from the southern North Sea, had in general much lower Si:N ratios.

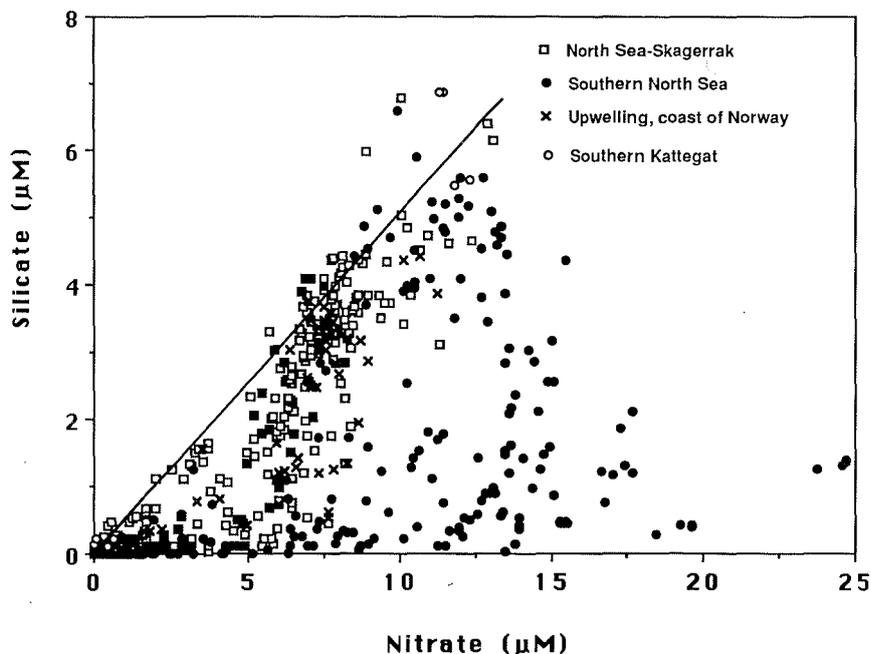


Figure 4.7 Plot of silicate versus nitrate in water samples from different water masses in the eastern North Sea and the Skagerrak/Kattegat in April 1988. Data from the Institute of Marine Research, Bergen.

4.2.2 Nitrate to phosphate ratio

Figure 4.8 shows a scatter plot of phosphate versus nitrate for the same stations as in Figure 4.7. The line shows the Redfield N:P atomic ratio of 16. The samples from the North Sea-Skagerrak stations had N:P ratios that were close to or somewhat lower than the Redfield ratio. The samples from the southern North Sea water mass, in contrast, had N:P ratios that were appreciably higher than the Redfield ratio.

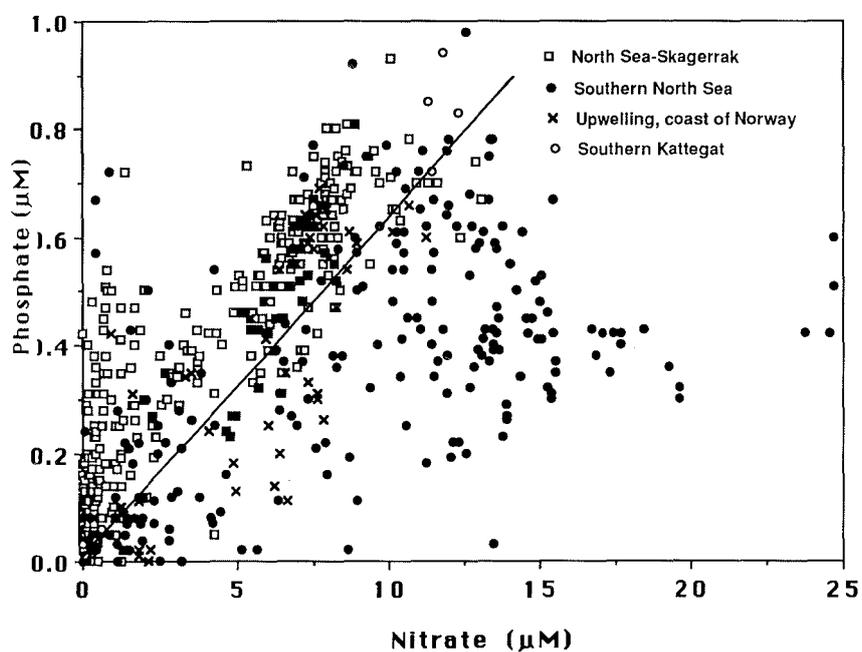


Figure 4.8 Plot of phosphate versus nitrate in water samples from different water masses in the eastern North Sea and the Skagerrak/Kattegat in April 1988. Data from the Institute of Marine Research, Bergen.

4.2.3 General remarks

Marine ecosystems have evolved in the presence of nutrient ratios, silicate to nitrate to phosphate, similar to those found today in unpolluted deep water. Anthropogenically created imbalances in these ratios are likely to disturb the normal structure and function of the ecosystem. A low content of silicate is likely to favour blooms of flagellates. A low nitrate may favour cyanobacteria blooms, while low phosphate may favour exceptional blooms of toxic algae such as dinoflagellates.

Anthropogenic nutrient input causes increased algal growth, which may create problems due to oxygen deficiency or otherwise reduced environmental quality. Reducing one nutrient, such as phosphate, in the freshwater outflow may improve the conditions locally by limiting the algal growth. This will have as a consequence, however, that the accompanying nitrogen will be utilized over an extended geographical area. This area will be characterized by phosphorus limitation, which may be inducive of the growth of toxic algae.

In a cost/benefit consideration of effluent water treatment, one needs to consider the relatively low cost of purification of phosphate in relation to the possible deleterious effect of creating an imbalanced nitrogen to phosphate ratio. It is probably a sound principle to attempt a balanced reduction of anthropogenic nutrient inputs. We also need to consider the possibility that an increased silicate concentration in riverine effluents may in some cases counteract the formation of noxious marine blooms and be conducive to less objectionable and perhaps more productive diatom blooms.

5. PHYTOPLANKTON

5.1 Diatom Spring Bloom

The diatom spring bloom was delayed for about 3 weeks in the Kattegat and Skagerrak area owing to reduced stabilization of the water column and poor light conditions. It did not present a high and narrow peak as usual, but was extended over a fairly long time. Since Chrysochromulina polylepis bloomed in Baltic Current waters, it might be useful to follow this water "upstream" and to consider the diatom spring bloom in the Belt Sea and Arkona Sea area. Here, Danish data are required. In the southwestern Baltic (Kiel Bight), there was no prominent diatom spring bloom, but there were higher than normal phytoplankton biomass levels throughout the whole winter.

In April 1988, the upper 30 m of the Kattegat water column was depleted of silicate but still showed some amount of nitrate (up to 6 μM). These data, however, integrate over a greater depth than that of the pycnocline and thus are somewhat misleading. Both sub-pycnocline waters and Jutland Current inflow waters exhibited high nitrate concentrations in relation to silicate and phosphate.

5.2 The Chrysochromulina polylepis Bloom

5.2.1 Early bloom stages

At the beginning of the bloom in the Gullmar Fjord (data from 3 May), nitrate was measured to be 1.3 μM and phosphate to be 0.13 μM (average concentrations for 0 - 15 m depth). This leads to an N:P ratio of 10, indicating nitrogen rather than phosphate to be the limiting nutrient. When the bloom arrived off Arendal (11 May), nitrate concentrations were 1.5 μM and phosphate concentrations were 0.04 μM at 0 and 5 m depth. In contrast to the Gullmar Fjord, the N:P ratio was greater than 25. Thus, nutrient concentrations in the upper layer at the beginning of the bloom were not unusually high in the coastal areas of

the Skagerrak/Kattegat. It should be noted, however, that this could have been at the edges of the bloom distribution at a time when the cell numbers were relatively high (of the order of a few million cells per liter).

The bloom was related to an unusual combination of high temperature and low salinity. At the beginning of the bloom, *C. polylepis* was found together with other phytoplankton species, but as the bloom developed further it became completely dominated by *C. polylepis*.

Based on the gross primary production measured in the Gullmar Fjord throughout the whole bloom event and the cellular content of nitrogen and phosphate as determined by Dahl *et al.* (1989), a gross uptake of 10 - 15 μM of nitrogen and 1.0 - 1.5 μM of phosphate must have occurred in the Gullmar Fjord. This would mean 10 times the amount of inorganic nutrients measured in the water column. Due to an apparent low remineralization of plankton organisms present in the water before *C. polylepis* occurred, there certainly was a strong need for inputs of "new" nutrients by some physical mechanisms in order to keep the bloom going on. The Gullmar Fjord is in open communication with the offshore waters, and advection plays a major role for the plankton dynamics in this fjord (Lindahl, 1987). Advection of nutrients and algae may have been such a mechanism, and one which complicates the interpretation of time series data. A further supply of nutrients may have come from the pool of dissolved organic matter (DOM). Brockmann and Dahl (1988) found fairly high concentrations of DOM in the euphotic zone of the Skagerrak, but very low concentrations within the horizon of the pycnocline where the *C. polylepis* population was mainly found.

The bloom seems to have originated from an initial population in the Kattegat. *C. polylepis* is probably present in the area all year round. While a sub-surface bloom built up in the central Kattegat, some part of that initial population was probably entrained into the Baltic current and formed the well-observed coastal toxic bloom near the surface. The latter was advected first towards the north by the Baltic Current and then to the west by the Norwegian Coastal Current (see Section 5.2.3, below).

5.2.2 Bloom development

Observations on the development of the *C. polylepis* bloom exist from the Gullmar Fjord on the Swedish Skagerrak coast (Lindahl and Rosenberg, 1989; Dahl *et al.*, 1989). High cell numbers were found on 22 and 24 May, with maximum densities of 26 and 40 million cells l^{-1} in a narrow layer at 6-8 m depth. The algal biomass was not particularly high, with a maximum depth-integrated content of chlorophyll-*a* of about 100 mg m^{-2} . The rate of primary production, on the other hand, was high, with an estimated production of 2.6 $\text{g C m}^{-2} \text{d}^{-1}$ on 19 May. This was the second highest daily rate of primary production ever recorded in the Gullmar Fjord.

The integrated primary production in the Gullmar Fjord was estimated as 27 g C m^{-2} for the period 6 to 26 May. This gross production corresponds to a requirement of 210 mmol m^{-2} of nitrogen. The estimated net production was about 1/3 of the gross production, corresponding to about 74 mmol m^{-2} of nitrogen. In comparison, the estimated entrainment of nitrogen from the deeper water into the outflowing Baltic water was 140 mmol m^{-2} for the same period. This shows that the nutrients supplied by entrainment were more than sufficient to account for the bloom as it was observed in the Gullmar Fjord (Lindahl and Rosenberg, 1989).

5.2.3 Transport and extension of the bloom in the Skagerrak

The development of the bloom of Chrysochromulina polylepis in the Skagerrak has been described in several reports (Aksnes et al., 1989; Dahl et al., 1989; Dundas et al., 1989). The first record of the occurrence of the bloom on the Norwegian Skagerrak coast was made on 13 May (position B in Figure 5.1) and 3 days later a fish farm east of Kristianssand (position C in Figure 5.1) was affected. This initial spread from the first record in early May on the Swedish west coast (position A in Figure 5.1) seems too rapid to be explained by advection only. It is, therefore, likely that a similar development due to growth of the bloom organism took place over an extensive area of the inner Skagerrak.

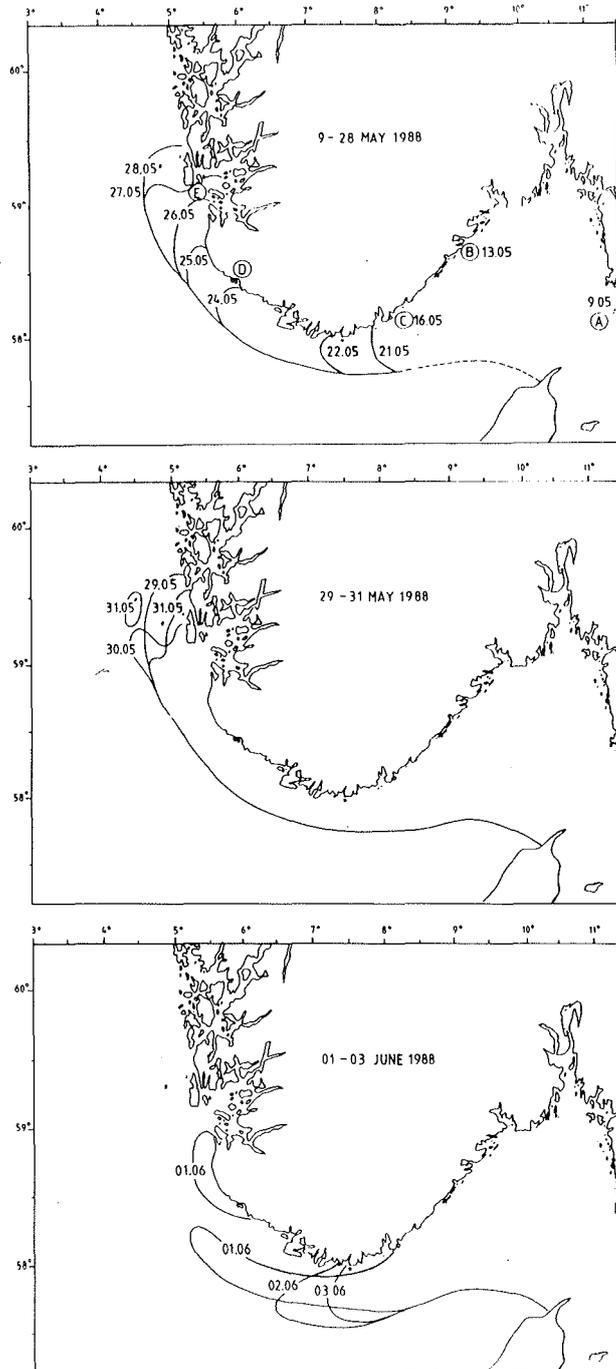


Figure 5.1 Distribution of the Chrysochromulina polylepis bloom in the Skagerrak. Dates indicate the position of the algal front between 9 May and 3 June 1988.

The further spread of the bloom westwards and northwards along the Norwegian coast was in good agreement with observations on physical conditions and was due mainly to advection. The westerly wind from 17-20 May (see Figure 2.2) blocked the outflow from the Skagerrak and the algal front remained stationary around Kristianssand until 21 May. As the wind ceased, the bloom was rapidly transported with the outflowing Skagerrak water in the Norwegian Coastal Current to reach its northernmost extension just north of the Boknafjord in Rogaland on 29 May (see Figure 5.1). Here the cell numbers of C. polylepis decreased rapidly and there was no further spread of the bloom (Aksnes et al., 1989).

When the bloom spread along the Norwegian Skagerrak coast and killed caged fish and natural biota, the cells were usually distributed evenly in the upper mixed layer of the coastal current.

5.2.4 Late bloom stages

At the end of the bloom, the population maximum was found in the region of the pycnocline. Thus, sub-surface pycnocline populations were found over much of the inner Skagerrak and the Kattegat in early June. During this time, C. polylepis was found in high densities (10-80 million cells l^{-1}) in a narrow layer of a few meters thickness. In the Gullmar Fjord, the bloom ended in late May. Off Arendal it declined around 2 June, with a bloom of the diatom Skeletonema costatum building at the surface.

In mid-June, the C. polylepis population could be detected only in the southern Kattegat and the Belt Sea.

5.2.5 Southwards extension in the Kattegat

Chrysochromulina polylepis was found as far south as the city of Korsør, Denmark. There it was associated with other nanoflagellates, such as Katodinium rotundatum, Gymnodinium sp. and Pyramimonas sp. In the southern Kattegat, C. polylepis built almost totally monospecies populations (Horstmann and Jochem, 1988).

6. PROPERTIES OF CHRYSOCHROMULINA POLYLEPIS

This chapter describes the morphology, taxonomy, nutrition, behaviour, and toxicity of the species Chrysochromulina polylepis. Because so little work has been done on C. polylepis in particular, much of the report on the properties of C. polylepis will depend on information general to the genus, as far as it is known.

6.1 Taxonomy

From work done by J. Larsen (University of Copenhagen) and J. Throndsen (University of Oslo) using the electron microscope, it is clear that the blooming species was a Chrysochromulina, and more specifically C. polylepis. Electron microscopy was necessary to identify this species because it is the structure of the scales (see Section 6.3, below) that defines the species, and these scales can be seen only with difficulty in the light microscope.

According to a current classification scheme, the genus Chrysochromulina belongs to the class Prymnesiophyceae within the Chromophyta (brown and golden algae). Close to fifty species of this genus have been described in the literature, and about half of these have been recorded from Scandinavian waters. A list of 42 species may be found in the publication by Estep et al. (1984). Three freshwater

species are known; all the others are marine. The species C. polylepis was described by Manton and Parke (1962), and the work of these authors contains much of the known information about its morphology and behaviour.

Related Prymnesiophycean flagellates of interest to marine management are the colonial species Phaeocystis sp., noted for mass occurrences in the North Sea and elsewhere (Cadée and Hegeman, 1986; Lancelot et al., 1989), and Corymbellus aureus, which was noted to form blooms in the North Sea for the first time in 1983 (Gieskes and Kraay, 1986). The closely related brackish-water species Prymnesium parvum is especially known for its toxicity to fish. Chrysochromulina is also closely related to the coccolithophorids.

6.2 Distribution

Chrysochromulina polylepis Manton et Parke 1962, which bloomed unexpectedly in the Kattegat and Skagerrak in May and June 1988, is not a recent immigrant to Northern European waters. It was recorded off southern England in the 1950s (Manton and Parke, 1962), and has been observed occasionally in Scandinavian waters before 1988. An early record suggests that it was present near Kiel, Germany, around 1911 (Büttner, 1911, as interpreted by J. Thronsen; Dahl et al., 1989) and only the introduction of the electron microscope in the 1950s made possible its routine identification.

The exact distribution of species within the genus Chrysochromulina is uncertain. Because special preparations are needed to detect these species, they are often not included in phytoplankton counts. However, where studies have been conducted that are amenable to their detection, Chrysochromulina species have been described from widely different localities around the world, a list of which may be found in Estep and MacIntyre (1989). Thomsen (1979), in a study of 500 electron microscope grids of samples from Danish waters, stated that "..... independent of season and geographical positions within the area, any water sample will hold one or more species of Chrysochromulina". Considering the fact that Chrysochromulina species have been identified in water samples from Europe, the Panama Canal, south Africa, Australia, Arctic Canada, Alaska, the Southern North Atlantic, the Galapagos Islands, and Japan, we may probably extend Thomsen's statement to most samples from the world's oceans.

6.3 Morphology

Chrysochromulina polylepis shares the attributes of other members of its genus. It is a unicellular (non-colonial) flagellate, with three appendages: two flagella and a "haptonema". The cell is about 10 μm long and typically has an obliquely pointed shape (see Figure 6.1A), though round forms may also be seen (see Figure 6.1B) (Manton and Parke, 1962).

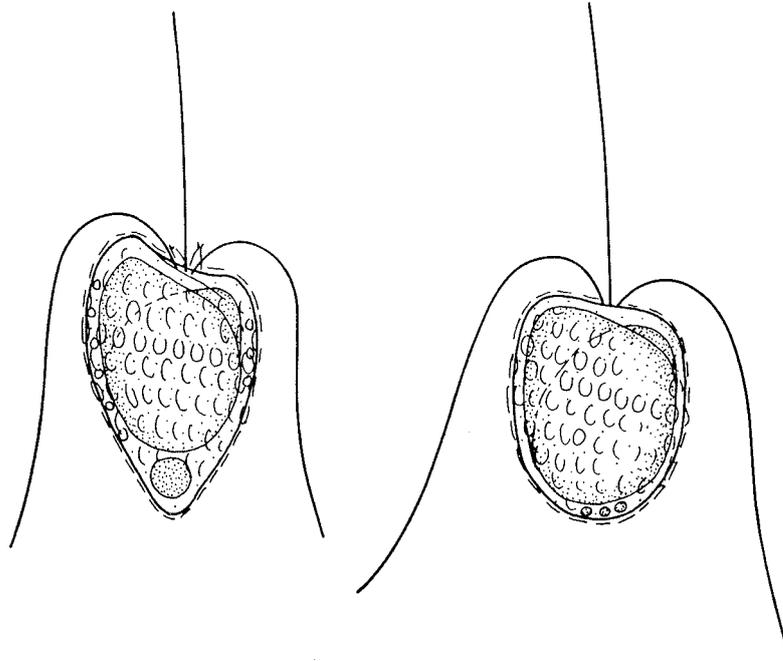


Figure 6.1 *Chrysochromulina polylepis*. Two morphological types with obliquely pointed shape (a) and rounded shape (b). Drawn by J. Throndsen (University of Oslo).

The flagella are used for locomotion. During swimming, they are directed backwards. Studies on the swimming speed indicate an ability to travel 3-6 m in a 12 hour period.

The third cellular appendage was originally described as a third flagellum, but is now known to be a different structure, termed haptonema (Parke *et al.*, 1955). The haptonema does not exhibit typical flagellar movement, and its usual motion is a coiling and uncoiling, though it may undergo erratic flipping or bending. Coiling is very rapid, occupying 1/60-1/100 of a second, while uncoiling takes several seconds (Leadbeater, 1971). During slow swimming, the haptonema may stretch directly out in front of or trail behind the cell (Parke *et al.*, 1956; Leadbeater and Manton, 1969). The only demonstrated function for the haptonema is attachment to surfaces. The importance of this ability in the life of the organism is uncertain (Leadbeater, 1971).

Like all other *Chrysochromulina* species, the surface of *C. polylepis* is covered with a layer of intricately patterned scales. These scales are produced in the golgi apparatus and transported to the surface (Leadbeater and Manton, 1969; Manton and Parke, 1962; Manton, 1972). Scales on a single species may be of one to four different types, two types being the most common. Scales may be flat plates or shallow cones, often rimmed, and the outer layer may be differentiated into a variety of patterns. Plate scales have a diameter that is usually about one-tenth to one-hundredth that of the cell diameter.

In *C. polylepis*, the scales are of four types: large rounded scales, 1.3 μm in diameter; small rounded scales, 0.7 μm in diameter; small elongated scales, 1.2 μm x 0.6 μm ; and large elongated scales, 2.5 μm x 0.9 μm (Manton and Parke, 1962). The large elongated scales are the most distinctive, bearing a forked projection in a characteristic position at one end (see Figure 6.2). The scales are composed of 65% protein and 32% carbohydrate (Allen and Northcote, 1975), and the carbohydrate appears to be cellulosic (Brown *et al.*, 1969). The close relationship of *Chrysochromulina* to coccolithophorids is indicated by studies showing that the latter initially produce unmineralized plate scales similar to *Chrysochromulina*, on which they then deposit calcium carbonate (Leadbeater 1970;

Leadbeater and Morton, 1973; Klaveness and Paasche, 1979). *C. polylepis* scales appear to be slightly mineralized (Manton and Parke, 1962), an observation confirmed by Thronsdén (unpublished results) using X-ray diffraction for the detection of calcium. Due to the organic nature of the scales, they represent a food source for other organisms and, therefore, it is extremely unlikely that they will remain intact in marine sediments.

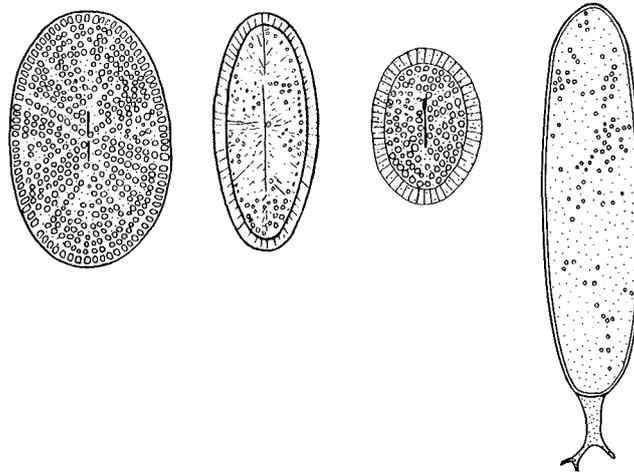


Figure 6.2 Scales of *Chrysochromulina polylepis*. Drawn by J. Thronsdén (University of Oslo).

The further distinguishing characteristic of *Chrysochromulina* cells is the possession of "muciferous bodies", electron-dense organelles near the surface of the cell that may discharge mucus into the surrounding water (Manton and Parke, 1962). Mucus may be liberated either quickly as threads or slowly as globules (Manton and Leadbeater, 1974). Threads may extend to a length of 90 μm (Parke *et al.*, 1956), or some 10 cell diameters. The function of this mucus discharge is at present unknown, though it has been suggested that it may bear some relationship to toxicity (Estep and MacIntyre, 1989).

6.4 Life Cycle and Behaviour

Little work has been done on the life cycle of *Chrysochromulina*. Species that have been studied exhibit a complex life cycle, with several different stages. For example, *C. ericina* reproduces asexually by fission into two progeny of equal or unequal size. After passing its maximum population density in culture, it forms amoeboid cells that collect on the bottom of the culture flask. These may then form four-walled progeny cells by successive fission. Motile cells are released from the walled cells (Parke *et al.*, 1956). *C. alifera*, *C. brevifilum*, *C. chiton*, *C. minor*, *C. kappa* and *C. ehippium* exhibit a similar life cycle (Parke *et al.*, 1955, 1956). *C. polylepis* has been observed only as motile cells and the amoeboid form, though the presence of other forms cannot be discounted based on the present information.

6.5 Nutrition and Photosynthesis

Each *Chrysochromulina polylepis* cell contains two chloroplasts of golden colour. The major pigments, as typical for other Prymnesiophycean algae, appear to be chlorophylls-*a*, *c*, and *c*₃, 19-hexanoyl-oxy-fucoxanthin, fucoxanthin, and diadinoxanthin (G. Johnsen, E. Sakshaug, and M. Vernet, pers. comm.). Thus, *C. polylepis* is equipped to live autotrophically. However, it can ingest particles, such as graphite or living bacteria and small algae, as has been found to be the case more generally within the genus *Chrysochromulina* (Manton and Parke, 1962).

Although C. polylepis has been in culture for about 30 years (the Plymouth strain), its physiology has been little studied. At least four strains of the species have been isolated from the 1988 bloom (L. Edler, University of Lund; J. Thronsen, D. Klaveness, E. Paasche, University of Oslo; J. Larsen, University of Copenhagen) and are now grown in culture in various Scandinavian laboratories. C. polylepis grows reasonably well in conventional seawater media, with nitrate and orthophosphate as the nitrogen and phosphorus sources. Three other species of the genus have been shown to require vitamins B1 and B12 (Pintner and Provasoli, 1968), and the same in all likelihood is true of C. polylepis. This species seems to have an unusually high demand for selenium (R.R.L. Guillard, pers. comm.; Dahl et al., 1989). The evidence for this is that cultures fail to grow to maximum density in media prepared from coastal sea water unless extra selenite (10 nM) is added. The growth seems to be best at salinities around 25 (Lindahl and Rosenberg, 1989).

One isolate has been grown as a bacteria-free culture (E. Paasche, University of Oslo). The significance of this is that C. polylepis does not require a supply of particulate food to meet its demand for, e.g., carbon, nitrogen or phosphorus, at least not at the elevated concentrations of dissolved nutrients in culture media. A similar conclusion was drawn earlier for three other Chrysochromulina species. Though Chrysochromulina cannot grow in the dark on particulate or dissolved food, it was found that heterotrophy may enhance growth in subdued light (Pintner and Provasoli, 1968). This capability may be important for the formation of high concentrations of Chrysochromulina cells at the pycnocline under sub-optimal light conditions, as was found during the 1988 bloom.

6.6 Biochemical Composition

The gross biochemical composition, in terms of carbohydrate, protein, lipid, etc., has been determined for the Plymouth strain (Ricketts, 1966). Analyses of cultures isolated from the 1988 bloom give the cellular content of some commonly determined components: 0.58-0.93 pg/cell of chlorophyll-a (Vernet, 1988; Dahl et al., 1989); 3.7 pg (0.26 picomol)/cell of nitrogen, and 0.8 pg (0.026 picomol)/cell of phosphorus (Dahl et al., 1989).

6.7 Toxicity

6.7.1 Chemistry and assays for detection of the toxin

Cooperative research in Norway and Japan on the structure of Chrysochromulina polylepis toxins has made considerable progress. Thus, the principal toxic components isolated are lipophilic and closely resemble hemolysin-2, a digalactosyl monoacyl glycerolipid produced by Amphidinium carterii (T. Aune, pers. comm.). In mass spectroscopy, fragments with mass/charge ratios near 700 dominate. The toxins are similar to hemolysin-I isolated from Prymnesium parvum (Kozakai et al., 1982).

C. polylepis toxins, like other algal toxins, appear to be a group of compounds rather than a single chemical. Chromatographic techniques are being developed to separate these closely related compounds.

During the determination of molecular structure, it is necessary to have rapid toxicity assays. The most useful in vitro test has been hemolysis of erythrocytes. Although hemolysis is not an observed cause of death in the natural environment, it is a useful model because it directly measures membrane failure. When thin-layer-chromatographic plates are sprayed with a suspension of erythrocytes, hemolytic spots show up as white areas. An assay method which reveals more details than simple hemolysis is the observation of morphological changes

of rat-liver cells exposed to toxins. Characteristic deformations of the membrane appear at concentrations well below those causing lysis, allowing a more discriminating analysis (Aune, 1988).

C. polylepis toxins are toxic to mice when administered intraperitoneally (Aune, 1988). Thus, the toxicity of C. polylepis may be determined by a mouse bioassay, similar to the measurement of diarrhetic shellfish poisons (DSP).

Groups of rats (20 animals per group) were administered perorally the following amounts of C. polylepis cells daily during two weeks: 0 (control), $0.175 \cdot 10^6$ or $0.350 \cdot 10^6$ cells per 100 g body weight. The C. polylepis cells were obtained from sea water (phosphorus content unknown), and concentrated by centrifugation. No clinical signs were observed during the two-week period. At termination, examination for gross pathology revealed no changes (Pedersen and Topsøe-Jensen, 1989).

6.7.2 Mode of action

The presumptive mode of action of C. polylepis toxins is cell membrane dysfunction.

The toxicity versus concentration curve for semi-purified toxin samples is highly non-linear and distinctly sigmoid, possibly because membrane disruption requires the cooperation of several toxin molecules. Laboratory data show that the duration of exposure is important, and that there is a threshold concentration of algal toxin below which no damage occurs (Leivestad and Serigstad, 1989). In addition, toxicity appears to be highly dependent upon the physiological condition of Chrysochromulina. The available data suggest that mortality in fish farms caused by C. polylepis toxins can be expressed by a hyperbolic relation (see Figure 6.3).

No data known to us conflict with the interpretation that the toxins exert their effect by disrupting cell membranes. Contrary to some early reports, gill mucus production is not increased by the toxins, and the respiratory problems seen in fish arise entirely from the failure of osmoregulation. Typical symptoms of mucus congestion are hyperventilation, coughing, and temporarily increased concentration of blood oxygen, followed by sudden death from exhaustion. None of these symptoms occur in C. polylepis poisoning. Death typically arises from damage to gill membranes with consequent loss of osmoregulation and increase of plasma chloride to lethal levels.

C. polylepis toxins seem to act similarly to the toxins of the closely related P. parvum (Shilo, 1982) and, more surprisingly, to the toxins produced by the dinoflagellates Gyrodinium and Amphidinium (T. Aune, pers. comm.).

DEADLY DOSE

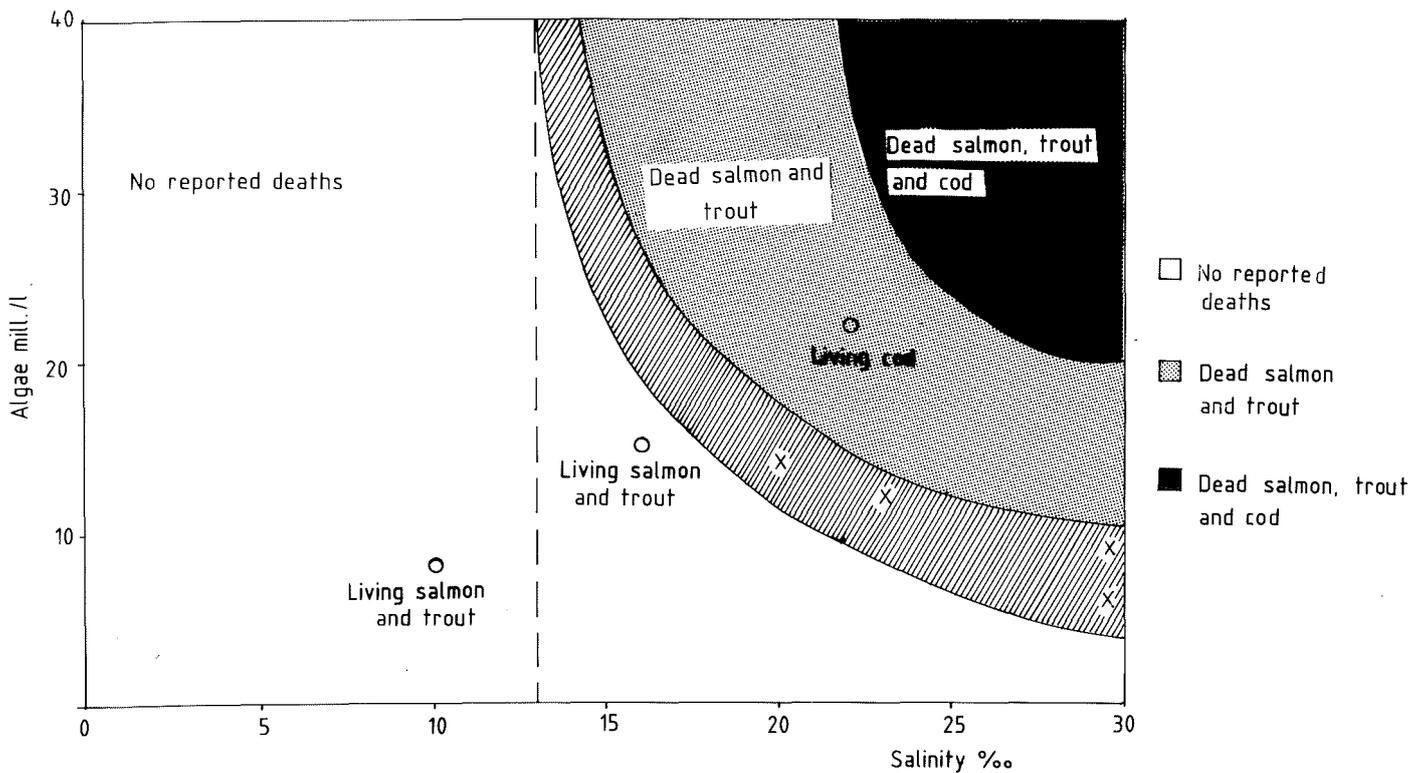


Figure 6.3 Reported mortality of salmon, rainbow trout, and cod in fish farms in relation to cell concentration of *Chrysochromulina polylepis* and salinity. From Leivestad and Serigstad (1989).

Two research groups (P. Gentien, IFREMER, and T. Aune and O. Stabell, Norwegian College of Veterinary Medicine) have independently used saponin - a well-known membrane disruptor - to mimic the effects of *Chrysochromulina* toxins *in vitro*, and have expressed toxicity in terms of "hemolytic units" (10 µg saponin = 1 HU). We suggest that this might become a useful standard in comparing the effects of membrane-disrupting toxins.

After the *C. polylepis* population collapses, the sea water rapidly loses toxicity. Mussels and oysters require 60 days for depuration (Aune, 1988).

6.7.3 Possible ecological implications of the toxin

It must be emphasized that *Chrysochromulina polylepis* strains are not always toxic. The Plymouth strain, when grown on standard media, was not toxic to fish (Manton and Parke, 1962) nor to a bryozoan, except for a slight toxicity in old cultures (Jebram, 1980). In fact, it served as useful food for this same bryozoan. During the bloom in the Skagerrak, *C. polylepis* was potentially toxic to a variety of animals and plants. Cultures of one strain established from the bloom were tested against a selection of organisms in the laboratory and displayed at most a weak inhibitory effect against diatoms, blue mussels, and cod (M. Nielsen and T. Strømngren, University of Trondheim). No effects were noted in other experiments with diatoms, red algae, and a copepod (Edvardsen *et al.*, 1990). Laboratory attempts to find potential grazers of *C. polylepis* suggested that certain heterotrophic dinoflagellates and a heliozoan might feed on *C. polylepis*, while some ciliates seemed unable to feed on the flagellate and appeared to be adversely affected by its presence (G. Tobiesen, University of Oslo). Extracts of *C. polylepis* cultures have been examined for cytotoxicity toward hepatocytes and for hemolytic effects on erythrocytes. In these artificial systems, toxicity

was noted in extracts made from phosphorus-deficient *C. polylepis*, but not from nutrient sufficient controls (Edvardsen *et al.*, 1990).

Prymnesium parvum, a related species, appears to develop toxicity primarily when stressed, such as by phosphate starvation (Shilo, 1981). *P. parvum* has recently (August 1989) formed a toxic bloom in the brackish surface water of a fjord in Rogaland on the west coast of Norway. This water was characterized by a high N:P ratio due to the low phosphate concentration in the freshwater runoff to the fjord (Skjoldal and Aure, 1989).

Available evidence suggests that the genus *Chrysochromulina* is ubiquitous and common, and that several species will be found at low cell concentrations in any water sample taken anywhere in the world. One may ask whether other *Chrysochromulina* species may also be capable of producing toxic blooms.

Two groups have independently suggested that the ability to secrete toxins may confer an ecological advantage on *Chrysochromulina*. P. Gentien (pers. comm.) mentions an "ectocrine detrimental to the growth of other algae", while Estep and MacIntyre (1989) discuss a nutritional mode which they call "dasmotrophy", or growth by taxation. In the dasmotrophy hypothesis, it is assumed that the *Chrysochromulina* toxicity is not primarily intended to kill other organisms, but to keep them alive and steadily milk them of nutrients.

6.7.4 Possible toxic effects on humans

The Workshop was not aware of any toxic effects on humans. Evidently, no human population was exposed to the 1988 bloom. No toxin was found in fish muscle, and no fish known to have been affected reached market. Mink that were fed on affected fish showed no symptoms of distress. Precautionary and apparently effective warnings were given concerning the possibility of toxic mussels. We know of no studies of peroral administration of the toxins, and so we have no way of assessing potential danger to humans. However, because filter feeders, such as mussels, accumulate the toxin, and because the toxin is heat stable to 100°C and has been recovered from cooked mussels, a direct route exists whereby the toxin may reach humans.

The possible adverse effect of *C. polylepis* on human skin has been investigated using five human volunteers. Sea water containing 80 million *C. polylepis* cells per liter was further concentrated by centrifugation and applied in two tests on human skin: the occlusion test and the scratch patch test, both revealing phototoxic properties. The tests were negative on all volunteers (Pedersen and Topsøe-Jensen, 1989). No evaluation of the human hazard of *C. polylepis* toxins perorally exposed can presently be performed, because there are so few toxicological data available.

7. POSSIBLE CAUSES FOR THE BLOOM

There is a tendency to look for single causes for noxious blooms and to believe that once a cause has been identified the bloom can be avoided. This "pin the blame" attitude is counter-productive for the understanding of complex phenomena such as algal blooms, which have many and interrelated causal factors.

7.1 A Plausible Scenario

Using known facts and some plausible assumptions, one may construct a scenario of the bloom event. Such a scenario may be of help in deciding what further research and monitoring efforts may be necessary in order to understand or predict future bloom events.

During the winter of 1987/1988, eutrophied water with a high nutrient content and with distorted N:P:Si ratios was advected by the Jutland Current from the southern North Sea into the Skagerrak/Kattegat area. Precipitation during the winter was higher than normal, causing increased nutrient inputs by land runoff into the Skagerrak/Kattegat area. A normal spring bloom of diatoms depleted the silicate, leaving a still high nitrate level and a high N:P ratio in the deeper water layer.

Atmospheric conditions allowed effective stratification of the water prior to the registered bloom, and Chrysochromulina polylepis is assumed to have grown at the pycnocline in an extensive area of the stratified waters of the Kattegat/Skagerrak during the late part of April and early May. C. polylepis at this stage was probably one of several species and occurred in a non-toxic mode. It seems likely that the "epicenter" of the bloom was in the Kattegat, possibly in the northern region due to doming or uplifting of nutrient-rich deeper water.

From this sub-surface layer, it is assumed that C. polylepis and nutrients were mixed into the upper mixed layer of the outflowing Baltic Sea water through entrainment and upwelling. The outflow from the Baltic Sea was considerably greater than normal and a rough calculation gives an entrainment of 1,000-2,000 tonnes per day into the outflowing water in the Kattegat. Here C. polylepis used up the nutrients fairly quickly and increased to moderate bloom proportions.

It seems possible that, owing to the high N:P ratio of the entrained or upwelled water, C. polylepis at this stage experienced P limitation and became toxic. The action of the toxin on accompanying pelagic biota may then have allowed further growth of C. polylepis.

7.2 The Role of Anthropogenic Nutrients

A central question is to what extent anthropogenic nutrient inputs may have been a contributing cause for the Chrysochromulina polylepis bloom. In 1980/1981, the yearly land runoff to the Kattegat/Skagerrak amounted to about 160,000 tonnes of nitrogen and the atmospheric deposition contributed some further 50,000 tonnes (ICES, 1987). Nitrogen in land runoff may be due to natural or anthropogenic sources and is subject to partial removal by denitrification in organically loaded estuarine systems. Nitrogen nutrient in atmospheric deposition is largely of anthropogenic origin and is not subject to removal mechanisms before being deposited in the sea.

The Jutland Current advects anthropogenically loaded water from the southern North Sea into the Skagerrak/Kattegat area. Together with the local runoff and the outflow from the Baltic Sea, this transport of anthropogenic nutrients undoubtedly contributes to the eutrophication of the Kattegat and the inner Skagerrak. The stratified conditions in this area are of particular importance in this respect. The Jutland Current carries well-mixed surface water that becomes layered below the outflowing Baltic Sea water. This surface water would normally have been nutrient depleted. However, due to the anthropogenic nutrient load, it now can still contain appreciable concentrations of nutrients remaining after the spring bloom. The distorted nutrient ratios, as observed in April 1988, are a reflection of this anthropogenic nutrient load.

It is likely that the high N:P ratio of the underlying water layer in the Kattegat and inner Skagerrak in April 1988 (see Figure 4.8) resulted in P deficiency in the upper water layer during the development of the Chrysochromulina polylepis bloom. There is experimental evidence that P deficiency results in a strong increase in the toxicity of this species, as well as of the closely related species Prymnesium parvum (see Section 6.7.3, below). Taken together, these observations suggest that the anthropogenic nutrient load to the affected

water masses played a role in the development of the toxic bloom of C. polylepis.

7.3 The Role of Physical Environmental Conditions

The special environmental conditions prior to and during the bloom of Chrysochromulina polylepis had important implications for the bloom development. The counter-clockwise circulation of the North Sea was hampered during the spring months, resulting in a long residence time of the water masses in the inner Skagerrak. The low wind activity and the large freshwater runoff resulted in strong stratification of the water masses as the bloom of C. polylepis presumably was building up.

Stratification seems to be an important factor, as a bloom of Chrysochromulina c.f. mactra Manton is reported to have occurred after enclosing a 25-m deep water column in the North Sea during May-June 1982 in a drifting enclosure (Brockmann et al., 1983). Growth occurred mainly above a stable thermocline at 15 m. During the bloom of C. polylepis, surface cell densities could be so low as to cause scarcely any water discoloration, while cell densities at specific depths could be so high as to give a scattering signal by sonar (Dundas et al., 1989).

The outflow of Baltic Sea water was particularly strong by the end of April and in the second week of May. This probably resulted in increased upward transport of nutrients from the nutrient-rich underlying water by entrainment. Southeastern winds from 8 May onwards may have caused uplifting of underlying water along the Swedish west coast, and westerly winds from 16 May caused upwelling along the Norwegian Skagerrak coast. These processes may have promoted the development and spread of the bloom.

The bloom was only noticed when it caused damage to farmed fish and at this stage major efforts were made to map its extent and progress. The front of the bloom along the southwestern coast of Norway correlated closely with a warm water front and could thus be followed by satellite infra-red (IR) imagery. In addition, water samples were monitored for C. polylepis cells. The propagation of the bloom is presented in Figure 5.1. It should be stressed that growth contributed to the spread of the bloom in the early phase, as the spreading cannot be explained by advection alone. This reflected similar biological developments over an extensive area. In the final stage, algal death was probably the cause for the retraction of the algal front against the current after its culmination off the southwestern coast of Norway.

7.4 Possible Role of Other Factors

Micronutrients have been considered as potentially contributing factors for the development of the Chrysochromulina polylepis bloom. C. polylepis has been shown to have a requirement for selenium in a nutrient-enriched sea water medium (see Section 6.5, above). However, there is no further information available to evaluate the possible role of micronutrients.

In order to investigate whether anthropogenic toxins might have influenced algal population species composition, water samples from the Gullmar region were subjected to analysis by the procedures "Priority Pollutants" (Center for Industrial Research, Oslo) and "Multi-analysis of biocides" (Governmental Agrochemical Laboratory, Uppsala). A water sample from early May showed the presence of 0.1-0.4 $\mu\text{g l}^{-1}$ of phenoxic acid MCPA (a biocide) and 3-5 $\mu\text{g l}^{-1}$ of phthalates and aromatics. It seems possible that MCPA might influence algal populations at the concentrations detected (Lindahl and Rosenberg, 1989).

The culmination of the bloom does not need to have been solely due to nutrient exhaustion. Thus, a Chrysochromulina bloom in the Baltic Sea culminated with most of the nutrients remaining (Niemi, 1983). Biological factors, such as competition and grazing, probably played a role in the culmination of the C. polylepis bloom. Microbial blooms may also culminate due to attack by specific viruses. Large quantities of viral particles, morphologically identical to those previously reported in association with Chrysochromulina, were detected in water samples from the C. polylepis bloom (G. Bratbak and M. Heldal, pers. comm.).

8. EFFECTS OF THE BLOOM

This report concentrates on the effects on the pelagic ecosystem, benthic ecosystem, and aquaculture. It also deals with subjects of public concern, such as tourism, trade in marine products, and legislation governing the siting of fish farms. The effects described below were recorded from coastal areas and, to a lesser extent, from the Skagerrak proper. Hardly any effects were observed within the Norwegian fjords and very few in the southern Kattegat, the Belt Sea, and the Sound area.

In general, the effects of the toxin were due to the damage of cell membranes. This general mechanism explains why so many different groups of organisms were influenced.

Literature references are mainly given to the summary reports from the different countries. These reports contain the detailed information and further references.

8.1 Pelagic Organisms

It is generally difficult to evaluate the effects of the bloom on the pelagic system, partly because of the movements of water masses, and partly because of the high patchiness and our restricted knowledge of "normal" species abundances in the pelagic system. The mobility of some organisms makes them less vulnerable to toxic events, since many of them can escape. Many dead organisms will obviously disappear from the system.

8.1.1 Microorganisms

There are no reports on negative effects on planktonic bacteria in connection with the bloom. Horstmann and Jochem (1988) reported heterotrophic colony-forming bacteria in water samples from the German cruise, with numbers almost one order of magnitude higher than normal. Some of these showed yellowish pigmentation, indicating a possible selective effect on these microorganisms.

8.1.2 Phytoplankton

Chrysochromulina polylepis, especially in the northern areas, formed almost a monospecific bloom (see Section 5.2), which might be due either to its effect on other phytoplankton species or to competitive advantage. However, observed effects on other phytoplankton species were few. Dahl et al. (1989) and T. Johnsen (pers. comm.) reported up to 90-100% of empty thecae of Ceratium spp. in waters above the pycnocline where the cell concentrations of C. polylepis were high. Below the pycnocline, the cells of Ceratium spp. had a normal appearance. Johnsen (pers. comm.) also found high abundances of single cells of the diatom Skeletonema costatum, which might be an effect of the C. polylepis bloom.

8.1.3 Zooplankton

Information on the effects of the bloom on zooplankton is sparse. Danish scientists reported normal concentrations of copepods in open waters (K. Vagn Hansen pers. comm.). Tintinnids were found among C. polylepis in the Belt Sea area (Horstmann and Jochem, 1988). In laboratory experiments, however, declining population densities were observed for ciliates, and egg production of three copepod species decreased drastically in the presence of cells of C. polylepis (Lindahl and Rosenberg, 1989). Copepod egg production has also proved to be a useful parameter in other studies of environmental impacts, and the use of this method should be encouraged in future cases of toxic blooms. Algal concentrations typical of the bloom period were also found in laboratory experiments to be acutely toxic to eggs and larvae of the ascidian Ciona intestinalis and the blue mussel Mytilus edulis (Granmo et al., 1988). Zooplankton genera such as Artemia and Daphnia were affected by C. polylepis at lower cell concentrations than were fish (Lindahl and Rosenberg, 1989).

8.1.4 Fish larvae

There is little evidence of effects on fish larvae in the open Skagerrak. However, the almost complete absence in some of the most seriously affected parts of the Norwegian coast of 0-group cod, whiting, pollack and saithe (Berge et al., 1988) may indicate an impact on the larval stages caused either by their escape or death.

8.2 Fish

The toxin produced by the alga destroyed the epithelial layer, particularly of the gills, leaving the fish unable to maintain ionic balance (Horstmann and Jochem, 1988; Leivestad and Serigstad, 1989; Lindahl and Rosenberg, 1989). Thus, it was osmotic stress owing to damaged membranes, and not lack of respiratory capacity, which killed both wild and farmed fish. No hemolysis was seen in experiments with fish (B. Serigstad, pers. comm.).

8.2.1 Pelagic species

There is little information on the impact on pelagic fish. However, avoidance of the bloom was reported for some species, e.g., inshore herring in Swedish coastal waters (Hagström, 1988), which escaped downwards from the pycnocline. The ICES Young Fish Survey in the Skagerrak/Kattegat during February 1989 showed no abnormal distribution in the area. Garfish (Belone belone) on the Swedish coast was one of the three fish species most often reported dead (Klang-Jonasson, 1988), while it was found to be only slightly affected in Norwegian coastal waters (Berge et al., 1988).

8.2.2 Demersal fish

Littoral fish species, especially labrids and gobiids, were badly affected in Norwegian coastal waters (see Table 8.1; Berge et al., 1988). Many of these species were found dead, while others were seen or caught in trawls at abnormal depths down to 60-130 m (cf. Klang-Jonasson, 1988). Along the Swedish coast of the Skagerrak, the influence on wild fish was somewhat less than that reported from the Norwegian coast, but many of the same species were found dead, including small cod and clupeids (Klang-Jonasson, 1988; Rosenberg et al., 1988; Lindahl and Rosenberg, 1989). Eels were found to aggregate and were caught in increased numbers in several Swedish coastal areas (Klang-Jonasson, 1988). In Norway, eel and catfish survived in cages in areas where other fish species died

(Leivestad and Serigstad, 1989). Along the Swedish Kattegat coast, fish were only slightly affected (Klang-Jonasson, 1988). In Danish waters, there are no reports of wild fish being killed by the bloom (Barth and Nielsen, 1989; Horstmann and Jochem, 1988).

8.3 Aquaculture

8.3.1 Fish

The bloom caused massive fish kills in areas with algal concentrations above about 5×10^6 cells l^{-1} . However, the toxic effect was greatly reduced at lower salinities, and large variations in tolerance were found between different species (see Figure 6.3). As is often found in cases of fish mortalities, young fish were found to tolerate the toxicity better than older specimens both in Norwegian and Swedish fish farms (Lindahl and Rosenberg, 1989; Leivestad and Serigstad, pers. comm.). Experiments where affected salmonids were transferred to non-toxic or less saline waters showed that the specimens recovered within hours in a manner analogous to recovery from anaesthesia (Leivestad and Serigstad, 1989). Crabs were also able to recover quickly from short-term exposure. However, the possible recovery after long-term exposure to algal cells has not been studied. Exposure of cod for 1 week showed more severe damage of gill tissues than was found in salmon that had died from exposure to C. polylepis (H. Leivestad and B. Serigstad, pers. comm.).

In Denmark, no farmed fish were reported to have died as a consequence of the bloom (Barth and Nielsen, 1989). Economic losses for Swedish and Norwegian fish farmers were estimated at about 10 million ECU. In Sweden, about 100 tonnes of salmon and rainbow trout were killed in marine farms, while one fish farm located in brackish water was not affected. In Norway, about 800 tonnes of fish, corresponding to 0.6 % of the total annual production in 1989, were lost. The low percentage is due to the fact that the area affected by the bloom is not a major fish farming area in Norway, and losses were furthermore avoided by towing cages into the brackish water of fjords.

8.3.2 Shellfish

The settlement of Mytilus edulis on ropes was low directly after the bloom, but unusually high later in July (Lindahl and Rosenberg, 1989). Extremely high settlement of Mytilus apparently occurred over much of the Swedish and Norwegian Skagerrak coasts that summer (J. Karlsson, M. Pedersén, E. Dahl, pers. comm.). No observations have been made for oysters.

8.4 Benthic Organisms

An impact was found on at least some species in all higher taxonomic levels (see Table 8.1). Due to the generally low amount of Chrysochromulina polylepis biomass which presumably sedimented onto the seabed, there was no wide-spread anoxia on the bottoms. Oxygen depletion caused by bacterial decomposition of dead organisms was, however, found locally after the bloom.

Table 8.1. Organisms strongly affected by the Chrysochromulina polylepsis bloom.

A. BENTHIC TAXA

Red algae

Delesseria sanguinea
Dilsea carnosa
Membranoptera alata
Ptilota plumosa

Polychaetes

Nereis sp.
Sabella penicillus

Chiton

Polyplacophora indet.

Snails

Buccinum undatum
Gibbula cinerea
Littorina littorea
Nassarius reticulatus
Nucella lapillus
Patella cf. vulgata

Mussels

Anomoniidae indet.

Seastars

Asterias rubens

Sea squirts

Ascidiella spp.
Ciona intestinalis
Corella parallelograma
Styela rustica

B. FISH

Centrolabrus exoletus
Ctenolabrus rupestris
Eutrigla gunardus
Gadus morhua (0- and 1-group)
Gobiidae
Labrus bimaculatus
Merlangius merlangius (0-group)
Platichthys flesus
Pollachius pollachius (0-group)
Pollachius virens (0-group)

8.4.1 Macroalgae

Severe effects were reported for four species of red algae, Delesseria sanguinea, Membranoptera alata, Dilsea carnosa and Ptilota plumosa. However, effects were also observed on other species of red, brown, and green algae, totaling more than 20 species, in Norway, Sweden and northern Jutland (Berge et al., 1988; Rosenberg et al., 1988; R. Nielsen, pers. comm.). Apparently this is the first time a toxic bloom has been reported to affect macroalgae. The effects were observed as discolouration of the thallus. The red algae first turned fluorescent orange and later greenish-brown, and subsequently part of the thallus died. Laboratory experiments in a flow-through system showed the same discolouration of red algae exposed overnight to water with similar high cell numbers of Chrysochromulina polylepis as those found in nature. Controls using deep water without C. polylepis showed no effect on the exposed macroalgae (Rosenberg et al., 1988; Lindahl and Rosenberg, 1989).

Since the changes in colour are easy to observe, and because the macroalgae are sessile, the perennial species are suitable indicators for this kind of toxin. The effects can also be checked under experimental conditions, and this can be used as a first warning.

Perennial algae such as Delesseria started to recover in July by growing a new thallus from the midrib, and the algae were well developed later in autumn and winter (Berge et al., 1988; J. Karlsson, pers. comm.). This indicates that the algal toxin had no long-term effects on the survival of seaweed tissues. The occurrence of Delesseria plants with small lamina in early autumn (an abnormal time for new "leaves") in the southern Kattegat above the pycnocline (M. Pedersén, pers. comm.) suggests that the bloom also had some impact there which had not been recorded during the spring.

8.4.2 Invertebrates

8.4.2.1 Observations by divers

Divers visited 90 transects along the Norwegian coast, recording visual effects on the biota on both hard and soft substrates (Berge et al., 1988; see Figure 8.1). The organisms most strongly affected were sea squirts and snails. The dog whelk populations were almost wiped out. In addition, sea urchins, starfish and some polychaetes were badly affected. Blue mussels and oysters, on the other hand, appeared to be little influenced, most probably due to their behaviour of closing their shells during unsuitable conditions. The impact on crabs seemed to be limited. A lack of observations made it difficult to determine whether there were any effects on lobster. The most severely affected taxa are listed in Table 8.1.

The main areas studied in Sweden were in the vicinity of the biological stations at Tjärnö and Kristineberg in the inner Skagerrak. The effects here were very much in accordance with the results from Norway (Rosenberg et al., 1988; Lindahl and Rosenberg, 1989). No effects were found on lobster, while some crabs were found dead. In Denmark, there were a few reports of effects on invertebrates off northern Jutland (Barth and Nielsen, 1989). Further south, the effects of the bloom were less (see Figure 8.1), and almost no effect was found in the Sound or the Belt Sea (Horstmann and Jochem, 1988; L. Edler, pers. comm.).

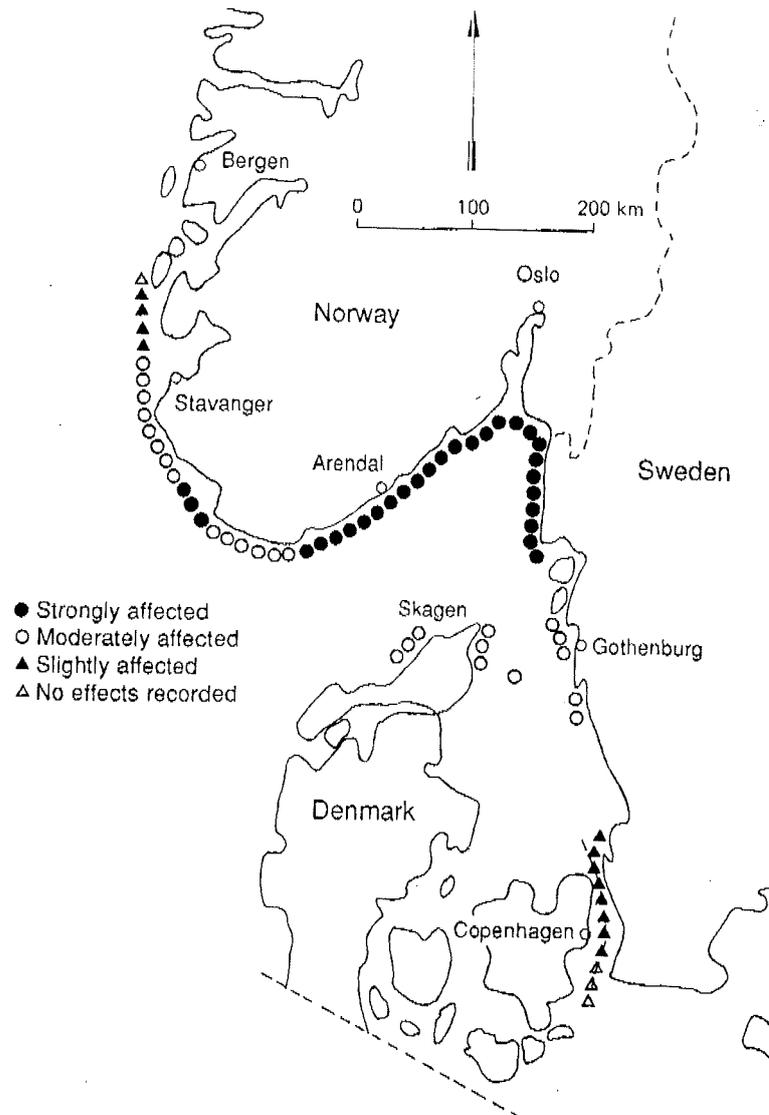


Figure 8.1 Coastal areas affected to various degrees by the *Chrysochromulina polylepis* bloom in the Kattegat and the Skagerrak.

8.4.2.2 Grab sampling

The soft bottom fauna at depths mainly between 10 and 30 metres was sampled on 65 coastal stations in Norway, while only a few littoral stations were monitored (Berge *et al.*, 1988). Generally, the impact on the fauna in these samples was significantly less than the effects noted by the divers. A survey in November in the most impacted areas on the Norwegian coast showed possibly delayed effects (A. Pedersen, pers. comm.). The reason for this is not clear, but it could reflect reduced survival of pelagic larvae. The samples from the littoral stations showed no effects.

The few soft bottom studies on the Swedish coast on the fauna in *Zostera* meadows (Lindahl and Rosenberg, 1989) did not show any significant changes in comparison to earlier studies, except for reduced abundance of two fish species during the first period after the bloom.

8.5 Public Concern

8.5.1 Tourism

There is evidence that there was some loss of tourist revenue, largely because of the very emotive media publicity during the algal bloom. The same is also true for the blooms of the closely related genus Phaeocystis on the North Sea coast of Denmark.

8.5.2 Trade in marine products

A loss of revenue to the mariculture industry and local fishermen was also attributable to the way in which the media presented partial and sometimes misleading information to the public. Thus, for future blooms it is important that, at an early stage, the authorities have the toxins identified and inform about in which organisms and organs the toxin has been found to accumulate. It is also essential that they clearly indicate for which organisms and areas there is no risk for human consumption, in order to avoid unnecessary economic losses.

8.5.3 Changes to the legislation governing the siting of salmon and trout farms

Existing legislation which governs the siting of marine fish farms takes no account of the economic impact which algal blooms may have on finfish mariculture. Some amendment to current legislation is urgently required in order that fish farmers may act "within the law" when sea cages have to be moved from designated areas in order to avoid or to mitigate the potentially harmful effects of algal blooms.

8.6 Specific Recommendations

Suitable test systems should be deployed as an "early warning" precaution and to obtain information on the effects of a bloom on a range of ecologically and economically important organisms:

- a) Small cages with salmonids should be deployed continually from spring to autumn at sensitive locations.
- b) Perennial red algal species, which have been shown to react to the Chrysochromulina toxin, should be exposed in flow-through systems and observed for pigmentation changes.
- c) Invertebrates noted to be highly sensitive to the toxins are also suitable test organisms.
- d) Eggs and larvae of cod and turbot may also be useful as test organisms.

In the event of a bloom, the following actions should be taken:

- a) Rapid identification of the bloom species is of great importance and procedures for this should be worked out in detail.
- b) Studies on the effects of the bloom should be carried out on a wide range of taxonomical groups.
- c) Specimens of commercial organisms should be properly preserved for later examination.

- d) An officially appointed spokesperson ought to be the only source of information to the public.
- e) The authorities should take account of the recommendations concerning information on toxicity, as given in Section 8.5.2, and changes of legislation governing the siting of fish farms, as given in Section 8.5.3.

9. GENERAL RECOMMENDATIONS FROM THE WORKSHOP

Our understanding of the general mechanisms underlying the occurrence of algal blooms is weak and largely qualitative. Knowledge of the physiology of C. polylepis was nearly nil before the bloom.

Specific recommendations were suggested by some of the workshop groups. In particular, the ameliorating group submitted a detailed list of recommendations. These suggestions have been condensed into four recommendation categories, as follows:

1. A better quantitative understanding of nutrient and carbon fluxes in marine microbial systems is urgently needed. Basic ecological interrelations between algae, protozoa, bacteria, and viruses need to be better studied also at the species level. Recent methodological advances make such studies possible.

Studies on the distribution, systematics, physiology, ecology, and toxicology of C. polylepis and other Chrysochromulina species should be encouraged. It would be ill-advised to concentrate studies exclusively on Chrysochromulina. Attention should also be given to other potential or proven noxious algae.

It is essential that a blooming alga be correctly identified, both for the monitoring of cell numbers in mixed populations and for accessing available information in the scientific literature as a basis for further research. A list of persons who may be contacted for assistance with C. polylepis and a list of Culture Collections holding Chrysochromulina cultures for research is appended in Annex III. It is recommended that similar lists concerning other relevant algae should be made available.

2. Further studies on the C. polylepis toxin should be encouraged; its mode of activity on marine species and its potential danger to humans by ingestion or aerosol inhalation should be firmly established.

It is of special interest to establish the conditions for toxin production and whether other species in the genus are potential toxin producers. Affected organisms, whether in test systems or otherwise, should be investigated for the toxin and toxin degradation products. The bodies, and particularly the livers, of some of the fish killed during the recent bloom could possibly have yielded important information on toxins and degradation products.

3. In order to make an early warning of future blooms, special attention should be given to monitoring those environmental parameters which observations during the recent bloom suggest were most closely related to the initiation and proliferation of the bloom.

Remote sensing, by satellite, aircraft or buoys, of parameters correlated with the bloom (turbidity, chlorophyll, pigments) should be considered.

The strongly stratified distribution of the C. polylepis population should be taken into account in future bloom monitoring.

4. Possible actions to counteract bloom effects include the following:

Test systems containing specially sensitive organisms, fish, algae or snails should be deployed in areas which are supposed to be impacted early in the event of a bloom.

Further research into the beneficial effects of low salinity on aquaculture organisms which have been exposed to Chrysochromulina should be carried out.

Methods for decreasing salinities and/or Chrysochromulina cell densities by pumping water from low salinity sources or from water depths with low concentrations of Chrysochromulina cells into "skirted cages" should be investigated.

Legal questions concerning emergency evacuation and the siting of aquaculture pens should be solved, in order to regulate possible controversies between owners of salmon river interests and fish farmers.

To avoid misinterpretations and confusion, information about a developing toxic bloom should be channelled through a single official channel. The unguarded use of the word "poison" in connection with the Chrysochromulina bloom may have caused a not inconsiderable monetary loss to the aquaculture industry.

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ANNEX 1

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ANNEX 2

ORGANIZATION OF THE ICES Chrysochromulina polylepis BLOOM WORKSHOP28 February

- 0845 - 0900 After the convener I. Dundas called the Workshop to order, the Director of the Institute of Marine Research, Odd Nakken, welcomed the participants and gave a short presentation of the scientific and managerial problems caused by the Chrysochromulina bloom.
- A plenary session followed, jointly chaired by I. Dundas and H.R. Skjoldal.
- 0900 - 1000 Plenary presentation on the physical and chemical oceanographic conditions prior to the bloom, given by R. Sætre.
- Plenary presentation on the biological conditions, given by O. Lindahl.
- 1000 - 1030 Coffee.
- 1030 - 1230 Presentation on the taxonomy and the physiology of Chrysochromulina, given by E. Paasche.
- Presentation on the research carried out on the toxin produced during the bloom, given by T. Aune.
- Presentation on the observed effects on the ecosystem, given by T. Bokn.
- Presentation of the observed effects on caged fish, given by B. Serigstad.
- Each presentation was followed by a short period for questions.
- 1230 - 1330 Lunch.
- 1330 - 1700 After the plenary presentations, the participants were divided into five groups:
- I. Group on Physical and Chemical Environmental Aspects
(Chairman S. Carlberg, rapporteur R. Sætre)
 - II. Group on Biological Environmental Aspects
(Chairman F. Jochem, rapporteur F. Rey)
 - III. Group on Taxonomy and Physiology of C. polylepis
(Chairman S.Y. Maestrini, Rapporteur K. Estep)

- IV. Group on C. polylepis toxin
(Chairman P. Krogh, Rapporteur F. MacIntyre)

- V. Group on Effects on Aquaculture and the Marine Environment
(Chairman K. Vagn Hansen, Rapporteurs T. Bokn and I. Wallentinus)

1900 Dinner at the Aquarium given by the Institute of Marine Research.

1 and 2 March

The five original groups, having finished their work the second day of the workshop, were rearranged so that members of Groups I and II jointly formed the Environmental Group
(Chairman R. Sætre, Rapporteur H.R. Skjoldal)

Members of Groups III and IV formed the Organism Group
(Chairman E. Paasche, Rapporteurs K. Estep and F. MacIntyre)

Group V continued its work as the Effects Group
(Chairman K. Vagn Hansen)

Some participants from the original five groups formed a new group, the Remedial and Ameliorative Measures Group
(Chairman B.I. Dybern, Rapporteur O. Lindahl)

These four groups presented their preliminary reports in a plenary session on the morning of the third day of the Workshop. The presentations were discussed and commented by the participants and, thereafter were amended and supplemented accordingly, forming the basis and the substance for the present Report.

1500 All participants joined in thanking the Institute of Marine Research for providing an agreeable venue for the Workshop. The plenary session was concluded by the convener with thanks to all participants for their diligent work during the Workshop.

It was agreed that the Editors would transmit to all participants a draft report by the end of April and that participants were to comment on this draft within a fortnight.

ANNEX 3

MEMBERS OF THE SUB-GROUPS

Group on Physical and Chemical Environmental Aspects

Ambjørg, C.
Aure, J.
Carlberg, S. (Chairman)
Dahlin, H.
Furnes, G.
Molvær, J.
Sætre, R. (Rapporteur)

Group on Biological Environmental Aspects

Dahl, E.
Dybern, B.I.
Edler, L.
Fraga, S.
Jochem, F. (Chairman)
Lindahl, O.
Rey, F. (Rapporteur)
Skjoldal, H.R.
Thordardottir, Th.
Willén, T.

Group on Taxonomy and Physiology of C. polylepis

Bauerfeind, E.
Dundas, I.
Erga, S.R.
Estep, K. (Rapporteur)
Heimdal, B.R.
Maestrini, S.Y. (Chairman)
Paasche, E.
Skulberg, A.
Thronsen, J.
Wallentinus, I.

Group on Toxin of C. polylepis

Aune, T.
Gentien, P.
Leivestad, H.
Krogh, P. (Chairman)
MacIntyre, F. (Rapporteur)
Stabell, O.

Group on Effects of C. polylepis Bloom

Bokn, T. (Rapporteur)
Eriksson, G.
Ervik, A.
Gaard, E.
Hansen, K. Vagn (Chairman)
Johnsen, T.M.
Naas, K.
Serigstad, B.
Seaton, D.D.
Wallentinus, I. (Rapporteur)

Environmental Conditions Group

Chairman: R. Sætre
Rapporteur: H.R. Skjoldal

Organism Group (Taxonomy, physiology and toxicology of C. polylepis)

Chairman: E. Paasche
Rapporteurs: K. Estep, F. MacIntyre

Effects Group

Chairman: K. Vagn Hansen
Rapporteurs: T. Bokn, I. Wallentinus

Group on Remedial and Ameliorative Action

Chairman: B.I. Dybern
Rapporteur: O. Lindahl

ANNEX 4

PERSONS WHO MAY BE CONTACTED FOR ASSISTANCE WITH C. polylepis IDENTIFICATION:

Norway: Jahn Throndsen, Kenneth W. Estep
Denmark: Øjvind Moestrup, Helge A. Thomsen
UK: John C. Green, Barry B.S.C. Leadbeater
Germany: Malte Elbrächter, Frank Jochem
Finland: Guy Hällfors
France: Marie-Josophe Chitriennot-Dinet, M. Billard

Culture collections that are a source of C. polylepis strains for research may be obtained from:

Provasoli-Guillard Center for Culture of Marine Phytoplankton, Bigelow, ME, USA.

Plymouth Culture Collection, Plymouth, UK.

Further assistance with culture collections may be obtained from:

Olav M. Skulberg
NIVA Culture Collection of Algae
Norwegian Institute for Water Research
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