

Environmental conditions and ecophysiological mechanisms which led to the 1988 *Chrysochromulina polylepis* bloom : an hypothesis

Chrysochromulina polylepis
Toxic-algal bloom
Grazer repellent
Phosphorus limitation
Eutrophication

Chrysochromulina polylepis
Efflorescence algale
Inhibiteur brouteur
Limitation du phosphore
Eutrophisation

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Received 9/11/90, in revised form 24/04/91, accepted 30/00/91.

ABSTRACT

Information available on the 1988 *Chrysochromulina polylepis* bloom in Scandinavian coastal waters is evaluated. Special attention is paid to the early bloom stage and the sequence of both environmental and physiological mechanisms leading to the bloom, and a tentative, integrated timing schema is given of causes which led to the observed events.

Environmental conditions favourable for *Chrysochromulina polylepis* are considered to have resulted from : a) an exceptionally high runoff of nitrogen-rich water in winter and early spring ; b) strong mixing of the water column, immediately followed by a long period of vertical stability and stratification ; c) a diatom bloom 30 % larger than usual, peaking around 20 March ; and d) a second diatom bloom in mid April, largely dominated by *Skeletonema costatum*. These events combined to cause the euphotic layer to become silicate-exhausted, phosphorus-poor and fairly nitrogen-rich. The lack of silicate prevented diatom growth. Weak turbulence and strong stratification favoured growth of non-siliceous, motile nanoplankton.

C. polylepis is believed to have outcompeted co-existing algal species by producing a toxin acting first as a grazer repellent, while its cell density was still below 10^4 individuals.l⁻¹. At the conjectured location of first appearance of the bloom (or at one of several locations), in the Skagerrak near Gullmar Fjord, the grazing repellent forced a shift of grazing to other algae around the latter part of April. With increased population density of *C. polylepis* (10^6 cells.l⁻¹), the toxin then became sufficiently concentrated to affect directly not only grazers, but all other organisms. From late April, the *C. polylepis* population increased free from grazing and other losses. In conditions of light and nutrient sufficiency, a high growth rate (corresponding to 0.8 div.d⁻¹) was achieved. Actively growing cells were buoyant and remained in the upper part of the water column.

With increasing population density (10^7 cells.l⁻¹), nutrients became exhausted and self-shading decreased available light. By mid May, the growth rate had decreased to zero, and the population started to become senescent. *C. polylepis* deteriorated in physiological state, perhaps partly because of self-poisoning, and this led to sinking. No further growth occurred, but cell densities showed higher

values (several 10^7 cells.l⁻¹, with maximum density between 5 and 10 m) because distribution became patchy both horizontally and vertically. At the end of May a significant part of the population had died, and cell leakage produced an increase in dissolved organic matter. The resultant lower turbidity and regenerated nutrients then allowed other flagellates and some diatoms to resume growth. The remaining *C. polylepis* cells sunk to the pycnocline (15-20 m), which acted as a barrier and greatly retarded this sinking, by which means the cells became concentrated, and produced the highest reported cell densities at the pycnocline. It is assumed that the bloom later sedimented.

Since relevant environmental conditions for the initiation of the bloom occurred over a very large area (75.10^3 km²) and the dominant currents were not altogether consistent with the spreading of the bloom, polygenesis of the bloom should be considered a possibility.

To what extent long-term global change and eutrophication might have contributed to this exceptional bloom remains unclear. Since the production of the toxin seems to be favoured by phosphorus deficiency, however, a large input of nitrogen in combination with a reduction in the phosphorus loading is believed to have contributed indirectly to the bloom, by changing the nutrient status of the coastal waters from being nitrogen- to phosphorus-limited.

Oceanologica Acta, 1991. 14, 4, 397-413.

RÉSUMÉ

Conditions environnementales et mécanismes écophysiologicals à l'origine de l'efflorescence à *Chrysochromolunia polylepis* de 1988 : une hypothèse

Toutes les informations disponibles au sujet de l'efflorescence à *C. polylepis* ont été examinées, en recherchant tout particulièrement les données objectives ayant trait au début du phénomène. Un schéma de la succession des conditions environnementales et des mécanismes écophysiologicals l'ayant rendu possible est proposé à titre d'hypothèse.

Suivant ce schéma, quatre conditions environnementales favorables se sont succédées : a) pendant l'hiver et au début du printemps, abondance exceptionnelle de neige et de pluie s'étant traduite par d'importantes quantités d'azote charriées à la mer ; b) fort mélange des eaux, immédiatement suivi d'une très longue période de stabilité et de stratification ; c) floraison de diatomées 30 % plus abondante qu'à l'accoutumée, maximale vers le 20 mars ; d) mi-avril, floraison dominée par *Skeletonema costatum*. Ces événements ont concouru à rendre les eaux de la couche euphotique épuisées en silicium, très pauvres en phosphore et relativement riches en azote. L'absence de silicium a prévenu toute croissance des diatomées ; l'absence de turbulence et la stratification ont favorisé la croissance des algues mobiles non silicifiées.

C. polylepis a indirectement pris l'avantage sur les autres phytoflagellés, en produisant une substance capable de repousser les brouteurs, alors que sa densité était encore inférieure à 10^4 cellules.l⁻¹. Au point hypothétique de première apparition du phénomène (ou à l'un des points), près du fjord Gullmar, dans le Skagerrak, la diminution de la pression de broutage sur *C. polylepis* et son détournement vers d'autres espèces algales a vraisemblablement eu lieu une semaine avant la fin avril. Avec l'accroissement de la densité de *C. polylepis*, jusqu'à 10^6 cell.l⁻¹, au moins, la toxine est devenue assez concentrée pour inhiber directement les autres organismes, y compris les brouteurs. A partir de fin avril, *C. polylepis* s'est développée sans perte de cellules ; là où l'intensité lumineuse et la concentration en nutriments ont été suffisantes, le taux de croissance a été maximal ($0,8$ div.j⁻¹). Ces cellules, étant flottables, sont restées dans la partie supérieure de la colonne d'eau.

Avec l'accroissement de la densité de *C. polylepis* (10^7 cell.l⁻¹), la réserve en nutriments a été épuisée et l'auto-ombrage a réduit l'énergie lumineuse disponible. Mi-mai, le taux de division s'est fortement réduit ($0,17$ div.j⁻¹), puis

la croissance a cessé. Le vieillissement accentué qui en a résulté a réduit fortement la flottabilité des cellules, qui ont alors sédimenté. Les fortes densités mesurées à cette époque (plusieurs 10^7 cell.l⁻¹) avaient pour origine une distribution inégale des cellules, avec des concentrations en «nuage» surtout localisées entre 5 et 10 m. Fin mai, une part significative des cellules étaient mortes. Les nutriments régénérés et une turbidité moins grande des eaux ont permis à d'autres espèces de phytoflagellés de croître à nouveau. Les cellules restantes de *C. polylepis* ont continué à sédimenter ; la pycnocline (15-20 m), ayant ralenti leur progression, la concentration s'est accentuée, donnant naissance, dans une couche pouvant avoir 1 m d'épaisseur seulement, aux très fortes densités (jusqu'à 10^8 cell.l⁻¹) mentionnées en juin. Aucune étude n'a porté au-delà de cette étape ; il est néanmoins admis que le reste de la floraison est parvenu au fond.

L'efflorescence ayant couvert une surface très grande (75.10^3 km²) et les courants dominants ne correspondant pas toujours aux directions de sa propagation apparente, la polygénèse du phénomène est considérée comme étant probable.

Le rôle éventuel des changements climatiques affectant la planète et celui de l'eutrophisation des eaux côtières dans la naissance de l'efflorescence n'ont pu être établis. Néanmoins, comme la production de toxine par *C. polylepis* semble être favorisée par une déficience en phosphore, les rejets croissants d'azote dans les eaux côtières et la réduction de ceux contenant du phosphore y ont sans doute contribué indirectement, en rendant le phosphore plus limitant que l'azote.

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INTRODUCTION

On 9 May 1988, caged fish (rainbow trout) in a fishfarm situated in the Gullmar Fjord, near Lysekil, Sweden, were observed behaving unusually, as if they lacked oxygen. Analyses, however, showed that the whole water column had a normal oxygen content, during both day and night (Lindahl, 1988). Notwithstanding, the fish began to die two days later; the largest individuals first, then the whole stock in decreasing order of sizes (Rosenberg *et al.*, 1988). The lethal phenomenon moved to the north. In Norway the first incidents of anomalous behavior were observed at Gamle Hellesund on 11 May in the County of Aust-Agder, and two days later mass mortalities occurred again in several areas with aquaculture installations (Underdal *et al.*, 1989).

The slightly yellowish green colour of the lethal waters soon led marine biologists to suspect that an algal bloom was associated with the fish kills. Microscopic examinations revealed the presence of between five and ten million cells per liter of a microalga identified on 17 May as the prymnesiophycean *Chrysochromulina polylepis* Manton and Parke. During the following two weeks, according to several reports (mostly non-scientific newspapers), the "algal front" spread along the coast of Norway, up to the Bokna Fjord just North of Stavanger (Nielsen, 1989). By the end of the third week, the bloom was also observed in the southern part of the Kattegat, in the Belt and the Sound (Rosenberg *et al.*, 1988), at the entrance of the Baltic Sea. The density of the alga was frequently higher than 10^7

cells.l⁻¹ (Nielsen, 1989), the yellowish green water with high density being located at or just above the pycnocline (Nielsen and Richardson, 1990; Horstmann and Jochem, 1990). In mid June the bloom began to disappear, and by late June the bloom was declining ; decayed cells of *C. polylepis* were overgrown by bacteria (Nielsen *et al.*, 1990) and observed to be attacked by fungi.

Due to the production of a non-selective toxin able to affect membrane permeability and disturb ion balance (chapter 6, in Dundas and Skjoldal, in press), not only did many metazoa suffer from the bloom, but also some seaweeds, especially those, such as *Delesseria sanguinea*, with a slender thallus (Berge *et al.*, 1988; Underdal *et al.*, 1989; Bokn *et al.*, 1990; chapter 8, in Dundas and Skjoldal, in press). Many grazers, *e.g.* the dominant copepods *Acartia*, *Temora* and *Centropages*, stopped feeding and produced few eggs. As a whole, zooplankton numbers were very low in the water bodies affected by the *C. polylepis* bloom (Lindahl and Dahl, 1990). Ciliates, usually voracious grazers, also became rare and apparently inactive, and algal cells were completely absent from their digestive vacuoles, where several are usually observed (Bernard and Rassoulzadegan, 1990). Moreover, other phytoplanktonic species became scarce or disappeared: 90-100 % of the thecae of *Ceratium*, for instance, were empty (Dahl *et al.*, 1989); the number of cryptophyceans was reduced by 98 % (Johnsen and Lømsland, 1990).

This noxious phenomena of great economic importance, which came as a total surprise to marine biologists, immediately promoted extensive co-operative research, both in

the field and the laboratory. Our aim here is to integrate all the available information, paying special attention to the early stages of the bloom, and to the sequence of environmental and physiological mechanisms which could have been responsible for allowing *Chrysochromulina polylepis* to outcompete its co-occurring species, and to affect a water body of a size never previously reported. We also discuss whether and how eutrophication could have contributed to the bloom, and the reasons for the bloom's final decline. Unfortunately however, the bloom was observed only in its later stages, when its lethal effects appeared; the initial period was not observed at all. Our interpretation is therefore somewhat speculative, and deliberately provocative in order to stimulate more long-term integrated studies in toxic-phytoplankton research.

THE CAUSES OF THE BLOOM

The environmental background and key hydrographic events

The winter of 1987-1988 was mild and wet in the whole Scandinavian area. During winter and early spring, precipitation in the Skagerrak was roughly 50 % above the mean value for 1936 to 1970, 150 % in the Kattegat, and between 150 % and 250 % in Sweden (Aksnes *et al.*, 1989; Rosenorn, 1989). The subsequent heavy runoff resulted in a critical increase in the input of terrigenous nutrients to coastal waters; the nitrogen concentration in *e.g.* the Gullmar fjord increased by 80 % before the spring bloom, and phosphorus by 50 % (Lindahl, 1988 *a*). During January and February, winds from the south were strong: up to 67 % above the average. On the contrary, in May and June, they were below average (the second lowest record in twenty eight years; Schroder, 1989 *a*). This sequence first mixed the upper layers and produced a nearly uniform vertical distribution of nutrients. Then vertical stability established, which prevented the deep, nutrient-rich reservoir from supplying the upper productive layer with nutrients. Deep waters over the whole Kattegat-Skagerrak area showed high nutrient values (NO_3 : 14 μM , in some places 18 μM ; PO_4 : 0.6 μM) with high N/P ratios (≈ 24 ; Aksnes *et al.*, 1989; Lindahl and Dahl, 1990). Unusually high NO_3 concentrations, up to 25 μM , were also reported from several areas along the Danish east coast near the Limfjorden. An extensive description of the hydrography and environmental conditions during the 1987-88 winter-spring period is given in Dundas and Skjoldal (chapters 2 and 3, in press); complementary details on 1987 features can be found in Rosenberg *et al.* (1990); data on meteorological and hydrological differences between "normal" and "*C. polylepis* abnormal year" are reported in Ambjörn *et al.* (1989).

The increase in silicate concentration was practically nil, reflecting the absence of anthropogenic silica input. Eutrophication of lakes and rivers generally leads to dia-

tom blooms which exhaust the natural silicate pool before this fresh water discharges to the sea, but large pools of available nitrogenous and phosphorous compounds remain (Weichart, 1986). Further inorganic nutrients available in the Kattegat and the Skagerrak were introduced from the North Sea *via* the Jutland current, whose waters were silicate-poor and nitrate-rich. After the rainy period, insolation was exceptionally high (70 % above average; Rosenorn, 1989), leading to an unusually rapid increase in water temperature: 16°C at 1 m depth by the end of May, instead of the usual 11°-12°C.

The sequence in algal development

The meteorological and hydrographic conditions described above led to massive diatom blooms. In the Kattegat-Skagerrak area, the spring diatom bloom was 30 % more intense than those of previous years (Lindahl, 1988 *b*; Lindahl and Carlberg, 1988), and highest available chlorophyll *a* content was recorded on 21 March (Fig. 1). Then, a second bloom, largely dominated by *Skeletonema costatum*, occurred in mid April (Fig. 2). During this bloom, persistently light winds and unusual, continuously high illumination allowed stratification to persist in the water

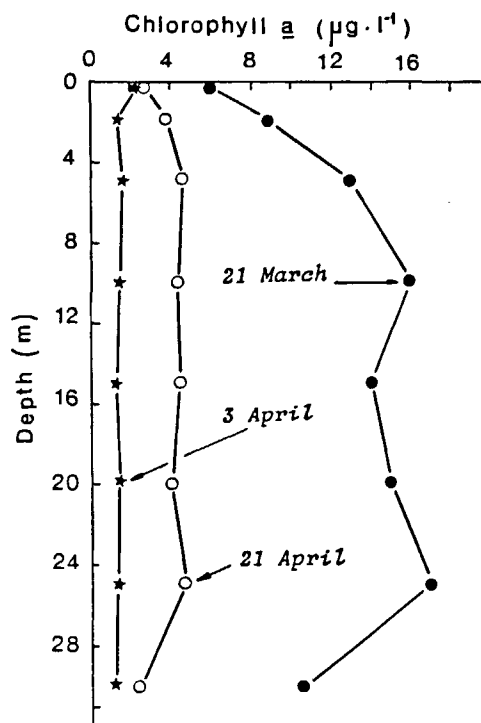


Figure 1

Chlorophyll *a* vertical distribution at Alsbäck station (Gullmar Fjorden, Skagerrak), from 21 March (diatom bloom) to 21 April (*Chrysochromulina polylepis* early-stage bloom). Unpublished data from courtesy of Odd Lindahl.

Profil vertical de la teneur en chlorophylle *a* à Alsbäck station (Skagerrak, Gullmar Fjorden), du 21 mars (floraison des diatomées) au 21 avril (premiers stades de l'efflorescence à *Chrysochromulina polylepis*). Données non publiées aimablement communiquées par Odd Lindahl.

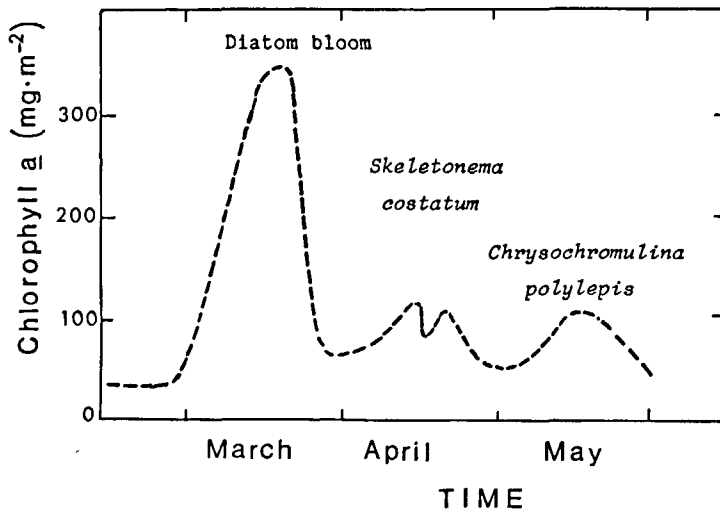


Figure 2

Typical evolution, during the spring of 1988, of chlorophyll *a* content of waters in which *Chrysochromulina polylepis* bloomed. Authors' scenario from available information (Lindahl, 1988 a; Dahl *et al.*, 1989; Lindahl and Rosenberg, 1989).

Évolution, pendant le printemps 1988, de la teneur en chlorophylle *a* dans les eaux où l'efflorescence à *Chrysochromulina polylepis* s'est développée. Reconstitution des auteurs à partir des informations disponibles (Lindahl, 1988 a; Dahl *et al.*, 1989; Lindahl et Rosenberg, 1989).

column : the surface layer (0-10 m) was well illuminated and warm, whereas deeper waters (below 10 m) were poorly illuminated and cold. At the beginning of May, the surface layer contained no silicate, very little phosphate and some nitrate (Aksnes *et al.*, 1990; Fig. 3). Below the pycnocline (Fig. 4), large amounts of nitrogen and some phosphate were available, while again no silicate was present (Aksnes *et al.*, 1989; chapter 4, in Dundas and Skjoldal, in press). In addition, dissolved organic nitrogen was present at significant concentrations, which later probably helped to support algal growth (Brockmann and Dahl, 1990).

Thus three conditions which favour non-siliceous algae were established: 1) shortage of silicate, which greatly reduced diatom growth potential (more than 80 % reduction according to Aksnes *et al.*, 1989); 2) absence of turbulence; and 3) stratification of waters, which favours many motile algal species (Margalef, 1975; 1978; Sournia, 1982; Paerl, 1988; Sommer, 1988). Under such conditions, it is not surprising that *Chrysochromulina polylepis* and other non-siliceous species began to increase; light energy was sufficient to allow photosynthesis, while nitrate, dissolved organic nitrogen and phosphate were available at concentrations high enough to support the production of a large algal biomass. The bloom then showed two different aspects in each of the two areas it covered, the Kattegat and the Skagerrak; in the Skagerrak, cell concentrations generally were lower than those found in the Kattegat (Dahl *et al.*, 1989). We nevertheless assume that initially the key mechanisms were practically the same in both areas; higher cell densities resulted from high concentrations of available nutrients and more marked concentration mechanisms (*see* "How were the highest cell densities..." chapter).

Such a sequence of physical, chemical and biological events is not unusual: similar features, except for phosphorus deficiency relative to nitrogen, but including dominance by flagellates, occurred in the Skagerrak and the Gullmars fjord in May 1987 (Rosenberg *et al.*, 1990). Silicate limitation also occurs in many other red-tides. Lancelot *et al.* (1987), for instance, have shown that soon after the silicate-limited spring bloom of diatoms in coastal

zones of the southern part of the North Sea, the surplus of N and P is used by the Prymnesiophyceae *Phaeocystis cf. pouchetii*, which produces massive blooms. Moreover, Lännergren (1978) demonstrated that during the course of a spring bloom in Lindåspollene (Norway), nitrogen was the nutrient limiting algal biomass in the early stages of the bloom while silicate limited the final stages, when small flagellates replaced diatoms as the dominant organisms.

The extreme dominance of *C. polylepis*, for many days virtually the only phytoplankton species (Lindahl and Rosenberg, 1989; Nielsen *et al.*, 1990), and the area affected by the bloom (75.10^3 km², according to Rosenberg *et al.*, 1988) had never been previously observed. Hence, two key questions arose: 1) how could this alga totally out-compete non-siliceous companion species, theoretically also able to take advantage of the same favourable condi-

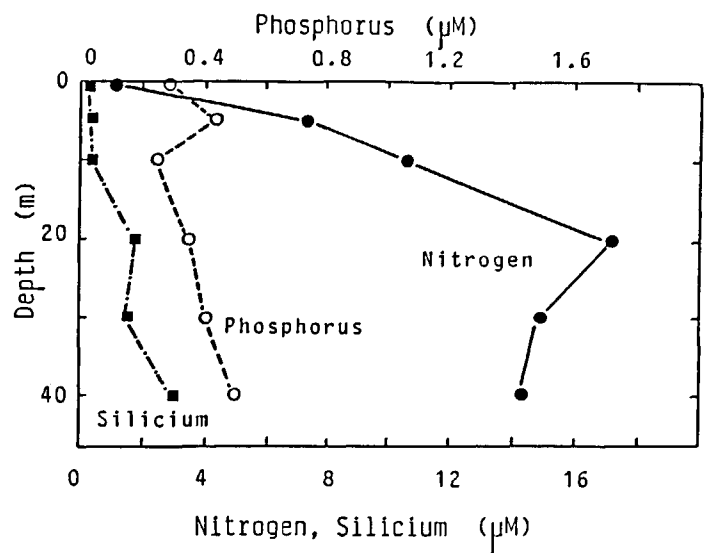


Figure 3

Inorganic nitrogen, phosphorus and silicium concentrations versus depth in the northern Kattegat, on late April 1988, soon after the diatom bloom (redrawn from Dundas and Skjoldal, in press).

Concentrations en azote, phosphore et silicium (formes minérales) dans le nord du Kattegat, en fonction de la profondeur, fin avril 1988, après la floraison des diatomées (recomposé d'après Dundas and Skjoldal, sous presse).

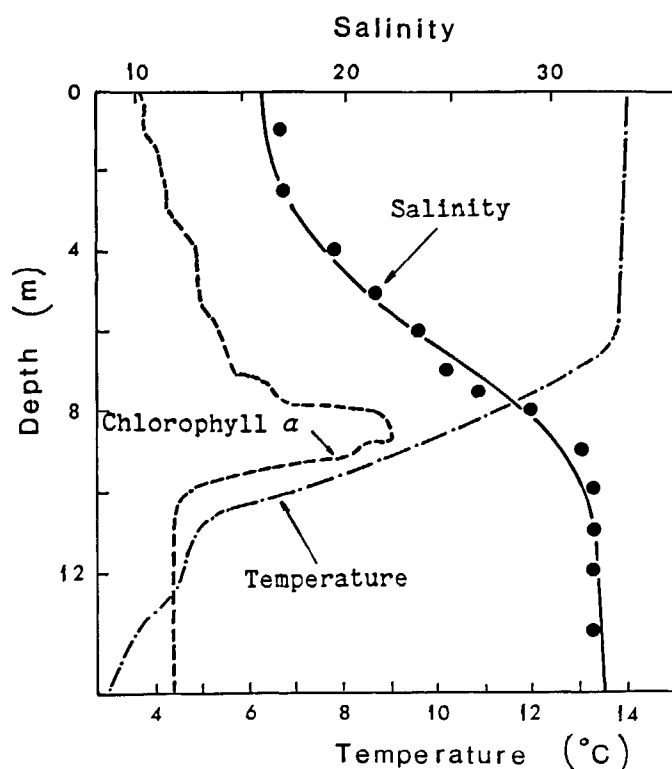


Figure 4

Typical vertical distribution of temperature, salinity and chlorophyll *a* fluorescence during the *Chrysochromulina polylepis* bloom. Redrawn from Haumann (1989; 31 May, Jutland east coast) and Horstmann and Jochem (1990; 1-3 June, Southern Kattegat).

Profils verticaux types de la température, de la salinité et de fluorescence de la chlorophylle *a* (unité arbitraire), pendant l'efflorescence à *Chrysochromulina polylepis*. Recomposé d'après Haumann (1989; 31 mai, côte est du Jutland) et Horstmann et Jochem (1990; 1-3 juin, sud du Kattegat).

tions ? 2) how could the population spread over a such large area ?

Timing of the main physiological-weapon activity of *Chrysochromulina polylepis*

Since propagation of the bloom required several weeks, different sites experienced different stages of algal growth and dominance at a given time. Any discussion of the temporal development of the bloom, as well as being tentative, can therefore be valid only for a limited area. Here we focus on the area in which the bloom was first noticed: the Gullmar fjord area. Fortunately the few pre-bloom data available also pertain to this area.

From the published data we analysed, it is likely that the key mechanism or set of mechanisms which displaced all unsilicified co-occurring species except *C. polylepis* was already acting in the early stage of the bloom before the end of April (although some competing species were still present by early May). As a matter of fact, Dahl (1988) and Lindahl and Rosenberg (1989) reported that 2.10^5 cells.l⁻¹ of the harmful dinoflagellate *Gyrodinium aureo-*

lum were present on 11 May when the first fish kills were observed, and so this species was first suspected to be the cause of the fish kills. However, by 17 May this species had apparently disappeared. On the other hand, Kaas (in Lindahl and Dahl, 1990) counted 18 400 *C. polylepis* per liter on 4 May, near Anholt in the Kattegat. The first fish kills were recorded five days later in the Gullmar Fjord with a cell count of a few million *C. polylepis* cells.l⁻¹. On this basis, and considering that counts were carried out in two different places, we suggest that from the beginning of May until May 11 *C. polylepis* had divided at its maximum growth rate and was totally free from losses. We also suggest that it established its capability to avoid cell losses and to make other algae unable to compete for nutrients just after the *Skeletonema costatum* bloom, i.e. roughly between the third week of April and the end of April. In other words, we hypothesize that *C. polylepis* took the upper hand with respect to co-occurring phytoplankton species even though its density was probably far less than 10⁴ cell.l⁻¹.

The nature of the main physiological "weapon"

Chrysochromulina polylepis is widespread in the North Sea and adjacent coastal waters but, like all other species of the genus *Chrysochromulina*, it is normally present in low cell densities and most often in an assemblage of 4 to 25 co-occurring species (Estep *et al.*, 1984). Before 1988 whether *C. polylepis* was autotrophic and/or heterotrophic or phagotrophic, for instance, remained unclear, as did many other aspects of its biology (Parke *et al.*, 1955-1958, cited in Sanders and Porter, 1988). Manton and Parke (1962) studying the original isolate of *C. polylepis* observed phagotrophic nutrition, while Pintner and Provasoli (1968), using three other species of the same genus, concluded that they were autotrophic, but with a requirement for vitamins B1 and B12. With the significant increase in research soon after the 1988 bloom, much new information about the species has been obtained, including: division rate (0.8 div. day⁻¹ and close to 1 div.day⁻¹, in F/2 medium at 15°C, according to Nielsen *et al.* (1990) and Dahl *et al.* (1989), respectively; the amounts of photosynthetic pigments, 0.58-0.93 pg.cell⁻¹ chlorophyll *a* (Vernet, pers. comm.); nitrogen, 0.26 pmole.cell⁻¹; and phosphorus, 0.026 pmole.cell⁻¹ (Dahl *et al.*, 1989); as well as on the assemblage of carotenoids serving to characterize the species (Bjerkeng *et al.*, in press), and P_{max} (≈ 1.2 mgC.mg Chl-*a*⁻¹.h⁻¹ at a light intensity of 150 μ mole.m⁻².s⁻¹; Nielsen *et al.*, 1990). Paasche *et al.* (in press) have also discovered the existence of a deviant cell form lacking one kind of scale, and have observed that cultures isolated from the 1988 bloom produce a mixture of the two types of cell, which it is not possible to grow separately on a permanent basis. It is not known, however, what this peculiar feature (perhaps a stage in the life cycle, according to Paasche *et al.*) could have meant for the development of the bloom. Phagotrophy has also been ascertained, at least for some stages of the living cycle (Estep and

MacIntyre, 1989). On the other hand, comparison of vertical profiles taken in early June did not indicate any vertical migration of *C. polylepis* to allow nutrients to be taken up in the dark at greater depths (Horstmann and Jochem, 1990), such as occurs in several other phytoflagellates. Nevertheless, given the present stage of knowledge, it seems likely that *C. polylepis* is not different from many other marine phytoflagellate species with respect to nutrient-based competitive ability (Maestrini and Bonin, 1981 *a*) and reaction to physical factors (Bonin *et al.*, 1981).

The single peculiar capability of *C. polylepis* seems to be its ability to release a toxin which disturbs the ionic exchange of many organisms to the point of causing their death. Nutrient-phosphorus deficiency enhances, and may even be necessary for the production of this toxin (Edvardsen *et al.*, 1990; Carlsson *et al.*, 1990; Tobiesen, 1990). The dinoflagellate *Alexandrium tamarense* (syn. *Protogonyaulax tamarensis*) also shows a 3- to 4-fold increase of toxin production in P-limited culture relative to that in control and in N-limited cultures (Boyer *et al.*, 1987).

The capability of *C. polylepis* to produce toxin is consistent with the theory of "dasmotrophy" proposed by Estep and MacIntyre (1989). According to these authors, all members of the genus *Chrysochromulina* (47 described species) may exhibit a variety of trophic modes: in the presence of organisms that they can prey upon, they consume them (= phagotrophy); when that is not possible, they induce nutrient leakage by producing a toxin which renders the cell membrane permeable but does not kill the prey (= "dasmotrophy"). This concept assumes that the biomass of the *Chrysochromulina* species would be small compared to that of their victims. Several species would then occur together because all the member species would profit from the leakage induced by one species in the genus.

This "altruistic" behaviour between species clearly did not occur during spring 1988, when only one member displaced all other species. On the other hand, it is not likely that direct allelopathic activity by *C. polylepis* prevented other algae from growing, because such inhibition usually requires concentrations of allelopathic substances higher than those which could have been produced by the still-scarce population of *C. polylepis* in the early stages (Berland *et al.*, 1974; Maestrini and Bonin, 1981 *b*).

Toxin produced by the still low-population of *C. polylepis* more probably acted as a "grazer repellent", thus reducing loss from grazing. Such a mechanism is possible, because most micrograzers, like ciliates, have to actively move toward their prey in order to enter in close contact and ingest it. Experiments made by Carlsson *et al.* (1990) support this assumption: these authors observed that the ciliate *Favella ehrenbergii* did not show any feeding reaction when it encountered *C. polylepis*. Similarly, it is likely that larger filtering organisms, such as copepods, may have

selected against repellent cells (Nielsen *et al.*, 1990) and chosen other more palatable ones. Such chemoreception-based feeding has been reported by Gill and Harris (1987) and Gill and Poulet (1988). Jebram (1980), who studied the influence of food-algal composition on grazer feeding rate, stated that *C. polylepis* was a good food, and therefore only weakly resistant to grazing. However, it should be noted that the algal culture medium used for his experiments was not phosphorus-deficient (P was present at 60 μM) and may not therefore have activated *C. polylepis*'s toxicity. Although similar experimental conditions (P was present at 36.3 μM) could have affected the results of Nielsen *et al.* (1990), they nevertheless reported that the copepod *Acartia tonsa* avoided feeding on *C. polylepis* although the culture was not toxic (*i.e.* no mortality of the copepod occurred) at the cell concentration tested. The authors stated that reduced swimming activity *in situ* contributed to the exclusion of copepods from the pycnocline where the algae gathered. On the other hand, reduced grazing pressure caused by inhibitory substances is widely considered to be important for the development of large populations of algae (Parker, 1987; Legendre, 1990); such a mechanism by which algal dominance may be established through repulsion of grazers has been already shown in *Olisthodiscus luteus* (Tomas, 1980). It is thus likely that the *C. polylepis* bloom in its early stages was not subject to the large grazing losses usual for most phytoplankton populations.

When the grazing pressure on *C. polylepis* had been reduced and shifted to competitive algal species (in late April - early May), the cell density of *C. polylepis* continued to increase. Subsequently, the toxin then reached a concentration at which it acted directly on the metabolism of all coexisting organisms. Carlsson *et al.* (1990), for instance, demonstrated that the feeding rate of a tintinnid ciliate upon a good prey was reduced by roughly 40 % by the presence of *C. polylepis* at a concentration of $1.5 \cdot 10^6$ cells.l⁻¹, and was completely suppressed at $3 \cdot 10^6$ cells.l⁻¹. Hence, as these authors pointed out, with a growth rate of 0.8 divisions per day (Dahl *et al.*, 1989), and under conditions of nutrient repletion and absence of grazing, an initial population of roughly 10^6 cells.l⁻¹ may potentially attain a density of several 10^7 cells.l⁻¹ in one week, which is consistent with increase of cell density observed in the field.

THE SPREADING OF THE BLOOM

Soon after unlimited growth was established, the *C. polylepis* cell-rich layer extended to the north and west at a surprising mean speed of 25 km.day⁻¹ (Dundas *et al.*, 1989). The presence of the algae close to the surface as well as deeper was noticed, especially in the Skagerrak, principally by the harmful effects produced on all kinds of organisms. The propagation of the later stages of the bloom was surveyed by several research vessels from different

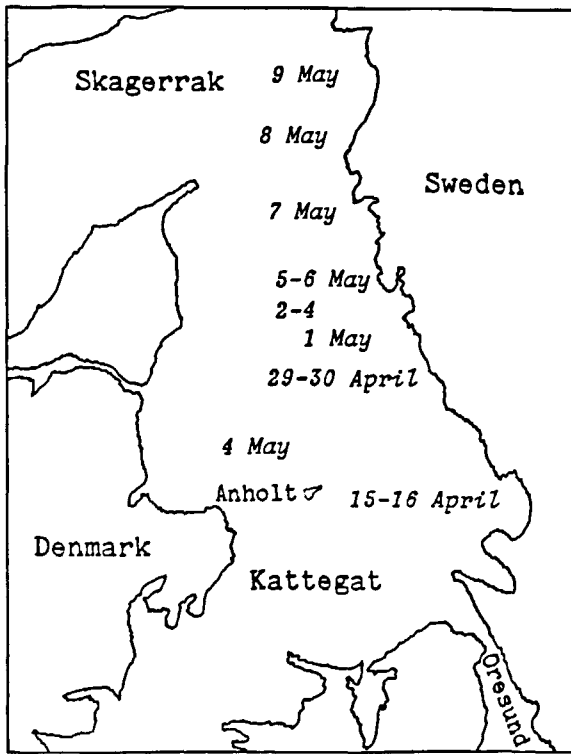


Figure 5

Speculated origin and initial spreading of the *Chrysochromulina polylepis* bloom, according to Lindahl and Rosenberg (1989).

Origine supposée et progression de l'efflorescence à *Chrysochromulina polylepis*, selon Lindahl et Rosenberg (1989).

countries, directed to investigate the hydrography, the algal distribution and the immediate ecological effects of the bloom (Rosenberg *et al.*, 1988; Haumann, 1989; Brockmann and Dahl, 1990; Horstmann and Jochem, Thronsen and Eikrem, 1990). In addition, because the "algal front" in the surface water coincided with the hydrological front of high-temperature and low-salinity water coming from the Baltic, satellite temperature-based pictures correlated well with the spreading of the bloom (Horstmann, 1988; Dundas *et al.*, 1989; Horstmann and Jochem, 1990), especially in the Skagerrak. Satellite pictures also showed that the Jutland current played an important role in transporting particle-rich waters from the North Sea towards the entrance of the Baltic Sea. However, since the water layer where the algae concentrated was mostly at 8 to 15 m (Kaas *et al.*, 1988), and thus partly decoupled from the surface current, the path indicated by satellite imagery should be carefully considered before stating that it exactly showed the spreading of the bloom and that no mechanism other than surface transport was involved. In view of the extent and spatial variability of the bloom, it should be discussed whether different regions experienced the same set of surface-transport mechanisms or whether propagation processes varied within this area.

The earliest available counts of several millions cells per liter were obtained with samples taken in the Gullmar

Fjord, soon after the fish death had attracted attention of scientists. Nevertheless, from an analysis of the hydrographic situation of the water where *C. polylepis* was found, Lindahl and Rosenberg (1989) supposed that the bloom started further South in the Kattegat, during the period 15-18 April (Fig. 5); then, in May, the water masses containing the blooming population would have been pushed up northward to the Skagerrak and west Norway. According to this hypothesis, *C. polylepis* bloomed within a unique spot area from which cells were spread by surface currents; in other words, there was a continuous frontal inoculation of water masses.

Such a mechanism is probably consistent with the fast propagation which occurred after 13 May along the coast of Norway, but it cannot explain the discrepancy between observed and predicted events prior this period. As a matter of fact, if the bloom had initiated by mid April further south from Gullmar fjord area, perhaps in Öresund, three weeks later deaths of metazoa should have been reported around this supposed south-Kattegat location. At the same time, due to the assumed delay for transportation from south to the north, no harmful effect should have been observed in the Gullmar fjord. On the contrary, it is clear that the bloom appeared rather late in the Kattegat (Anonymous, 1988), whereas Gullmar fjord fish farms experienced first reported lethal effects of the bloom.

The alternative hypothesis to the one of Lindahl and Rosenberg (1989), namely initiation of the bloom in the Gullmar fjord area and transportation from there, both to the north and the south, is also not convincing, because such an unique origin would mean that the bloom invaded the whole southern part of the Kattegat and even entered the Baltic Sea against the direction of the surface Baltic

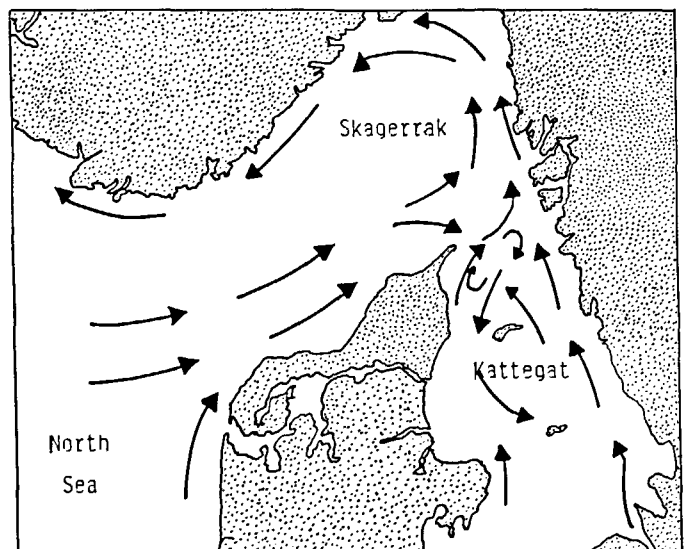


Figure 6

Main basic surface currents in the Kattegat and the Skagerrak (redrawn and simplified from Aksnes *et al.*, 1989).

Principaux courants de surface dans le Kattegat et le Skagerrak (recomposé et simplifié d'après Aksnes *et al.*, 1989).

current (Fig. 6). Moreover, observations made during the development of the bloom led Danish scientists to think that it was not transported in the Kattegat by sea currents, but resulted from growth of the permanent local *C. polylepis* population (Anonymous, 1988). As a matter of fact, *C. polylepis* is likely to be permanently present in all coastal Scandinavian waters (Nielsen *et al.*, 1990) and thus does not need any inoculation to initiate growth.

Hence, all included, it is our opinion that a polygenesis of the bloom should be considered as a possibility. This would have required the existence of suitable bloom-producing conditions over a very large area, which indeed seems to have been the case throughout the Scandinavian coastal area during the late spring of 1988. The simultaneous appearance of blooms of a noxious species at several separated sites has already been observed elsewhere with *Gyrodinium cf. aureolum* (Partensky and Sournia, 1986).

DID THE ANTHROPOGENIC DISCHARGES PRODUCE THE TOXIC BLOOM ?

During the past few decades, nitrogen and phosphorus inputs from man-made sources have increased markedly, yet estimates are variable. Schroder (1989 *b*), for instance, stated that the total nitrogen load in the North Sea has increased by a factor of 2.5 between 1950 and 1980, but that the phosphorus load had stayed rather constant. On the other hand, Gran, as early as 1931, suspected that the high productivity of coastal waters could be explained by terrestrial iron-containing humus compounds carried to the sea by freshwater runoff. Graneli and Moreira (1990), using algal assays, showed that river water originating in forested areas is growth-promoting to potentially toxic dinoflagellates such as *Prorocentrum minimum*, a species that was seen in the Skagerrak for the first time in 1979 (Tangen, 1980). The transport of humic substances to the coastal waters in Sweden seems to have increased during the last 15 years due to acid precipitation falling on forested soils (Forsberg and Ahl, 1990, cited in Forsberg and Petersen, 1990). This increase in humic substances in river water during the last decade may also be connected to a higher than average runoff. Based on the *op. cit.* assumptions, Graneli *et al.* (1989) have hypothesized that the increase in humic compounds being discharged in the Scandinavian coastal waters might be promoting dinoflagellate growth. In coastal waters, through "conditioning" (Johnston, 1964; Barber and Ryther, 1969), leakage of metals (Graneli *et al.*, 1986 *b*) and/or decreased grazing effects (Graneli *et al.*, 1989 *b*), humic substances promote more frequent algal blooms, and play a role in shifting the species composition from diatoms to algal flagellates, mostly dinoflagellates (Graneli *et al.*, 1989 *a*; Graneli and Moreira, 1990). Present concentrations of nutrients in North-Sea coastal waters are at least twice as high now as they were fifty years ago. For the Kattegat, Edler (1984) calculated that nitrogen has increased by a factor of 4 and phosphorus by a

factor of 3 to 7 during the period 1930-1980, and Andersson and Rydberg (1988) showed that dissolved inorganic nitrogen has increased approximately two-fold between 1971 and 1982, while changes in dissolved inorganic phosphorus were insignificant. Recently, Haumann and Jorgensen (1989) reported an increase of 10 $\mu\text{mole.l}^{-1}\text{N}$ near the pycnocline, within an area covering 14000 km^2 , reflecting a loading surplus of 22 400 tonnes from 1987 to March 1988.

On the other hand, in marine ecosystems, individual species are controlled by a large set of environmental factors. If any one changes significantly, it upsets the existing balance and ultimately generates a new ecological equilibrium which fits the new conditions. In such a process, substantial effects on final algal yields are ultimately regulated by macronutrients. Micronutrients, in contrast, appear to regulate species occurrence, growth rate, competitive ability and perhaps community structure (Frey and Small, 1980; Smayda, 1990). Hence, whether or not such macronutrient depletion and/or an exceptional increase in concentration of one or more growth-promoting micronutrients may have generated the *C. polylepis* bloom is considered below.

The role of the load of N and P

Chlorophyll *a* concentrations of 10 $\mu\text{g.l}^{-1}$ were found when $20 \cdot 10^6$ cells. l^{-1} of *C. polylepis* were present (Lindahl and Rosenberg, 1989). Taking the mean value for the ratio of chlorophyll *a* increase/nitrogen uptake in flagellate algae (*i.e.* 1.1 $\mu\text{g Chl } a^{-1} \mu\text{mole}^{-1}$; Healey, 1975; Charpy-Roubaud *et al.*, 1982), production of that biomass requires a maximum of 9 $\mu\text{mole.l}^{-1}$ nitrogen. Such a supply could be sustained by the pool of nutrients present below the pycnocline. Calculation of the algal-growth potential (Oswald and Golueke, 1966), *i.e.* natural nitrogen reservoir ($\mu\text{mole.volume}^{-1}$) versus minimum cell quota ($\mu\text{mole.cell}^{-1}$; Droop, 1974), provides another estimate of the nutrient supply needed to support the observed algal densities. On the basis of the nutrient content present in the water and cell nutrient content (Dahl *et al.*, 1989), 15-20 $\cdot 10^6$ *C. polylepis* per litre could be produced from the pool of nutrients in the upper layer.

But the estimated need for nutrients by the production of observed biomass of *C. polylepis* was frequently higher than the surface-water pool (Berge *et al.*, 1988). It is therefore likely that deep waters supplied the upper layer with nutrients, either through advection, vertical mixing or cell migration. However, the exact magnitude of nutrient inputs and origins is not of prime importance here. We argue that the bulk of nutrients had no effect per se and cannot explain the total success of *C. polylepis*, because the excess of nitrate and phosphate left by the early diatom bloom, together with the regenerated nutrients and humic acids could have supported growth of most or all of the non-silicious species present before *C. polylepis* started to

bloom. Moreover, *C. polylepis* has been reported to grow in waters poor in inorganic nutrients (Johnsen and Lömsland, 1990). Hence, environmental mechanisms other than eutrophication must have been involved in the process which led to the observed phenomenon of dominance by a single species.

The role of micronutrients

Edvardsen *et al.* (1990) demonstrated that the presence of selenium greatly enhances the maximum cell density of *C. polylepis* in culture. But Harrison *et al.* (1988) did not observe any selenium requirement. Since, however, there is no useful available data on selenium concentrations in Scandinavian coastal waters during April-May 1988, whether or not micronutrients played a role in differentially stimulating the growth of non-siliceous species must remain an open question.

The role of the nutrient balance

We have already suggested that toxin production may have been the primary mechanism by which *C. polylepis* avoided being grazed, and which allowed it to outcompete co-occurring algal species. In this case the key environmental condition which permitted this advantage is likely to have been the high nitrogen to phosphorus ratio in the water (Dahl *et al.*, 1989), relative to the mean N/P ratio in phytoplankton (Redfield, 1934). Enhanced saxitoxin production by phosphorus deficiency in dinoflagellates (Hall, 1982 in Boyer *et al.*, 1985; 1987) led to the suggestion that algal-toxin excretion could be an adaptation to manipulate environmental conditions, *i.e.* eliminate excess nitrogen from the water column by diverting arginine, methionine and energy from growth, and releasing a stable high-nitrogen-content compound (Wyatt and Reguera, 1989; Wyatt, 1990). The main toxin of *C. polylepis* is obviously not generated by such a mechanism, since it does not contain any nitrogen (Yasumoto *et al.*, 1990). The greatly enhanced toxicity of *C. polylepis* in phosphorus-starved cells is nevertheless documented by experimental evidence (Edvardsen *et al.*, 1990; Carlsson *et al.*, 1990; Tobiesen, 1990), and stimulation of production of a nitrogen-free hemolysin by phosphorus-nutrient deficiency has been also reported with *Prymnesium parvum* (Shilo, 1971, in Edvardsen *et al.*, 1990). Ultimately, since discussing whether Wyatt's hypothesis is realistic and whether *C. polylepis* produces other toxic compounds (Yasumoto *et al.*, 1990) is beyond the scope of the present paper, we assume that limitation of algal growth by phosphorus promoted its toxin production and efficiency.

In oceanic waters, except the Mediterranean Sea (Berland *et al.*, 1980), nitrogen has often been reported to be the nutrient most limiting the potential algal growth (Ryther, 1954; Ryther and Dunstan, 1971). In the Baltic Sea area

and the Kattegat/Skagerrak, nitrogen is also generally found to be the most limiting nutrient (Skulberg, 1966; 1970; Gargas, 1975; Sakshaug and Mykkestad, 1973; Graneli *et al.*, 1986 *a*; Graneli, 1987). However, there is now evidence that phosphorus is limiting at least locally or during limited periods (Gargas *et al.*, 1978; Graneli, 1987; Graneli *et al.*, 1990). Some authors furthermore consider P to be the most limiting nutrient in general (Mykkestad and Sakshaug, 1983) or in areas such as the coastal North Sea (Veldhuis *et al.*, 1987; Bauerfeind *et al.*, 1990). In the Oslofjord, Paasche and Erga (1988) demonstrated that the first bloom in spring 1986 was limited by nitrogen, while phosphorus limitation was the rule in summer flagellate-dominated plankton. During the early phase of the 1988 *C. polylepis* bloom, nutrient analyses conducted in Skagerrak waters showed NO₃-N/PO₄-P ratios well above the Redfield value, thus indicating a shortage of phosphorus relative to nitrogen (Dahl, 1988). At the end of May 1988, the cell quotas of *C. polylepis* still reflected phosphorus deficiency (Brockmann and Dahl, 1990). Hence we assume that phosphorus limitation in the Kattegat and the Skagerrak waters during spring 1988 could have resulted from an increased nitrogen concentration due to high precipitation and runoff.

Whether excess of N over P might appear again in the Kattegat/Skagerrak and become a recurrent condition cannot be stated at present. However, it is likely that the European goal to reduce, by 1995, nutrient input from land sources to the half of the 1985 level (Anonymous, 1987) might have unexpected negative effects; since reducing phosphorus in waste water is easier than reducing nitrogen, coastal waters are likely to receive waste water with an increasing N/P ratio (Graneli *et al.*, 1990). In addition, although improvements in sewage treatment plants and agricultural practices will reduce river-transported nitrogen, the wastes produced by combustion sources and delivered by the atmosphere (25-33 % total input) continue to grow (Migon *et al.*, 1989; Huebert, 1990).

HOW WERE THE HIGHEST CELL DENSITIES GENERATED ? WHY DID THE BLOOM TERMINATE ?

Although many papers have appeared which describe the bloom, no set of time-series data covering the whole period from peak to disappearance is available (Table). In addition, the bloom affected a very large area and was perhaps generated separately to some extent in different areas, which led to different bloom stages at different points at any one time. Some results also pertain to areas where the dominance of *C. polylepis* was only relative, for instance in Western Norway, where coexisting species declined, but remained present (Johnsen and Lömsland, 1990). Any "typical" cause-and-effect schema has therefore to be rather hypothetical. There is evidence, however, that both high cell densities, 10⁷-10⁸ cells.l⁻¹, and disappearance of

Table

Summary of available informations: key events and time sequence. For *Chrysochromulina polylepis*: division rate (division.day⁻¹), maximum cell density (cell dens.; cells.l⁻¹), depth (m) of maximum cell density (depth max. cell.) and total number of cells in the water column (10⁹ cells.m⁻²). DIN = dissolved inorganic nitrogen; DON = dissolved organic nitrogen; Chla = chlorophyll a; Phaeo = phaeopigments.

Résumé des informations disponibles : événements clés et séquence temporelle. Critères descriptifs afférents à *Chrysochromulina polylepis*: taux de division (div.j⁻¹), densité cellulaire maximale (cellules.l⁻¹), profondeur (m) du maximum de densité cellulaire et nombre total de cellules dans la colonne d'eau (10⁹ cells.m⁻²). DIN = azote minéral dissous ; DON = azote organique dissous ; Chla = chlorophylle a ; Phaeo = phéopigments.

Time	January February		March		April				May							June			
			20	31	1	15	21	30	1	4	9	11	15	17	23	26	31	1	13
Environmental conditions	Rain and snow 15 % more than mean Winds 67 % above normal activity		Sun 70 % more than usual Winds below normal activity		Surface temperature 4°C higher than usual; absence of turbulence Stratified water column														
Nutrients	Heavy input of nitrogen from terrigenous origin				Si reservoir exhausted P limiting versus N				Much DIN + DON, little P, no Si available							Regenerated nutrients			
Co-occurring algae	Normal winter population		Diatom bloom (30 % biomass more than previous years)		<i>Skeletonema costatum</i> bloom				Sharp decrease of most species							Some algae flagellates resume growing including <i>S. costatum</i>			
<i>C. polylepis</i> Division rate (div. d ⁻¹)			?						0.80 → 0.25 → 0.17 → Nil							Decay → Bacterial attack			
Cell density (cell.l ⁻¹)			?						10 ⁶ → 10 ⁷ → 10 ⁷ → 10 ⁷ → patches							8 x 10 ⁷ → ?			
Depth (m) max. cell.									0-5 → 5-10 → 8-15 → 15-20 → ?										
Total cell (10 ⁹ cell. m ⁻²)			?						49 → 103 → 98 → 40-80 → ?										
Grazers	Normal activity				Avoid <i>C. polylepis</i> feed on other algae				Reduction of grazing as a whole							No grazing, then grazer death → End of toxicity			
Comment					<i>C. polylepis</i> toxin acting as a grazer repellent				Direct allalopathic effect First fish deaths							Heavy losses in the whole biota Rate of sedimentation of POC twice as such as usual Chl a/Phaeo = 0.3-1.3			

the bloom resulted from three main ecophysiological processes acting while environmental conditions remained essentially unchanged. There is in fact no paper which mentions that the stratification of the water column had been disrupted when competitive species resumed growth. On the contrary, Horstmann and Jochem (1990) and Nielsen *et al.* (1990) report that between 30 May and 16 June there was a pronounced pycnocline at several different stations in the Kattegat. Significant input of inorganic nutrients which could have supported growth of "r" species was also not reported, and furthermore 2/3 of the growth of *C. polylepis* from 10 May to 2 June was supported by regenerated nutrients (Lindahl, 1988). In other words, the cause of the bloom decline is to be found in *Chrysochromulina polylepis* itself.

As pointed out above, *C. polylepis* cells presumably divided at nearly maximum rates (0.8 div. d⁻¹) up to densities

at which fish deaths appeared, a few million cells per litre. Then, prior to the peak in cell density, the increase was slow (0.17 div. d⁻¹), and finally division stopped. Meanwhile, the layer of maximum algal biomass deepened from 0-5 m to 15-20 m, and cell densities in concentrated layers increased by one order of magnitude. From information given by Lindahl and Dahl (1990) and related papers, it also appears that peak concentrations of *C. polylepis* cells were recorded when total number of cells in the water column had remained constant or even had decreased significantly. Based on this information the following sequence and timing of events (Table) are likely to pertain to at least the area of Skagerrak near Gullmar fjord.

Stage 1 (from late April to about 11 May)

Growth was rapid (0.80 div. d⁻¹) and led to densities in the range of a few 10⁶ cells.l⁻¹. Cells were distributed in the

surface waters (0-5 m), and the number of co-occurring species decreased sharply.

Stage 2 (from 11 May to about 15 May)

Growth slowed down (mean rate = 0.25 div. d⁻¹), leading to maximum concentrations close to 10⁷ cells.l⁻¹. The total number of cells in the water column rose slightly (from 49 to 103.10⁹ cells.m⁻² in four days), and cells began to concentrate in deeper water. *Gyrodinium aureolum* was the only co-occurring alga.

Stage 3 (from 15 May to about 23 May)

The growth rate was zero or very low (0.17 div. d⁻¹). Cell densities showed maximal values (several 10⁷ cells.l⁻¹). Total number of cells in the water column nevertheless remained unchanged (98.10⁹ cells.m⁻²), and cell distribution was patchy both horizontally and vertically, with maximum densities between 5 and 10 m (Fig. 7). However, the rate of primary production showed the highest values at 2-4 m, and photosynthetic activity (¹⁴C uptake) was virtually absent below 8 m. The Secchi depth was 5 m. No other algal species coexisted with *C. polylepis*.

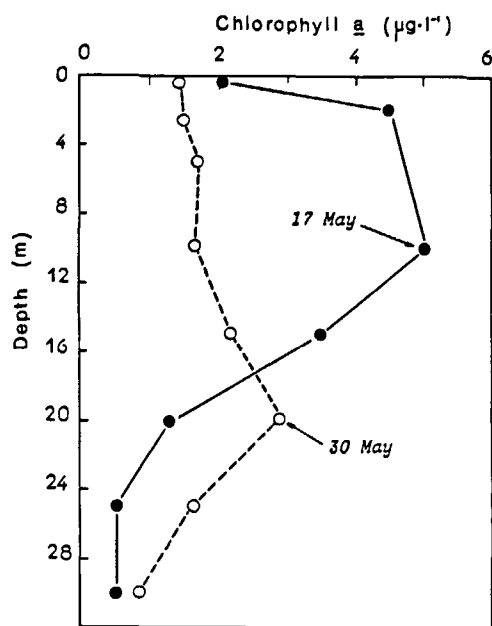


Figure 7

Chlorophyll *a* vertical distribution at Alsbäck station (Skagerrak, Gullmar Fjorden) on 17 May (peak of *C. polylepis* bloom) to 30 May (late stage of *C. polylepis* bloom). Unpublished data from courtesy of Odd Lindahl.

Distribution, en fonction de la profondeur, de la teneur en chlorophylle *a* à Alsbäck station (Skagerrak, Gullmar Fjorden), le 17 mai (pic de l'efflorescence à *C. polylepis*) et le 30 mai (stade tardif de l'efflorescence). Données non publiées aimablement communiquées par Odd Lindahl.

Stage 4 (from 24 May to 13 June ; no subsequent data available)

No further growth occurred. On the contrary, a significant number of cells probably died and lysed, the total number of cells present in the water column ranging between 40.10⁹ and 80.10⁹ cells.m⁻²; elsewhere, a significant concentration of dissolved organic nitrogen was reported in late May (10-15 µM in the 0-7 m upper layer, and 7-10 µM below; Brockmann and Dahl, 1990). Nevertheless, cell densities up to 80.10⁶ cells.l⁻¹ were reported in a thin layer close to the pycnocline, between 15 and 20 m (Fig. 8; Dahl *et al.*, 1989). During this period, the rate of sedimentation of particulate organic carbon was twice the mean value for previous years (Lindahl, 1988 *b*). Another flagellate, whose taxonomic position has not been stated, was reported to become gradually more abundant. Elsewhere, bacteria were seen overgrowing *C. polylepis* (Nielsen *et al.*, 1990).

It is likely that, while free from losses due to grazing, the *Chrysochromulina polylepis* aged progressively, as evidenced by a marked increase in the ratio of phaeopigments to chlorophyll *a*, which increased sharply from 0.3 on 26 May to 1.3 on 1 June (Johnsen and Lømsland, 1990). In the area they studied, in western Norway, collapse of the bloom reduced the standing stock by 93 % in 34 hours, even though hydrological conditions were ascertained to be of minor importance.

High sinking rates often occur during and after blooms (Lännergren, 1979), and it has been demonstrated that nutrient-replete cells of some dinoflagellates are positively buoyant, while nutrient-depleted ones are neutrally or negatively buoyant (Kahn and Swift, 1978). Furthermore, Bienfang (1981) showed that the sinking rate of *Cricosphaera carterae*, an alga belonging to the same class as *C. polylepis*, increases with age in phosphate-limited cultures. Hence sinking of actively growing cells may be interpreted in general as resulting from adaptations to a change in nutritional conditions: when the nutrient reservoir in the upper layers becomes exhausted, sinking allows the algae to reach deeper waters richer in nutrients. Such behaviour was certainly not that of the *C. polylepis* cells, because they continuously sank from the peak period to the collapse (Fig. 8; Table). Their behaviour corresponds to findings of Smayda and Boleyn (1965), Eppley *et al.* (1967) and Smayda (1970) who demonstrated that senescent cells usually sink faster than actively growing ones.

From this trend of observations concerning of *C. polylepis*, and from similar features reported by Nielsen *et al.* (1990), we assume that cells of stage 1 were buoyant and that they experienced nutrient sufficiency and high light : they thus remained in the upper part of the water column. From stage 2, due to the marked increase in cell density, up to about 10⁷ cells.l⁻¹, two unfavourable processes were established : exhaustion of nutrients and self-shading. Whether self-poisoning also took place is still not known, but appears possible, since this occurs in blooms of other algae

(Bardour and Gergis, 1965; Pincemin, 1971; Opute, 1974). Suffering from severe nutrient limitation, the cells began sinking. During stage 3, no growth whatsoever occurred, and the cells continued to sink and accumulate in patchy stains, reaching a layer where no photosynthesis could occur because of insufficient light. At the end of May, a significant part of the population had died, so cell leakage would have increased levels of dissolved organic material. Clearance of water in the upper layer together with regenerated nutrients now allowed growth of other algae (flagellates and some diatoms, mainly *Skeletonema costatum*, Dahl *et al.*, 1989) to resume. The remaining *C. polylepis* cells sedimented to the top of the pycnocline (roughly 15 m according to figures in Lindahl, 1988), and met a density barrier that delayed further sinking. Cells therefore became concentrated here and gave the highest reported cell densities. No survey was made of the later fate of these cells (the deepest sediment traps were installed at only 20 m), but on the basis of growing evidence that a significant part of the particulate matter sinks in most blooms (Skjoldal and Wassmann, 1986; Zeitzschel, 1986), we assume that those cells which did not disrupt sedimented. From this scenario, which is in agreement with the one formulated by Nielsen *et al.* (1990), the evidence suggests that the *Chrysochromulina polylepis* bloom had to end because of lack of grazing: if a significant part of dividing cells had been continuously eliminated, the population would not have become senescent and thus would have remained in the euphotic layer. In other words, this alga has created a new unbalanced environment, and finally could not live in it.

CONCLUSION

The most extensive noxious algal bloom ever recorded, that of *Chrysochromulina polylepis* in 1988, did not result from hitherto unknown mechanisms allowing the species to better acquire nutrients and/or avoid cell losses. The causes were due to ecophysiological processes already understood, and are consistent with the theory of Tett (1987). The bloom was probably caused by an exceptional sequence, coupling physiological capabilities with the environmental conditions needed to activate them. To what extent long-term global changes, including eutrophication, might have contributed to these exceptional processes is still unclear. An unbalanced N/P loading ratio, however, may have upset the normal ecosystem equilibria in the marine coastal system, thus allowing *C. polylepis* to use a previously unknown physiological weapon.

Acknowledgements

We warmly thank Dr. Odd Lindahl (Kristinebergs Marinbiological Station) and Dr. Maria Vernet (Scripps Institution of Oceanography) for providing useful unpublished data, Prof. Eystein Paasche (University of Oslo) and

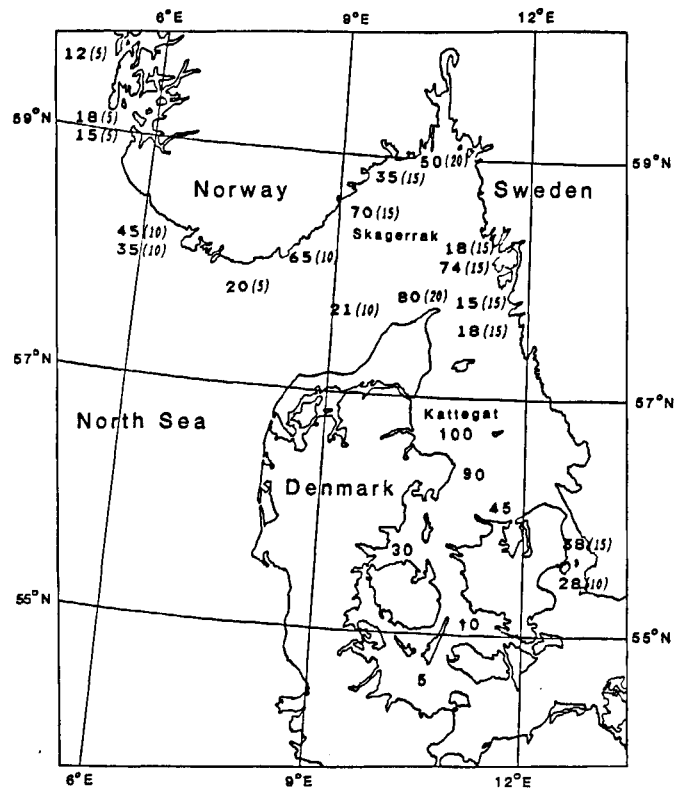


Figure 8

Maximum cell density of *Chrysochromulina polylepis* (10^6 cells.l⁻¹) in the Kattegat and the Skagerrak; numbers within parentheses indicate respective depths (m) at which the values were recorded. Redrawn from Berge *et al.* (1988), Nielsen (1989), Nielsen and Richardson (1990) and Bokn *et al.* (1990).

Densités cellulaires maximales (10^6 cells.l⁻¹) de *Chrysochromulina polylepis* dans le Kattegat et le Skagerrak; les nombres entre parenthèses indiquent les profondeurs (m) auxquelles ont trait les valeurs mentionnées. Reconstitué d'après Berge *et al.* (1988), Nielsen (1989), Nielsen et Richardson (1990) et Bokn *et al.* (1990).

three unknown referees for helpful comments, Dr. Ian Jenkisson (ACRO, La Roche Canillac) for improving the English version, and Mrs. Evelyne Travers (L'Houmeau) for typing and correcting the manuscript. The financial help of the "Programme national Efflorescences algales marines" is also greatly acknowledged.

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