LA FLORAISON D'ALGUES TOXIQUES

DE BLOEI VAN GIFTIGE ALGEN

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Mededeling / Communication :

'Phaeocystis Blooms and Nutrient Enrichment in the Continental Coastal Zones of the North Sea'

(Ambio, Vol. 16, n° 1, 1987, pp. 38-46, Royal Swedish Academy of Science)

Studie- en Beleidsdag

DE NOORDZEE :

EEN ZEE VOOR HET LEVEN

Oostende, 20 mei 1989

Journée d'étude scientifique et politique

LA MER DU NORD :

UNE MER POUR LA VIE

Ostende, le 20 mai 1989

(Mededeling : Phaeocystis Blooms and Nutrient Enrichment in the Continental Coastal Zones of the North Sea' - Abstract)

Het voorkomen van algenbloei van het planktonisch wier Phaeocystis pouchetii in de continentale kustzones van de Noordzee is de laatste twintig jaar steeds frequenter vastgesteld. Dit is vermoedelijk het gevolg van een aanrijking aan voedingsstoffen door de aanvoer van rivieren. De specifieke fysiologie van dit kolonievormende wier beïnvloedt grondig de struktuur en de werking van het kustecosysteem. Vanwege de vorming van volumineuze schuimbanken die op de kust samenhopen, is deze algenbloei eveneens een grote hinder geworden.

(Communication : Phaeocystis Blooms and Nutrient Enrichment in the Continental Coastal Zones of the North Sea' - Abstract)

Des efflorescences de l'algue planctonique Phaeocystis pouchetii dans les régions côtières continentales de la mer du Nord ont été observées de plus en plus fréquemment et de manière de plus en plus intense au cours de ces vingt dernières années, et résultent probablement de l'enrichissement en nutriments causé par les apports fluviaux. La physiologie particulière de ce flagellé colonial influence profondément la structure et le fonctionnement de l'écosystème côtier. Cette algue constitue une nuisance importante principalement parce qu'elle provoque le développement de couches massives de mousse qui s'accumulent sur les rivages.

Phaeocystis Blooms and Nutrient Enrichment in the Continental Coastal Zones of the North Sea

Article

By Christiane Lancelot, Gilles Billen, Alain Sournia, Thomas Weisse, Franciscus Colijn, Marcel J.W. Veldhuis, Anthony Davies and Paul Wassman

Blooms of the planktonic alga *Phaeocystis pouchetii* in the continental coastal zones of the North Sea have been observed to occur more and more frequently and intensively over the past twenty years, probably as a result of nutrient enrichment from river discharge. The peculiar physiology of this colony-forming flagellate strongly influences the structure and function of the coastal ecosystem. It is a major nuisance alga mainly because it can lead to the development of massive foam banks which accumulate near shore.

At certain times, generally during the second half of June, beaches of the Dutch and German coasts of the North Sea are covered with a layer, up to 2 m thick, of slimy light foam resembling the beaten white of eggs (Figure 1). This foam is not the result of an accidental discharge of detergents; it is simply the most spectacular of several consequences of the proliferation in coastal waters of a photosynthetic microorganism: *Phaeocystis cf. pouchetii*.

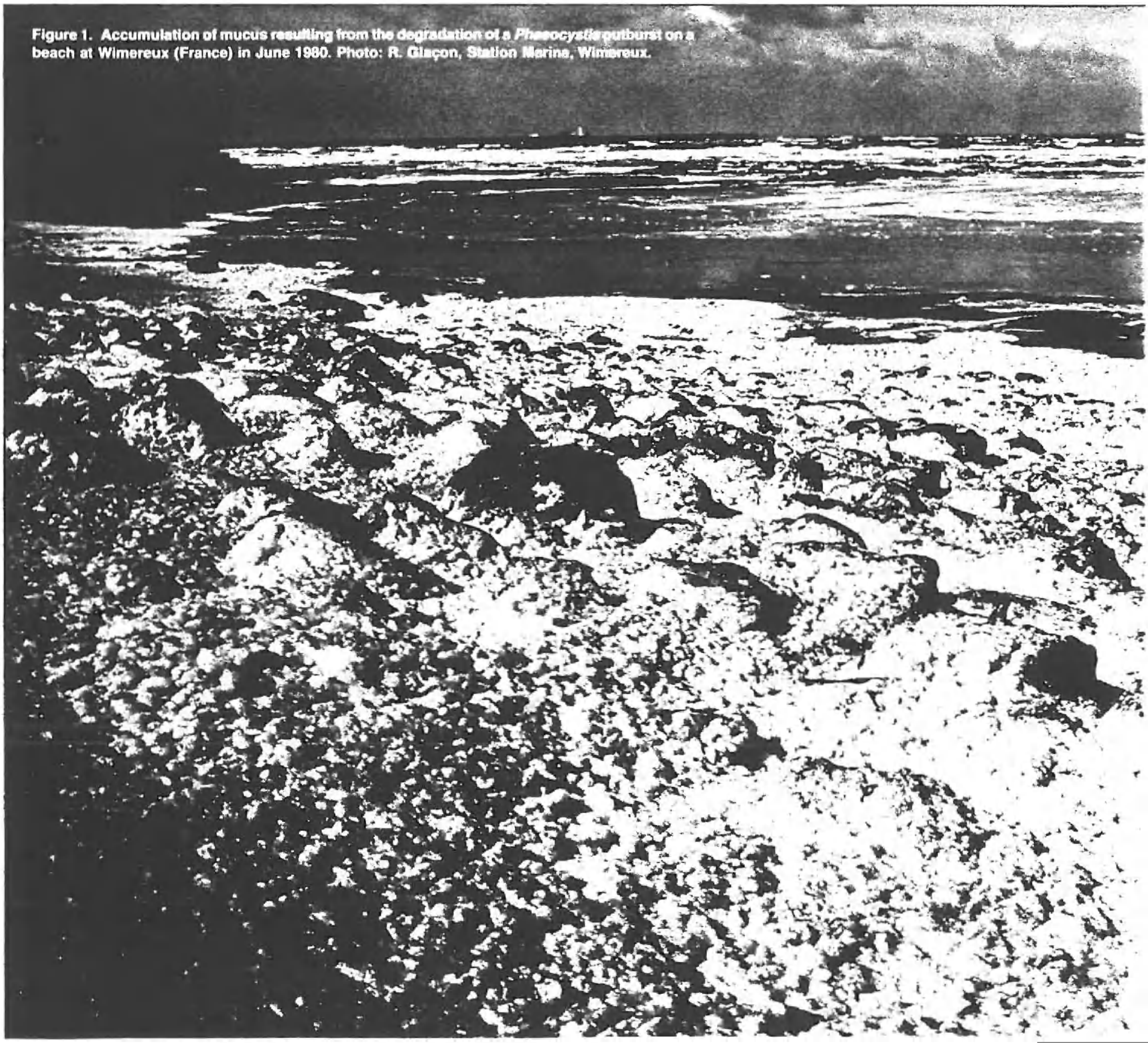


Figure 1. Accumulation of mucus resulting from the degradation of a *Phaeocystis* outburst on a beach at Wimereux (France) in June 1980. Photo: R. Glaçon, Station Marine, Wimereux.

Figure 2a. Map showing major rivers discharging into the Channel and the Southern Bight of the North Sea and the population of their watershed. The general residual circulation of the seawater masses is also shown.

Phaeocystis is one of the numerous genera which compose the marine phytoplankton, i.e. that community of unicellular algae, drifting in the water masses, that are responsible, due to their photosynthesis, for most of the biological production at the first level of the food chain in the seas. Compared to other phytoplankton organisms, *Phaeocystis* exhibits several peculiarities which cause it to alter significantly the working of coastal marine ecosystems.

Phaeocystis proliferation is not a recent phenomenon. Furthermore, it is not restricted to the coastal zones of the North Sea. Nevertheless, the increasing pressure of human activities on these coastal areas has almost certainly led to the recently observed increase in intensity and duration of *Phaeocystis* blooms in the Southern Bight of the North Sea. In particular, the anthropogenic discharge of nutrients (i.e. those inorganic compounds of nitrogen, phosphorus and silica which normally represent the limiting factors of phytoplankton growth) into coastal ecosystems may enhance, sometimes with negative results, certain features that normally distinguish shallow nearshore systems from offshore zones.

A group of European and North American scientists (who called themselves the "*Phaeocystis* Club"!) met at Texel (The Netherlands) on the 19–21st of March 1986 to take stock of available information on the behavior of *Phaeocystis* in coastal ecosystems and its disquieting increase, in particular along the continental European coast of the North Sea. This paper is a summary of the material discussed at the Texel meeting (1). It will address the difficult questions of why *Phaeocystis* blooms occur and what the consequences are. The answers to these questions are not yet fully known. Some elements, however, will emerge from consideration of three subjects:

(i) the general enrichment of coastal zones by the discharge from rivers;

(ii) the ecological characteristics of coastal ecosystems, some characteristics being reinforced by increased river discharges;

(iii) the peculiar physiology of *Phaeocystis* which makes it particularly adapted to growth in enriched coastal systems.

These three aspects will be discussed separately. We will first discuss why the continental coast of the North Sea, from the Straits of Dover to the German Bight, is particularly subject to nutrient enrichment. A basic discussion of the structure and function of coastal ecosystems will show us that the main effect of nutrient enrichment will be to enhance temporary explosive blooms of phytoplankton. Under these circumstances some phyto-

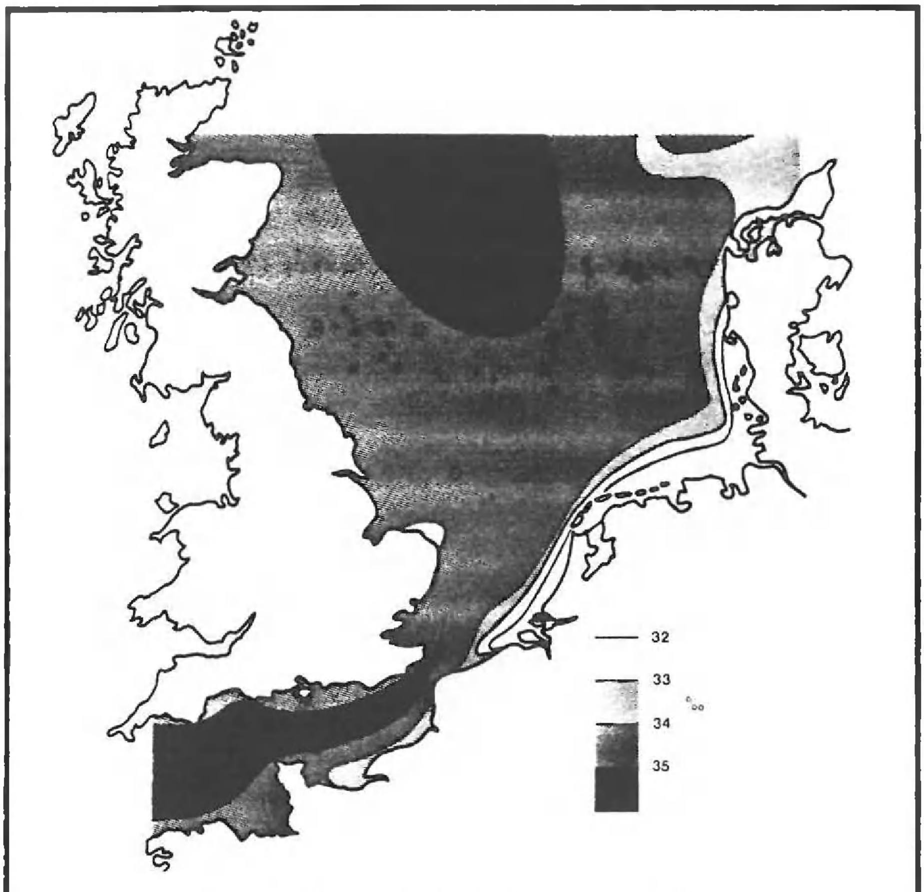


Figure 2b. Mean distribution of salinity (‰) in the Channel and the Southern Bight of the North Sea.

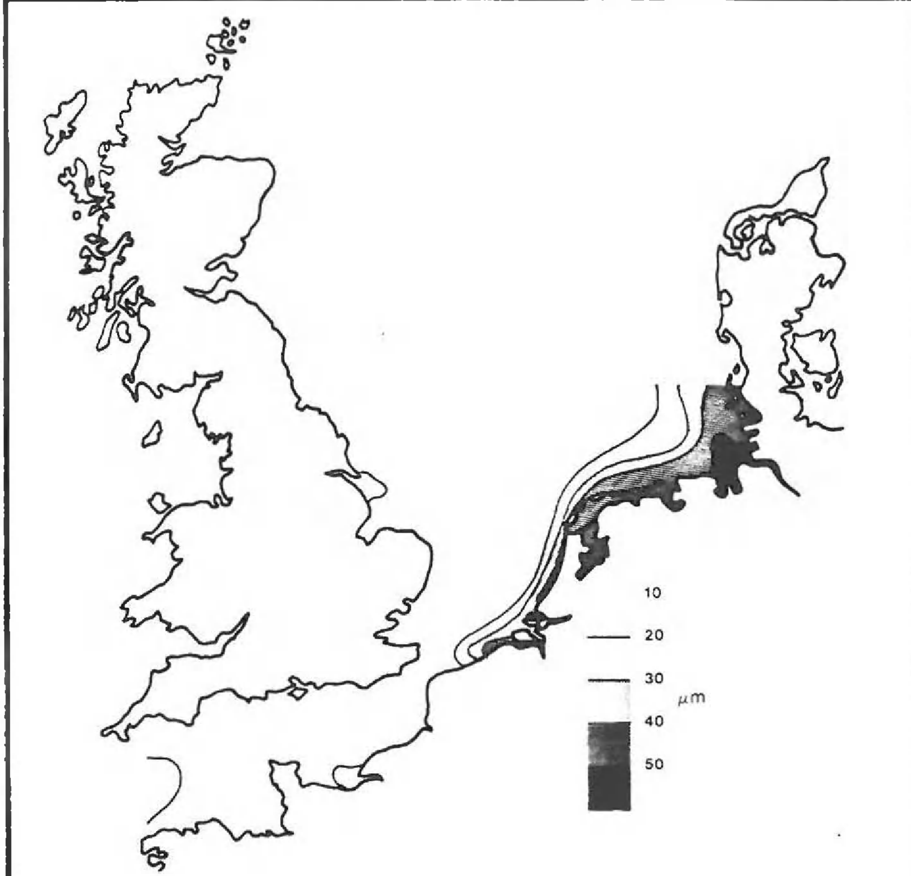


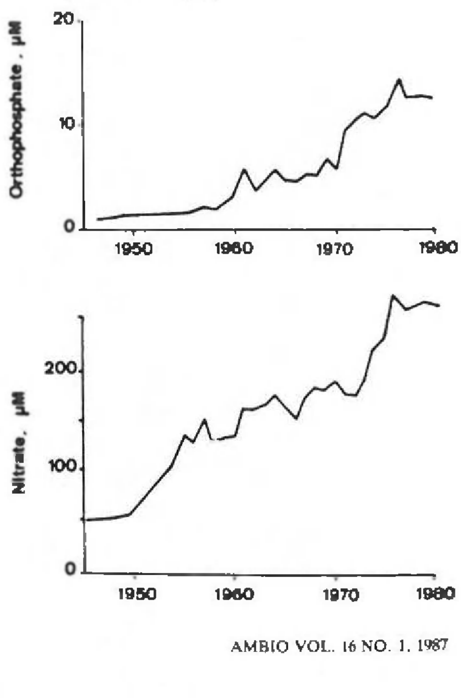
Figure 2c. Mean distribution of winter nitrate concentration in the Channel and the Southern Bight of the North Sea.

plankton species will dominate more than others. A summary of what is known on the peculiar physiology of *Phaeocystis* will help us to understand why this species often entirely overwhelms other species during blooms, and the consequences of its proliferation on the overall working of the ecosystem. Lastly, the question of the possible control of *Phaeocystis* blooms will be briefly considered.

INCREASED TERRESTRIAL NUTRIENT INPUTS

The continental coastal zone of the southern North Sea receives discharge from several major estuaries. Their catchment areas cover one of the most densely populated and industrialized regions in the world. The mean residual circulation of the water masses in this region is directed to the northeast, along the coast. Oligotrophic Atlantic water, with a high salinity and a low nutrient content, enters the English Channel and flows through the Straits of Dover into the North Sea at a mean rate of 0.15 $km^3 s^{-1}$ (Figure 2a) (2). In this way the effects of the successive major rivers discharging into the North Sea (the Seine, Somme, Yser, Scheldt, Rhine, Ems,

Figure 3. Orthophosphate and nitrate concentration in the River Rhine at Lobith (German-Dutch border) since 1950 (24).



Weser and Elbe) are cumulative. Thus, the salinity decreases gradually from 35 g L^{-1} in the Western Channel to 30–32 g L^{-1} in the northern part of the continental coastal zone of the Southern Bight (Figure 2b). Note, in addition, that active tidal currents ensure a complete mixing of the water column, so that no stratification occurs in the coastal regions where the depth is less than 30 m.

The present nutrient load of the major rivers discharging into the continental coastal zones of the Channel and the North Sea is summarized in Table 1. Together these inputs represent more than the import of nutrients from the Atlantic, and considerably affect the concentration of these elements in the Southern Bight. This is clearly seen during winter when nitrate concentrations reach their maxima due to reduced uptake by phytoplankton (Figure 2c).

The amounts of nutrients discharged by rivers have increased considerably during the last 20 years. This is illustrated in an example from the Rhine in Figure 3. This trend obviously reflects the increasing discharges by domestic, industrial and agricultural activities; growing use of polyphosphates in detergents; growth of industrial sectors like basic chemistry and food processing industries; application of increasing amounts of fertilizers on agricultural soils; intensification of cattle farming, and so on.

In agreement with this observed trend a general rise in winter nutrient levels has been monitored in coastal waters: observations performed since the 1960s at Helgoland in the German Bight show an increase in winter nitrate and phosphate concentrations by factors of 4 and 1.5, respectively (3). Data from the Dutch coastal zone show similar trends (4, 5).

DYNAMICS OF ENRICHED COASTAL ECOSYSTEMS

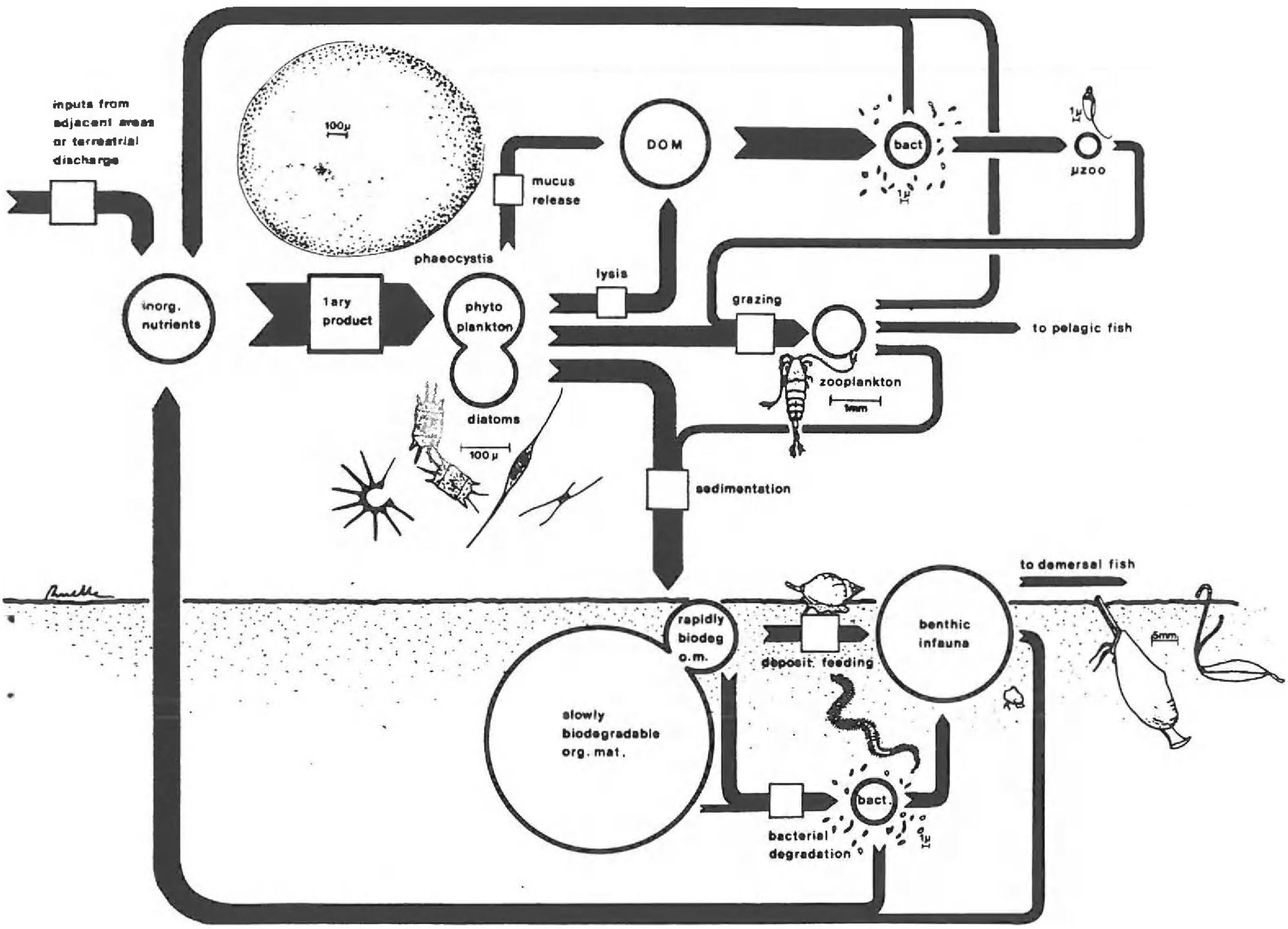
In the preceding paragraph winter nutrient levels have been taken as an index of coastal water enrichment. This index, however, does not entirely reflect the dynamic nature of the marine ecosystem, which is the seat of a rapid circulation of elements between several abiotic and biotic compartments. A schematic picture of this circulation at the first trophic levels of the food chain in an unstratified coastal marine ecosystem is presented in Figure 4.

Uptake of nutrients is an essential process for phytoplankton growth. Part of the

Table 1. Freshwater and nutrient inputs from the major rivers discharging into the continental coastal zone of the North Sea and the Channel. (Data communicated at the Consultation meeting on Nutrients in the Eastern and Southern North Sea, Skagerak and Kattegat under art. 9 of the Paris Convention (Copenhagen, 26–29 November 1985).)

River	Mean freshwater discharge $m^3\ sec^{-1}$	SiO_2	N	P
		10^3 t yr^{-1}		
Seine	440		90	
Somme	60		12	
Yser	5		4	
Scheldt	105	42	35	2.2
Rhine	2,500	410	408	50
Lake Ijssel	600		66	4
Ems	120		42	3
Weser	500		42	8.5
Elbe	1,150		250	14

Figure 4. Schematic representation of the dominant fluxes of nutrient elements through the first trophic levels of the food-web of a coastal ecosystem. (DOM = dissolved organic matter.)



phytoplankton produced may be grazed by zooplankton, initiating the food web that finally leads to fish. A characteristic feature of North Sea coastal ecosystems, however, is the limited role of zooplankton in consuming primary production, particularly in spring, when phytoplankton production is at its highest (6, 7). Most of the phytoplankton lyses or settles. Lysis produces dissolved organic matter used by planktonic bacteria whose development closely follows phytoplankton growth and is responsible for a rapid remineralization of nutrients. Most of the phytoplanktonic material deposited on the sediments is also rapidly degraded or eaten by deposit-feeders. However, part of it is more refractory and accumulates in the benthos where it forms a very large stock. The slow biodegradation of this stock is responsible for a continuous input of nutrients back to the water column (8, 9).

Nutrient levels are highest in late winter, because uptake by phytoplankton is at its lowest due to low solar radiation and temperature, while mineralization continues to some extent during the winter. The onset of phytoplankton development in early spring corresponds to the moment when available light is high enough to allow the growth rate to match losses by sinking and mortality. When this is the case a rapid growth of phytoplankton occurs, up to the point where the required nutrients are exhausted. From that moment, and during the whole summer, growth of phytoplankton is controlled by the rate of nutrient remineralization or supply from external sources. A steady and generally lower biomass level results during the whole period from June to October.

This seasonal pattern of phytoplankton biomass is observed in the available data from the coastal zones of the Channel and the North Sea (Figure 5). The river inputs of nutrients, the effects of which are cumulated from the Channel to the German Bight, result both in a higher and longer lasting phytoplankton spring bloom and a higher biomass during the summer steady state, as clearly shown in Figure 5. These general trends can be adequately simulated by a very simple mathematical model of the dynamics of the first levels of the trophic web, taking into account the seasonal variations of light and temperature, the residual circulation of the water masses and the amounts of nutrients discharged by the major rivers (Figure 5) (8, 9).

What are the effects of the enhanced primary production clearly shown in Figure 5? Does it simply provide more food for the herbivorous zooplankton and hence contribute to higher fish yields? Unfortunately, the reality seems much more complex.

First of all it must be stressed that, as is apparent from Figure 5, enrichment mostly results in increasing short-lived, explosive blooms of phytoplankton. We already saw that the decline of these blooms in the North Sea is generally not caused by significant zooplankton grazing, but the phytoplankton is decomposed by planktonic bacteria or deposited on the sediments. In some areas, with a partially or temporarily stratified water column, as for example in the German Bight and the western coast of Denmark, the sudden deposition of organic material can result in severe oxygen depletion of the bottom waters, leading to fish and shellfish mortality. Such events were already observed at the beginning of the century (10), but seem to be occurring more and more frequently during recent years. Again, the recent man-made enrichment is reinforcing a natural tendency.

DYNAMICS OF *PHAEOCYSTIS* BLOOMS

In order to discuss the effects of nutrient enrichment on the coastal zones more qualitative information is required, both on the nutrients discharged by the rivers and on the phytoplankton composition.

An important distinction must be made within the phytoplankton between diatoms, which are characterized by the presence of a siliceous frustule, and other algae, mainly represented by flagellates. The former require silica as an essential nutrient, the latter do not. The terrestrial input of silica, which mostly originates in river water from the dissolution of rocks and soil minerals, remained essentially constant during the time nitrogen and phosphorus inputs were increasing considerably. As a consequence, growth of flagellates is now favored while that of diatoms is rapidly becoming limited by silicate deficiency. Thus, observations made in Helgoland clearly show a long-term increase in biomass of flagellates while there is no such trend for diatoms (3).

Phaeocystis is one among the numerous genera composing the flagellates. Consideration of the peculiarities of its life cycle and physiology can explain its frequent dominance over other flagellates in the spring and its influence upon the working of the ecosystem. *Phaeocystis* may appear in two different forms. One is a motile stage, 3–10 μm in size, with two flagella and one flagellum-like appendage (haptonema), two chloroplasts, a unique thread-like material up to 50 μm long, and a coverage of minute organic scales (Figure 6). The other form consists of colonies of cells (devoid of flagella and scales) in a common gelatinous matrix. As colonies may reach several millimeters in diameter, they can be seen with the naked eye (Figure 7).

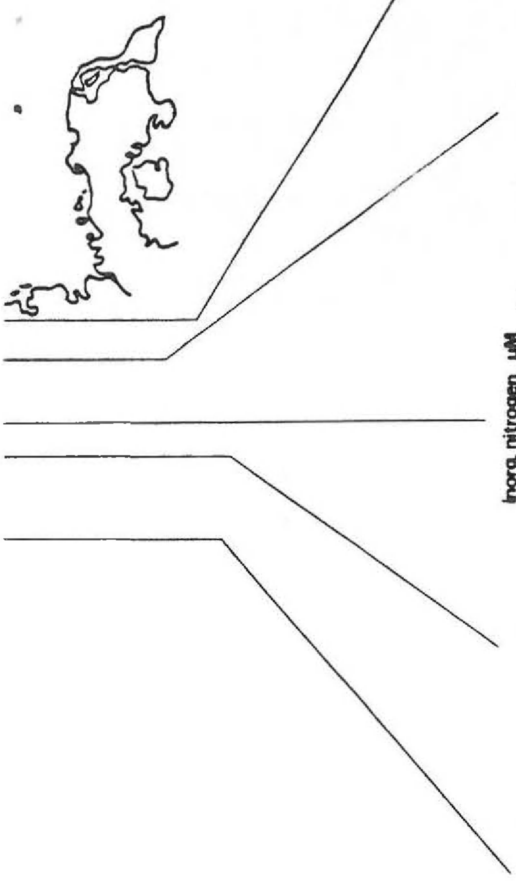
The colonies offer an interesting example of a biological entity in which the separate cells, growing and dividing inside the mucous matrix, lose part of their individuality. Therefore, this organism can be considered as intermediate, between unicellular and multicellular algae. This in itself warrants scientific interest.

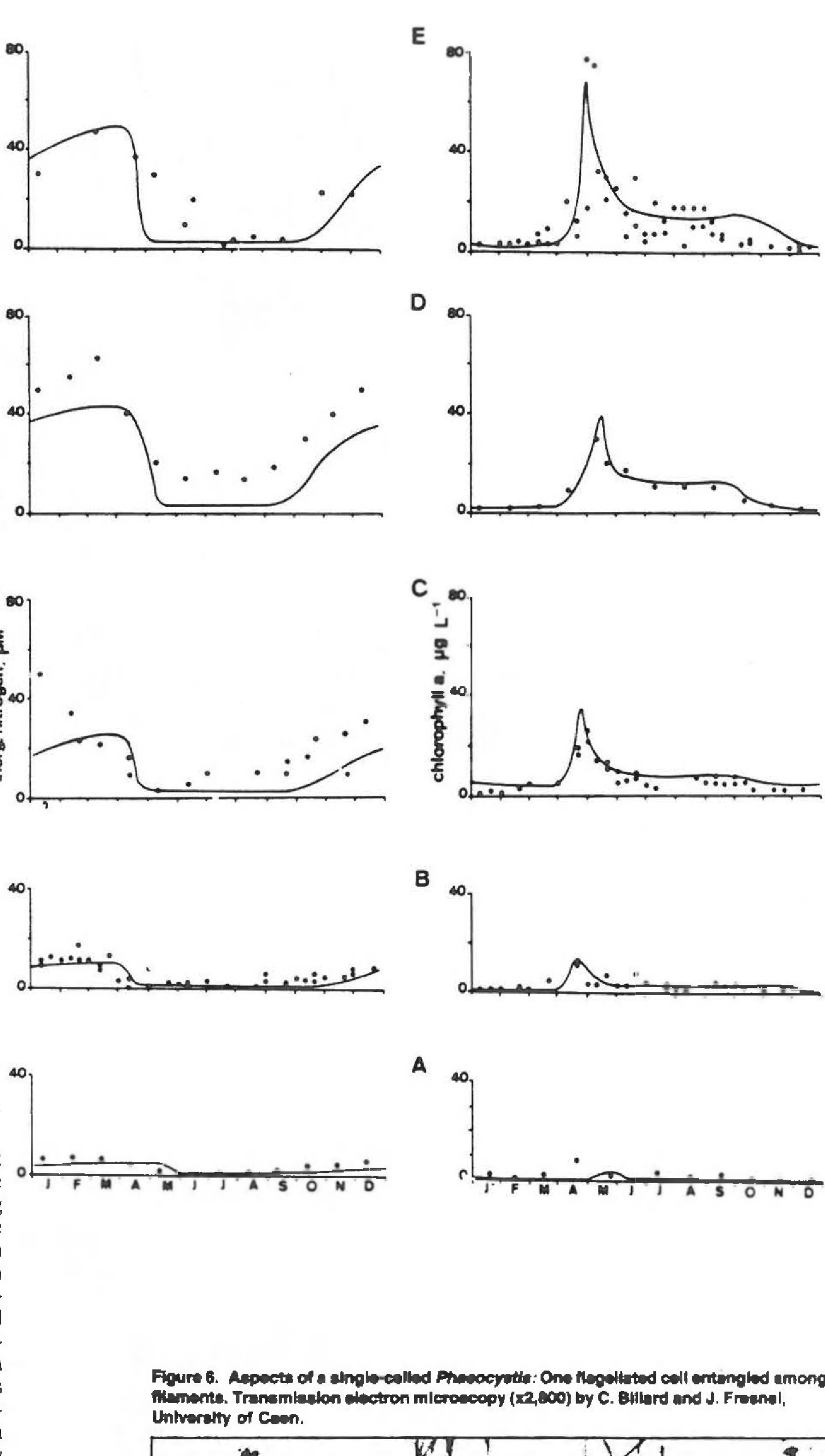
When receiving light, the cells actively secrete the mucus which constitutes the envelope of the colony. Mucus secretion can represent more than 50 percent of the carbon fixed by *Phaeocystis* (11). Apart from its structural role this mucus seems to play important physiological roles. It has been demonstrated that the polysaccharides composing the mucus, constitute an energetic substrate that is catabolized by the cells during the dark period to meet their energetic and biosynthetic requirements (12). This mechanism enables the algae to continue growing during the night without the need to accumulate large energy reserves inside their cells. There is also evidence which suggests that the mucous matrix may act as a reservoir for phosphorus, providing the cells with the possibility of further growth after phosphate exhaustion in the surrounding medium (13).

Figure 5. Seasonal variations in nitrate concentration (μM) and phytoplankton biomass (μg chlorophyll a L^{-1}) in different stations from the Western Channel to the Wadden Sea area. The points refer to observations gathered from different sources (25–29). The curves are the re-

In the light of these recent findings, colony formation by *Phaeocystis* appears to be quite an efficient strategy in response to the reduction of nutrient concentrations, which occurs in late spring. Indeed, it is in the colonial form that *Phaeocystis* proliferates in large abundance, generally after the diatoms have initiated the process of nutrient depletion. Moreover, when *Phaeocystis* blooms occur this species often entirely dominates the phytoplankton community, as is regularly observed in the coastal zones of the Southern Bight from mid-April to the end of May.

During these periods, the peculiar physiology of *Phaeocystis* colonies strongly influences the working of the whole marine ecosystem. First of all, the large size of *Phaeocystis* colonies prevents them from being grazed by most of the zooplankton species and stages present at that time of sults of a simulation using a simplified model (8, 9) taking into account the control by light and temperature on the basic ecological processes, the hydrodynamics of the coastal areas and the discharge of nutrients by rivers.





the year. *Temora longicornis* is the most important zooplankton species in the Southern Bight of the North Sea during the spring bloom of *Phaeocystis*. These zooplankton species thrive much better on diatoms (14). However, it has been proven that *Phaeocystis* flagellates and medium-sized colonies could be efficiently grazed by various zooplankton species (summarized in (1)). The extent to which a complete *Phaeocystis* bloom is used as food by zooplankton and benthic organisms is still an open question. Moreover, a major part of primary production by *Phaeocystis* blooms is in the form of mucilagenous material. Little is known of the exact structure of this mucus. Its nitrogen content seems to be rather low. For this reason this mucilagenous material is probably not degraded as rapidly by bacteria as is cellular material that is much richer in nitrogen. Consequently, at the end of the bloom, *Phaeocystis* mucus often transiently accumulates in large concentrations in the dissolved form (15, 16). The polymeric structure of the mucus makes it subject to foaming. During storms a large amount of foam can be formed on the surface of the sea. During onshore winds, a 1–2-meter thick, gluey layer of light

Figure 6. Aspects of a single-celled *Phaeocystis*: One flagellated cell entangled among filaments. Transmission electron microscopy (x2,800) by C. Billard and J. Fresnel, University of Caen.

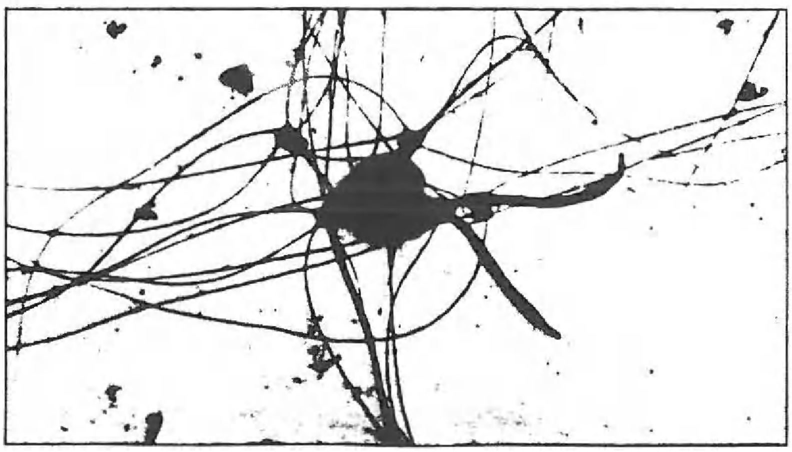
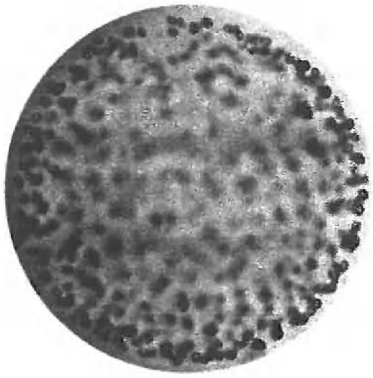
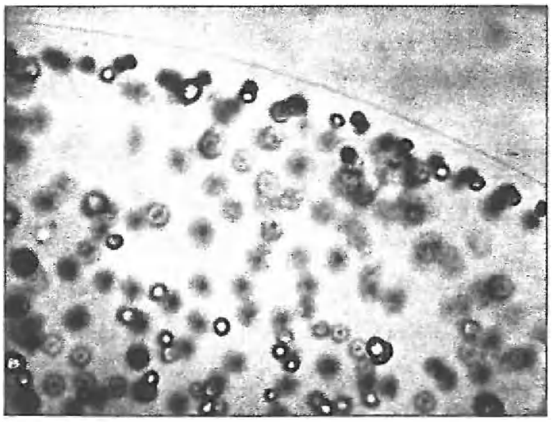


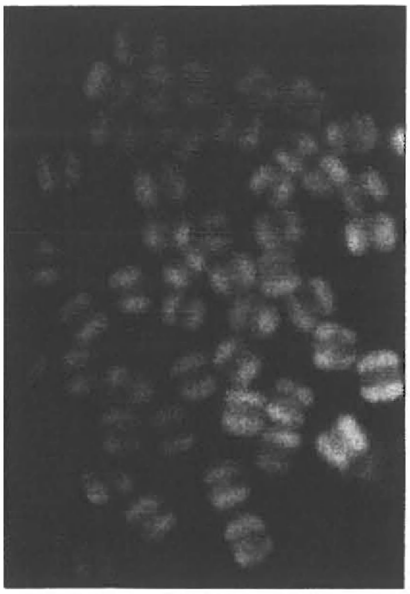
Figure 7. Aspects of colonial *Phaeocystis*: Different views under the light microscope.



a. An entire globular colony (diameter 1.5 mm).



b. Details of the colony; size of an individual cell (ca. 5 μm).



c. Still higher magnification under epi-florescence, showing the red florescence of chlorophyll. Photos: (a), C. Billard and J. Fresnel, University of Caen. (b, c), Department of Marine Botany, University of Groningen.

brownish slime can accumulate on the beaches causing a great nuisance for recreational activities (Figure 8).

Whether the mucus is degraded by bacteria in the water column, washed ashore in the form of foam, or deposited on the sediments, a large part of the primary production by *Phaeocystis* may escape the pelagic food web. Therefore, and because of the short time periods over which *Phaeocystis* blooms typically last, nutrient enrichment of the coastal ecosystem does not result in a significantly increased fish yield.

Phaeocystis blooms not only alter the marine environment, but may also have an impact on the atmosphere. Indeed, these organisms actively produce reduced sulfur compounds—among which dimethylsulfide (DMS) is the most important—which are emitted into the atmosphere (17–19). On a global basis, emission of sulfur from the ocean to the atmosphere equals approximately that from industrial sources (about $65 \cdot 10^{12}$g $S \cdot yr^{-1}$) (17–19). This production of DMS is restricted to only a few phytoplanktonic species (Prymnesiophytes and dinoflagellates). Large blooms of *Phaeocystis* may thus contribute significantly, both locally and globally, to the acidity of rainwater.

RECENT EXTENSION OF *PHAEOCYSTIS* BLOOMS

The blooming of *Phaeocystis* is obviously not a recent phenomenon. Discoloration of the sea surface, characteristic of these blooms, and clogging of fishing nets caused by colonies have long been noticed by fishermen, and colloquial terms like "weedy water," "baccy juice" or "stinking waters" have been used to describe these

Figure 8. Accumulation of *Phaeocystis* mucus on a Netherlands beach in June 1986. Photo: M. Veldhuis.

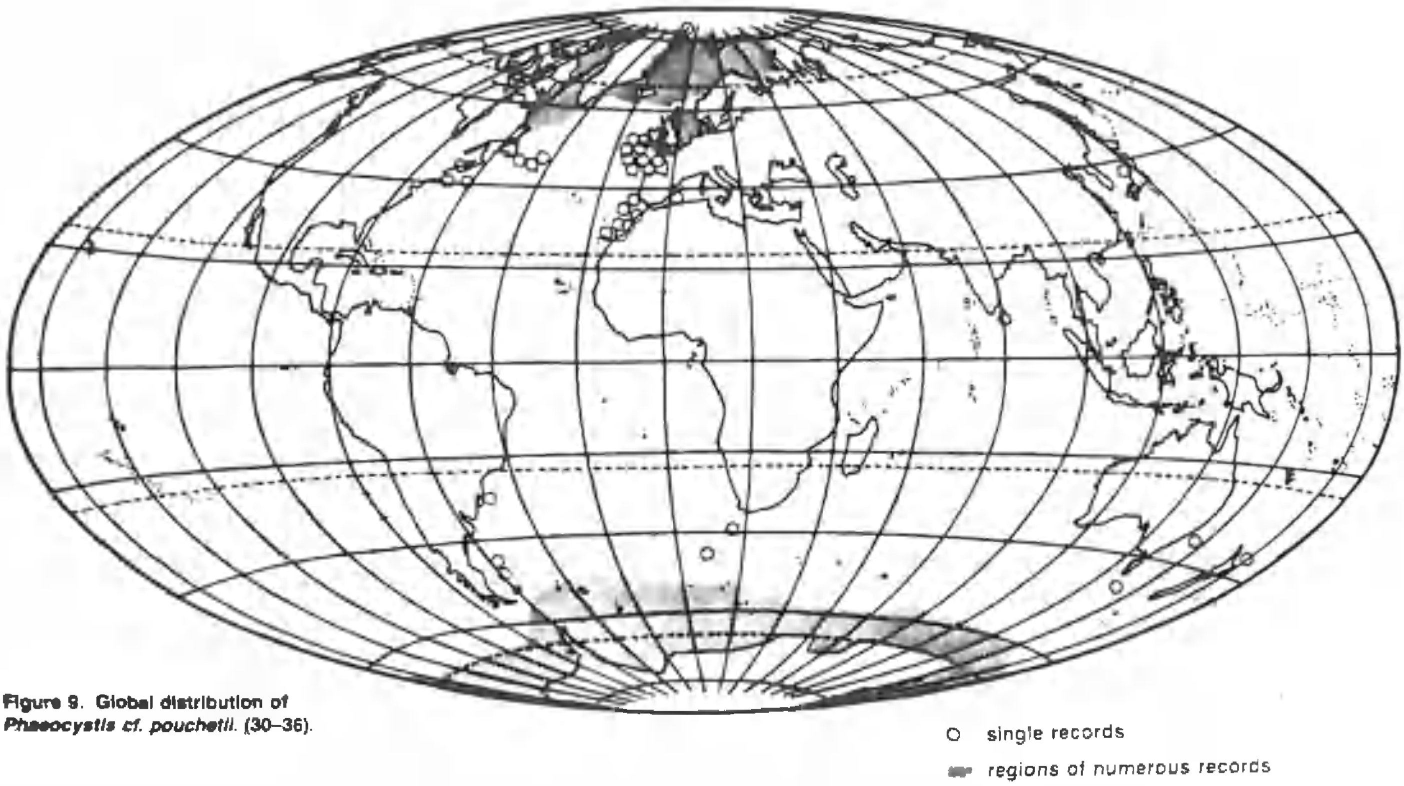


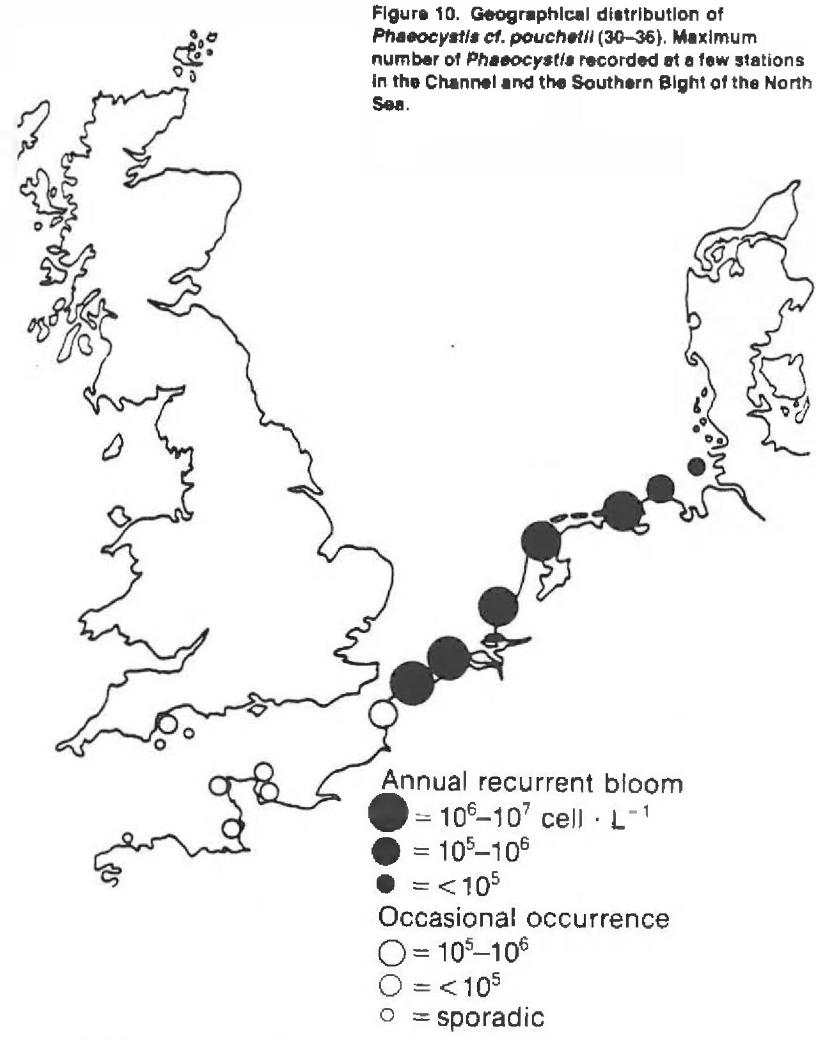
Figure 9. Global distribution of *Phaeocystis cf. pouchetii*. (30–36).

natural events (20). However, detailed long-term observations of Dutch coastal waters over the last 12 years (21) have shown a significant increase in the duration of the spring peak and the length of the period that *Phaeocystis* occurs in the plankton.

In this area, as in most coastal zones of the North Sea and the Barents Sea, *Phaeocystis* blooming is a recurrent phenomenon observed each year from April to June. In other regions blooms of this species seem more episodic. They have been recorded, however, in a wide variety of sites all around the world, as shown in Figure 8, even if the most spectacular blooms were recorded in the North Sea, the Arctic and the Antarctic waters.

A question then arises which although apparently academic, is actually a central one: Is there one single species of *Phaeocystis*, or are there several species? Since the description of the genus by G. Lagerheim in 1893 some eight species have been described in the scientific literature. These descriptions have mainly been based on the shape of the colonies, a feature which no longer seems reliable. On the other hand, the latest species described is based upon the ultrastructural features of the motile stage without consideration of the colony. At present most *Phaeocystis* outbursts are attributed arbitrarily to *Phaeocystis pouchetii*, the name of the type species, since scientists are unable to tell "why" outbursts appear or fail to appear. Temperature, salinity, freshwater runoff or nutrient discharge have all been advocated, but no explanation has withstood more than 2–3 publications! As seen in Figures 9 and 10, the genus can no longer be said to prefer cold waters as it is actually universally distributed in the

Figure 10. Geographical distribution of *Phaeocystis cf. pouchetii* (30–36). Maximum number of *Phaeocystis* recorded at a few stations in the Channel and the Southern Bight of the North Sea.



oceans of the world. Fortunately, (and again for unknown reasons) it does not bloom everywhere. The answer may well be that several species are contained within the genus, each having its own ecological preferences.

CONCLUSIONS

In an attempt to throw some light onto this obscure problem, the whole "*Phaeocystis* story" could be summarized in the following way.

Some strains of this organism have acquired adaptative mechanisms that make it particularly suited for growth in the environmental conditions created in enriched coastal zones by the early spring growth of diatoms. Increased anthropogenic inputs of nutrients, unbalanced in favor of nitrogen and phosphorus with respect to silica, have promoted these conditions and reinforced the natural tendency of *Phaeocystis* to develop temporary explosive blooms. The peculiar physiology of this alga, which devotes a large part of its phytosynthetic capacity to producing mucus, markedly affects the structure and function of the ecosystems it dominates. A decrease in food resources for zooplankton, increased deposition of organic material to the bottom, accumulation of organic material, either dissolved in seawater or in the form of slimy foam, and emission of volatile sulfur compounds into the atmosphere are the main harmful consequences of these blooms.

This simplified summary leaves many questions to be answered. For example, what are the factors promoting the transition from single cells to colonial *Phaeocystis* forms; what are the conditions required for blooming; what is the fate of mucus and why is it only slowly degraded by bacteria? Answers to these questions are required for a complete understanding of the processes involved in *Phaeocystis* blooms and, hence, for learning how to prevent and control them.

The means of control, however, are far from obvious. Some measures which *a priori* may be thought beneficial for the quality of coastal waters, may actually increase their eutrophication. The case of the Scheldt is a striking example. The river system of the Scheldt is one of the most polluted in Europe. Large segments of the tributaries are either anoxic or comprise anoxic sediments. These segments are prone to intensive denitrification (the anaerobic microbial process by which organic matter is oxidized at the expense of nitrate, the latter being reduced into gaseous form). Denitrification has been shown to remove as much as 70 percent of the total nitrogen entering the system (22, 23). A large scale waste-water purification program started in Belgium aims to eliminate 90 percent of the organic load by standard primary and secondary treatment processes and should indeed restore the oxic status of most of the river system. This kind of sewage treatment, however, does not capture more than about 30 percent of the nitrogen load. On the contrary, disappearance of the anoxic reaches of rivers and reduction of the organic matter content of the sediments should lead to a severe reduction in denitrification, resulting in an increase in the nitrogen output of the Scheldt by at least a factor of two (23). Thus, paradoxically, the spread of waste-water treatment as it is practiced now in Europe (i.e., without tertiary treatment for eliminating nutrients) is a contributing factor for the increase in nutrient input into the coastal zones of the North Sea.

This example indicates the difficulties involved in controlling nutrient enrichment of coastal zones. We shall probably have to live with coastal eutrophication for a long period.

In the meantime, it is possible that mankind can take advantage of the production of mucus by *Phaeocystis*. Food, cosmetic, textile and pharmaceutical industries are using large amounts of mucilaginous substances such as alginates or carrageenans. These substances are presently being extracted from large macrophytic algae (*Fucus* and *Laminaria* species) that grow on rocky shores. European sites for the exploitation of these algae are gradually approaching depletion. Why should not *Phaeocystis* mucus, particularly that accumulated on the beaches, constitute an alternative source of raw material for the production of polysaccharides? Here again more investigations are required to evaluate the feasibility of such exploitation, particularly in regard to the structure and properties of the mucus.

Studies on *Phaeocystis* cover a large variety of topics, from geochemical oceanography and organic chemistry to algal physiology and taxonomy. It also offers a wide range of perspectives in environmental management and, possibly, in industrial exploitation. Because of these perspectives and because of the international nature of the problems addressed, research on *Phaeocystis* could well become a privileged area for European scientific cooperation.

References and Notes

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