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PHYTOPLANKTON OF THE NORTH SEA AND ITS DYNAMICS: A REVIEW

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ABSTRACT

Phytoplankton is the major contributor to algal biomass and primary production of the North Sea, although crops of macroalgae can locally be up to 2000 g $C.m^{-2}$ along the coast of the U.K. and Norway, and microphytobenthos dominates production in the shallow tidal flat areas bordering the coasts of England, the Netherlands, Germany and Denmark. Data collected since 1932 during the Continuous Plankton Recorder Survey show consistent patterns of geographical, seasonal and annual variation in the distribution of phytoplankton and its major taxonomic components. There is a trend of increased colouration in Recorder silks in the southern North Sea until approximately 1975 since when Colour levels (assumed to be indicative of algal biomass) have declined. In the eutrophic Dutch Wadden Sea the algal crop continued to increase; in Dutch coastal North Sea waters a trend of biomass increase reversed since 1984, apparently due to a reduction in Rhine river outflow. Long-term observations made at Helgoland since the 60's also show trends of increasing nutrients and phytoplankton biomass only to 1984.

Adverse effects such as deoxygenation, foam formation and toxin production have been linked to mass concentrations of algae known as blooms. There is no evidence from existing reports for an increase in their frequency, although some years stand out with larger numbers. Occurrence of blooms can partly be explained by hydrographic conditions. More than 30 taxa are recognised as occurring in bloom proportions in the North Sea, approximately one third of which can be toxic.

The crop of Bacillariophyceae (diatoms) is not likely to increase with eutrophication due to silicate limitation. An extensive subsurface maximum of armoured dinoflagellates, its abundance gouverned by hydrographic conditions, is the most characteristic feature of the central and northern North Sea in the summer months. Abundance, sometimes dominance, of picoplankton and of species that are not readily detected by microscopic observations has been documented by measurements of taxon-specific pigments such as chlorophyll *b* (green algae), alloxanthin (Cryptophyceae) and 19' - hexanoyloxyfucoxanthin (Prymnesiophyceae or Haptophyceae).

Analysis of time series of satellite images is a promising way to assess in a quantitative and, more important, synoptic way the patchy distribution of phytoplankton over large regions. Growth processes of the phytoplankton respond according to variables amenable to such satellite remote sensing. Empirical and theoretical relationships that can be established between chlorophyll *a*, ^{14}C uptake, turbidity, stratification, suspended sediment type, irradiance and temperature in some well-investigated areas make remote sensing a potential tool to obtain reliable estimates of primary production in the whole North Sea. The ^{14}C method for estimates of the rate of algal growth processes appears to agree reasonably well with other methods, both involving incubation of samples and *in situ* measurements of temporal changes of oxygen and pH. The level of net primary production is 250 g $C.m^{-2}.a^{-1}$ in the central North Sea, 150 to 200 g $C.m^{-2}.a^{-1}$ in the northern North Sea, and 200 g in the South. The main metabolic processes involved in phytoplankton growth have been modelled mathematically in terms of the most important controlling en-

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vironmental parameters. Such parameters comprise not only those of a chemical signature (micro- and macronutrients, both inorganic and organic) but also physical effects of vertical mixing and sinking, and biological effects including allelopathic interactions, antibiotic excretions, vertical migration, and mortality due to grazing and parasitism. The balance between primary production and consumption of organic matter appears to vary both geographically and seasonally. The process of regeneration of primary products both in the water column and in and near the bottom seems to be of major importance.

Future research should center around a study of growth-controlling parameters in laboratory culture experiments. The studies should include uptake of dissolved organic compounds by all taxonomic groups, including pico- and nanophytoplankton, and all aspects of ecosystem structure and function involving the relation between algae and microheterotrophs making up the small food web. There is a need to synthesize existing information on phytoplankton in the North Sea and the factors gouverning its growth, such as nutrients, river input and stratification intensity. Complicated inter-relationships and successional patterns between individual species which are limited by varying physiological requirements and adaptation to differing hydrographic regimes reemphasizes the importance of species identification in phytoplankton studies. Many future problems in phytoplankton research will not be resolved without accurate identification of algal species. Taxonomic expertise takes many years to acquire; there is at present a shortage of skills in this area and more resources should be turned towards training and long-term support.

1. INTRODUCTION

After more than a century of observations of phytoplankton in the North Sea and two decades of measurements of its activity it has become clear that the causes and consequences of the observed temporal and spatial variability of algal biomass and its primary productivity cannot adequately be characterized and analyzed by shipboard measurements alone. Material collected in the field during cruises will remain the basis and a *conditio sine qua non* for a realistic interpretation of data collected by the most advanced tool now available for studies of the structure of the phytoplankton component of the ecosystem of the North Sea: remote sensing from satellites. This sophisticated way of synoptically surveying the algal standing crop, which includes the feasibility of distinguishing the distribution of its major taxonomic components, is promising and attractive. Its use will not easily overshadow the value of results obtained by more conventional means in the field, whether made with established methods or futuristic ones. Field results also need to be supplemented with investigations in the laboratory because a relation between standing crop data and growth processes can only be established through ecophysiological studies.

Our insight into the hydrographical, chemical and biological factors that affect the seasonal and geographical fluctuation in the abundance of the most important species of diatoms, dinoflagellates and microflagellates, and the long-term variation of their biomass in the North Sea has slowly but steadily increased from the time of the first surveys by German, Dutch, Belgian, Norwegian, Danish, Swedish and British scientists (HENSEN, 1887; CLEVE, 1886, 1887, 1900, 1902; LOHMANN, 1903, 1908; GRAN, 1902, 1905; REDEKE, 1922; VAN BREEMEN, 1905, 1906; MEUNIER, 1915; SAVAGE, 1930; SAVAGE & WIMPENNY, 1936; BRAARUD *et al.*, 1953; FRASER, 1952; GRØNTVEDT, 1952; HARDY, 1956; VAN GOOR, 1923; VAN DER WERFF, 1938; SCHULZ, 1961). The early studies were devoted mainly to an inventory of phytoplankters caught by nets. Near the beginning of this century HENSEN (1887) and LOHMANN (1903) stressed the importance of phytoplankters that pass the meshes of nets coarser than 50 μm or even less. These cells are nowadays categorized under the names of nanophytoplankton (less than 20 μm), picophytoplankton (less than 3 μm) and femtophytoplankton (less than 1 μm diameter). The Continuous Plankton Recorder Survey which started in the North Sea in 1931 (HARDY, 1935; GLOVER, 1967; ANON., 1973; COLEBROOK, 1975) has sampled the phytoplankton of most regions of the North Sea on a monthly basis. The meshes of the silks used in the Recorders are again too wide to catch the smaller phytoplankton cells but the structure of the silk threads and the speed of passage through the water appear to cause green to brown colouration of the silk when a Recorder is towed through blooms of small microflagellates (REID, 1975, 1977; GIESKES & KRAAY, 1977a; ROBINSON & HIBY, 1980). Recent observations on nano- and picoplankton by microscope (DE PAUW, 1972, 1975; HAGMEIER, 1978; CADÉE & HEGEMAN, 1986), with fractionation procedures (MOMMAERTS, 1973a, b), and by analysis of taxon-specific pigments (GIESKES & KRAAY, 1984a, 1986) confirm the abundance of small-celled forms.

Microscopy was partly abandoned as a tool in phytoplankton research during the sixties and early seventies because studies of 'bulk phytoplankton' growth processes were considered of more importance. This impetus in the direction of investigations of 'primary production' was given by the introduction of

the ^{14}C method of Steemann-Nielsen in the early fifties (1952). A succeeding wave of studies centered around the 'Systems Approach', earlier made popular in the U.S.A. by Odum and applied to the North Sea by STEELE (1974; see also REID, 1987). This stimulated the development of budgets and the modelling of primary production processes, with the purpose of improving our understanding of the position of phytoplankton in the food web and its role in the flow of organic matter cycling through the ecosystem (FRANSZ & VERHAGEN, 1985; URSIN & ANDERSEN, 1978; JOIRIS *et al.*, 1982; PODAMO, 1973). However, the Systems Approach has until now not appeared to be sufficiently advanced to explain succession phenomena, *i.e.* the temporal sequence of species as a response to environmental conditions. This all-important aspect of phytoplankton research can only be resolved by ecophysiological studies of key species. Such investigations, which can best be done with material regularly transferred from the sea to the laboratory, have been the subject of work done by several groups (LANCELOT *et al.*, 1986; SAKSHAUG & OLSEN, 1986; VELDHUIS & ADMIRAAL, 1987).

Interestingly, since the arrival of these laboratory studies species have become popular again. To unravel the metabolism of individual species, laboratory culturing has been accompanied by a return to taxonomy (PARKE & DIXON, 1976; LOUIS *et al.*, 1974; LOUIS, 1977; KAT, 1977, 1982a, b, 1988). These changes have also led to a return to microscopy, the latter now supplemented by modern techniques: scanning electron microscopy (WANDSCHNEIDER, 1980) and high-performance liquid chromatography (GIESKES & KRAAY, 1983, 1984a, 1986). Epifluorescence techniques are now commonly in use. Flow cytometry, molecular methods in the areas of recombinant DNA techniques, immunology, DNA probe technology, and molecular genetics are starting to be applied to studies of trophic dynamics, phylogenetic characterization, speciation, productivity potential, and distribution of strains of species.

In the following we will not treat the North Sea as a single entity, but discuss the phytoplankton and the environmental conditions that govern its abundance and activity in the geographical subdivisions chosen by the Flushing Group of the International Council for the Exploration of the Sea (I.C.E.S., 1983) covering an area of 575,000 km^2 (Fig. 1). Hydrographic characteristics of these subdivisions are outlined in REID *et al.* (1988).

In the past, other proposals for a subdivision have been based on the source and properties of water bodies, as described by BÖNECKE (1922), CARRUTHERS (1925), LAEVASTU (1963), LEE (1970), HILL (1973), NIHOUL (1973), RAMSTER *et al.* (1976), and POSTMA (1973). For the Continuous Plankton Recorder Survey, the North Sea has been divided into eight boxes which are approximations of the flushing areas (Fig. 1). Others have distinguished water masses with a similar seasonal species succession and production cycle (GIESKES & KRAAY, 1975; LEEWIS, 1985). The I.C.E.S. boxes (Fig. 1) have a different content due to differences in surface area and depth: from a mean of 25 m in the Southern

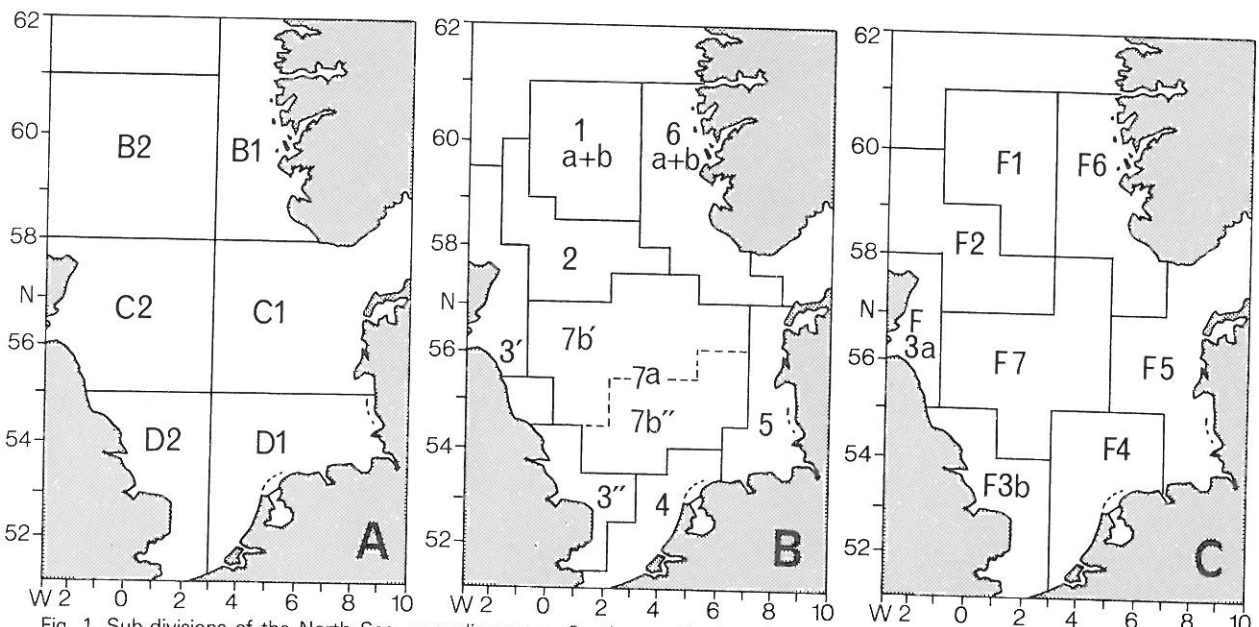

Fig. 1. Sub-divisions of the North Sea, according to: a. Continuous Plankton Recorder Survey. b. the Flushing Times Group. c. Combination of a and b (proposed).

Bight, to 200 m in the North, to 600 m in the deep trough at the north-eastern margin along the Norwegian coast.

For distribution of macronutrients and other factors that are of importance for phytoplankton, such as turbidity, regional and seasonal distribution in stratification, the location of frontal regions, suspended sediment characteristics, temperature and salinity distribution and circulation we refer to recent reviews by BROCKMANN *et al.*, (1988), NELISSEN & STEFELS (1988) and REID *et al.* (1988).

2. PHYTOPLANKTON GROUPS AND THEIR SPATIAL AND TEMPORAL VARIATION

A diversity of phytoplankton taxa with wide morphological variation have been described from the North Sea ranging in size from 300 μm to tiny cyanophyte picoplankton 1 μm in diameter. Some idea of this heterogeneous form is seen in Fig. 2 which illustrates examples from the classes described below. Guides illustrated with photographs of the more than 160 species found in the North Sea were published by DREBES (1974) and drawings of dinoflagellates by DODGE (1982). Taxonomic lists of species that are likely to be found in the North Sea have been published for Helgoland (DREBES & ELBRÄCHTER, 1976), the British Isles (PARKE & DIXON, 1976; HARTLEY, 1986) and Norway (HEIMDAL *et al.*, 1973). Distribution atlases have been published for species found in the Continuous Plankton Recorder Survey (ANON, 1973); for dinoflagellates by DODGE (1981).

The North Sea flora is primarily made up of autochthonous meroplanktonic species which are present in the water (or at times on the bottom) throughout the year, or overwinter as resting cysts in bottom sediment. Tychopelagic species may at times be an important component of the plankton in shallower waters. Superimposed on the above flora is an element of oceanic forms which may be seeded, to a varying extent

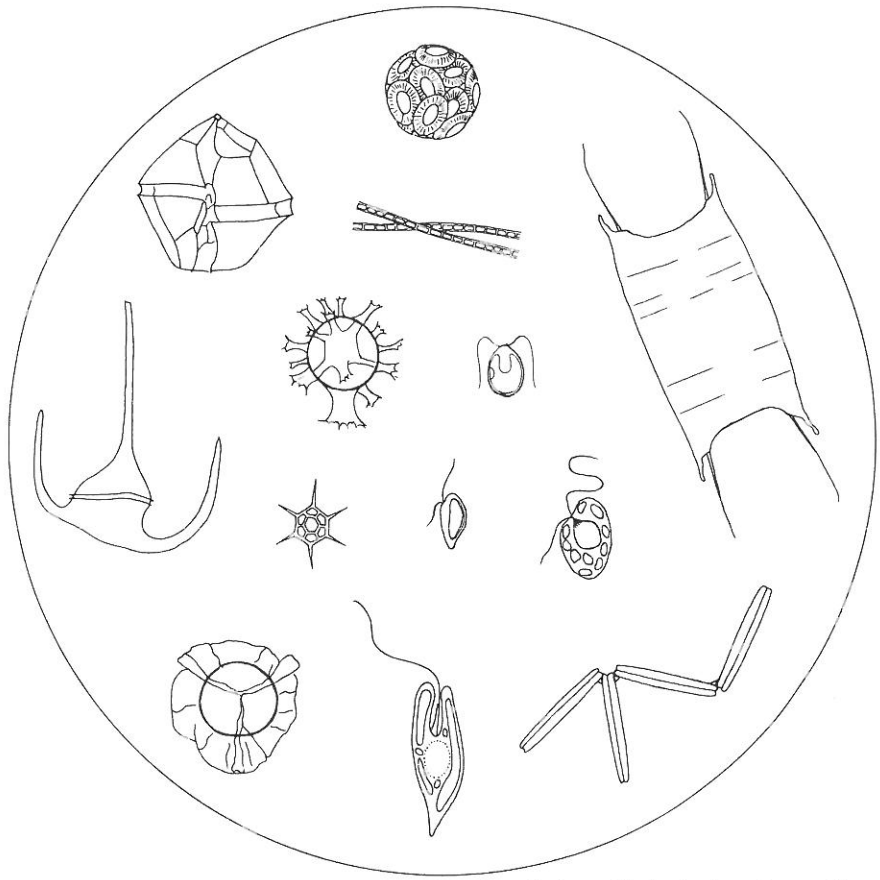

Fig. 2. Line drawings illustrating the variety of from of North Sea phytoplankton. Clockwise from top: a. *Coccolithus pelagicus* b. *Odontella sinensis* c. *Thalassionema nitzshioides* d. *Euglena* sp. e. *Pterosperma vanhoeffeni* f. *Ceratium tripos* g. *Gonyaulax polyedra* h. Oscillatoria j. *Dunaliella* sp. k. *Olisthodiscus luteus* l. *Plagioselmis* sp. m. *Destephanus* sp (Silicoflagellate) n *Spiniferites* sp (cyst of *Gonyaulax spinifera*)

each year, from the Atlantic.

Photoautotrophic marine phytoplankton including the Myxophyceae or Cyanobacteria can be divided into twelve classes, each with its own distinctive morphology, chemical composition, food reserves and set of photosynthetic pigments. Many protozoa and some higher animals have algae incorporated as symbionts (STOECKER *et al.*, 1987). Such protozoa, *e.g.* oligotrich ciliates, acantharia, radiolaria and foraminifera, may at times be important contributors to chlorophyll levels and primary production. Algal symbionts in some dinoflagellates may have originated from more than one source (DODGE, 1979).

2.1. DIVISION INTO CLASSES

1. *Cyanophyceae*

Procaryotic unicellular algae occur as minute 1 μm coccoid single cells or aggregates (JOINT, 1986). The common use of fluorescence microscopy in the 1980s has demonstrated their ubiquitous occurrence but little is known of their taxonomy and ecology. Distributions of picoplankton in the North Sea are given in GEIDER (1988) and HOWARD & JOINT (in press). They can grow very rapidly with generation times of the order of two hours. Filamentous forms, *e.g. Trichodesmium*, which may occur as mats on the sea surface in the Baltic and on Atlantic coasts, may rarely be advected into the North Sea.

2. *Cryptophyceae*

These small 3-20 μm flattened, bean shaped, darting flagellates have been largely ignored in the past as they do not preserve easily, although they are known to be common in coastal waters of the North Sea (BUTCHER, 1967; THRONDSEN, 1976). Using H.P.L. chromatography GIESKES & KRAAY (1983) demonstrated that Cryptophytes can form an important part of the spring bloom flora in the Central North Sea.

3. *Dinophyceae*

These spirally swimming organisms propelled by flagellae are main primary producers of the phytoplankton in summer (DODGE, 1982). The class also includes a large number of heterotrophic and phagotrophic species. *Ceratium*, the predominant autotrophic genus in the North Sea, succeeds diatoms in the second half of the year as the main algal group in the plankton. It may undergo large diurnal migrations in response to changing light levels (WANDSCHNEIDER, 1979). Dinoflagellates may form dense blooms colouring the water red (Red Tides), may be toxic (see Section 5) and heterotrophic forms may be important grazers.

4. *Chrysophyceae*

Golden brown silicoflagellates are the main marine representatives of this algal class which normally forms only a minor component of North Sea populations. Tubular siliceous rods which show great variation in morphology support the protoplasm. A form in which the skeleton had not developed was described as occurring in bloom proportions in the Kattegat (THOMSEN & MOESTRUP, 1985).

5. *Rhaphidophyceae*

Representatives of this class were thought to be rare, but are now known to form blooms in coastal waters of Japan and on the east coast of the USA. The class includes *Olisthodiscus luteus*, a species described from Belgian coastal waters, which is toxic and responsible for fish kills.

6. *Haptophyceae (Prymnesiophyceae)*

These organisms are covered in organic or calcareous scales and have a unique organelle, the haptonema, which is thought to be used for attachment. They may occur as unicellular flagellates or non-motile palmelloid colonies in mucus. Colonial forms usually occur after the spring diatom increase when silica has been depleted (GIESKES & VAN BENNEKOM, 1973; LANCELOT *et al.*, 1987). Calcareous forms known as coccolithophorids have a complicated life cycle. Large concentrations may be clearly reflected in satellite imagery (HOLLIGAN *et al.*, 1983). Representatives of all morphotypes are known to form blooms and may produce dimethyl sulphide (TURNER *et al.*, 1988).

Chrysochromulina polylepis, the species responsible for the massive bloom which caused fish kills and other impacts off the Swedish and Norwegian coasts in May/June 1988 (BERGE *et al.*, 1988; GRANMO *et al.*, 1988) is both autotrophic and phagotrophic, ingesting particles the size of bacteria.

7. *Eustigmatophyceae*

This is a new class since 1970; species now attributed to it were formerly allocated to the Xanthophyceae. Marine species exist but nothing is known of their occurrence in the North Sea.

8. *Bacillariophyceae*

Diatoms are the dominant algal group in the North Sea especially during the spring bloom. The class is divided into 'pennate' and 'centric' forms, the former elongate and appearing symmetrical and the latter radial having the basic structure of a 'pill box' with a wide range of height/diameter ratios (HENDEY, 1964). Because of their relatively large size diatoms are a favoured food source of the main herbivores, the copepods; they are grazed by filtration or raptorial capture. They may also be predated on by dinoflagellates which suck out the contents of cells after enclosing them in a protoplasmic web.

9. *Xanthophyceae*
These small species have two flagellae of unequal length with a wall that contains silica. Like diatoms they produce auxospores. They typically occur in brackish water and have not been described from the open North Sea. They may, however, be a dominant taxon in Norwegian Fiords (HALLDAL & HALLDAL, 1973).

10. *Euglenophyceae*
These free swimming flagellates have a characteristic undulating movement caused by cytoplasmic flow within an elastic wall. They are common in brackish and eutrophic waters, but also occur in the open North Sea at levels of 200-20,000 l^{-1} (THRONDSEN, 1969). Both phototrophic and heterotrophic forms exist.

11. *Chlorophyceae*
Unicellular representatives of the green algae occur in the plankton as coccoid non-motile and motile forms with two to four flagellae of equal length. They are characteristic of estuarine and polluted waters, but also occur in the North Sea (THRONDSEN, 1976). The beautifully illustrated guide of BUTCHER (1959) is still invaluable for references to identification.

12. *Prasinophyceae*
Green algae with 1 to 8 flagellae which are covered in characteristic scales and have complicated life histories. The class includes *Halosphaera* (DREBES, 1974) which has a large globular non-motile 'Phycoma' stage and *Pachysphaera* and *Pterosperma* (PARKE *et al.*, 1978), living fossils where the phycoma may split to release vast numbers of flagellates.

2.2. HISTORY

2.2.1.

The first attempt to evaluate the geographical variability of phytoplankton over the whole North Sea was made by CLEVE (1887) using nets hauled in the inappropriate month of January. An international programme of quarterly surveys (February, May, August and November) using Cleve's methodology was started in 1902 under the auspices of ICES. In these surveys fine nets were drawn vertically through the water from a known depth to give an integrated plankton sample of the whole water column. Estimates of the abundance of the plankton were made into three categories: present, common, abundant. Reviews of the results for the period 1902-1908 were made for the *Halosphaera*/Flagellata and for the Bacillariophyceae by OSTENFELD (1910, 1913), for the genus *Ceratium* by JØRGENSEN (1911) and for other dinoflagellates by PAULSEN (1913). In 1910/11 the international studies concentrated on a number of bi-weekly surveys from lightships throughout the whole year. Tables for these results are given in ICES (1914). This early period of international collaboration ended with the beginning of the First World War.

In the 1920/30s research based on net hauls was linked to the herring fishery, with an emphasis on autumn blooms as this was the time when the herring migrated to shoal on banks in the southern North Sea. Large patches of phytoplankton, sometimes over 100 miles long, were believed to block the migratory routes of the herring and influence the size of catches (SAVAGE, 1930; SAVAGE & HARDY, 1934; SAVAGE & WIMPENNY, 1936). Doubt was thrown on this hypothesis by CUSHING (1955) in a postwar study. Primitive sampling methods make it difficult to fully evaluate these studies, but it is clear that *Phaeocystis* formed large patches in the southern North Sea in the late autumn of the 1920s and that similarly large patches of *Rhizosolenia styliformis* and *Odontella sinensis* (formally called *Biddulphia sinensis*) occurred in autumn months throughout the 1920/30s in the southern North Sea.

2.2.2. DISCRETE WATER SAMPLES

The objectives of the international collaborative sampling programme of ICES changed in 1912 when a need for information on the vertical distribution of phytoplankton was recognised. In May/June 1912 discrete water samples were taken from a number of standard depths on surveys which covered almost the whole of the North Sea and the north eastern Atlantic (GRAN, 1915). For the first time samples were preserved, using acidic 'Flemings Fluid' concentrated by centrifugation, and analyzed quantitatively under low magnification on a counting plate.

The few phytoplankton studies in the interwar years *e.g.* (WULFF, 1925, 1934; VAN GOOR, 1923) were on a smaller and less extensive scale.

2.2.3. POST 1945 STUDIES

North Sea wide surveys were carried out in 1947 and 1948 by GRØNTVEDT (1952) and BRAARUD *et al.* (1953) both of whom used the 'Utermöhl' settling technique with buffered formalin to preserve samples. In consequence calcareous algae such as the coccolithophores were preserved and provided the first evidence for their importance in the North Sea. Braarud's early studies paved the way for an active school of phytoplankton taxonomists and ecologists in Norwegian fjords and coastal waters, *e.g.* BRAARUD *et al.* (1974).

Studies evaluating possible links between phytoplankton production and the pelagic herring fishery and the impact of grazing on algae were initiated at about the same time at the Fisheries Laboratory in Lowestoft (*e.g.* CUSHING, 1955, 1959, 1963).

More recent work has attempted to relate

phytoplankton occurrence to the physics of the water as seen from modelling and remote sensing (*e.g.* HOLLIGAN, 1978, 1987; HOLLIGAN & GROOM, 1986; HOLLIGAN *et al.*, 1980; PINGREE *et al.*, 1978, 1982, 1986). Detailed studies of the development of the phytoplankton spring bloom in the Fladen Ground area of the central northern North Sea were evaluated by GIESKES & KRAAY (1980, 1986), and by WANDSCHNEIDER (1983).

In continental coastal waters at Helgoland a long time-series of daily phytoplankton measurements has been compiled since 1962 (HAGMEIER, 1978; RADACH *et al.*, 1984). A ten-fold increase in flagellates occurred between 1962 and 1984 paralleling changes in nitrate with no increase, possibly a slight decrease, in diatoms. A similar progressive increase in flagellates was also described for the Marsdiep entrance to the Wadden Sea by CADÉE (1986). *Phaeocystis pouchetii* formed an important component of this apparent upward trend in flagellates (CADÉE & HEGEMAN, 1986). This Marsdiep study also revealed a repetitive alternation of taxa throughout the year, a pattern that was also evident in the results of LOUIS *et al.* (1974) described later and which differs from the traditional view of phytoplankton succession.

The important work of STADEL (1968) in August 1953 provided one of the first records of the importance of *Ceratium* species in the thermocline of the Central North Sea during summer. Vertical distributions of dinoflagellates were described by DODGE & HART-JONES (1974, 1977), DODGE (1977) and WANDSCHNEIDER (1979).

2.2.4. SERIAL SAMPLING TECHNIQUES

Many small flagellates are difficult to identify and observe unless they are alive and concentrated. Serial sampling techniques have been developed to provide suitable quantities of the organisms and estimates of their abundance in the water column (THRONDSEN, 1976). These techniques may possibly lead to the selective concentration of specific species as a consequence of the culture media used and may not truly represent their abundance in the plankton.

2.2.5. PHYTOPLANKTON STUDIES WITH THE CONTINUOUS PLANKTON RECORDER

All the above surveys and methods have given a limited insight into the temporal and spatial variability of phytoplankton species in the North Sea. Varying techniques and levels of identification have been used, generally wih a limited geographical coverage and with restricted sampling throughout the year. The majority of cruises (or sections) for both net and bottle samples are in May followed by late autumn cruises in October/November. Little is known of the seasonal development of the phytoplankton. To overcome some of these problems and to attempt to relate the plankton to fishery problems a modification of the CPR used by Hardy in the Antarctic was developed in 1931, to be towed behind merchant ships in the North Sea (LUCAS, 1940, 1941, 1942). This instrument filters plankton through a moving band of bolting silk of 270 μm mesh. The silk transport is regulated to the speed of the ship so that approximately 4 inches of silk represents 10 nautical miles and 3 m^3 of water filtered. Like net samples much of the phytoplankton passes through and the instrument is thus unsuitable for a full quantitative analysis of the phytoplankton. Nevertheless, a considerable proportion of the phytoplankton is retained on the silks to colour it and provide information on species occurrence and semiquantitative estimates of abundance (ROBINSON & HIBY, 1980). With a gap for the war, CPR's have been towed in the North Sea regularly each month since, 1931 to the present, to give a unique long record of phytoplankton variation at a depth of 10 m. References to recent papers on phytoplankton are included in GIESKES & KRAAY (1977a), COLEBROOK (1986), ROBINSON (1983), REID *et al.* (1987), and see ANONYMOUS (1973).

Annual and seasonal means for CPR phytoplankton have been calculated for subdivisions of the North Sea which approximate to the Flushing areas and represent differing hydrographic regimes (Fig. 1).

2.2.6. CPR PHYTOPLANKTON: ANNUAL CHANGES

A marked reduction of diatoms throughout the North Sea from approximately the mid 1960s, with similar changes evident in the northeast Atlantic, was described by GIESKES & KRAAY (1977a) and REID (1977). This pattern of change was particularly evident in the central and southern North Sea and has continued through to 1986 (Fig. 3) with some evidence for a possible slight increase in the last few years especially in the central and northern North Sea (Areas F1 and F7; see Fig. 1). Patterns of annual change in *Ceratium* spp. (Fig. 3c) show little relationship to the diatoms other than possibly in area F 3A where numbers declined markedly until 1980. A short period of years from 1971 showed higher numbers throughout the North Sea and especially in Area 3B (see also DICKSON & REID, 1983) and coincided with generally lower numbers of diatoms. Like Diatoms, *Ceratium* spp were also at a minimum in 1980 (see ROBINSON, 1983); this pattern may also have partly been due to reduced sampling in the southern North Sea at this time. Phytoplankton Colour (3a) shows little evidence for long-term trends except possibly in the southern North Sea where there was a general increase in levels until the mid 1970s since when colour has

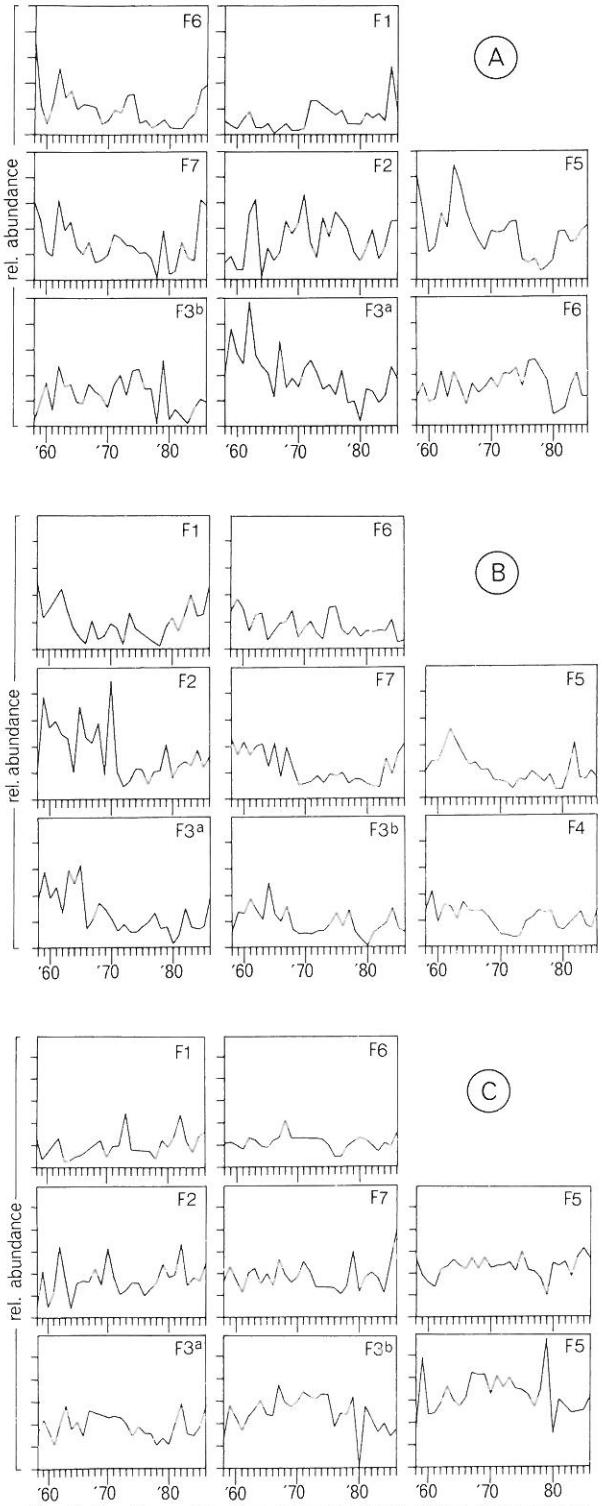

Fig. 3. Continous Plankton Records: Plots of the annual mean variation in phytoplankton abundance between 1958 and 1985 for the areas given in Figure 1c. a. Silk Colour (Phytoplankton Colour) b. Diatoms c. *Ceratium* spp.

declined. An apparent inverse relationship between colour and diatoms in the period 1958-1973 (REID, 1978) appears to have broken down since the mid 1970s.

In a long sequence of papers Colebrook (COLEBROOK, 1986) has analyzed temporal changes in the phytoplankton and zooplankton of the North Sea and Atlantic from CPR samples. An overall downward trend of zooplankton to approximately 1980 appears to have reversed. The widespead occurrence of the same trend suggests mediation through a link to long-term changes in climate and not via biological processes in the plankton.

2.2.7. CPR PHYTOPLANKTON: SEASONAL CYCLES

Descriptions of seasonal patterns for important species from the CPR have been presented by ROBINSON (1983). For area location see Fig. 1. A pronounced Spring maximum in April (May in area 3B) is shown by the Diatoms with much lower numbers after June. A less marked secondary increase in the late Summer is evident in areas 2 and 3A with evidence for a small Autumnal increase in October in areas 7, 5 and 3B. Ceratia exhibit a single summer peak with maximum levels in areas 2 and 3A. In these areas and the southern North Sea the dinoflagellates peak in July/August. A longer season with the peak in September is evident in the eastern and northern North Sea.

Phytoplankton Colour is divided into a Spring and Autumn peak of differing magnitude in all but the southern-most areas 3B and 4 where high levels of Colour continue into the later Autumn after the Spring increase. Moderate colour levels are evident in these two areas very early in the year. A distinction can be made between the three western areas 1, 2, 3A and the central and eastern North Sea areas 7, 6, 5. The season starts earlier and at a higher level in these latter regions with the peak of the Spring bloom in April. Areas 3A, 7 and 5 in the middle of the North Sea exhibit a higher peak of Colour in the Autumn than in the Spring which cannot be completely explained by *Ceratium* spp which is at lower levels here than in area 2. A shorter season is evident in the west with the peak of the spring bloom in May. Combined together Diatoms and Ceratia contribute the major part of the seasonal pattern of Phytoplankton Colour in the areas of the central and northern North sea. This is not so in the two southern areas where Colour remains high in the early Summer when Diatoms and Ceratia are low. This period coincides with the occurrence of *Phaeocystis* and is possibly also evident in area 5. Late October peaks in Colour as seen in areas 7, 5, 3B and 4 are possibly attributable to blooms of large diatoms such as *Odontonella sinensis* and *Coscinodiscus* sp. which contain dense concentrations of chloroplasts and may contribute more significantly to Phytoplankton Colour than their

numbers would indicate (GIESKES & KRAAY, 1977a). Maximum levels of Diatoms and Ceratia recorded between 1958 to 1986 show the same seasonal pattern as the mean values but have peaks that are 2-4 times as high with more pronounced late Autumn peaks in the Diatoms.

2.2.8. SEASONAL PATTERNS OF PHYTOPLANKTON

The only comprehensive seasonal analysis of phytoplankton other than the CPR was undertaken by LOUIS *et al.* (1974) from surface water samples taken at a number of standard sites between Ostend and Iceland on 17 cruises in 1970-1971. He includes tabulated results for 143 taxa. The route is restricted to the western North Sea and passes from Belgian coastal waters (25), to the central Southern Bight (24) to shallow East Anglian coastal water (23, 22), to the Flamborough Front (21, 20), to the seasonally stratified west central North Sea (16-21), to mixed waters off Buchan (15) to the outer Moray Firth (14).

Diatoms predominated in the south and dinoflagellates in the north with a pronounced peak in the region of the Flamborough Front. The seasonal cycle was markedly different from north to south. Phytoplankton (diatoms) was limited to March/September in the north, with the first bloom in the middle of April and the last in September. In contrast, on the Belgian coast dense blooms of diatoms, with numbers ranging up to $1.74 \cdot 10^6$ l, occurred as early as February, with smaller blooms as late as September, and common diatoms until December. The spring bloom did not start until late April/May off East

TABLE 1

Synthesis of tables from LOUIS et al. (1974) as a matrix of months/cruises against sampling stations showing the species that occurred at an abundance of more than 10,000 l^{-1}. St. 14 off Scotland; st. 25 off Belgium; other stations in between.

Dinoflagellates

Monthly Means

Station	*Prorocentraceae*	*Dinophyceae*	*Peridinea*	*Gymnodinaceae*	*Total*	*Mean*
14	4.23	109	552	0.41	665.7	166.43
15	22.00	218	1521	20.00	1781.0	445.25
16	3.29	127	1984	28.00	2142.3	535.51
17	7.52	2180	1386	36.00	3609.5	902.38
18	13.00	862	897	0.47	1772.5	443.12
19	61.00	1711	461	1.64	2234.6	558.66
20	66.00	2004	4635	0	6105.0	1676.25
21	33.00	193	245	0	471.0	117.75
22	12.00	34	111	1.17	158.2	39.54
23	18.00	109	478	26.00	631.0	157.75
24	54.00	45	255	49.00	403.0	100.75
25	85.00	76	425	33.00	619.0	154.75

Diatoms

Monthly Means

Station	*Centrales*	*Pennates*	*Total*	*Mean*
14	10437	5086	15523	7761.5
15	8246	2119	10365	5182.5
16	13105	3466	16571	8285.5
17	12080	1083	13163	6581.5
18	11230	605	11885	5942.5
19	15674	423	16097	8048.5
20	14262	7773	22035	11017.5
21	13887	30140	44027	22013.5
22	12033	49616	61649	30824.5
23	16141	3378	19519	9159.5
24	27097	11938	39035	19517.5
25	149385	26972	176357	88178.5

Anglia. A short and late season after April occurred in stratified waters further north, although surface samples may not truly represent water column populations in this area. Table 1 lists the species that occurred at $>10{,}000\ l^{-1}$ by month and station. While this table is a gross simplification of the total species representation it does help to illustrate some of the patterns that are evident in this data set. Diatoms dominate at all months and sites and a seasonal succession is not particularly pronounced. Species occur throughout the year, may bloom more than once, and may have high numbers in up to three consecutive months. For example, the dominance of *C. debilis, C. curvisetum* and *C. didymum* in the spring of the west central North Sea and the repetitive occurrence of *R. shrubsoleii* at station 25. The importance of *Thalassiosira* in the spring of the northernmost station is a pattern which is confirmed by the CPR. *Rhizosolenia* spp. are seen to be virtually restricted to the south of the Flamborough Front as dominant species and *Asterionella japonica* appears to be associated with this front.

The importance of tychopelagic species is indicated in the two southern sites and site 23, but not the shallow site 15 (LOUIS *et al.*, 1974). *Skeletonema costatum* which may at times be an important species in the North Sea only occurred in small numbers at three sites. *Guinardia flaccida* with its poorly silicified frustule is an important species in coastal waters of the southern North Sea after the spring bloom, filling a gap when other species are rare or absent.

3. VARIATION IN BIOMASS

The concentration of chlorophyll *a* is used as the most convenient index of phytoplankton biomass. Within this measure the carbon-to-chlorophyll ratio is highly variable, however. It is normally between 25 and 50 in healthy diatoms, microflagellates and dinoflagellates; young populations containing relatively high levels of pigment are found in spring, and at the first stages of bloom formation at other times of the year. In most of the many samples taken during an intensive exercise in oceanography in the northern North Sea in 1976 (Fladen Ground Experiment FLEX-76) chlorophyll *a* concentrations and phytoplankton carbon estimates based on cell counts resulted in C: chl. *a* ratios well under 10 - quite unrealistically low and certainly wrong. The ratio is between 50 and 150 in populations with a mixed physiological condition, and may be up to 300 or even more in declining blooms of *Phaeocystis* and other colonial species whose cells are embedded in mucus consisting of polysaccharides (*Corymbellus aureus; Chaetoceros socialis*). FRANSZ & GIESKES (1984) presented an example of a bloom of the diatom *Leptocylindrus danicus* in the Southern Bight of the North Sea that gradually lost its chlorophyll in the course of 3 weeks, while the number of cells, or at least of the frustules, remained nearly constant. This indicates how difficult it is to estimate biomass of phytoplankton: even counting algal cells and converting numbers to carbon using formulae produced by Hagmeier may lead to large overestimates. Measurements of particulate organic carbon (POC) are normally not useful because a distinction cannot be made between detrital carbon and phytoplankton carbon. POSTMA & ROMMETS (1984) reported that even in the central North Sea, far from the influence of rivers, much of the non-living particulate matter is refractory; yet, the contribution of living phytoplankton to the total load of POC in the open North Sea was found by GIESKES & KRAAY (1984a) to be between 25 and 65% in the vegetative season - higher than reported earlier by KREY (1954, 1960) and STEEL & BAIRD (1965). In dense blooms the algae contribute close to 100% of the 'labile' POC, *i.e.* the fraction readily available for consumption and mineralization by heterotrophs. In the southern North Sea, the close coupling between primary production of organic matter in spring and its consumption by heterotrophs (in casu bacteria and possibly other micro-organisms, in the near-absence of copepods) has been discussed by GIESKES & KRAAY (1977b). They noted an additional source of organic matter available for mineralization in the coastal North Sea, namely from the river Rhine, consumed (presumably by bacteria) at a rate as high as 250-500 mg $Cm^{-2}\ day^{-1}$ in late winter and early spring - far in excess of consumption of phytoplankton biomass at this time of the year.

Specific products of the growth processes of phytoplankton have been used by LANCELOT (1980) to estimate biomass parameters by a linear regression method not only of POC but also of protein, carbohydrate, and lipid on chlorophyll *a;* and new chlorophyll *a,* formed during growth, has been successfully used by GIESKES & KRAAY (1984b) to estimate North sea phytoplankton biomass with the chlorophyll labelling technique of REDALJE & LAWS (1981) after separation of Chl. *a* by HPLC.

Such methods may give reliable results but they are too sophisticated for general or routine use. An equally time-consuming method is to count particles with a Coulter Counter, then subtracting the phytoplankton volume in each size category after visual observations by microscope so the plankton can be subtracted from other suspended matter (EISMA & GIESKES, 1974). Interestingly, peaks in the phytoplankton size spectrum are often mirrored in the non-living fraction, which suggests rapid detritus production from phytoplankton. In the season without algal growth, the size spectrum of suspended matter shows the background, with a peak of smaller particles near the coast, coarser particles offshore, in oceanic water. The distribution of non-living suspended matter, measured with the 'subtraction pro-

cedure' here described, has also been presented by EISMA & GIESKES (1974). The concentration near Belgium is the highest of the whole North Sea; it is due to resuspension from the bottom in this shallow, silty area. HAGMEIER (1962) showed that tripton (dead particulate matter) by weight may exceed the contribution of plankton even in the central North Sea and spring bloom.

All methods based on microscopy, including the ones just mentioned, suffer from the fact that an unknown proportion of the algal crop is destroyed during fixation or is not recognized by the microscopist for other reasons. It is possible to detect such 'lost' cells by analysis of taxon-specific pigments in suspended matter. In this way, the abundance of nanoplanktonic microflagellates (Cryptophyceae, green algae and Prymnesiophyceae) has been documented in the central and northern North Sea by GIESKES & KRAAY (1983, 1984a). It may even be possible to differentiate with this method between species that until recently (JAHNKE & BAUMANN, 1987) were considered to be one: *Phaeocystis pouchetii* of the Southern Bight contains only fucoxanthin, *Phaeocystis globosa* both fucoxanthin and 19'-hexanoyloxyfucoxanthin. However, BUMA & BANO (1990) warn that physiological differences may influence fucoxanthin ratios. Measurements of the concentration of all algal pigments provides a great opportunity to differentiate between water masses containing different pigment fingerprints, the fingerprints being a precise reflection of the taxonomic composition, *e.g.* across fronts (Fig. 4).

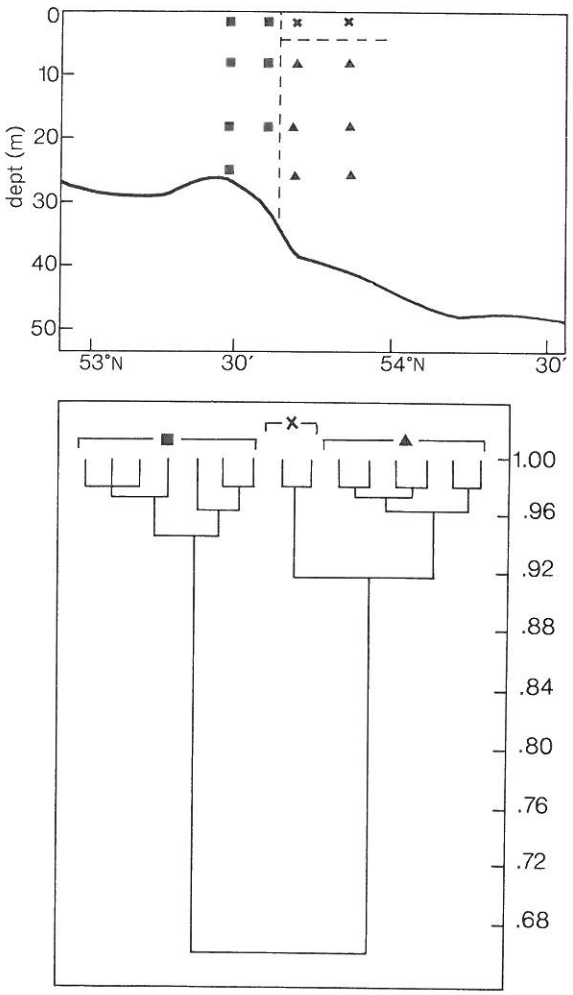

Fig. 4. Dendrogram of similarity between algal pigment chromatogram fingerprints developed by HPLC in samples taken on a north-south section through the Friesian front, along 4° 30'E. Gieskes and Kraay: SCOR Wg 78 (1985). ■: diatoms dominant (fucoxanthin); x: *Mesodinium* and *Cryptophyceae* dominant (alloxanthin); ▲: Microflagellates dominant (Chl.b, lutein/Zeaxanthin).

Another reliable, but much simpler and therefore widely used, method for detection of the relative abundance of micro-, nano- and picophytoplankton is size-fractionation by filtration over Unipore or Nucleopore filters, then measuring chlorophyll *a* in the fractions. The first results using this method in the North Sea are given in HOWARD & JOINT (in press).

In short, algal colour due to the pigment chlorophyll appears to be the most useful, best available means of detecting gradients in algal distribution, both horizontal and vertical. The use of *in situ* fluorometers of various types (AquaTracka; VarioSens) is now common for recording large- and finescale distribution, *e.g.* for registration of the thin layer (5 m) of the deep-dwelling dinoflagellate population that causes the deep chlorophyll maximum at 25-35 m so typical of the central and northern North Sea during summer (KREY, 1954; STADEL, 1968; GIESKES & KRAAY, 1984a), or the narrow patches of phytoplankton expected in frontal regions (REID *et al.*, 1983). Discrete sampling for measurements of chlorophyll *a* in acetone or methanol extracts remains, however, the most common method for estimates of the phytoplankton biomass, and series of surveys give a convincing picture of the development of biomass of phytoplankton in the course of the vegetative season (Fig. 5). The distribution patterns obtained in this way, based on sampling from a ship, are not synoptic, as is imagery from satellites given appropriate algorithms (see Chapter 6). Remote sensing cannot reveal, however, the significant accumulations of phytoplankton deep down in the water such as the summer's deep chlorophyll maximum at mid-depth in the central and northern North Sea, or accumulations near the bottom, *e.g.* after mass sinkings of spring diatoms in the central North Sea (GIESKES & KRAAY, 1984a), diatoms and Coccolithophorids in the northern North Sea (DAVIES & PAYNE, 1984; CADÉE, 1985), or after transport from elsewhere, *e.g.* the large algal

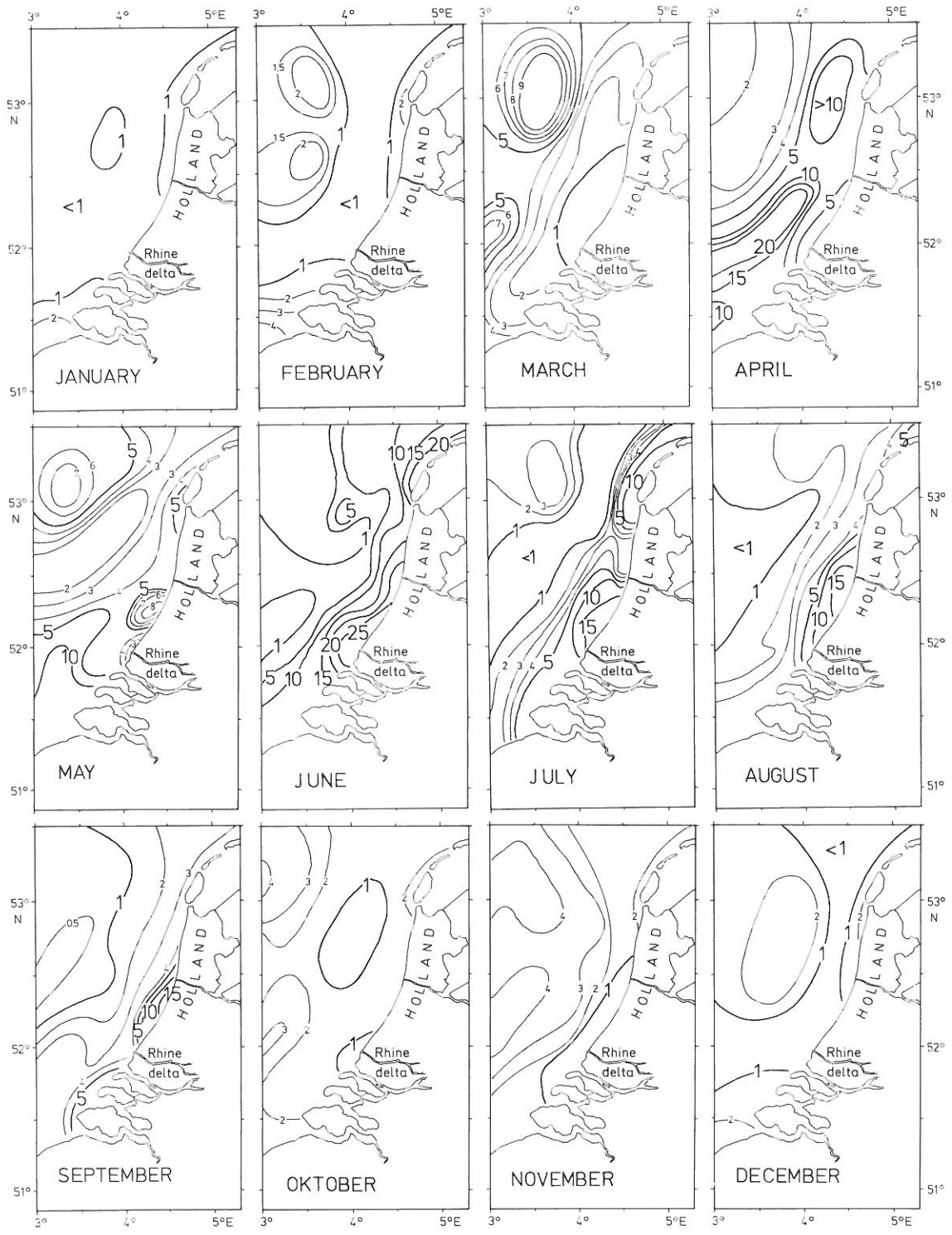

Fig. 5. Mean surface chlorophyll distribution (μg per liter) near the Dutch coast throughout a year; representative situation for 1974-1979.

masses found near the bottom at the Friesian Front, with an origin from more southern regions (JOORDENS, 1987; see Fig. 6). Thus, shipboard measurements with the 'good old' methods for the measurement of chlorophyll *a* will remain a necessity well into the next century.

4. PHYTOPLANKTON DYNAMICS

The distribution of phytoplankton biomass in the aquatic environment results from the balance between growth and mortality. These are governed by the physical processes that determine the light environment, the water column stability and the temperature, the chemical processes that determine the nutrient level, the physiological processes which express the adaptative changes of the cells in response to environmental stress, and the biological interactions with higher trophic levels.

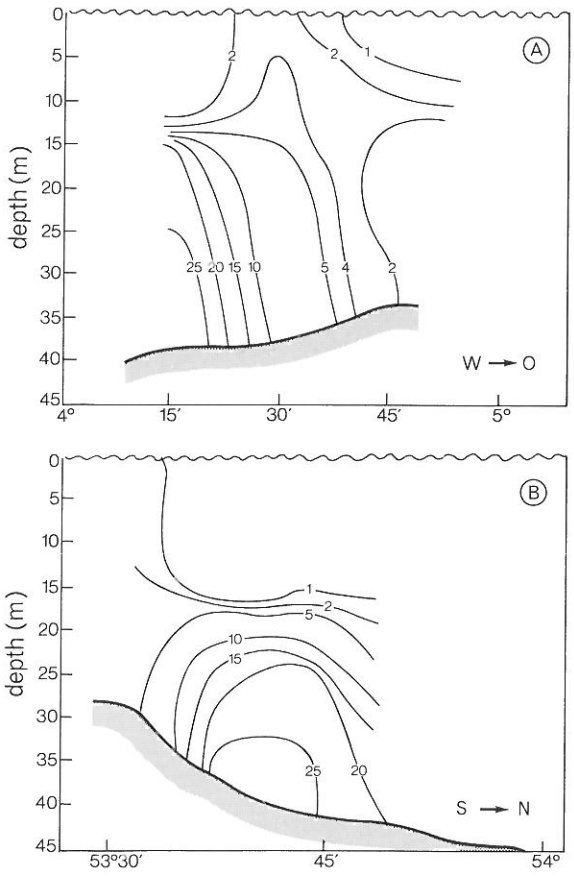

Fig. 6. Vertical distribution of Chlorophyll a in the Friesian Front (North of the Netherlands) a: June 12-16 1986 b: July 1 1986. Data of JOORDENS (1987).

4.1. PHYTOPLANKTON GROWTH

4.1.1. ENVIRONMENTAL CONTROLLING FACTORS

Light from the sun is essential for algal growth. Incident Photosynthetically Active Radiation (PAR) averaged for the whole North Sea and available for phytoplankton growth was calculated by REID (1987) as 48.3 W m^{-2}. This calculation averaged seasonal latitudinal and cloud cover variation, the effect of which is considerable. For example, the lower winter light level in the northern North Sea is reflected in a shortening of the growing season from south to north. Cloud which covers the North Sea on average for more than 50% of the year further reduces available light to phytoplankton varying by a factor of five between overcast and clear conditions. Spatial variability of cloud cover in different regions of the North Sea is considerable; and this is likely to be a major factor behind year-to-year differences in phytoplankton communities and their succession.

Light penetration in the water column is determined by suspended matter content and phytoplankton biomass. Euphotic depths as calculated on the basis of vertical light extinction coefficients measured in the Central North Sea and in the Belgian and Dutch coastal waters (GIESKES & KRAAY, 1975, 1977b; LANCELOT & MATHOT, 1989) range respectively between 70 and 8 m in offshore and between 12 and 3 m in nearshore areas indicating the great influence of tidal current and river discharge on light penetration in the latter biotope.

The physical environment of the North Sea can be divided into two regions: one where the water column is mixed throughout the year and one where stratification develops. In stratified waters the boundary between mixed and stable water (thermocline, halocline, pycnocline) has particular importance for phytoplankton growth as it divides, as a density discontinuity, the water column with bottom water rich in inorganic nutrients and a wind mixed upper layer where nutrients may be limiting. Algal concentrations track the thermocline, giving high chlorophyll measurements in summer months. In the summer 30 - 80% of the total production in the euphotic layer may take place in the thermocline (FRANSZ & GIESKES, 1984). Where the thermocline 'outcrops' at the surface it forms a 'front' which may at times be marked by blooms of algae, characteristically of large dinoflagellates. As the thermocline gets deeper they are replaced by flagellates or *Ceratium* spp. in the central North Sea. In waters mixed by tidal or wind action, light penetration, varying light levels and residence time within the photic zone are important to cells.

Residual currents transport patches of phytoplankton, disperse new immigrant species and may advect seed populations from the Atlantic into the North Sea. As an example, the oceanic species *Thalassiothrix*

longissima which is only common in the North Sea in certain years (*e.g.* 1952-1958 and 1967; REID & SURVEYGENT, 1980) reappeared again in the spring of 1989. This species grows in the early spring apparently from a seed population advected in the previous winter.

The inorganic nutrients nitrate, ammonia, phosphate and silica are part of the building blocks of phytoplankton cellular structure and may at times be limiting growth. Deep mixing during winter months in the Atlantic and North Sea recycles nutrients into the water column to give high levels before the spring bloom.

Winter values of nitrate, silicate and phosphate are respectively 8.6, 3.69 and 0.6 μmole·l^{-1} in the Central North Sea (BROCKMANN *et al.*, 1988). In continental coastal waters these levels have been supplemented by increasing anthropogenic inputs possibly causing eutrophication (LANCELOT *et al.*, 1987; BROCKMANN *et al.*, 1988). Depending on human activities and rainfall, winter nitrogen levels of coastal waters reach concentrations as high as one order of magnitude higher than oceanic levels.

Nutrient requirements for different algal groups differ. Silicon which is not rapidly recycled is used up first by

TABLE 2

Usual methods for measuring phytoplankton activity in the North Sea.

Method	*Variable measured*	*References*
Open System		
Diurnal measurement of concentrations in water mass	O_2	TYSSEN & EIJGENRAAM, 1980 JOIRIS & HECQ, 1982
	pH	WEICHART, 1980, 1985
	Dissolved PO_4^{3-} decrease	WEICHART, 1980
	Dissolved NO_3^- decrease	EBERLEIN et al., 1983
	Particulate P & N increase	EBERLEIN et al., 1983
Enclosure system (bottles experiments) in simulated in situ conditions		
1) Tracers		
^{14}C	(^{14}C-POC)light-(^{14}C-POC)dark	MOMMAERTS, 1973 GIESKES & KRAAY, 1975, 1984, 1986 HAGMEIER, 1984
	(^{14}C-POC + ^{14}C-DOC) light -(^{14}C-POC + ^{14}C-DOC) dark	LANCELOT, 1983 LANCELOT & BILLEN, 1984 COLIJN, 1983 VELDHUIS et al., 1986
	^{14}C-assimilation into macro-molecules during light:dark cycles	LANCELOT & MATHOT, 1985 a,b LANCELOT et al., 1986 VELDHUIS et al., 1986
^{15}N	uptake and assimilation during light:dark cycles	LANCELOT et al., 1986
^{32}P	short-term-uptake measurements	VELDHUIS & ADMIRAAL, 1987
2) Concentration measurements	(O_2 increase) light + (O_2 decrease) dark	FRANSZ & GIESKES, 1984 GIESKES & KRAAY, 1984a, 1986

diatoms and the seasonal succession to flagellates during spring bloom is a common feature of temperate marine systems. Changing N:P:Si ratios due to excessive anthropogenic inputs have been implicated in the increasing relative importance of flagellates in continental coastal waters during the spring bloom (VAN BENNEKOM *et al.*, 1975; GIESKES & KRAAY, 1977a; LANCELOT *et al.*, 1987).

4.1.2. ESTIMATE OF PHYTOPLANKTON GROWTH IN THE NORTH SEA

An accurate estimate of phytoplankton growth is essential from an ecological point of view as it determines available food for higher trophic levels. Interpretation of existing data on primary production is however complicated due to the interplay of environmental, physiological and methodological factors. There is now good evidence that phytoplankton has developed varying behaviour in response to nutritional and physical environmental fluctuations. Particularly well-known is the varying behaviour of phytoplankton when undergoing light fluctuations, partly because of the diurnal rhythm of solar radiation, partly induced by the vertical mixing of the water column and by surface waves. Also well reported are the mechanisms of nitrogen assimilation under transient situations of nutrient pulses. Depending on the time scale, the possible adaptative changes include alterations in intracellular pathways, changes in cellular composition, and/or change in cell size and species composition of the phytoplankton community. The phytoplankton ecologist is therefore confronted with the problem of the interpretation of more or less steady state measurements of process rates exhibited by populations taken from fluctuating environments and exposed to more constant experimental conditions. In addition each technique among those currently used for measuring phytoplankton processes during incubation experiments gives results which are often ambiguous and fail to give a complete description of community metabolic rates. One of the strategies adopted here to evaluate the meaning of measurements of phytoplankton processes in the field involves a comparison of data determined by different methods applied in the North Sea (Table 2). Comparison is difficult, however, because the compared data refer to different phytoplanktonic processes.

Another approach is to consider biochemically the phytoplankton processes that would lead to the establishment of a mathematical model which describes the main metabolic processes involved in phytoplankton growth on the basis of the knowledge of their control by environmental fluctuations. This approach was applied in the North Sea with different degrees of complexity in the biochemical characterization of processes: from the most oversimplified by RADACH *et al.* (1984) in the central northern North Sea to a more elaborated one by LANCELOT *et al.* (1986) in Belgian coastal waters. In our opinion, only with this approach it is possible to clarify data and integrate the interplay of environmental and physiological factors and produce accurate estimates of phytoplankton development in any aquatic system.

In the following, methods and literature data on North Sea phytoplankton activity are reviewed with regards to these two complementary approaches. Both are discussed in the light of an idealized model of phytoplankton metabolism. Also data are reviewed with regards to taxonomic groups, since succession of flagellate to diatom is common in the North Sea (see 2.) and to the physical properties of the watermass as subdivided into summer stratified waters (central, open North Sea) and well-mixed waters (coastal areas).

4.1.2.1. PHYTOPLANKTON PROCESSES

4.1.2.1.1. DESCRIPTION, TERMINOLOGY AND CONTROL FACTORS

Primary production refers theoretically to photosynthetic carbon fixation by phytoplankton cells. In the literature a distinction is made between gross and net production (minus phytoplankton respiration) *i.e.* available food for higher trophic levels. However, because a confusing debate presently rages in the literature regarding the exact meaning of the methods currently used for estimating gross or net primary production, a rigorous definition of phytoplankton processes in their biochemical context is required. In Fig. 7a, b, c diagrams are presented of the main metabolic activities of phytoplankton - photosynthesis, growth, excretion, respiration, physiological death - during a light, a short dark and a long dark period. It is an illustration of the different environmental situations encountered by phytoplankton in the turbulent well-mixed coastal waters of the North Sea and in the stratified waters of its central part during summer. The most important cellular and external components involved in these processes are the pools of active small metabolites including Calvin and Krebs intermediates and the oligomer precursors for macromolecular synthesis, the pool of reserve products composed of polysaccharides and/or lipids and the pool of functional (enzymes, DNA, ATP) and structural products which contain nutrients and are mostly composed of proteins.

Because of the biological function and their slow turnover rate the macromolecules can be considered as a good index of growth (LANCELOT & MATHOT, 1985a; LANCELOT *et al.*, 1986). External components are divided into CO_2/O_2 involved in photosynthesis/respiration processes and macronutrients N which control the growth process and are composed of nitrate, ammonia,

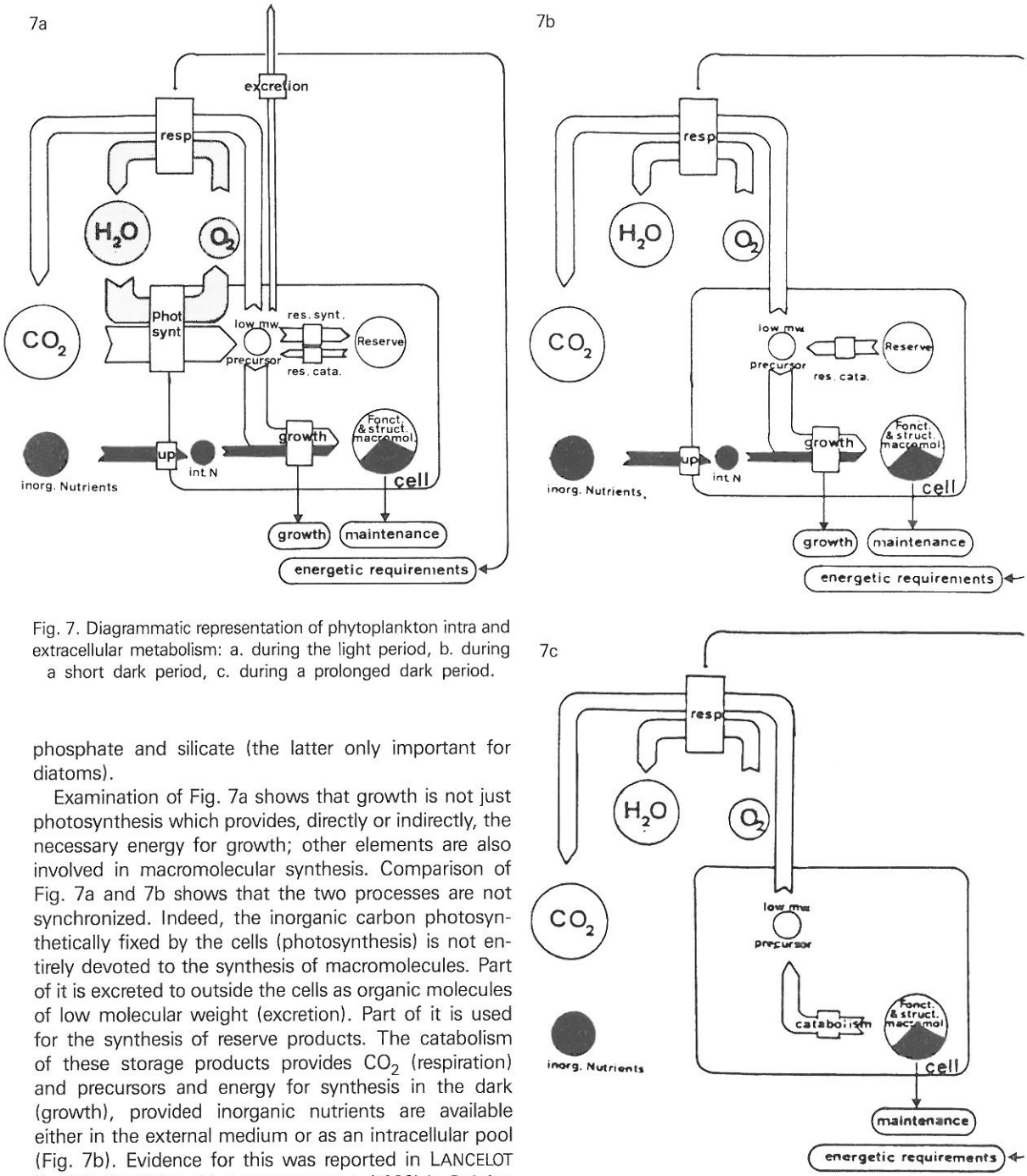

Fig. 7. Diagrammatic representation of phytoplankton intra and extracellular metabolism: a. during the light period, b. during a short dark period, c. during a prolonged dark period.

phosphate and silicate (the latter only important for diatoms).

Examination of Fig. 7a shows that growth is not just photosynthesis which provides, directly or indirectly, the necessary energy for growth; other elements are also involved in macromolecular synthesis. Comparison of Fig. 7a and 7b shows that the two processes are not synchronized. Indeed, the inorganic carbon photosynthetically fixed by the cells (photosynthesis) is not entirely devoted to the synthesis of macromolecules. Part of it is excreted to outside the cells as organic molecules of low molecular weight (excretion). Part of it is used for the synthesis of reserve products. The catabolism of these storage products provides CO_2 (respiration) and precursors and energy for synthesis in the dark (growth), provided inorganic nutrients are available either in the external medium or as an intracellular pool (Fig. 7b). Evidence for this was reported in LANCELOT & MATHOT (1985a, b); LANCELOT *et al.* (1986) in Belgian coastal waters and by VELDHUIS *et al.* (1986) in Dutch coastal waters.

A prolonged stay in the dark by phytoplankton cells due to sinking or because the mixed layer is much deeper than the euphotic zone (as is usual in the turbid coastal waters of the southern North Sea) could lead to the exhaustion of storage products. Under these circumstances, catabolism of structural and functional compounds occurs, causing either encystment or the physiological death of the cells as illustrated in Fig. 7c. From this diagram, gross primary production is better defined as photosynthesis and net primary production as growth minus autocatabolism.

4.1.2.1.2. PHOTOSYNTHESIS

(i) Analysis of methods

One of the current methods for measuring phytoplankton photosynthesis is derived from that introduced in 1952 by Steemann-Nielsen. This method involves the sampling of natural plankton communities at different depths and at different times during the day. Samples are enclosed in light and dark bottles inoculated with ^{14}C-bicarbonate as a tracer. Carbon fixed after a set time period is determined by counting radioactivity on the filter. Photosynthesis is defined by the difference between organic carbon fixation measured in the light bottle and in the dark one (anaplerotic fixation). Daily integrated photosynthesis is then estimated by the sum of the hourly data and their vertical integration up to the depth of the photic layer. Only apparent photosynthesis rates can be measured by this procedure as ^{14}C losses are known to occur during the incubation, both by phytoplankton respiration and excretion. Many improvements to the initial ^{14}C method have been and are still being suggested. They concern both the experimental procedure (*e.g.* additional measurement of excretion by counting radioactivity in dissolved organic matter) and the concept of the experiment (*e.g.* development of kinetic procedures). Also, the method used by different workers for calculating integrated daily primary production from experimental data is often different.

Incubations are generally performed either *in situ* or under simulated *in situ* conditions reproducing different light intensities or spectral qualities (neutral light common, but blue filters are now in use). Photosynthetic rates are calculated either simply from long-term (6-12 h) incubations by means of a factor expressing the ratio between daily available light and available light during the incubations as recommended by BIOMASS (O'REILLY & THOMAS, 1983) or by means of a mathematical model from ^{14}C data on short-term (2-4 h) incubations performed under different light intensities. These last experimental data allow the estimation of the parameters that characterize the photosynthesis-light relationship. Equations of both VOLLENWEIDER (1965) and PLATT *et al.* (1980) have been used in the North Sea. Daily integrated photosynthesis rates are then calculated from integration of one of these equations on the daily variation of solar radiation and on depth. Both procedures have been used for estimating daily photosynthesis rates in the North Sea. Original data are summarized in Table 3. As previously mentioned, these data concern apparent photosynthetic rates. How far from true photosynthetic rates these values are depends on the incubation period, the filtration procedure and the physiological state of the algae.

Measurements of oxygen production and consumption during light and dark incubations have been proposed as an alternative to the ^{14}C method. Good agreement is generally observed between the two methods, on the condition that the photosynthetic quotient PQ used for conversion of oxygen into carbon is adjusted following the inorganic nitrogen source. WILLIAMS *et al.* (1979) and GIESKES & KRAAY (1986) report PQ values ranging from 1.2 to 1.8 for marine phytoplankton growing respectively on ammonia and nitrate. A typical example is illustrated in Fig. 8 which reports data on parallel ^{14}C and oxygen light-and-dark bottle incubations by GIESKES & KRAAY (1984a). Agreement between the two methods is not necessarily obvious in natural environments because they are relevant to different groups of the planktonic community. Indeed, while the ^{14}C method refers mostly only to phytoplankton, the oxygen decrease observed in the dark bottle measures the dark respiration of the whole planktonic community (autotrophs + heterotrophs) enclosed in the bottle. The oxygen increase in the light bottle measures the budget between photosynthesis and respiration by this whole community. The latter process includes light respiration by phytoplankton which was shown through tracer experiments with $H_2{}^{18}O$ to represent up to 40% of photosynthesis. Data relative to physiological studies conducted on natural diatoms in Belgian coastal waters (LANCELOT & MATHOT, 1985a) indicate that light respiration amounts to 34% of photosynthesis when algae are incubated at maximal incident solar radiation.

This short inventory of methods used in phytoplanktonology indicates that photosynthesis cannot be accurately measured in marine environments except by the very sophisticated ^{18}O method. However, the complexity of this method and the required equipment excludes it as a routine procedure to estimate photosynthesis in marine environments.

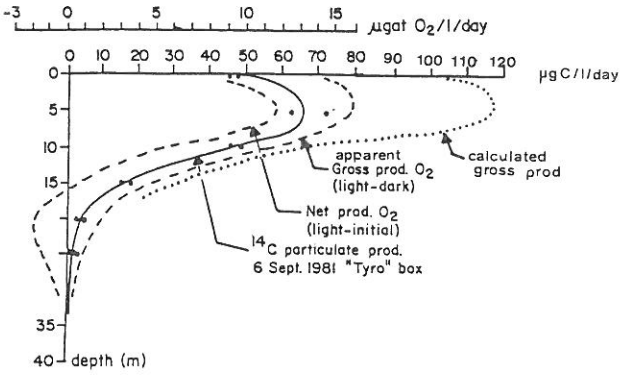

Fig. 8. Comparison between primary production data calculated from classical ^{14}C and O_2 incubation (GIESKES & KRAAY, 1984b) and gross primary production extrapolated for the same day. See Text.

(ii) Comparability of ^{14}C data

An alternative approach is to make a careful biochemical analysis of the tracer method using the diagram illustrated in Fig. 7 as a framework. Phytoplankton is considered in Fig. 7 as a multicompartment system, where each cellular constituent needs time to reach isotopic equilibrium. Clearly photosynthesis can never be measured by the classical ^{14}C method except when short incubation periods are used. LANCELOT & MATHOT (1985a) showed that important losses are attributable to light respiration of carbohydrates. Daily photosynthesis calculated on the basis of 2-4 hours incubation experiments are underestimated by about 30%. Longer incubations, as for instance in the protocol recommended by BIOMASS, results in still higher underestimates of photosynthesis (about 50%), as was shown during a ^{14}C experiment conducted in April 1986 (LANCELOT & MATHOT, unpublished). These correction factors were used to reassess the data gathered in Table 3.

4.1.2.1.3. EXCRETION

Excretion is commonly defined as the active production by phytoplankton of organic molecules outside their cells. Exudation, extracellular release or dissolved primary production are the usual synonyms reported in the literature. A distinction must be made between true excretion of organic molecules in the external medium and secretion. Some colonial species in the North Sea, like the diatom *Chaetoceros socialis* (GIESKES & VAN BENNEKOM, 1973) or the flagellate *Phaeocystis* (LANCELOT & MATHOT, 1985b; VELDHUIS *et al.*, 1986), actively produce outside the cells the mucilaginous substances forming the colonial matrix in which the cells are embedded. This distinction is essential from an ecological point of view. Indeed, excreted organic molecules are directly available for bacterial utilization (LANCELOT, 1979), whereas mucilaginous substances are most important for the physiology of *Phaeocystis* colonies. LANCELOT *et al.* (1986) and VELDHUIS *et al.*

TABLE 3a

North Sea primary production data: well-mixed coastal waters.

Month period	*Method*	*Dominant phyto-plankton*	*Incu-bation time*	*Characte-rization*	*pp gC.m^{-2}d^{-1} min-max*	*pp gC.m^{-2}ds period^{-1}*	*pp. gC.m^{-2} corrected period^{-1}*	*Sources*
Belgian coastal waters								
12 1971-1975	B	D+P	2-4	total	0.2-5	320	410	JOIRIS *et al.*,1982
3 (April-June) 1982	B	D+P	2-4	total	0.16-1.4 0.2	73	93	LANCELOT & BILLEN, 1984
1 February	B	D	2-4	total	0.2	6	77	
1 (April-May) 1984	C	P	2	total	0.4-5.2	94	126	LANCELOT & MATHOT, 1987
Dutch coastal waters								
6 (Febr. July) 1974	A	D+P	6-8	cells	0.1-3	78-153	162-306	GIESKES & KRAAY, 1975
3 (March-May) 1984	C	D+P	2	total	0.5-5	176	225	VELDHUIS *et al.*, 1986
1 (April-May)	C	P	2	total		94	120	
0.03 (May) 1986	C	P	2	total	2.97	2.97	4	Lancelot & Mathot, unpubl. results
Western Dutch Wadden Sea								
12 1964-1965	S_1		2	cells	0.04-1.5	120-170	150-210	POSTMA & ROMMETS, 1970
12 1972-1973	S_2		3			100	125	CADÉE & HEGEMAN, 1974
12 1981-1982	S_2	P+D	3	cells	0.5-6.5	340	425	CADÉE, 1986
German Bight								
0.03 (May) 1986	C	D	1	cells	2.92	2.92	4	Lancelot & Mathot, unpubl. results

Legend: S_1 = Original Steeman-Nielsen's method
S_2 = Steeman-Nielsen's method modified following POSTMA & ROMMETS, 1970
A = Biomass method
B = Mathematical integration on light variation of Vollenweider's equation
C = Mathematical integration on light variations of Platt *et al.*, equation
D = Diatom
P = *Phaeocystis pouchetii*
F = Flagellate

(1986) have shown that these mucilaginous substances act as storage products for the colony and provide energy for the growth of *Phaeocystis* cells inside the colony.

Current methods for measuring excretion are modifications of the ^{14}C method of STEEMANN-NIELSEN (1952), as first developed by HELLEBUST (1965). In this method the radioactivity of the organic carbon contained in a filtrate after a fixed incubation time is regarded as phytoplankton excretion. Incubation time adopted by authors varies generally between 1 and 12 h. Again, incubation duration is important for the estimate of gross phytoplankton excretion rate because of the physiology of the cells, as clearly shown in Fig. 7, and the presence of heterotrophic micro-organisms in natural plankton communities. Both can lead to a serious underestimation of phytoplankton excretion rates by up to 68% (LANCELOT, 1979).

On the other hand, excretion rates may be overestimated because secretion and excretion cannot be distinguished at present. The filtration procedure commonly used after ^{14}C incubation causes disruption of the colonial matrix and solubilization into the filtrate. Therefore, the excretion rates measured during *Phaeocystis* blooms by LANCELOT (1983), COLIJN (1983) and LANCELOT & BILLEN (1984) are mostly attributable to secretion rather than to true excretion.

Ultrafiltration and gel filtration techniques used on ^{14}C *Phaeocystis* filtrates by LANCELOT (1983) and VELDHUIS *et al.* (1986b), suggest that secreted mucilaginous substances are polymeric and can thus be distinguished from excreted small molecules.

Daily changes in dissolved organic substrate concentrations like dissolved carbohydrates have been proposed by EBERLEIN *et al.* (1983) as an alternative to the ^{14}C method. In Table 4 available literature data on excretion rates by North Sea phytoplankton are summarized. Values have been corrected for incubation time. The occurrence of colonial species was taken into account for the distinction between excretion and secretion. Clearly, gross excretion is too low to be of significance. Secretion, on the other hand, ranges between 21 and 64% of photosynthesis (Table 4); it appears to be inversely correlated with the inorganic nitrogen content of the ambient medium (data not shown). This is in agreement with the storage nature of these compounds.

4.1.2.1.4. NUTRIENT UPTAKE

Nutrient uptake by phytoplankton communities has been little studied in the North Sea. Only nitrogen and phosphate utilization were considered. Little work has been done on silicon uptake, except by GIESKES & VAN BENNEKOM (1973). Field studies on nitrogen and phosphate uilization during the spring bloom, *i.e.* refering to new primary production, have only been made

TABLE 3b

North Sea primary production data: Central and northern North Sea

period Month^{-1}	*Method*	*Dominant phyto-plankton*	*Incu-bation time h.*	*Characte-rization min-max*	*pp gC.m^{-2}d^{-1} period^{-1}*	*pp gC.m^{-2} period^{-1}*	*pp corrected gC.m^{-2}*	*Sources*
Fladen Ground (open North Sea)								
1.5 (March 25-May 10) 1976	B	D	3-13	cells	0.14-2.9	36	46	GIESKES & KRAAY, 1980
1. (May 10-June 16) 1976	B	F+D	3-13	cells	0.2-2.8	46	59	GIESKES & KRAAY, 1980
Oyster Ground (central North Sea)								
0.2 (May 3-9) 1981	A	D	8	cells	1.04-1.53		15.6	GIESKES & KRAAY, 1984a
0.2 (July 23-29) 1983	A	D+F	8	cells	0.93-1.21		12.6	GIESKES & KRAAY, 1984a
0.2 (Sept. 3-10) 1983	A	D+F	8	cells	0.91-1.23		12.6	GIESKES & KRAAY, 1984a
Open North Sea								
0.3 (Apr. 29-May 8) 1983	A	D	12	cells	0.65-1.22	14.2	25.2	GIESKES & KRAAY, 1986
0.5 (May 8-May 22)	A	F*	12	cells	0.45-3.2	26.	52	

Legend: A = BIOMASS method
B = Mathematical integration on light variation of Vollenweiders' equation
C = Mathematical integration on light variations of Platt *et al.* equation
D = Diatom
P = *Phaeocystis poucheti*
F = Flagellate
F* = *Corymbellus aureus* (colonial Haptophyceae)

TABLE 4

Percentage of extracellular release P.E.R. in different areas of the North Sea.

Area	*Period*	*Dominant phyto-plankton species*	*P.E.R.* *Excretion %*	*Secretion %*	*Reference*
Coastal areas					
Belgian coastal waters	Winter	Diatoms	0		LANCELOT & BILLEN, 1984
	Spring	Colonial diatoms		25	
		Colonial *Phaeocystis*	7-11	31-64	LANCELOT, 1983
	Autumn	Diatoms	1-16		LANCELOT & MATHOT, 1987
					LANCELOT & BILLEN, 1984
Dutch coastal waters	Spring	Colonial diatoms		25	GIESKES & VAN BENNEKOM, 1973
		Colonial *Phaeocystis*		28	VELDHUIS *et al.*, 1986
Ems estuary	Spring	Colonial *Phaeocystis*		40	COLIJN, 1983
Open Sea					
Fladen Ground	Spring	Diatoms	0-10		GIESKES & KRAAY, 1980
Oyster bank	Autumn	Diatoms	5		GIESKES & KRAAY, 1984a

P.E.R.* = dissolved primary production
cellular + dissolved primary production

in Belgian (LANCELOT *et al.*, 1986) and Dutch (VELDHUIS *et al.*, 1986b; VELDHUIS & ADMIRAAL, 1987) coastal areas. The recent study on nitrogen by OWENS *et al.* (1990) covers the whole North Sea area with emphasis on the summer regeneration period.

Relative preference index (RPI) values calculated for two nitrogenous nutrients in Belgian waters indicate that ammonia was by far the preferred substrate, in agreement with other studies on marine phytoplankton *e.g.* GLIBERT *et al.* (1982). Nitrate, ammonia and phospate uptake rates by *Phaeocystis* colonies have been shown to obey Michaelis-Menten kinetics (LANCELOT *et al.*, 1986; VELDHUIS *et al.*, 1986b, 1987). In some cases, in addition, organic forms of nutrient (nitrogen and phosporus compounds) can be used by phytoplankton. Thus, VELDHUIS & ADMIRAAL (1987) reported high alkaline phosphatase activity in *Phaeocystis* colonies induced by the exhaustion of inorganic phosphate; VAN BOEKEL & VELDHUIS (1990) have continued to study the role of organic P and N compounds for growth of North Sea phytoplankton.

4.1.2.1.5. GROWTH

Growth, *i.e.* net primary production, refers to the net synthesis of new cellular structures. It can be expressed in terms of biomass production or increases in cell numbers. It is this component of production that is important as it is the part that is available for higher trophic levels. Growth is a complex process involving the uptake and assimilation of nutrients into macromolecules. Monomeric carbon precursors for macromolecular synthesis on the other hand are provided either by photosynthesis or by the catabolism of storage products. Because of this, growth of natural phytoplankton communities is not easy to determine.

Both tracer techniques and measurements of diel changes in O_2, CO_2, nutrient concentrations in the external medium, or particulate nitrogen and phosphorus have been used to estimate net primary production in the North Sea. These methods are only applicable when the measurements are made within the same water mass and the currents are relatively weak. Table 5 summarizes data of phytoplankton net primary production for the Fladen Ground area from pH, phosphate, particulate phosphorus and nitrogen measurements. Good agreement was reported by WEICHART (1980) between growth estimates from pH and ambient phosphate concentration. However, growth estimates based on CO_2 or O_2 changes could be underestimated because of the light respiration of phytoplankton which is not taken into account in the CO_2 budget calculation. Also estimates of phytoplankton growth based on phosphate budgets could be either underestimated because of its regeneration by bacteria or overestimated since all the phosphate taken up by phytoplankton cells is not necessarily assimilated.

On the other hand, sophisticated methods combining tracer technology and biochemical fractionation (LANCELOT & MATHOT, 1985) show good evidence that the measurement of protein synthesis constitutes the best method now available for estimating phytoplankton growth in marine environments. Hourly specific protein synthesis rates of 0.004 to 0.04 h^{-1} were measured during the course of a *Phaeocystis* bloom in Belgian (LANCELOT & MATHOT, 1985 a, b; LANCELOT *et al.*, 1986) and Dutch (VELDHUIS *et al.*, 1986b) coastal waters. This work was developed with a mathematical model of daily integrated growth (LANCELOT *et al.*, 1986) using incident light, vertical light attenuation coefficients and ambient inorganic nitrogen.

TABLE 5

North Sea phytoplankton growth data.

Period	*Biotope*	*Method*	*Growth gC.m⁻² period⁻¹*	*Source*
21.04.76-01.05.76	Fladen Ground	A	20± 4	WEICHART, 1980
		B	20± 3	WEICHART, 1980
		C	8-20	EBERLEIN et al., 1980
		D	14-28	EBERLEIN et al., 1980
Spring	German Bight	A	20-40	WEICHART, 1985
Year	Fladen Ground	B	54-82	STEELE, 1956, 1958
24.04.84-21.05.84	Belgian coastal waters	E-D	84	LANCELOT & MATHOT, 1987

A : CO_2 budget based on pH measurements
B : Phosphate budget
C : Particulate phosphorus budget
D : Particulate nitrogen budget
E : Modelling of protein synthesis

4.1.2.2. A MATHEMATICAL MODEL FOR CALCULATING PHYTOPLANKTON GROWTH IN THE NORTH SEA

As discussed above, no good method exists at present to measure net phytoplankton growth. Net growth can be calculated, however, by incorporating field results into a suitable mathematical model which takes into account physiological and environmental fluctuations. The equations of the model and the meaning of the parameters describing the kinetics of the different metabolic processes involved will be described elsewhere. The model is applied here to two regions of the North Sea:

(i) A well mixed coastal environment (Belgian Coastal zone)

(ii) A stratified open sea environment (The Fladen Ground).

4.1.2.2.1. PHYTOPLANKTON GROWTH DURING SPRING IN BELGIAN COASTAL WATERS

Belgian coastal waters are dominated during spring by *Phaeocystis* colonies that succeed diatoms. Growth of diatoms is limited by silicon availability, whereas *Phaeocystis* is under the control of nitrogen (LANCELOT & MATHOT, 1987). Runs of the model were performed using parameters for nutrients and light conditions encountered by the cells at the different sampling days. The mean depth of the area was 18 m, and only one nutrient was considered as limiting: silicon during the diatom bloom and inorganic nitrogen during the *Phaeocystis* bloom. Parameter values were determined experimentally (LANCELOT *et al.*, 1986) or derived from the literature. Results of these simulations are given in Fig. 9. Validation of the model is supported by a comparison of observed and predicted phytoplankton biomass. The latter was calculated from chlorophyll *a* data and daily specific growth rate (0.03-0.3 d^{-1}) as deduced from Fig. 9. Further information on model predictions and observational verification will be presented by LANCELOT & MATHOT (in prep.). A budget of metabolic activities of phytoplankton was calculated by integration of the prediction curve (Fig. 9) Respiration rates can be deduced by difference between photosynthesis, growth and excretion. The model implies that diatoms and *Phaeocystis* contribute respectively 20 and 30% of the spring bloom in Belgian coastal waters. Phytoplankton respiration was high, amounting to 50-60% of photosynthesis. This can be explained by the high turbidity of these shallow coastal waters where only one third of the water column is illuminated. Catabolism of storage products proceeds therefore at a high rate in order to maintain basal metabolism when cells spend time in the dark.

4.1.2.2.2. SPRING PHYTOPLANKTON BLOOM IN THE FLADEN GROUND

Several runs of the model were performed using data on the physics, inorganic nutrients, and Chl*a* reported

in the Flex Atlas for the Fladen Ground spring bloom of 1976. Parameters of the equation were estimated from the particulate primary production atlas or from literature, using correction factors reported previously. Results of these simulations can be seen in Fig. 10. Predictive daily specific growth rates ranged between 0.04 d^{-1} in the winter to 0.38 d^{-1} during the spring bloom. Biomass calculations are also presented in Figs 9 and 10. Good agreement was found between predicted and observed phytoplankton biomass during the growing phase of the bloom. A discrepancy observed during the decay of the two blooms is attributable to phytoplankton mortality and/or sedimentation. Growth averaged 40% of the photosynthesis in agreement with the 35% calculated in Belgian coastal waters. Also, good agreement was found between predicted phytoplankton growth and that estimated by WEICHART (1980) from an inorganic phosphate budget. This indicates that phosphate is not stored by phytoplankton as an inorganic intracellular pool and that regeneration does not proceed to a significant extent during the growing stage of the phytoplankton bloom. Comparison between prediction curves and primary production daily rates confirms that ^{14}C data from experiments lie between true photosynthesis and growth.

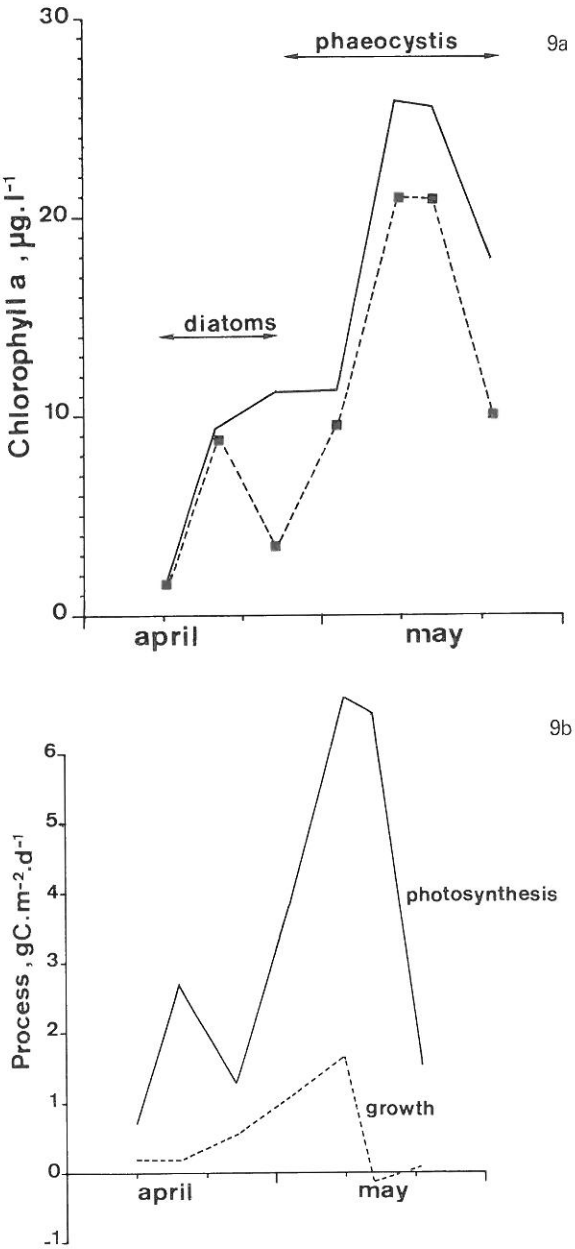

Fig. 9. a. Photosynthesis and growth of phytoplankton during the spring bloom in Belgian coastal waters as calculated by Lancelot's model (see text); b. Calculated and observed Chlorophyll *a* concentration during the 1984 spring bloom in the Belgian coastal zone.

4.1.2.2.3. PHYTOPLANKTON GROWTH IN THE NORTH SEA

Simulations of phytoplankton growth during its exponential phase indicates that the described mathematical model is convenient for calculating phytoplankton growth in any aquatic system. However, during summer, when phytoplankton growth is dependent on nutrients regenerated by bacteria and zooplankton or diffused across the thermocline when waters are stratified, a whole ecosystem model describing hydrodynamic and nutrient regeneration processes would be required. Nevertheless, previous simulations of photosynthesis and growth indicate that a mean growth yield of 40% should be considered for North Sea phytoplankton as a first approximation.

4.2. PHYTOPLANKTON MORTALITY; LYSIS

The phytoplankton biomass formed is destroyed by mortality or deposited on the bottom. Mortality results either from grazing by zooplankton and protozoa of from spontaneous or parasite-induced cell lysis. The former process transfers part of the phytoplankton biomass to higher trophic levels, while the latter results in shorter recycling. Very little is known of phytoplankton cell lysis in the water column although this mechanism greatly determines the supply of organic matter for heterotrophic bacteria.

Although the wane of the spring bloom was classically explained by high pressure of zooplankton grazing (CUSHING, 1955), it has been shown in the North Sea and adjacent areas that zooplankton grazing does not contribute significantly to the reduction of phytoplankton biomass following the spring and autumn bloom (FRANSZ & GIESKES, 1984; RADACH *et al.*, 1984; DAVIES & PAYNE, 1984). In coastal areas, however, there

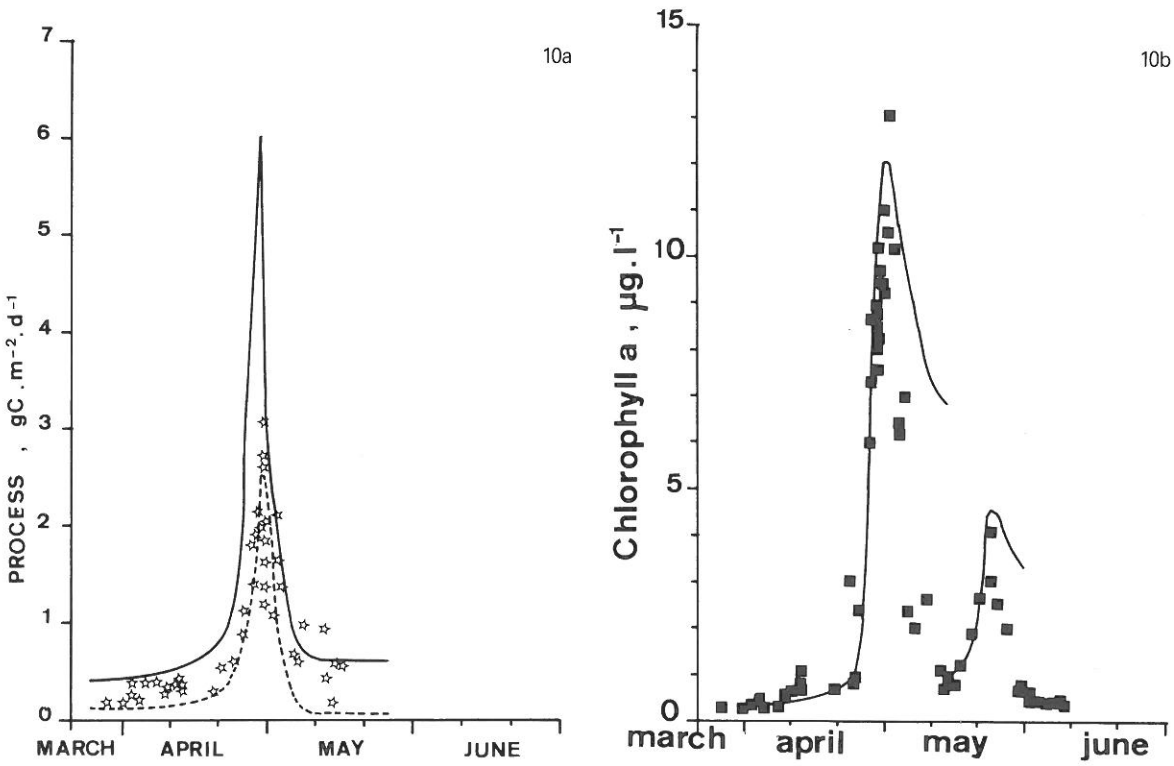

Fig. 10. a. Photosynthesis and growth of phytoplankton during the 1976 spring phytoplankton bloom in the central northern North Sea (Fladen Ground) as calculated by Lancelot's model (solid line), and as measured experimentally (Flex Atlas) (dotted line and symbols); b. Calculated (solid line) and observed (symbols) chlorophyll *a* concentration during the 1976 spring bloom in the central northern North Sea (Fladen Ground).

is increasing evidence that protozoa like tintinnids and *Noctiluca* play a key role in the reduction of *Phaeocystis* single cells during spring (ADMIRAAL & VENEKAMP, 1986; BÄTJE & MICHAELIS, 1986). During summer, on the other hand, copepod grazing matches primary production in all areas of the North Sea (FRANSZ & GIESKES, 1984).

Direct sedimentation of phytoplankton cells in the North Sea has been shown to be very important, particularly during and at the end of phytoplankton blooms (FRANSZ & GIESKES, 1984; GIESKES & KRAAY, 1984a; CADÉE, 1985). Sediment trap measurements indicate that 20 to 35% of primary production deposits to the benthos during spring in the northern North Sea (DAVIES & PAYNE, 1984; CADÉE, 1985). Similar measurements in coastal areas indicate a higher contribution by sinking as well during the spring bloom when it may represent up to 65% of primary production.

5. BLOOMS: CAUSES AND CONSEQUENCES

The term 'bloom' was orginally used, by analogy with terrestrial plants, to describe the spring 'flowering' of the diatoms which characterises most temperate waters. More recently it has come to be equated with high concentrations of planktonic organisms, usually but not always autotrophic algae, which represent the maximum development of the organism(s) at a particular time or place. Blooms are normally dominated by one species. Visible discolouration of the water is usually associated with blooms when organisms in the nannoplankton size range occur at concentrations >5. 10^5 cells l^{-1}, or are represented in biomass terms by chlorophyll concentrations (TETT, 1987) >10 mg m^{-3}. These are minimal concentrations to discolour water levels of >100 mg m^{-3} and 30. 10^6 cells l^{-1} are more typical and may range up to 2000 mg chl *a* m^3 and 100. 10^6 cells l^{-1}. Such high concentrations are necessary for pigments or skeletal mineralogical components to absorb and algal cells to scatter a substantial part of incoming radiation causing the colour of the water to change.

Depending on the characteristic pigments or mineralogy of the dominant organisms the water may appear white (coccolithophores) to various shades of green (diatoms, euglenids, chlorophytes) to brown (*Phaeocystis*) to purple (the ciliate *Mesodinium*), to red or coffee brown (dinoflagellates). Blooms of the latter

organisms are often referred to as 'Red Tides', an emotive term which is often linked with a catastrophy, poisoning or other harmful consequence. The red discolouration of the River Nile described in Exodus 7 v17 may possibly be one of the first references to a Red Tide. Phagotrophic organisms such as the dinoflagellate *Noctiluca* which is pigmented by orange carotenoids may also form blooms which have the consistency and colour of tomato soup. The ciliate *Mesodinium* and oligotrich ciliates which contain symbiont algae of possible cryptomonad affinity may also concentrate and form blooms.

Discolouration of water caused by blooming phytoplankton may be so extensive as to be visible from aircraft (BERGE *et al.*, 1988) or in imagery taken by satellites (HOLLIGAN, 1981). White reflection from the calcareous coccoliths of coccolithophores in the northern and central North Sea provides particularly dramatic evidence of bloom formation (HOLLIGAN, 1987).

Blooms may develop from rapid rates of production combined with reduced grazing pressure, active swimming or buoyancy changes and/or processes of physical concentration in conditions of favourable light and nutrient concentration. Inhibitory biological factors may also be important in their success. An initial inoculum is required which may derive from a resident population via sediment seed beds, by advection or by upwelling. They are thus a consequence of a complex interaction of biological, chemical and physical processes which may develop over a range of different temporal and spatial scales. Physical processes, because of their link with light and nutrient supply, are believed to predominate at least in the initial development of blooms. Dinoflagellates in particular are known to actively swim to the surface in calm weather as a response to self shading. Turbulence due to strengthening winds rapidly reduces the number of near surface aggregates (GILLBRICHT, 1983); in this paper an increasing C/N ratio, with higher numbers of *Ceratium*, was put forward as evidence of transport and concentration of blooms from adjacent waters. A framework for the development of different types of blooms based on changing patterns of dominant phytoplankton and linked to gradients of turbulence and water column stability was outlined by HOLLIGAN (1987). Different growth and reproductive strategies and responses to physical changes in the water column were shown to develop in concert with these gradients. Growth rates and physiological requirements of known bloom forming taxa may differ significantly. Dinoflagellates for example are slow growing and reach bloom proportions by avoiding grazers, and via positive buoyancy and vertical migration. While light, nutrients and mixing are essential for phytoplankton growth, TETT (1987) has shown they are not sufficient to explain bloom development. Often blooms are found at much higher levels than could be inferred from nutrient concentrations alone so they must be a consequence of active migration or physical concentration.

At times, blooms of certain species may develop to exceptional levels when they may have serious effects on the ecosystem. Worries that such exceptional events, with associated detrimental consequences, are increasing in frequency in Atlantic Coastal waters and especially in the North Sea were the subject of a special ICES symposium in 1984 (PARKER & TETT, 1987). Criteria for distinguishing between blooms which are part of the normal seasonal pattern and 'exceptional blooms' were outlined in this meeting by HOLLIGAN (1987) and REID *et al.* (1987).

A wide range of effects has been attributed to blooms, ranging from de-oxygenation, foam formation, unpleasant odours, mortality of fish and benthic organisms, toxicity to marine organisms including seals and whales, and man, and changes to the ecosystem via plankton-benthos and plankton-macroplankton feed back loops. An increasing occurrence of medusae, for example, is one of the phenonema that has been linked to bloom formation (LINDAHL & HERNROTH, 1983).

5.1. BLOOM ORGANISMS

More than 30 taxa have been described as occurring in bloom proportions in the North Sea and adjacent waters; a brief outline of the important groups is given below under the following headings: Ceratia, *Noctiluca, Gyrodinium*, Gymnodinium, Dinophysis, Gonyaulax, Prorocentrum, small dinoflagellates, cryptophytes, diatoms, silicoflagellates, prasinophyceans, and coccolithophores. Taxa that are asterisked are included in a later section on toxic phytoplankton.

1. Ceratia

The following species of *Ceratium* have formed blooms in the North Sea or adjacent waters: *C. fusus, C. furca, C. tripos* and *C. lineatum*. Relatively small concentrations to 5.10^5 cells l^{-1} can have a major impact because of the size of the cells (up to 250 μm). In particular, mass sedimentation of Ceratia have been implicated in deoxygenation of bottom waters in the German Bight (WESTERNHAGEN *et al.*, 1986) and Kattegat (EDLER, 1984). A large bloom of *C. furca* in July/August 1981 was studied from its initiation by GILLBRICHT (1983) at Helgoland in the German Bight. A relationship between the size of the *Ceratium* stock and salinity was determined. As salinity decreased, *Ceratium* numbers increased, a pattern which was represented spatially by an onshore gradient of increasing numbers. Nutrients were in excess throughout the bloom except in waters of a mean salinity of 30.4 ‰. An outline of the spatial

distribution of the bloom is given in HICKEL (1982).

Blooms of *Ceratium furca* and associated dinoflagellates ranging up to 5.7 10^5 l^{-1} have occurred in the Gullmarn Fjord of the Swedish Skaggerak (LINDAHL & HERNROTH, 1983). The very large bloom with chlorophyll levels up to 70 mg m^{-3} which formed in this Fjord in 1981 at the same time as the *Ceratium* bloom in the German Bight consisted almost exclusively of *Gyrodinium aureolum*.

2. *Noctiluca*

Blooms of *Noctiluca* have been recorded on a regular basis off the Belgian coast since 1971 (MOMMAERTS, 1985, 1986a, b) and have also been noted in Norwegian offshore waters (TANGEN, 1979). In the German Bight, *Noctiluca* is most abundant off the east and north Friesian islands in the first ten days of July (UHLIG & SAHLING, 1982).

3. Gymnodinium

Blooms of this genus were recorded as early as 1937 in the Oslo Fjord (BRAARUD, 1945) and have occurred more recently as *G. sanguinum* with concentrations up to $35 \cdot 10^6$ l^{-1} (TANGEN, 1979).

4. Small dinoflagellates

Heterocapsa triquetra regularly forms summer blooms in the Oslo Fjord with concentrations that reached $260 \cdot 10^6$ l^{-1} in 1974. *Katodinium rotundatum* is an unusual dinoflagellate as at times in the early spring, it blooms in cold water of 9°C (PINGREE *et al.*, 1986), but more typically in summer. In the Oslo Fjord levels as high as $2883 \cdot 10^6$ l^{-1} were reached in April/May 1978 (TANGEN, 1979).

5. Diatoms

Few diatoms are recorded as reaching bloom concentrations, possibly because the visible impact is less spectacular and the phenomenon of the spring bloom is accepted as a regular natural phenomenon. Two diatom species have been reported by KAT (1982b) as occurring in bloom proportions in Dutch coastal waters. *R. delicatula* formed blooms (>$1.3 \cdot 10^6$ cells l^{-1}) in a 30 km wide band parallel to the coast in a number of years since 1978. In the summer of 1973 only, *S. costatum* bloomed in a similar but more restricted area just north of the mouth of the Rhine, reaching levels of $4 \cdot 10^6$ cells l^{-1}. Spring blooms dominated by *S. costatum* appear to be a regular feature of Swedish coastal waters in the Skagerrak with concentrations reaching $53 \cdot 10^6$ cells l^{-1} in March 1981 (LINDAHL & HERNROTH, 1983).

An exceptionally early bloom of diatoms which occurred off the mouth of the Rhine in 1977 consisted of *Phaeoceros, Navicula, Bacillaria* and *Biddulphia* species (REID *et al.*, 1983). This bloom was attributed to unusual hydrographic and meteorological conditions (temperature >2°C and salinity >0.1‰ above average) in the central Southern Bight combined with heavy run-off from the Rhine causing a pronounced density stratification.

Large concentrations of *Coscinodiscus* sp. breaking down and causing oil slicks on the surface were reported by GRØNTVED (1952). Blooms of this species were also recorded off the Dutch coast in the mid 19th century (ENDE, 1849) and more recently in 1972 (GIESKES, 1973). The decline of both these blooms was accompanied by a foul smell presumably due to decaying cell material- which was following oxygen depletion.

6. Haptophyceae or Prymnesiophyceae

Massive blooms of palmelloid mucilaginous algae attributed to *Phaeocystis* in the southern North Sea (GIESKES & KRAAY, 1975, 1977b; GIESKES & VAN BENNEKOM, 1973; LANCELOT *et al.*, 1987) and *Corymbellus* in the northern North Sea (GIESKES & KRAAY, 1986) have been recorded in recent years. Blooms of *Phaeocystis* off the Dutch coast may occur with levels of chlorophyll as high as 50 mg m^{-3} day^{-1} in a 25 m water column (GIESKES & KRAAY, 1977). Banks of froth on beaches from the breakdown of these blooms are a visible and olfactory nuisance (photographs in LANCELOT *et al.*, 1987 and BROCKMANN *et al.*, 1988). Sulphurous products from the blooms may also contribute to the formation of acid rain (TURNER *et al.*, 1988). A progressive increase in the numbers and season length of *Phaeocystis* in Wadden Sea water (CADÉE & HEGEMAN, 1986) has been linked to increasing eutrophication but also to freshwater quantities discharged from lake Yssel (de Jonge, pers. comm.). A link between freshwater Rhine river discharge and algal abundance in Dutch coastal waters has also been reported (GIESKES & SCHAUB, 1990). Two morphotypes of *'Phaeocystis'*, the *'globosa'* and *'pouchetii'* forms (BÄTJE & MICHAELIS, 1986) may represent different species and possibly even different genera. This suggestion is based on ultrastructure (JAHNKE & BAUMANN, 1987) and HPLC chromotographic signatures (A. Buma, pers. comm.), but this may not be sufficient to support separation into two species (A. Buma, pers. comm.). Most interesting is a bloom of *Corymbellus aureus* in the Fladen Ground area of the open northern North Sea, far from eutrophicated waters, found in May 1983 (GIESKES & KRAAY, 1986). This colonial species, resembling *Phaeocystis*, was never seen in the North Sea before.

7. Coccolithophorids

Emiliania huxleyi is a common element of Norwegian coastal water in the summer and has formed blooms on a semi-regular basis in the Oslo Fjord and other coastal areas since the beginning of this century (TANGEN, 1979). The progress of a large bloom of this species in the coastal waters and fjords of west Norway in May/June 1955 was traced in detail by BERGE (1962). Concentrations of up to $115 \cdot 10^6$ cells l^{-1} were recorded with the highest levels near the surface. The bloom coincided with clear weather so that the surface maxima were open to high light intensities. Distinct boundaries between pale green discoloured and normal blue water seen in aerial photography in some areas *e.g.* the Korsfjord were attributed to transport of the surface waters by dominant northerly winds leading to upwelling on northern shores. The discolouration of the water was enhanced by a turbid suspension of detached coccoliths from earlier production which were still present in the water. BRAARUD (1945) attributed blooms of *E. huxleyi* in the Oslofjord to an influx of Skagerrak waters with a high initial stock into an area which was enriched by sewage.

In the summer dense populations of *E. huxleyi* may form a shallow subsurface chlorophyll maximum in the central Skagerrak (PINGREE *et al.*, 1982). This feature forms as a response to doming of the seasonal isopycnals by geostrophic forces and increased surface transport due to freshwater outflow from the Norwegian coasts and Baltic.

5.2. TEMPORAL AND SPATIAL OCCURRENCE

The traditional view of the normal seasonal sequence of phytoplankton development in temperate waters is of a spring bloom of diatoms followed by a later autumn bloom generally dominated by other algal groups. As seen in earlier sections there may be considerable deviations from this standard pattern in different areas of the North Sea. The majority of blooms occur in the summer months of the year but may develop at any time in the growing season given favourable conditions. Different responses to light, temperature, stability and nutrients are likely to be the main factors governing this sequence.

5.2.1. GEOGRAPHY OF BLOOMS

The majority of reports of blooms or red tides have been made from near-shore waters (<10 nm out to sea) which are accessible and most readily investigated by marine biologists. There is little information on blooms found in deeper waters though WYATT (1979) showed that they are a frequent phenomenon; a conclusion which has been substantiated recently by the results from remote sensing studies. Most blooms occur near shore; the continental and Norwegian coasts are most at risk. Individual bloom forming taxa are found in relatively limited geographic areas suggesting that their physiological requirements are closely linked to specific hydrographic/chemical needs.

Using data from the Continuous Plankton Recorder Survey, REID *et al.* (1987) characterised seasonal patterns and long-term changes in the occurrence of blooms in the open waters of the North Sea. In the CPR data blooms represented by all organisms show a progressive movement in their centres of abundance from the North Sea into the north eastern Atlantic throughout the year. In the open North Sea blooms of diatoms are virtually restricted to the months of March to May. They develop first off the southern coast of Norway in March in the haline stratified waters of the Baltic outflow. The maximum frequency of diatom blooms occurs in April and further to the north west in May coinciding with the establishment of stratification. By June diatoms are a minor part of the phytoplankton in almost the whole North Sea.

Blooms of *Ceratium* start to appear on the western and southern margins of the stratified area, a pattern that is consolidated in the following month. As the CPR only samples at 10 m the machine may not be adequately sampling these dinoflagellates which may be present at greater depths. Evidence from other surveys (*e.g.* STADEL, 1968) suggests that dense bands of *Ceratium* occur every year at depths of 20-30 m in the thermocline throughout the central North Sea. By September/October this dominant feature of the central North Sea summer phytoplankton is evident as a band of blooms with an east-west axis from approximately Newcastle to the Skagerrak.

Phytoplankton Colour which is a visual estimate of chlorophyll based on the colour of the CPR silks indicates the importance of blooms of other algal groups at certain times of the year. For example, high 'Colour' in the southern North Sea from May to September which cannot be explained by diatoms or *Ceratium* is consistent with the known occurrence of *Phaeocystis* off the Dutch coast. A high colour intensity in the central North Sea in October/November may be attributable to late blooms of large diatoms like *Odontella sinensis* and *Coscinodiscus* spp, which are not numerically abundant, but are large and contain numerous chloroplasts.

Coccolithophorids are frequently recorded in CPR samples. They may form spectacular blooms in the central and northern North Sea during the summer months and formed an important component of the phytoplankton in the Fladen Ground in 1984 (CADÉE, 1985; GIESKES & KRAAY, 1986).

Frequency

An analysis of bloom occurrence in the Oslo Fjord since the early twentieth century by TANGEN (1979) showed no trend of increasing frequency. The 1984 symposium came to a similar conclusion (PARKER & TETT, 1987), qualifying the statement by noting that the data input is limited. In particular, it must be remembered that most reports of blooms are only from surface water and may not give a true representation of the extent and spatial coverage of the phenomenon. Reports of blooms in the last two decades in the North Sea are included in tables compiled by MOMMAERTS (1985, 1986a, b). These records are drawn from scattered und unrelated surveys and provide evidence for a bias towards sea areas such as Norwegian coastal waters where intensive studies of phytoplankton have been carried on for a long time. There is no evidence for an increasing trend in the frequency of blooms in Mommaerts' data, but they do provide evidence for an increase in the number of blooms in particular years, namely, 1968, 1971, 1977, 1978, 1982, 1984. Like the *Chrysochromulina* bloom in 1988 many of the years experienced higher levels of snowmelt and run-off contributing to increased nutrient inputs and intensified stratification.

5.4. TOXIC PHYTOPLANKTON

A range of phytoplankton taxa of which dinoflagellates are the dominant group have been shown to contain toxins which may lead to massive mortality of marine life or be transferred through the food chain to man, leading to severe illness or sometimes death. Species from which toxins have been isolated may not always contain poisons and distinguishing characteristics between species or varieties that are toxic, or not, or the conditions which induce possible temporary toxicity are still the subject of considerable debate and are poorly understood.

High concentrations are not essential for toxic taxa as some species which are the supposed source of toxins in the North Sea need only occur at concentrations of 20,000 l^{-1} to induce toxicity in shellfish. Highly toxic resting cysts, containing up to 10 times the toxin of vegetative cells, may be an alternative source of poison to benthic organisms and may be the source of toxins well after the species disappears from the water column (DALE & YENTSCH, 1978).

Known or potentially toxic algae recorded or possibly occurring in the North Sea can be divided into 10 groups based on the taxa and proven or inferred associated poison.

1. *Gonyaulax tamarensis* complex - Paralytic Shellfish Poisoning 2. *Dinophysis* species - Diarrhetic Mussel Poisoning 3. *Prorocoentrum* species - Venerupin Shellfish Poisoning 4. *Gonyaulax polyedra* - Paralytic Shellfish Poisoning·5. *Gyrodinium aureolum* - Ichthyotoxin 6. *Chatonella* - Ichthyotoxin 7. *Dictyocha fibula* - Ichtyotoxin 8. *Chrysochromulina* - Ichtyotoxin 9. Species in which toxic products have been found in culture. 10. Species that are believed to be non-toxic but have been implicated in fish kills.

5.4.1. PARALYTIC SHELLFISH POISONING

The taxonomy of this group is the subject of much wrangling. A clear distinction or synonymy between the type species *G. tamarensis* and *G. alexandrium/G. excavata* is still not universally accepted; they are thus referred to as a complex here. Outbreaks of PSP have occurred on a recurrent basis on the north east coast of Britain and along the Norwegian coast in the spring and early summer months (April to July), specifically in the Oslofjord, Trondheimfjord and near Bergen, Nesset, Sognefjord and Ronsdalfjord (AYRES & CULLUM, 1978; TANGEN, 1983; WEST & CULLUM, 1986). A mass mortality of fish in an enclosed fish farm in the Faeroes was linked to this complex and by implication farms in the Shetlands and Orkneys are at risk.

The last major outbreak of PSP in Britain was in 1968. While levels of toxin found then have not been seen since a regular monitoring programme has shown that highly toxic shellfish are found in nearly every year. A similar monitoring system was established in Norway after 1962. The extremely high PSP titre of 42,000 mouse units found near Bergen in June 1980 (TANGEN, 1983) was comparable with the maximum values recorded in the 1968 event near Holy Island, England (WEST & CULLUM, 1986). High levels of toxicity may also be found in the benthic resting cysts of these dinoflagellates (DALE & YENTSCH, 1978). Cysts were recorded as common (15,000 l^{-1}) during peak mussel toxicity off Holy Island in 1970 by AYRES & CULLUM (1978). Blooms of 'tamarensis' are not necessary to produce PSP; continued exposure to low concentrations (>4000 cells l^{-1}), of the organisms appears to be sufficient to induce toxicity. *Gonyaulax polyedra*, which is a common species in European waters, has been implicated in PSP toxicity elsewhere in the world.

5.4.2. DIARRHETIC MUSSEL POISONING

The symptoms of this poisoning are sickness, diarrhoea and fever induced after eating mussels contaminated with DMP toxins. The relationship between DMP toxins and dinoflagellates of the genus *Dinophysis (D. fortii)* was first discovered in Japan, but toxic compounds have not yet been proved to occur in North Sea representatives of the genus. *Dinophysis* type toxins have been identified, however, in shellfish at a time when the related species *D. accuminata* was common in Dutch offshore waters (KAT, 1988). Shellfish con-

taminated by DMP have been observed regularly in Dutch coastal water (E. Scheldt and Wadden Sea) since 1961 (KAT, 1982b), and in Norwegian Fjords (Oslofjord, Sognefjord and near Bergen) on three occasions since 1971 (TANGEN, 1983).

5.4.3. VENERUPIN SHELLFISH POISONING

Prorocentrum minimum, the dinoflagellate linked to this type of poisoning in Japan, is an ubiquitous species in the North Sea and may at times occur in large numbers *viz.* $1777 \cdot 10^6$ cells l^{-1} in Oslofjord (TANGEN, 1983). TANGEN (1983) suggested that an epidemic outbreak of mussel poisoning where 40 people were affected at Tvedestrand was a possible example of VSP since large populations of *P. minimum* were present in the affected area. There is no standard bioassay for this poison and no studies have been made of possible toxins in North Sea species.

5.4.4. ICHTHYOTOXIC SPECIES

Gyrodinium aureolum

This species was first documented in European waters in 1966 by BRAARUD & HEIMDAL (1970) when it occurred in dense populations along the whole Norwegian coast; a pattern that was repeated in 1976 (TANGEN, 1977). It was also noted off Plymouth in the United Kingdom at about the same time (BOALCH, 1987) and became a dominant alga of frontal systems in the entrance to the English Channel (HOLLIGAN, 1979) and in the eastern North Sea (RICHARDSON & KULLENBERG, 1987). The species shows many of the characteristics of an immigrant phytoplankter occurring in bloom concentrations for the first few years until a new balance is assumed and appears to show a progressive colonisation of new waters. Mortality of littoral marine animals and farmed fish is often associated with blooms that may reach concentrations $>30 \cdot 10^6$ cells l^{-1}. In shallow areas migration or sinking of blooms to the bottom may cause deoxygenation of bottom waters. WIDDOWS *et al.* (1979) showed that *G. aureolum* produced or contained a substance cytotoxic to mussels. This toxin causes gill lesions in caged salmonid fish, is heat stable and its production appears to be mediated by high levels of biotin in cultures (TURNER *et al.*, 1987).

Silicoflagellates

A variety of *Distephanus speculum* without a siliceous skeleton formed a bloom (9 to $25 \cdot 10^6$ cells l^{-1}) in Danish coastal waters of the Kattegat in early May 1983 (THOMSEN & MOESTRUP, 1985). The bloom spread to the north-east causing mortality of fish in Als and Langeland Sounds.

Chrysochromulina polylepis and other small flagellates

In the spring of 1988 massive fish kills and mortality of a range of other marine organisms, including benthic macro-algae, affected extensive areas of the Swedish and Norwegian coasts. Blooms of *Chrysochromulina* were implicated as the cause and the species has since been shown to be acutely toxic to eggs and larvae of an ascidian and the mussel *Mytilus*. The toxin may be similar to the haemolytic exotoxin of the related freshwater species *Prymnesium parvum* which may cause massive fish mortality.

6. REMOTE SENSING: A NEW TOOL

Images of the North Sea made by the Coastal Zone Colour Scanner (CZCS) on Nimbus 7 are available from 1978. Much of the information is still on file. Processing these data and producing an Atlas with selected, cloud-free or cloud-poor scenes is a difficult task (*e.g.* MITCHELSON *et al.*, 1986; VIOLLIER & STUMM, 1984). Appropriate algorithms have yet to be calculated to retrieve chlorophyll from the signal and correct for aerosol scatter, presence of particulate detritus and other suspended matter, and dissolved yellow substance, all masking the phytoplankton signal. A full set of calibration data has still to be developed, but this cannot be achieved yet because there is a general lack of calibration measurements of the most important bio-optical properties, in both coastal and sediment-rich areas. Regions with much dissolved organic matter near rivers or in the North Sea influenced by the Skagerrak can be expected to affect the signal received by the satellite-borne scanner most.

The CZCS, which was launched in 1979 and continued to operate until 1986, has obtained synoptic images of near-surface concentrations of phytoplankton pigments and suspended sediments by detecting the backscattered radiance in the following spectral bands: around 443 nm (blue chlorophyll and carotenoid absorption); 520 nm (green; chlorophyll correlation); 550 nm (yellow; 'Gelbstoff', yellow substance); 670 nm (red; chlorophyll absorption). Surface vegetation (*e.g.* macroalgae) was scanned in the 750 nm range (far-red), and surface temperature in the infra-red (11.5 micrometers). Many scenes of the situation in the Pacific, the Atlantic, and the Southern Ocean are now available from the US National Aeronautics and Space Administration, Goddard Space Flight Center, Space and Earth Sciences Directorate, Greenbelt, MD 20771, U.S.A; but few scenes of the North Sea have been published until now. Those that have been processed show the occurrence of blooms, the distribution of optical properties related to fronts, and other interesting oceanographic features related to phytoplankton distribution. We present as Fig. 11 a picture of features

associated with suspended matter and algal distribution patterns that could not have been viewed in any other way. This imagery is a colour composite of CZCS channels 1, 2 and 3 which have been processed to remove molecular and aerosal scattering in the atmosphere. Areas with both higher levels of chlorophyll and high sediment load appear as darker colours.

Within the phytoplankton community one taxonomic group can readily be distinguished if present in significant amounts, *i.e.* corresponding to 'bloom' levels of 2-3 μg chlorophyll a per liter: the Coccolithophorids (Haptophyceae). A reflectance signal is generated by their calcite scales and by detached coccoliths. Typical maximum reflectance values as measured by CZCS are about 1 gram $CaCO_3$ per m^3 surface seawater. The influence of coccolith reflectance on the chlorophyll algorithm is hard to define; maximum reflectance is seen in Channel 1 and significant reflectance in Channel 4 (HOLLIGAN *et al.*, 1983). *Emiliania huxleyi* is the most important Coccolithophorid species in the North Sea, mainly restricted to the north. It should be noticed that wax esters of copepods can give a similar signal on remote sensing pictures.

Because of the feasibility of remotely sensing blooms of other taxonomic groups individually it will in the future be useful to study phytoplankton with all the characteristics determining its optical signature, including chlorophyll *b* and *c* and all the various carotenoids, preferable by HPTLC and HPLC. It is known that blooms of plankton colour the surface of natural waters in various shades of green, brown and red, often corresponding to the dominant pigments contained in the bloom-forming organisms: 'red tides' by red peridinin containing dinoflagellates, 'brown tides' by *Gyrodinium aureolum*, the dinoflagellate not containing peridinin but rich in 19' hexanoyloxyfucoxanthin; 'orange tides', looking like paint, caused by *Noctiluca miliaris*; greenish hues where apple green algae dominate; and pinkish shades of purple of *Mesodinium rubrum*, a flagellate containing Cryptophycean symbionts (GIESKES & KRAAY, 1983). The concentration of all these pigments can readily be measured by modern chromatographic methods. Pigment degradation products may be indicative of the presence of detritus, and

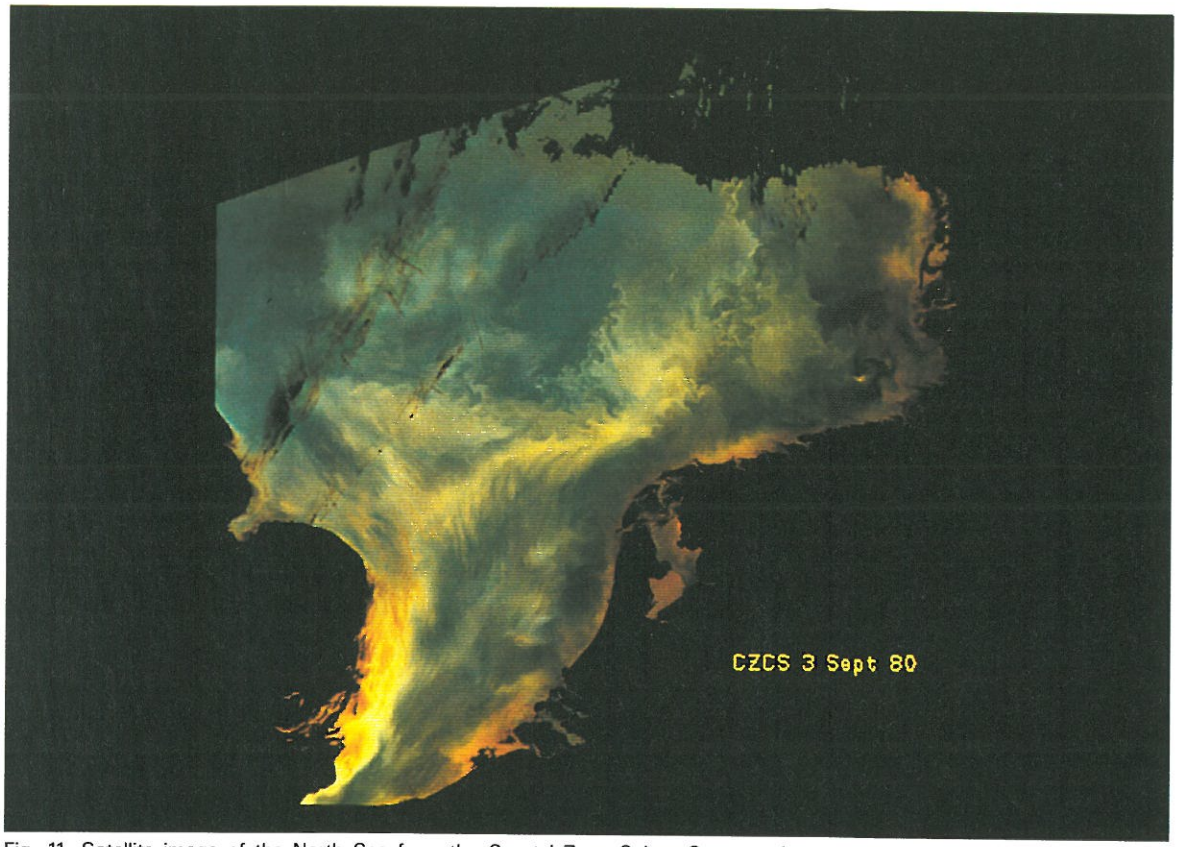

Fig. 11. Satellite image of the North Sea from the Coastal Zone Colour Scanner. A composite of channel 1 to 3 processed to remote scattering due to atmospheric processes; Mercator projection. The high reflectance and white colour portrays an extensive coccolithophore bloom in the northern North Sea. The dark tones in the southern North Sea partly reflect suspended sediment loads. Image processed by S. Groom, NERC Image Analysis Unit, Polytechnic South-West, Plymouth PL 4, 8AA, U.K.

we recommend that the absorption spectra of total suspended matter, readily measured on material freshly collected on glass fiber filters, be measured frequently during all cruises in order to provide us with a better insight into the contribution of detritus to total light absorption.

This detrital absorption due to sediment and yellow substance and living plankton absorption together influence the remote sensing signal. It is of importance to distinguish these individual contributions to absorption because an important goal of remote sensing imagery analyses is to estimate primary production from satellite measurements. The parameters of models of the dependence of water column productivity on chlorophyll and irradiance are variable, especially of phytoplankton, which are influenced by absorption by other suspended matter. It is imperative that we develop the capacity to partition light attenuation in its components, and estimate the fraction of light absorbed by phytoplankton detritus, sediment, etc. An analysis of satellite imagery other than that by CZCS, *e.g.* that derived from LandSat, may help in the determination of the distribution of total suspended matter (in the open North Sea consisting mostly of phytoplankton during blooms, near the coasts mostly sediment at all times of the year). Temperature, another factor of great importance to the amount of primary production per unit clorophyll per unit of incident photosynthetically active irradiance (the light utilization index: see CAMPBELL & O'REILLY, 1988) is also amenable to remote sensing techniques.

7. CONCLUSIONS AND RECOMMENDATIONS

An overriding impression on completing this review is the great complexity of phytoplankton dynamics in the North Sea as visualised spatially in the surface layer from CZCS satellite imagery and vertically in the water column, over short and long time periods and in the biology and taxonomy of the represented organisms. Algal succession often does not follow a classical pattern and species groups may reappear and 'flower' more than once in a year. The North Sea cannot be considered as one unit either geographically or vertically, but is divisible into a number of sub-regions which have characteristic floras.

When the historical record of phytoplankton surveys in the North Sea was evaluated we were struck by the inadequacy of the coverage in both time and space. The majority of surveys were in spring and we know little of the distribution of phytoplankton in winter, summer and autumn months. Some areas of the North Sea have been studied intensively and others hardly at all and the one detailed survey over more than twelve months by LOUIS *et al.* (1974) was restricted to the western North Sea. While the Continuous Plankton Recorder is an exception to these comments because of its frequent and wide coverage it provides only a semiquantitative measure of phytoplankton, at one single depth. There is, however, considerable scope for a greater evaluation of the phytoplankton archive in the CPR data base. The recent German ZISCH programme, the British North Sea Project and the EEC *Phaeocystis* project give opportunities for a very necessary improvement in the survey of North Sea phytoplankton.

Chlorophyll a is usually used as a measure of phytoplankton biomass, but we want to stress again the variability in chlorophyll to carbon ratios. It is envisaged that shipboard and remote measurement of chlorophyll a will remain a standard technique for measuring gradients of algal distribution well into the future.

Despite all this complexity we now have a sufficient understanding of physical and physiological processes governing net phytoplankton growth in mixed waters to be able to model this process. One of the achievements of this review is a comparative assessment of net growth in two contrasting areas of the North Sea during the spring bloom, for Belgian coastal waters and the Fladen Ground. The little information that is available in earlier literature on production rates using the ^{14}C method needs careful evaluation as rates are highly dependent on the methodology used, the incubation period, the filtration procedure, and the physiological state of the algae. A good agreement was found between different methods such as oxygen, CO_2 and ^{14}C determinations. Gross excretion by phytoplankton was shown not to be an important process in North Sea phytoplankton whereas secretion may range up to 64% of photosynthesis; it is inversely correlated to the inorganic nitrogen content of the seawater.

Technological advances in field measurements, satellite remote sensing and modelling have greatly improved our understanding of the physical environment of the North Sea. Evaluation of earlier phytoplankton literature and new data shows that distribution patterns are closely linked to hydrographic regions and boundaries with a primary emphasis on water stability and turbidity linked to light penetration; of the complex factors governing phytoplankton life and death, two stand out as needing further study: parasitism and dormancy.

Our review has also drawn attention to the distinction between changes in the open North Sea and coastal waters. Eutrophication, the effect of elevated nutrients levels on phytoplankton, is clearly visible in continental coastal waters, but not offshore. Moreover, eutrophication has not increased greatly since the late seventies, whereas microflagellates seem to have continued to rise in abundance. Even the length of their season of occurrence seems to have increased. The question is, where do the products of phytoplankton end up? Do they sink

and concentrate at fronts, do they accumulate in the Wadden Sea, do they end up as foam on beaches or settle into the Norwegian trench?

A final concluding remark is related to blooms of algae. Blooms are natural phenomena; there is no evidence for an increasing trend in their frequency with the possible exception of *Phaeocystis*. However, the CPR time series 1931-1989 indicates a progressive decline in *Phaeocystis* from 1948 to present. Furthermore, Dutch work suggesting an increase of this species does not take into account the large and extensive blooms reported from the 1920/30s in the Southern Bight. Some years do stand out in the North Sea with higher numbers of blooms; these years coincide with periods of higher snowmelt, rainfall and river runoff, possible causing heightened stability of the water column and certainly increased levels of nutrient input (GIESKES & SCHAUB, 1990). There is evidence to suggest that deoxygenation periods in the early 1980s and other negative impacts from blooms coincided with a period of high runoff and low salinity in the North Sea.

What needs to be done in the future?

First, there is a need for a return to the microscope complementing 'bulk' measurements with new ways of studying species at a fine scale. After many years of promoting primary production modelling effort and chemotaxonomy we need material to explain succession phenomena by studying why, when and where species occur. The response of taxa to changing environmental conditions should be studied in parallel in the laboratory, setting up single and multiculture experiments to evaluate ecophysiological processes and interactions.

Second, the processes involved in lysis, breaking, death, decay, sedimentation and transport of suspended organic matter derived from algal growth need to be studied in more detail.

Third, phytoplankton biologists and ecologists should work closely with modellers to provide the information necessary at the first trophic level to build accurate predictive models of the important levels of the marine ecosystem. Through observation we can improve our understanding but models can also be a tool to help understanding, to indentify gaps in knowledge, and enable policy makers to evaluate the effects of different options.

Fourth, improved cooperation with physical oceanographers should be encouraged since physical phenomena, light and turbulence especially, determine phytoplankton growth. Collaboration at this level is especially important in improving our understanding of bloom dynamics.

Fifth, a secure future should be guaranteed to the few long time-series of phytoplankton observations that have been made in the North Sea such as the Continuous Plankton Recorder survey, and on a local scale by CADEÉ near Texel and by German workers near Helgoland. These observations are essential to understanding long-term variability, to climatic changes and to evaluation of anthropogenic impacts on the coastal and offshore North Sea ecosystem.

Sixth, the development of new techniques to characterise the activities of individual species in the field should be stimulated. Flow cytometry, immunological techniques and aspects of modern cell biotechnology are examples of new methodologies still at the development stage.

Seventh, in order to interpret satellite images we need more information on the bio-optical signals of suspended matter and phytoplankton. Development of this work and future plans to launch new sensor packages will require continuing partnership between European and American laboratories.

Eighth, the role of phytoplankton in the biogeochemical cycling of many important elements such as manganese and sulphur must be studied intensively.

Ninth, an improved understanding of the relationship of nutrient dynamics to algal growth and succession needs to be determined. This should include work on the relative effect of different nutrient ratios, allelopathic interactions, and the effect of reduced nutrient loadings to the North Sea as agreed by the North Sea Ministers.

8. REFERENCES

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