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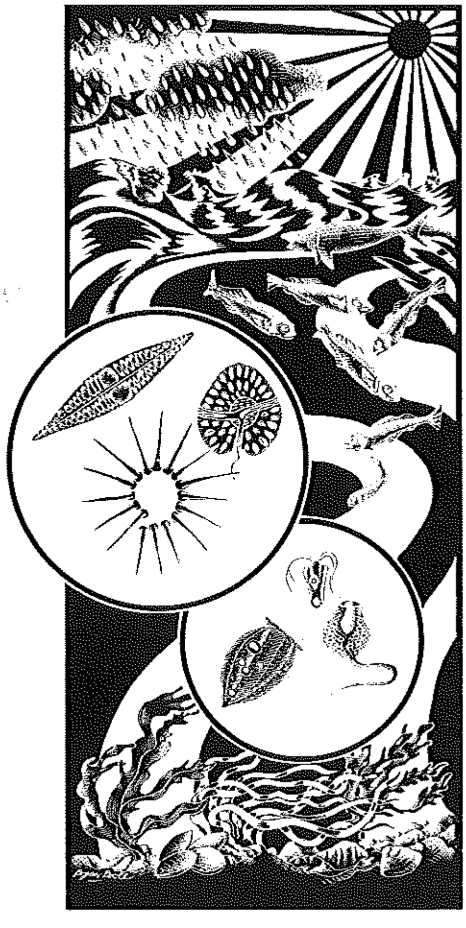
A Synthesis of Phyto- and Zooplankton Dynamics of the North Sea Environment



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"A Synthesis of Phyto- and Zooplankton Dynamics of the North Sea Environment"

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A SYNTHESIS OF PHYTO- AND ZOOPLANKTON DYNAMICS IN THE NORTH SEA ENVIRONMENT

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CONTENTS

VIII. GLOSSARY

I. A GENERAL INTRODUCTION TO THE NORTH SEA PLANKTON AND ITS ENVIRONMENT

The word "plankton" was introduced in the early days of marine research by Victor Hensen (Hensen 1887). It is derived from the greek word "πλαγκτος" which literally means to wander about. Hensen used this conception to circumscribe those organisms that live freely in the water and which because of their limited locomotive powers are subject to external hydrographic forces like currents or turbulence.

Plankton comprises both bacterio-, plant (phyto-) and animal (zoo-) plankton. It ranges in size from minute one-celled organisms to large jelly fish. Most of its animal and some of its bacterial and algal constituents can actively swim. However, being in general of rather small size, their absolute speed is slow in relation to the current speed and turbulent diffusion.

In order to understand the plankton distribution patterns in the North Sea some knowledge on the current patterns is necessary. But as will be shown later the relation between plankton and hydrography goes further than the mere transport of organisms: Hydrodynamics determine to a large extent the structure of the plankton community.

I.1 THE NORTH SEA ENVIRONMENT

I.1.1 Geography and Hydrography

The North Sea is a shallow basin that gradually deepens from appr. 30 m in the south to 200 m in the north. It encompasses a surface area of 575.000 km^2 (Kossinna 1921). Two of the most pronounced geographic features are the Dogger Bank in the central North Sea with depths of appr. 20 m and a trench along the Norwegian coast - the Norwegian Trench - with a maximum depth of 705 m (Fig. I.1). Other areas that are frequently referred to in the forthcoming chapters are also indicated.

The Dogger Bank plays an important role in the hydrographic structure of the North Sea. It separates the North Sea in two hydrographically different parts:
The northern part is strongly influenced by water from the Atlantic Ocean. It is relatively deep (40-200 m) and during summer much of the area is stratified. The influence of Atlantic water in the northern North Sea reaches to the northern margin of the Dogger Bank.
The southern part is shallow (20-40 m) and in most areas the water column is mixed throughout the year. Here Atlantic Water intrudes via the Dover Channel. In contrast to the northern part, the southern North Sea is under strong continental influence since it receives most of the continental run-off.

The different water masses in the North Sea can be distinguished by their salinity. "Atlantic Water" is characterized by salinities >35‰. The major part enters the North Sea in the north between the Shetland Islands and the Norwegian coast. In general, it intrudes the North Sea deeper in winter than in summer. Atlantic Water entering the North Sea via the Dover Channel can be identified by a tongue with salinities >34.75‰.

Apart from oceanic influences, the North Sea also experiences strong continental influences. Along the Scottish, British and Continental coasts low salinity water masses are formed by the admixture of fresh run-off with Atlantic Water. Along the Scottish and British coast salinities usually lie between 34‰ and 35‰, along the Continental coast salinities reach as low as 29-30‰.

Another important water mass is the Baltic Sea outflow which enters the North Sea via the Kattegat and the Skagerrak in the northeast. It has salinities of 24-30‰ most of the year.

I.1.2 Currents

The most important hydrodynamic force in the North Sea is the tidal motion (Otto *et al.* 1990). It is among others responsible for the predominantly anti-clockwise residual currents that affect all North Sea coasts. Lee (1980) reviewed the various concepts about the North Sea current system (Fig. I.2): Two major currents enter the North Sea from the north and the north-west. The latter current splits up in two branches around 57°30' N. One heads directly to the Skagerrak in the east (Dooley 1974), the other follows the English coast southward. The major part of the southbound current branches off to the northeast around 53°N. It follows the southern margin of the

Table I.1: Flushing times of the ICES boxes (ICES 1983) and model estimates (Backhaus 1984).

Box	Flushing time (days) ICES estimate	Model Calculations min	- max
1	150	35	48
2	100	9	39
3'	1000*	13	41
3"	500*	15	30
4	70	21	29
5	70	10	27
6	50	41	61
7'	700*	32	49
7"	500*	31	39

* estimates are too high because turbulent diffusion was not considered (Becker 1990).

Dogger Bank and heads towards the Skagerrak. Between the Lancastershire Coast and the Dogger Bank an anti-clockwise gyre exists.

The Channel Water moves in an approximate northeasterly direction through the North Sea towards the Skagerrak. It mixes with the Scottish and English Coastal Water at its western margin. Along its eastern side it mixes with continental run-off. The latter mixture - called Continental Coastal Water- follows the continental coast northbound. It forms a complex system of gyres in the German Bight (Goedecke 1968). The Continental Water moves further along the Danish west coast and enters the Skagerrak as the "Jutland Current". In the Skagerrak a complex set of currents dominated by an anti-clockwise current exists (Tomczak 1968, Svansson 1975, Lee 1980): The Jutland Current moves along the northern Danish coast in an eastward direction and joins the north-flowing "Baltic Current". Together with run-off from Norway they form the "Norwegian Current" that follows the Norwegian coast first in a westward and then in a northward direction.

In the central North Sea currents are variable and depend on wind direction. The impact of wind has been illustrated by the model calculation of Backhaus & Meier-Reimer (1983) and Backhaus (1984).

I.1.3 Water Budget and Flushing Times

On average $1.8 \cdot 10^6$ m^3 of water enter the North Sea each second . The major part is of Atlantic origin (99.2%). Fresh water input only amounts to 0.8% of the North Sea input budget (Lee 1980). Of the total water input 72% enters the North Sea between the Shetland Islands and Norway, 18% enters between the Orkneys and the Shetlands and only 8% enters via the English Channel. Precipitation and evaporation balance each other (Becker 1983). To put these numbers in perspective: The inflow of Atlantic Water is about 820 times the mean discharge of the Rhine ($2.2 \cdot 10^3$ m^3 s^{-1}, RIZA 1982). The annual input of Atlantic Water ($63.8 \cdot 10^3$ km^3, Lee 1980) compares with a North Sea volume of 54 10^3 km^3 (Kossinna 1921).

Flushing times are defined as the amount of water advected into an area divided by the water volume of the area. It is a measure for how fast the water in an area is renewed. The ICES Flushing Group has proposed a water budget and calculated flushing times for 7 different North Sea regions. These so-called ICES boxes (Fig. I.2) were chosen on both hydrographic and biological criteria. The ICES (1983) estimates for the flushing times are listed in Table I.1. Lowest flushing times were estimated for the continental coast (50-70 days). In the northern North Sea values of 100-150 days were estimated. The estimates for the central North Sea and along the English coast are very high (500-1000 days).

Since no direct observations on flushing times are available, better estimates are only possible with numerical models. Backhaus (1984) presented the results of a baroclinic (wind-driven) three-dimensional model using real atmospheric data (January-June 1979, Table I.1). He concluded that "A fairly reasonable agreement with observations is obtained for the boxes 1, 2, 4, 5, 6 when the model estimates are extrapolated for an annual mean assuming that flushing times of the calm summer months are about a factor three smaller than those of the stormy winter months. However, considerable mismatches are obtained for the box regions 3 and 7". The reason probably is that the ICES estimates did not consider turbulent diffusion (Becker 1990, see also Otto in ICES 1983). Thus, the flushing times of the different ICES boxes are in the order of 10-150 days depending on location and season. The model calculations of BACKHAUS (1984) further illustrate the influence of wind on the currents and flushing times of the North Sea.

I.1.4 Stratification

Next to tidal motion and wind, temperature is the third factor of importance in the North Sea hydrodynamics. In summer, warming of the water can result in a layering of the water column (stratification) with the warmer, lighter water on top of the colder, heavier bottom water (both layers being separated by a thermocline). The importance of this phenomenon lies in:
(1) the oxygen supply of the bottom water,
(2) the influence on regional production and species composition (PINGREE *et al.* 1978).
Besides thermal stratification, stratification of the water column can also be caused by low salinity, relatively light water overriding high salinity, denser water (both water masses being separated by a halocline). This type of stratification can be found all year-round along the Norwegian coast where the outflow of the Baltic Sea forms a layer of 15-35 m deep on top of the saltier North Sea water (DIETRICH 1950) and sometimes also along the Dutch coast (POSTMA 1954) and in the German Bight (GOEDECKE 1968).
"DIETRICH (1954) has analyzed the factors controlling the degree of thermal stratification. The turbulence generated in the surface layer by the shearing stress of the wind creates a homogeneous mixed layer at the sea surface, the depth to which this layer extends increasing with increasing wind speed. In late spring and summer when the sea surface is receiving more heat than it loses, the mixed layer will be warmer than that below it and the two will become separated by a thermocline. However, turbulence also results from the friction of the sea bed on the tidal streams. The velocity of these decreases, usually logarithmically, as the sea bed is approached, and the resulting shear stress gives rise to vertical turbulence. In regions of strong tidal streams and sufficiently shallow depth this turbulence is so great as to reach up to the surface mixed layer, and thus there is sufficient vertical turbulence throughout the water column to ensure mixing from the sea surface to the sea bed so that the formation of a thermocline is prevented." (From LEE 1980).
In short: summer (temperature) stratification and haline stratification cannot take place when tidally induced turbulence reaches throughout the entire water column. The so-called Simpson-Hunter criterion h/u^3 (SIMPSON & HUNTER 1974) relates the water depth (h) with the tidal current velocity (u). Below a certain value (350 m^{-2} s^3, PINGREE & GRIFFITHS 1978) stratification cannot occur. PINGREE *et al.* (1978) used the Simson-Hunter relation to calculate where the North Sea can be expected to be stratified (Fig. I.2). The thermocline is usually found at a depth of 20-40 m. It should be noted that the water column off the Norwegian Coast has a permanent haline stratification.

I.1.5 Fronts

Fronts are the bounderies where two water masses meet. Their hydrodynamics have been described by OTTO *et al.* (1990) and VAN AKEN *et al.* (1987). One type of front, the so-called tidal front, is found where a stratified water mass meets a tide-induced vertically mixed water mass. These fronts can be expected to occur in the transition zones between the stratified and well mixed water masses shown in Figure I.2.

Along the tidal fronts deep nutrient-rich water can be mixed across the front into the well mixed (surface) layers. This results in an enhanced primary production generally observed in frontal areas (*e.g* PINGREE *et al.* 1978, CREUTZBERG 1985). Another mechanism leading to an enhanced productivity is the mixing of two water masses each of which is depleted with another nutrient (LODER & PLATT 1985). Examples of frontal zones and their influence on local productivity will be given later when the different subareas of the North Sea are described.

I.1.6 The Distribution of the Major Nutrients

Strictly speaking, a description of the chemical environment in relation to phytoplankton growth should take into account both all the chemical factors necessary for growth, *i.e.* inorganic macronutrients (nitrogen as NO_3^-, NO_2^- or NH_4^+, phosphate and silicate), organic N- and P-compounds, essential metals (*e.g.* Fe, Cu, Zn, Mn), vitamins but also toxic substances like haloginated hydrocarbons. Here we restrict ourselves to macronutrients which at the moment probably exert the strongest influence phytoplankton composition, biomass and in consequence zooplankton dynamics. The subject of toxicants will be dealt with in chapter IV.

The distribution of nutrients is studied best in winter when phytoplankton growth is at a minimum (VAN BENNEKOM & WETSTEIJN 1990). One of the best data sets covering the entire North Sea were collected during the ZISCH project (BROCKMANN *et al.* 1990). Figure I.3a-d shows the distribution of phosphate, nitrate+nitrite, ammonium and silicate during winter 1987 (January 28th-March 6th). With the exception of ammonium, the nutrients show a more or less comparable distribution pattern. In general, lowest concentrations were found in the central North Sea (phosphate <0.5 $\mu mol{\cdot}dm^{-3}$, nitrate+nitrite < 6 $\mu m{\cdot}dm^{-3}$ and silicate <5 $\mu m{\cdot}dm^{-3}$). The extreme low silicate levels in the Dogger Bank area (<1 $\mu mol{\cdot}dm^{-3}$) are caused by an early diatom bloom (BROCKMANN *et al.* 1990, RICK 1990). Concentrations all increased towards the coasts as a consequence of an increased admixture of fresh, nutrient-rich water. Phosphate concentrations up to 3 $\mu mol{\cdot}dm^{-3}$ and silicate and nitrate concentrations above 50 $\mu mol{\cdot}dm^{-3}$ were observed. Of course, these concentrations will be higher near the river mouths as the fresh water contribution increases (*e.g.* VAN BENNEKOM & WETSTEIJN 1990, WEICHART 1986). In the Atlantic Ocean Water nutrient concentrations (phosphate ~0.75 $\mu mol{\cdot}dm^{-3}$; nitrate ~10 $\mu mol{\cdot}dm^{-3}$, silicate ~6 $\mu mol{\cdot}dm^{-3}$) are higher compared to the central North Sea. The Atlantic Ocean thus acts as an important source of nutrients for the North Sea.

During summer, the nutrient concentrations are generally very low (*e.g.* BROCKMANN *et al.* 1990). WOODWARD & OWENS (1990) studied the nitrate and nitrite distribution during July 1987 using an extremely sensitive chemoluminescence detection method. Their results showed that nitrate and nitrite levels are extremely low (NO_3^- <10-100 nm dm^{-3} and NO_2^- <5-100 nm dm^{-3}) over large parts of the North Sea. N/P levels were also very low (<0.1 compared to ±16 in winter) indicating that during summer the phytoplankton was potentially nitrogen limited. This is supported by *in situ* nutrient uptake studies by RIEGMAN *et al.* (1990a).

I.2 THE PLANKTON DWELLERS

Plankton comprises both bacteria (bacterio-) plant (phyto-) and animal (zoo-) plankton. In this review we will constrain ourselves largely to the phyto- and zooplankton. Phytoplankton generally spends all of its active life in the water column (holoplanktic, holopelagic). But some species of dinoflagellates or diatoms can form resting spores or cysts that survive adverse periods within or on the sediment. Zooplankton includes next to holoplanktic groups also so-called meroplanktic lifeforms like the juvenile stages of fish (nekton) and of benthic dwellers. Therefore, the planktonic realm or pelagial first constitutes the nursery and later the feeding grounds for these groups.

For practical reasons, the plankton is usually classified into different size classes (here after SIEBURTH *et al.* 1978):

☐ picoplankton (0.2-2.0 μm)
☐ nanoplankton (2.0-20 μm)
☐ microplankton (20-200 μm)
☐ mesoplankton (0.2-20 mm)
☐ macroplankton (2-20 cm)
☐ megaplankton (>20 cm)

Phytoplankton in the traditional sense, *e.g.* diatoms and dinoflagellates, belongs to the microplankton. Consequently, this group has been studied best. Recently, the pico- and nanoplankton, consisting of bacteria and small flagellates, has been given increasing attention. The zooplankton groups being studied best are megaplankton and macroplankton, mesoplankton and microplankton. The best studied zooplankton organisms, the copepods, are classified as mesoplankton.

The many different types of plankton are linked to each other by a multitude of uni- or bilateral "feeding and seeding" relationships: Phytoplankton generally depends on light and nutrient for production. Zooplankton may either feed on the primary producers or on other, smaller zooplankton organisms, itself nourishing the largest zooplankton like fishlarvae, euphausids and jelly fish. However, zooplankton not only harvests the phytoplankton, it also fertilizes the sea with its excretory products and degrades the plants for further mineralization. A large phytoplankton standing stock, as for example accumulated during the spring bloom, results in high sedimentation rates of degradable material, nourishing the benthic dwellers which in turn release their offspring to the plankton. Consequently, plankton, benthos (the bottom dwellers) and nekton (the active swimmers) are tightly coupled to each other.

Table I.2: *Summary of the major taxonomic classes of North Sea phytoplankton in approximate order of importance (after* Reid et al. *1990) and present study).*

Class	Size	Occurrence	Important representatives
Bacillariophycea	5-500 µm	ubiquitous, dominant during spring blooms	*Chaetoceros, Thalassiosira, Coscinodiscus, Rhizosolenia, Odontella*
Prymnesiophyceae[1]	5-15 µm; Colonies: 1-10 mm	ubiquitous, peaks usually after the spring diatom bloom	*Phaeocystis, Chrysochromulina, Emiliania*
Dinophyceae	5-200 µm	ubiquitous, main primary producer during sommer in central North Sea	*Ceratium, Gonyaulax, Alexandrium, Dynophysis*
Cryptophyceae	3-20 µm	common in coastal water, summer central North Sea	*Chroomonas*
Chrysophyceae		Minor component	Silicoflagellates (*e.g. Distephanus*)
Cyanophycea	1 µm	ubiquitous	*Synechococcus*

[1] Synonym: Haptophyceae

I.2.1 Phytoplankton

Reid *et al.* (1990) gave a short description of the different taxonomic classes represented by the North Sea plankton. It is summarized in Table I.2. Of particular importance for the North Sea are in order of their seasonal appearance: Bacillariophyceae, Prymnesiophyceae (synonym Haptophyceae) and Dinophyceae.

The most important group of algae are the Bacillariophycea or diatoms (Reid *et al.* 1990). They are solitary or colonial algae with an intricate cell wall made from silicate (H_4SiO_4). As will be shown later, these algae dominate the phytoplankton during the spring bloom in all North Sea areas. In most areas the diatom bloom is succeeded by a bloom of algae that do **not** depend on dissolved silicate (see chapter II). Especially Prymnesiophyceae are prominent after the vernal diatom bloom: Along the Belgian, Dutch and German coast the post-diatom bloom is dominated by the colonial alga *Phaeocystis* (Lancelot *et al.* 1987). In the northern and central North Sea other Prymnesiophyceae like the coccolithophorid alga *Emiliania huxley* (Braarud *et al.* 1953, Rick 1990) or *Corymbellus aureus* (Gieskes & Kraay 1986) also occur. Several other small flagellates (*e.g.* Cryptophyceae, Chrysophyceae; Wandschneider 1980, Rick 1990, Peeters & Peperzak 1990) and cyanobacteria (Howard & Joint 1989) can also dominate during summer. In the stratified parts of the North Sea the summer phytoplankton is further characterized by a high dinoflagellate biomass which peaks around August (Dickson *et al.* 1992).

I.2.2 Zooplankton

Practically every major group of animals has its planktonic representatives, which either spend all their life or only a certain part of it in the water column (Tab.I.3).

The total number of zooplankton species in the North Sea is >300 (de Wolf & Zijlstra 1988). Copepods, mostly holopelagic mesoplanktic crustaceans, generally constitute the predominant fraction of the zooplankton in terms of abundance and biomass all year-round. Only in the very shallow coastal areas like the Wadden Sea or *e.g.* the Limfjord, do other groups, such as meroplanktonic larvae of benthic dwellers, outnumber the copepods during certain time periods.

Copepods are the group with the highest diversity (number of species), 20 different species regularly occurring in the northern North Sea, including the five most common zooplankton species groups, *Calanus finmarchicus, Acartia* spp., *Temora longicornis,* the *Pseudocalanus group (P. elongatus, Paracalanus parvus, Microcalanus pusillus*) and *Oithona similis* (Rae & Rees 1947). Corresponding to a general increase in species diversity towards the open ocean (Bowman 1971), there are only about 7 copepod species with very high abundances in coastal waters,

Tab. I.3: *Some common taxonomic groups with zooplankton representatives.*

Phylum	common name	zooplankton representatives
Protozoa	single celled ...	oligotrich and tintinnid ciliates, radiolaria, foraminifera
Coelenterata	jelly fish	Hydrozoa (*i.e. Phialidium* sp.), Scyphozoa (*i.e. Aurelia sp.)*
Ctenophora	comb jellies	*i.e. Pleurobrachia sp., Beroe* sp.
Chaetognatha	arrow worms	*i.e. Sagitta spp.*
Annelida	polychaetes	*i.e. Tomopteris*
Crustacea (class)		Copepods, cladocerans, ostracods, mysids, euphausiids, amphipods, isopods
Urochordata (sub-phylum)	salps, appendicularians	
Mollusca	molluscs	Heteropods, Pteropods

compared to 12-25 main species in the oceanic regions (RUSSELL 1935, COLEBROOK *et al.* 1961a).

Euphausids occur in the North Sea with three oceanic species (*Meganyctiphanes norvegica, Thyssanoessa longicaudata*), restricted to the Atlantic inflow, and three typical North Sea forms (*Thyssanoessa inermis, T. raschi, Nyctiphanes couchi*). (GLOVER 1952, LINDLEY 1977, 1982a). In the southern North Sea, euphausids are rarely found (KRAUSE *et al.* in prep.). Due to the high species diversity in the benthos, there is a great wealth of meroplanktic decapod larvae (28 taxa, of which 8 taxa are found only NE of Scotland, LINDLEY 1987), lamellibranch (max. 40 species in October, REES 1951) and echinoderm larvae (NEWELL & NEWELL 1977) regularly occurring in the plankton. Two pteropod species (*Clione limacina, Limacina retroversa*), two chaetognath species (*Sagitta elegans, S. setosa*), and only one commoner species of amphipods (*Parathemisto abyssorum*) are found. Besides, the macroplankton consists of fish larvae, three regularly occurring species of scyphomedusae (*Aurelia aurita, Cyanea lamarcki, C. capellata,* HAY *et al.* 1990), two species of ctenophores (*Pleurobrachia pileus, Beroe cucumis*), one common trachymedusa (*Aglantha digitale*), and some anthomedusae.

In the microzooplankton (passing 200 µm gauze), there are 3 species of cladocerans (*Podon intermedius, P. leuckarti, Evadne nordmanni,* GIESKES 1971a,b) common in the North Sea plankton. Among the ciliates, non-loricate forms like *Strombidium* and *Lohmanniella* and loricate forms like *Tintinnopsis* are dominating (STEIFF 1988). *Noctiluca spp.* is a large heterotrophic dinoflagellate, known to form mass occurrences (UHLIG & SAHLING 1982).

In coastal and estuarine areas, the species diversity is generally diminished (DE WOLF & ZIJLSTRA 1988) due to the very variable and physiologically difficult living conditions. For an inventory of species occurring in the Dutch, German and Danish Wadden Sea and the Southern North Sea see FRANSZ (1980a).

II. PHYTOPLANKTON OF THE NORTH SEA

II.1 A GENERAL OVERVIEW OF THE PHYTOPLANKTON IN THE NORTH SEA

From the short description of the North Sea hydrography in the previous chapter it is clear that the North Sea is a sea of extremes. It comprises both shallow parts that are constantly well mixed and deep areas where the water column is stratified during summer, but also regions like the Belgian, Dutch and German coasts that are affected by heavily polluted rivers or areas like the northern North Sea that are strongly influenced by the practically undisturbed Atlantic Ocean. It is evident that in such a diverse system there is no such thing as a typical "North Sea Plankton".

Before the different regions -each of them with a unique hydrographic, geographic and chemical setting- will be dealt with in the next chapter (II.2), a short overview of the North Sea as a whole will be presented. First, some information about primary production in general and about the most important taxonomic groups will be made. Next, data sets of primary production and biomass that cover the whole or at least the major part of the North Sea will be presented. The bird`s eye view on the North Sea phytoplankton will finish with the description of long-term trends which have been observed throughout the open North Sea.

II.1.1 SOME GENERAL REMARKS ON PRIMARY PRODUCTION

The significance of the phytoplankton for the North Sea ecosystem is that it forms the basis of all food webs through its ability to transform light and inorganic carbon into high energy organic compounds through the process of photosynthesis. Together with inorganic nutrients like phosphorus (as HPO_4^{2-}), nitrogen (as NO_3^-,NO_2^- or NH_4^+) or silicium (as H_4SiO_4), vitamins (*e.g.* B_{12}) and numerous trace metals (like iron, copper, zink etc.) these organic compounds can be turned into new cellular componds.

The biogeochemical pathways of the newly formed organic carbon -the primary production- are numerous and take place on quite different time scales. Part of the photosynthetic products are released into the environment within minutes after their fixation by the algae and can immediately be re-mineralized by bacteria. On the other hand, some carbon will move through the entire food web (including the human population) before it is remineralized to its inorganic constituents. A small portion of the newly sequestered carbon might even get "permanently" buried in the sediment.

Photosynthetic carbon can be used by the algae for the formation of cell components (anabolism), as energy source for physiological processes (metabolism), it can be excreted or passively diffuse out of the algae. Excretion includes true excretion which can be useful during nutrient depleted conditions (see below) and secretion. The latter refers to the formation of an external organic matrix by some algae in which the individual cells are embedded and which is not directly available for bacterial consumption (REID *et al.* 1990). Examples of secreting algae are the colonial Prymnesiophyceae *Phaeocystis* spp. and *Corymbellus aureus* or the colonial diatom *Chaetoceros socialis* and the unicellular diatom *Coscinodiscus wailesii*. The latter was a nuisance to English fishermen during the 70's because the enormous amounts of slime produced by this alga clogged their nets (BOALCH & HARBOUR 1977a).

The amount of total photosynthetic carbon (or gross primary production) that is used for growth (formation of biomass) is the so-called net photosynthesis. The ratio between gross and net primary production depends on different factors like nutrient status, light conditions, motility and algal size: If enough nutrients are available the photosynthetic carbon can be turned into biomass. However, if carbon fixation exceeds incorporation into new cell material due to lack of nutrients release of excess photosynthates is observed (IGNATIADES & FOGG 1973, MYKLESTAD 1977, JOIRIS *et al.* 1982). Also, during saturating light intensities excess photosynthates can be excreted (WOOD & VAN VALEN 1990). It is obvious that active motility has a high energy requirement.

Several methods are used to estimate primary production, the most widly applied being the ^{14}C method (STEEMANN NIELSEN 1952). Basically, a sea water sample is spiked with radioactive bicarbonate ($H^{14}CO_3^-$) and after a certain amount of time (mostly 2-24 hours) the sample is filtered and the radioactivity on the filter is measured. Since part of the incorporated radioactive carbon is excreted again during the measurement this method yields results somewhere between gross production and net production. Alternative methods have been proposed on the basis of O_2 (TIJSSEN & EIGENRAAM 1980), phosphate budgets (WEICHART 1980) or ^{15}N incorporation (LANCELOT *et al.* 1986). The latter authors claim that nitrogen incorporation is a better measure for growth because it is built into macromolecules with a relatively low turn-over time as compared to photosynthetic metabolites, which are both actively and passively excreted. An overview of problems related to ^{14}C measurements is given by PETERSON (1980) and COLIJN *et al.* (1983).

The best measure for phytoplankton biomass obviously is its carbon content. This review, however, is restricted to the pigment content or more specifically the chlorophyll *a* (Chl *a*) content as an indication of biomass because this indicator was most widly used. As a rule of thumb Chla *a* can be converted into carbon content by multiplying with a factor of 50. However, when applying this conversion factor one should be aware of the large variation of C/Chl *a* ratios (*e.g.* DE JONGE 1980).

Comparability of primary production data is less complicated since almost all measurements were carried out with the radiocarbon method. Nevertheless, even here different approaches in estimating the daily production exist between the data sets. These differences will be addressed shortly when the data are presented.

II.1.2 PHYTOPLANKTON BIOMASS AND PRIMARY PRODUCTION

During the past 20 years only a limited amount of primary production data from the North Sea have been published (RIEGMAN & COLIJN 1991). Most of the primary production measurements were carried out in coastal water and only a few cover a complete annual cycle. Recently, however, a few data sets have become available that cover large parts of the North Sea (OWENS *et al.* 1990, RICK 1990, JOINT & POMROY 1992). These data sets will now be presented in order to give a general picture of biomass and primary production in the North Sea during different seasons.

The only quasi-synoptic data set (data aquisition took 6 weeks) of biomass and primary production covering the whole North Sea originates from the German North Sea project ZISCH (**Z**irkulation und **Sch**adstofftransfer in der Nordsee; circulation and transfer of pollutants in the North Sea). Biomass (as Chl *a*) and production data[1] are available for two seasons: winter (Feb. 1987) and summer (Mai/June 1986). There is a general agreement between biomass (as Chl *a*) and primary production distribution as might be expected. Therefore, only primary production data are presented.

During February 1987 the phytoplankton biomass generally was low (<3 $\mu g \cdot dm^{-3}$). Also in the continental coastal water biomass was little in excess of 3 $\mu g \cdot dm^{-3}$. Primary production rates of around 10-30 mg C hr^{-1} m^{-2} (~0.05-0.15 g C m^{-2} day^{-1}) prevailed over most of the North Sea. Three areas of high biomass and primary production were present: in the Skagerrak, in the Dogger Bank and in the off-shore area along the Dutch coast Chl *a* concentrations up to 15 $\mu g \cdot dm^{-3}$ and production levels up to 400 mg C hr^{-1} m^{-2} (1.1 g C m^{-2} day^{-1}) were observed (Fig. II.1a). During summer Chl *a* concentrations and primary production ranged from <1 to 5 $\mu g \cdot dm^{-3}$ Chl *a* and 20-200 mg C hr^{-1} m^{-2} (~0.15-1.5 g C m^{-2} day^{-1}) in the central parts of the North Sea. Along the Dutch and German coasts Chl *a* concentrations up to 10-20 $\mu g \cdot dm^{-3}$ and production levels up to 1000 mg C hr^{-1} m^{-2} (8 g C m^{-2} day^{-1}) were found. Especially in Dutch coastal water very high values were encountered (Fig. II.1b).

The importance of the ZISCH data lies in the fact that they give the first synoptic overview of various biologically relevant parameters over the entire North Sea during winter and early summer. However, the data set does not give any information on the duration of the algal blooms in the different parts of the North Sea and therefore no estimates of annual productivity are possible.

A second set of primary production and biomass data from the North Sea was collected during the UK NERC North Sea Project. The North Sea south of 56°N was sampled from August 1988 until October 1989 at monthly intervals. This data set gives a

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[1] It should be noted that primary production is expressed as mg C fixed per m^2 per hour. I have converted Rick's data to daily fixation rates by multiplication with half the day length (~5 for the winter cruise and ~8 for the summer cruise, c.f. CADÉE & HEGEMAN 1974).

unique picture of the development of phytoplankton growth in the central and southern part of the North Sea and for the first time allows a reliable estimate of primary productivity for off shore regions in the North Sea. In winter, primary production is generally low. Highest rates occurred in the central region (Dogger Bank Area). During early March carbon fixation rates exceeding 1 g C m^{-2} day^{-1} were observed. During April primary production had increased along all coasts. Highest production rates were encountered along the continental coast with maximum values in excess of 2.4 g C m^{-2} day^{-1} in the German Bight in May. Lowest primary production rates were found along the English coast.

During summer, extremely high production and biomass values disappeared from the entire North Sea except from the continental coast. In the central North Sea production decreased to low values and remained low during the rest of the year.

The late summer distribution of primary production in 1988 and 1989 -relatively high production values along the continental coast and low values elsewhere- showed great similarities suggesting a reproducable seasonal pattern in phytoplankton production (JOINT & POMROY 1992).

OWENS *et al.* (1990) presented primary production data aquired during July 1987, and covering the whole North Sea. They only measured primary production in surface samples and therefore their results are not directly comparable to the ZISCH and NERC data who gave production estimates per unit surface. In addition to total primary production OWENS *et al.* (1990) differentiated between production in the larger than 5.0 µm and smaller than 5.0 µm size fraction. During their survey much of the North Sea showed thermal stratification. Nutrient and Chl *a* concentrations in these regions were low and up to 75% of the primary production was attributable to algae <5.0 µm. In contrast, nutrient concentrations, biomass and primary production were higher in the well mixed coastal water. Here the majority of primary production occurred in the larger than 5.0 µm fraction. The results from OWENS *et al.* (l.c.) are in support of ideas that in stratified, nutrient poor areas primary production is dominated by small autotrophic algae whereas in nutrient rich, well mixed coastal water larger phytoplankter dominate (e.g. MARGALEF 1978, FOGG 1991, TETT & MILLS 1991). However, it should be noted that OWENS *et al.* only sampled the surface layer. Other studies in the stratified parts of the North Sea show the presence of high concentrations of larger phytoplankter within the thermocline (*e.g.* RIEGMAN *et al.* 1990a).

II.1.3 LONG-TERM CHANGES IN PHYTOPLANKTON BIOMASS

There are only few time series available that document the changes -both in species composition and in the seasonal cycle- that took place in the North Sea plankton community. The most prominent time series are those from the Plymouth Marine Laboratory (BOALCH 1987), the Netherlands Institute for Sea Research (*e.g.* CADÉE & HEGEMAN 1991a, b), the Biologische Anstalt Helgoland (BERG & RADACH 1985, RADACH & BOHLE-CARBONELL 1990, RADACH *et al.* 1990a) and the time series based upon the Continuous Plankton Recorder Survey (*e.g.* COLEBROOK 1986, REID *et al.* 1990). They reflect each in their unique way the reactions of the plankton community to a changing environment. The first three time series are based on observations of coastal areas carried out from near-by research institutes and therefore bear a strong influence of local conditions. For that reason they are not representive of the North Sea as a whole.

The only data set that overcomes the disadvantage of being too local originates from the Continuous Plankton Recorder Survey (hence called CPRS data). Since 1948 the plankton of the North Atlantic Ocean and the North Sea is surveyed routinely on a monthly basis using Continuous Plankton Recorders. The Plankton Recorder was originally developed for monitoring zooplankton. Because of the large mesh size (270 µm) it does not quantitatively sample phytoplankton. Nevertheless a considerable proportion of the phytoplankton is retained on the silks to color it and provide information on species occurrence and semiquantive estimates of abundance (ROBINSON & HIBY 1980).

The methods for assessing the phytoplankton on the silk changed in 1958. For that reason the time-series for phytoplankton are 10 years shorter that for zooplankton. The method applied can be summarized as follows: Plankton recorders are towed by merchant ships on regular routes at a standard depth of 10 m. The plankton is filtered on a slowly moving band of silk of 270 µm mesh that is stored in a formaline containing box. In the laboratory the silk band is cut into lenghts representing 10 miles of tow and the "content" of approximately 3 m^3 sea water.

Two indices of phytoplankton abundance are discerned: The first one is based upon the greenness of the silk. According to GIESKES & KRAAY (1977b) and REID (1978) the greenness is largely derived from microphytoplankton and flagellates that disintegrate in the formaline used to conservate the silk. Also the chloroplasts of larger phytoplankton that are disrupted can contribute to the greenness. The second index of phytoplankton abundance is based on counts of larger phytoplankter, mainly diatoms and dinoflagellates. These are not retained by the silk mesh which obviously is too large for phytoplankton, but are probably entangled in the individual threads of the silk twines. A recent example of the trends that have been observed during the Continuous Plankton Recorder Survey is presented in Figure II.2.

The most important aspect of the CPR data is that their unchanged methods have enabled to track changes in the plankton communities especially in "remote areas".REID (1975, 1977, 1978) showed that in the North Sea a general decline of diatom abundance was observed in the North Sea from 1958-1973. The decline was particularly clear for the summer, autumn and winter populations, *i.e.* a marked decrease in season length had taken place. This decline coincided with a delay of the spring phytoplankton maximum of about three weeks (GLOVER *et al.* 1972).
No common trend was observed for *Ceratium* spp. except for an earlier start in the southern and eastern North Sea during the 70's.
An interesting aspect was that changes in numbers of diatoms and *Ceratium* spp. were not reflected in the phytoplankton color index. Whereas the number of identifiable phytoplankton decreased, the phytoplankton color index (the greenness of the silk) increased over much of the North Sea. The organisms that are responsible for the color increase are not preserved on the CPR silk. REID (1975, 1977, 1978) and GIESKES & KRAAY (1977b) assumed that microflagellates are responsible for the increased phytoplankton color. They suspect that these organisms disintegrate in the formalin preservation solution but that their more resistant chloroplast added to the coloration of the silk[2].

COLEBROOK (1982a) described the year-to-year fluctuations of zooplankton and phytoplankton in the North-East Atlantic and in the North Sea from 1958-1980. It should be noted that in Colebrook's analyses the index of phytoplankton abundance was not the greenness of the silk but was based on the number of 18 abundant phytoplankter (12 diatoms and 6 species of *Ceratium*). Principal component analysis showed a common pattern of change -*in casu* a continuous decrease of abundance- for both the phytoplankton group and zooplankton.

COLEBROOK *et al.* (1984) noticed that a reversal of the downward trend of both zooplankton and most of the phytoplankton (see note above) had taken place around 1980. The same trend (*i.e.* a downward trend from 1946-1980 and an increase afterwards) was also observed for *Phaeocystis* spp. (OWENS *et al.* 1989). The upward trend of phytoplankton and zooplankton lasted at least until 1990 (CPR-SURVEY TEAM 1992).

II.1.4 NEWLY INTRODUCED SPECIES IN THE NORTH SEA

Since the early days of marine biology some conspicuous changes have occurred in the North Sea phytoplankton through the introduction of new species. In 1903, Ostenfeld (OSTENFELD 1908) observed a large new diatom *Odontella sinensis* which previously was only known from the Pacific Ocean. Since then species new to the area have frequently been observed. When dealing with the question about new species of phytoplankton in the North Sea, however, three different cases have to be discerned: true novel species not previously described, introduced novel species which were already known from other remote areas and species from adjacent areas which are only transported into the areas during exceptional hydrographic conditions. A listing of novel species introduced in the North Sea from other, remote areas is given in Table II.1. Much of the information is taken from BOALCH (1987).

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[2] Recently, the limited applicability of the "greenness" as a direct measure of phytoplankton standing stock was shown by HAYS & LINDLEY (1994).

Table II.1: *Novel species in the North Sea.*

Species	Author
Odontella sinensis	OSTENFELD (1908)
Coscinodiscus wailesii	BOALCH & HARBOUR (1977a)
Pleurosigma planctonicum	BOALCH & HARBOUR (1977b)
*Thalassiosira punctigera**	HASLE (1983)
Gyrodinium aureolum	BRAARUD & HEIMDAHL (1970)
Prorocentrum minimum	TANGEN (1983)

* When this species was first observed along the Dutch coast it was named *Thalassiosira angstii* (KAT 1982)

BOALCH (1987) noticed that in most cases the new arrivals made some sort of impact on the ecosystem and then settled down to occupy a rather insignificant part in the ecosystem. This statement seems to hold for the novel diatoms, although *Coscinodiscus wailesii* still can reach high biomasses in the German Bight (M. KRAUSE, pers. comm.). The last two algae of Table II.1, however, both represent flagellates that still are known for their frequent blooms (MOMMAERTS 1985, 1986a,b, SMAYDA 1990). *Gyrodinium aureolum* - a toxic dinoflagellate - now even is a dominant species in frontal areas of the English Channel (HOLLIGAN *et al.* 1984) and in the Skagerrak (RICHARDSON & KULLENBERG 1987).

Examples of species that are only found during changes in the general hydrographic conditions of the North Sea are the oceanic diatom *Thalassiothrix longissima* that was found in the North Sea from 1951/52 until 1958 and again in 1967 and 1989. Its presence coincided with the passage of oceanic water into the North Sea in the previous autumn and winter (REID *et al.* 1992).

A serious problem with the interpretation of novel species was put forward by SMAYDA (1990). Due to the recent interest in plankton and the concomittant observer effort, species are discovered that before were part of the hidden flora. Changed environmental conditions for instance can cause part of the hidden flora to proliferate. *Chrysochromulina polylepis* - well known because of the massive bloom in the Skagerrak in 1988 - certainly would have been an example of the deleterious effect of novel blooms if it had not previously been identified as a rare component of the indigenous community (SMAYDA 1990).

II.2 REGIONAL CHARACTERISTICS OF PHYTOPLANKTON DYNAMICS

II.2.1 INTRODUCTION

In the previous section an attempt was made to give a comprehensive picture in both space and time of the actual status of phytoplankton production and of long term trends in the North Sea as a whole. In this chapter the plankton dynamics in the different subregions of the North Sea will be discussed in more detail. We have chosen a compartmentation after ICES for two reasons. Firstly, the ICES division of the North Sea (ICES 1983, (Fig. I.2) is based on hydrographical characteristics but also recognizes biological criteria. Secondly, it has been agreed upon by the Ministerial Conference for the protection of the North Sea to prepare a Quality Status Report based upon the ICES subdivision (QSR, to be prepared by the North Sea Task force for the 4th Minister Conference for the protection of the North Sea). Following the same divisions renders some compatability of the present review with the official QSR.

For each subarea, the major hydrographic and chemical features will be addressed. Next, an overview will be given of the phytoplankton seasonal cycle including a compilation of primary production data and annual production

Table II.2: Compilation of primary production data from the northern North Sea (ICES 1, 2).

Week/Year	mean prim. prod. (g C m^2 day^1)	min. - max.	Reference
5-10/1986	0.06	0.05-0.07	Estimated from RICK 1990
09/1988	0.15		NIELSEN & RICHARDSON 1989
18/1976^F (during spring peak)	1.6	1.5-1.9	GIESKES & KRAAY 1980
20/1983^F	1.69	0.45-3.2	GIESKES & KRAAY 1986
18-24/1986	0.63	0.13-2.81	Estimated from RICK 1990
25/1976^F (after spring peak)	0.06	0.04-0.08	GIESKES & KRAAY 1980
28/1987^F	0.4		OWENS *et al.* 1990[1]
38/1984^B	0.35		RICHARDSON *et al.* 1986
41-42/1985^B	0.35		KIØRBOE *et al.* 1988a
Annual production	**125 g C m^{-2} a^{-1}**		own estimate: see text

[1] Estimated from Fig. 6 of OWENS *et al.* (1990)
^{F} Fladen Ground
^{B} Buchan Front (stratified side)
The location of the various areas can be found in Figure I.1.

estimates. If data are available, interannual phytoplankton trends will be addressed.

II.2.2 NORTHERN NORTH SEA (ICES 1 & 2)

The northern part of the North Sea is under a strong influence of the Atlantic Water which intrudes the area from the north and west. Depth ranges from 100-200 m in the northwest to 700 m in the Norwegian Trench. In winter the water column is completely mixed while during summer (May-October) a thermocline at approximately 20-40 m is present (TOMCZAK & GOEDECKE 1962). Nutrient concentrations in winter are relatively high compared to the central and western part of the North Sea (Si: ~5 µmol·dm^{-3}; P: ~0.8 µmol·dm^{-3}; N: ~10 µmol·dm^{-3}, LEE 1980, BROCKMANN & WEGNER 1985, BROCKMANN *et al.* 1990, RADACH *et al.* 1990b).

II.2.2.1 Seasonal cycle of phytoplankton biomass, primary production and dominant species

During winter, the biomass and primary production (Table II.2) are very low. RICK (1990) observed Chl *a* levels of 1 µg·dm^{-3} and an average primary production of 0.06 g C m^{-2} day^{-1}. NIELSEN & RICHARDSON (1989) measured carbon fixation rates of 0.15 g C m^{-2} day^{-1} along the eastern margin of ICES box 1 and 2 during the end of February 1988.

The spring bloom in the Fladen Ground area was extensively studied during the international Fladen Ground Experiment in 1976 (FLEX '76) and later in 1983 during REFLEX. Figure II.3 shows - as an example of the open North Sea phytoplankton bloom- the evolution of biomass (as Chl *a*) and nutrients during the FLEX study. The spring bloom started during the first week of April. Biomass first peaked during the last week of April with maximum values fo 12 µg·dm^{-3} (RADACH *et al.* 1980). It was dominated by diatoms, mainly *Chaetoceros* spp. and *Thalassiosira* spp. (WANDSCHNEIDER 1980). The collapse of the diatom bloom coincided with the depletion of dissolved silicate. A second peak (~3 µg·dm^{-3}) occured during the third week of May which was dominated by several species of flagellates like *Rhodomonas* spp., *Emiliania huxleyi* and *Phaeocystis* spp. (WANDSCHNEIDER 1980). The latter author presents a complete list of species observed during FLEX. The development of the spring bloom during the REFLEX experiment in 1983 was remarkably similar. The first peak occured during the first week of May and was dominated by diatoms (mainly *Chaetoceros* spp.). It was followed by a second peak two weeks later dominated by the Haptophycea *Corymbellus aureus*

(GIESKES & KRAAY 1986). Both FLEX and REFLEX data showed that primary production peaked during the spring bloom and reached values up to 3.2 g C m^{-2} day^{-1} with a mean value of 1.7 g C m^{-2} day^{-1} (GIESKES & KRAAY 1980, 1986).

During May and early June 1986 RICK (1990) observed a biomass of 1-2 $\mu g \cdot dm^{-3}$ and production levels of 0.63 g C m^{-2} day^{-1} which are in good agreement with the FLEX data. Phytoplankton was dominated by several diatoms (among others *Thalassiosira* spp.), *Phaeosystis* sp. and several *Ceratium* species. During July 1987 OWENS *et al.* (1990) found considerably lower Chl *a* values (<0.5 $\mu g \cdot dm^{-3}$). From their Figure 6 primary production rates of 0.35 g C m^{-2} day^{-1} can be estimated for the Fladen Ground area. Similar values were observed by RICHARDSON *et al.* (1986) and KIØRBOE *et al.* (1988) at the western margin of the ICES box 2 (stratified side of the Buchan front) during late summer and autumn. During summer and autumn phytoplankton is dominated by dinoflagellates (REID 1978, RICHARDSON *et al.* 1986).

II.2.2.2 Annual primary production

At present no production data are available for the northern North Sea that cover a complete annual cycle. A first estimate of annual production which was based upon the FLEX and REFLEX spring bloom data amounted in excess of 100 g C m^{-2} a^{-1} (FRANSZ & GIESKES 1984). On the basis of recent observations for winter and summer primary production the above estimate can be precised: FRANSZ & GIESKES (l.c.) used for their estimate a mean winter primary production of 0.3 g C m^{-2} day^{-1} for January-February. Recent primary production measurements in the northern North Sea, however, showed much lower winter values of appr. 0.06 g C m^{-2} day^{-1} (RICK 1990) and 0.15 g C m^{-2} day^{-1} (NIELSEN & RICHARDSON 1989). Thus a winter primary production of 0.1 g C m^{-2} day^{-1} seems more realistic. The winter period can be assumed to last from November to March. On the basis of FLEX and REFLEX data FRANSZ & GIESKES (l.c.) calculated a mean primary production of 1 g C m^{-2} day^{-1} during the spring bloom which is assumed to last from April-May. In June very low production rates of appr. 0.06 g C m^{-2} day^{-1} were observed by GIESKES & KRAAY (1980). The data of OWENS *et al.* (1990), RICHARDSON *et al.* (1986) and KIØRBOE *et al.* (1988) suggest a rather constant daily production from July-October of 0.35 g C m^{-2} day^{-1}. This is supported by the results of the CPRS Survey who observed rather constant biomasses throughout the summer in this area (COLEBROOK 1979). Using the above estimates an annual primary production in the northern North Sea (ICES 1-2) of 125 g C m^{-2} a^{-1} is proposed.

II.2.2.3 Recent chemical and biological changes

No data other than the results from the Continuous Plankton Recorder Survey are available that show long-term changes in this area. These have already been presented in chapter II.1.

II.2.3 SCOTTISH AND ENGLISH COAST (ICES 3)

The Scottish and English Coastal Water has a salinity between 34‰ and 35‰. Along the coast the water is well mixed. During summer the mixed water is separated from the thermally mixed central North Sea water by a tidal front. Nutrient concentrations are generally low: DICKSON *et al.* (1988a) concluded that winter nitrate concentrations did not show any significant trend during the past three decades and vary around 6 $\mu mol \cdot dm^{-3}$. HORWOOD (1982) reported similar nitrate concentrations and in addition winter phosphate and silicate levels of ~0.6 and 4.5 $\mu mol \cdot dm^{-3}$.

II.2.3.1 Seasonal cycle of phytoplankton biomass, production and dominant species

During winter the primary production is very low and ranges from 0.05-0.13 g C m^{-2} day^{-1} (RICK 1990, Table II.3).

HORWOOD (1982) described the seasonal cycle of among others zooplankton, Chl *a* and nutrients on the basis of a series of cruises off the north-east English coast during 1976. In winter highest phytoplankton biomass was observed at the edge of the Dogger Bank area. From here the bloom spreaded over much of the investigated area by the end of April. Maximum biomass amounted up to 4-5 µg Chl *a* dm^{-3} during the first two weeks of May. During mid-May dissolved silicate was depleted (<0.1 $\mu mol \cdot dm^{-3}$) with some nitrate and phosphate left. This suggests that the spring bloom was silicate limited. A second phytoplankton peak was observed during September.

HORWOOD *et al.* (1982) studied the seasonal changes of phytoplankton in ICES area 3'.

Table IV.3: Compilation of primary production data from the English coast (ICES 3)

Week/Year	mean prim. prod. (g C m^2 day^1)	min. - max.	Reference
6/1987 (ICES 3')	0.07	0.05-0.13	Estimated from RICK 1990
7/1987(ICES 3")	0.13	0.03-0.26	Estimated from RICK 1990
19-21/1986 (ICES 3')	0.54	0.18-1.30	Estimated from RICK 1990
19-21/1986 (ICES 3")	2.73	0.19-8.05	Estimated from RICK 1990
38/1984^B	0.52	0.20-0.97	RICHARDSON *et al.* 1986
41/1985^B	0.33	0.12-0.55	KIØRBOE *et al.* 1988
Annual Production	**g C m^{-2} a^{-1}**		
1988-1989 (ICES 3')	**75**		JOINT & POMROY 1992
1976 (ICES 3")	**40**		HORWOOD 1982
1988-1989 (ICES 3")	**79**		JOINT & POMROY 1992

^{B} Buchan Front

They used a high-speed water sampler, which in addition to its main net was also fitted with an auxiliary phytoplankton sampler with a mesh of 35 µm. Thus their results do not represent the total phytoplankton composition since the pico- and nanoplankton will have passed through the net. The spring phytoplankton was dominated by the diatoms *Coscinodiscus concinnus* and *Chaetoceros* spp. During summer dinoflagellates took over the lead. The autumn bloom in September was again dominated by diatoms but now with a larger contribution of dinoflagellates.

RICHARDSON *et al.* (1986) and KIØRBOE *et al.* (1988) studied the frontal zone in the Buchan area (Fig. I.1) during the late summer/autumn of 1984 and 1985. They showed that highest phytoplankton biomass and production occurred parallel to the front. In agreement with HORWOOD *et al.* (1982), RICHARDSON *et al.* (l.c.) found that dinoflagellates were the dominant species. But significant numbers of small flagellates (monads and cryptomonads of 6-10 µm) were also present (which could not have been observed with the sampling method of Horwood *et al.* l.c.). Only on the coastal side of the front some diatoms formed part of the phytoplankton. The studies of RICHARDSON *et al.* (1986) and KIØRBOE *et al.* (1988) showed the frontal zone to be an area of high secondary production.

II.2.3.2 Annual primary production

The first estimate of primary production along the English east coast was made by HORWOOD (1982). This estimate was, however, not based on direct measurements. Horwood interpreted actual Chl *a* meaurements with a mathematical model. This model adequately explained timing and development of the spring bloom. Algal development during the rest of the year, however, was poorly represented. HORWOOD (1982) inferred from his calculations an annual primary production of 40 g C m^{-2} a^{-1}.

JOINT & POMROY (1992) showed that this area generally had the lowest productivity compared to the rest of the North Sea (see chapter II.1). The annual primary production estimated on the basis of the NERC North Sea Project data amounts to 75-79 g C m^{-2} a^{-1} which is substantially higher than Horwoods estimate (see Table II.3).The data from RICK (1990) suggest that the production levels in the northern part of ICES 3', which was not sampled by the NERC North Sea Project, are even lower than in the southern part.

II.2.3.3 Recent chemical and biological changes

DICKSON *et al.* (1988a) compiled data on winter nitrate concentrations in ICES box 3. Winter nitrate concentrations were around 6 µmol·dm^{-3}. They could not discern any long-term trends. Further, no data are available that show any biological or chemical changes.

Table II.4: Compilation of primary production data from the Southern Bight (ICES 4): Belgian Coast.

week/year	mean prim. prod. (g C m^{-2} day^{-1})	min. - max.	Reference
6/1982	0.2	0.2	Lancelot & Billen 1984
7/87	0.3		estimated from Rick (1990)
14-26/1982	0.78-1.0	0.16-1.4	Lancelot & Billen 1984
15-20/1984	3.03	0.4-5.2	Lancelot & Mathot 1987
21/86	1.6		estimated from Rick (1990)
Annual production	**(g C m^{-2} a^{-1})**		
1971-1975	**170 (320)***	0.2-5	Joiris *et al.* 1982

* The production estimate in parenthesis refers to particulate plus dissolved production.

II.2.4 BELGIAN AND DUTCH COAST (ICES 4)

Due to the shallow depths and strong tidal currents the water column in the Southern Bight (the North Sea between Belgium, the Netherlands and England) is thoroughly mixed. The Belgian and Dutch coastal waters have relative low salinities of around 29-33‰ caused by the admixture of river water. Along the Belgian coast the rivers Seine and Scheldt are the predominant fresh water sources. The Dutch coastal water is mainly influenced by the river Rhine. The high contribution of river water causes winter nutrient concentrations to be relatively high. In the Belgian coastal zone winter concentrations are for Si around 20 µmol·dm^{-3} , for PO_4 up to 5 µmol·dm^{-3} and for NO_3 around 45 µmol·dm^{-3} (Lancelot & Mathot 1987). Along the Dutch coast the following (salinity dependent) concentrations nowadays prevail during winter: PO_4 ~1-3 µmol·dm^{-3}, NO_3 ~10-60 µmol·dm^{-3}, SiO_4 ~5-30 µmol·dm^{-3}, (van Bennekom & Wetsteijn 1990, Brockmann *et al.* 1990, Klein & van Buuren 1992). Nutrient concentrations in winter are directly related to salinity (*e.g.* van Bennekom & Wetsteijn 1990, Klein & van Buuren 1992).

II.2.4.1 Seasonal cycles of phytoplankton biomass, primary production and dominant species

Belgian coast The spring bloom in the Belgian coastal water occurs in April with maximum biomass and primary production of 15-50 µg Chl *a* dm^{-3} and 2-5 g C m^{-2} day^{-1} (Joiris *et al.* 1982, Lancelot & Billen 1984, Lancelot & Mathot 1987). The first part of the spring bloom is dominated by diatoms (e.g. *Chaetoceros socialis*) and is terminated by silica depletion. It is followed by a *Phaeocystis* bloom which mainly occurs in its colonial form and during which the maximum production levels are reached. After the *Phaeocystis* bloom the plankton is dominated by small flagellates (Lancelot & Mathot 1987) and single-celled *Phaeocystis* (Riegman 1991). During summer the phytoplankton is nitrogen limited (Lancelot 1983). Production levels gradually decrease during summer to reach typical winter levels of 0.2 g C m^{-2} day^{-1} during October (Lancelot & Billen 1984). The annual primary production in the Belgian coastal zone amounts to 320 g C m^{-2} a^{-1} (Joiris *et al.* 1982). This estimate is substantially higher than the annual production estimate by Joint & Pomroy (1992) of 199 g C m^{-2} a^{-1} for ICES 4. The difference is probably related to the fact that the estimate by Joiris *et al.* (1982) also included dissolved primary production which reached very high levels of almost 50% of the annual primary production. Particulate primary production was 170 g C m^{-2} a^{-1}. Furthermore, the estimate by Joiris *et al.* (1982) is strongly influenced by stations close to the coast with generally much higher nutrient levels. A compilation of primary production data from the Belgian coastal zone is given in Table II.4.

Dutch coast The Southern Bight is one of the three areas where plankton blooms start first. In some years (1962, 1968, 1969, 1976) local silicate mimima - indicative for diatom blooms - were observed as early as January/February

(VAN BENNEKOM & WETSTEIJN 1990). REID *et al.* (1983) reported an early diatom bloom in February 1977. The area of early blooms lies off the Dutch coast east of the maximum salinity tongue (Atlantic Water) and is probably the result of shallow depths and a minimum of suspended matter in that area (POSTMA 1981, VAN BENNEKOM & WETSTEIJN 1990). Light is the decisive factor in the timing of the spring bloom (GIESKES & KRAAY 1975). CADÉE (1986a) has used the occurrence of the spring diatom peak rather than the onset of diatom growth as a measure of the timing of the spring bloom in the Marsdiep area because the sampling frequency around the peak was higher. To his opininion, however, a correlation exists between the onset of the spring diatom bloom and the timing of the peak. The timing of the peak was not correlated with water temperature. A good correlation was found using a multiple regression analysis with both turbidity and the amount of solar radiation received during the months January-March ($n = 19$, $r = 0.61$).

The seasonal cycle of surface Chl *a* off the Dutch coast (GIESKES & KRAAY 1975, REID *et al.* 1990, JOINT & POMROY 1992) also shows that the spring phytoplankton bloom starts in the off-shore area. The phytoplankton reaches its maximum biomass during March with values of 10-20 µg Chl *a* dm^{-3}. The maximum then gradually moves towards the coast. Near shore, the phytoplankton biomass reaches maximum values of 20-30 µg Chl *a* dm^{-3} during April and May (GIESKES & KRAAY 1977a, REID *et al.* 1990). In tidal inlets like the Marsdiep area or the outer Ems estuary spring values of around 40 $\mu g \cdot dm^{-3}$ Chl *a* are often reached (CADÉE & HEGEMAN 1991a, CADÉE 1992a, b, COLIJN & LUDDEN 1983).

The available primary production values (Table II.5-6) also indicate early phytoplankton activity. RICK (1990) reported a maximum (hourly) production equal to 0.5 - 0.7 g C m^{-2} day^{-1} during mid-February. During the spring bloom production levels of 3-4 g C m^{-2} day^{-1} prevail. (CADÉE 1992a, b, COLIJN & LUDDEN 1983, JOINT & POMROY 1992) but can reach maximum values of 10 g C m^{-2} day^{-1}.

During the first part of the spring bloom diatoms dominate. Both experimental and circumstantial evidence exists that the diatom bloom is terminated by silicate limitation (GIESKES & VAN BENNEKOM 1973, VAN BENNEKOM *et al.* 1975, GIESKES & KRAAY 1975, 1977a, COLIJN 1983, PEETERS & PEPERZAK 1990). Van Bennekom and co-workers further showed that enough nutrients were left for an ensuing non-diatom bloom. This second bloom occurs everywhere in the Dutch Coastal Water and is dominated by *Phaeocystis* spp. (GIESKES & KRAAY 1975, 1977a, VELDHUIS *et al.* 1986a, RICK 1990, PEETERS & PEPERZAK 1990). The *Phaeocystis* bloom is probably terminated as a consequence of phosphate limitation. This is inferred from the high N/P ratios prevailing during the bloom (VAN BENNEKOM *et al.* 1975, VELDHUIS *et al.* 1986a). This contrasts with the situation in the Belgian coastal zone and in the central North Sea where nitrogen is the limiting nutrient (LANCELOT 1983, OWENS *et al.* 1990). Using a bioassay method PEETERS & PEPERZAK (1990) showed that in the near-shore area silicate and phosphate were the potentially limiting nutrients but that in the off-shore areas inorganic N was potentially limiting.

In contrast to the seasonal cycle off the English coast, where a pronounced spring bloom is followed by a summer minimum and an autumn bloom (HORWOOD 1982, MADDOCK *et al.* 1981), the Southern Bight is characterized by a continued series of blooms during the summer period (COLEBROOK 1979). VELDHUIS *et al.* (1986a), for instance, observed a second diatom bloom after the collapse of the spring *Phaeocystis* bloom. CADÉE (1986a) described the average seasonal cycle in the Marsdiep as consisting of three sequences of a diatom bloom followed by a flagellate bloom. The maximum cell densities during the subsequent blooms gradually decreased. Whereas *Phaeocystis* is the dominant flagellate species after the spring diatom bloom (and in the Marsdiep area even during the major part of the summer, CADÉE & HEGEMAN 1986, CADÉE 1992a, b), µ-flagellates like *Croomonas* spp, *Rhodomonas* spp. and Dinoflagellates are the dominant non-diatoms during summer in the rest of the Dutch coastal water. In general, dinoflagellates are more important in off-shore areas than in near-shore areas (*e.g.* COLIJN & LUDDEN 1983, PEETERS & PEPERZAK 1990, KAT 1992, COLIJN 1992). Lists of dominant species are given by GIESKES & KRAAY (1975), LEEWIS (1985), CADÉE (1986a), VELDHUIS *et al.* (1986a), KAT (1988) and PEETERS & PEPERZAK (1990).

Table II.5: Compilation of primary production data from the Southern Bight (ICES 4) Dutch Coast (off-shore).

Week/year	Mean prim. prod. (g C m^{-2} day^{-1})	min-max	Reference
7/1987	0.25	0.05-0.50	Estimated from RICK 1990
21/1986	2.8	0.53-8.0	Estimated from RICK 1990
~22/86	3.0		LANCELOT & MATHOT (in REID *et al.* 1990)
Vernal production	(g C m^{-2})		
7-29/74	142	0.1-3	GIESKES & KRAAY 1975
5-23/75	114	0.02-2.4	GIESKES & KRAAY 1977a
11-20/84	121	0.5-4.8	VELDHUIS *et al.* 1986a
Annual production	(g C m^{-2} a^{-1})		
1971-1981^{W}	**250**		FRANSZ & GIESKES 1984
1974^{W}	**~210^{V}**		based on GIESKES & KRAAY 1975
1975^{W}	**~170^{V}**		based on GIESKES & KRAAY 1977a
1989^{W}	**212**		PEETERS *et al.* 1991
1988-1989^{I}	**199**		JOINT & POMROY 1992
1990^{W}	**191**		PEETERS *et al.* 1991
1989^{N}	**92**		PEETERS *et al.* 1991
1990^{N}	**149**		PEETERS *et al.* 1991

W	Western part of Dutch coastal water.
N	Northern Part of Dutch coastal water.
V	Based on a vernal budget and assuming that annual production equals 1.5 times the vernal production (JOIRIS *et al.* 1982, cf. annual production at Fladen Grounds).
I	Integral value for the whole ICES 4 box.

Evidence exists that large nutrient fluxes are instrumental in the sustenance of the high biomass and production levels in the Southern Bight. GIESKES & SCHAUB (1990) and SCHAUB & GIESKES (1991) noted that not the concentration of nutrients but their loads into the area are decisive for the phytoplankton growth potential of the area. They demonstrated that the variation of total nutrient input via the river Rhine into the Dutch coastal zone over the period of investigation (1972-1984) amounted to a factor of ~2 for all nutrients. Accordingly, they investigated whether a relation existed between phytoplankton biomass in the Dutch coastal zone and nutrient discharge by the river Rhine. First, they showed that the nutrient concentrations in the river Rhine were remarkably constant despite large fluctuations in river flow. This enabled them to use river water discharge as a measure of nutrient input. A statistical analysis showed no correlation between water discharge and phytoplankton biomass (as Chl *a*) during winter. This corroborates with the previously cited studies that during winter phytoplankton is light-limited and not nutrient-limited. During the growing season (April-September), however, a positive relation was found between river discharge (and thus nutrient discharge) and phytoplankton biomass (as Chl *a*). This correlation was significant ($r = 0.77$, $0.01<P<0.05$) for the period July-September. In other words, the weak correlation between phytoplankton biomass and nutrient input during the spring bloom suggests that its dynamics are largely dependend on local nutrient sources (high winter nutrient concentrations) although extra nutrients have some positive effect. During summer, when the phytoplankton is nutrient limited (see above) an extra nutrient input as a consequence of increased river discharge had

Table II.6: Compilation of primary production data from the Southern Bight (ICES 4): Dutch Coast (near-shore and Marsdiep).

Week/year	Mean prim. prod. (g C m^{-2} day^{-1})	min-max	Reference
7/1987	0.27	0.14-0.5	estimated from RICK 1990
20/1986	6.3	2.9-10.1	estimated from RICK 1990
vernal production	(g C m^{-2} 0.33 a^{-1})		
7-29/1974	79	0.01-1.5	GIESKES & KRAAY 1975
5-23/1975	96	0.02-3.5	GIESKES & KRAAY 1977a
Annual production	(g C m^{-2} a^{-1})		
1949-1951^{M}	**50***		POSTMA 1954
1964-1965^{M}	**170**	0.04-1.5	POSTMA & ROMMETS 1970
1972-1973^{M}	**200**	0.02-0.8	CADÉE & HEGEMAN 1974
1974^{M}	**145**		CADÉE & HEGEMAN 1979
1981-1982^{M}	**340**	0.05-6.6	CADÉE 1986B
1985^{M}	**400**	?-?	CADÈE 1991
1986^{M}	**370**	?-?	CADÉE 1991
1986^{M}	**303**	?-3.2	VELDHUIS *et al.* 1988
1990^{M}	**254**	?-4	CADÉE & HEGEMAN 1991b
1991^{M}	**385**	?-5.7	CADÉE & HEGEMAN 1993
1992^{M}	**370**	?-4.9	CADÉE & HEGEMAN 1993
1974^{W}	**~120^{V}**		based on GIESKES & KRAAY 1975
1975^{W}	**~150^{V}**		based on GIESKES & KRAAY 1977a
1988^{W}	**185**		PEETERS *et al.* 1991
1989^{W}	**273**		PEETERS *et al.* 1991
1990^{W}	**441**		PEETERS *et al.* 1991
1988^{N}	**272**		PEETERS *et al.* 1991
1989^{N}	**272**		PEETERS *et al.* 1991
1990^{N}	**391**		PEETERS *et al.* 1991

W Western part of Dutch coastal water.
N Northern Part of Dutch coastal water.
M Marsdiep area.
V Based on a vernal budget and assuming that annual production equals 1.5 times the vernal production (JOIRIS *et al.* 1982, *cf.* annual production at Fladen Grounds).
* Based on changes in Chl *a* levels. This value should be considered with care (see DE JONGE 1990 and CADÉE 1992a, b).

a strong effect on the phytoplankton biomass during the summer months. A similar relation between Rhine water discharge (which was positively related to nitrogen discharge but not to phosphate discharge at Lobith (German-Dutch border) and phytoplankton biomass was found by CADÉE (1992b) for the Marsdiep area.

Some critical comments on the above analysis by GIESKES & SCHAUB (1990) were mentioned by KLEIN & VAN BUUREN (1992). They noticed considerably higher ammonium and phosphate concentrations near the mouth of the river Rhine compared to the concentrations measured at Lobith (Dutch-German border). KLEIN & VAN BUUREN (l.c.) suggest that the relation between nutrient discharge and phytoplankton biomass could be precised more if the nutrient loads were estimated on the basis river data from as close to the mouth of the river as possible.

II.2.4.2 Annual primary production

In Tables II.5-6 production data from ICES box 4 have been compiled. A subdivision was made between the Belgian coast and the near- and off-shore Dutch coast. In general, the highest daily production rates are observed during the late spring bloom in the near-shore areas. Here the highest daily production values of ~10 g C m^{-2} day^{-1} were observed.

The recent annual primary production estimates show the same tendency to be higher in the near-shore areas. Estimates of annual production for the off-shore part of the Dutch coast amount to 200-250 g C m^{-2} a^{-1} for the western part and 90-150 g C m^{-2} a^{-1} for the northern part. They agree well with the integral estimate for ICES box 4 as a whole of 199 g C m^{-2} a^{-1} by JOINT & POMROY (1992). Recent estimates for the near-shore areas are substantially higher and range from 250-440 g C m^{-2} a^{-1} in 1990 (PEETERS *et al.* 1991).

II.2.4.3 Recent trends in nutrients and phytoplankton biomass, species composition and primary production

The longest time series of phytoplankton in Dutch coastal water is being carried out by CADÉE and co-workers. Since 1969, the phytoplankton composition (using the Utermöhl method), phytoplankton biomass (Chl *a*) and on a less regular basis primary production (^{14}C) are monitored in the Marsdiep area (see Fig. I.1). The long series of observation in the Dutch coastal area render the possibility to study the impact of the heavily polluted river Rhine on the coastal plankton ecosystem. First, an overview of the nutrient trends in both the River Rhine and the coastal water will be presented. Next, the main changes in the plankton community will be discussed.

<u>Changes in the chemical composition of the River Rhine</u> VAN BENNEKOM & WETSTEIJN (1990) and KLEIN & VAN BUUREN (1992) reviewed the changes in nutrient load of the river Rhine at the German/Dutch border and at the river mouth as part of their studies about changes in the nutrient status of the Southern Bight. Nitrogen and phosphorus nutrients showed marked changes during this century. Both particulate and dissolved P peaked in the 70's. At the German-Dutch border dissolved P increased from almost 2 μmol·dm^{-3} around 1930 to 15 μmol·dm^{-3} around 1975 and decreased again to 5 μmol·dm^{-3} in 1988. The conspicuous increase of dissolved P in the 60's and its decrease since 1975 is probably related to the use of phosphate containing detergents. Further downstream, however, the decrease of dissolved P since the 70's was less conspicuous and P concentrations ranged from 10-15 μmol·dm^{-3}. This indicates that in the Dutch part of the river considerable amounts of phosphate are added (KLEIN & VAN BUUREN 1992). Particulate nitrogen and ammonium also peaked in the 70's. Their decrease together with the decrease of particulate P are related to the waste water treatment. In contrast, the nitrate concentrations constantly increased. As was the case for phosphate, nitrate concentrations at the river mouth are higher (~25%) compared to the German Dutch border and presently amount to ~340 μmol·dm^{-3}.

No clear trend in winter concentrations of dissolved silicate could be discerned. In contrast, to phosphate and nitrogen, dissolved silicate shows a pronounced seasonal cycle due to diatom growth. Its mean annual concentrations in the river Rhine remained practically unchanged from 1968-1979 (VAN BENNEKOM & WETSTEIJN 1990). Also the winter concentrations near the river mouth showed no trend (KLEIN & VAN BUUREN 1992).

The sharper regulations for the chemical industry had a marked effect on the heavy metal concentrations of the river Rhine which clearly decreased from 1972 to 1987 (Table II.7).

Two recent trends are noteworthy. Firstly, in contrast to phosphate and ammonium, the nitrate concentrations further increased since the 70's; a trend which only recently seems to stabilize. BILLÉN (1990) suggested that the nitrate increase during the 70's and 80's was not due to an increased input into the environment. He claimed that due to the sewage treatment and the subsequent higher oxygen levels denitrification takes place at a much lower rate and therefore caused an increase of nitrate levels. Secondly, a marked decrease in summer dissolved silicate concentrations has taken place recently. This decrease is in fact a return to former

Table II.7: Mean annual dissolved particulate metal concentrations ($\mu g \cdot dm^{-3}$) in the river Rhine at Lobith (German/Dutch border) in 1972 (: 1973), 1980 and 1987. (From Heymen 1990).*

	1972		1980		1987	
Metal	diss.	part.	diss.	part.	diss.	part.
Cd	1.79	1.89	0.62	0.96	0.02	0.08
Cr	1.0	64	4.6	14.8	0.6	6.9
Cu	9.8	29.1	5.3	8.8	2.5	2.8
Hg	0.38	1.96	0.04	0.14	0.01	0.04
Ni	10.7	3.5	5.2	3.9	2.7	1.2
Pb	6.5*	28.2*	1.3	13.4	0.2	3.8
Zn	166	115	41	61	9	25

conditions: Early measurements from 1928-1933 indicate very low dissolved silicate levels (7 $\mu mol \cdot dm^{-3}$ during summer, Biemond 1940). But during the 60's and 70's the summer silicate concentrations were appreciably higher (~50 $\mu mol \cdot dm^{-3}$, van Bennekom & Wetsteijn 1990). Admiraal & van der Vlught (1990) observed again minimum silicate concentrations in the Rhine < 5 $\mu mol \cdot dm^{-3}$. van Bennekom (pers. comm., Laane 1992) suggested that the recently observed low silicate concentrations in summer are due to enhanced diatom growth as a consequence of a decreased toxicity of the Rhine water (*cf.* Table II.7).

<u>Changes in the nutrient status of the Southern Bight</u> van Bennekom & Westeyn (1990, winter data until 1979) and Klein & van Buuren (1992, additional data until 1990) reviewed the distribution of nutrients in the Southern Bight. We will only discuss winter data because during this season the phytoplankton activity is at a minimum (see van Bennekom & Westeijn (1990). In Dutch coastal water dissolved phosphate, nitrate and silicate directly depend on salinity (the relative contribution of river water) during this season. Thus two factors influence the actual nutrient status in aane 1992Dutch coastal water: Riverine nutrient concentrations and the river discharge (see also previous paragraph).

During winter 1935/36 the phosphate concentrations in the coastal water were below 1 $\mu mol \cdot dm^{-3}$ (Kalle 1937). They have sharply increased especially since appr. 1960. This increase and the maximum winter concentrations in 1977 are consistent with the phosphate time series of the river Rhine presented earlier. Since 1977 the phosphate concentrations in the Dutch coastal water tend to decrease.

Nitrate concentrations also increased but in contrast to phosphate no decrease but a further (small) increase was observed since 1977.

No conspiciuous trend for dissolved silicate could be discerned (see also van Bennekom *et al.* 1975).

<u>Changes in species composition</u> In a comparison of their own observations with earlier records (back to 1897) of phytoplankton occurrence in the Marsdiep area, Cadée & Hegeman (1991a) concluded that at least as far as the microphytoplankton is concerned no drastic changes in species composition took place. In a comparison of the results from a recent Dutch governmental monitoring programme with older data from Gieskes & Kraay (1975) and Kat (1988), Colijn (1992) came to a similar conclusion that there is no clearcut long term trend in species composition. Colijn (1992) also compared his data with data (only diatoms) from van Breemen (1905) from the beginning of this century. More than 60% of the species observed by van Breemen were still present with the difference being mainly due to the genus *Chaetoceros*. Whether new species had emerged was difficult to assess due to taxonomic problems. In the relative contribution of the different species to the total phytoplankton biomass, however, large shifts occurred.

<u>Changes in annual biomass and species composition in the Marsdiep area</u> In Figure II.4 a compilation of trends in phytoplankton biomass and composition is presented. Mean annual phytoplankton biomass (as Chl *a*) in

the Marsdiep area has increased from 3-6 µg·dm^{-1} in 1971-1976 to 6-15 µg·dm^{-1} nowadays (CADÉE & HEGEMAN 1991b, 1993). This change was accompanied with by a shift in the relative composition of the phytoplankton. Quantitative data on the total numbers of diatoms are available since 1965. They show that large fluctuations occur in the duration of the diatom bloom, but that no clear trend was present except for a minimum in the mid 70's which was observed everywhere in the North Sea and adjacent Atlantic Ocean (REID 1978). For the most conspicuous non-diatom phytoplankter, *Phaeocystis* sp., however, clear trends could be discerned. This alga has attracted general interest because of the large amounts of foam that occasionally cover the Dutch and German coasts after the collapse of its blooms (EBERLEIN *et al.* 1985, LANCELOT *et al.* 1987). The major bloom of this alga peaks approximately 3 weeks after the spring diatom bloom (CADÉE 1986a). The duration of the *Phaeocystis* bloom increased from appr. 20 days in 1974-1976 to appr. 90 days in 1984-1985 (CADÉE & HEGEMAN 1986). This trend continued to reach levels of 120-140 days in 1989-1990 (CADÉE & HEGEMAN 1990a, b). Phytoplankton observations by CLEVE (1897, 1900a, b) suggest that *Phaeocystis* was already present in the Marsdiep area in large numbers around the turn of the last century. In an attempt to quantify CLEVE's data CADÉE & HEGEMAN (1991a) estimated the duration of the *Phaeocystis* bloom at a maximum of 52 resp. 55 days in 1897-1899 which implies an increase during the past century of at least a factor of three (Fig. II.4). The duration of other non-diatom blooms increased parallel to the bloom duration of *Phaeocystis* (CADÉE 1992a).

Changes in primary production From the production data compiled in Tables II.5-6 some trends can be discerned: The data from the off-shore area show no conspiciuous trend in annual production levels. However, there is some indication that the maximum daily rates have increased from 2-3 g C m^{-2} day^{-1} during the early 70's to 5-8 g C m^{-2} day^{-1} during the 80's. In the coastal areas a clear increase has been observed. The longest series of primary production measurements is available for the Marsiep. Earliest production estimates (50 g C m^{-2} a$^{-1)}$ were made by POSTMA (1954). This value was not obtained by direct measurement but estimated on the basis of chlorophyll. First estimates based on direct measurements with the ^{14}C method date from 1963-1965 (POSTMA & ROMMETS 1970, corrected by CADÉE & HEGEMAN 1974). Production levels remained around 150 g C m^{-2} a^{-1} in the Marsdiep area from 1964-1976 and then increased to 300-400 g C m^{-2} a^{-1} during the early 80's (CADÉE 1986). These high values persisted until recently (1992) although in 1990 a somewhat lower value of 254 g C m^{-2} a^{-1} was measured (CADÉE & HEGEMAN 1991b, 1993). In the near-shore areas off the Dutch west coast production levels increased from around 130 g C m^{-2} a^{-1} during the 70's to 200-400 g C m^{-2} a^{-1} during the 80's. Thus in the near-shore areas production levels have at least doubled from the 70's to the 80's. The approximate doubling agrees well with the increase of primary production in the outer Ems estuary (eastern Dutch Wadden Sea, ICES box 5) from 240 g C m^{-2} a^{-1} in 1972-1973 to 400-500 g C m^{-2} a^{-1} in 1976-1980 (COLIJN & LUDDEN 1983).

CADÉE (1986b) first indicated that the increased primary production in the Marsdiep area was related to increased phosphorus levels. DE JONGE (1990) further elaborated the relation between phosphorus levels and primary production. He calculated the loads of phosphate carried into the area via the IJselmeer and related the changes in primary production to changes in phosphate loads from the IJselmeer. The results show a significant correlation between both parameters and suggest a direct relation between nutrient loads carried into the area and primary production. Similar results albeit for phytoplankton biomass were obtained by GIESKES & SCHAUB (1990, see above). Recently, CADÉE (1992b) CADÉE & HEGEMAN (1993) demonstrated a relation between the nitrate discharge by the river Rhine and mean annual Chl *a* levels in the Marsdiep area.

Table II.8: Compilation of primary production data from the eastern North Sea (ICES 5).

Week/year	Mean pp (g C m^{-2} day^{-1})	min-max	Reference
~2/89[GB]	0.31		Aletsee *et al.* 1990
7/87[GB]	0.17	0.10-0.29	estimated from Rick 1990
~7/89[GB]	0.26[1]		Aletsee *et al.* 1990
~15/89[GB]	0.47[1]		Aletsee *et al.* 1990
~15/89[GB]	0.89[1]		Aletsee *et al.* 1990
17/92[D]	0.28	0.12-0.30	Richardson & Christoffersen 1992
17/92[GB]	2.85	0.14-6.3	Richardson & Christoffersen 1992
19/91[D]	0.64	0.08-1.25	Richardson & Christoffersen 1992
19/91[GB]	1.75	0.16-5.1	Richardson & Christoffersen 1992
~20/89[GB]	7.9[1]		Aletsee *et al.* 1990
~20/86	2.9		Lancelot & Mathot (in Reid *et al.* 1990)
22/86[GB]	1.50	0.04-9.52	estimated from Rick 1990
23/85[GB]		0.05-6	Colijn *et al.* 1990
Annual production	(g C m^{-2} day^{-1})		
1972-1973[E]	**240**		Cadée & Hegeman 1974
1976-1980[E]	**400-500**		Colijn & Ludden 1983
1988-89[GB]	**261**		Joint & Pomroy 1992

[D] Danish coast.
[E] Ems estuary.
[GB] German Bight (south of 55°.30').
[1] Calculated from hourly estimates after Colijn *et al.* (1990) and Cadée & Hegeman (1974): production·day^{-1} = daylength·0.5·hr^{-1}.

II.2.5 GERMAN BIGHT (ICES 5)

The German Bight is characterized by a complicated hydrography (see Krause *et al.* 1986). Along the East- and North-Frisian Islands the water column is permanently mixed and rich in nutrients due to the admixture of river water from the rivers Ems, Weser and Elbe. A relatively deep channel - an old river bed of the Elbe river which was formed during the last ice age - of approximately 30-40 m depth stretches from Helgoland to the northwest. In this area a seasonal stratification occurs which is caused both by temperature and salinity.

II.2.5.1 Seasonal cycles of phytoplankton biomass, primary production and dominant species

In the entire area the spring bloom is dominated by diatoms. It peaks during the second half of April (Colijn & Ludden 1983, Weisse *et al.* 1986, Radach *et al.* 1986, 1990a, Bauerfeind *et al.* 1990). The biomass reaches up to 20-50 µg Chl *a* dm^{-3} in the coastal areas (Colijn & Ludden 1983, Weisse *et al.* 1986) but hardly exceeds 10 µg Chl *a* dm^{-3} in the off-shore areas (Richardson & Christofferson 1992). After the spring diatom bloom a *Phaeocystis* bloom is observed in the entire area which reaches biomasses comparable to the preceeding diatom bloom. Again highest biomasses are observed near-shore (*e.g.*

EBERLEIN *et al.* 1985, RICHARDSON & CHRISTOFFERSEN 1992). The *Phaeocystis* bloom occurs during May-June. But also during July *Phaeocystis* blooms have been observed along the East Frisian Islands (VOSJAN *et al.* 1992). Calculations by COLIJN (1983) indicate that the spring diatom bloom was limited by silicate depletion. WEISSE *et al.* (1986) and BAUERFEIND *et al.* (1990) also concluded that the spring bloom was potentially limited by silicate (diatoms) and phosphate ("flagellates").

After the *Phaeocystis* bloom often a second diatom bloom is observed (WEISSE *et al.* 1986, COLIJN & LUDDEN 1983). The occurrence of several diatom blooms during the growing season seems to be a general feature of the German Bight: RADACH *et al.* (1986) showed that the mean annual cycle of phytoplankton is characterized by several (2-3) diatom blooms. During summer flagellates gain increasing importance. They reach highest numbers during July-August (COLIJN & LUDDEN 1983, RADACH *et al.* 1986, see also the following paragraph on changes). Among the dinoflagellates the larger *Ceratium* sp. are only observed in the off-shore areas (COLIJN & LUDDEN 1983, VOSJAN *et al.* 1992). Dinoflagellates are in terms of biomass the major contributors to the flagellate biomass around Helgoland although high numbers of other unidentified naked flagellates occur (HICKEL *et al.* 1992, 1993).

II.2.5.2 Annual primary production

Only recently primary production data for the German Bight proper have become available. The first data (spring 1985) were published by COLIJN *et al.* (1990). The available data are presented in Table II.8. During the spring bloom in the German Bight COLIJN *et al.* (1990) observed production values of 0.05-6.0 g C m^{-2} day^{-1}. RICHARDSON & CHRISTOFFERSEN (1992) observed similar values of 0.13-6.3 g C m^{-2} day^{-1}. In the Ems estuary primary production also reached values of 6 g C m^{-2} day^{-1} (COLIJN & LUDDEN 1983). The highest values were always found in the coastal areas of the German Bight. This is also clearly shown by the NERC data (JOINT & POMROY 1992, see chapter II.1).

For the summer period a limited amount of data is availble. The NERC data suggest that similar to the situation off the Dutch coast production levels remain high (1-2 g C m^{-2} day^{-1}). In the outer Ems estuary summer production levels lie around 1 g C m^{-2} day^{-1} (COLIJN & LUDDEN 1983).

Both data sets show that low winter production values (<0.2 g C m^{-2} day^{-1}) are reached in October/November.

The annual primary production in the German Bight (ICES 5) was estimated by JOINT & POMROY (1992) at 261 g C m^{-2} day^{-1}. The most recent estimate for the outer Ems estuary of 400-500 g C m^{-2} day^{-1} (COLIJN & LUDDEN 1983) suggests that the production levels near-shore are appreciably higher.

II.2.5.3 Recent trends in nutrients and phytoplankton biomass, species composition and primary production

For the German Bight a unique time series with respect to both its length as to the number of monitored parameters is available. The sampling location is situated close to Helgoland (Fig. I.1). Details on sample collection and the analytical methods applied are given by RADACH *et al.* (1990a). Apart from biological parameters the observations also include chemical variables. This renders the "Helgoland Reede" data set a unique position among the other long-term data sets because it enables a ***direct*** comparisons between changes in the chemical environment and the biological reactions thereupon which is not possible with the other long term observations discussed above. The Helgoland Reede data for the period 1962-1984 were statistically analyzed by RADACH and co-workers (BERG & RADACH 1985, RADACH *et al.* 1986, RADACH & BOHLE-CARBONELL 1990, RADACH *et al.* 1990a). HICKEL *et al.* (1992, 1993) and HICKEL (1993) present additional information that include data until 1991.

Chemical changes A trend analysis based on the 5-year running average was carried out by RADACH & BOHLE-CARBONELL (1990, TABLE II.9). The mean annual phosphate concentrations increased from 0.55 µmol·dm^{-3} in 1962 to 0.9 µmol·dm^{-3} in 1975. Especially during the early 70's a strong increase occurred. From approximately 1976-1986 the mean winter concentrations remained on a rather constant level of ~1.2 µmol·dm^{-3}. Since 1985 a decrease was observed (HICKEL 1993) to 1991 winter concentrations of ~0.55 µmol·dm^{-3} and summer concentrations of ~0.25 µmol·dm^{-3}.

The changes in nitrate concentrations were quite different. Until 1980 no conspicuous changes occurred with mean annual levels of ~6 µmol·dm^{-3}. During the last decade the mean annual concentrations doubled. Nowadays winter concentrations between 23 and 40 µmol·dm^{-3} are found (HICKEL *et al.*

Table II.9: Initial and end concentrations for nutrients and phytoplankton biomass in the German Bight (Helgoland Reede) as calculated from the five year running average (From RADACH *&* BOHLE-CARBONELL *1990).*

Parameter	analyzed period	Initial conc.	last conc.	factor of change
Silicate (µmol·dm^{-3})	66-84	5.3	3.4	-0.69
Phosphate (µmol·dm^{-3})	62-84	0.55	0.95	+1.67
Nitrate (µmol·dm^{-3})	62-84	6.07	15.12	+2.49
Diatoms (µg C dm^{-3})	62-84	3.36	2.25	-0.67
Flagellates (µg C dm^{-3})	62-84	3.82	17.75	+4.65

1992, HICKEL 1993). High winter concentrations are related to high Elbe river discharges (HICKEL 1993).
In contrast to nitrate and phosphate, silicate concentrations decreased from an annual mean of 5.3 µmol·dm^{-3} in 1966 to 3.4 µmol·dm^{-3} in 1984. The decrease was especially noticable during winter in the relatively fresh, Elbe-influenced water masses around Helgoland (BERG & RADACH 1985).

In addition to the Helgoland Reede data, some interesting data sets exist on the nutrient distribution that document the chemical changes that have taken place in the German Bight. One of the oldest chemical data sets for the north Sea was originated by KALLE (1937) who reported the nutrient distribution during January/February 1936. WEICHART (1986) compared this data set with own measurements from January 1978. He concluded that the silicate distribution had not greatly changed. During winter 1936 and 1978 the silicate concentrations showed the same relation with salinity. The 1978 data were, however, somewhat higher. This might, however, be due to analytical uncertainties in 1936. WEICHART (1986) further observed a strong increase in phosphate concentrations from 1935 to 1978. In the northwestern German Bight the increase was hardly significant with phosphate concentrations during both surveys of 0.5-0.6 µmol·dm^{-3}. In the coastal zone, however, phosphate concentrations increased by a factor of 4 from 0.7 to 3 µmol·dm^{-3}. During both surveys phosphate concentrations correlated with salinity which pinpoints the river Elbe as the most significant source of phosphate. The observed increase from 1935 to 1978 near Helgoland by a factor of ~2 agrees well with the increase in phosphate observed at Helgoland Reede of 1.7 (see Tables II.9, but note the recent decrease described above).

KÖRNER & WEICHART (1992) presented additional data from winter 1985, 1987, 1989 and 1990. Again they observed approximate linear relations between dissolved nutrients and salinity. During this period a slight decrease of phosphate was observed, dissolved silicate decreased by 50% at a salinity of 33‰ but the decrease was less (30%) at a salinity of 30‰. No conspicuous trends were observed for nitrate.

The Expert Group on nutrients of the Oslo and Paris Commision stated that at salinities higher than 33 no nutrient increase could be detected. This thesis was tested by HICKEL (1993). He noted that in the German Bight a nutrient increase ***could be*** detected. The increase has a time lag of 3 years for nitrate and ~10 years for phosphate compared to the increase at mean salinities. HICKEL argues that the redistribution of organic particles with the sediment acting as a temporary buffer could explain this phenomenon. It is interesting to note that phosphate has a higher affinity for sediment particles than nitrate[3] which could explain the difference in time lag of these nutrients.

Biological changes The above-mentioned chemical changes had a significant impact on the phytoplankton structure. Total phytoplankton biomass increased 3-4 fold from 10-20 µg C dm^{-3} during the early 60's to 60-80 µg C dm^{-3} nowadays. Until the early 80's the

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[3] This can be inferred from the conservative behaviour of nitrate in the Elbe estuary compared to the non-conservative behavior of phosphate (own analysis of original data published by ARGE ELBE.

diatom biomass increased from ~10 to ~20-50 µg C dm^{-3}. Since then no conspicuous trend can be discerned (e.g. HICKEL *et al.* 1992). The trend analysis, however, suggested a decrease that seems to be more pronounced in the North Sea influenced water masses around Helgoland than in the coastal, Elbe river influenced water masses (BERG & RADACH 1985). In contrast to the absence of a clear trend in diatom biomass, the flagellate component strongly increased from ~10 µg C dm^{-3} during the early 60's to 30-130 during '78-'82. The increase was most pronounced in the Elbe river influenced water masses around Helgoland (a factor of 16; BERG & RADACH 1985). From 1985-1990 a flagellate biomass of 20-80 µg C dm^{-3} were observed. The phytoplankton time series reported by HICKEL and co-workers illustrate the problems inherent to trend analyses of these data: interannual variation is much larger than any trend.

Although the phosphate concentrations have decreased, no downward trend in annual phytoplankton has been observed (HICKEL 1993).

It is tempting to interprete the above trends in terms of limiting nutrients. Only flagellates have clearly taken advantage of the increased nitrogen and phosphate levels. A closer look reveals that during the early sixties diatom biomass approximately doubled but could not take full advantage of the increased phosphate levels. Possibly, a shift from phosphate to silicate limitation occurred. Recent studies support that nowadays diatoms are silicate-limited (see above). The sharp increase in flagellate biomass during the early 80's suggests that before that time flagellates were nitrogen limited. However, GILLBRICHT (1989) pointed out that in summer the phytoplankton was not nutrient limited. HICKEL *et al.* (1992) suggested that the changed N/P ratios during summer in the German Bight could have caused changes in the phytoplankton composition.

Also, during the winter months marked changes have occurred: Diatom biomass decreased whereas the flagellate component increased. The latter group probably consists of heterotrophic flagellates (HICKEL *et al.* 1992) and currently reaches winter biomasses comparable to the summer populations during the early 60's.

Primary production Unfortunately, no long-term observations on primary production exist. Only in the Ems estuary a rise in production levels from around 250 g C m^{-2} a^{-1} from 1972-1978 to 400-500 g C m^{-2} a^{-1} in 1980 could be confirmed (CADÉE & HEGEMAN 1974, 1979, COLIJN & LUDDEN 1983). However, phytoplankton biomass in the German Bight has increased four-fold from 1962 to the present (RADACH & BOHLE-CARBONELL 1990, HICKEL *et al.* 1992). The close agreement between phytoplankton biomass and primary production (e.g. JOINT & POMROY 1992) suggests that the primary production levels in the German Bight must have increased significantly since the early 60's.

II.2.6 CENTRAL NORTH SEA (ICES 7)

The central North Sea (ICES box 7) comprises three hydrographically different areas (cf. REID *et al.* 1988, LEE 1980):

☐ the Northern area (ICES 7') with depths from 200 m in the north to 50 m in the south. This area is stratified in summer.

☐ the Dogger Bank (northern part of ICES 7") with depths of 20-50 m. Here the water column is completely mixed due to the shallow depths (cf. RIEGMAN *et al.* 1990b).

☐ the southern part with depths of around 40m which is stratified in summer.

The Dogger Bank forms a physical barrier for the intrusion of the Atlantic Water that enters the North Sea from the north. It thus separates the central North Sea in a northern, ocean influenced part and a southern part which is under influence of a mixture of Atlantic Water entering through the Channel and coastal water.

Winter nutrient concentrations are relatively high along the northern and southern margins of the central North Sea and reach a minimum in the Dogger Bank area (cf. chapter II.1). In the northern and southern part winter nutrient concentrations reach values of 0.6-0-8 µmol·dm^{-3} phosphate, ~10 µmol·dm^{-3} nitrate and 5 µmol·dm^{-3} silicate. In the Dogger Bank area nutrient concentrations reach a minimum of 0.2 µmol·dm^{-3} phosphate, 4 µmol·dm^{-3} nitrate and 1 µmol·dm^{-3} silicate (RADACH *et al.* 1990b, BROCKMANN *et al.* 1990).

Table II.10: Compilation of primary production data from the northern central North Sea (ICES 7').

Week/year	Mean pp (g C m^{-2} day^{-1})	min-max	Reference
5-10/1987	0.15	0.04-0.28	estimated from RICK (1990)
9/1988		0.17-0.27.	NIELSEN & RICHARDSON (1989)
18-24/1986	0.87	0.1-4.4	estimated from RICK (1990)
28/1987	0.5		OWENS *et al.* 1990[1]
31/1988	0.6		RIEGMAN & COLIJN 1991
Annual production	(g C m^{-2} a^{-1})		
1988-89	**100**		JOINT & POMROY 1992

Because ICES box 7 comprises three hydrographically different areas, the phytoplankton of these areas will be discussed separately.

II.2.6.1 Seasonal cycles of phytoplankton biomass, dominant species and primary production in the northern central North Sea (ICES 7')

RICK (1990) reported a winter biomass of ~1 µg Chl *a* dm^{-3}. From his data production levels of 0.05-0.28 g C m^{-2} day^{-1} can be calculated. Similar values (~0.5 µg Chl *a* dm^{-3}, 0.20-0.27 g C m^{-2} day^{-1}) were found by NIELSEN & RICHARDSON (1989). The latter authors reported that several diatom species dominated the phytoplankton.

During early summer (May-June 1986) RICK (1990) reported biomass levels of 1-3 µg Chl *a* dm^{-3} and a mean production equal to 0.9 g C m^{-2} day^{-1}. In the eastern part primary production was low. Here the phytoplankton was dominated by several dinoflagellates and small diatoms. Towards the west high production levels up to 4.4 g C m^{-2} day^{-1} were observed. In the central part diatoms and dinoflagellates dominated the phytoplankton whereas along the western margin of the area diatoms and *Phaeocystis* prevailed.

In summer the northern North Sea area is stratified. This has important implications for the phytoplankton biomass distribution. RIEGMAN *et al.* (1990b) reported that during July 1988 along the southern margin of the area a thermocline was present at a depth of 30 m. In the thermocline a shallow layer with chlorophyll concentrations from 0.5-3.2 µg Chl *a* dm^{-3} was observed whereas above the thermocline Chl *a* concentrations below 0.1 µg Chl *a* dm^{-3} prevailed. Above the thermocline small flagellates and *Ceratium furca* dominated but at the thermocline diatoms (*Rhizosolenia stolterfolthii*, *Chaetoceros curvisetum*) and again *Ceratium furca* dominated.

During July small flagellates seem to play an important role in the phytoplankton. OWENS *et al.* (1990) reported that during July 1987 small algae (<5 µm) were responsible for around 75% of the total primary production. PEETERS & PEPERZAK (1990) observed dominance of µ-flagellates, *Chroomonas* spp. and other cryptophytes during July 1988. OWENS *et al.* (1990) and PEETERS & PETERZAK (1990) gave evidence that primary production is nitrogen-limited during July.

During late summer and autumn large dinoflagelllates like *Ceratium fusus* and *C. furca* dominate. Diatoms play an additional role during autumn (PEETERS & PEPERZAK 1990).

Available primary production data have been compiled in Table II.10. No annual production estimates that cover the whole area are available. JOINT & POMROY (1992), however, reported an estimate for the southern part of ICES 7' (along 56° N) of 100 g C m^{-2} a^{-1}.

II.2.6.2 Seasonal cycles of phytoplankton biomass, dominant species and primary production in the Dogger Bank area (ICES 7")

The Dogger Bank is one of the areas where extremely early plankton blooms occur. HORWOOD (1982) already observed that the blooms off the English coast first started in the Dogger Bank area. The occurrence of early

Table II.11: Compilation of primary production data from the Dogger Bank area (ICES 7").

Week/year	Mean pp ($g\ C\ m^{-2}\ day^{-1}$)	min-max	Reference
5-10/1987	0.9	0.6-1.3	Own estimate from RICK (1990)
9/1988		0.5-2.1	NIELSEN & RICHARDSON (1989)
20-21/1986	0.2	0.1-0.32	Own estimate from RICK (1990)
28/1987	1.4		OWENS *et al.* 1990[1]
31/1988	1.2	0.3 -2.2	RIEGMAN & COLIJN 1991
Annual production	($g\ C\ m^{-2}\ a^{-1}$)		
1990	**135**		PEETERS *et al.* 1991

blooms (or even a permanent winter production) is expressed by the low nutrient concentrations that prevail in this area (BROCKMANN *et al.* 1990, BROCKMANN & WEGNER 1985). These authors suggested that due to the shallow depths phytoplankton production is possible throughout the year.

JOINT & POMROY (1992) reported production levels of 0.3-0.6 g C m^{-2} day^{-1} during early January 1989; the highest of the entire North Sea at that time. During mid-February 1987 RICK (1990) observed a dense phytoplankton population dominated by the diatom *Thalassiosira gravida* with biomasses up to 15 µg Chl *a* dm^{-3} and production levels locally exceeding 1 g C m^{-2} day^{-1}! NIELSEN & RICHARDSON (1989) found somewhat lower values during the end of February (~0.5 g C m^{-2} day^{-1}). But at a shallow bank (20 m) just south of the Dogger Bank an intense diatom diatom bloom (mainly *Rhizosolenia* sp.) was observed with a biomass up to 7.3 µg Chl *a* dm^{-3} and production levels of 2.1 g C m^{-2} day^{-1}.

From the above cited data and the NERC data (chapter II.1) it can be inferred that in and around the Dogger Bank area a spring diatom peak occurs during February-March with production levels of around 1-2 g C m^{-2} day^{-1}. An impression of the further seasonal cycle of species composition is given by PEETERS & PEPERZAK (1990). During mid-April diatoms (*Rhizosolenia hebetata, Nitzschia seriata*) still dominated the phytoplankton but some dinoflagellates were already present. Dinoflagellates and µ-flagellates (*Chroomonas* spp. and other Cryptophytes) took over phytoplankton dominance during June/July 1988. At the same time RIEGMAN & COLIJN (1991) observed primary production levels of 1.2 g C m^{-2} day^{-1}. From August to October 1988 the large dinoflagellates *Ceratium fusus* and *Ceratium furca* dominated. PEETERS & PEPERZAK (1990) and OWENS *et al.* (1990) gave evidence that the plankton was nitrogen-limited during most of the summer.

In Table II.11 primary production data from the Dogger Bank area are compiled. The production levels seem to be higher compared to the northern central North Sea: This is partly due to the high winter production levels, but also during summer the daily production rates of1.2-1.4 g C m^{-2} day^{-1} are twice as high as observed in the northern North Sea (ICES 2) and northern Central North Sea (ICES 7'). The annual primary production estimate from PEETERS *et al.* (1990) amounts to 135 g C m^{-2} a^{-1} which is somewhat higher than the estimate for the entire ICES box 7" of 100 g C m^{-2} a^{-1} (JOINT & POMROY 1992).

II.2.6.3 Seasonal cycles of phytoplankton biomass, dominant species and primary production in the southern central North Sea (ICES 7")

During winter biomass and production levels are intermediate and range from 1 to 3 µg Chl *a* dm^{-3} and from <0.1 to 0.5 g C m^{-2} day^{-1} (Rick 1990, NIELSEN & RICHARDSON 1989). About the spring peak little is known. The NERC data (JOINT & POMROY 1992, see chapter II.1) suggest that biomass peaks during the end of March with values of ~4 µg Chl *a* dm^{-3} and production levels of 1-2 g C m^{-2} day^{-1}. During April/ May 1981 diatoms like *Rhizosolenia setigera* and *Chaetoceros* sp. dominated the phytoplankton as identified by microscopy (GIESKES & KRAAY 1984) but high numbers of Chryptophyceae must also have been present as indicated by high alloxanthin concentrations, a pigment which is typical for

Table II.12: Compilation of primary production data from the southern central North Sea (ICES 7").

Week/year	Mean pp (g C m^{-2} day^{-1})	min-max	Reference
5-10/1987	0.28	0.05-1.31	estimated from RICK 1990
9/1988	0.5		NIELSEN & RICHARDSON 1989
18/1981	1.24	1.04-1.53	GIESKES & KRAAY 1984
21/1987	0.35	0.10-0.76	estimated from RICK 1990
26/1981	1.06	0.93-1.21	GIESKES & KRAAY 1984
36/1981	1.03	0.91-1.23	GIESKES & KRAAY 1984
Annual production	**(g C m^{-2} a^{-1})**		
1981	**200-250**		GIESKES & KRAAY 1984
1988-89	**119**		JOINT & POMROY 1992
1989	**92**		PEETERS *et al.* 1991
1990	**135**		PEETERS *et al.* 1991

Cryptophyceae (GIESKES & KRAAY 1983). Biomass ranged from 1-3 µg Chl *a* dm^{-3} with primary production values of ~1.2 g C m^{-2} day^{-1}.

During July-September a thermocline is present at a depth of 20 m (TOMCZAK & GOEDECKE 1962). PEETERS & PEPERZAK (1990) and GIESKES & KRAAY (1984) found that during July dinoflagellates (*Ceratium fusus, C. tripos, C. furca*) and several µ-flagellates (Cryptophyceae, Prymnesiophyceae) dominated. The latter authors showed that *Ceratium* formed a dense layer at the thermocline. Here primary production levels (1.1 g C m^{-2} day^{-1}) also peaked (~80% of total production). During July the area is nitrogen-limited (OWENS *et al.* 1990, RIEGMAN *et al.* 1990a, PEETERS & PEPERZAK 1990).

During August 1988 PEETERS & PEPERZAK (1990) found that due to a storm the thermocline had disappeared. This caused diatoms (*Rhizosolenia* sp.) to become dominant again but *Ceratium* sp. was still present in high numbers.

During September 1981 first the Prymnesiophyceae *Emiliania huxleyi* dominated but was later replaced by the diatom *Leptocylindricus danicus.* A biomass of ~0.8 µg Chl *a* dm^{-3} and production levels of ~1 g C m^{-2} day^{-1} prevailed (GIESKES & KRAAY 1984).

Primary production data have been compiled in Table II.12. Summer production levels in the southern central North Sea are about twice as high as in the northern North Sea and similar to values found in the Dogger Bank area. Several estimates of annual primary production exist. GIESKES & KRAAY (1984) estimated on the basis of the three primary production measurements in 1981 and a mean phytoplankton cycle for the area as presented by COLEBROOK (1979) an annual primary production of 200-250 g C m^{-2} a^{-1}. The more recent estimates listed in Table II.12 for 1988-1990 are remarkably similar (92-135 g C m^{-2} a^{-1}) but are almost twice as low as the 1981 estimate. Possible explanations for the discrepancy are that the latter are based a 5-12 measurements compared to 3 for the estimate by GIESKES & KRAAY (1984) or that the vernal production which was not directly observed by GIESKES & KRAAY (l.c.) has been overestimated. On the other hand it should be noted that the NERC data indicated a gradient with increasing production levels from the west to the east where GIESKES & KRAAY (l.c.) carried out their investigations.

II.2.6.4 Chemical and biological changes in the central northern North Sea (ICES 7)

Apart from the Continuous Plankton Recorder survey data that already have been discussed no long term observations for this area are available. RIEGMAN *et al.* (1990b) compared the species composition north of the Dogger Bank area as observed during July 1988 with observations from BRAARUD *et al.* (1953) from May 1948. They concluded that basically the same distribution in biomass and species composition was present. RICK (1990) carried out a similar comparison of his data (May-June 1986) with the observations from BRAARUD *et al.* (l.c.) and GRAN (1915). He arrived at the same conclusion. This indicates that no significant changes in the species composition of the phytoplankton in the central North Sea have occurred.

II.2.7 SKAGERRAK AND KATTEGAT

Three water masses enter the Skagerrak: From the south the Jutland Current transports continental coastal water into the area. It moves eastward along the north Danish coast and joins the north-flowing Baltic current off the Swedish coast. In the southwestern Skagerrak and in its deeper parts Atlantic Ocean water can be found. Due to the low salinity Baltic outflow, the Kattegat and Skagerrak is stratified. The intensity of stratification increases from winter to summer -probably due to the additional effect of temperature (RICHARDSON & CHRISTOFFERSEN 1991). As a result of the anti-clockwise currrent in the Skagerrak the deep heavy water domes In the central Skagerrak and causes there a strong pycnocline at 10 m. Towards the margins of the area the density gradient in the water column becomes less strong and shifts to ca. 60 m along the periphery (PINGREE *et al.* 1982, KIØRBOE *et al.* 1990). As will be shown, the phytoplankton distribution in the Skagerrak/Kattegat area is strongly influenced by the hydrodynamic structure of the area.

Winter nutrient concentrations in the surface of the Kattegat and in the Baltic outflow are respectively: nitrate = 6.4/7.7 µmol·dm^{-3}; phosphate = 0.8/0.9 µmol·dm^{-3}; silicate = 5.8/6.8 µmol·dm^{-3} (RICHARDSON & CHRISTOFFERSEN 1991).

II.2.7.1 Seasonal cycles of phytoplankton biomass, dominant species and primary production

The permanent halocline due to the low-salinity Baltic Outflow and the concomittant shallow mixing depth enables early plankton blooms along the Norwegian/Swedish coast. RICK (1990) recorded production levels up to 1.7 g C m^{-2} day^{-1} late February 1987. The peak of the spring bloom occurs during March, about a month earlier than in the other coastal areas of the North Sea (COLEBROOK 1979) but comparable to the situation in the Dogger Bank area. The spring peak is dominated by diatoms (MAESTRINI & GRANÉLI 1991, PETTERSON 1991). The latter author reported *Chaetoceros* sp. as the dominant species. During the spring bloom Chl *a* levels up to 22 µg Chl *a* dm^{-3} and production levels up to 3.6 g C m^{-2} day^{-1} have been observed (RICHARDSON & CHRISTOFFERSEN 1991). MAESTRINI & GRANÉLI (1991) reported a second diatom bloom during April 1988 which was dominated by *Skeletonema costatum*. According to the latter authors diatom growth during summer is silicate limited. During April 1984 RICHARDSON (1985) studied the phytoplankton distribution in the Skagerrak-/Kattegat. Low phytoplankton biomass was found in the North Sea water and in low salinity Baltic Outflow but peaked in the vicinity where Baltic and North Sea water met. Primary production in the frontal area (0.9 g C m^{-2} day^{-1}) were about 25 times higher than in the surrounding waters. Dense blooms (>20 µg Chl *a* dm^{-3}) were further observed in association with a strong pycnocline. Richardson did not report on species composition.

During May 1987 ROSENBERG *et al.* (1990) observed dominance of choanoflagellates and several other flagellates/monads in the central Skagerrak. Second to these algae small diatoms (*Chaetoceros* spp.) and dinoflagellates (e.g. *Gonyaulax* spp.) prevailed. Biomass varied from 1-4 µg Chl *a* dm^{-3} but never exceeded values of 9 µg Chl *a* dm^{-3}. Primary producion ranged from 0.16-1.1 g C m^{-2} day^{-1}. Production was generally limited by nitrogen but occasionally phosphate limitation was observed. At the same time KIØRBOE *et al.* (1990) studied a transect through the central Skagerrak from Norway to Danmark (May 1987): In the central Skagerrak a shallow pycnocline was observed whereas along the margins the surface mixed layer deepend. The hydrographic structure of the Skagerrak at that time had a marked influence on the plankton community structure: In the central part the phytoplankton was characterized by small flagellates. Along the periphery of the Skagerrak, however, large, chain-forming diatoms dominated. In its turn the phytoplankton composition influenced the energy transfer through the food web. The fecundity of copepods (a measure for the quality of phytoplankton as a food for copepods) was dependent on the concentration of larger algae (> 8 µm: for instance diatoms) in a linear way. Thus in the periphery of the Skagerrak, where the larger phytoplankton prevailed a large proportion of the primary production was directly sluiced to

Table II.13: Compilation of primary production data from the Skagerrak/Kattegat

Week/year	Mean pp ($g\ C\ m^{-2}\ day^{-1}$)	min-max	Reference
9/1987	0.56	0.05-1.7	estimated from Rick 1990
9/1988	0.5		Nielsen & Richardson 1989
15/198		0.02-0.9	Richardson 1985
17/1992	0.20	0.01-0.45	Richardson & Christoffersen 1992
19/1991	0.11	0.05-0.26	Richardson & Christoffersen 1992
20/1987	0.46	0.16-1.1	Rosenberg *et al.* 1990
21/1987	0.82	0.44-1.26	estimated from Rick 1990
Annual production (Kattegat only)	**($g\ C\ m^{-2}\ a^{-1}$)**		
1955-1984[M]	**105**		Rydberg *et al.* 1990
1981-1985[SE]	**144**		Rydberg *et al.* 1990
1989[SE]	**290**	0.14-3.6	Richardson & Christoffersen 1991

[SE] south-eastern Kattegat
[M] mid-Kattegat

higher trophic layers. In the central Skagerrak, however, the major part of the primary production was respired by bacteria and flagellates and dissipated within the community.

The phytoplankton observations by Petterson (1991) along the Swedish coastal zone of the Skagerrak showed that during May and July 1988 flagellates (e.g. Choanoflagellates) and monads were dominant. Diatoms (*Rhizosolenia, Chaetoceros*) were responsible for 20% of the phytoplankton biomass.

During September (1988) a bloom of the dinoflagellate *Gyrodinium aureolum* was observed.

In (the previous) October (1987) the phytoplankton was totally dominated by diatoms (*Chaetoceros* sp., *Skeletonema costatum*). Her study further indicated that the phytoplankton in summer was basically nitrogen limited but that occasionally phosphate limitation could occur.

In Table II.13 primary production data from the Skagerrak-Kattegat area have been compiled.

II.2.7.2 Chemical and Biological Changes in the Skagerrak Area

There are no indications that the annual primary production in the mid-Kattegat has increased. In the 1950's Steemann Nielsen recorded values between 70 and 110 g C $m^{-2}\ a^{-1}$ (Svannson 1975). Rydberg *et al.* (1990) estimated a mean annual production during the period 1955-1984 of 105 g C $m^{-2}\ a^{-1}$. South of the Kattegat, however, Wassmann (1990) estimated a 50-150% increase from 1955-1976. A recent estimate by Richardson & Christoffersen (1991) of annual production in the southeast Kattegat (290 g C $m^{-2}\ a^{-1}$) also suggests that production levels might have increased compared to annual values in 1981-1985 (144 g C $m^{-2}\ a^{-1}$, see Table II.13). As far as species composition is concerned it should be noted that the novel dinoflagellate *Gyrodinium aureolum* now is one of the dominating species in frontal areas (*e.g.* Lindahl 1986, Richardson 1989b).

II.3 BLOOMS

II.3.1 Some general remarks on blooms

A special point of interest with regard to recent trends in North Sea phytoplankton is the question whether there has been a change in frequency and magnitude of phytoplankton blooms. A phytoplankton bloom as such is a perfectly normal phenomenon and part of the annual phytoplankton cycle (Richardson

1989a). Examples are the spring diatom bloom, the late summer dinoflagellate proliferation which both are ubiquitous in the North Sea and the autumn bloom that is observed in some areas during the breakdown of the thermocline (*e.g.* HORWOOD *et al.* 1982). It is, however, a matter of dispute when a bloom is exceptional. During an ICES symposium on the subject of "exceptional blooms" (ICES 1983) several definitions were proposed. TETT (1987) regarded Chl *a* concentrations exceeding 100 $\mu g \cdot dm^{-3}$ as exceptional. HOLLIGAN (1987) suggests spatial and/or temporal dimensions of >10 km and >10 days as a measure (which can be scaled up or down according to the size of the system). In terms of biomass Holligan (l.c.) suggested a Chl *a* concentration able to absorb the available light in the surface layer (~300 mg Chl *a* m^{-2}). REID *et al.* (1987) considered phytoplankton blooms as exceptional if:

1. They occur in an area where they have been previously unrecorded
2. the species forming the bloom is new to the area or has not previously been recorded as a bloom-forming species
3. the timing differs from normal
4. the blooms are more extensive than normal
5. they have some delerious effect (deoxygenation, poisoning, etc.)

CADÉE & HEGEMAN (1986) define a (*Phaeocystis*) bloom when cell densities larger than 10^6 dm^{-3} occur. COLIJN (1992) used the similar definition to identify phytoplankton blooms in Dutch coastal water. Dinoflagellate blooms, on the other hand, were defined by Colijn when cell densities exceeded 10^3 dm^{-3}. The large interspecific range of biomass per cell is, however, a large disadvantage of cell density dependent definitions.

MOMMAERTS (1985, 1986a, b) compiled data on blooms in the ICES area. These and newer data from 1984 until 1990 were mapped by COLIJN (1992). One striking conclusion by the latter author was that there is a close relation between areas where blooms are observed and the vicinity of scientific institutes. Colijn concluded that the observer effort, mentioned as one of the possible causes for the increased number of observations of algal blooms by SMAYDA (1990) is really one of the factors to be dealt with. The observations compiled by Colijn and Mommaerts further indicate that sampling is biased towards the coasts which are more accesible (COLIJN 1992). Thus compilations of scattered bloom observations are as yet not a reliable tool for assessing trends in the incidence of blooms. Again the long term observation discussed in the previous chapters are the back-bone for trend analyses.

II.3.2 THE OPEN NORTH SEA (CPR DATA)

One of the critisisms against the CPR survey is that it seldom samples appropriately the coastal zones (RADACH *et al.* 1990, CADÉE 1990a). Its results therefore cannot be used to assess trends in the coastal zones. On the other hand it has produced a data set that has been gathered under almost identical conditions during the past decades and that covers a large part of the less accessible parts of the North Sea. The CPR data are thus an important "mirror" against which the coastal observations should be seen.

REID *et al.* (1987) analyzed the CPR data in order to reveal any trends in the incidence of blooms. Their operational definition of blooms was: (1) when the color of the silk section has been assessed as the top category in the color analysis and (2) if species were present in at least 14 out of 20 microscopic fields. (Here the reader is reminded that one sample represents 10 miles of tow with the recorder and that pytoplankton is identified in 20 microscope fields.) REID *et al.* (1987) drew the following conclusions:

1. Within the area sampled by the CPR there has been a general **decline** in the incidence of phytoplankton blooms over the period 1958 to 1983; *Gyrodinium aureolum* may be an exception to this generalization.
2. The incidence of diatoms, *Ceratium* spp., and to some extent "Phytoplankton Colour" blooms, parallels long-term changes in phytoplankton abundance.
3. There is a progressive movement in the occurrence of blooms spreading from the North Sea to the Atlantic as the seasons advance.
4. There is only slight evidence for an association between blooms and tidal fronts at the scale of sampling used by the CPR.
5. Most records of high numbers of phytoplankton from the CPR survey are not unusual but part of the normal variation seen in the seasonal development of the phytoplankton.

The incidence of "Phytoplankton Colour" blooms tended to increase during the early eighties.

II.3.3 THE CONTINENTAL COASTAL WATER

In the previous chapter we have shown that the *Phaeocystis* blooms in the Dutch coastal water have increased by a factor of about 3 during the last century (CADÉE & HEGEMAN 1991a). Also in the German Bight the summer flagellate bloom has increased both in length and magnitude since 1962 (RADACH *et al.* 1990). If we follow the above definition by REID *et al.* (1987) the recent trends in the Dutch and German coastal water suggest that we are indeed dealing with exceptional blooms. It is interesting to note that in the coastal zone the overall decline of blooms in the open North Sea from the sixties until the mid-eighties are overruled by local effects (*e.g.* GIESKES & KRAAY 1977b). There is a general acceptance that the above mentioned increases in coastal flagellate blooms are related to eutrophication (RADACH *et al.* 1990, SMAYDA 1990, CADÉE & HEGEMAN 1991b). The exact relation, however, is more complicated than that more nutrients automatically leading to a higher biomass: This will be examplified by the investigations of two recent bloom events: the *Chrysochromulina polylepis* bloom in the Skagerrak area in 1988 and the above mentioned proliferation of *Phaeocystis* in the Dutch coastal water.

II.3.3.1 The 1988 *Chrysochromulina* Bloom

"During May 1988 fish mortalities were observed in fish farms along the Swedish and Norwegian coast (ROSENBERG *et al.* 1988). The slightly yellowish green colour of the lethal waters soon led marine biologists to suspect that an algal bloom was associated with the fish kills. Microscopic examinations revealed the prymnesiophycean *Chrysochromulina poylepis* to be responsible. Towards the end of May the bloom had spread from Stavanger to the southern part of the Kattegat and had reached densities up to 10^7 per liter near the pycnocline (NIELSEN 1989). The bloom began to disappear during the second half of June."

MAESTRINI & GRANÉLI (1991) - from whom the above introduction has been taken - studied the ecophysiological mechanisms that led to this bloom. The winter before the bloom was mild and wet, resulting in high nitrate and phosphate concentrations with a high N/P ratio of ~24. Silicate concentrations on the other hand were normal (LINDAHL & DAHL 1990). The mild wet winter was followed by high insolation in spring. This lead to a massive spring diatom bloom in March during which a strong thermocline was formed. The first diatom bloom was followed by a second one during mid-April which was dominated by *Skeletonema costatum.* At the beginning of May silicate was neither present above nor below the pycnocline. Some phosphate and especially larger amounts of nitrate were available, especially just below the pycnocline. Thus three conditions which favour non-silicious algae were establihed:

1. shortage of silicate (*ergo* no diatom growth potential)
2. absence of turbulence
3. stratification which favours motile algal species (*e.g.* MARGALEF 1978)

It is not surprising that under such conditions *Chrysochromulina* and other non silicious algae could develop. The main question remaining, however, is why it came to the observed extreme dominance of *C. polylepis.* Maestrini and Granéli suggest that *C. polylepis* established its capability to avoid cell losses and to make other algae unable to compete for nutrients just after the spring diatom bloom. It did so by producing a toxin, that at low *C. polylepis* concentrations acted as a grazer repellent. At high cell densities the toxin reached a concentration at which it acted directly on the metabolism of all coexisting organisms. Experimental support is given by CARLSSON *et al.* (1990). They demonstrated that the feeding of a tinntinnid upon a good prey was reduced by roughly 40% at *Chrysochromulina* cell densities of $1.5 \cdot 10^6$ cells dm^{-3} and was completely suppressed at $3 \cdot 10^6$ cells dm^{-3}.

The factor that induced *C. polylepis* to produce the toxin was probably the phosphorus deficiency which enhances or may even be necessery for toxin production (CARLSSON *et al.* 1990, EDVARDSEN *et al.* 1990, TOBIESEN 1990). Phosphorus deficiency is also observed to enhance toxin production of the dinoflagellate *Alexandrium tamarensis* (BOYER *et al.* 1987). Possibly, excess nitrate in combination with another limiting nutrient is a general rule in algal toxicity. Silicate deficiency in combination with a nitrate surplus initiates toxin production in *Pseudonitzscha pungens* var. *pungens* (BATES *et al.* 1991).

In summary, the factors suggested by MAESTRINI & GRANÈLI (1991) leading to the *C. poylepis* bloom were in order of "occurrence":

1. an exceptionally high runoff of nitrogen-rich water in winter and early spring.
2. strong mixing of the water column followed immediately by a long period of vertical stability and stratification.
3. a diatom bloom 30% larger than usual followed by a second diatom bloom dominated by *Skeletonema costatum*.
4. a silicate depleted, phosphorus-poor, failry nitrogen-rich euphotic surface layer (N/P ~24), which prevented diatom growth and possibly initiated toxin production.
5. outcompetition of co-existing algae first through grazer repellent and later through direct effect on all other organisms.

MAESTRINI & GRANÈLI (1991) further concluded that the *Chrysochromulina* bloom did not result from hitherto unknown mechanisms. The bloom was probably caused by an exceptional sequence, coupling physiological capabilities with the environmental conditions needed to activate them. To what extent eutrophication as such has contributed to the bloom is still unclear, but possibly an unbalanced N/P ratio triggered *Chrysochromulina polylepis* to express its previously unknown toxicity.

II.3.3.2 The *Phaeocystis* Blooms in Dutch Coastal Water

In contrast to the above mentioned unique *Chrysochromulina* bloom, the *Phaeocystis* blooms along the Belgian, Dutch and German coast have a recurrent character. *Phaeocystis* belongs just like *Chrysochromulina* to the Prymnesiophycea (Haptophyceae). It occurs in two forms: as a free-living flagellate or as non-motile free-floating colonies. These colonies can become as large as 1 cm and can contain up to 10.000 cells. When these blooms collapse large amounts of foam develop that can accumulate on the beaches in thick layers (LANCELOT *et al.* 1987). Moreover, the enormous amounts of organic matter produced may enhance hypoxia and thus thread bottom dwelling organisms (MICHAELIS 1993). As has been shown during the description of the phytoplankton in the Dutch Coastal Water, the length and intensity of its blooms have strongly increased during the past 20 years (CADÉE & HEGEMAN 1991a, see chapter II.2).

During recent years, much attention has been paid to understand the mechanisms behind the increase in *Phaeocystis* blooms (LANCELOT *et al.* 1987, RIEGMAN *et al.* 1992). As in the case of the *Chrysochromulina* bloom, the *Phaeocystis* bloom is preceded by a spring diatom bloom that consumes all dissolved silicate but leaves enough phosphorus and nitrogen nutrients to enable an ensuing flagellate bloom (VAN BENNEKOM *et al.* 1975, LANCELOT *et al.* 1987). RIEGMAN *et al.* (1992) give some clues why *Phaeocystis* is so succesful during summer in the Marsdiep area. In multi-species competition experiments carried out in nutrient-limited continuous cultures these authors investigated the influence of different nutrient regimes on the dominance of algae. They showed that *Phaeocystis* was a good competitor under nitrate limitation, whereas under phosphate limitation other algae dominated. A further and important aspect of their experiments was that they observed that under nutrient limited conditions *Phaeocystis* only formed colonies when low ammonium/nitrogen ratios prevailed. Under phosphate limitation no colony formation occurred.

RIEGMAN *et al.* (1992) linked the increase of *Phaeocystis* in the Marsdiep area to changes in the nutrient regime in the mid seventies. During that period hydrodynamic measurements in the IJselmeer - an artificial fresh water lake through which part of the Rhine water is sluiced into the Wadden Sea - caused a shift in the N/P ratio during summer from 38 in 1975 to 13 in 1978. Taking a N/P ratio of 16 as critical (REDFIELD *et al.* 1963), RIEGMAN *et al.* (l.c.) suggest that the shift from P control to N control in the Marsdiep in summer after 1977 favoured *Phaeocystis* dominance.

Waste water treatment along the Rhine resulted in a low ammonia/nitrate ratio (VAN BENNEKOM & WETSTEIJN 1990). Between 1972 and 1986 nitrate discharge from the Rhine increased from 5 to 10 kg N s^{-1} whereas ammonium discharge decreased from 4 to 1 kg N s^{-1} (VAN DER VEER *et al.* 1989). The low ammonium/nitrate ratio stimulated colony formation by *Phaeocystis*. Because of their large size these colonies are not eaten by predators (VERITY & SMAYDA 1990), whereas the flagellate stage is controlled by predation for instance by tintinnids (ADMIRAAL & VENEKAMP 1986, WEISSE & SCHEFFEL-MÖSER 1990).

In conclusion, at least three factors have been responsible for the proliferation of *Phaeocystis* in the Marsdiep area according to RIEGMAN *et al.* (1992):

1. as a consequence of increased N/Si and P/Si ratios in the river Rhine enough N and P was left after the spring diatom bloom to enable an ensuing flagellate bloom,
2. a shift from phosphate limitation before 1975 to nitrate limitation after 1977 enabled *Phaeocystis* to succesfully compete against other flagellates,
3. a shift in the ammonium/nitrate ratio stimulated the formation of colonies. The resulting reduced grazing pressure enabled an unbridled growth of *Phaeocystis* and contributed to the observed sharp increase in annual primary production in the Marsdiep area.

It should be noted that *Phaeocystis* colonies occur in large parts of the North Sea after the spring diatom bloom and that they are not confined to the strip of eutrophicated coastal water (e.g. OWENS *et al.* 1989, RICK 1990). The former authors noted on the basis of data from the Continuous Plankton Recorder Survey a decrease of *Phaeocystis* in the North Sea as a whole was observed until approximately 1980. Since then the trend reversed just as in the case of phytoplankton and zooplankton. Their observation seems to contradict the reported increase by CADÉE & HEGEMAN (1991a, b) but one should remember that the CPRS does not effectively sample the coastal zone and therefore does not represent trends in coastal areas (OWENS *et al.* 1989, CADÉE 1990a).

RICHARDSON & CHRISTOFFERSEN (1992) noted that in April and May 1991 and 1992 (also after the spring diatom bloom) large concentrations of colonies were present over the entire southeastern North Sea. Highest concentrations were found either off-shore in the bottom water or near shore mixed throughout the homogeneous water column. They argued that the *Phaeocystis* blooms along the Danish coast were seeded from the open North Sea. Once mixed into the mixed coastal water, high growth rates were possible because of both high ambient nutrient concentrations and a better light regime. On the other hand the spring bloom generally occurs earlier in the off-shore areas (chapter II.1 and II.I2) and for that reason alone an earlier *Phaeocystis* bloom will occur there.

In summary, *Phaeocystis* blooms after the spring diatom bloom seem to be a normal part of the annual phytoplankton cycle. In the Marsdiep area, however, the long duration of the *Phaeocystis* bloom is striking. RIEGMAN *et al.* (1992) suggest that a shift in nutrient ratios in summer rather than an absolute enrichment with P and N enabled the *Phaeocystis* proliferation (as a consequence of reduced predation) and the consequent increase in primary production. However, one should not forget that relative large nutrients loads are a *sine qua non* to sustain large algal blooms (*e.g.* FRANSZ & VERHAGEN 1985). Moreover, it should be noted that although *Phaeocystis* is the dominant flagellate, long-term changes in the duration of blooms of *Phaeocystis* and other non-diatom algae in the Marsdiep area showed a similar pattern (CADÉE 1992a, see chapter II.2).

II.4 A REVIEW OF CURRENT THEORIES ON PHYTOPLANKTON DYNAMICS

In the previous chapter it has been shown that the observed changes in phytoplankton biomass and primary production can be explained by the following factors: (1) the physical setting, (2) the nutrient status and nutrient ratios and (3) grazing. In this chapter a more theoretical approach on the relation between phytoplankton dynamics and its physical and chemical environment is presented. In principle it is based on two review articles by FOGG (1991) and MARGALEF (1978).

In order to understand phytoplankton dynamics we have to be aware of the size spectrum of phytoplankton cells and its implications for the interactions with their environment. The size spectrum ranges from large diatoms (up to a few 100 µm) to small autotrophic cyanobacteria of approximately 1 µm (see Table I.2). The larger phytoplankton is often designated as microphytoplankton (> 20 µm). The smaller phytoplankton comprises picoplankton (0.2-2.0 µm) and nanoplankton (2.0-20 µm). Only recently the importance of the pico- and nanoplankton in the marine environment has become evident (e.g. WATERBURY *et al.* 1979).

The size of an alga has important implications for nutrient uptake. MUNK & RILEY (1952) and GAVIS (1976) showed that a growing microphytoplankton cell can become nutrient limited even before ambient nutrient concentrations have dropped to limiting concentrations. The reason for this is the small surface-to-volume ratio which can result in a situation where nutrient requirements are not met by the flux of these nutrients through molecular diffusion to the uptake sites in the cell wall. On the other hand RAVEN (1986) showed that for small phytoplankter with a high surface-to-volume ratio nutrient limited growth is very unlikely. He calculated that at ambient phosphate concentrations of 0.1 $\mu mol \cdot dm^{-3}$ - the lower end of concentrations in the marine environment- the molecular diffusion to the cell wall of a 1 µm picoplankter is 400 times the nutrient requirements of this cell. Thus one would expect the small phytoplankter to be able to outcompete the larger phytoplankter under all circumstances. That this is not the case is due to to grazing controll of the autotrophic pico- and nanoplankton by heterotrophic flagelates and ciliates which have generation times similar to or even exceeding those of the pico- and nanoplankton (JOHNSON *et al.* 1982, GOLDMAN & CARON 1985, TURLEY & LOCHTE 1985).

The high surface-to-volume ratio of the pico- and nanoplankton also has its price. BJØRNSEN (1988) suggested that part of the photosynthetic products of algae is lost through passive diffusion through the cell wall. He calculated that a 10 µm cell daily loses 5% of its biomass due to passive diffusion. The portion lost would increase with decreasing cell diameter due to the increased surface-to volume ratio. The excreted carbon is an important source for bacterial production (e.g. LARSSON & HAGSTRÖM 1982, AZAM *et al.* 1983)

Fogg (1991) pictures the pico- and nanoplanktonic community as a "*highly dynamic and closely knit community based on photosynthetic primary production, in which the population densities of the component species are set by the kinetics of their trophic relationships rather than by the input of materials from outside. High efficiencies of uptake and rapid cycling of mineral elements enable the community to function at low ambient nutrient concentrations and to hold sufficient amounts of scarce nutrients to permit rapid multiplication. Since the organisms are so small as to sediment at a negligible rate, or, if larger are motile, loss of nutrients by sedimentation does not occur and the community is potentially capable of maintaining itself indefinitely in surface waters. ......*
The ultraplankton [the pico- and nanoplankton] *is the ultimate in plankton existence.*" Fogg further noticed the cosmopolitan nature of the ultraplankton community. A review of all aspects of the dynamics of the pico- and nanoplankton community is beyond the scope of this review. The reader is referred to the excellent paper by FOGG (1991) from which the above information has been taken.

Whereas the ultraplanktonic community is controlled by grazing and not by nutrient limitation or loss through sedimentation, the opposite seems to hold for the microplanktonic community. Their relatively large size makes them prone to nutrient limitation due to the small surface-to-volume ratio (MUNK & RILEY 1952, GAVIS 1976) and to loss from the euphotic zone through sinking (WALSHBY & REYNOLDS 1980). The advantage of being big, however, lies in the fact that the generation times of the microplankton (in the order of days or less) allows them to escape grazing control by mesozooplankton which has generation times in the order of weeks (FOGG 1991).

MARGALEF (1978) discussed the different survival strategies of the microphytoplankton in the marine environment. He envisaged the extreme case of a stagnant ocean. There, eventually a complete segregation would occur between the two factors essential for autotrohpic growth -light and nutrients- since any atom in particulate form is more likely to sink than to float. The connecting factor between light above and nutrients below is turbulence. Thus the two extremes between which the stage of microplankton growth is set are excess turbulence and extreme stagnation. An excess of turbulence will cause the algae to spend more time in the dark and respire more than can be compensated for by photosynthesis and therefore does not allow growth despite nutrient-rich conditions. The other extreme is a complete stagnant water column with no nutrients which is unable to support any life[4]. He postulated that within this spectrum of different turbulent conditions the (micro)phytoplankton has evolved different survival strategies. Under turbulent, nutrient rich conditions diatoms will prevail. Their

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[4] It shoud be noted that at that time the concept of the microbial loop and the importance of pico- and nanoplankton was not known yet. FOGG (1991) postulates that under nutrient depleted conditions the self-contained equilibrium community of pico- and nanoplankton could last indefinitely.

potential to dominate the other algae has been demonstrated in several experiments (THOMAS *et al.* 1978, PARSONS *et al.* 1978, EGGE & ASKNES 1992). Adaptions to exploit the situation best include the absence of active motility. In a turbulent environment this would be a waist of energy. Instead they use the possiblilities of turbulence to their own advantage. As has been stated before, one of the disadvantages of being big is the relative inefficient nutrient uptake. MUNK & RILEY (1952) and GAVIS (1976) mathematically showed that the movement of sinking cells relative to the water steepens the diffusion gradien of nutrients around the cells and thus promotes nutrient uptake. RAVEN (1986) calculated that a cell of approximately 10 µm could double its nutrient uptake by sinking. CANELLI & FUHS (1976) gave experimental evidence that slowly sinking cells display slower uptake rates than fast sinking cells.

Another mechanism to exploit the turbulence is the construction of protruberances and/or colonies. This enables them to exloit the turbulence more effectively. MARGALEF (1978) used the following image: *"a small boat dances on the waves, a large boat is washed by the waves"*. CHASE (1979) showed that organic substances can reduce the friction of sinking particles. PICKET-HEAPS *et al.* (1992, and references therein) suggested that the construction of a silica frustule -typical for diatoms- requires approximately ten times less energy compared to the formation of an organic cell wall. Thus the advantage of having a silica cell wall might be two-fold: Firstly it is cheaper and secondly its high specific weight would have a positive effect on sinking and therefore enhance nutrient uptake and growth. The above life-style is accompanied by a certain loss through sedimentation, but when this is compensated for by growth and an upward turbulent diffusion of cells a net growth is still possible.

When the stabilization of the water column progresses, the loss of non-motile algae from the surface layer by sinking and grazing cannot be compensated for anymore by growth due to the combined effect of reduced turbulence and nutrient levels. In this situation it pays the organism to invest some energy in swimming (MARGALEF 1978). This not only allows it to choose its optimum position in the nutrient-light gradient, but it also helps to keep a steep nutrient gradient around the cell upright.

For nutrient limited cells to survive it is important to live long enough to gather as many nutrients as necessary to enable a cell division. Margalef further suggested that using part of the available energy in toxic, grazer-repellent substances might be a wise investment.

II.5 PHYTOPLANKTON IN THE NORTH SEA: A SUMMARY

In the previous chapters a review was presented of the seasonal cycle of phytoplankton biomass (as Chl *a*), primary production and species composition and succesion. If available, data were presented that showed if any changes had taken place in the annual phytoplankton cycle. Special attention was given to algal blooms. In this chapter the above information will be summarized and some general - and for the "Conservation of the North Sea Plankton" important - trends of phytoplankton dynamics in the North Sea will be extracted.

II.5.1 SPRING BLOOM

Light is the predominant factor that determines the start of phytoplankton blooms both in coastal and oceanic areas. The availability of light is controlled by day length and cloudiness on the one hand and by turbulence (mixing of the water column) and suspended matter content on the other hand. In the deep areas of the North Sea excess turbulence will cause the phytoplankton to dwell longer in the dark and lose more energy through respiration than can be compensated for by photosynthesis during their residence in the euphotic zone. In shallow coastal areas the mixing depth is fixed. Here a horizontal suspended matter gradient directed towards the coast exists that determines the vertical light gradient. Thus the spring bloom first starts in the off-shore regions and gradually intrudes the near-shore, more turbid areas as soon as the available light allows growth. Differences in the timing of the spring bloom in coastal areas are probably related to a combination of average amount of sunlight (cloudiness) and turbidity as found by CADÉE & HEGEMAN (1991b) for the Marsdiep area

Extremly early blooms (January-February) correspond to profitable light conditions (shallow mixing depth, low suspended matter content) such as prevail in the centre of the Southern Bight (ICES 4), the Dogger Bank (ICES 7") and the Skagerrak. In these areas the spring peak occurs during March and gradually spreads from there to the other areas. In the continental coastal water the spring peak occurs during April. In the northern North Sea the spring peak occurs during late April-early May.

In all areas of the North Sea diatoms dominate the first phase of the spring bloom. In those cases where the spring bloom has been studied evidence exists that the diatom bloom is limited by silica depletion. After the diatom bloom a second bloom of algae that do not have a silicate requirement is observed. Prymnesiophyceae (syn. haptophyceae) play a dominant role during this phase of the phytoplankton annual cycle. "Follow-up" blooms of these algae after the spring diatom proliferation have been observed in the northern and central North Sea and along the continental coasts (ICES 1/2, 4, 5, 7"). Noteworthy are the blooms dominated by colonies of the Prymnesiophyceae *Phaeocystis* sp. along the continental coast.

The phytoplankton biomass and primary production during the spring bloom are highest along the nutrient-rich continental coastal zone. There they reach a biomass up to 15-40 µg Chl *a* dm^{-3} and production levels of 3-10 g C m^{-2} day^{-1} compared to 4-12 µg Chl *a* dm^{-3} and up to 3 g C m^{-2} day^{-1} in other areas. Interestingly, the maximum biomass and primary production was observed in the Northern North Sea during the diatom bloom, whereas along the continental coast (Marsdiep, Ems-Estuary) the highest biomass and production levels were observed during the (*Phaeocystis*-dominated) post-diatom bloom.

II.5.2 SUMMER PHYTOPLANKTON

The development of the summer plankton strongly depends on hydrographic conditions and nutrient supply. In the off-shore region, where water depth exceed ~30 meters a thermocline develops. As a consequence of algal growth in the upper euphotic zone the thermocline divides the water column in an upper, euphotic, low turbulent, nutrient poor surface layer and a relative nutrient-rich, dark bottom layer. In the upper, euphotic zone the phytoplankton evolves towards a community which is dominated by small flagellates. During summer a second component slowly gains importance: large Dinoflagellates like *Ceratium* spp.

Evidence exists that the summer phytoplankton in these stratified regions of the North Sea is nitrogen-limited. When, however, due to strong winds the mixed surface layer is deepened and nutrients are transported into the euphotic surface layer combined flagellate-diatom blooms can occur. The question as why flagellates are best adapted to nutrient poor conditions and why diatoms can gain importance under nutrient rich conditions has been discussed in the previous chapter.

In the near-shore, well-mixed coastal zone the annual phytoplankton cycle is characterized by a series of blooms which follow after the spring bloom. In contrast to the central North Sea, diatoms are an integral part of the phytoplankton throughout the entire growing season. In the coastal zone the phytoplankton is phosphate limited. There is evidence to suggest that the phytoplankton biomass and primary production in summer is related to the nutrient input (GIESKES & SCHAUB 1990, DE JONGE 1990, CADÉE & HEGEMAN 1993).

II.5.3 ANNUAL PRIMARY PRODUCTION

In chapter II it was shown that highest primary production values are found along the continental coast where nutrient levels are highest. Here annual primary production levels up to 500 g C m^{-2} a^{-1} have been observed. Lowest production values were observed along the English coast (75 g C m^{-2} a^{-1}). These low production levels coincided with the lowest winter nitrate concentrations (~6 µmol·dm^{-3}). In Figure II.5 an attempt is made to relate the winter nutrient concentrations with the annual primary production. The rationale behind this exercise is: the more nutrients available at the onset of the growing season, the more biomass can be produced (= new primary production) and the more nutrients can be recycled (regenerated primary production). Indeed nutrient levels after the vernal bloom reach very low levels in the entire North Sea indicating that all nutrients have been turned into biomass.

We related the annual primary production presented in chapter II.2 to nitrogen (as NO_3^-) because it is assumed to be the limiting nutrient during summer (OWENS *et al.* 1990, RIEGMAN *et al.* 1990a) over much of the North Sea. The production data were taken from JOINT & POMROY (1992). The Dogger Bank values, however, were excluded because the permanent phytoplankton production does not allow an estimate of true winter nitrate concentrations. Our estimate for the northern North sea is also included. The winter nitrate concentrations were estimated from winter distribution pattern presented by BROCKMANN *et al.* (1990) except for the FLEX estimate (ICES 1 and 2), which were taken from BROCKMANN *et al.* (1980) and the English coast estimate which was taken from DICKSON *et al.* (1988a).

As Figure II.5 shows there exists a very good agreement between winter nitrate concentrations and annual primary production. Of course a more rigorous analysis with respect to the nutrient budget is needed, including nutrient fluxes into and out of the different ICES boxes. Nevertheless, the relation substantiates the hypothesis that nutrient input into the North Sea has a direct effect on primary production.

It has been pointed out before that large amounts of nutrients enter the coastal areas via rivers. There is, however, an extra anthropogenic source of nitrogen that affects the whole North Sea -both near-shore and offshore. Through the combustion of fossil fuels and for instance through the modern livestock industry large amounts of nitrogen-nutrients are transported directly to the North Sea via the atmosphere. NELISSEN & STEFELS (1988) made a tentative budget on N input into the North Sea. They estimated that 40% of the nitrogen is transported into the North Sea via the atmosphere.

II.5.4 LONG-TERM TRENDS

Two trends can be discerned in the North Sea: a climatic driven and a nutrient driven change.

In the open North Sea and in the Atlantic Ocean a similar change in phytoplankton and zooplankton biomass was observed. There is information to suggest that the observed changes are of global extent. In the Pacific Ocean trends in phytoplankton biomass similar to those in the North Sea were observed (CPR SURVEY TEAM 1992). The changes in phyto- and zooplankton possibly exerted an impact on higher trophic levels. AEBISCHER *et al.* (1990) showed that changes in phytoplankton and zooplankton biomass were closely followed by for instance changes in Kitty Wake clutch size and young herring standing stock.

Several hypotheses have been put forward to explain the observed changes. They all relate the observed changes to climatic changes. The exact mechanism is not yet clear, but all hypotheses acknowledge the importance of light availability during winter/spring due to changes in turbulence and mixing depth.

Along the continental coast the influence of changing weather patterns on the phytoplankton is overriden by the influence of increased nutrient input and nutrient ratios. For the Dutch coastal zone a direct relation between annual phosphate input and primary production (DE JONGE 1990) and between mean phytoplankton biomass in the Marsdiep area and nitrogen loads of the river Rhine (CADÉE 1992a) have been suggested. In the German Bight increased nutrient levels resulted in an increased annual phytoplankton biomass.

Apart from the above mentioned quantitative impact of nutrient status on phytoplankton biomass the nutrient ratios (Si/P/N) also exert a strong influence on phytoplankton composition. First of all the importance of dissolved silicate should be mentioned. The Dutch and German time series have shown that diatoms have not been able to take advantage of the increased nutrient levels. Instead their annual biomass is most probably limited by silicate availability. Only those algae that do not depend on silicate have been able to use the increased P and N levels. But also changes in N/P ratios might have a strong influence on phytoplankton composition. HICKEL *et al.* (1992) suggested that the increase of flagellate biomass during the mid seventies was rather due to an increase N/P ratio than to increased nutrient levels as such. RIEGMAN *et al.* (1992) presented evidence that the increased *Phaeocystis* standing stocks were related to extreme low NO_3/PO_4 ratios. MAESTRINI & GRANÉLI (1991) suggested that the *Chrysochromulina* bloom in the Skagerrak in 1988 was related to high extreme high N/P ratios that induced toxin production in this alga. Thus it escaped from predation and high nutrient availability (through diffusion into the euphotic zone) enabled unbridled growth. In both the *Phaeocystis* and the *Chrysochromulina* case the escape from predation was assumed to be the underlying mechanism for the proliferation of these algae.

III. ZOOPLANKTON

III.1. ZOOPLANKTON COMMUNITIES: SPECIES DISTRIBUTION AND ABUNDANCE

The North Sea is a shelf sea and therefore basically a neritic area, *i.e.* autochthonous neritic populations dominating in the most sheltered parts and mostly allochtonous oceanic populations being transported into the area with the currents. Hence, the zooplankton community composition in the North Sea is dominated to a large extent by the current systems, carrying specific species communities into and out of the North Sea, as well as by the degree of mixing of the water column as a factor of depth and tidal currents. The physiological capacities of the species, *e.g.* growth, reproduction etc. and thus the population's survival in turn are subject to water quality and water column stability. Therefore, the deep central and northern North Sea (north of the 50 m depth isopleth, stretching from the Humber estuary to the northern tip of Denmark, see Fig. I.1), as characterized by Atlantic water inflow and summer thermal stratification, has to be considered a different type of ecosystem compared to the shallow southern North Sea. Here, tidal stirring is responsible for a continuously mixed water column, with some salinity stratification occurring at the mouth of the great rivers.

Following the first differentiation of LAEVASTU (1963), FRASER (1965, 1973) listed 8 different hydrographical regions within the North Sea, each containing a specific zooplankton community.

III.1.1. NORTHERN AND CENTRAL NORTH SEA

(1) Water masses and indicator species

With progressive "dilution" of the Atlantic water, the zooplankton species composition in the northern North Sea is characterized by a decreasing number of Atlantic intruders towards the Central North Sea (FRASER 1968): North of Scotland, 13-18 different copepod species were found in the Continuous Plankton Recorder Surveys (CPRS), of which only 7-12 species crossed the edge of the shelf and entered the North Sea (COLEBROOK *et al.* 1961b, their Text-Fig. 1). Between September and February each year, the inflow of Atlantic water to the east of Shetland is at a maximum (STEELE 1957). Correspondingly, HAY *et al.* (1990) found an increased abundance of Atlantic water indicator species (*i.e.* those which can withstand a change in the environment/water mass as older life stages, but are unable to reproduce) in the northwestern North Sea between October and January. However, FRASER (1968) showed that the highest number of Atlantic water indicator species enters the North Sea through the Orkney-Shetland Channel in July/August each year, and round the north of Shetland in August/September. In the central North Sea, the highest number of oceanic species occurs in September (FRASER 1968). Probably, the high oceanic species diversity in the northern North Sea reflects more the seasonal abundance of the species in the Atlantic surface waters than the quantity of the inflow to the North Sea.

The intrusion of mixed oceanic and Scottish coastal water through the Orkney-Shetland Channel is indicated by the presence of the copepods *Metridia lucens, Candacia armata,* the pteropods (thecosomates) *Spiratella (Limacina) retroversa, Clione limacina,* and the thaliacean *Dolioletta gegenbauri;* on the other hand, the chaetognath *Eukrohnia hamata,* the copepods *Calanus hyperboreus, Metridia longa, Pareuchaeta norvegica, Aetidius armatus* and the salp *Salpa fusiformis* point to the inflow of arctic-boreal water north of the Shetlands and via the Norwegian Deep (KRAUSE 1990, based on COLEBROOK *et al.* 1961a and b, FRANSZ *et al.*, 1991).

The Central North Sea Water characterized by high abundances of the cyclopoid copepod *Oithona* spp. (mainly *O. similis*), the chaetognath *Sagitta elegans,* and echinoderm larvae (RUSSELL 1939, FRANSZ *et al.* 1984, KRAUSE *et al.* SUBM.).

(2) Zooplankton communities

During and after the spring bloom in the northern North Sea, calanoid copepods (in particular *Calanus finmarchicus, Pseudocalanus elongatus, Microcalanus pusillus*), cyclopoid copepods (*Oithona similis* and *O. nana*) and the harpacticoid *Microsetella norvegica* predominate. The only other relatively abundant organism is the appendicularian *Oikopleura spp.*, which occurs during the bloom in April/May. In June, only copepods are found. Only a few protozoans occurred (Fransz & van Arkel 1980, Williams & Lindley 1980a, Krause & Trahms 1982).

In winter (from Krause et al. subm.), *Oithona spp.* (mainly *similis*), *Paracalanus parvus* and *Microcalanus pusillus* are the most prominent zooplankters over wide areas of the central and northern North Sea, reaching mean densities of 1000-10000 ind. m^{-2} with maxima of 33000 and 13000 ind. m^{-2}, respectively. In contrast, *Calanus finmarchicus* as well as all the large carnivorous copepods (*Pareuchaeta norvegica, Scolethricella minor, Heterorhabdus norvegicus, Chiridius armatus*) occur mainly restricted to the Norwegian Deep in the Skagerrak and around the southern tip of Norway. This is an effect of depth and season: While the carnivorous species live below the euphotic zone in deeper waters year-round, the oldest *C. finmarchicus* life stages (mainly CIV and CV) spend the phytoplankton-poor season in a passive, non feeding state (diapause) at great depths (see *e.g.* •stved 1955, Krause & Radach 1989) predominantly off the continental shelf and in the Norwegian Deep. In spring each year, this species repopulates the North Sea with the prevailing Atlantic inflow from the north and from the Norwegian Deep (Krause & Martens 1990, Backhaus *et al.* 1991).

Euphausids (*Nyctyphanes couchi, Thysanoessa inermis, T. raschi*) constitute important members of the zooplankton community of the northern North Sea in winter and spring, reflecting to a large extent the Atlantic water inflow to the North Sea (Marshall 1948, Glover 1952).

III.1.2. SOUTHERN NORTH SEA

(1) Water masses and indicator species

English and Continental Coastal Waters are highly influenced by the riverine freshwater runoff and to a lesser extent by the admixture of "Channel Water" ($S >34.75*10^{-3}$, Lee 1980), Atlantic water entering the North Sea through the English Channel.

There are only a few zooplankton species with a distribution limited to the southern North Sea: *Sagitta setosa, Centropages hamatus, Temora longicornis, Isias clavipes* and *Labidocera wollastoni* (Krause 1990). The latter two copepods are considered to be the only truely neritic species of the North Sea (Colebrook *et al.* 1961b) with a distribution confined to the southern North Sea. The chaetognath *Sagitta setosa* enters the North Sea with the English Channel water, as does probably the calanoid copepod *Calanus helgolandicus*.

(2) Zooplankton communities

The mesozooplankton communities of the Southern Bight, in the western and northern Wadden Sea and in the German Bight are dominated by the calanoid copepods *Temora longicornis, Pseudocalanus elongatus, Acartia clausi* and *Centropages hamatus*, which together constitute from 90 % of the total zooplankton biomass in winter to 50 % or less in summer (Fransz 1976, 1980b,c, Hickel 1975). *Temora longicornis* predominates in spring and autumn, *Acartia clausi* and *Centropages hamatus* dominate in summer (Fransz 1980c). In winter, *Pseudocalanus elongatus*, *Paracalanus parvus* and *Acartia clausi* are the most frequently met taxa with 5000-2000 ind. m^{-2}, maximal 25000, 17000 and 33000 ind. m^{-2}, respectively (Krause et al. subm.). *Calanus helgolandicus* is a warm water form, reaching highest densities in summer-autumn in the deeper parts of the southern North Sea (Matthews 1969) but never predominates in the way *Calanus finmarchicus* does in the northern North Sea. In the shallow coastal areas in summer, copepod numbers are occasionally outnumbered by the meroplanktic larvae of polychaetes, lamellibranchs, echinoderms, cirripeds and decapods, the appendicularian *Oikopleura dioica*, and isopods (Martens 1980, Fransz 1980b, Bosselmann 1989). In the German Bight, echinocardium larvae at times constitute up to 80 % of the total meroplankton individuals (Gerdes 1985, Bosselmann 1989). According to Martens (1980), besides the above mentionned four calanoid copepod species, *Acartia discaudata, Podon sp.*, and *Oikopleura dioica* also belong to the indigenous coastal fauna of the German Bight. *Paracalanus parvus*, *Oithona similis* and *Rathkea octopunctata* on the other hand are considered non-productive immigrants.

Tab. III.1a Regularly occurring holopelagic zooplankton species of the northern North Sea.
Origin: A: autochthonous; a: allochthonous
Immigration paths: 1: Scotland-Shetlands; 2:Shetland-Norway;
3: Norway Deep/Skagerrak; 4: Channel
*Legend: * = few; ** = common; *** = stock forming.*

Group	Species	Rel. frequency		Origin	Entering via	Distribution center
		summer	winter			
Scyphomedusae	Cyanea capillata	*		A		
Trachymedusae	*Aglantha digitale*	*		a	1, 4	Atlantic
Polychaeta	*Tomopteris spp.*	*		A		
Mollusca	*Clione limacina*	***		a	1, 3	Norway Deep, shelf edge
	Spiratella retroversa		***	a	1, 3	Norway Deep, shelf edge
Copepoda	*Calanus finmarchicus*	***	*	a	1, 3	North. N.S.
Calanoida	*Microcalanus pusillus*	***	*	A,a	3	North. N.S., Atlantic water
	Pseudocalanus elongatus	***		A		
	Paracalanus parvus		**	A		Centr. N.S.
	Acartia clausi		***	A,a		
	Centropages typicus		**	a	3	Atlantic, NW N.S.
	Metridia lucens	*	**	a	1	Atlantic
	Anomalocera pattersoni	*		a	1	Atlantic
	Pleuromamma robusta	*		a	1	Atlantic, NW N.S.
	Aetidius armatus	*		a	3	Norway Deep
	Candacia armata		*	a	1	Atlantic, NW N.S.
	Rhincalanus nasutus	*		a	1, 2	Atlantic, NW N.S.
	Chiridius armatus	*		a	3	Norway Deep
	Scolethricella minor	*		a	3	Norway Deep, shelf edge
	Pareuchaeta norvegica	*		a	3	Norway Deep, shelf edge
	Calanus hyperboreus	*		a	3	Norway Deep
	Metridia longa	*		a	3	Norway Deep, Centr. N.S.
Cyclopoida	*Oithona similis*	**	***	A,a		Centr. N.S., Skagerrak
	Oithona plumifera	*		a	3	N N.S., Atlantic
Harpacticoida	*Microsetella norvegica*		**	A		Centr. N.S.
Ostracoda	*Conchoecia elegans*			a	3	Norway Deep, allover N.S.
	Conchoecia borealis			a	3	Norway Deep, NW N.S.
Euphausiacea	*Thysanoessa inermis*	*	***	A,a	1	NW N.S.
	Thysanoessa longicaudata		**	a		West. N.S. to Doggerbank
	Thysanoessa raschii		**	a		NE N.S.
	Meganyctiphanes norvegica		**	a	3, 1	Norway Deep, Skagerrak
	Nyctiphanes couchi		**	a		NW N.S.
Amphipoda	*Parathemisto abyssorum*		**	A,a	3	
Chaetognatha	*Sagitta elegans*		**	a		Centr. N.S., NW N.S.,Atlantic
	Sagitta maxima	*	*	a	3	Norway Deep
	Eukrohnia hamata		*	a	3	Norway Deep, shelf edge
Tunicata	*Salpa fusiformis*		***	a	3	shelf edge
	Oikopleura dioica	**		A		Centr. N.S.

In the German Bight, the mesozooplankton species composition and density differ between near-coastal and more offshore areas (MARTENS 1978, GERDES 1985): Several types of water bodies can be distinguished, which are at times separated by strong salinity fronts (HESSE *et al.* 1989). The zooplankton community composition depends on a more or less extensive admixture of Central North Sea Water, characterized by high copepod abundances, with coastal water, containing a majority of meroplanktic larvae. The closer to the coast, the lower is the relative density of copepods, being replaced by cladocerans and meroplanktic larvae of polychaetes and cirripeds in particular in April/May (MARTENS 1980) and/or June (GERDES 1985).

The protozoan fraction of the microzooplankton of the German Bight is dominated by non-loricate ciliates most of the year, the genera *Lohmaniella* and *Strombidium* at times producing spring biomass maxima. Loricate forms, like the tintinnids *Helicostomella subulata* and *Favella denticulata* may also reach considerable densities. The autotrophic ciliate *Mesodinium rubrum* almost matches the biomass of all other ciliates together, in some years constituting up to 40 % of the total phytoplankton biomass (STEIFF 1988). From May/June to August, the heterotrophic dinoflagellate *Noctiluca miliaris* may reach considerable densities in the southeastern and southwestern North Sea (UHLIG & SAHLING 1982, DAAN 1987).

The metazoan zooplankton <200 µm is dominated by copepod nauplii and meroplanktic larvae of molluscs and polychaetes, but never takes an important part in the total microzooplankton biomass.

The macroplanktonic predators of the Southern Bight are dominated by a variety of gelatinous carnivores (scyphomedusae, ctenophores and hydromedusae) and, to a lesser extent, by fish larvae and chaetognaths (DAAN 1989). The most common scyphomedusae are *Aurelia aurita* (in May/June), and *Cyanea lamarcki* (in June-August), showing strong interannual fluctuations in abundance (VAN DER MAADEN 1942, VERWEY 1942, VAN DER BAAN 1980, in DAAN 1989). The ctenophore *Pleurobrachia pileus* and fish larvae reach peak densities in May/June, while hydromedusae, in particular *Phialidium hemisphericum*, dominate from July onwards. The chaetognath *Sagitta setosa* is most abundant in fall (FRANSZ *et al.* 1978, FRANSZ & VAN ARKEL 1983, FRANSZ 1980a, b, DAAN 1989).

Based on all available literature, a list of the regularly occurring holopelagic zooplankton species of the northern/central North Sea and the southern North Sea is given in Tab. III.1a-b.

III.1.3. SEASONAL VARIABILITY OF ZOOPLANKTON ABUNDANCE

(1) Offshore areas of the North Sea

Based on data acquired with the Continuous Plankton Recorder Survey CPRS, the seasonal abundance of all copepod species together can be described for each 1 by 2 degree latitude by longitude rectangle of a sampling grid covering the North Sea and the Skagerrak, but not the continental coastal zone (FRANSZ *et al.* (1991): Generally, the copepods have their minimum abundance during the winter months. The stocks start to increase in February, and mostly maintain high abundances between April and September/October. The highest seasonal abundance maxima are found along the southeastern coast (outer German Bight) and decrease towards the north and northwest. Due to relatively large winter stocks in the south, the difference in abundance between summer (June-August) and winter (January-March) amounts to a factor of 10-15 in the south, compared to 30-40 in the north.

However, the CPRS samples are taken in appr. 10 m depth only. This means that two sources of mistakes obscure the picture of the seasonal amplitudes in abundance of copepods: 1. In the deep northern North Sea, other than in the turbulent waters of the shallow southern North Sea, most copepods undertake distinct diurnal and some also seasonal migrations - especially in winter the median depth of occurrence of almost all species is below 10 m depth. 2. the copepod community of the northern North Sea in summer is dominated by *Calanus finmarchicus*, a species which is not present in winter, but immigrates into the North Sea every year in spring with the Atlantic waters overflowing the shelf - the copepod community of the southern North Sea on the other hand consists more or less of autochtonous species.

Tab. III.1b The regularly occurring holopelagic zooplankton species of the sourthern North Sea
Origin: A: autochthonous; a: allochthonous
Immigration paths: 1: Scotland-Shetlands; 2:Shetland-Norway;
3: Norway Deep/Skagerrak; 4: Channel
Legend: * = few; ** = common; *** = stock forming.

Group	Species	Rel. frequency		Origin	Entering via	Distribution center
		summer	winter			
Dinoflagellata	*Noctiluca miliaris*	***		A		German B., South. B.
Tintinnidae		***		A		Skagerrak, Norway Deep, coastal
Scyphomedusae	*Chrysaora hysoscella*	**		A		German B.
	Cyanea lamarcki	***		A		South. B.
	Aurelia aurita	***		A		Baltic, Wadden Sea, South. B.
Trachymedusa	*Aglantha digitale*	*		a	4	South. B.
	Rathkea octopunctata		*	A		coastal
	Sarsia	***		A		coastal, max. April
	Phialidium	***				South. B.
	Bougainvillia	*		A		southern coastal
Ctenophora	*Pleurobrachia pileus*	***		A		German B., South. B.
	Beroe cucumis	*		A		German B., South. B.
Polychaeta	*Tomopteris*	*		A		
Cladocera	*Podon leuckarti*	**	*	A		"British waters"
	Podon intermedius	**	*	A		
	Evadne nordmanni	**	*	A		
Copepoda, Calanoida	*Temora longicornis*	***	***	A		
	Acartia clausi	**	**	A		Channel, Skagerrak, NW N.S.
	Acartia longiremis	*		A		Baltic, Kattegat, Skagerrak, coastal
	Paracalanus parvus		***	A,a		S N.S. offshore
	Pseudocalanus sp.	**	***	A		Centr. N.S.
	Centropages hamatus	***		A		Channel, South. B., Kattegat, Skagerrak, coastal
	Calanus helgolandicus	**	*	A? a?	4?	
	Labidocera wollastoni		*	A		German B.
	Isias clavipes			a	4	SW North Sea, Channel
Cyclopoida	*Oithona nana*	*	**	A		south of 53°N
	Corycaeus anglicus		**	A		S, SE N.S., German B., South. B.
Harpacticoida	*Microsetella norvegica*	**		A		
Ostracoda	*Conchoecia elegans*			a		
Euphausiacea	*Thysanoessa raschii*		**	A,a		SW N.S.
Chaetognatha	*Sagitta setosa*		**	a	4	South. N.S.
Tunicata	*Oikopleura dioica*	**	*	a	4	Channel, South. B., estuaries

Very distinct species-specific seasonal abundance patterns underly the above geographical pattern for all copepods (FRANSZ *et al.* 1991). In the long-term (1948-1986) average of seasonal abundances of 18 zooplankton taxa in the offshore areas of the North Sea, *Pseudocalanus elongatus* (probably the *Pseudocalanus* group since *Paracalanus parvus* was not identified and *Microcalanus sp.* not sampled quantitatively) appears to be the most abundant species, *Metridia lucens* among the least abundant. However, this may only partly be true, because small species, like *Oithona spp.*, *Evadne/Podon spp.* etc. and young developmental stages of most other species cannot be sampled quantitatively by the CPRS due to the large meshsize of 270 µm employed. Furthermore, species or stages with a median depth of occurrence deeper than the sampling depth of 10 m, like *Metridia, Microcalanus, Microsetella, Para- and Pseudocalanus spp.* (KRAUSE & RADACH 1989), will be underrepresented. Nevertheless, the CPRS data give a unique impression of the relative seasonal (and long term, see chapter III.1.4.) abundances of most mesozooplankton species.

Most taxa show a single more or less distinct abundance peak in summer, some in fall like *Centropages typicus and Corycaeus spp.*. In general, the peak abundances vary between May and October. The most abundant, mainly herbivorous taxa like *Calanus finmarchicus* and *Temora longicornis* peak earlier in the year than the omnivorous and carnivorous taxa - chaetognaths, hyperiid amphipods and euphausids also occur in winter in relatively high densities.

(2) The zooplankton community off the Northumberland coast

All groups of meso- and macrozooplankton sampled at a fixed station 8 km off the Northumberland coast (ca. 55 °N, 1 °W; water depth 53 m) during a 15 year period were analyzed by ROFF *et al.* (1988). The authors consider the sampling location to be representative for the western central North Sea, quadrant (C2) of the CPRS.

The phytoplankton spring bloom starts, on average, in March, when the copepod abundance reaches its seasonal minimum. The copepods (only small species) start their seasonal production in April, but the abundance peak is formed two months after the phytoplankton peak. The seasonal maximum in June/July (uni-modal distribution) corresponds with the summer decline of phytoplankton, and the second peak of phytoplankton begins with the seasonal decline of the copepods starting usually in July. Peak abundances of potential copepod predators occurred at various times: ctenophores in August, decapods and fish larvae in September, medusae having high abundances from May to at least September. In contrast, chaetognaths, euphausids and the hyperiid amphipod *Themisto gaudichaudi* have their seasonal maxima in winter.

The abundances of copepods are "tracked" both seasonally and inter-annually by the abundances of their summer-autumn predators (ctenophores, medusae, larval fish, decapods), and the authors assume this to indicate food limitation of predators or "top-down" (predator) control of the secondary producers. Also in winter, chaetognaths, advected euphausids and the amphipod *Themisto gaudichaudi* control the stock of overwintering herbivorous zooplankton.

(3) Southern Bight, eastern coastal area

In Dutch coastal waters, the herbivorous copepod populations build up peak densities during May/June (FRANSZ 1976). Later in June/July, the herbivore populations break down to very low abundance levels (FRANSZ *et al.* 1978). Such a summer decline was also observed in the Kattegat by ERIKSSON (1973a) and in the English Channel by DIGBY (1950). Probably, the decline is caused by an insufficient feeding regime which inhibits further reproduction. Predation by ctenophores, with a maximum abundance in May/June, by hydromedusae (*Phialidium hemisphaericum, Sarsia tubulosa*) and by the egg predator *Noctiluca sp.* was shown to have only a minor impact (DAAN 1986, 1987, 1989, KUIPERS *et al.* 1990). Locally, high densities of fish larvae may cause a rapid decline of copepods. In some years a second abundance peak of copepods develops in August.

(4) German Bight

The seasonal abundance of small copepods (*Temora longicornis, Acartia clausii, Pseudocalanus elongatus, Paracalanus parvus, Centropages hamatus, C. typicus*) in the German Bight is subject to very large interannual variations (GREVE 1988). In a series of observations from 1974 to 1982, a consistent trend of two abundance peaks occurring increasingly later in the year becomes apparent. The ctenophore *Pleurobrachia pileus* and its predator *Beroe gracilis* show very distinct single abundance peaks in almost every year in May/June (GREVE & REINERS 1988). In the 9-year-mean, the small copepods reach their maximal abundance only after *Pleurobrachia pileus* has disappeared as a predator. Only after the population of *Pleurobrachia pileus* is grazed away by another ctenophore, *Beroe gracilis*, copepods increase in abundance again. Therefore, GREVE (1988) considers predation by the ctenophore *Pleurobrachia pileus* to be responsible for the summer decline of the copepods (in June/July; same species as in Southern Bight).

Noctiluca sp. is a heterotrophic dinoflagellate (up to to 1 mm diameter), typical for the southern North Sea, which forms very dense patches in *e.g.* the German Bight in summer (UHLIG & SAHLING 1982, SCHAUMANN *et al.* 1988): These patches are located at the water surface and consist of aging *Noctiluca* cells which release nutrients (nitrate and phosphate) to the water during cell lysis. The regenerated nutrients stimulate new phytoplankton production (mainly typical spring diatoms), which then constitutes the preferred food for *Noctiluca*. Besides, large amounts of organic substances are set free, some of them gelatinous, causing a mucilaginous consistency of the surface water. A microheterotrophic food web establishes in and around the *Noctiluca* patch, consisting of bacteria and fungi that degrade the organic material and an association of bacteriovorous protozooplankton such as ciliates, heterotrophic dinoflagellates, small amoebae and uncoloured nanoflagellates. On the other hand, mesozooplankton, with the exception of meduseae, seems to be largely excluded from the patch, mechanically by the slime consistence of the water, partly by predation of *Noctiluca* on small mesozooplankters, and possibly by the feeding impact of the abundant meduseae. Thus locally, *Noctiluca* occupies the grazer position in the food web, escluding the copepod food competition by its own special microheterotroph feed-back system.

III.1.4. LONG TERM TRENDS IN ZOOPLANKTON ABUNDANCE IN THE NORTH SEA

There are only a very few long-term studies available for zooplankton abundance in the North Sea: From 1920-1960, the variations in zooplankton composition and abundance in the Faroe-Shetland Channel and further off the west coast of Scotland were studied in relation to the inflow of Atlantic water (FRASER 1969). From 1932-1961, the Lowestoft laboratory collected (but almost did not publish) zooplankton along the "Flamborough line" (east-north-east from Flamborough Head till 2°E, following more or less the Flamborough front (COLEBROOK 1966). Other time series are well documented: *(1)* the Continuous Plankton Recorder Survey, covering the offshore areas of the North Sea, hence in particular the northern and central North Sea; *(2)* the zooplankton community off the Northumberland coast; *(3)* the phenomena summarized as "Russell cycle" in the English Channel; *(4)* a stationary time series in the German Bight: the Helgoland Reede and LV Elbe I data; but here the analysis of the mesozooplankton was not seriously published; *(5)* observations at a tidal inlet to the western Wadden Sea (Marsdiep) and in the coastal Southern Bight since the 1970s.

(1) Offshore areas of the North Sea - Continuous Plankton Recorder Survey 1948-1987

In 1932, the Continuous Plankton Recorder Survey (CPRS) started, but only since 1948, sampling routes and methodology have been fairly consistent and comparable. Despite the insufficiencies inherent in the sampling method (see III.1.3., RADACH 1984, KRAUSE 1990), this is the only suitable data set available for the establishment of geographical distribution patterns and for interannual comparisons of mesozooplankton abundance (at appr. 10 m depth) in the offshore areas of the whole North Sea.

From the beginning of the survey to about 1979/1980 (32 years), the dominant pattern in the annual fluctuations of zooplankton abundances is one of a decreasing trend in relation to the long-term average. Since the early eighties, 15 out of 20 neritic and oceanic zooplankton taxa increased in their overall abundance again. Interspecific differences exist mainly with respect to the seasonal variations in abundances. The long-term trend is common to the zooplankton in the whole CPRS area, *i.e.* throughout the North Sea and also in the Atlantic shelf areas and in the open ocean from Iceland to Biscay to about 20 °W. Underlying the long-term decline until the early eighties, there is "an element of variability" with a period of about 3 years (FRANSZ *et al.* 1991, CPR Survey Team 1992).

(2) The zooplankton community off the Northumberland coast, 1969-1983.

The generally declining trend of mesozooplankton abundance at least from 1971 to 1980, followed by a substantial increase was also derived from investigations on the zooplankton community off the Northumberland coast (ROFF *et al.* 1988, for details see III.1.3.(2)). Here, the mean annual abundance of copepods was positively correlated to the previous winter's minimum abundance (thus confirming COLEBROOK 1982a), and inversely related to the previous winter's abundance of euphausids and chaetognaths. The authors suggest (contrary to COLEBROOK 1982a, see above) that the euphausids, the chaetognath *Sagitta elegans* and the hyperiid amphipod *Themisto gaudichaudi*, all well-known copepod predators and abundant in winter, are responsible for the copepod winter mortality. Copepods declined in average abundance by a factor of about 5 between 1974 and 1980.

(3) Western English Channel - The Russell Cycle 1924-1970s

There is another long-term, possibly periodic change known in the pelagic system of the North Sea: the Russell Cycle. This is the name given to the series of changes throughout the marine ecosystem since 1924 in the western English Channel (RUSSELL 1973). A system of herring and macroplankton was replaced in 1930-1931 by one of pilchards and smaller zooplankton and it reverted to its earlier state in 1970-1971. Possibly, overfishing in the 1920s and 1930s had contributed to the decline of the herring stocks (CUSHING 1975). During the pilchard period the numbers of spring-spawned and summer-spawned larvae were much reduced as was the winter phosphorous content of the water. The indicator species *Sagitta elegans* was in 1931 replaced by *Sagitta setosa* and returned only in 1972, being abundant again by 1973. In addition there were changes in the species composition of elasmobranch and teleost fishes, in the benthos, in seaweeds and in the species composition of the phytoplankton. The Russell cycle passed through its low pilchard, low macroplankton and low phosphorous condition during a period of warming of the surface waters (positive anomaly of 0.5 °C in the northeast Atlantic), which peaked in 1945 (from CUSHING 1978). In 1971-1974, a change in wind direction over the northeast Atlantic to more western directions, related to the reversal of the Greenland high-pressure anomaly, caused a stronger inflow of Atlantic water into the English Channel which brought back the original fauna of the beginning of this century. Directly or indirectly linked to these events, the sea surface temperature, the nutrient content and the vertical stability increased in the Channel and in the Southern Bight (COLEBROOK *et al.* 1978, DICKSON & REID 1983 in RADACH 1984).

(4) German Bight - Helgoland Reede and LV Elbe I data 1962-1984

In the German Bight, which is not covered by the CPRS, a long time series (1962-1984) of meteorological and hydrographic parameters, nutrients and phytoplankton biomass was investigated at a fixed station (meteorology at LV Elbe 1, the other parameters at Helgoland Reede; RADACH *et al.* 1990). Here, the increase in wind velocity betweeen the 1950s and the 1970s was least compared to all other regions of the North Sea (DICKSON *et al.* 1988b). Accordingly, most meteorological and oceanographic parameters show unchanged annual cycles within their natural variability, except for the air and sea surface temperature which rose by 1°C during the 23 y of observation. This increase was due to temperature increases in coastal waters, influenced by river discharges and could not be detected in Central North Sea water (RADACH *et al.* 1990).

RADACH *et al.* (1990) state conspicious changes in the annual cycle of plant nutrients and an increase in phytoplankton biomass due to an increasing abundance of flagellates. Microzooplankton (ciliates, *Notiluca sp.*) was determined from 1962-1975 and was observed to increase as well (RADACH *et al.* 1990). Likewise, GREVE (1991) shows a general increase in small copepod density at Helgoland from 1974-1989 decreasing thereafter. Until 1989 the copepod biomass, as inferred from their densities in spring, increased continuously, pointing to increasingly larger overwintering stocks. The trend of increasing copepod abundance in the winter months parallels the features of flagellate abundances (see chapter II.2.5.3). RADACH *et al.* (1990) suggest that the observed ecosystem changes may be due to anthropogenic eutrophication, overriding possible influences of large-scale climatic changes.

(5) Western Wadden Sea, NL - Marsdiep 1973-1991

From 1973 to 1991, the average abundance of successive developmental stages of the copepod *Temora longicornis* increased by factors between four and eight in the period March-June in the eutrophicated western Wadden Sea (FRANSZ *et al.* 1992). The seasonal peak of this species, originally between March and May, extended into the summer months. Egg production peaked at the highest *Phaeocystis sp.* density. The authors conclude that eutrophication, leading to increased stocks of detritus, bacteria, microheterotrophs, free *Phaeocystis* cells and other flagellates (see HANSEN & VAN BOEKEL, 1991), had a stimulating effect on productivity and development of *Temora longicornis* (see IV.1.4.).

III.2. ZOOPLANKTON BIOMASS

The seasonal development of zooplankton and phytoplankton biomass in temperate seas can be described roughly as follows: The start of the copepod season is closely related to the onset of the phytoplankton bloom, the zooplankton peak usually occurring somewhat later (0-3 months) than the algal maximum. The zooplankton decline in autumn coincides approximately with the algal decline, at least in the northern and central North Sea. In all areas, the phytoplankton spring bloom is underexploited due to the temperature-limited development of the small overwintering zooplankton stocks. The algal biomass sediments to a large extent, stimulating the benthos to release their meroplanktic larvae. In summer, the high temperatures result in high production rates at low biomass, the phytoplankton being limited by nutrient availability, the zooplankton being food-limited.

III.2.1. STANDING STOCK

(1) Spring/summer

(a) ZISCH North Sea survey

During ZISCH (Zirkulation und Schadstofftransfer in der Nordsee, Univ. Hamburg, FRG), two quasi-synoptic surveys of the whole North Sea were accomplished in terms of the vertically integrated zooplankton standing stock (g DW m^{-2}) in different depth strata and in the whole water column, biomass concentration (g DW m^{-3}) as well as species composition and abundance (KRAUSE & MARTENS 1990, KRAUSE & KNICKMEYER 1992, KRAUSE ET AL. SUBM.).

The spring/summer survey (2 May-13 June, 1986) represents a late spring situation (after the spring bloom, Fig. III.1.): The highest zooplankton standing stock (> 10 g DW m^{-2}) is found off the great river plumes (Rhine, Elbe, Firth of Forth), in the Strait of Dover, the Skagerrak/Kattegatt frontal area and in the offshore areas of the northern North Sea. South of 56 °N and west of Norway, the standing stock amounts to less than 5 g DW m^{-2}. This is not only due to the larger depth in the northern North Sea but corresponds to a significantly higher biomass concentration north and east of the Dogger Bank. Seemingly, the zooplankton biomass distribution pattern reflects the anti-clockwise circulation pattern of the Atlantic water masses in the northern and central North Sea through all depth strata sampled (0-20 m, 20-60 m, 60-150 m, KRAUSE & MARTENS 1990).

The zooplankton biomass as indicated above is, of course, representative for only one particular time of the year and is subject to large temporal and spatial variations as well as being dependent on the sampling gear.

(b) Fladen Ground Experiment (FLEX)

Between March and June 1976 in the FLEX-box (59°20' to 58°26'N and 00°00' to 01°44'30'E), KRAUSE & RADACH (1980, rosette water sampler) found an increase of zooplankton biomass from almost zero until mid April to about 10-12 g DW m^{-2} or roughly 80 mg DW m^{-3} in the period from end of May to early June, which fits rather well with biomass measured with the High Speed Loch Ewe net by WILLIAMS & LINDLEY (1980b). During the same experiment, FRANSZ & VAN ARKEL (1980, high speed sampler) sampled 19 mg DW m^{-3} during the phytoplankton spring bloom in April/May and 41 mg DW m^{-3} after the phytoplankton spring bloom at the end of June, 1976. WILLIAMS & LINDLEY (1980a, CPR and UOR) measured an increase from about 5 mg DW m^{-3} in March to only 10-20 mg DW m^{-3} in June 1976.

Fransz & Gieskes (1984) summarized these data (from the FLEX Atlas) and calculated that the mesozooplankton standing stock increased from about 0.2 g C m^{-2} in April and early May to up to 4 g C m^{-2} at the end of May, steeply declining after having reached the peak. In early May and mid June 1986, Krause *et al.* (subm., WP-2 and "Meßhai", 200 µm) on the other hand measured 24 g DW m^{-2} and 21 g DW m^{-2}, respectively, roughly corresponding to about 12 g C m^{-2}, on two sampling stations in the same area. Their total zooplankton biomass concentration amounted to about 160 mg DW m^{-3}.

(c) Oyster Ground

During three cruises to the Oyster Ground south of the Dogger Bank, Fransz *et al.* (1984) measured a mesozooplankton biomass equivalent of 2, 6 and 3 g ADW m^{-2} in May, July and September 1981, respectively. This compares well to the data of Krause *et al.* (subm.), who found about 3 g DW m^{-2} (ADW = ca. 0.9 DW) in the same area in May 1986.

(d) Southern Bight

In the Southern Bight, in the Dutch and Belgian coastal area, the zooplankton biomass starts to increase in March/April, peaks at about 1 g C m^{-2} and ca. 100 mg C m^{-3} in June/July, and returns to very low levels in August. Offshore, the zooplankton standing stock varies seasonally to a lesser extent and always stays below 1 g C m^{-2} and 40 mg C m^{-3} (Fransz 1980b, Fransz & Gieskes, 1984). Spatially, the mean copepod biomass decreases from 200 mg DW m^{-3} directly off the Rhine/Maas/Scheldt estuary to less than 50 mg DW m^{-3} further offshore (Fransz *et al.* 1978, Fransz 1986). Krause *et al.* (subm.) found >200 mg DW m^{-3} off the Rhine-/Maas/Scheldt estuary and >100 mg DW m^{3} (C = ca. 0.5 DW) allover the Channel north of the Strait of Dover in May 1986.

At a permanent station right off the Dutch coast, Daan (1989) measured 50-100 mg C m^{-3} (or approx. 100-200 mg DW m^{-3} in June/July and a maximal copepod biomass of up to 80 and >160 mg C m^{-3} (approx. 150-300 mg DW m^{3}) in July/August 1984 and July 1985, respectively, which is about twice as much as indicated by Fransz *et al.* (1978). In the Belgian coastal zone, Joiris *et al.* (1982, samples taken at 3 m depth) measured more than 100 mg C m^{-3} in early May 1979, followed by a pronounced minimum in June/July, and a subsequent secondary peak of ca. 40 mg C m^{-3} in July/August. However, these authors state a rather uniform horizontal distribution of zooplankton biomass between coastal and offshore sampling stations.

The data of Joiris *et al.* (1982) do not include macroplankton predators. Fransz *et al.* (1978) found a mean biomass of common predator species (fish larvae, medusae, ctenophores, 16 species) of ca. 4.5 mg m^{-3} offshore and 2.5 mg m^{-3} in the coastal area of the Southern Bight in June/July 1977. In 1973, the same authors had found ca. 73 mg m^{3} in the nearcoastal area. This illustrates impressively the huge spatial and temporal variability of plankton distribution.

(e) German Bight

The seasonal development of microzooplankton biomass was studied by Steiff (1988): She found a monthly mean microzooplankton biomass of 5 and 3 mg C m^{-3} in 1985 and 1986, respectively, at Helgoland Reede. The peak biomass amounted to 10-15 mg C m^{-3} in April/May 1985 and 1986, contributing up to 21 % of the total plankton biomass (phyto- and microzooplankton, Fig. III.2, III.3). The biomass of the metazoan zooplankton contributed little to the total microzooplankton biomass compared to that of the protozooplankton. Non-loricate ciliates alone contributed 70 % of the spring peak biomass in 1985 while tintinnids dominated in 1986.

(2) Fall/winter

(a) ZISCH North Sea survey

During the ZISCH winter survey (26 January to 9 March, 1987, Krause et al. subm.) the zooplankton standing stock was generally lower by about a factor of 10 compared to the spring/summer cruise (Fig. III.4). The highest depth-integrated biomass (> 5 g DW m^{-2}) was observed in the deep Skagerrak and off the Norwegian coast. A tongue of increased zooplankton biomass (> 10 mg DW m^{-3}), evident in all water layers, stretches from here towards the south. Another one, limited to the surface layer, flows to the northwest and west into the central North Sea. The biomass of the northern North Sea is situated almost entirely in the bottom-near layer (60-150 m). A considerable inflow from the Atlantic seems to

Tab. III.2: Mesozooplankton biomass in the northern/central and southern North Sea in spring and summer
Sampling gear: 1 - water bottle; 2 - pump; 3 - vertical net; 4 - high speed sampler
5 - CPR (Continuous Plankton Recorder), UOR (Undulating Oceanographic Recorder);
6 - IKMT (Isaak Kidd Midwater Trawl).

Area North./Centr. North Sea	Period Spring/Summer	Standing stock g m^{-2}	Concentration mg m^{-3}	Reference	Gear
Fladen Ground	Mar. '76		5 (DW)	Williams & Lindley 1980a	5
Fladen Ground	before mid Apr. '76	n.n.	n.n.	Krause & Radach 1980	1
Fladen Ground	Apr./May '76	0.4 (C)	19 (DW)	Fransz & van Arkel 1980	4
Fladen Ground	early May '76	0.2 (C)		Fransz & Gieskes 1984	4
Fladen Ground	early May '86	24 (DW)	164 (DW)	Krause & Martens 1990	4,3
Fladen Ground	end of May'76 (peak)	3.5-4 (C)		Fransz & Gieskes 1984	4
Fladen Ground	end May/early June '76	10-12 (DW)	80 (DW)	Krause & Radach 1980	1
Fladen Ground	mid June '86	21 (DW)	157 (DW)	Krause & Martens 1990	3,4
Fladen Ground	June '76		10-20 (DW)	Williams & Lindley 1980a	5
Fladen Ground	end of June '76		42 (DW)	Fransz & van Arkel 1980	4
Southern North Sea	Spring/Summer				
Oyster Ground	May '81	2 (AFDW)		Fransz et al. 1984	4
Oyster Ground	July '81	6 (AFDW)		Fransz et al. 1984	4
Oyster Ground	Sept. '81	3 (AFDW)		Fransz et al. 1984	4
Oyster Ground	May '86	3 (DW)		Krause et al in prep.	3,4
S.B. offshore	March '80		10-20 (AFDW)	Fransz 1980b	4
S.B. offshore	April/May '73		20 (C)	Fransz 1980b	4
S.B. offshore	July '73		<50(DW)	Fransz et al. 1978	4
S.B. offshore	Aug./Sept. 1973 (peak)		30-40 (C)	Fransz 1980b	4
Channel	May/June		100 (DW)	KRAUSE ET AL. SUBM.	3,4
off Delta Rhine/Scheldt	May/June		>200 (DW)	KRAUSE ET AL. SUBM.	3,4
off Delta Rhine/Scheldt	July '73		100->200 (DW)	Fransz 1976	4
S.B. Dutch coast	June/July '73 (peak)	1 (C)	50-100 (C)	Fransz & Gieskes 1984 Fransz 1980b	4
S.B. Dutch coast	June/July '73(peak)		>200(DW)	Fransz et al. 1978	4
S.B. Dutch coast	July/Aug. '84 (peak)		80 (C)	Daan 1989	2
S.B. Dutch coast (peak)	July '85 (peak)		160 (C)	Daan 1989	2
S.B. Belgian coast	early May '79 (peak)		>100 (C)	Joiris et al. 1982	1?
S.B. Belgian coast	June/July '79 (min.)		<10 (C)	Joiris et al. 1982	1?
S.B. Belgian coast	July/August '79 (peak)		40 (C)	Joiris et al. 1982	1?
Western Wadden Sea	June/July '73-'75 (peak)		50-100 (C)	Fransz 1980b	4
North. Wadden Sea Sylt	April/May '72 (1. peak)		10 (C)	Hickel 1975	1?
North. Wadden Sea Sylt	June/July '72 (2. peak)		13 (C)	Hickel 1975	1?
North. Wadden Sea Sylt	Sept./Oct.'72 (3. peak)		18 (C)	Hickel 1975	1?
German Bight	Apr./May '85-'86 (peak)		10-15 (C)	Steiff 1988	1

take place around the Orkney Islands. This band of increased zooplankton biomass apparently follows the general circulation pattern in the northern North Sea, with an anticlockwise turning north of the Dogger Bank area (where depths decrease to less than 50 m). In the southern North Sea, the generally rather low standing stock is increased under influence of the inflowing Channel water and off the mouth of Rhine/Schelde (up to 57 mg DW m^{-3}).

(b) Northern/central North Sea

NIELSEN & RICHARDSON (1989) found a zooplankton biomass of 23 mg C m^{-3} (or about 5 g DW m^{-3}, using their dry weight to carbon conversion factor of 0.45) in the reach of the Skagerrak outflow in February/March 1988. This is much less compared to the minimal 10 mg DW m^{-3} that KRAUSE *et al.* (subm.) found in the same area. HAY *et al.* (1991) measured a total zooplankton biomass of 3.2, 4.1, 1.1, and 1.4 g C m^{-2} in the northern North Sea in October, December, January and February 1987/88, respectively (when molluscs which were weighed including their shell are excluded 2.0, 0.92, 0.65 and 0.73 g C m^{-2}). This fits well with KRAUSE *et al.*'s (subm.) 0.5-1 g DW m^{-2} (or < 5 mg C m^{-3} in the northwest and 5-20 mg C m^{-3} towards the Central North Sea) in the same area. KIØRBOE & JOHANSON (1986) for comparison sampled zooplankton with an average dry weight of 5-15 and 2.5-8 mg C m^{-3}, respectively, on two transects across the Buchan Front in September 1984. In September/October 1985, KIØRBOE *et al.* (1988a) measured 3-7 and 2.5-10.1 mg C m^{-3}, respectively, on comparable transects in the same area (compare Table III.3).

(c) Southern North Sea

In winter, the mesozooplankton biomass of the southern North Sea is low (s.a. FRANSZ & GIESKES 1984, compare Tab. III.3): In the western Wadden Sea, the nearshore and the more offshore Dutch and Belgian coastal area, it decreases to less than 10 mg C m^{-3} (JOIRIS *et al.* 1982, FRANSZ 1980b). Macrozooplankton biomass is reduced to almost zero in the nearcoastal Southern Bight (FRANSZ *et al.* 1978).

In the German Bight at Helgoland, the biomass of microzooplankton is near zero from October to February (STEIFF 1988). This finding corresponds to similar results of NIELSEN & RICHARDSON (1989). However, the latter authors measured egg production and elevated nauplii and copepodid abundance of various copepod species in shallow, fertile parts of the southern North Sea during the winter months, while STEIFF (1988) did not find any copepod nauplii in the water column until after the spring phytoplankton bloom in May. Probably, the winter phytoplankton concentration is too low at Helgoland to initiate copepod reproduction. No data are available on meso- and macrozooplankton biomass at Helgoland. In the northern Wadden Sea of Sylt, the mesozooplankton biomass amounts to less than 2 mg C m^{-3} (HICKEL 1975).

(3) Summary and comments

There is only one data set on the zooplankton biomass distribution available, which covers the entire North Sea area in both winter and summer (KRAUSE & MARTENS 1990, KRAUSE ET AL. SUBM., ZISCH cruises). The studies reveal that the zooplankton biomass (standing stock and density) of the northern North Sea is higher in both seasons compared to the southern North Sea. This is in contrast to the phytoplankton data, which suggest a higher biomass in the shallow, southern part. An explanation for this discrepancy could be that in the south, more energy is recycled by heterotrophic microbial activity (JOIRIS *et al.* 1982), while in the north, most of the primary production is channelled straight through to fish production, along the "classical" short food chain. ZIJLSTRA (1988) considers this to be the explanation for the lower fish production in the southern, compared to the northern North Sea (HUMMEL & ZIJLSTRA 1978)

Comment: Except for the data of KRAUSE & MARTENS 1990, KRAUSE *et al.* (subm.), DAAN (1989), and STEIFF (1988), the biomass values presented above are rather old - in view of the continuing eutrophication of the coastal zone there is reason to believe that the overall biomass of the southern North Sea has increased during the last 20 years: FRANSZ (1986) states that "there is no doubt that river-induced high food levels stimulate the late spring and summer development of herbivore populations in the coastal area of the Southern Bight". A comparison of the data of FRANSZ *et al.* (1978) and DAAN (1989) on the copepod biomass in the coastal Southern Bight implies such an increase but due to the large natural spatial and temporal variability, such a conclusion is premature. However, Fransz (pers. comm.), having studied the data from all sampling programmes in the Wadden Sea and the Southern Bight from 1977 to 1991, found an overall general increase in zooplankton biomass after 1979. The trend originates from biomass increases of the copepod *Temora longicornis*, the appendicularian *Oikopleura* and the dinoflagellate *Noctiluca*, as well as polychaete and lamellibranch larvae, indicating higher activity of benthic species. Predators also increased in biomass: fish (eggs and larvae), the ctenophore *Pleurobrachia*, decapod larvae and hydrozoans.

Tab. III.3: *Mesozooplankton biomass in the northern/central and southern North Sea in fall/winter Sampling gear: 1 - water bottle; 2 - pump; 3 - vertical net; 4 - high speed sampler 5 - CPR (Continuous Plankton Recorder), UOR (Undulating Oceanographic Recorder); 6 - IKMT (Isaak Kidd Midwater Trawl).*

Area	Period	Standing stock	Concentration	Reference	Gea
Northern North Sea	Autum/Winter	g m^{-2}	mg m^{-3}		
Buchan front 1. transect	Sept. '84		5-15 (C)	Kiørboe & Johansen 1986	2
Buchan front 2. transect	Sept. '84		2.5-8 (C)	Kiørboe & Johansen 1986	2
Buchan front 1. transect	Sept./Oct. '85		3-7 (C)	Kiørboe *et al.* 1988a	2
Buchan front 2. transect	Sept./Oct. '85		2.5-10.1 (C)	Kiørboe *et al.* 1988a	2
Northwestern N.S.	Oct. '87	2.0 (C)^{1})		Hay *et al.* 1991	2,4
Northwestern N.S.	Nov./Dec. '87	0.92 (C)^{1})		Hay *et al.* 1991	2,4
Northwestern N.S.	Jan. '88	0.65 (C)^{1})		Hay *et al.* 1991	2,4
Northwestern N.S.	Feb. '88	0.73 (C)^{1})		Hay *et al.* 1991	2,4
Northwestern N.S.	Feb./Mar. '87	0.5-1 (C)	<5 (C)	Krause & Martens 1990	4
Central N.S.	Feb./Mar. '87		5-20 (C)	Krause & Martens 1990	4
Central N.S.	Feb./Mar. '87		>10-100 (DW)	Krause & Martens 1990	4
North of Doggerbank	Feb./Mar. '88		2.5-4 (C)	Nielsen & Richardson 1989	2
Skagerrak Outflow	Feb./Mar. '88		2-3 (C)	Nielsen & Richardson 1989	2
Southern North Sea	Autum/Winter				
S.B. offshore	Jan./Feb. '73		<10 (C)	Fransz 1980b	4
Off Delta Rhine/Scheldt	Feb./Mar. '87		>57 (DW)	Krause & Martens 1990	4
S.B. Dutch coast	after July/Aug. peak '84-'85	<0.04(C)		Daan 1989	?
S.B. Dutch coast	Aug.-Nov., Jan. '73-75	<0.05 (C)?		Fransz & Gieskes 1984	4
S.B. Dutch coast	Jan. '73		<10	Fransz 1980b	4
S.B./ Belgian coast	Sept.-Dec. 78, March-Apr. '79		<10 (C)	Joiris *et al.* 1982	1?
Western Wadden Sea	Jan./Feb. '73-75		<10 (C)	Fransz 1980b	4
North. Wadden Sea Sylt	Nov.-March '71/72		< 3 (C)	Hickel 1975	1?
South of Doggerbank	Feb./Mar. '88		8.8 (C)	Nielsen & Richardson 1989	
German Bight	Oct. '85-Mar. '86		<1 (C)^{2})	Steiff 1988	1

^{1}) Molluscs excluded (see Hay et al. 1991)
^{2}) Microzooplankton

III.2.2. BIOMASS - SEASONAL SUCCESSION OF STOCK-FORMING TAXA

(1) Northern/central North Sea

Adult chaetognaths (predominantly *Sagitta elegans*), euphausids (*Meganyctiphanes norvegica, Nyctiphanes couchi, Thysanoessa inermis, T. raschi*) and the hyperiid amphipod *Themisto gaudichaudi* have their seasonal maxima in winter (December-January), probably all feeding on the overwintering stocks of copepods (ROFF *et al.* 1988, but compare HAY *et al.* 1991) Hence in early spring (before the phytoplankton spring bloom), euphausids constitute up to 90 % of the zooplankton biomass in the northern North Sea (WILLIAMS & LINDLEY 1980a). In April/May a shift from dominance of euphausids to dominance of the calanoid copepod *Calanus finmarchicus* takes place. This is due to a replacement of adult by juvenile euphausids and therefore a decreasing euphausid biomass, and on the other hand an increasing biomass of *Calanus*. During and after the phytoplankton bloom the proportion of *C. finmarchicus* in the total zooplankton biomass is steadily increasing to 90 % in June (WILLIAMS & LINDLEY 1980a, FRANSZ & VAN ARKEL 1980). At that time, *C. finmarchicus* enters the diapause (*i.e.* no molting to adults and reproduction take place) and possibly starts to get carried out of the "shallow" northern North Sea so that after June, the *Calanus* biomass is strongly reduced and small copepods (*Paracalanus parvus, Centropages typicus*) dominate the zooplankton biomass in the warm surface layer above the thermocline (WIBORG 1954, in DAVIS 1987).

In fall and winter, after *C. finmarchicus* almost disappears from the relatively shallow (less than 200 m) parts of the North Sea (see *e.g.* FRANSZ *et al.* 1991, BACKHAUS *et al.* 1991), molluscs, esp. the pteropod *Limacina retroversa*, contribute substantially (23-63 %, if shell weight excluded, euphausids not listed, HAY *et al.* 1991, their Table 3) to the overall zooplankton biomass in the northwestern North Sea. Among the copepods, which comprise in November/December another 32 % at the minimum, in other winter months about 60 % of the biomass, the relative proportion of large and small calanoids, *Oithona* spp. and Harpacticoids is about equal in November and February. During October and January, large calanoids had a significantly higher, harpacticoids a much lower biomass than the other two groups. Overall, the copepod biomass decreased from 1.8 g DW m^{-2} in October through 0.8 g DW m^{-2} in November/December to 0.5 g DW m^{-2} in January. In February, a standing stock of 0.6 g DW m^{-2} was measured, due to the high harpacticoid biomass. Chaetognaths contributed max. 7 % of the overall biomass, the trachymedusae *Aglantha digitale* up to 5 %, but was not present at all in November/December and February. The same holds for amphipods (*Parathemisto* spp.) which did not exceeded 1.3 % of the biomass. Euphausids were encountered only irregularly, the highest biomass being found at the northernmost stations (north of 57°N).

The results presented by HAY *et al.* (1991) on the biomass distributions of larger predator species in the northwestern North Sea are in obvious contradiction to the abundance estimates of ROFF *et al.* (1988) for a fixed station off the Northumberland coast. However, also the CPRS data for the northern North Sea suggest that in terms of biomass, euphausids are important members of the zooplankton community in winter and spring, reflecting to a large extent the Atlantic water inflow to the North Sea (MARSHALL 1948, GLOVER 1952).

(2) Southern North Sea

In the offshore areas, NIELSEN & RICHARDSON (1989) found an average copepod biomass of 2.5-4 mg C m^{-3} north, and 8.8 mg C m^{-3} just south of the Dogger Bank in February/March 1988. Microzooplankton neither played a role in terms of density nor with respect to biomass at that time of year. Close to the latter site, in the Oyster Ground area, copepods contributed almost 70 % of the registered zooplankton biomass in May, 35 % in July and 48 % in September (FRANSZ *et al.* 1984). At times, blooms of meroplankton may outweigh the copepod biomass, as observed by FRANSZ *et al.* (1984) in July 1981. The carnivores (mainly medusae and in September also the chaetognath *Sagitta setosa*) represented 15, 9 and 25 % of the biomass in May, July and September, the appendicularian *Oikopleura dioica* 11, 6 and 11 %, respectively.

In the coastal areas of the North Sea, biomass peaks tend to occur in spring (March-May), summer (June/July) and fall (September-/October) and may be linked with temperature extremes and food minima. The early spring peak is formed by polychaete larvae, mainly spinoids, and sometimes cirriped and lamellibranch larvae. This peak is most distinct in the northern and western Wadden Sea, and weak in the North Sea. The summer peak is constituted of copepods and a new outbreak of spinoids and other herbivores, the autumn peak in the coastal area stems from the copepods or again polychaetes (HICKEL 1975, MARTENS 1980, FRANSZ 1980b, see Fig. III.5). A comparison of data given by HICKEL (1975) and MARTENS (1980) for the northern, and also the 3-year study of FRANSZ (1980b) in the western Wadden Sea outline the large interannual variations which are possible with respect to overall biomass and the formation of biomass peaks by the various taxa - *i.e.*

meroplanktic larvae do not form a substantial biomass every year.

The further offshore, the more do copepods, in particular the calanoid copepods *Temora longicornis, Pseudocalanus elongatus, Acartia clausi* and *Centropages hamatus*, form almost exclusively the copepod biomass, dominating the mesozooplankton biomass in the eastern Southern Bight (FRANSZ 1976, 1980b). In shallow coastal areas like the northern and western Wadden Sea, the biomass of meroplanktic larvae at times matches or outweighs the one of the copepods. Protozoans like the dinoflagellate *Noctiluca* sp. can be numerous in summer (cf. DAAN 1987), but their biomass is usually negligible (FRANSZ 1980b).

In summer, either *Pleurobrachia pileus* or *Phialidium hemisphaericum* (hydromedusa) predominate the macroplankton of the Dutch coastal area of the Southern Bight, fish larvae, crustacean larvae, chaetognaths, mysiids, scyphomedusae etc. being of minor importance (DAAN 1989). However, in the western Wadden Sea, carnivores (mainly hydromedusae, ctenophores, *Sagitta setosa,* cladocerans and mysids, but without large jelly fish) in some years contribute a great deal to the overall zooplankton biomass (FRANSZ 1980b).

For the first week of July 1973, FRANSZ *et al.* (1978) present a biomass budget comprising meso- and makrozooplankton off the Dutch coast in the Southern Bight: the four dominant copepod species alone comprise 67 %, fish larvae another 28 % and hydromedusae of 5 % of the total 224 mg DW m^{-3}. Contrary to the western Wadden Sea, here the chaetognath *Sagitta setosa* and ctenophores only play a negligible role.

The release of meroplanktic larvae in spring results from spawning activities of the usually perennial benthic fauna, which responds to food availability and water temperature. Later, the holozooplankton biomass builds up with the rising temperature in April/May, reaching peak values in June, and collapsing thereafter. Early predator peaks, usually of *Sarsia tubulosa* (hydromedusa) and *Pleurobrachia pileus* (ctenophore), occur stimulated by the spring peak of polychaetes and cirripeds in the southwestern North Sea (after FRANSZ 1980b).

Among the microzooplankton, non-loricate ciliates of the genera *Lohmanniella* and *Strombidium* constitute the most prominent component (STEIFF 1988). But at times also loricate ciliates like tintinnids may form blooms. The biomass of the functional autotrophic ciliate *Mesodinium rubrum,* bearing symbiontic algae, may reach similar levels to the one of all heterotrophic ciliates. Its seasonal maximum is attained in July/August. Copepod nauplii always contributed more than 50 % of the comparatively low metazoolankton biomass.

In the southern North Sea in winter, when overall plankton biomass is low, a few large organisms like hyperiid amphipods or the trachymedusae *Aglantha digitale* may dominate the biomass distribution despite the high numerical abundance of *e.g.* small copepods like *Pseudocalanus elongatus, Temora longicornis* and *Acartia spp.* (KRAUSE & MARTENS 1990, KRAUSE ET AL. SUBM.).

III.3. POPULATION DYNAMICS AND PRODUCTION

Secondary and tertiary production is the biomass produced by consumers of primary production (herbivores) and secondary or higher trophic production (carnivores), respectively.

Estimates of secondary and tertiary production of zooplankton populations in the sea are even more difficult to carry out than abundance or biomass measurements. The problem is that next to representative abundance and biomass estimates, the factor time is involved. Thus, the rate of change in one and the same population is asked for, which involves the problem of sampling in one water mass over a longer period. The other possibility is to measure the abundance once and determine experimentally the possible growth and development rates of the most prominent species, extrapolating the derived production to the field. Measuring stage-specific growth rates is very laborious and bears many ambiguities. However, the carbon invested into eggs by the non-growing female (as carbon produced per female carbon weight per unit time, or specific egg production) can be used as an approach of the daily P/B ratios (corresponding to growth rates) of the copepodid stages (SEKIGUSHI *et al.* 1980). Egg production is either determined in laboratory experiments, or simply figures as female:egg ratio in the water column, divided by the temperature dependent hatching time (= residence time in the water).

Hence, the intensity of secondary production is indicated by species- and stage-specific development, growth and egg production rates. All these processes are to a certain degree size-dependent and temperature- and food-determined, if not limited. VIDAL (1980a,b,c) has shown that the small copepod *Pseudocalanus spp.* requires lower food concentrations for maximum growth than the larger *Calanus pacificus.* The growth efficiency (energy produced in relation to energy consumed) of the larger species decreased with increasing temperature (8-15.5 °C) and body size (5-175 µg). The critical food concentration for maximal egg production is lower in the smaller *Acartia* and *Paracalanus* sp. than in *Calanus* (RUNGE 1984).

If this holds true for the zooplankton community in general, then the small-sized species have a selective advantage during the warm summer months when the phytoplankton biomass is low, compared to the time of the spring diatom bloom in cold waters. In addition, the transition of large-sized diatoms in spring, to a small-sized, flagellate dominated, phytoplankton community in summer favours small herbivorous and omnivorous grazers to large ones. Consequently, any large-scale change of the water temperature will alter the zooplankton community structure due to differential rates of growth and reproduction of the various species and life stages.

The above mentionned physiological constraints are reflected in the seasonal production cycles: In spring, when the temperatures are low, a high zooplankton biomass coincides with a relatively low production, based mainly on large species, while during the warm months of summer and fall, a higher production is achieved at a lower biomass of predominantly small species. Thus, in spring the P/B ratio is rather low, and in fall high, which indicates losses to predation rather than increases in herbivore stock, as occurs in spring (DAVIS 1987).

III.3.1. SPATIAL VARIABILITY OF PRODUCTION

The rate of secondary and higher trophic production is to a large extent determined by physical constraints, temperature being the most ubiquitous one. In the sea, discontinuities like thermal or salinity fronts and pycnoclines not only seperate distinct water masses from each other, but also play a role as convergence zones for accumulating matter (for example *Noctiluca miliaris* cells, SCHAUMANN *et al.* 1988), traps for fine detritus particles, and not least in enhancing pelagic production.

(1) Production in stratified/unstratified waters

The extent of permanent vertical mixing or summer stratification is of utmost importance to the annual plankton (and esp. phytoplankton) cycle (LEFÈVRE 1986). The "classical" cycle for temperate waters, with two diatom outbursts, one in spring and one in autumn, with a less productive summer dinoflagellate maximum inbetween, is actually found where a summer thermocline develops after the spring diatom maximum (*e.g.* northern North Sea, Fig. III.6). Where year-round vertical mixing prevails (*e.g.* southern North Sea), several diatom and flagellate maxima follow the spring diatom bloom, highest biomass and primary production being observed during the flagellate bloom following the diatoms in spring.

The "classical" or traditional food chain comprises a large biomass of algae, a smaller biomass of herbivores and a still smaller quantity of carnivores (cf. station M in mixed water in Fig. III.7). Microzooplankton and bacterioplankton does not play a significant role. The large size of the plant cells (diatoms) favours direct consumption by larger herbivores which in turn are preyed upon by large carnivores like fish.

The physical and biological setting in the thermally stratified temperate sea in summer is comparable to that of the oligotrophic ocean (CUSHING 1990, Fig. III.6): Due to the high summer water temperatures, a small standing stock of phytoplankton with high primary production, fuelled by regenerated nutrients, supports a large standing stock of zooplankton with high turnover rates (Stat. E5 in Fig. III.7). In the summer phytoplankton, flagellates outcompete diatoms with decreasing nutrient pool and rising temperatures; the overall smaller size distribution of the phytoplankton favours a food chain transfer of energy through small-sized grazers like ciliates, small copepods, mainly invertebrate carnivores to jelly fish and fish as end consumer (Fig. III.8).

This is what KIØRBOE *et al.* (1990) observed in the Skagerrak in May 1987: The Skagerrak is characterized by a doming of the pycnocline, with a deep mixed layer along the periphery and a very shallow pycnocline in the central parts. With increasing thickness of the upper mixed layer, the average size of the phytoplankton and also the egg production rates of two abundant small copepod species (*Temora longicornis, Acartia spp.*) increased. In the strongly stratified central parts, a microbial loop-type of food web predominated, compared to the more "classical" picture along the margins.

FRANSZ *et al.* (1984) describe the effect of stratification on species composition in plankton sampled at the Oyster Ground: "*In summer the conditions in the stratified area were in favour of armoured dinoflagellates* Ceratium *spp. and microflagellates (*GIESKES *&* KRAAY *1977a 1984). The dinoflagellate-to-diatom ratio in summer has been very high in the central North Sea since 1970 (*POULET *1978). The numerous echinopluteus larvae observed in July 1981 ... probably used Ceratium as food. They contained cell wall remains of these algae.*" The cyclopoid copepod *Oithona similis* is very abundant in stratified waters. A positive effect of stratification on copepod production (and primary production) was not found, when compared to the isothermal Southern Bight (FRANSZ *et al.* 1984).

In permanently unstratified waters, as in the coastal zone of the southern North Sea, fronts may play a role in initiating the spring diatom bloom (REID *et al.* 1990) and in subsequently enhancing secondary production. But here, the seasonal production pattern of copepods is to a lesser extent subject to seasonal fluctuations, compared to the stratified northern North Sea, because the year-round dominating small species reproduce all through the year (*e.g.* NIELSEN & RICHARDSON 1989, HAY *et al.* 1991), have short generation times (KLEIN BRETELER *et al.* 1982) and feed omnivorously on a large variety of food. Based on a very high primary production all through the summer in coastal areas (>30 km) of the Southern Bight, a single broad copepod production peak of up to 300 mg C m^{-2} d^{-1} (potential production) develops in June/July. However, further offshore, the high spring peak in primary production is not used up for secondary production, which remains rather low (<100 mg C m^{-2} d^{-1}) during all the year (FRANSZ & GIESKES 1984). This contrasts clearly to the northern North Sea production system, where the high primary production in spring is, after a time lag, reflected in a secondary production peak (>500 mg C m^{-2} d^{-1} during FLEX, FRANSZ & GIESKES 1984).

(2) Production in frontal systems

Fronts can be interpreted as the boundaries between regions, each with a different hydrographic structure and a different annual plankton cycle. They are characterized by special dynamic properties, which make them a place of exchanges as well as a boundary between contrasting ecosystems (LEFÈVRE 1986).

There has been a long debate as to what degree passive accumulation and cross-frontal advection, and enhancement of production, respectively, are responsible for the observed increased biomass in frontal areas (for review see LEFÈVRE 1986). As concerns the zooplankton production, in recent years egg production studies were introduced as an indicator for the spatial and temporal distribution of productivity on the same time scale as the physical and phytoplankton dynamics - along and across frontal systems (RICHARDSON 1985 - North Sea/Skagerrak-Kattegatt front, KIØRBOE & JOHANSON 1986, KIØRBOE *et al.* 1988a).

In the Buchan front area, to the northeast of Scotland, phytoplankton biomass and primary production as well as copepod egg production peak in the transitional zone between isothermal and temperature-stratified water compared to low rates in mixed as well as strongly stratified waters (KIØRBOE *et al.* 1988a). Egg production of small and large copepods varies as a function of food quantity and quality (see *e.g.* RICHARDSON *et al.* 1985, KIØRBOE *et al.* 1985, KIØRBOE *et al.* 1988a,b) and may therefore only indirectly be coupled to the physical features. Overall zooplankton biomass shows no apparent relationship to frontal features - this may be a question of the time scales involved: usually we have only short-term knowledge on the dynamics and previous development of the hydrographic features observed. This allows only the interpretation of distributional relationships of *e.g.* eggs or nauplii, which have a short residence time in the water, and can be considered more or less passive particles as concerns their mobility. The older and larger the life stages, the more difficult is the establishment of a relationship between hydrographic features and biomass distribution (KIØRBOE & JOHANSON 1986).

Thus, the transition period from mixed to stabilized water columns, as characterizing frontal areas or, for example, also the time after a storm which breaks up the summer thermocline, can be considered as indirectly enhancing zooplankton production (KIØRBOE & JOHANSON 1986, KIØRBOE *et al.* 1988a,b). The same physical factors, resulting in increased nutrient supply and subsequent growth of large phytoplankton, are responsible for the development of the spring diatom and zooplankton bloom. Colebrook (1982) has shown that the spring outburst in the northeast Atlantic is more or less complete before the upper layers finally become stratified; this is because the exponential diatom growth depends on the constant replenishment of their nutrient pool at the water-cell interface by turbulent mixing. However, wind-induced mixing should not exceed the compensation depth, which explains why strong winds, leading to deep mixing in spring, may delay the spring bloom (see phytoplankton).

III.3.2. SEASONAL VARIABILITY OF PRODUCTION

From south to north, coinciding with an increased water depth, the vernal stratification and thus also the onset of vernal primary production, takes place increasingly later (CUSHING 1983). In the frontal zones of the southern North Sea, the first diatom bloom may occur as early as February (REID *et al.* 1990) spreading further and reaching the turbulent coastal waters in March/April. In the Central North Sea, COLEBROOK & ROBINSON (1965) observed the peak in "greenness" in CPRS samples by about mid April, and in the northern North Sea at the beginning of May.

In the northern and southern North Sea, eggs and nauplii of large (*Calanus sp.*, *Metridia lucens*), as well as small copepod species *Acartia* spp., *Paracalanus parvus* , *Pseudocalanus* spp., *Temora longicornis, Centropages typicus, Oithona* spp.) sampled in fall and winter point to ongoing reproduction and recruitment allover the year (NIELSEN & RICHARDSON 1989, HAY *et al.* 1991). However, the common summer species, as *e.g.* *Centropages hamatus* and *Acartia clausi* disappeared more or less completely during winter (HAY *et al.* 1991). The latter authors found a seasonal minimum for *Acartia clausi* in January, with a marked increase in reproductive intensity and naupliar abundance by February/March. Egg to female ratios for all species investigated were highest in the southeastern and lowest in the northwestern North Sea both in November/December and February/March, indicating an earlier start of secondary production in the southern part.

The reproductive output and the juvenile standing stock of resident populations surviving the winter (mortality due to food scarcity and predation) form the basis for the successfull exploitation of the spring phytoplankton increase, thus determining to a large extent the later summer standing stock (*e.g.* COLEBROOK 1986). In the southern North Sea, it is mainly the local populations which determine the annual production, while in the northern North Sea, the spring and early summer secondary production is highly dominated by *Calanus finmarchicus* (*e.g.* FRANSZ *et al.* 1991) after immigration from its hibernation area (BACKHAUS *et al.* 1991).

Most herbivorous copepods like *e.g.* *Calanus finmarchicus* start intensive reproduction in spring as soon as the diatom increase takes place. Eggs are released and after a while, the overwintering adults fade. The juvenile stages of the spring generation at first form a low biomass at high abundances and have a temperature-limited production. Only after the phytoplankton biomass maximum is over, the zooplankton biomass maximum, now consisting of the grown up spring generation, is attained. However, the production of phytoplankton is high enough to maintain this generation. A large fraction of the *Calanus* generation hatched in spring halts development after having reached the overwintering stages in June/July, migrates to deeper water layers and gets carried out of the shallow North Sea, or becomes victim to heavy predation by carnivores (KRAUSE pers. comm.).

In the northern North Sea in summer, the secondary production above the thermocline is probably based on small grazers and carnivores. The generation times of small copepod species are much shorter than those of larger ones (*i.e.* at the same temperature, the production/biomass ratio is higher compared to large copepods) and vary *e.g.* for *Temora longicornis* from 2 months at 5 °C at the beginning of March to 1 month at 10 °C at the end of April (KLEIN BRETELER & GONZALEZ 1986) on the condition that no food shortage occurs. Food shortage may indeed be responsible for the decline in copepod abundance after a peak in May/June in the southern North Sea (by mid July, DAAN 1987):

the increasing density of herbivorous grazers originating from very high spawning intensities during and after the spring diatom bloom may gradually limit the phytoplankton production, which leads to a quick decline in phytoplankton standing stock, and consequently lower egg production rates (FRANSZ *et al.* 1989) in herbivores. At the same time, abundance and production in carnivores (which may also contribute to the depletion of the phytoplankton stock, before feeding as a carnivore, like *Noctiluca miliaris* or *Phialidium hemisphericum*) are increasing. But probably neither predation nor cannibalistic feeding of nauplii at low food levels are responsible for the summer copepod decline (VAN DER VEER & OORTHUYZEN 1985, DAAN 1986, DAAN 1987, 1989, KUIPERS *et al.* 1990).

During summer, herbivorous copepods are assumed to grow at reduced rates due to food limitation in all parts of the North Sea (KLEIN BRETELER *et al.* 1982, FRANSZ & GIESKES 1984). However, only recently, the importance of protozooplankton for the marine food web was recognized: Ciliates are important grazers on small algae, like flagellates or the single cell stage of colonial algae like *Phaeocystis* (WEISSE & SCHEFFEL-MÖSER 1990) which dominate the summer phytoplankton composition. Most copepod species which used to be classified as strict herbivores have now been recognized as omnivorous feeders, being able to exploit the ciliate stocks accompanying the wax and wane of flagellate blooms (WIADNYANA & RASSOULZADEGAN 1989, STOECKER & MCDOWELL CAPUZZO 1990, HANSEN *et al.* 1993). Possibly, the eutrophication-induced increased biomass of flagellates and ciliates in summer accelerates the hitherto food-limited growth rates of copepods.

III.3.3. ANNUAL ZOOPLANKTON PRODUCTION IN THE NORTH SEA

Table III.4 lists all available data on annual or shorter term zooplankton production in the North Sea. The various methods applied to estimate the production are indicated. With the exception of four papers dealing with euphausids (LINDLEY 1980, 1982b,c, LINDLEY & WILLIAMS 1980) and one concerned with *Aurelia aurita* in the Wadden Sea (VAN DER VEER & OORTHUYZEN 1985), all others are restriced to mesozooplankton (MARTENS 1980) or one (*Calanus*; WILLIAMS & LINDLEY 1980a, FRANSZ & VAN ARKEL 1980, FRANSZ & DIEL 1985) or more copepod species (EVANS, 1977, FRANSZ *et al.* 1984, FRANSZ & GIESKES 1984, KIØRBOE & JOHANSON 1986, ROFF *et al.* 1988, NIELSEN & RICHARDSON 1989).

FRANSZ *et al.* (1991) concluded that the Oyster Ground (south of the Dogger Bank) and the Buchan area (to the east of Scotland) "are not much different in terms of copepod production. The same correspondence can be found between the Oyster Ground, the Northumberland coastal area, and the Southern Bight. The near-coastal mixed areas have somewhat higher production, and the species composition may vary to some extent (*Acartia tonsa* being more significant in the western coastal areas and *Oithona similis* in the northern stratified areas), but small-sized neritic species dominate and produce 5-20 g C m^{-2} a^{-1}." In the northern (stratified) North Sea in spring and summer, *Calanus finmarchicus* is the stock-forming species and therefore the *Calanus* production may be a good indication of the overall zooplankton production. In summary, production data on North Sea zooplankton are scarce and random. They do not allow a thorough comparison between different areas, nor between seasons.

Tab. III.4: Literature review of zooplankton production data.

Code	Area / Group	Period	Production	Units	Reference	meth
N	Northumberland coast	1 year	10-44 (ÝØ 17)	$gCm^{-2}y^{-1}$	Roff *et al.* 1988	3
N	Northumberland coast		3.5	$gCm^{-2}y^{-1}$	Evans 1977	1
S	North. Wadden Sea Sylt		0.02	$gCm^{-2}y^{-1}$	Martens 1980	2
S	South. B. - Dutch coast		>12 (12-23)	$gCm^{-2}y^{-1}$	Fransz 1986	4
S	West. Wadden Sea		12-17	$gCm^{-2}y^{-1}$	Fransz 1980b	
S	Southern Bight offshore		5-15	$gCm^{-2}y^{-1}$	Fransz 1986	4
N	NW N.S./ Euphausids		0.01	$gCm^{-3}y^{-1}$	Lindley 1980, 1982 a,b	
N	Fladen Ground / *Calanus*	May	490-910	$mgCm^{-2}d^{-1}$	Williams & Lindley 1980b	4
N	Fladen Ground / *Calanus*	29/4-2/5	20-50	$mgCm^{-2}d^{-1}$	Fransz & van Arkel 1980	4
N	Fladen Ground / *Calanus*	May	Ø 44	$mgCm^{-2}d^{-1}$	Fransz & Diel 1985	4
S	Oyster Ground	Apr.-Oct.	1.3	$mgCm^{-3}d^{-1}$	Fransz *et al.*1984	6
N	Buchan area, mixed/frontal	Sept./Oct.	Ø 0.2-0.3	$mgCm^{-3}d^{-1}$	Kjørboe & Johansen 1986	5
N	Buchan area, stratified	Sept./Oct.	Ø 0.05-0.15	$mgCm^{-3}d^{-1}$	Kjørboe & Johansen 1986	5
N	Centr. N.S.	Feb./Mar.	Ø 0.07	$mgCm^{-3}d^{-1}$	Nielsen & Richardson 1989	5
S	south of Doggerbank	Feb./Mar.	Ø 0.3	$mgCm^{-3}d^{-1}$	Nielsen & Richardson 1989	5
	West. Wadden Sea/ *Aurelia aurita*	May/June	1-2	$mgCm^{-3}d^{-1}$	van der Veer & Oorthuyzen 1985	

Methods

1 mean annual biomass x no. of generations, based on adult size distributions in 5 species of copepods
2 summation of biomass peaks of successive generations over the year
3 mean copepod biomass x instantaneous growth rate x no. of generations/y, estimated from Belehradeks equations
4 biomass x instantaneous growth rate, determined experimentally or from literature, adapted to actual temperature with Belehradeks equations
5 biomass x specific egg production rate as a measure for daily P/B ratio. Specific egg production determined experimentally or by egg ratio *in situ*
6 biomass x weight increase during one generation / generation time

IV POSSIBLE HAZARDS/POTENTIAL CAUSES OF CHANGE FOR THE PLANKTON OF THE NORTH SEA

In this chapter we will discuss the possible hazards for plankton development in the North Sea. In the first part of this chapter we will focus on those factors for which evidence exists that they have altered the community structure of the plankton community. As has been shown in the previous chapters these factors are eutrophication and climate. This by no means implies that a third possible anthropogenic factor - the contamination of the North Sea with hydrocarbons, synthetic organic substances and heavy metals - has no influence on the plankton community. Indeed, numerous experiments show the detrimental effect of these substances on the plankton community. However, until now their impact has not been demonstrated as being the primary cause for the observed changes in the North Sea plankton community. Nevertheless, the discussion of contamination is indispensible for the present review as the effect of these substances has been demonstrated in many experiments and because its influence can not be ruled out.

IV.1. EUTROPHICATION

Two aspects of the nutrient status in an area and its influence on phytoplankton growth should be discerned: the absolute concentrations and the ratio between the major nutrients. In chapter II.4 it was shown that in the North Sea at large the annual primary production is closely related to the winter nitrate concentrations (which reflect the nutrient input into an area). But changes in phytoplankton composition and thereby in productivity are also strongly influenced by the nutrient ratios. This chapter summarizes the most important conclusions on the relation between nutrients and phytoplankton. Emphasis is put upon the possible effects of recently observed nutrient trends on the future plankton development.

IV.1.1 Nutrient enrichment

In the summary of chapter II it was shown that if we look at the North Sea at large, phytoplankton is nitrogen-limited during much of the growing season. It is therefore not surprising that a good agreement between the winter nitrate concentrations and the annual primary production exists. Highest production levels are encountered in the northern North Sea where nutrient rich Atlantic water enters and along the coasts where rivers (and thus anthropogenic sources) are reponsible for high nutrient concentrations.

Along the eutrophic coastal zone the relation between nutrient input and phytoplankton biomass and production is somewhat complicated. In general, there is no doubt that the increased nutrient input has also increased biomass and production levels. Since the sixties these levels ***have increased by a factor of two to three***. GIESKES & SCHAUB (1990) showed that the mean annual biomass along the Dutch coast is directly related to the discharge and nutrient load of the river Rhine. DE JONGE (1990) and DE JONGE & ESSINK (1991) presented evidence that in the western Wadden Sea (including the Marsdiep area) biomass and primary production were related to the phosphate load into the area via the IJselmeer. However, the latter authors already showed that during the late eighties the phytoplankton biomass was higher than would be expected on the basis of the phosphate load into the area. During the last decade the phosphate concentrations in the Marsdiep area have decreased. The primary production levels, however, remained high (CADÉE 1992a, b, CADÉE & HEGEMAN 1993). They demonstrated a good relation between mean annual phytoplankton biomass in the Marsdiep area and nitrogen loads of the river Rhine.

The above controversy indicates that although there is no doubt that nutrient enrichment causes enhanced phytoplanton productivity the exact relation between nutrient enrichment and production enhancement is not yet clear. Recently, a growing interest has arisen to explain the observed eutrophication effects in terms of nutrient ratios. HICKEL *et al.* (1992) did not observe a direct relation between the increase of either nitrate or phoshate and biomass increase in the German Bight. They suspected the changed N/P ratio to be instrumental in the increase of phytoplankton biomass in the German Bight. Indeed, high N/P ratios seem to be instrumental in driving the phytoplankton composition towards unpalatable species (see chapter II.5). Thus increasing N/P ratios in the Dutch coastal water might have increased the relative contribution of unpalatable phytoplankton thereby increasing the standing stock and primary productivity. In the Marsdiep area, the increased productivity was mainly due to recent blooms of *Phaeocystis*. Its proliferation was also explained by changed nutrient ratios (*in casu* an increased NO_3/NH_4 ratio). The aspect of nutrient ratios will be discussed in the next paragraphs. It should, however, be borne in mind that although nutrient ratios possibly play a dominant role in the phytoplankton composition and subsequently in biomass formation, the availability of nutrients is a *sine qua non* for phytoplankton blooms.

IV.1.2. Silica and the diatom-flagellate shift

Dissolved silica is an esential element for diatoms, the most important primary producers in the North Sea (REID *et al.* 1990). OFFICER & RYTHER (1980) evaluated the role of dissolved silicate in species succession. They stressed the fact that there is a marked difference in the time scales of nitrogen and phosphate remineralization on the one hand and of silica on the other. There is an obvious interest of various heterotrophic organisms in the remineralization of organic materials (including nitrogen-rich proteins and phosphate rich membranes) which results in a rapid turn-over of organic matter. No interest is, however, present for biogenic silica (diatom cell walls). Since silica remineralization is slower than that of nitrogen compounds and phosphate (OFFICER & RYTHER 1980), a continuous decrease of the Si/P and N/P ratios occurs during a plankton bloom. This eventually can lead to a Si depleted situation with enough P and N left for ensuing flagellate blooms that do not depend on Si.

It has been shown in chapter II that in all North Sea areas the spring phytoplankton is dominated by these algae. Furthermore, evidence was presented that the spring diatom bloom in all North Sea subareas was terminated by silica depletion. The dominance of diatoms over other algae under nutrient rich conditions has been demonstrated in several experiments (PARSONS *et al.* 1978, THOMAS *et al.* 1978, EGGE & ASKNES 1992). Because of the increased loads of nitrogen nutrients and phosphate in the coastal North Sea zone the available amounts of these nutrients exceed the optimal N/Si and N/P ratios and consequently these nutrients are left over and can nourish phytoplankton populations that do not depend on dissolved silica (*e.g.* VAN BENNEKOM *et al.* 1975).

Evidence from the Dutch and German North Sea coast presented in chapter II.2 shows that total phytoplankton biomass has sharply increased but that diatoms have not been able to take advantage of the increased nutrient loads. In other words the phytoplankton community has changed from a diatom dominated to a flagellate dominated system.

Negative effects of eutrohication are usually connected with flagellate blooms (cf. OFFICER & RYTHER 1980, in chapter II.3 it was for instance shown that silica depletion always preceeded noxious flagellate blooms). Thus changes in the silica cycle would influence the diatom population and therefore affect the diatom to flagellate-shift. There are three major sources of dissolved silica: import via rivers, via the Atlantic Ocean and *in situ* regeneration of biogenic silica (*e.g.* VAN BENNEKOM *et al.* 1975, RAGUENEAU *et al.* 1994).

Fresh water: The eutrophication of our fresh water system has led to increased fresh water phytoplankton blooms. Since nitrogen and phosphate are remineralized more quickly than biogenic silicate these blooms will cause a shift in the Si/P and Si/N ratios of the nutrients entering the sea. There are several indications that silica concentrations in fresh water systems have dropped (*e.g.* SCHELKE & STOERMER 1971, ELSTER 1974) whereas the phosphate and nitrogen nutrients clearly have increased. Thus fresh water eutrophication aggravates the effects of marine eutriphication in that it decreased the Si/P and Si/N ratio thereby stimulating the diatom-flagellate shift. Other ways of reducing the dissolved silica transport into the North Sea are the construction of weirs and artificial lakes: They are built for instance to enable a better use as ship ways (increased depth). These constructions have already led to a decreased silica input into the sea (VAN BENNEKOM & SALOMONS 1981). The increased residence time will enhance phytoplankton growth thereby decreasing the Si/(N,P) ratio.

Recently, a decrease in the summer silica concentrations in the river Rhine has been observed. It is possibly due to a reduced toxicity of the Rhine water which has enabled a stronger diatom growth. Consequently, the silica load into the North Sea coastal must have decreased. The - as such favorable development of a declining Rhine water toxicity - caused the effects of eutrophication in previously highly contaminated fresh water now to become apparent.

Remineralization: The rate at which biogenic silica is being remineralized depends among other factors of its aluminium content with higher concentrations leading to a slower remineralization rate and a smaller portion of the biogenic silica being dissolved (VAN BENNEKOM 1981). It has been suggested that due to the increased loadiing of the coastal zone with organic matter (DE JONGE & POSTMA 1974) and the increased atmospheric dust load, the aluminium flux into the sea has increased and thereby has decreased the amount of remineralized silica (VAN BEUSEKOM & WEBER 1992). Therefore, an increased aluminium flux and subsequent decreasing remineralization rates might have contributed to the observed decrease of dissolved silicate in the German Bight (KÖRNER & WEICHART 1992). Although the trend analyses by Radach and co-workers (see chapter II.5) did indicate a downward trend for diatom biomass, it should be noted that the interannual variation is very large. In an area like the German Bight, the summer diatom population is entirely dependent on (and therefore sensible to changes in) remineralization processes since during summer the amounts of dissolved silica carried into the German Bight by the river Elbe are very low (*e.g.* ARGE ELBE 1992).

IV.1.3. Phosphorus/nitrogen ratios and the flagellate proliferation

There is no *per se* reason that flagellates have a negative impact on an ecosystem. Indeed, many flagellates are a preferred food for copepods and filter feeders. Many marine ecosystems, like the oligotrophic oceans, are actually based upon a dominant flagellate phytoplankton population. Still, the negative consequences of eutrophication are related to the increase of flagellate biomass. There are two reasons for this:
Firstly, only flagellates have been able to take advantage of the increased nutrient load of the coastal water. The organic matter produced during blooms of these algae threats the benthic community by reducing the oxygen concentration to reducing levels. One of the consequences might be the recently observed "Black Spot Disease" in the Wadden Sea (MICHAELIS 1992) or anoxia in bottom water as observed in the German Bight after massive *Ceratium* blooms in the German Bight (VON WESTERNHAGEN *et al.* 1986)

Secondly, phytoplankton blooms with obvious negative consequences like the *Phaeocystis* blooms along the Dutch/German/Danish coast or toxic blooms like the *Chrysochromulina* blooms or the toxic *Dinophysis* blooms (shellfish poisoning) are all caused by flagellates.

Firstly, one of the major problems in coastal eutrophication is the increased sedimentation of organic matter to the extent that the ecosystem cannot cope with it.Since especially flagellate production has increased, this group of algae is held responsible. It should, however, be noted that the total organic production and not the question who produced it matters.

As has been mentioned above, there is no linear relation between increased nutrient levels and increased phytoplankton biomass. Recently, an increased interest has emerged in the possible role of nutrient ratios as a factor regulationg phytoplankton species composition and blooms. In chapter II.3 two well known phytoplankton blooms in the North Sea - the recurring *Phaeocystis* blooms in the Dutch and German coastal zone and the unique 1988 *Chrysochromulina* bloom in the Skagerrak - were discussed. Both blooms have in common that they could reach very large proportions through the escape of grazing controll by herbivorous zooplankton. In both cases the defense mechanism was triggered by specific nutrient ratios. *Phaeocystis* escaped grazing control by forming large colonies. Colonie formation was triggered by high NO_3^-/NH_4^+ ratios. *Chrysochromulina* escaped grazing control by the formation of toxins which was presumably triggered by high N/P ratios.

It is important to note that toxin production has been observed in all three major algal groups, diatoms, Prymnesiophyceae and Dinophyceae. In all cases toxine production was triggered by phosphate limitation (or silicate limitation in the case of diatoms) in combination with excess nitrate. Once these blooms were initiated the large nutrient flux guarantees unbridled growth.

The danger of these mass blooms for the coastal ecosystem is that the benthic system which already is under severe stress through fisheries and its high loads with organic matter, gets a sudden and large input of fresh organic material when mass blooms collapse. Anoxia in the sediment and in stratified areas also in the bottom water mayl kill a large part of the benthic fauna.

The present trends in nutrient input show a decreasing phosphate and ammonium input (KLEIN & VAN BUUREN 1992), a stabilizing or even increasing nitrate input (BILLÉN 1990) and stable silica inputs with recently a slight decrease during summer (LAANE 1992, p. 21). In other words, the present trend aims towards high nitrate/(Si, P, NH_4^+) ratios. These conditions trigger the escape from grazing and therefore might lead to enhanced (toxic) mass blooms despite decreasing phosphate concentrations.

IV.1.4 Effects of phytoplankton changes on zooplankton

The increased nutrient loads and especially the changed nutrient ratios have altered the phytoplankton community in coastal areas. Since herbivorous zooplankton, mainly copepods and microzooplankton, are seriously affected by any change in their food source, an indirect effect of eutrophication on zooplankton can be expected.

In contrast to the overwintering stocks in spring, the large zooplankton standing stocks in summer may be food limited and could therefore gain from an increased primary production (FRANSZ 1976). However, food quality is a more decisive factor for its trophic transfer than quantity. One of the consequences of coastal eutrophication is an increased flagellate production. There are several indications that apart from microzooplankton (BURKILL *et al.* 1987), also copepods can utilize the flagellate energy source for production: For instance, the "usual" summer phytoplankton in the Southern Bight, consisting to a fairly large extent of µ-flagellates like *Rhodomonas* spp., *Chroomonas* spp. and dinoflagellates is used efficiently for secondary production. This was shown in several experimental series carried with the dominant copepods of that area by KLEIN BRETELER (1980) and KLEIN BRETELER *et al.* (1982, 1990). It was demonstrated that the copepods fed on the heterotrophic dinoflagellates, which in their turn prey upon µ-flagellates. However, not all kinds of dinoflagellates constitute palatable food for herbivores: Various dinoflagellate species are reported to cause chemically-mediated rejection, eventually regurgitation, elevated heart rates and loss of motor control, and hence reduced grazing rates in copepods (HUNTLEY *et al.* 1983, 1986, SYKES & HUNTLEY 1987).

Microzooplankton may also show a food preference for dinoflagellates and other chlorophyll b-containing phytoplankton (BURKILL *et al.* 1987) and is itself part of the copepod diet (HERNROTH 1983, STOECKER & EGLOFF 1987, SHELDON *et al.* 1986).

According to a comparable trophic pattern, copepods may profit of *Phaeocystis* blooms. Neither the colonial nor the unicellular form of occurrence of this mass algae are considered a suitable food for the medium-sized copepods like *Acartia spp.* and *Temora longicornis,* dominating the mesozooplankton community of the southern North Sea (VERITY & SMAYDA 1989, HANSEN & VAN BOEKEL 1991). This fits to observations of BAUTISTA *et al.* .(1992), who report from drastically decreasing copepod abundances and a copepod grazing impact of less than 1 % during a *Phaeocystis* bloom in the English Channel. Thus, only a small proportion of the *Phaeocystis* blooms is directly transferred to the zooplankton.

Ciliates probably constitute the major consumers of *Phaeocystis* single cells (ADMIRAAL & VENEKAMP 1986, WEISSE & SCHEFFEL-MÖSER 1990) and are in turn known to be a protein and lipid-rich food source to copepods (VERITY & LANGDON 1984, CLAUSTRE *et al.* 1988 in KLEPPEL *et al.* 1991). Although copepods do not graze directly of *Phaeocystis sp.*, they may exert a considerable indirect effect on its mass development by selectively removing competing phytoplankton (VERITY & SMAYDA 1989) or by preying upon ciliates (HANSEN & VAN BOEKEL 1991, HANSEN *et al.* 1993). Especially in near-coastal areas this could be the case: FRANSZ *et al.* (1992) report of a thriving copepod population (*Temora longicornis*) and maximal egg production rates during the peak of a *Phaeocystis* bloom, accompanied by a bloom of ciliates in the Marsdiep. More offshore, on the other hand, it seems that no such mediated feeding by protozoans couples the flagellate bloom to secondary production: ADMIRAAL & VENEKAMP (1986) did not find any conspicious tintinnid populations in samples taken by VELDHUIS *et al.* (1986a) at offshore stations in the North Sea. Consistently, the *Phaeocystis* blooms did not decline as abruptly as at the near-shore stations, possibly due to reduced grazing (ADMIRAAL & VENEKAMP 1986).

Similar to *Phaeocystis* another hayptophycean microalga - *Corymbellus aureus* -also avoided grazing through colony formation. The release of grazing pressure enabled this flagellate which for the first time was observed in 1983 to form an extremely dense bloom (up to $9 \cdot 10^6$ cells per liter, constituting up to 85% of all phytoplankton cells) in the Fladen Ground, northern North Sea (GIESKES & KRAAY 1986). During its bloom, the water turned thick and slimy and growth and reproductive rates of the copepod *Calanus finmarchicus* were reduced (FRANSZ & DIEL 1985, DIEL & KLEIN BRETELER 1986). Filtering rates were lower compared to the preceeding diatom spring bloom (BAARS & OOSTERHUIS 1985) and the ingested phytocarbon hardly covered the demands for maintenance (HELLING & BAARS 1985).

By virtue of their large size (up to 250 µm), several dinoflagellates of the genus *Ceratium* may constitute unpalatable food for herbivorous copepods (HARGRAVE & GEEN 1970). However, others (ELBRÄCHTER 1973, SCHNACK 1976 in LINDAHL & HERNROTH 1983) suggest that the copepods use the cells by sucking them out. FRANSZ *et al.* (1984) assume *Ceratium* to be grazed by echinocardium larvae. Furthermore, Cladocerans and heterotrophic dinoflagellates graze efficiently on *Ceratium* spp. (NIELSEN 1990 in DICKSON *et al.* 1992), the abundance of which increased in recent years up to a factor of four in the central North Sea, especially in summer after the onset of stratification, (REID 1990, REID *et al.* 1990, DICKSON *et al.* 1992).

The avoidance of algae by zooplankton is an important factor in the formation of dense phytoplankton blooms. It is not exclusively limited to flagellates. In the German Bight a summer bloom of the diatom *Coscinodiscus wailesii* was recently observed. Its large size and lack of adaptation by the zooplankton community possibly helped this large diatom to reach a high biomass. (KRAUSE pers. comm., ROY *et al.* 1989, RICK & DÜRSELEN 1992).

A mechanism comparable to the grazer repelling effect of the *Chrysochromulina polylepis* toxin, which inhibited bacterial production, feeding and growth rates of ciliates as well as copepod feeding and egg production (CARLSSON *et al.* 1990, NIELSEN *et al.* 1990, see also chapter II.3) seems to determine the ecological impact of *Alexandrium tamarense* (formerly *Gonyaulax excavata, G. tamarensis*) blooms. This dinoflagellate species is well known to cause the Paralytic Shellfish Poisoning (PSP). At low cell densities, *e.g.* the beginning of a bloom, grazing by zooplankton may slow down the development of the bloom. At higher cell densities, inhibition of zooplankton grazing is induced, the treshold being determined by the cell toxin content (being clone specific and dependent on the growth phase) and the physiological state of the dinoflagellates (HANSEN 1989). At high cell densities, the exudates of *A. tamarensis* poison the zooplankton, which may continue to ingest the cells but subsequently suffer from incapacitation (IVES 1987, HANSEN 1989). In the case of lower cell densities, the dinoflagellates constitute a valuable food for copepods, cladocerans barnacle nauplii, polychaete larvae and pteropods and ciliates (*e.g.* WHITE 1977, 1979, 1981, TURNER & Anderson 1983, 1989). The toxin of the dinoflagellate is then transferred to higher trophic levels, *e.g.* bivalves, fish, birds and man where it may cause Paralytic Shellfish Poisoning (PSP), without affecting the zooplankton themselves (*e.g.* ADAMS *et al.* 1968, WHITE 1981).

IV.1.5 Conclusions

In the North Sea at large, a correlation exists between the winter nitrate concentrations and the mean primary production. Thus on a large scale (ICES boxes) it can be assumed that the increase in riverine and atmospheric nitrogen input during the past decades has raised production levels in the North Sea. Long term observations along the North Sea coast support that with increased nutrient load the production and biomass levels also have increased. However, on a local scale a direct correlation between nutrient loading and production increase is not observed. Reason for this is probably the role of nutrient ratios in regulating the phytoplankton composition: In the first place, the annual diatom biomass is limited by the availability of dissolved sillica. The remaining phosphate and nitrogen nutrients are used by flagellates. Some of these flagellates can form dense blooms that are not consumed by herbivorous zooplankton. These flagellates escape predation either by becoming toxic or by being unpalatable. There is evidence to suggest that high nitrate concentrations during silicate- or phosphate limiting conditions may induce grazer repellent tactics. The extent of phytoplankton blooms that are not controlled by grazers depend on nutrient fluxes into a bloom and are for that reason largest in coastal areas.

Thus two factors seem to regulate the consequences of eutrophication in our coastal zone: (1) absolute nutrient levels and (2) nutrient ratios. Future plans to reduce the effects of eutrophication in our coastal zone should therefore not only be directed towards a general reduction of nutrient. It is just as important to consider at the same time the ratios between the four major nutrients silicate, phosphate and nitrate and ammonium and be aware to keep the nutrient ratios in our coastal zone at "natural" levels (N/P/Si ~1/16/7, REDFIELD *et al.* 1963, SCHOTT & ERHARDT 1969). In a broader context this implies that coastal management starts with the management of continental surface waters (and atmosphere management because of its importance as additional nitrogen-source).

The recently observed nutrient trends observed in the fresh water are: decreasing phosphate concentrations due to phosphate elimination in wastewater treatment plants, slightly decreasing silica concentrations due to enhanced diatom growth and decreased ammonium concentrations and strongly increased nitrate concentrations due to agriculture on the one hand and waste water treatment on the other. The latter has probably decreased the denitrification levels in the fresh water systems through the increased oxygen levels.

The above mentioned trends - increasing NO_3^-/P, NO_3^-/Si and NO_3^-/NH_4^+ ratios all aggravate rather than reduce the present day eutrophication phenomena in our coastal area by stimulating grazer repellent tactics - the prerequesite for large phytoplankton blooms. Recent trends seems to support this view: In the Marsdiep area annual primary production levels remained high despite a marked phosphate decrease.

Some secondary producers can profit of the increased primary production levels, thus supporting supporting a higher standing stock of macrozoobenthos and of tertiary producers like fish and birds. FRANSZ *et al.* (1992) reported rising fecundity and productivity of the copepod *Temora longicornis* in a nutrient-enriched Dutch tidal inlet, BEUKEMA & CADÉE (1986) and BEUKEMA (1992) found a doubling in macrozoobenthos biomass (1970-1985) and BODDEKE & HAGEL (1991) noted for the same period a higher-than-average fish production in the same area. In the German Bight, SALZWEDEL *et al.* (1985), DUINEFELD *et al.* (1987) and RACHOR (1990a) found an increased benthic biomass at altered species compositions compared to several decades ago. KRÖNCKE (1990) stated the same for the benthic macrofauna of the Dogger Bank area. As concerns the fish-eating seabirds (gulls, terns, auks) of the southern North Sea, HARTWIG ET AL. (1990) reported of a continuous increase in breeding and migrating stocks during the last 15 years. They related this to ameliorated feeding conditions due to increased stocks of small fish (sandeel, sprat and others; TIEWS 1983, PRÜTER 1988). However, TIEWS (1990) emphasized that since the early eighties, some of these species decline in abundance again.

However, biomass production *per se* cannot be taken as an indicator for an undisturbed ecosystem. Increased standing stocks just imply that any a component of the food web is able to produce under the prevailing conditions. This is what happened in the coastal benthic communities: large, long-lived species which need deeply aerobic sediments for borrowing their tubes, recede for example in the inner German Bight, and small, fast growing species like polychaetes fill their niches (*e.g.* BERGHAHN 1990, RACHOR 1990b).

Shifts in species composition also seem likely in the zooplankton: Due to the differential growth requirements of the various algal groups, an additional supply of N and P but not of Si increased the total phytoplankton biomass but also changed the species composition towards an increased ratio of flagellates over diatoms. This means a change in food quality and size composition for herbivores. Furthermore, the time period during which algal food is available has extended into and over the winter months.

More opportunistic zooplankters like for example *Temora longicornis* (see FRANSZ *et al.* 1992) that are able to profit from the changed trophic conditions will have a great competitive advantage. These species and their branch in the pelagic food web will probably be strengthened. Hence, depending on the rate of change in algal composition, it is to be expected that a few opportunistic species will dominate the species composition, the most specialized species disappearing sooner or later. Depending on the rate of change in the pelagic system, species diversity may decrease to low levels.

IV.2. THE INFLUENCE OF CLIMATIC CHANGE ON PLANKTON DYNAMICS

IV.2.1. The relation between plankton dynamics and climate

The long-term changes of phyto- and zooplankton abundance in the offshore areas of the North Sea, as documented by the Continuous Plankton Recorder Survey records, were remarkably similar. The abundances continuously decreased from the fifties until the early eighties followed by a partial recovery during the past decade. These changes in phytoplankton and zooplankton biomass were paralleled by similar trends in herring abundance, in the northwestern North Sea, as well as by Kittiwake egg laiyng date, clutch size and chick production in a colony on the northeast coast of England (AEBISCHER *et al.* 1990). It emphasizies the tight coupling of all components of the marine ecosystem.

Various processes with sufficient temporal and spatial scales have been suggested to be the cause of the trends. They all base on long term climatic variations (RADACH 1984). These include: (1) a decline in solar radiation due to an increasing aerosol concentration (GLOVER *et al.* 1972), (2) long-term changes in the frequency and magnitude of the intensity of various wind fields over the north-east Atlantic, and the concomitant oceanographic effects, for example on salinity (TAYLOR & STEPHENS 1980a), temperature (COLEBROOK 1985a), and the latitudinal displacement of the gulf stream (TAYLOR & STEPHENS 1980b). Furthermore, wind speed directly influences timing and magnitude of the phytoplankton production by altering the water column mixing and the thermal stratification process in spring. Two groups of authors, the "Dickson & Cushing-group" and the "Colebrook-group" selected two different components of the same North-east Atlantic climate pattern, the "northerly wind component" and the "westerly weather frequency", respectively, to correlate with changes in plankton abundance observed with the CPRS:

DICKSON *et al.* (1988b) demonstrate that a long-term (1950s-1970s) increase in the northerly wind component over the North-east Atlantic in particular in March/April (due to a pressure anomaly over Greenland, leading to decreased temperatures and increased storminess during winter and spring (*i.e.* more frequent and deeper mixing, and later stabilization of the water column) is strongly associated with the downward trend in the whole plankton community, particularly in the central North Sea. In evaluation of the above hypothesis, CUSHING (1990) shows that particularly in the western central North Sea, where the frequency of gales increased most, the productive season of 12 phytoplankton species had a delayed start and was diminished in magnitude, with consequences for zooplankton production. He emphasizes that in particular the decline in production (abundance) of *Pseudo-* and *Paracalanus sp.*, the principal food for the very young autumn spawned herring larvae, lead to a reduction in herring recruitment in the 1950s to 1970s (*i.e.* overfishing of the herring stocks was imposed on naturally reduced year classes, due to a reduction in recruitment).

The second group of authors (e.g. COLEBROOK 1985b, 1986, AEBISCHER *et al.* 1990) searched the origin for the declining trend in phyto- and zooplankton plankton abundance in the declining frequency of occurrence of westerly weather over the UK. COLEBROOK (1985b, 1986) identifies two different elements determining the relationship between the frequency of westerly weather and the biological components: Firstly, a long-term trend of decline until 1979/1980 and a subsequent recovery is a common pattern of all parameters. Secondly, a periodicity of 3-4 years is underlying the long-term decrease in all parameters, but most clearly in the westerly weather frequency. However, weather and plankton abundance are inversely related and out of phase by about 9 months. The complex relationship is interpreted in terms of the same forcing mechanism (the weather, *i.e.* wind-induced vertical mixing) having different effects in different phases of the seasonal cycle: The origin of the long-term trend of decline and recovery lies in the differential survival of the overwintering stocks of zooplankton (COLEBROOK 1985b,1986), which subsequently determine the size of the summer stocks and thus the annual production (see also ROFF *et al.* 1988, chapter III.2.3 (2)). Most species have a limited potential for growth and reproduction so that a reduction of the stock size beyond a certain level in winter, will lead to a lower population density during the following year and beyond, even under optimal growth conditions (called persistency by COLEBROOK 1982c, 1985b). The shorter-term effects, on the other hand, appear to relate to events in spring and summer and may be due to variations in the rates of *in situ* nutrient regeneration modulated by a feed-back loop involving the nutrient demand for phytoplankton growth and the nutrient supply by zooplankton grazing and excretion (COLEBROOK 1982a, b, 1985b, 1986).

AEBISCHER *et al.* (1990) reason about the nature of the causal relationships between the trends in climate and the parallel developments across the four trophic levels observed: phytoplankton, zooplankton, fish and bird. Either, there is a causal connection straight up the food chain, or each trophic level could independently be affected by the climatic (physical) factor. The authors come to differential preliminary answers for each trophic level considered: while phytoplankton seems to be directly linked to climate, zooplankton is affected by climate and by phytoplankton: The northerly displacement of the Gulf Stream is thought to have contributed to the decreasing annual abundances by changing the advection to the overwintering stocks (COLEBROOK 1985b). On the 3-4 year scale, zooplankton abundance seems climate-driven through surface heat exchange phenomena, influencing the vertical stability of the water column (COLEBROOK & TAYLOR 1984). The effect is mediated by phytoplankton, possibly in a zooplankton-phytoplankton nutrient-feed-back system as indicated above. Any trophic interaction between fish and plankton turned out to be indirect and climate-driven (this result seems questionable, see CUSHING 1990), while the trend in the bird parameters were likely to be produced by a combination of climate and prey (fish).

It is not only the climate that influences the plankton dynamics, but the phytoplankton may also influence the climate by a positive feed-back loop (WOODS & BARKMANN 1993): As a consequence of the increased concentration of atmospheric carbon dioxide, the global temperatures are expected to increase (greenhouse effect). The elevated temperatures diminish the depth of winter convection, reduce the annual supply of nutrients to the euphotic zone and therefore the annual primary production. This reduces the amount of CO_2 that can be taken up by the ocean (removed from the atmosphere) and thereby enhances the greenhouse effect.

IV.2.2. Man-induced atmospheric changes

(1) Changes in atmospheric composition

In contrast to terrestrial plants which almost certainly were limited in their photosynthesis capacity by the availability of atmospheric CO_2 in pre-industrial times (HEKSTRA 1990), in the marine environment, CO_2 is present in large excess over the amount generally required for plant growth (PARSONS *et al.* 1984). Therefore, any increase in CO_2-concentration in the water by way of atmosphere-sea surface exchange will not alter the phytoplankton production. However, RIEBESELL *et al.* (1993) indicate that photosynthesis might become limited by diffusion of CO_2 to the cell wall. The authors suggest that an increase in atmospheric CO_2 and consequently higher concentrations in the sea water will increase the primary production to a limited extent. Similar to nutrient uptake (see chapter II.4), CO_2 limitation will affect large algae more than small algae.

According to BROUNS (1988), there is general agreement on a 0.3 lowering of pH (in the sea on average between 8.0 and 8.2, range 7.5 - 8.5) at a doubling of atmospheric CO_2. This is in the same order of magnitude as the daily amplitude (7.8 - 8.3) caused by photosynthesis and respiration of phytoplankton. HEKSTRA (1990) further mentions the acidifying effects of SO_2, NO_x and sulphide deposition in the sea. Acidification of the sea water will result in an increased bioavailability of copper ions (also others???) and enhance copper toxicity to marine life.

Marine acidification will also reduce the remineralization of biogenic silica in two ways: an increased pH will increase the aluminium flux through precipitation (MARING & DUCE 1987) and hence the aluminium content and remineralization of biogenic silica (VAN BEUSEKOM & WEBER 1992). A pH decrease as such will also reduce the silica remineralization (ILLER 1979). Hence atmospheric and marine acidification will intensify the diatom-to-flagellate shift.

(2) Global warming

General atmospheric circulation models predict that the increase in atmospheric CO_2 content will result in rising air temperatures and a higher precipitation (MANABE & STOUFFER 1980). Temperatures will increase most at high latitudes (>70° N) and in winter. The increased precipitation will lead to higher river runoff north of 45° N. There is also evidence that there may be a slight decrease (about 10 %) of wind stress at temperate latitudes (MANABE & WETHERALD 1980). As a consequence, a general increase in temperature and a reduction in salinity of the shelf waters was predicted for the Atlantic coast of Canada (WRIGHT *et al.* 1986 in FRANK *et al.* 1990). The authors expect a weakening of the Gulf Stream. This implies that on the one hand winter temperatures will decrease. On the other hand increased summer temperatures (next to weaker winds and, in the coastal area, greater freshwater discharge) will intensify the vertical stratification. As a consequence, the area of tidally mixed waters will be reduced and the position of the frontal zones will be situated nearer to the coast and experience a stronger nutrient flux.

The North Sea, as a shallow shelf sea, is expected to follow almost immediately any change in the atmospheric weather pattern. Due to its tight connection to the North Atlantic Ocean, which reacts much slower to changing weather patterns, a second, long-term component of possible future alterations has to be considered (BACKHAUS 1993). For example, a southward displacement of the Gulf Stream will probably affect the North Sea in a similar way as described by FRANK *et al.* (1990) for the Canadian Atlantic coast. This would imply:

(1) Intensification of stratification - Higher temperatures and less wind stress will further extend the area of seasonal stratification and intensify and prolong its duration. Stronger stratification is expected to enhance a predominance of flagellates over diatoms. Under oligotrophic conditions the transfer of organic material to the bottom due to intensified recycling above the pycnocline will be reduced. Under nutrient rich conditions, large blooms might develop above the thermocline. When such blooms collapse, large amounts of organic matter are transported into the bottom layer where they can cause oxygen deficiency. Supposedly, the reduction in the average size composition of the phytoplankton strengthens a flagellate⇒ciliate⇒copepods energy transfer, reducing the energy available for fish production.

(2) Higher water temperatures - In the southern North Sea, the higher water temperatures may allow for a higher zooplankton production and growth rate in winter and spring, in particular during the spring phytoplankton bloom. Hence, the grazing impact on the spring bloom might increase and change the energy flux towards the benthic community. Warm water species may intrude via the Channel into the southern North Sea. Due to differential growth and development rates of the various phyto- and zooplankton species, a temperature increase will result in a change in community composition.

(3) Increased fresh water input - Stronger precipitation and the resulting increase in freshwater run-off will extend the low salinity coastal zone with a reduced zooplankton species diversity. The increased fresh water input causes a higher nutrient input. As a consequence, phytoplankton production will increase.

Furthermore, a change in the nowadays predominantly westerly wind pattern will substantially reduce the Atlantic Water inflow and the flushing of the North Sea (BACKHAUS 1993). Northerly and easterly winds may reverse the anti-clockwise circulation and induce local gyres that can trap phytoplankton blooms (DIPPNER 1993).

(3) Ozone reduction in the stratosphere - intensified UV-B radiation

Ultraviolet radiation is known to induce photochemical changes in the DNA resulting in mutations of the genome. UV-B is harmful to most aquatic organisms (WORREST 1982, TITUS 1986 in VOYTEK 1990) by reducing growth and production of terrestrial plants, phytoplankton, bacteria, zooplankton and fish (POLNE & GIBOR 1982, GEIGER *et al.* 1982, LUTZ & YAYANOS 1986, DAMKAER & DEY 1982, PEAK & KUBITSCHEK 1982, HUNTER *et al.* 1982, ZIGMAN 1982). Observations of a number of aquatic organisms suggest that their tolerance of UV-B is remarkably close to their present exposure (CALKINS *et al.* 1976, GEIGER *et al.* 1982).

In general, organisms floating at the sea surface are particularly vulnerable. Among the phytoplankton, the ^{14}C fixation was found to be substantially reduced (LORENZEN 1979) and the species-specific survival of diatoms exposed to UV-B radiation resulted in an altered community structure with implications for the herbivorous feeders (DOEHLER 1984a, b; WORREST *et al.* 1981 in KRAMER 1990). As concerns the zooplankton, there is evidence that UV-B radiation, at DNA effective levels, as currently occurring in the upper layers of the water column (in Oregon, 44°35'N), may reduce the fecundity of adults and the survival of naupliar stages of *Acartia clausii* (KARANAS *et al.* 1979, 1981). The viability of nauplii was a more sensitive indicator of UV-B radiation impact than egg production itself. The survival of the older stages was not affected by the radiation levels tested.

The impact on the actively moving plankton will be reduced by vertical migrations to less exposed strata and mixing (see also review by KRAMER 1990). Older life stages of copepods, for example, undertake diurnal vertical migrations, feeding close to the surface at night and spending the day in deeper layers. However, egg production takes place near the surface and the sensitive young stages remain in the phytoplankton-rich surface layers. Also other less mobile, small taxa are not likely to be able to escape intensified radiation.

The continuing reduction of the ozone concentration in the stratosphere causes an increasingly higher UV-B radiation to reach the earth's surface. In clear waters, UV-B can penetrate to depths of 20-30 m (VOYTEK 1990), possibly affecting most of the productive zone above the pycnocline in the northern North Sea or the Skagerrak. In contrast, in the turbulent coastal areas the impact will be marginal due to the high turbidity and the optical properties of the water. The phytobenthos on the tidal flats of the Wadden Sea, however, would be severely exposed to increased UV-B levels. As this community plays an important and in winter even major role in the energy transfer in tidal flat ecosystems (DE JONGE & VAN BEUSEKOM 1993) increased UV-B radiation will indirectly affect the coastal ecosystem.

IV.2.3. Conclusions

Whereas in the coastal eutrophic waters the nutrient status is the main factor determining the plankton dynamics, changes in the offshore plankton community reflect the reactions of this community to changed hydrographic conditions. The most important factor seems to be the degree of mixing of the water column. This factor determines during the light limited winter season the growth rate of the phytoplankton (and hence the food supply to the food-limited zooplankton). During the nutrient-limited summer, however, increased mixing will stimulate the larger-sized phytoplankton and enhance secondary and higher productivity.

How these climatic changes exactly influence the plankton dynamics is largely speculative. This matter will be dealt with in the next chapter in which our ideas of how the plankton system works and reacts on external factors like climate, nutrient enrichment and toxicants will be discussed.

The recent changes in atmospheric composition all seem to have either directly or indirectly the same effect: an increased flagellate to diatom ratio. Global warming will intensify the stratification - directly through increased surface temperatures and indirectly through an increased run-off - and therefore create a situation that favors flagellate blooms. But also the acidification and atmospheric nitrate input will slow down the silica remineralisation and enhance flagellate growth.

The overall effect of UV-B is difficult to assess. In any case, the shallow stratified areas and the tidal flats seem to be most susceptible to this influence.

The increased radiation may reduce primary production and alter the population dynamics of marine copepods directly by reducing the survival of their off-spring in the upper water layers. The radiation dose as it occurs at present, is sufficient to directly induce genetic changes and alter the population dynamics of marine copepods.

IV.3. CONTAMINANTS

IV.3.1. Introduction

The input of man-made substances like organohalogenous compounds and the discharge of additional substances of natural origin like biologically essential or non-essential metals, oil or oil products to the sea alike, change the ambient environment for fauna and flora of the pelagial and benthal. The organisms experience an environment, in which not only the concentrations of essential elements are elevated, but also the ratio of these elements is altered, so that possibly the "wrong" element wins the competition for the free binding place (for example Cu - Zn, Cd - Fe, Cd - Mg, Cd - Zn, *cf.* SUNDA *et al.* 1987). In addition, "unknown" compounds, which means structures, to which the organisms are not adapted, *e.g.* organochlorines, may accumulate in the body substance and cause changes in the physiological performance.

Apart from direct lethal impacts of pollutants, sublethal stress on individuals ultimately affects the production of the whole population. The production of the population in turn determines the role of this population in the community structure and the food web. Responses of Plankton populations to pollutant stress can be determined at four levels of biological organization: 1. biochemical and cellular responses; 2. Organismal responses, including the integration of physiological and behavioral changes; 3. population responses, including alterations in population dynamics; and 4. community responses, resulting in alterations in community structure and dynamics.

As the individuals of a population are concerned, any pollutant that interferes with normal energy utilization and storage mechanisms will produce an alteration of the metabolic rate, with possible consequences in feeding and reproductive activity. Therefore these are the most sensitive physiological indicators of sublethal stress which also have the advantage of being measurable both in shipboard experiments and in the laboratory. However, the most sensitive species may not survive capture and experimental stress so that only the most resistant and hardy species and life stages will be studied.

Although feeding and egg production rates can easily be determined for the individuals tested, it is very difficult to verify rates and processes on the population and community level due to the high natural variability. As an intermediate between laboratory assay and field estimate, mesocosm studies offer the opportunity to observe the behaviour of natural plankton communities upon discharge of selected pollutants. However, mesocosms keep a number of artefacts compared to natural waters. In particular, advection is completely prevented and vertical migration of the organisms is restricted. Therefore, no emigration to more favourable living conditions is possible, nor can resistant species immigrate. Nonetheless, mesocosm studies provide a very good indication of the potential damage of chemical pollution to the pelagic food web.

IV.3.2. Transport and accumulation pathways in the food web

(1) Heavy (trace) metals

Trace metals take part in all biogeochemical processes of the soluble and the particulate phase, as well as in the biosphere. From the biological point of view, the essential trace metals may on the one hand become limiting factors in biological processes (Fe, Zn, Cu, Mn, Co, Mo, Ni), on the other hand metals may have inhibitory or toxic effects (Cu, Hg, Ag, Cd, Cr, Zn, Ni, Pb). Zinc is an example of an element which is essential to the silicate uptake of diatoms, becoming a limiting factor at concentrations of less than 10^{-11} mol (as Zn^{2+}), and on the other hand has toxic effects at concentrations of more than 10^{-8} mol (as Zn^{2+}, ANDERSON *et al.* 1978).

The concentrations of trace metals in the water depend on interactions between the soluble and the particulate phase, on exchange processes with the sediments as well as on input through the atmosphere and rivers. In the water column, the metals occur in solution either in complexed form (*e.g.* Pb, Zn, Cu), as carbonates, hydrates (*e.g.* Cu), salts/chlorides (*e.g.* Cd) or as free ion (*e.g.* Cu, Zn). The latter form of appearance is considered to have the highest toxicity for phytoplankton (SUNDA & GUILLARD 1976), zooplankton (ANDREW *et al.* 1977, SUNDA *et al.* 1978) and fish (DAVIES *et al.* 1976). The importance of the chemical form of the elements is also demonstrated by the fact that euphausiids assimilate methylated mercury with a retention efficiency of 97 %, compared to only 36 % for the inorganic form (FOWLER *et al.* 1976 in FISHER *et al.* 1991a).

One way of entry into the food web is ad- and absorbtion by the phytoplankton cells, which generally have higher metal concentrations than zooplankters. Phytoplankton also incorporates metals actively into the cells, as *e.g.* known for cadmium (ROMEO & GNASSIA-BARELLI 1985). Hence, the heavy metal concentrations in the sea water tend to reach a minimum during periods of high primary production, maximum concentrations occur during the winter (RICK *et al.* 1990, SCHMIDT & DICKE 1990).

Zooplankters on the one hand accumulate the trace metals indirectly by consumption of contaminated phytoplankton (main source of Cd, POHL 1991). The metals were found to accumulate in particular in the inner organs (hepatopankreas, ICELY & NOTT 1980). The second way of uptake is adsorbtion by the body surface, to be ultimately incorporated into the exoskeleton (JENNINGS & RAINBOW 1979a,b; main source of Pb, POHL 1991; see also Fig. IV.1). Lighter metals like Cu and Zn adsorb less to particulate material than heavier metals. This means that the heavier metals are channelled faster and in greater quantities to the benthos and thus have a smaller impact on the pelagic food web (MENZEL 1977).

The metals are incorporated into the body substance, the chitin exoskeleton and/or eliminated with the fecal pellets (chitin-metal-chelate-complexes in the peritrophic membrane) and to a lesser degree with the eggs (FOWLER 1977). For example, except for Cu which is an essential part of the animal's blood pigment haemocyanin, the concentrations of metals (Pb, Cd, Zn) in euphausids from the Mediterranean Sea are lowest in the organisms themselves, intermediate in the exuviae and highest in the fecal pellets (FOWLER 1977).

Non-essential metals like plutonium or americium cannot be assimilated by crustaceans. In copepods, zinc, cadmium, mercury, silver, and americium have retention efficiencies of 47 %, 30 %, 21 %, 17 % and 0.9 %, respectively (FISHER *et al.* 1991a, REINFELDER & FISHER 1991). The metals assimilated by the copepods solely derive from the cytoplasm of the phytoplankton cells, whereas elements associated with the cell walls and plasmalemmae are defecated (REINFELDER & FISHER 1991).

The pellets and exuviae containing trace metals may sink across thermo- or haloclines to the bottom or reenter the food web through ingestion by bacteria, microzooplankton or herbivores (coprophagy) in the euphotic zone. FISHER *et al.* (1991a) suggest that copepods rapidly defecate the unassimilated elements (*e.g.* Pu) which sink to the bottom without being much recycled in surface waters. The assimilated/essential metals on the other hand remain in the food web via predation and therefore have a much longer residence time in surface waters. However, fecal pellets, at least those of copepods, are now being recognized as fertilizers of the depleted nutrient regime in summer, *i.e.* sustaining the regenerated production, because they disintegrate in the upper water column (SMETACEK 1980, KRAUSE 1981, MARTENS & KRAUSE 1990). Therefore it seems likely that metals mainly sediment with the phytoplankton bloom in spring, but remain in the euphotic zone during summer.

Contrary to previous findings on long residence times of metals in fecal pellets (FOWLER *et al.* 1976 in FISHER *et al.* 1991a, FISHER *et al.* 1983, FISHER *et al.* 1991a) suggest that except for mercury, which has a very strong affinity to sulphur/proteins, metals deposited in a dissolved state in the fecal pellets diffuse out of the pellets within a day in clean sea water. On the other hand, sedimenting fecal pellets could function also as scavenging agents of dissolved or colloidal metal from ambient water (FOWLER *et al.* 1983, FISHER *et al.* 1991b). Elevated metal concentration levels in the fecal material should result in higher contamination levels of the consumers than through feeding on algae alone.

Possibly, copepods and other zooplankters possess mechanisms for detoxification of small amounts of heavy metals. Proteins, known as metallothioneins, were found by PULIDO *et al.* (1966) to complex cadmium, zinc, mercury, and copper and were demonstrated to exist in marine fishes (OLAFSON & THOMPSON 1974) and in two invertebrates (a crab and a chiton, OLAFSON unpubl. manuscript, from REEVE *et al.* 1977a).

(2) Organochlorines

Several groups of anthropogenic organochlorine compounds have been observed in the marine environment. These are for example the insecticides like DDT, cyclodiene, and HCH, industrial compounds such as PCBs, and fungicides like HCB and PCP, which may also be released as industrial byproducts. However, LOHSE (1990) estimated that those well known compounds which are readily identified today in gaschromatograms account for less than 5 % of the actually emitted substances. Common characteristics of the organochlorine compounds are their persistency in the environment and the high fat-solublility. They are volatile and thus ubiquitously distributed via atmospheric transport and the food web.

The persistency of organochlorines in the environment derives from the fact that during evolution no enzymatic route was developed to metabolize ingested/assimilated chlorine compounds, *i.e.* to break up or eliminate the compounds. Higher chlorinated compounds like Hexachlorbenzol (HCB) or Hexachlorcyclohexan (HCH, e.g. Lindane) are not metabolized at all (adapted from LOHSE 1988a).

As a rule, the potential for accumulation is increasing with decreasing volatility and decreasing water-solubility. Accumulation and storage take place in the biotic and abiotic compartments, such as suspended particles and sediments, of the ecosystem. The accumulation and elimination rates in organisms (actively by metabolic transformation, excretion, reproduction, or passive exchange at the body surface) depend on hydrographic factors such as temperature, salinity, oxygen content and turbidity of the water, as well as nutrients and substrate available for growth of phytoplankton and bacteria (adapted from LOHSE 1990).

Copepods can accumulate organochlorines directly by sorption from seawater and by ingestion of particulate matter in the seawater or by contaminated prey: WYMAN & O'CONNORS (1980) and O'CONNORS *et al.* (1982) investigated these relationships on the example of PCBs in the copepods *Acartia tonsa* and *A. clausi.* Uptake of PCBs by feeding on contaminated algae resulted in much higher accumulation levels than uptake from seawater alone. Starved copepods reach an equilibrium concentration between seawater and their lipid fraction within a few hours. Upon feeding on contaminated food, the equilibrium level of 22 ng PCB/mg dry weight is reached at a faster rate compared to uptake from seawater alone - transient inputs of PCBs are reflected in the copepods within a few hours. Ingestion of PCB's with the food means excretion of PCB residues with the fecal pellets and also uptake of PCB by predators with their contaminated prey or via recycling of fecal pellets.

There are no indications for biomagnification within the pelagic food chain (TEN BERGE & HILLEBRANDT 1974, DUURSMA *et al.* 1986, DELBEKE & JOIRIS 1988). This is in agreement with previous findings of FALKNER & SIMONIS (1982), who analyzed the available literature for evidence of the biomagnification hypothesis. They concluded that for aquatic organisms, the lipid-specific organochlorine concentrations were not different for the various trophic levels.

Copepods eliminate *e.g.* PCBs not only with the fecal pellets (39 and 49 % in females and males, respectively), but also with the lipid-rich eggs produced by the females (23 %, MCMANUS *et al.* 1983). The weight-specific PCB concentration in the eggs is four times higher than in the females, which eliminate the PCB by this way twice as fast as males do during depuration experiments. Individuals that were fed during depuration experiments eliminate the PCBs more rapidly than starved copepods, due to their higher metabolic activity.

Apart from sinking of fecal pellets, mass sedimentation of algae may also supply organochlorines to the benthos: KNICKMEYER & STEINHART (1989) showed that the colony-forming gelatinous Prymnesiophyceae *Phaeocystis* sp. particularly concentrates organochlorines from the ambient sea water. Little of the enormous biomass built up during *Phaeocystis* blooms is consumed by herbivores in the water column. Most of it sediments out and may not only be one factor leading to oxygen-deficient zones on the sediments (TETT & MILLS 1991), but also transports organochlorines to the benthic food web.

The sediments are not the ultimate sink for organochlorines: At least in shallow coastal waters, resuspension due to wind mixing, bioturbation and temperature-dependent release makes organochlorines available for plankton and fish (LARSSON 1983, 1985, 1986): PCBs readily desorb from resuspended PCB-contaminated sediments into water within a few hours and redistribute to uncontaminated particles, incl. plankton (O'CONNOR *et al.* 1982).

Therefore, one can assume organochlorines to be recycled to a large extent within the pelagic food web, with zooplankton occupying a key function in transforming its mode of appearance (dissolved, fixated in or adsorbed at phytoplankton, feces, zooplankton etc., HARDING 1986).

(3) Petroleum hydrocarbons

Unsubstituted petroleum hydrocarbons behave in many ways like chlorinated hydrocarbons during food chain transfers (TEAL 1977): both groups have a low polarity and are several orders of magnitude more soluble in lipids than in water. Like DDT or PCB's, many petroleum hydrocarbons contain aromatic rings. The original hydrocarbon compounds get sooner or later metabolized by the organisms, which increases the petroleum hydrocarbon's toxicity and its water solubility. The rate of metabolization is compound- and species-specific, and temperature-dependent (concluded from LEE 1975, CORNER *et al.* 1976a, b).

Copepods under oil spills have been shown to consume particles of oil which were subsequently excreted into the faeces

(CONOVER 1971). Laboratory work with crustacean zooplankton, primarily copepods, has demonstrated that they can take up a variety of aromatic and paraffinic hydrocarbons from either food or water (CORNER *et al.* 1976a,b, LEE 1975). The studies of CORNER *et al.* (1976a) and HARRIS *et al.* (1977) showed that for naphtalenes the dietary route of entry was more important than direct uptake from the water, the lipid content (probably the triglycerides) of the organisms determining the amount of uptake. About half the assimilated fraction is released in water-soluble form during feeding, either as unchanged hydrocarbons or as metabolites, and the other half is retained (HARRIS *et al.* 1977). Most of the aromatic hydrocarbons could not be traced back in the animals in depuration experiments, 50 % being lost after 2-3 days, but even a 28 d depuration period was not sufficient to discharge all hydrocarbon (CORNER *et al.* 1976a). Adults developing from Nauplii I, depurated after 24 h exposure to ^{14}C-1-naphtalene, still contained considerable amounts of the hydrocarbon (HARRIS *et al.* 1977). Therefore, even if the plankton is exposed to oil-contaminated water only for a short period of time, the physiology of the exposed and the following generations will be affected. Residues of petroleum hydrocarbons enter the food web via predation, ingestion of fecal pellets or adsorption of soluble excretory products to particulate material and may end up in the sediments, thus being incorporated in the benthic food web.

(4) Conclusions

Neither heavy metals, nor organochlorines or oil are completely removed from or degraded in the water column and sediment. Sooner or later all substances that are not permanently buried in deeper sediment layers are resuspended, recycled and temporarily accumulated in the food web. The accumulation of pollutants in the biota is first of all highly species-specific. The organisms regulate the pollutant gradient between body fluid and seawater by release of undesired elements/compounds assimilated by way of feeding, with the chitin exoskeleton during moulting, with the fecal pellets or, for lipophilic substances, also with the eggs. Adsorption is limited by the body surface and its contribution to the total contamination may be a function of the surface to volume ratio in the animals: The smaller the organisms, the more important is the contamination due to adsorption in relation to consumption with the food.

Elevated ambient pollutant concentrations in the sea water will raise the contamination levels in the organisms of the different trophic levels. However, within the pelagic food web, feeding on particles with higher pollutant concentrations does not increase the pollutant concentration in the consumer beyond a species- and size-specific accumulation level. If large amounts of particulate material (phyto- and zooplankton, suspended matter) is present in the water, then more of the absolute quantity of pollutants can be fixated, thereby decreasing the average pollutant concentration in the water and consequently in the particles. Therefore, the concentrations of pollutants in the biota are lower in summer than in winter. Possibly, the large amounts of particulate matter present in the southern North Sea decrease the average pollutant level in the organisms there, compared to in the more oligotrophic northern North Sea.

IV.3.3. Concentration and load of pollutants in plankton

(1) Heavy metals

Data on the concentrations of heavy metals in North Sea zooplankton became available only recently: WITZEL (1989) measured the cadmium, copper, lead and nickel concentrations in mixed copepod samples from the inner German Bight before, during and after the phytoplankton spring bloom in February, April and June 1985 (Tab. IV.1). She found a consistent trend of decreasing metal concentrations in the copepods from the innermost (southeastern) German Bight towards the Central North sea and correlates the decreasing concentration gradients between February and June with the weaker inflow of Atlantic water towards the summer (KÜNNE 1952). The rivers Elbe and Weser are considered to be the main sources of metal contamination (except Pb) in the German Bight. In February, before the phytoplankton increase, WITZEL (1989) found a significant correlation between the sample weight and the metal concentrations in the copepods. Smaller sized copepods had higher relative concentrations, indicating adsorption as the main accumulation mechanism at that time of the year. Later on, when phytoplankton was present in the water column, most of the metal contamination in the copepods was due to food uptake. HEYER *et al.* (1994) analyzed the concentrations of lead and cadmium in several zooplankton taxa, sampled during 6 monthly cruises to the German Bight between December 1988 and May 1989. In Fig. IV.2, the average concentrations of both metals per unit dry weight of the organism groups are presented. Fishlarvae and mysids seem to accumulate only low levels of heavy metals compared to the cumaceans and meroplanktic larvae, which contain up to the 45-fold concentration. Mixed zooplankton samples were considered unreliable estimates of metal contamination due to a very high variability introduced by sample contamination with detritus, mucous, phytoplankton and/or suspended sediments or particularly large individuals.

During the German ZISCH Project, which ended in October 1993 KRAUSE & ZAUKE (unpubl.) extended the above measurements. They studied the heavy metal (cadmium, copper, lead, nickel, zinc) contamination of various zooplankton taxa during four cruises to the northwestern North Sea (September -October 1990), the German Bight (April and August 1991), and the German Bight and Central North Sea (October 1991). The zooplankton was sorted on board ship into the following groups: fish larvae, decapods, euphausids, hyperiids, chaethognats, copepods mixed sample, copepod genera *Calanus, Acartia, Temora, Centropages, Pareuchaeta, Anomalocera.*

Tab. IV.1: Concentrations of cadmium, lead, copper and zinc (mg kg^{-1} DW, means and standard deviations) and accumulation factors with respect to ambient sea water in Calanus finmarchicus *and mixed plankton in the North Sea and northeast Atlantic.*

A. *Calanus finmarchicus*

Region, period	Cd Conc. mg kg-1	Acc.	Pb Conc. mg kg-1	Acc.	Cu Conc. mg kg-1	Acc. mg kg-1	Zn Conc.	Acc.	Reference
Greenland Sea 1989	8.8±4.4	$8.2*10^5$	1.3±1.0	$2.7*10^4$	6.7±3.6	$4.5*10^4$	176±77	$1\text{-}2*10^6$	Pohl 1991
Greenland Sea 1990	6.6±2.1	$7.0*10^5$	2.0±2.0		8.4±3.2	$1.3*10^4$	152±49		Pohl 1991
Framstrait 1989	4.1±1.7	$3.7*10^5$	0.6±0.4		4.3±0.8	$5.0*10^4$	207±48	$1.1*10^6$	Pohl 1991
Framstrait 1990	8.9±5.0	$7.1*10^5$	0.9±0.6		7.9±1.5	$7.5*10^4$	176±60	$4.0*10^6$	Pohl 1991
NW N.S. Oct.91	5.4±3.1	$1.7*10^5$	1.1±0.5	$2.4*10^4$	7.0±2.7	$7.6*10^4$	104±31	$2.3*10^5$	Haarich *et al.* 1992
Centr. N.S.,Germ. B. Oct.91	2.6±0.9		1.4±0.7		6.9±2.4		130±19		Krause & Zauke unpubl.
German Bight Dec. '88-May '89	1.2±0.5		0.6±0.4						Heyer *et al.* 1994
German Bight Apr.91	1.3±0.7				4±2		105±21		Krause & Zauke unpubl.

B. Mixed plankton

Region	Cd Conc. mg kg-1	Acc.	Pb Conc. mg kg-1	Acc.	Cu Conc. mg kg-1	Acc.	Zn Conc. mg kg-1	Acc.	Reference
German Bight before Feb., Copep.	0.52±0.087		1.76±0.74		9.62±1.24				Witzel 1989
German Bight Apr., Copep.	0.92±0.46		1.80±0.8		10.1±2.3				Witzel 1989
German Bight June, Copep.	2.03±0.57 (s.e.)		2.70±0.37 (s.e.)		8.6±2.1 (s.e.)				Witzel 1989
German Bight Apr., Copep.	1.0±0.6				10±1		257±106		Krause & Zauke unpubl.
German Bight	0.7±0.9		570±258						Heyer *et al.* 1994

mean values ± standard deviation (s.e. = standard error)

A general result is that the concentration of each element (Cd, Cu, Zn) is highly taxon-specific: for example, hyperiids accumulate by far the highest cadmium, but only moderate zinc concentrations. Fishlarvae are among the least contaminated in all areas, while the most abundant copepod species carry a rather high load of all elements.

All taxa show a trend of increasing cadmium contamination towards the northern North Sea. On the other hand, the copper and zinc load seems to be highest in the central North Sea and German Bight with copper decreasing towards the German Bight and zinc decreasing towards the northern North Sea. The measured lead concentrations all amount to 0.5 - 3.0 mg kg^{-1}. The nickel concentration varied only taxon-specifically at a low level, not regionally.

An intraspecific regional comparison of the heavy metal concentrations per unit dry weight is possible only for one species, the copepod *Calanus finmarchicus* in the northern and central North Sea (HAARICH *et al.* 1992, KRAUSE & ZAUKE unpubl.).

The cadmium concentrations range from 1 to >13 mg kg^{-1}, the highest values being found along the shelf edge and between Norway and the Shetlands. The mean concentrations are 5.4 (s.d. 3.1) and 2.6 (s.d. 0.9) mg kg^{-1} in the northern and Central North Sea, respectively.

The copper concentrations amount up to >14 mg kg^{-1}. No particular regional trend is apparent, the mean concentrations being comparable with 6.9 (s.d 2.4) and 7.0 (s.d. 2.7) mg kg^{-1} in the northern and Central North Sea, respectively.

The lead concentrations are generally very low and range from ca. 0.4 to >3 mg kg^{-1}. There are no particular regional trends, the mean concentrations being 1.1 (s.d. 0.5) and 1.4 (s.d. 0.7) mg kg$^{-1,}$ in the northern and Central North Sea, respectively.

The nickel concentrations are generally very low and range from ca. 0.4 to 11 mg kg^{-1}. There are no particular regional trends, the mean concentrations being 2.5 (s.d. 1.8) and 2.2 (s.d. 1.4) mg kg$^{-1,}$ in the northern and Central North Sea, respectively.

The zinc concentrations range from ca. 39 to 189 mg kg^{-1}, the higher values being concentrated in the central North Sea. This is reflected in the higher mean concentration of 130 (s.d. 19) mg kg^{-1} in the central compared to 104 (s.d. 31) mg kg^{-1} in the northern North Sea.

The accumulation factors with respect to the average concentrations of cadmium, copper and zinc measured in the sea water (SCHMIDT & HAARICH 1992, HAARICH, pers. comm.), can so far only be given for the northern North Sea: the concentration of cadmium is between $1*10^4$ (fish larvae) and $1.7*10^6$ (hyperiids) times higher in the organisms than in sea water. For copper, the accumulation factor is at the minimum $2.1*10^4$ (fishlarvae) and at the maximum $2.71*10^5$ (euphausids), for zinc $7.5*10^4$ (euphausids) and $2.8*10^5$ (*Pareuchaeta*), respectively. These factors give only a rough indication of the level of heavy metal accumulation in the various organisms and may not be extrapolated to a "general" accumulation level in the northern North Sea.

Data comparable to the ones presented by HEYER *et al.* (1994), KRAUSE & ZAUKE (unpubl.), HAARICH *et al.* (1992) on *Calanus finmarchicus* are available only from the Fram Strait and the Greenland Sea (POHL 1991, Tab. IV.1). The mixed copepod samples can be compared to data presented by WITZEL (1989).

Surprisingly, the concentrations of cadmium and zinc per unit dry weight as well as the accumulation factor of zinc in *Calanus finmarchicus* are far lower in the North Sea compared to the northern North Atlantic - despite lower concentrations in the sea water. Also within the North Sea, the cadmium concentration in *Calanus finmarchicus* and hyperiid amphipods, as an example of small pelagic carnivores, are significantly lower in the German Bight compared to the northern and central North Sea.

If these data are no measuring artefacts, then three factors may contribute in determining the north-south gradient of the cadmium concentrations in *Calanus finmarchicus*:

1. the longer life cycles in the north: Cadmium is actively incorporated into the phytoplankton cells and is therefore passively accumulated by herbivores during the feeding period. Crustaceans do not possess regulating mechanisms for cadmium uptake themselves so that the accumulation is a linear function of time, concentration (in water, food) and growth efficiency (WITZEL 1989). Towards the north, the water temperatures and the length of the feeding period decrease, resulting in slower growth and development rates, thus prolonged stage duration and ultimately longer generation times. The longer the stage duration, the more cadmium can be accumulated in the body substance through food uptake, but also in the chitin exoskeleton by adsorption from the ambient sea water.

2. The lack of seston other than phytoplankton in northern waters may lead to higher accumulation levels of cadmium in phytoplankton relative to the turbulent southern North Sea. This would mean that the level of cadmium in phytoplankton and consequently in herbivorous zooplankton are not necessarily correlated to the cadmium concentration in the water.

(2) Organochlorines

Zooplankton: contamination levels

The organochlorine contamination of the North Sea plankton was investigated by KNICKMEYER & STEINHART (1989) in late spring 1986 (02 May - 13 June 1986) and in winter 1987 (26

Tab IV.2: *Range (min-max) of organochlorine residue concentrations in North Sea plankton in summer and winter. (from* KNICKMEYER *1990)*

PLANKTON	n	ΣPCB	HCB	p,p'-DDE	Lindan
Zooplankton Summer	112	220 -8300	1 - 49	4 -115	2 - 130
Zooplankton Winter	16	760 - 4300	9 - 42	30 - 120	26 - 290
P. globosa Summer	12	11700 -28000	21 -380	60 - 810	60 - 810

January - 09 March 1987, KNICKMEYER 1990). They analyzed mixed net plankton samples which were grouped according to the predominant mesozooplankton species into *Calanus finmarchicus*- and *Temora longicornis*-dominated samples. In addition, *Phaeocystis globosa*-dominated plankton samples from the continental coastal area were analyzed. The *Calanus finmarchicus*-dominated samples denote the area of the northern/central North Sea (north of 56 °N), the *Temora longicornis*-dominated samples origin from the southern North Sea (south of 56 °N).

Low chlorinated biphenyls dominated the pattern of PCB congeners in all samples, but the amount of higher chlorinated isomers was greater in *Temora longicornis*-dominated samples compared to *Calanus finmarchicus*-dominated samples. This could be an indication for optional detritus feeding of *Temora,* since higher-chlorinated biphenyls get preferably absorbed at the extensive surface of fine suspended sediments (DUINKER & HILLEBRAND 1983, DUINKER 1986).

The geographical distribution patterns of the cyclic organochlorine concentrations in zooplankton are rather uniform for PCBs (Polychlorinated biphenyls, 24 components), HCB (Hexachlorobenzene), p,p'-DDE (DDT-derivate), Lindane (=γ HCH) and α-HCH (Hexachlorocyclohexane, Figs. IV.3-7). The highest concentrations (expressed as ng g^{-1} n-hexane extractable lipids of zooplankton, = Triacylglycerides TAG) of contaminants were found in the *Phaeocystis globosa*-dominated samples from the near coastal areas of the southern North Sea. The level of all measured contaminants was about 5 times higher than in the neighbouring zooplankton-dominated samples. The *Temora longicornis*-dominated samples of the southern North Sea and the British east coast show a higher contamination level with, in particular, PCBs, α HCH and Lindane than the *Calanus finmarchicus*-dominated samples of the northern North Sea. Here, the above mentioned substance classes show elevated concentrations in plankton sampled off the Norwegian southwestern coast (Bergen) and in the waters between Scotland and the Shetlands. KNICKMEYER (1990) gives a table with minimal and maximal concentrations of ΣPCB's, HCB, DDE, and Lindane (α-HCH; Tab. IV.2).

DELBEKE & JOIRIS (1988) determined the PCB concentration of e.g. zooplankton at a large number of stations along a transect from the Belgian coastal zone north to 57 °N (ca. 2-3 °E) in September 1983 . They found high PCB levels (ca. 3 mg kg^{-1} DW) in the Belgian coastal zone, decreasing in the northern direction. Around the Dogger Bank (53-54 °N), increased values up to 13 mg kg^{-1} DW were measured, then decreasing to concentrations <1 mg kg^{-1} DW towards the north.

Since DELBEKE & JOIRIS (1988) present the PCB concentration as a fraction of zooplankton dry weight, the results are not directly comparable to those of KNICKMEYER & STEINHART (1989), who gave the PCB concentration as a fraction of n-hexan extractable lipid in zooplankton. However, the decreasing trend of PCB concentrations from the continental coast towards the north becomes visible in both studies.

In summary, organochlorines are up to 50 times more concentrated in zooplankton sampled off the Dutch and German coast compared to samples taken in the North Atlantic (KNICKMEYER & STEINHART 1989). In particular the mucous-rich *Phaeocystis globosa*-dominated plankton off the southern coast accumulates organochlorine compounds from the water column and the suspended matter. DUURSMA *et al.* (1986) calculated accumulation factors for PCB's of 1.1-38*10^6 in suspended matter and 0.1-0.9*10^6 for zooplankton in the Oosterschelde estuary; the accumulation factor of *e.g.* Lindane in Zooplankton is 10^5 with respect to average North Sea water (KNICKMEYER & STEINHART 1990).

The highly contaminated waters discharged by the big English, Dutch and German rivers into the North Sea are sources of the elevated

Tab IV.3: Estimated quantities of total zooplankton (tons dry weight) in the North Sea during the ZISCH-Survey (02 May-13 June, 1986) as well as of its incorporated pollutants (ΣPCB, HCB, p,p'-DDE, α-HCH, τ-HCH) (after KRAUSE & KNICKMEYER 1992).

	Stations (N)	Total amount (t)	Relative contribution (%) of contaminant to total contaminant load in zooplankton
Zooplankton (DW)	127	4962522	
Σ PCB	87	1.3	96.7
HCB	84	.0064	0.4
p,p'-DDE	85	.0193	1.4
α HCH	87	.0056	0.4
τ-HCH	87	.0120	0.9

organochlorine contamination in coastal zooplankton (KNICKMEYER & STEINHART 1989). This regional distribution pattern corresponds well with the distribution pattern of dissolved organochlorines in the water column (GAUL & ZIEBARTH 1983, CARLSON 1986, SCHULZ-BULL *et al.* 1991) and with the results of simulation studies on the riverine input of pollutants into the North Sea (MÜLLER-NAVARRA & MITTELSTAEDT 1985; modified after KNICKMEYER 1990).

Zooplankton: Seasonal variation

The Σ PCB concentration in the zooplankton of the southern North Sea and the Skagerrak was higher in May/June 1986 than in January-March 1987, while in the central and northwestern North Sea, the relationship was inverse (KNICKMEYER 1990). The PCB-concentrations in the zooplankton at sampling stations with a relatively high primary production was usually low compared to stations with low primary production (KNICKMEYER 1990). This implies that the contaminants adhere to supended particles, this way being removed from the water phase. The higher the phyto- and zooplankton stocks are, the lower is the average pollutant concentration in the organisms. The same trend, though less pronounced, was visible for HCB, DDE and lindane (KNICKMEYER 1990, Tab. IV.2).

(3) The load of organochlorines in the zooplankton standing stock

The load of organochlorines accumulated by the zooplankton standing stock (ng m^{-2}) of the North Sea in May/June 1986 (Figs. IV.3-7) was estimated by KRAUSE & KNICKMEYER (1992): Despite the decreasing concentrations of pollutants in the animals towards the north, the load of all investigated organochlorines is significantly increased in the zooplankton standing stock of the northern and central North Sea and off the mouth of the Thames, Rhine and Elbe.

In general, the increased pollutant load reflects the higher zooplankton biomass in the northern areas (see chapter III.3, KRAUSE & MARTENS 1990). Nonetheless, a quite variable picture is derived for the various substances: Clearly, the load of Σ PCBs is increased all over the northeastern part of the North Sea and the Skagerrak, compared to the region south of 56 °N. For HCB, the impacts of the Firth of Forth, Thames, Rhine and Elbe become evident. The load of HCB in the zooplankton stock north of 56 °N seems elevated, but variable. In DDE and α-HCH, the riverine impact is obvious as well, but besides, all values north of 56 °N are higher than those south of it. The lindane (γ-HCH) load is of similar magnitude all over the North Sea, and the high concentrations in the southern North Sea are being counterbalanced by the high biomass in the north.

In total, an estimated zooplankton biomass of $5*10^6$ t (dry weight) in the North Sea in May/June 1986 carried about 1.3 t of cyclic organochlorines (Tab. IV.3). The ΣPCBs alone constitute almost 97 % of this load. KRAUSE & KNICKMEYER (1992) assume the estimated amount of 1.3 t PCBs to represent only about 50 % of the amount actually present. The resulting 2.6 t constitute at most 2 % of the total ΣPCB load of 150 t in the water of the North Sea (LOHSE 1988). However, LOHSE (1990) estimates, that the above mentionned substances constitute, at most, about 5 % of the absolute quantities of all organochlorines regularly released into the North Sea.

(4) Conclusions

It becomes clear that so far only very few studies on the amount of pollutants fixated in the North Sea zooplankton exist. In fact only WITZEL (1989), HEYER *et al.* 1994, KRAUSE & ZAUKE unpubl., KNICKMEYER & STEINHART (1989) and KRAUSE & KNICKMEYER (1992) provide data on the concentration levels of some heavy metals and a few organochlorine compounds, respectively, present in zooplankton samples from all over the North Sea. So far these investigations have focused on the metals cadmium, copper and zinc, lead, and nickel, thus comprising those heavy metals which have been introduced to the North Sea in the highest quantities. Other metals, like mercury or tin might be worth investigating as well, although their impact will probably be locally restricted.

As concerns the chlorinated hydrocarbons, at most 5 % of the absolute quantities of all organochlorines regularly released into the North Sea, can nowadays be analyzed in the marine ecosystem (LOHSE 1988a, 1990). Most of the compounds measured (like Σ PCBs, HCB, DDT, DDE, HCH etc.) are now recognized as being harmful and dangerous to the environment and their discharges will be restricted or abandoned in future. The problem consists in the other 95 % of the organochlorine input to the North Sea, consisting of a fairly unknown number of compounds: The analysis will always lag behind the chemical development. Also solvents, which make up ca. 5 % of the total riverine organochlorine input to the North Sea are usually not incorporated into the measuring programmes.

The fact that most compounds occur only in trace amounts in the water column, does not make them harmless - the dose-effect level may be reached at very low ambient concentrations. Synergistic effects may occur at much lower element concentrations than observed in tests with individual elements.

The results of the investigations carried out so far, show that there is no simple relationship between ambient pollutant level in the water and the concentrations found in the zooplankton organisms. The amount of heavy metals and organochlorine compounds accumulated in the zooplankton turned out to be highly species-specific. On the intraspecific level, the concentrations depend on the size (surface to volume ratio), the amount of lipids accumulated (Triacylglycerides are most important) and the general level of physiological activity (a function of temperature and season). Since heavy metals adhere to suspended matter, the amount of suspended matter, including phytoplankton, in the sea may be decisive for the contamination level actually present. Consequently, in the turbulent waters of the southern North Sea, the high amount of suspended matter may prevent the pollutant concentrations in the organisms from being even higher. On the other hand, the continuous resuspension of the sediments due to the tidal currents and storms, especially in fall and winter, will keep large amounts of heavy metals in the water column.

The importance of the pelagic turnover for the determination of the geographical distribution pattern of pollutants, as reflected by the sediments and relatively immobile bottom dwellers, was indicated by KRAUSE & KNICKMEYER (1992): The authors assume a vertical flux of pollutants to the bottom by means of the vertically migrating, stock-forming copepod *Calanus finmarchicus* (fecal pellets, exuviae, dead animals?) and the sedimenting spring phytoplankton bloom (KNICKMEYER 1989). This pelagic-benthic coupling could explain the elevated concentrations of mercury, cadmium and lead measured in the hermit crab *Pagurus bernhardus* (KARBE *et al.* 1988), as an example for an abundant benthic organism, and in the sediments (KERSTEN & KLATT 1988, SÜNDERMANN & PULS 1990) of the northern North Sea. The hypothesis is supported by the pattern of mainly low-chlorinated PCB congeners characterizing the contamination of the dominant plankters as well as the sediments. Furthermore, *P. bernhardus* eggs contain higher amounts of Σ PCBs (in particular low chlorinated PCB congeners) in late spring, after the spring phytoplankton bloom, than in late winter.

IV.3.4. Sublethal effects of pollutants on zooplankton

In this chapter, the available literature on sublethal effects of pollutants on zooplankton will be reviewed. Studies on acute toxicity tests (24, 36 or 96 hour LC_{50} concentrations, or pollutant concentrations which kill 50 % of the experimental animals within 24 h, 36 h or 96 h) will mostly be neglected, since they will have only a local and short-term effect on the zooplankton community, if these concentrations should ever be reached in the sea. Sublethal impairments like reduced fecundity or nauplii viability, however, can be assumed to have long lasting effects on the whole food web.

IV.3.4.1 Heavy metals

Copper - The effects of copper on elements of the pelagic food web were studied in two large mesocosm experiments, carried out in Loch Ewe, Scotland (GAMBLE *et al.* 1977) and Saanich Bay, B.C., Canada in the 1970s (Controlled Ecosystem Pollution EXperiment, CEPEX; summary given by MENZEL, 1977).

In Loch Ewe, copper at a concentration of 10 mg m^{-3} was added to one of two pairs of cylindric plastic enclosures (3 m in diameter, 17 m deep) after an adaptation period of 35 d (during which nutrients were added twice). The background levels were 1 mg m^{-3} of copper in Loch Ewe and 1-2, max. 5 mg m^{-3} in British coastal waters (PRESTON *et al.* 1972, in GAMBLE *et al.* 1977). Indications for a reducing effect of the applied copper concentrations on the zooplankton biomass and species composition were vague due to differential predator abundance in the mesocosms. However, the reduced egg to female ratios and ingestion rates of copepods in the enclosures indicate a possible detrimental effect of the copper additions (GAMBLE *et al.* 1977).

GAMBLE *et al.* (1977) emphasize that in addition to the pollution-induced stress excerted on the plankton community, physical and biological alterations within the enclosures may also alter biological rates and processes, the effects finally being more or less indistinguishable from each other. They consider the effects of copper on plankton to be at most comparable in scale to those induced by the enclosures themselves, unless for communities which are stressed already upon capture.

The Controlled Ecosystem Pollution EXperiment, CEPEX in Saanich Bay was carried out in three steps: 1. short term acute toxicity laboratory experiments on zooplankton; 2. Sub-lethal toxicity laboratory measurements; 3. Two series of mesocosm experiments.

1. short term acute toxicity laboratory experiments on zooplankton (LC_{50} tests) which had previously been exposed to various concentrations of copper and mercury showed that toxicity is directly related to the size of the organism, smaller animals being more sensitive. Sensitivity to mercury is about 2-4 times higher than to copper (see also SOSNOWSKI & GENTILE 1978).

Relative to their size, the ctenophores *Mnemiopsis* and *Pleurobrachia* and the euphausid *Euphausia pacifica* were more sensitive than the studied chaetognaths, copepods or the "hardy laboratory pets" *Artemia* or *Brachionus.* No systematic differences between inshore, offshore and oceanic species were detected. However, different populations and generations of *Acartia tonsa* showed differential sensitivity to comparable copper concentrations at the same ambient environmental conditions.

2. Sub-lethal toxicity laboratory experiments with the estuarine copepod *Acartia tonsa* revealed a significantly decreased feeding activity and egg production at 10-20 mg m^{-3}, or 1-1.5 orders of magnitude lower than in the 24 h LC_{50} experiments (ca. 300 mg m^{-3}). At 50 mg m^{-3}, the faecal pellet production was reduced to half the control level and egg production almost ceased. Subsequent experiments by REEVE *et al.* (1977a, b) confirmed that copper levels of 5 mg m^{-3} can produce a measurable effect over a few days on a variety of zooplankton exposed, both under laboratory conditions and in the enclosures.

3. Two series of mesocosm experiments with four enclosures of 66 m^3 each (2.5 m in diameter, 15 m deep) were carried out in June (25d) and September 1974 (20d), with initial copper concentrations of 0, 10, 50 (reported in REEVE *et al.* 1976) and 0, 5 and 10 mg m^{-3}, respectively (REEVE *et al.* 1977b). In the course of both experimental series, the density of zooplankton rapidly declined in all enclosures mainly due to predation impact by ctenophores. The diversity did not change significantly due to the copper treatment. However, the population reduction in *Pseudocalanus sp.* and *Acartia longiremis* took place the more rapidly, the higher the copper concentrations were (GIBSON & GRICE 1977). In the enclosures treated with copper, the rate of faecal pellet production (as an index of the feeding intensity) and egg production of mesozooplankton was significantly reduced compared to the controls. *Euphausia pacifica* and *Pleurobrachia bachei* showed enhanced mortality and decreased feeding rates in the copper treated bag, which confirmed their high sensitivity to low levels of copper, as previously derived from laboratory incubations.

In the microzooplankton, initial copper concentrations of more than 5 mg m^{-3} led to shifts in species composition and dominance at reduced abundances, ciliates and copepod nauplii particularly being affected (BEERS *et al.* 1977a). The observed effects are considered to be indirect, via uptake of contaminated food such as detrital material, which may adsorb large amounts of metals, relative to its volume. As a direct consequence of the copper treatment, the species composition and size distribution in the phytoplankton switched from large *Chaetoceros* chains to microflagellates and diatoms <10 µm during the experiment (THOMAS & SEIBERT 1977) which should provide good food for the microzooplankton.

The copper concentrations actually found in the near coastal waters of the southern North Sea, German Bight and the Skagerak amount to 0.5-1 mg m^{-3} at 10 m depth (SCHMIDT & DICKE 1990) and thus may still be below, but nonetheless close to, the observed "effect level" for the plankton communities. However, the amount of copper accumulated in detritus, entering the food web via feeding by microzooplankton and other facultative detritivores, is much higher. Therefore, the concentration of dissolved metals is not the most relevant parameter to asses the ambient contamination level.

Mercury - The effects of mercury pollution on plankton communities were investigated by BEERS *et al.* (1977b), KUIPER (1977) and DAVIES & GAMBLE (1979). BEERS *et al.* (1977b) and DAVIES & GAMBLE (1979) added an aliquot of 1 mg m^{-3} mercury to two out of three 95 m^3 enclosures, filled with Saanich Bay and Loch Ewe plankton, respectively. In both experiments, no longer-term sublethal changes were detected. Effects on the microbial population and photosynthesis lasted only for 4 days, while the mesozooplankton community apparently remained unaffected. However, in the Loch Ewe experiment, the addition of mercury resulted in immediately decreasing numbers of copepod eggs and nauplii, in absolute terms as well as in relation to copepod density. After a few days numbers increased again, which may be due to the decreasing mercury concentrations in the water (3 days after addition of a nominal concentration of 1 mg m^{-3} Hg , little more than 0.2 mg Hg m^{-3} occurred in reactive form). After 20 days, DAVIES & GAMBLE (1979) added a further 10 mg m^{-3} mercury to the enclosures and noted a marked reduction of the zooplankton density, corresponding to a 10-fold decrease in biomass. The species composition changed in favour of benthic larvae and larvaceans, calanoid and cyclopoid copepods being more sensitive.

KUIPER (1977) worked with an initial mercury concentration of 5 mg m^{-3} in two out of four 1.5 m^3 enclosures of coastal North Sea plankton. As a consequence of the mercury treatment, nauplii and copepodid development rates of *Centropages hamatus* were lowered. The population densities of *Temora longicornis, Acartia clausi* and *C. hamatus* (nauplii, copepodids and adults) were significantly reduced compared to the control bags. Only *Euterpina acutifrons* had a significantly higher density in the polluted enclosures. Mercury at initial concentrations of >1.5 mg m^{-3} reduced the growth rate of phytoplankton and 5 mg m^{-3} changed the species composition.

The highest mercury concentration measured in the North Sea at 10 m depth amounts to 0.030 mg m^{-3} in summer 1986 (SCHMIDT & DICKE 1990), but high concentrations seem to be local exceptions deviating from the generally low values (<0.005 mg m^{-3}) over the entire North Sea. Thus even the highest concentrations are 1-2 orders of magnitude below the initial concentrations in the mesocosm experiments.

Cadmium - KUIPER (1981) studied the effect of cadmium pollution on North Sea coastal plankton communities, enclosed in 1.5 m^3 enclosures (2 experiments, 6 bags). Initial cadmium concentrations of 1, 5 and 50 mg m^{-3} cadmium were later supplemented to final nominal concentrations of 100 and 250 mg m^{-3}, respectively, in two bags. In both experiments, the species composition of the phytoplankton remained unchanged. The zooplankton showed species-specific very distinct reactions: The growth and development rates of the ctenophore *Pleurobrachia pileus* were inhibited already at 1 and 5 mg m^{-3}, and no individuals sustained at higher concentrations. From the copepods, *Centropages hamatus* and *Acartia clausi* were the most sensitive, nauplii and copepodid development being reduced and mortality increased at 50 mg m^{-3}. Thus, at an overall reduced biomass, the relative abundance of the other dominant copepods *Temora longicornis* and *Euterpina acutifrons* increased. Higher concentrations increased the mortality of *Centropages hamatus* and *Temora longicornis*.

Cadmium concentrations of ca. 0.020 - 0.050 mg m^{-3} occurred all along the Belgian, Dutch, German and Danish coast of the North Sea and in the Skagerak in winter 1987 (SCHMIDT & DICKE 1990). In summer, the cadmium concentrations were even lower, probably due to their incorporation into the biological processes. Consequently, cadmium is present in maximum concentrations which are about one to two orders of magnitude below those for which shifts in the copepod species composition can be expected, based on the experimental results. For the ctenophore *Pleurobrachia pileus*, however, which is very abundant in coastal waters, the "no effect level" might be exceeded much sooner.

Cupric and zinc ion activities The effects of cupric and zinc ion activities on the survival and reproduction of the estuarine copepod *Acartia tonsa* were investigated in laboratory experiments by SUNDA *et al.* (1987): Whereas adult survival and egg hatching was little affected by copper and zinc addition, egg laying was most sensitive to zinc (reduction at zinc ion activities of ~0.006 mg m^{-3}), and naupliar survival was most sensitive to copper (reduction at cupric ion activities of ~0.0006 mg m^{-3}, and zinc ion activities ~0.6 mg m^{-3}; no survival at all at 0.002 mg m^{-3} Cu and 6 mg m^{-3} Zn, respectively).

In the near-coastal areas of the North Sea, the copper and zinc concentrations in the water column reach values of up to 1 mg m^{-3} and 2 mg m^{-3}, respectively (QSR 7a report). In the south eastern North Sea and off the SE coast of England, average copper concentrations of ca. 0.3 and 0.35 mg m^{-3}, respectively, were measured in 1986 (SCHMIDT & HAARICH 1990). According to SUNDA & HANSON (1987, in SUNDA *et al.* 1987), 97-99.9 % of the copper dissolved in seawater is organically complexed, compared to only 1-16 % of the dissolved zinc (VAN DEN BERG & DHARMVANIJ 1984, in SUNDA *et al.* 1987). Therefore, it can be estimated on the basis of the presently occurring Zn and Cu concentrations in the near-coastal waters that the Cu and Zn activities are of about the order of magnitude where biological effects can be expected.

Iron (acid-iron waste) No study was conducted on the effects of acid waste disposal in the discharge area north of Helgoland on the zooplankton. Laboratory experiments (GRICE *et al.* 1973) as well as a field study on small scale abundance and biomass distributions of the plankton communities in New York Bight (WIEBE *et al.* 1973) support the conclusion that acid waste disposal is not a noticeable factor for mortality in the zooplankton communities. In the experiments, detectable effects of acid-iron waste on copepods occurred only at combinations of concentrations of waste solution and time periods which have been demonstrated not to persist on the dumping grounds. The acidity of the waste solution rather than the effect of enhanced iron concentrations caused mortality in the copepods in laboratory tests.

However, NEWELL *et al.* (1991) did not measure a considerably increased acidity *in situ* at or near dumping grounds and suggest that the metallic components of the acid waste are responsible for the locally observed changes in the macro- and meiobenthic communities. These changes consist in an altered species composition, presumably through removal of species susceptible to the effluents and their replacement by other more resistant species. Very few species dominate in abundance, the diversity apparently being not diminished (at least during the observation period).

The effects of iron-containing "red mud", which is a waste product of aluminium production, on mortality and growth of *Calanus helgolandicus* juvenile stages as well as herring eggs and larvae, were investigated by PAFFENHÖFER (1972) and ROSENTHAL (1971), respectively. In both cases, the detrimental effects were primarily supposed to be due to the physical impact of the suspended and sedimenting material, rather than due to the toxicity of the product.

Summary and conclusions

The sensitivity of zooplankton organisms towards increased concentrations of biologically available heavy (trace) metals varies with the element (*e.g.* mercury acts more toxically than copper) and is size- and species-specific. Size-specific means that inter- and intraspecifically, smaller animals are more sensitive than larger ones. Hence, juveniles are generally more sensitive than adults. Besides, intraspecifically, subsequent generations or different populations may react differently to the same environmental conditions due to inherent genetic variability. In the interspecific comparison, relative to their size, medusae and ctenophores proved to be the most sensitive zooplankters with respect to metals.

Egg production and naupliar survival of copepods are the most sensitive indicators known for detrimental impacts of increased heavy metal concentrations. Furthermore, feeding activity (as ingestion rate or indirectly in terms of fecal pellet production) are other indicators of environmental stress, whereas respiration and excretion rates are less sensitive. In absolute terms, there may be processes or species which react to even lower concentrations, but probably, these would not thrive in the laboratory either - our understanding is biased towards what we are able to investigate!

So far, the heavy metal concentrations causing demonstrable effects in the experiments are ca. 1-2 orders of magnitude higher than the highest concentrations measured in the North Sea. However, this is valid only if each element is studied individually - synergisms were not studied yet at all. However, the amount of copper accumulated in detritus, entering the food web via feeding by microzooplankton and other facultative detritivores, is much higher. Therefore, the concentration in the water alone does not have any significance for the biological processes.

More importantly, usually the total metal concentration in the animals or in sea water is measured and used as pollution indicator. However, it is the free metal ion concentration (or activity), not the total metal concentration which determines the biological effect (SPRAGUE 1968, SUNDA *et al.* 1987). Furthermore, the metal ion activity ratios are important: Competition among metals for binding to cellular sites leads to various uptake rates; antagonistic effects between "toxic" and "nutrient" metals have been reported for *e.g.* copper and zinc (PRICE & QUIGLEY, 1966, RUETER & MOREL 1981, STOECKER *et al.* in press, in SUNDA *et al.* 1987), cadmium and iron (FOSTER & MOREL 1982, HARRISON & MOREL 1983), cadmium and manganese (PERRY & SILVER 1982) and cadmium and zinc (OAKDEN *et al.* 1984, SUNDA *et al.* 1987).

Different water bodies possess different complexing capacities, which renders not only comparisons between localities of the same nominal metal concentrations very difficult, if not impossible, but also the extrapolation of experimental results to ambient environmental conditions.

In summary, the effects of metals on zooplankton must vary between localities, depending on the species composition (already adapted/insensitive populations?) and life stage, water temperature and the complexing (detoxifying) capacities of the ambient seawater. The species-, size- and age-specific sensitivity of zooplankton to increased metal contaminations in the ambient sea water will probably lead to an altered community composition already in the case of small deviations of the natural range of biological metal availability.

Nothing is known about the metal ion activities in the North Sea. However, SUNDA *et al.* (1987) name several estuaries in which the copper and/or zinc ion activities reach levels which may inhibit the physiological functioning of the very abundant estuarine copepod *Acartia tonsa*.

IV.3.4.2 Petroleum hydrocarbons and related chemicals

After the "Torrey Canyon" oil spill, SMITH (1968) observed high numbers of *Chrysochromulina* sp.. This finding coincides with experimental observations of PARSONS *et al.* (1976) that low oil concentrations can lead to microflagellate blooms and in particular to predominance of *Chrysochromulina kappa*.

For zooplankton, in particular copepods, ingestion of contaminated food was shown to be the main pathway of hydrocarbon uptake (CORNER *et al.* 1976a) leading to much longer residence times of naphtalene during depuration experiments compared to adsorption from sea water. The retention of the hydrocarbons in the animals ensures either the transfer to a higher trophic level in the food web, or its sedimentation.

It has been long known that refined petroleum products are very toxic to marine organisms (ANDERSON *et al.* 1978). In laboratory studies petroleum hydrocarbons reduce egg production and viability of the estuarine copepod *Eurytemora affinis* (BERDUGO *et al.* 1977, OTT *et al.* 1978). Later, mesocosm studies have been performed often confirming these effects. The concentration range applied in mesocosms varied, from 250-550 mg m^{-3} crude oil simulating the upper 5 m near the BRAVO-blow-out site (GRAHL-NIELSEN *et al.* 1977, in DAHL *et al.* 1983), concentrations of production water expected 500-1000 m downstream from an oil production platform (HAY *et al.* 1988), to lower concentrations of

50-60 mg m^{-3} and 40 mg m^{-3} of fuel oil (LEE *et al.* 1977).

Crude oil - DAHL *et al.* (1983) enclosed natural water columns by hauling plastic bags (1 m in diameter) from the bottom in 12 m depth to surface in Rosfjord, Norway. At the start of the experiment in early March 1979 the plankton was in a prebloom stage of development. One of two enclosures was layered with about 5 mm thick Ekofisk crude oil (>300 mg m^{-3}). In the untreated enclosure, the phytoplankton developed as a typical spring bloom in natural waters. In the oil-treated enclosure, no diatom bloom occured but bacteria and protozoa flourished. This caused a change in food supply at the disadvantage of copepods and in favour of the small grazers like tintinnids. Additionally, copepod recruitment was directly diminished by inhibition of the development of copepod eggs and naupliae. By these two effects, copepods almost disappeared.

In the laboratory, solutions of crude oil in seawater reduced the feeding rate and although egg production was maintained, no nauplii of *Centropages hamatus* survived past NIII (COWLES & REMILLARD 1983, see also GAMBLE *et al.* 1987). Crude oil and crude oil/sea water suspensions (0.1 ml l^{-1}) lead to abnormal organogenesis in sea urchins (LØNNING & HAGSTRÖM 1975) and marine fish larvae (LØNNING 1977) and an impact of the oil on the genome has been suggested. At high oil concentrations, the deformations of the fish embryos led to their death.

Fuel oil - The increase of phytoplankton standing stock in mesocosms due to fuel oil was condidered a result of reduction in predator pressure (VARGO *et al.* 1982).

A water-extract of fuel oil No. 2 was pumped throughout the water column of one of two large vertical enclosures of 2 m diameter and 12 m depth in Saanich Bay, B.C., Canada, up to an average final concentration of 50-60 mg m^{-3}. The control enclosure contained about 10 mg m^{-3} and this level was also reached in the oil-treated enclosure after 15 days.. The initially dominating centrate diatoms were replaced by a bloom of microflagellates which supported a large increase in tintinnids abundance. This change in phytoplankton may have caused some food shortage thus reducing the growth rate in *Pseudocalanus minutus,* which accounted for 44-91 % of the total zooplankton population. However, this did not alter the zooplankton standing stock substantially (LEE *et al.* 1977). Similar effects were observed by DAHL *et al.* (1983).

Effects of produced water - Waste water from oil production platforms contains oil and chemicals used in the drilling process. By using the waste water in experiments it cannot be fully established which part of the contamination affects the organisms (DAVIES *et al.* 1981, HAY *et al.* 1988). The effects of production water on the population dynamics of copepods were tested in Loch Ewe (Scotland) in four enclosures of 4.7 m in diameter and 310 m^3 each, filled with water at 22 m depth and lifted to the surface during a period of 100 days. Two of the four enclosures were treated twice with an initial dose of 7-8 mg m^{-3} of produced water, concentrations expected 500-1000 m downstream from an oil production platform.

In the water mixed with production water recruitment of copepods was significantly reduced by lowered hatching success and/or survival of nauplii. Development and mortality rates were not significantly different in treated and untreated enclosures. However, a differential development of the copepods *Temora longicornis* and *Acartia clausi* at the different treatments supposedly indicate a higher sensitivity of *Temora* compared to *Acartia* (HAY *et al.* (1988, see also GAMBLE *et al.* 1987). GAMBLE *et al.* (1987) found indirectly elevated phytoplankton stocks and depressed larval growth rates due to decreased copepod abundance. Fish larvae showed no measurable effect, but larvae of benthic invertebrates proved to be highly vulnerable.

Dispersant-treated oil - After the use of dispersants the oil concentration in water can be 100 to 1000 times higher than would have been the case under natural oil weathering conditions (WARD & DAVIES 1978, in DAVIES *et al.* 1981). In Model Plankton Ecosystems (MOP's) the effects of oil-solutions on zooplankton were investigated. Dispersant-treated oil increased the concentrations of oil dispersed in the water and reduced the abundance and biomass of copepods to a much greater extent than oil (0.5 mm) or dispersants alone (KUIPER *et al.* 1986, in: KUIPER & GAMBLE 1988). Microplanktonic ciliates are also affected by all kinds of oil, dissolved, as droplets or dispersed. They either die or migrate out of the polluted surface layers. Heterotrophic ciliates react less sensitively to oil but more sensitively to dispersant-treated oil than autotrophic ciliates and dinoflagellates. Nutrient addition to oil-polluted mesocosms accelerated recolonization by heterotrophic but not by autotrophic ciliates (DALE 1988a, b).

The fertilization process of sea urchins and the early development of marine fish proved to be particularly sensitive to oil dispersants. Also barnacle nauplii, calanoid copepods and decapod larvae and hydromedusae showed a delay or inhibition in development (LØNNING & FALK-PETERSEN 1978).

Disturbance of chemical communication - - Chemical communication, by pheromone, takes place at all trophic levels and probably affects most of the essential biological processes. Evidence for disturbed chemically mediated reactions already at exceptionally high dilutions of hydrocarbons in the sea water was given for lobsters, fishs, seeslugs and crabs, and also for brown algae (see GUNKEL & GASSMANN 1980).

Conclusions - Crude oil, fuel oil and production water from platforms and oil dispersants all affect zooplankton population: directly through the hydrocarbon content of their food and indirectly through a change in the structure of the food web. They lower egg production, egg viability and offspring mortality and therefore alter the population dynamics of zooplankton. The effects of dispersant-treated oil are much stronger than those of untreated oil.

It is important to note that the experimental methodology applied to manifest the effects of contaminants on the plankton determiones to some extent the obtained results: *E.g.* a singular input of fuel oil which is very volatile, to clear sea water will have only a limited, short term effect on the plankton community. In the study of LEE *et al.* (1977), the natural variation of the community composition was larger than the variation caused by the addition of fuel oil. However, in the long run, the observed slight alterations in reproduction of some species will change the species community. This should be true for all kinds of oil. The long-term, multiple generation effect of increased sublethal concentrations of oil in the sea and thus a possible sublethal genetic impact was not studied yet, but there is no doubt that the wide-spread, permant low level oil contamination is a greater threat to marine life than locally restricted large oil spills.

However, high oil concentrations may cause deformation of fish embryos leading to their death. Thus oil spills of a major scale and at sensitive times may cause the loss of a fish generation.

One aspect which might be of utmost importance is the possible disturbance of chemical communication in all kinds of organisms. It could be that already very low concentrations of hydrocarbons released in the sea influence the behavior of the pelagic and benthic communities on a very large scale. However, the resulting changes will probably be subtle and difficult to recognize. Also, possible genetic changes may be measurable only after very long observation periods. But these hypotheses need further verification.

In conclusion, the effects of an oil spill may be much more extensive, spatially and temporally, than to be expected at first view.

IV.3.4.3. Synthetic and other hydrocarbons

It must be kept in mind that our knowledge on the distribution and toxicity of synthetic contaminants is limited to a small number of compounds (comp. IV.4.2).

Diatoms are more sensitive to organic contaminants, than are flagellates (MOSSER *et al.* 1972a, b). A few parts per billion of PCB's can already cause a shift from diatoms to flagellates. PCB concentrations in the North Sea are lower (in the range of parts per trillion; ERNST *et al.* 1988) which makes a direct impact unlikely. It should, however be noted that PCB's are widely spread in marine sediments (LOHSE 1988a, b) and are rapidly transferred from particles to algae (Harding & Phillips 1978).

The impact of organochlorines on herbivorous zooplankton is not only a direct one, but also acts indirectly via the phytoplankton species and size composition. PCB's may reduce the average size composition of a natural phytoplankton community by suppressing the growth of large diatoms more than the growth of small diatoms and flagellates (O'CONNORS *et al.* 1978, 1982). As a consequence, herbivores have to cope with quantitatively and qualitatively altered food conditions.

Effects - Despite the ubiquitous distribution of the numerous organochlorine and other synthetic organic compounds, only very few investigations on possible sublethal effects on zooplankton exist: Mesocosm (1.5 m^3) studies on fate and effects of 4-Chlorophenol (4CP), 2,4-Dichlorophenol (DCP, 1984a), and 3,4-

coastal plankton revealed that initial concentrations of 1000 mg m^{-3} 4CP or DCP and 100 mg m^{-3} or more of DCA in seawater significantly affected the zooplankton community (KUIPER & HANSTVEIT 1984 a,b): Development and therefore secondary production of the dominating copepods *Acartia clausi, Temora longicornis* and, mostly, *Centropages hamatus* were reduced to a variable extent in the three succeeding experimental series with 4CP and DCP, the latter showing less strong effects. No effects were registered at lower concentrations. DCA concentrations of 100 mg m^{-3} changed the species composition of both phyto- and zooplankton, 1000 mg m^{-3} or higher concentrations significantly increased the mortality of copepods. The authors assume a direct impact of the compounds on the zooplankton which, as a consequence, excerted a reduced size-selective grazing pressure on the phytoplankton community in the treated bags. In one experiment, the phytoplankton was inhibited a few weeks after the chemical (4CP or DCP) could not be traced in the water anymore. It was assumed that the metabolite formed behaved more toxic than the original compound.

WYMAN & O'CONNORS (1980) and O'CONNORS *et al.* (1982) found a significant increase in mortality rates among *Acartia* copepodids exposed to PCB-contaminated food (Aroclor 1254) when compared to mortality of copepods without PCB in their diet, and suggest that also fecundity could be affected. This could so far only be proven to be caused by γ-HCH (Lindane, 10-100 mg m^{-3}, HANSEN 1987) and Atrazine (1-10 mg m^{-3}) on *Daphnia sp.* (LAMPERT 1987, SCHWOERBEL 1987). Atrazine also reduces the filtration rate and may therefore indirectly lower the egg production rates.

TESTER & COSTLOW (1981) tested the effects of 1-1000 mg m^{-3} Dimilin, a chitin synthesis-inhibiting insect growth regulator, on *Acartia tonsa:* a 1-4 d treatment of females with 1-100 mg m^{-3} Dimilin did not significantly reduce their fecundity, but the hatch of viable nauplii was reduced from 90 % or more to less than 50 % in 1 mg m^{-3} after 12 h of treatment and to less than 5 % in 10 mg m^{-3} after 24 h of treatment.

The impact of discharged DuPont Grasselli waste water (an alkaline solution of sodium sulfate, containing trace amounts of methyl sulfate, methanol, phenol and other organic compounds) on three neritic copepod species was evaluated by CAPUZZO (1985). A reduction of feeding rates was observed which was suspected to be due to the methanol and phenol content of the waste, either by impairment of the feeding mechanisms or by inhibition of the chemosensory receptors used to detect food items. Other chemicals may interfere with the oxidative metabolism. These organochemicals therefore mimic starvation stress and as a consequence, egg production rates were decreased in all three species, the level being determined by the individual life history strategy.

Summary and conclusions - Organochlorine compounds are accumulated in the lipid fraction of phyto- and zooplankton. With respect to the lipid content, no food chain magnification takes place, but the physiological functioning of the organisms seems to be affected, *i.e.* hatching rates and nauplii survival of copepods are reduced. There is no data available, which concentrations of the diverse organochlorine compounds in the water cause these effects. Virtually nothing is known about synergistic effects of different compounds. The quoted studies only worked with copepods - we do not have the slightest idea of how sensitive other members of the zooplankton community behave to organochlorine stress.

Egg viability, hatching rates and nauplii survival are by far the most sensitive indicators of toxic stress on copepods: females deposit large amounts of the lipophilic organochlorines in their eggs, and thus ultimately in their offspring. MCMANUS *et al.* (1983) have shown that the first-laid eggs of *Acartia tonsa* contain the highest level of contamination. High mortality of first-laid eggs could serve as a mechanism for clearing the copepod population of organochlorines. However, it could equally well endanger the species since females produce only a few clutches before removal from the population by predation (PETERSON 1979) and the first clutch is demographically the most important (SLOBODKIN 1966, from HARDING 1986).

SLOOF & MATTHIJSEN (1988) estimated "safe levels" for α-HCH, γ-HCH and δ-HCH of 1 mg m^{-3}, 0.002 mg m^{-3} and 0.001 mg m^{-3}, respectively, for marine organisms, based on very few acute toxicity studies. They found γ-HCH to be 20-40 times more toxic in salt water than in fresh water. The possibly different sensitivity of estuarine and oceanic species/communities to organochlorines (and other pollutants) needs verification.

In the case of lindane (γ-HCH), the proposed safe level of 0.002 mg m^{-3} has already been reached or is even exceeded in the southern North Sea, with concentrations >0.004 mg m^{-3} being measured in the inner German Bight (LOHSE 1990). In view of the widespread and manifold contamination of coastal waters with solvents, detergents, PCB's, pesticides, insecticides, etc. more detailed long-term community studies are urgently required.

IV.3.5 Sublethal effects of pollutants on phytoplankton

The potential of heavy metals to influence the phytoplankton composition has been shown in many laboratory experiments (e.g. RICK 1990) and mesocosm experiments (THOMAS *et al.* 1977a, b, KUIPER 1981). These experiments show that in general large diatoms are more sensitive to heavy metals than certain flagellates (*e.g.* GRAY 1982). Thus the contamination of the marine environment with these metals could have induced a shift in the diatoms to flagellate ratio. However, the problem with applying the results of the above type of experiments to the North Sea situation is that these experiments are generally carried out under unnaturally high metal concentrations.

No data is available that show that changes observed in the North Sea phytoplankton could be attributed to toxic levels of heavy metals. Therefore, it is difficult to assess whether the present heavy metal concentrations have contributed to the observed changes in the phytoplankton system. RICK (1990), however, concluded on the basis of his study in which he used a natural range of metal and nutrient concentrations as well as natural light intensities such as prevail in the North Sea, that in the German Bight the copper concentrations are in the range where an impact cannot be excluded. Also DAVIES & SLEEP (1980) suspect that in the coastal zone copper could have influenced the phytoplankton composition.

As was shown in chapter II the heavy metal loads of the river Rhine decreased markedly. It should be worthwhile to investigate whether the decreased heavy metal loads could have had an influence on the increase in primary production off the Dutch west coast (by a factor of appr. two, see chapter II.2.4).

V. THE PLANKTON ECOSYSTEM: HOW IT FUNCTIONS AND IS AFFECTED

In the first chapters of this review we have described the phyto- and zooplankton systems separately. In the previous chapter the possible factors influencing the dynamics of both systems were discussed. It has become clear that both systems can neither be regarded as independent entities nor in a strictly hierarchical way. In this final chapter we will try to depict the plankton system as one entity. We will describe the interconnection of the plankton system with its physical and chemical environment and identify where and when the system is sensitive to external forces. With the aid of this conceptual framework some scenarios of local environmental change will be investigated for their impact on the North Sea plankton ecosystem.

V.1 AN ASSESSMENT OF THE PRINCIPAL FORCING FACTORS

There are two lines of explanation for the recent changes that have been observed in the North sea: climate and eutrophication. Whereas climate is the principal factor in the open North Sea, its influence is overruled by eutrophication in some coastal areas. This by no means implies that contaminants do not play any role in the North Sea plankton system. Its influence on plankton dynamics was shown in various experiments. Furthermore, the levels of toxic substances like copper have reached such levels that they might influence the plankton dynamics. However, there are no adequate time series or even incidental large scale observations demonstrating the effect of contaminants on the plankton dynamics.

Therefore, we have restricted the following description of the plankton system to the two above mentioned factors climate and nutrients. In some critical situations the possible influence of increased contaminants is indicated.

V.2 THE PLANKTON SYSTEM

In the pelagial, two main dietary routes of energy transfer exist (comp. Fig III.8). During nutrient rich periods, the classical type of food chain dominates: microphytoplankton (diatom) production is directly transferred into secondary (herbivore) and higher trophic levels. In contrast, during calm, nutrient poor periods the ultraphytoplankton (flagellates) prevail. Its production is channeled through heterotrophic flagellates and ciliates as primary grazers and from there via macrozooplankton (copepods) to the higher trophic levels. Thus, on the one hand, less energy will reach the highest trophic levels, because each additional step in the food web costs ~90 % of the available energy. On the other hand, the heteroflagellate⇒ciliate ⇒copepod link makes extra food sources accessable by coupling bacterial production via heteroflagellates etc. with higher trophic levels. Thus depending on the physical and chemical conditions for plankton growth during the four seasons, the efficient, short food chain or the longer, less efficent food chain dominates.

V.2.1 Winter

Winter is the period of low biological activity. The entire North Sea with the exception of the Skagerrak and Kattegat is vertically mixed and nutrient rich. Both phyto- and zooplankton are limited by energy availability. The phytoplankton is light-limited, whereas for zooplankton food is the limiting factor. Thus the one major factor determining both phytoplankton and zooplankton abundance in winter is light availability. Light availability is determined by the degree of water column mixing. In the open sea a high degree of mixing causes the phytoplankton to spend more time in the deep, dark zones, thus loosing more energy through metabolic processes than can be compensated for by production in the photic zone. In the coastal zone the mixing depth is fixed by the water depth. Here, light availability is determined by water turbidity. Light availability is also reduced by cloudiness.

Thus, during cloudy, stormy winters, the phytoplankton standing stock and production will be very low and in consequence the survival of the zooplankton stocks is reduced. During relatively calm, clear winters primary production is to a lesser extent light limited, larger phytoplankton stocks are present and a larger zooplankton population can survive. At times, the strong winterly predation on the zooplankton can be compensated for by (food-dependent) reproduction.

Two additional factors can modify the effect of the winter weather situation in coastal waters: contaminants and eutrophication:
The general effect of contaminants is an increased metabolic rate in order to restore the physiological damages caused. In that sense a plankton population in a contaminated area has a lower chance to survive an energy-limited period than an uncontaminated population.
The most apparent effect of eutrophication in coastal areas during winter is an increase of flagellate and zooplankton biomass As zooplankton is food limited any increase in food availability would increase its survival during the winter period. One such food source that has recently increased is the winter flagellate population in the German Bight near Helgoland (RADACH *et al.* 1990a). It is not conceivable that the winterly flagellate increase is due to an increased light availability. Possibly, the increased loading of the coastal zone with organic matter has formed an additional or even a major energy source for this group of heteroflagellates during winter.
Thus increased contaminant load and eutrophication have an opposite modifying effect: Whereas contaminants enhance the effect of increased storminess or cloudiness, eutrophication indirectly increases the survival rate of smaller zooplankton at least in some coastal areas.

In conclusion, during winter the primary factor determining the plankton dynamics in the open North Sea is the weather (cloudiness, storminess). It controls the exposure of the phytoplankton community to light which in turn determines the size of the phytoplankton population and consequently the zooplankton standing stock. In coastal areas, contaminants and nutrient enrichment may interact with the natural cause of events: contaminants generally enhance the respiration of the plankton (energy required to restore damages) and thus aggravates its energy-limited situation. Eutrophication indirectly nurtures the hetero-(auto)trophic flagellate community that serves as an additional food source for especially the smaller copepods.

V.2.2 The end of the light limitation: The start of the plankton season.

During winter net phytoplankton growth is only possible under favourable local conditions as found in the Dogger Bank area or under favorable weather conditions (temporal stratification cf. COLEBROOK 1979). With increasing day length, the chances for net phytoplankton growth also increase and culminate in the spring phytoplankton bloom. These blooms, which are dominated by diatoms, can occur as early as January-February in the shallow low turbidity waters like off the Dutch west coast, the Dogger Bank area or the Skagerrak (here the "shallow depth" is the permanent haline stratification which keeps the algae in the surface layer). From there it spreads into the turbid coastal water and into the deeper parts of the central and northern North Sea. Here the spring bloom first peaks during April. Again light availability (water mixing, turbidity) determines the timing of the spring bloom. During adverse conditions it can be delayed up to six weeks. In the open North Sea early blooms are supposedly related to transient thermal structures which can be formed before the permanent summer stratification is established. They have a higher probability to occur when large differences between winter and summer temperature exist. The timing of the bloom influences its shape: In general, early blooms develop slower (less light) and therefore last longer.

Nutrient availability determines the size of the spring bloom. Thus in the eutrophic coastal zone peak concentrations of 40 µg Chl *a* dm^{-3} are common as compared to only 6 µg Chl *a* dm^{-3} in the western central North Sea. A common characteristic of the North Sea spring bloom is its two-stage appearance. It is determined by nutrient ratios: The first stage is dominated by diatoms and limited by silicate availability. The second stage is dominated by flagellates. The potential size of this bloom is determined by the amount of N and P nutrients left after the diatom bloom. The nutrient ratios ($SiO_4/NO_3/NH_4/PO_4$) possibly exert a strong influence on species composition of the flagellate bloom (see next paragraphs).

The start of the spring phytoplankton bloom triggers the zooplankton population to reproduce. Since the generation times of the phytoplankton are much shorter than the zooplankton generation times, the phytoplankton bloom is largely unaffected by the zooplankton. The amount of phytoplankton grazed by the zooplankton depends on two factors:

(1) Size of the initial zooplankton population.
(2) Ratio between phytoplankton and zooplankton generation times.

The size of the initial zooplankton population depends on three factors:

(1.1) Size of the population that enters the food-limited period.
(1.2) Length of the food-limited period.
(1.3) Food availability during the food-limited period (which is determined by the phytoplankton standing stock which is determined by light availability).
(1.4) Predation upon zooplankton

The ratio between phytoplankton and zooplankton growth rates during the spring bloom depends on:

(2.1) Timing of the spring phytoplankton bloom (earlier blooms develop slower than late blooms).
(2.2) Temperature (higher temperatures allow a faster zooplankton reproduction and higher growth rates and *vice versa*).

The degree of phytoplankton-zooplankton interaction has important consequences for the energy- and nutrient flow. In the absence of grazers most of the phytoplankton population (and the sequestered nutrients) will sink out of the water column and will be channeled into the benthic food web. This triggers the release of meroplanktic larvae of the benthic fauna. During intense grazing, however, a considerable portion of the primary production will flow via the zooplankton (secondary production) into the pelagic system. The cycling of organic matter within the water column will also keep a larger portion of the nutrients available for further phytoplankton production.

V.2.3 A schism in the plankton community: summer stratified versus permanently mixed.

During spring, water temperature continuously rises due to the increasing intensity of solar radiation. In the deeper parts of the North Sea this causes the water column to be stratified. In the shallower parts of the North Sea, however, the turbulence caused by tidal currents prevents this layering. These totally different hydrographic conditions have a profound influence on the plankton development. The two closely entwined factors - nutrient availability and turbulence - segregate the plankton community during summer into the low turbulent, nutrient poor central and northern North Sea, and the nutrient rich, turbulent coastal zone.

Under stratified conditions, nutrients in the upper water column will soon be depleted and a phytoplankton community will evolve that is optimally adapted to low nutrient, low turbulent conditions. Such communities usually consist of small (<10 µm) so-called ultraphytoplankton (see chapter II.4). In contrast to the larger microphytoplankton, their high surface to volume ratio guarantees that even under very low nutrient concentrations enough nutrients can be taken up to enable optimum growth. Because of their small size sedimentation out of the photic zone is negligible compared to the microphytoplankton.

Due to their small size (a high surface-to-volume ratio), a relative large part of the photosynthetically produced organic matter is lost to the environment by passive diffusion. This pool of organic matter is being used by bacteria. Since these bacteria are preyed upon by ciliates and heteroflagellates, this "microbial loop" forms an important alternative link of primary production to higher trophic levels. However, the number of steps involved makes it an a rather inefficient link in terms of for instance fish yield.

The ultraphytoplankton is preyed upon by heteroflagellates and ciliates. These predators have generation times comparable to the ultraphytoplankton. Therefore, ultraphytoplankton is tightly controlled by grazing and blooms of these algae are rare.

Under nutrient rich, turbulent conditions the microphytoplankton (diatoms and larger flagellates) prevail. In contrast to the ultraphytoplankton their generation times are much shorter than those of their main predators, the copepods. This allows the microplankton to escape grazer control and form large blooms.

It has important implications whether the phytoplankton is dominated by the ultra- or the microphytoplankton. It takes at least one to two steps more to transfer the ultraphytoplankton biomass for instance via ciliates, small copepods, large copepods to fish than in the microplankton dominated plankton systems where a relatively short food chain (phytoplankton, copepods, fish) is present. Remember that during each transfer of one trophic level to the next about 90% of biomass is lost by respiration.

V.2.4 The stratified central and northern North Sea

Of course, the actual summer plankton distribution in the stratified North Sea never has a 100% "stratified" appearence. Both the microplankton-based and the ultraplankton-based systems are found at the same locality. The contribution of the "short" food chain, however, determines the productivity of the system. Two factors seem to influence the microphytoplankton (diatom)-macrozooplankton (copepod) abundance:

(1) The extent of phyto-zooplankton interaction during the spring bloom
(2) The amount of turbulence during the stratified season.

The effect of phytoplankton-zooplankton interaction can be visualized as follows: If no or too little zooplankton is present at the start of the spring phytoplankton bloom, this bloom will grow until nutrients are depleted and sink from the euphotic zone to the bottom. In this way, a large part of the primary production is channeled directly into the benthic system. If, however, a relative large zooplankton population is present before the spring bloom, the zooplankton population can graze a substantial part of the phytoplankton standing stock. Both the so-called superfluous feeding and the fact that the fecal pellets of zooplankton can remain for a long time in the upper water column are responsible for a shift of the remineralization of organic matter from the benthic to the pelagic system. In this manner the zooplankton is refertilizing "its own meadow".

The amount of turbulence during summer has an important influence on microphytoplankton growth and thus on the overall productivity. A high degree of turbulence, which in the deeper parts of the North Sea is entirely due to wind, will increase the nutrient flux from the deep, nutrient rich water layer across the thermocline into the nutrient depleted, euphotic surface layer. It also stimulates microphytoplankton growth by preventing it from sinking out of the euphotic zone and by enhancing nutrient uptake. On the other hand, extreme stratification (low wind speeds, high temperatures) will force the plankton system into a low productive ultraphytoplankton-microzooplankton system (compare chapter II.4).

V.2.5 The well-mixed coastal zone

In contrast to the open North Sea, the coastal zone is subject to a continuous nutrient input. Main sources are fresh organic matter, which remains available for remineralization due to the constant mixing of the water column and fresh water input. After the spring phytoplankton bloom, one to two additional diatom blooms occur. They are mostly followed up by non-diatom (flagellate) blooms. Presently, the annual primary production levels in the Dutch coastal zone which receives most of the continental run-off and nutrients are approximately 3-5 times higher (up to 500 g C m^{-2} a^{-1}) compared to the open North Sea (75-125 g C m^{-2} a^{-1}) and compared to the near shore productivity during the sixties and early seventies. The changes that occurred in the coastal zone plankton are without any doubt related to eutrophication. In other words, the principal forcing factor in the coastal zone is the nutrient status. However, there is not a simple one-to-one relation between nutrient availability and plankton productivity. Of course, the potential of phytoplankton growth is determined by nutrient availability. But recent evidence suggests that nutrient ratios have a profound influence on phytoplankton species composition. Shifts in phytoplankton composition can be intensified by zooplankton selective grazing. Thus the interaction between nutrient ratios, phytoplankton species composition and zooplankton grazing determine the actual biomass and production levels during summer in the coastal zone.

Diatoms are better adapted to the nutrient rich, turbulent conditions such as prevail in the coastal zone. However, the availability of silicate limits the annual diatom biomass. The nitrogen and phosphate nutrients left over enable flagellates to take over phytoplankton dominance. Since flagellates are in general smaller than diatoms, especially the small copepods and ciliates can take advantage of this food source. It implies that longer food chains are necessary to transfer the primary production to higher trophic levels compared to the shorter and therefore more efficient diatom, large copepods, fish chain. Eutrophication thus reduces the overall efficiency of the coastal food web. GREVE & PARSONS (1977) suggested that the shift towards smaller copepods might change the pelagic food web from fish as the top predators to medusae (*Pleurobrachia*) as the top predators. Since these medusa prey upon fish larvae and large copepods such food web changes would have far-reaching consequences for the fish yield of coastal areas.

If herbivores are present in large enough numbers (such as during summer) they can control phytoplankton growth. However, part of the phytoplankton induces grazer avoidance tactics, the absence of grazing allows an unbridled growth for this part of the phytoplankton. A Prymnesiophyceae which is well known for its massive blooms along the continental coasts is *Phaeocystis*. Its grazer avoidance tactic involves the formation of large colonies that cannot be preyed upon by zooplankton. If toxin production is involved in the grazer repellent tactics, such blooms can have disastrous effects on the entire ecosystem (*e.g.* fish kills, anoxia). What exactly triggers toxicity in algae is not yet clear. However, a common factor seems to be phosphate or silicate limitation in combination with excess nitrate. This was shown to induce toxicity in the three dominant classes of algae in the North Sea: diatoms, Dinophyceae and Prymnesiophyceae.

Whatever triggers grazer avoidance tactics and wherever this occurs, if such patches of algae originate in or are drifted into the eutrophic coastal zone an unbridled growth is possible. When such blooms collapse the benthic system has to cope with a sudden and large flux of fresh biomass. If the oxygen demand necessary to remineralize the organic matter exceeds the oxygen flux into the benthic system, hypoxic conditions will occur.

V.2.6 The end of the growing season

Just like the annual debut, the end of the growing season is determined by light availability. In the open North Sea, the cooling of the surface layer together with autumn storms break down the thermocline. The accompanying nutrient injection can lead in some areas to an autumn bloom of diatoms and dinoflagellates (the latter dominating the phytoplankton towards the end of the summer). Both the timing of the end of the growth season and the size of the zooplankton community at this point will have an important impact on the plankton development during the following year. The larger the zooplankton standing stock, the larger the population that will survive the winter, the larger the interaction with the spring phytoplankton bloom, the larger next years zooplankton summer population can be. A late thermocline break down will also enhance the survival of the zooplankton.

In the coastal zone, the end of the plankton season will depend on the solar radiation (cloudiness) and turbidity (sediment resuspension by wind-wave action).

V.2.7 Contaminants

In the previous paragraphs we have depicted how the plankton system is intertwined with its environment. We have mentioned the role of contaminants only if its synergistic effect on the plankton system was clear. In this paragraph we will summarize the role of contaminants in the plankton dynamics.

V.2.7.1 Antropogenic impact: pollution and eutrophication

It is not possible to distinguish the overall effects of pollutants on the ecosystem structure from the effect of increased nutrient input. Both impacts change the pelagic system in the same direction: Eutrophication changes the system from diatom dominance to flagellate dominance due to the unchanged or even enhanced silica limitation of diatoms and increased N and P levels. The same shift is to be expected from pollutants since diatoms are in general more sensitive to *e.g.* organochlorine and oil pollution.

In the zooplankton the pattern of change is comparable: specialists like *Calanus* spp. which depend on diatoms for reproduction and growth will be replaced by generalists (small species, feeding preferentially on small food items, having a higher temperature optimum, shorter generation times and needing lower critical food concentrations for attaining maximum growth and reproduction rates). This corresponds to the normal reaction of an ecosystem under stress (compare GRAY 1979) and can further be amplified by increasing temperatures, for instance caused by "global warming".

V.2.7.2 Sensitivity to pollution

The threshold concentrations at which phyto- and zooplankton organisms show measurable (short term!) changes depends on the element or compound tested and the species and life stage in question. In general, zooplankton seems to be more sensitive to metal pollution (*e.g.* Cd, Cu, Zn) than phytoplankton, and less sensitive to organochlorine pollution. However, the effects of pollution on zooplankton are always twofold: a direct toxic impact of the substance on the metabolism, and an indirect impact originating from a qualitatively and/or quantitatively altered phytoplankton community (food supply). As mentioned before, this will ultimately lead to a change in herbivore species composition and its effect will propagate up the food chain. The system is coupled by a feed-back loop: Any change in the grazer community will effect a change in the phytoplankton community.

Zooplankton as a rule has much longer generation times than phytoplankton. Any a disturbance of the zooplankton population (differential reproductive success leading to an altered community composition) will therefore have much longer lasting effects on the zooplankton community than on phytoplankton. The shorter the generation time, the better can an organism group adapt to environmental changes. However, since in the eutrophic coastal zone grazer control is very important to curtail the phytoplankton biomass (by preventing mass blooms), zooplankton population dynamics changed by pollution would on the long run also influence the phytoplankton dynamics (and the carbon flow within the system).

V.2.7.3 Seasonal variation in susceptability to pollution stress

In winter, the concentration of organochlorines (metals not known) in zooplankton is generally higher than in summer due to reduced particle concentrations in the water (less surface for adsorption). No data are available for phytoplankton, but due to the same factors as mentioned above, a stronger contamination can be expected. Therefore, pollution stress may add an additional mortality (enhanced metabolic requirements and slower growth rate in combination with continuous predation) to the light-limited phytoplankton and the food- and temperature limited zooplankton. The nauplii, which constitute considerable portions of the winter copepod biomass (HAY *et al.* 1991), are particularely vulnerable because they are slow moving, do not possess food reserve capacities and are highly susceptible to pollutant stress. It should be remembered that the zooplankton stock surviving the winter determines to a large extent the potential peak density of both the phyto- and zooplankton during the following summer.

In summer on the other hand, the population density is much higher compared to the winter levels. The turnover rates are increased, and mortality by predation is high, so that an additional mortality or a reduction in feeding, growth and reproduction due to pollutant impact will not play a significant role in the system at large compared to the natural impacts. However, locally changed zooplankton dynamics can reduce its control over the phytoplankton giving way to sudden (and in the coastal zone large) phytoplankton blooms.

V.2.7.4 Atmospheric contamination

The subject of climatic change has already been discussed in the previous paragraphs. The general effect of atmospheric contamination is:

(1) The distribution of air borne pollutants over a large area.
(2) Enhanced N input.
(3) Acidification of the sea water.

The increased N input will effect an enhanced flagellate growth in the N-limited central and northern North Sea (OWENS *et al.* 1990). It also adds to the high N/P ratios that prevail in the coastal area and possibly increase the potential of toxic blooms.

The acidification has the same effect of enhancing the diatom⇒flagellate shift through an enhanced copper toxicity and reduced silica remineralization rates.

As far as pollutants are concerned, it is difficult to assess their effect on the plankton system. It should, however, be considered that atmospherically borne contaminants can reach the open North Sea, where the suspended matter concentrations are extremely low. Therefore, the impact on the biological particles in these remote areas can be higher compared to the suspended matter rich coastal zone.

V.3 WHAT IF.....?

In the previous chapter we have presented our view on how the North Sea plankton system works and is intertwined with its physical and chemical environment. In this chapter we will restructure the above presented ideas with respect to the question how the plankton system might react to environmental change. Our "answers" should not be interpreted as predictions of what will happen. It is an attempt to structure the available information. On the basis of this information we speculate on how

Table V.1: *Possible effects of increased storminess on the North Sea plankton community.*

	Winter	Spring	Summer
Central stratified	lower light availability (increased mixing) ⇩ lower phytopl. st. stock ⇩ lower survival zoopl. (little/no reproduction)	retarded, shorter phytopl. bloom ⇩ less grazing increased sedimentation less pelagic remineralization	enhanced diatom blooms ⇩ enhanced sec. production ⇩ shorter food chains (higher fish yield)
Coastal mixed	lower light availability (higher susp. matter) ⇩ lower phytopl. st. stock ⇩ lower survival zoopl (little/no reproduction)	retarded phytopl. bloom	

the plankton system might react to changes in their environment being fully aware that:

(1) our understanding of how the plankton system reacts to perturbations is still very limited.

(2) any a prediction in a non-linear system has only a limited value.

V.3.1 Nutrients

The present nutrient trends are: decreasing phosphate concentrations, with possibly increasing nitrate concentrations and decreasing silicate concentrations. The present biological reaction on this trend is that despite the decreasing phosphate input into the presumably phosphate-limited coastal zone the annual productivity remains high. It has been suggested hat the increased N/P ratio has changed the phytoplankton composition towards less edible species, thereby allowing part of the phytoplankton to escape grazer control and to reach high biomasses. The possible influence of high N/P and N/Si ratios is demonstrated by some algae in which toxicity is triggered by phosphate or silicate limitation in combination with high nitrate concentrations. It can be speculated that a continuing reduction of phosphate input without a simultaneous nitrogen reduction may drive the phytoplankton towards unpalatable species. This would uncouple the phytoplankton from grazer control initiating a highly variable and sometimes massive carbon flux to the benthic system far beyond what it can cope with. It is needless to say that restoring the N/P ratio by increasing the phosphate load is not the way to solve the present eutrophication problem.

Any measures in the fresh water system that enhance blooms aggravate the marine eutrophication problem by reducing the Si flux into the sea since Si is remineralized slower than N and P compounds. Enhanced fresh water blooms will thus reduce marine diatom growth and stimulate marine flagellate growth and the danger of large and sometimes toxic blooms. For instance, the construction of weirs in rivers for an increased accessability of rivers for larger ships will also increase the residence time of phytoplankton, allowing larger blooms.

It is a cynical aspect of our environmental concern that the reduced toxicity in some fresh water systems like the Rhine river - an as such very positive feat - seems to stimulate fresh water diatom growth thereby aggravating marine eutrophication problems by consolidating marine flagellate growth.

V.3.2 Climate

There is still a large uncertainty on how global climatic change will exactly affect the local weather conditions in western Europe. However, three factors are often mentioned (*e.g.* Goodness & Palutikof 1990):

(1) increased storminess,

(2) increased temperatures and

(3) increased precipitation

To discuss all the possible combinations of climatic change on the plankton dynamics is beyond the scope of this review. Moreover, the available knowledge does not allow more than general estimates of what might happen to the plankton ecosystem under certain climatic conditions. The next paragraphs should therefore be seen as a first attempt to structurize the available information on climate-plankton interaction.

V.3.2.1 Increased storminess

In Table V.1 we have summarized the possible effects of increased storminess (increased mixing) on the plankton community. One of the major problems in interpreting these effects on the overall functioning of the system is the fact that the phytoplankton, the zooplankton and their interaction react upon changed environmental conditions on different time scales. Whereas the reaction of phytoplankton is immediate, the zooplankton reacts much slower because of its longer generation times. Thus changes in the zooplankton are characterized by a certain degree of persistency: Its population structure and therefore its interaction with the phytoplankton has a memory effect.

For the open North Sea the effect of changed mixing characteristics can be predicted with some probability when the change takes place only during one season: However, depending on which season, the effect on the plankton system can be almost opposite: Whereas increased mixing in winter and spring results in a retarded phytoplankton growth, in an uncoupling of phyto- and zooplankton productivity and in a shift in the carbon flow from the pelagial to the benthos which ultimately leads to a diminished phytoplankton production during the summer, the opposite occurs when the increased mixing takes place during the summer in which case an increased plankton production can be expected. Thus the combination of increased winter and spring mixing (a late, short, intense spring bloom and subsequent sedimentation) in combination with a decreased summer mixing would shift the the energy flow from the pelagial to the benthos. However, to predict the overall effect of altered mixing during more than one season when opposite effects are involved (like decreased winter mixing, increased spring mixing and unchanged summer mixing) is very difficult. Here the development of conceptual models could be of great value.

V.3.2.2 Temperature changes

In Table V.2 the effects of a changed temperature regime are listed. In general, decreasing temperatures will uncouple the phyto-zooplankton system because of the temperature limited growth of zooplankton. It will reduce the pelagic productivity. Increased temperatures will tighten the phyto-zooplankton coupling resulting in a higher pelagic productivity. Higher temperatures will speed up the nutrient cycles. This will shift the phytoplankton community towards flagellate dominance.

When interpreting the information on climate-plankton interaction we should be aware that only in a limited number of cases this interaction is of a linear type. Mostly we are dealing with strongly non-linear relations like the interaction between phytoplankton and grazers. Also one should bear in mind that whereas phytoplankton reacts almost immediately to changing environmental conditions, the zooplankton community is much slower in its reaction. Moreover, its reaction to environmental change shows some degree of persistency. All this reduces the predictability of the plankton system (if such predictability exists at all). Therefore, tendencies are maybe a better expression for the above-mentioned forecasts.

V.3.2.3 Precipitation

One of the possible consequences of global warming is an increased precipitation. This will cause a lower salinity and higher nutrient concentrations in the coastal zone. The coastal ecosystem seems to be particularly sensitive to an increased river discharge during summer (GIESKES & SCHAUB 1990, HICKEL 1993) According to GIESKES & SCHAUB (1990) an increased river discharge (and hence an increased nutrient discharge) will lead to a higher phytoplankton biomass. However, an increased river flow will also increase the N/P ratio (CADÉE 1992b, HICKEL 1993) since nitrogen nutrients are washed from soils more easily than phosphate. As already discussed above, this might drive the plankton community towards less edible phytoplankton species, giving way to uncontrolled blooms. Consequences for the coastal ecosystem include a shift in the carbon flow from the pelagic to the benthos, a higher variability of the carbon flow including an increased danger of anoxic conditions and a less efficient coupling between primary and secondary production.

Table V.2: *Possible effects of increased temperature differences (identical winter temperatures, higher summer temperatures) on the North Sea plankton community.*

	Winter	Spring	Summer
Central stratified		earlier, slower phytopl. bloom (less light) ⇩ enhanced grazing enh. pelagic remineralization flagellate ⇒ diatom shift ⇩ short food chains increased fish yield	enhanced stratification faster cycles enh. nutrient limitation ⇩ diatom ⇒ flagellate shift ⇩ long food chains (lower fish yield)
Coastal mixed		faster cycles ⇩ diatom ⇒ flagellate shift ⇩ long food chains (lower fish yield)	faster cycles ⇩ diatom ⇒ flagellate shift ⇩ long food chains (lower fish yield)

V.4 RISK EVALUATION

Eutrophication is the major threat for our coastal ecosystem. The past decades of marine eutrophication have loaded the coastal zone with nutrients enabling a higher primary production. Subsequently, secondary production probably increased. The large growth potential for the phytoplankton can, however, turn into a major threat for the ecosystem if the phytoplankton cannot be eaten by herbivore zooplankton (for instance the recent *Phaeocystis* blooms): The threat is caused by decaying phytoplankton blooms, which suddenly can supply more organic matter than can be coped with by the ecosystem. This will give way to anoxic conditions.

Future threats are caused by the increasing N/P and N/Si nutrient ratios which seems to shift the phytoplankton community towards unpalatable species giving way to large, uncontrolled phytoplankton blooms. This threatens the coastal benthic ecosystem in the same way as mentioned above: anoxia. Toxic blooms can have disastrous ecological and economic consequences as has been shown by the recent *Chrysochromulina* bloom.

Climatic change Our knowledge of the interaction between the plankton and the physical environment is at present too little to make exact predictions on what will happen under certain scenarios of climatic change. However, an overall increased storminess threatens to uncouple the phyto- and zooplankton seasonal cycles through reduced winter survival of the zooplankton. This will reduce the overall productivity of the pelagic system and shift the North Sea ecosystem from pelagic production to benthic production.

Enhanced temperatures will enhance flagellate dominance. In combination with coastal eutrophication noxious or even toxic blooms occur.

Enhanced precipitation will increase the N/P and N/Si ratio in the coastal zone, affect the phytoplankton population and increase the danger of noxious or even toxic blooms.

Contaminants are at present no direct threat to the plankton at large. However, it should be borne in mind, that the overall effect of contaminants is to enhance flagellate growth and to uncouple phytoplankton growth from grazer control. Contamination thus aggravates the impact of eutrophication on the marine ecosystem. Locally, oil pollution can form an important threat to the plankton system .

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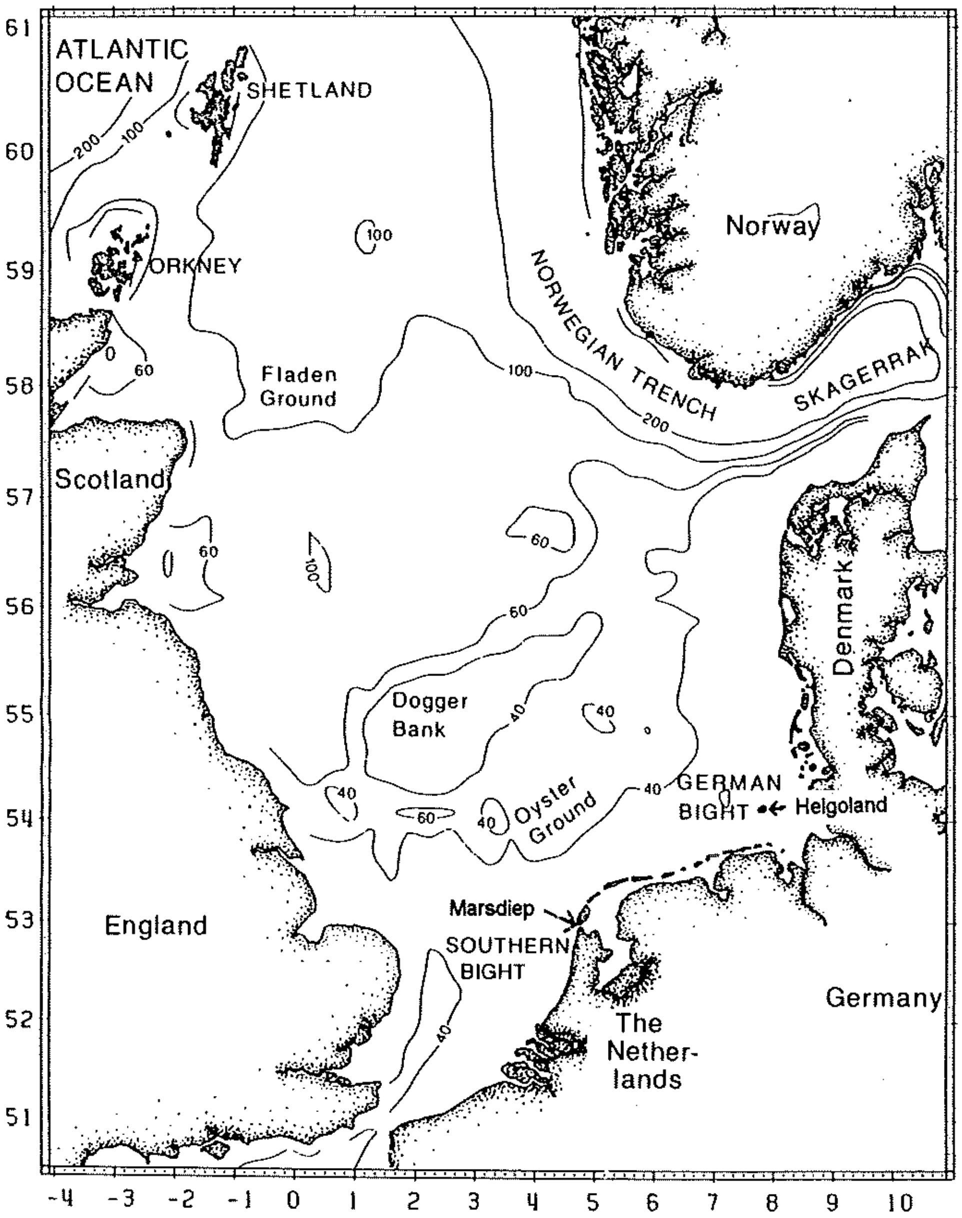


Fig. I.1 Geography of the North Sea.

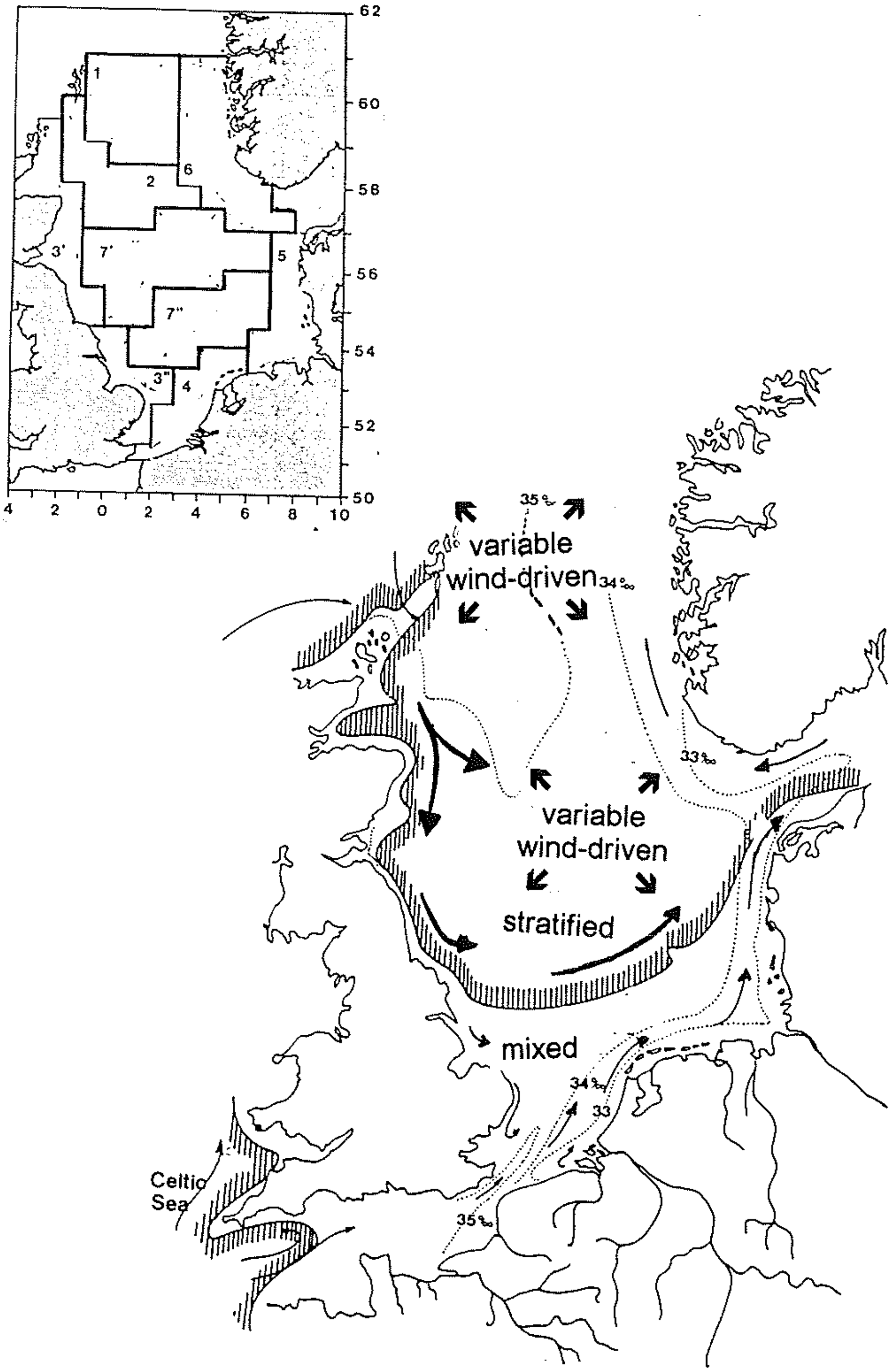


Fig.I.2 Hydrography of the North Sea.

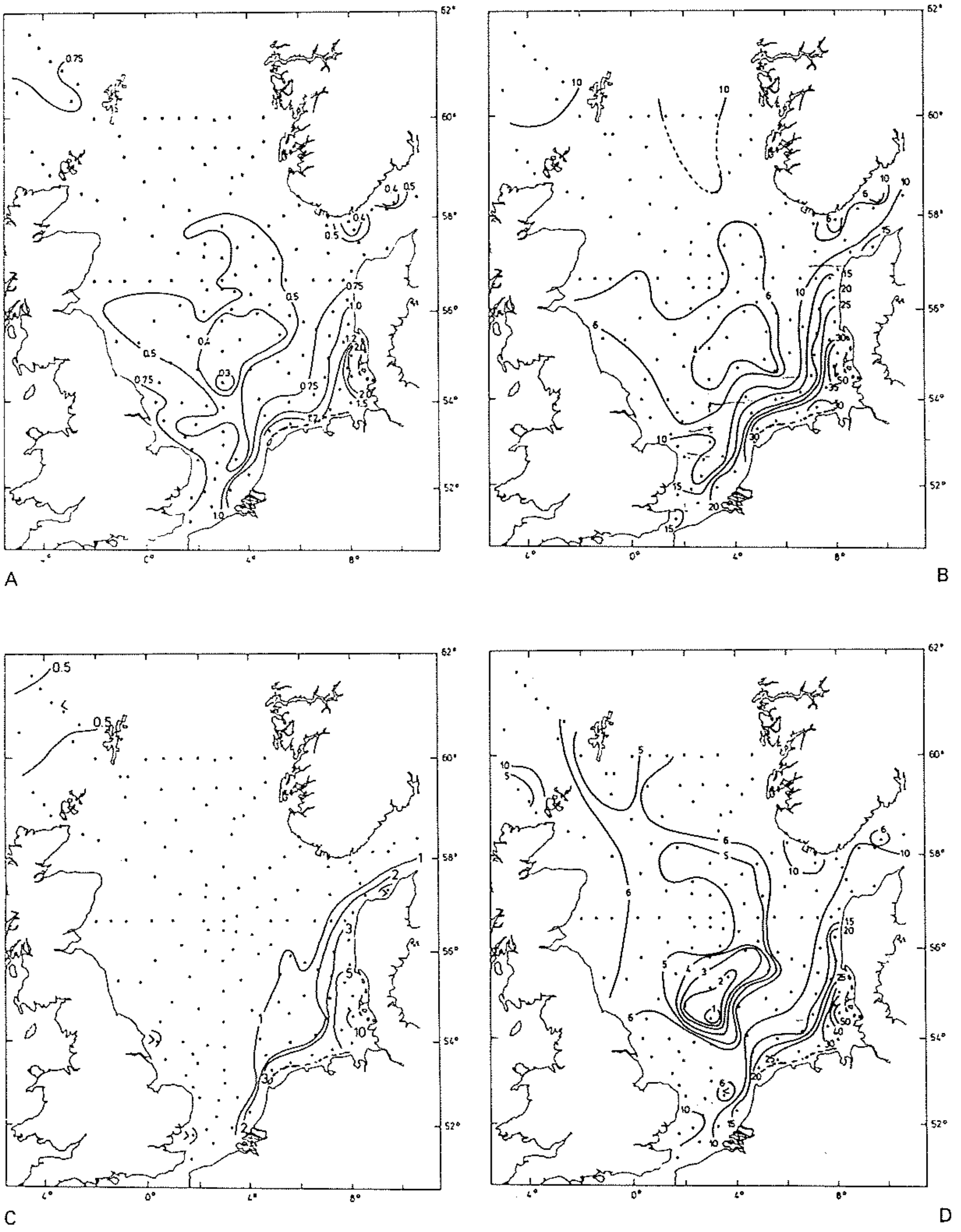
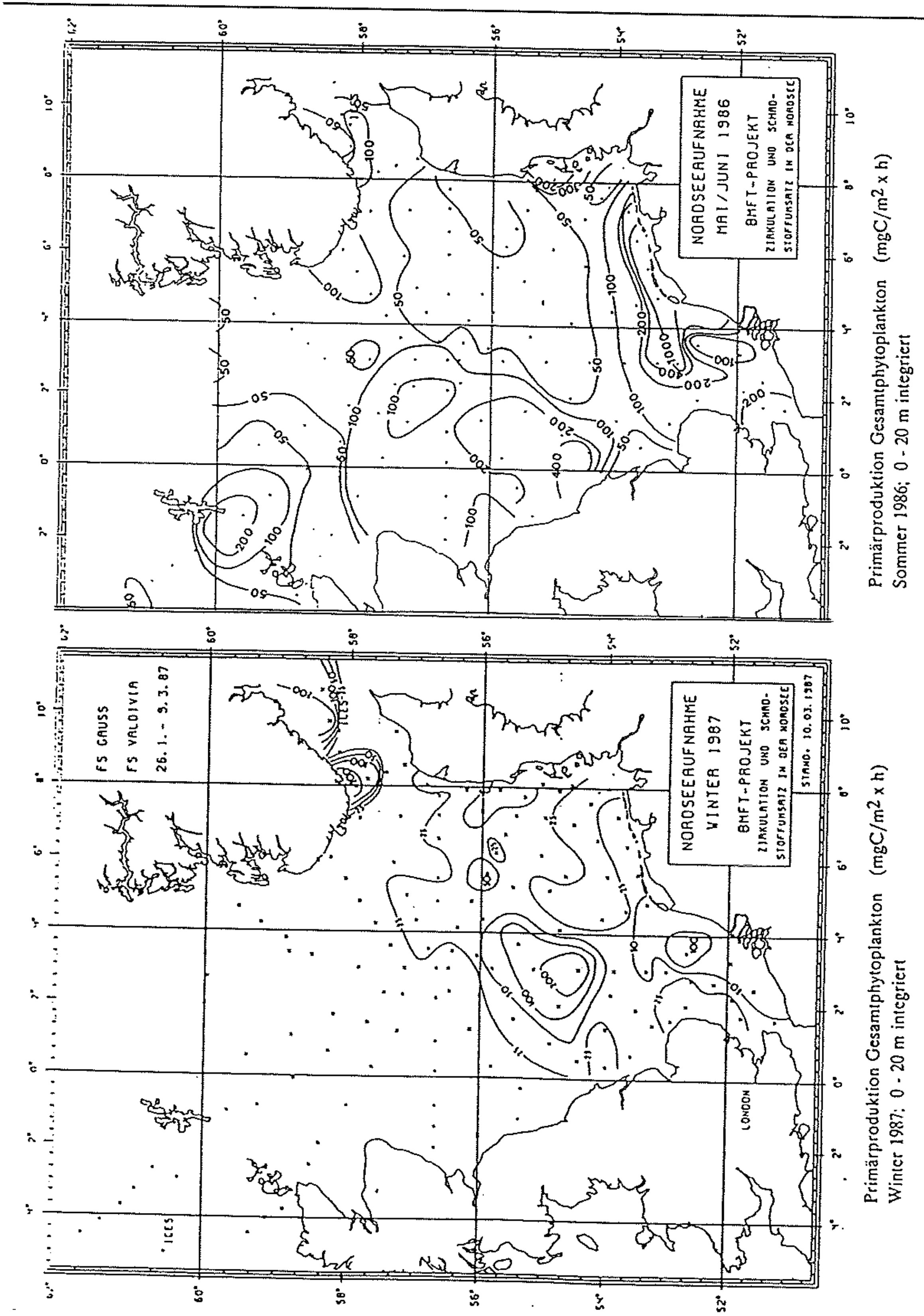


Fig. I.3 Surface distribution (5 m) of dissolved phosphate (A), nitrate+nitrite (B), ammonium (C) and silicate (D) during January-March 1987. (From BROCKMANN *et al.* 1990)



Primärproduktion Gesamtphytoplankton (mgC/m2 x h)
Sommer 1986; 0 - 20 m integriert

Primärproduktion Gesamtphytoplankton (mgC/m2 x h)
Winter 1987; 0 - 20 m integriert

Fig. II.1 Distribution of phytoplankton primary production (mgC m^{-2} hr^{-1}) during winter (A) and summer (B). (From RICK 1990)

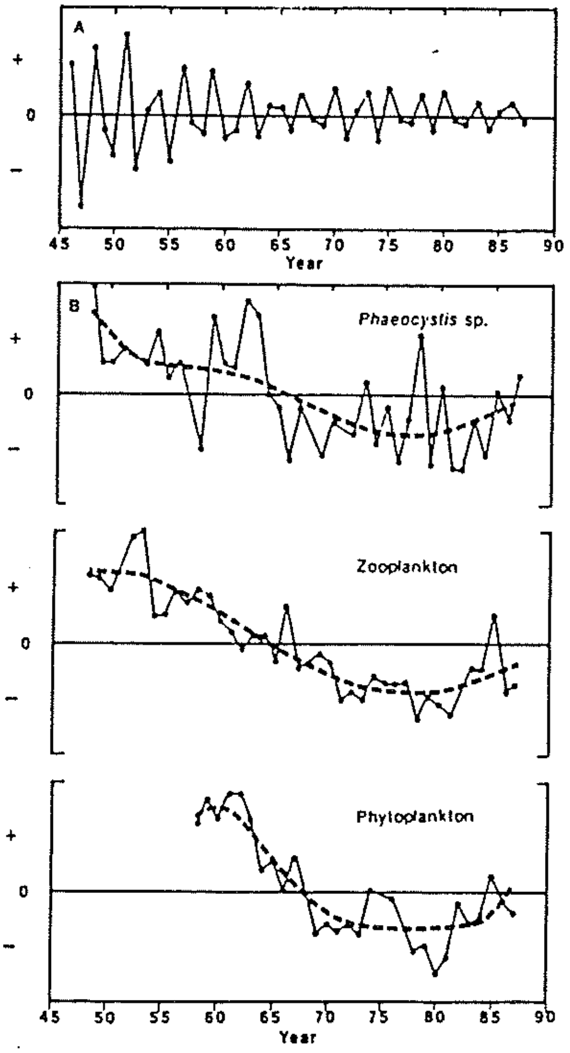


Fig. II.2 Long-term trends of *Phaeocystis*, phytoplankton (23 species) and zooplankton in the north-east Atlantic and North Sea. (From OWENS *et al.* 1989)

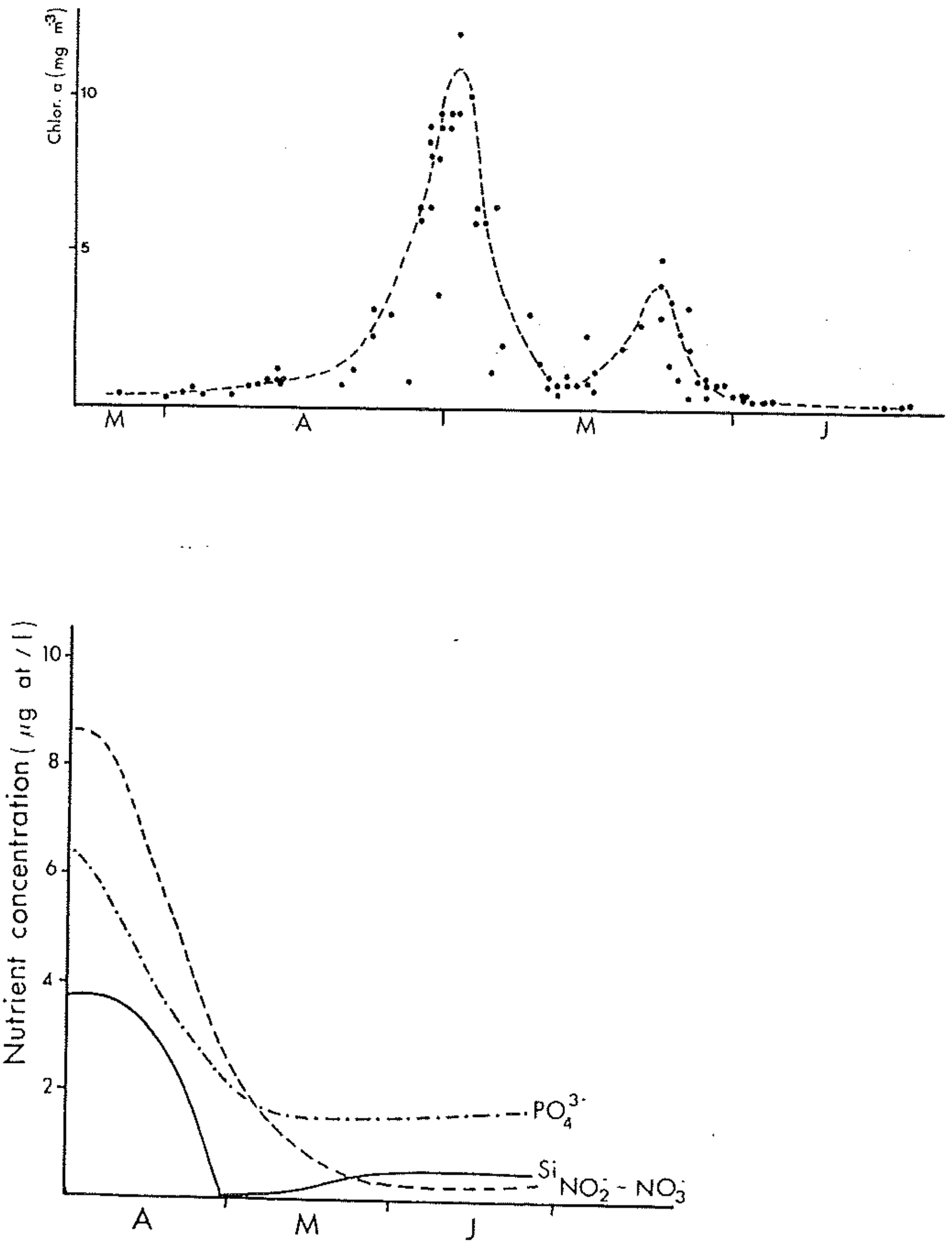


Fig. II.3 Evolution of the Chlorophyll *a* and of themajor nutrients in the euphotic zone during the Fladen Ground Experiment. Units for P: x10^{-1}. (From MOMMAERTS 1980).

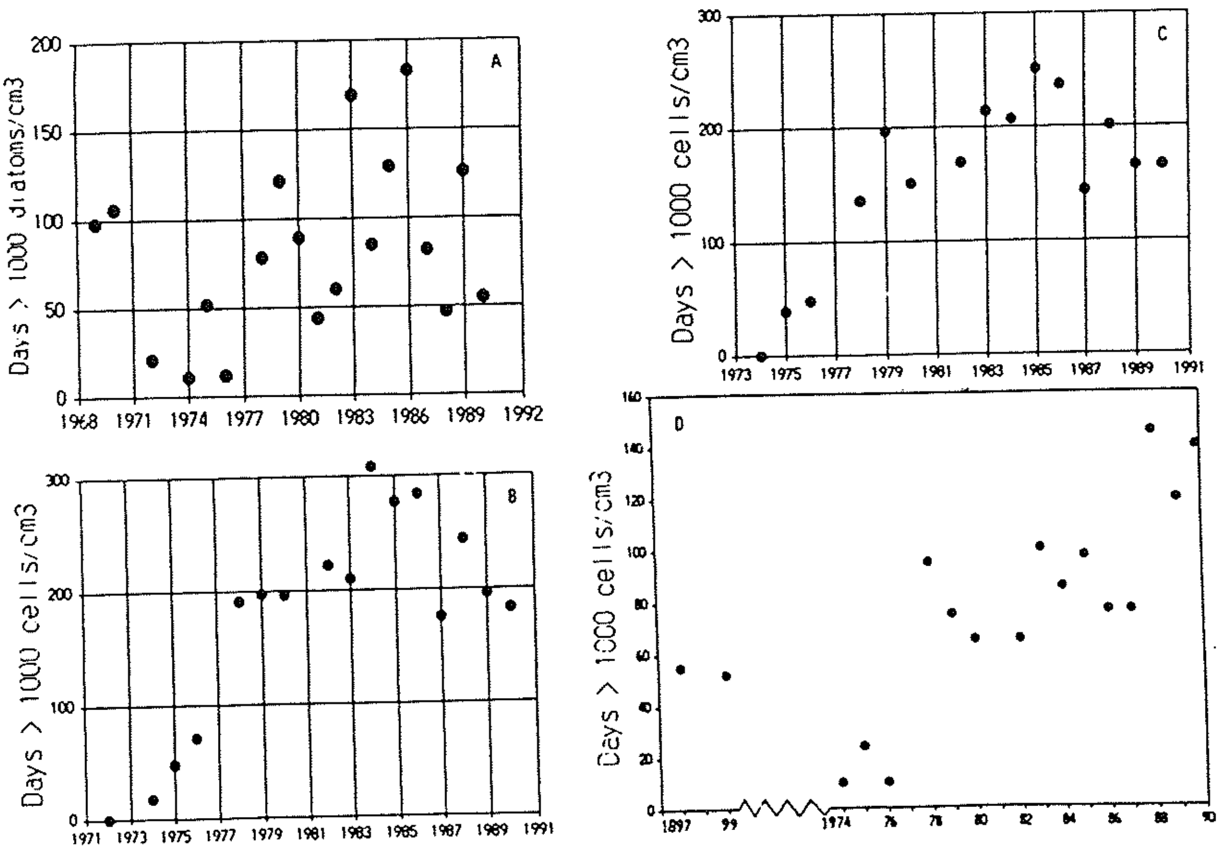


Fig. II.4 Length of "algal blooming periods" (days with cell numbers exceeding 1000 cells ml^{-1}in the Marsdiep for the different years. A = diatoms, B = all non-diatoms, C = non-diatoms minus *Phaeocystis* and D = only *Phaeocystis* and including historical data of CLEVE (1898-1900). (From CADÉE 1992a).

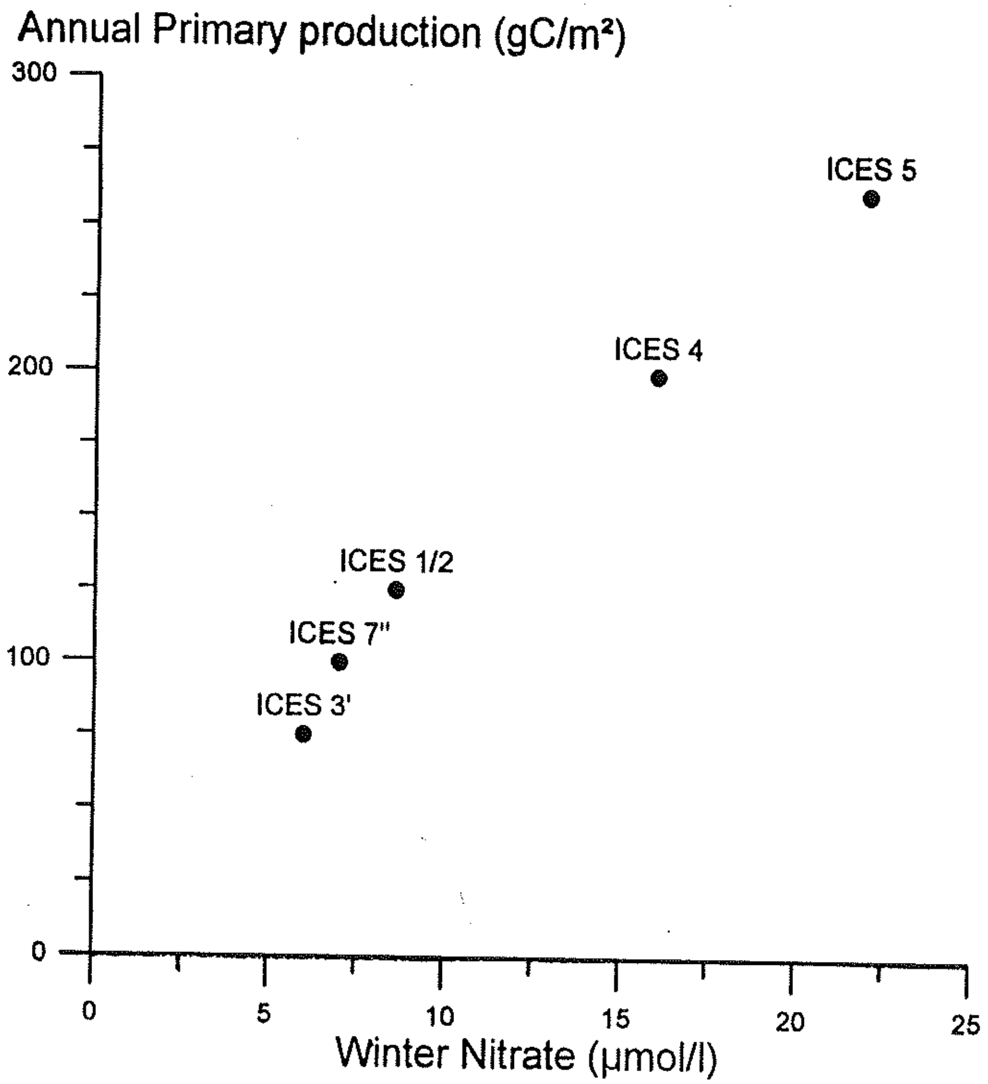


Fig.II.5 Relation between annual primary production and winter nitrate concentrations in the North Sea.

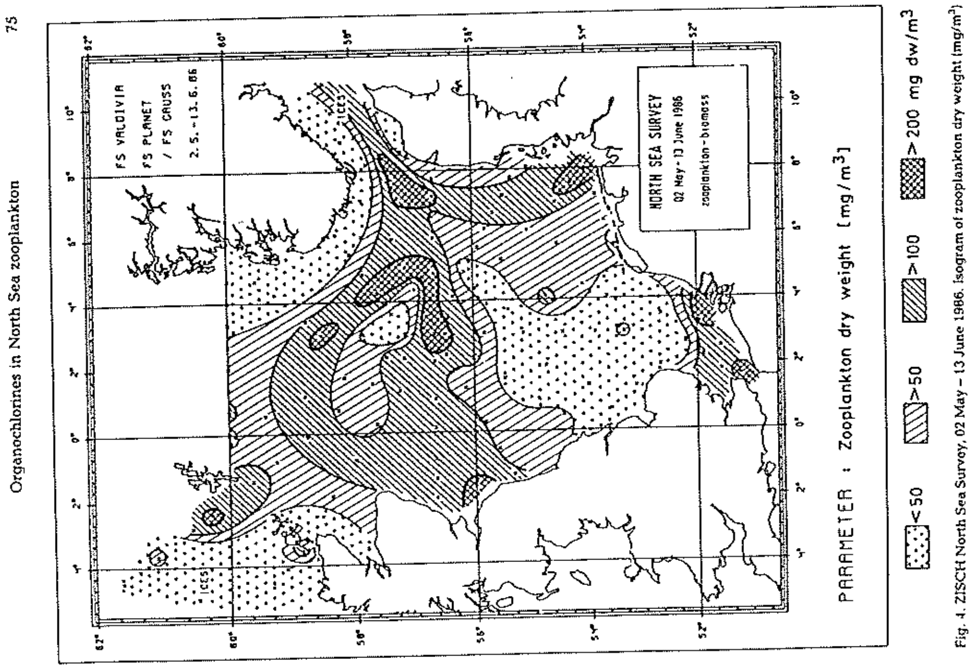


Fig. 4. ZISCH North Sea Survey, 02 May – 13 June 1986. Isogram of zooplankton dry weight (mg/m³)

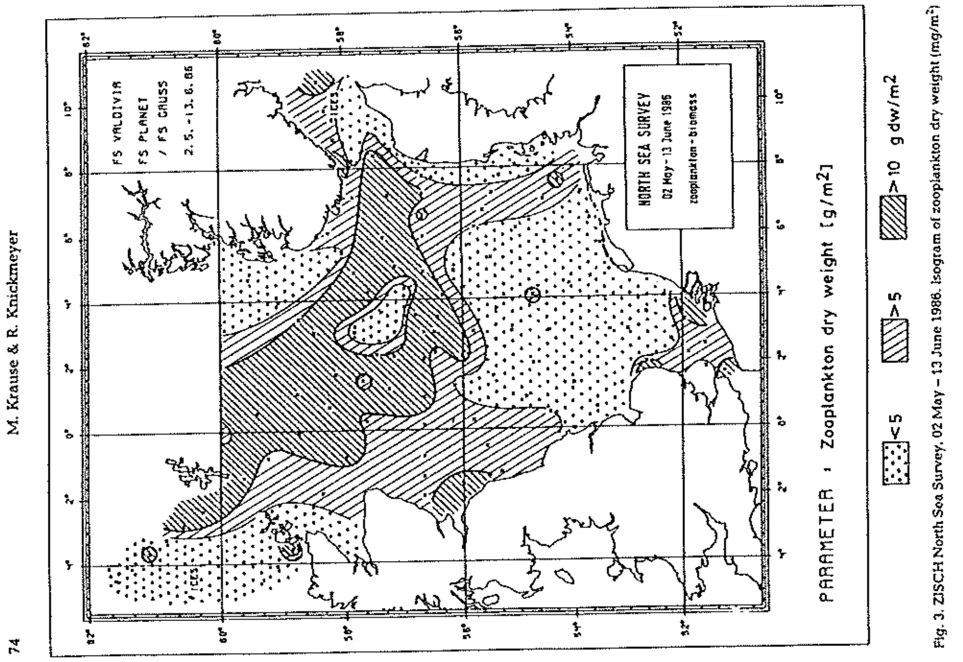
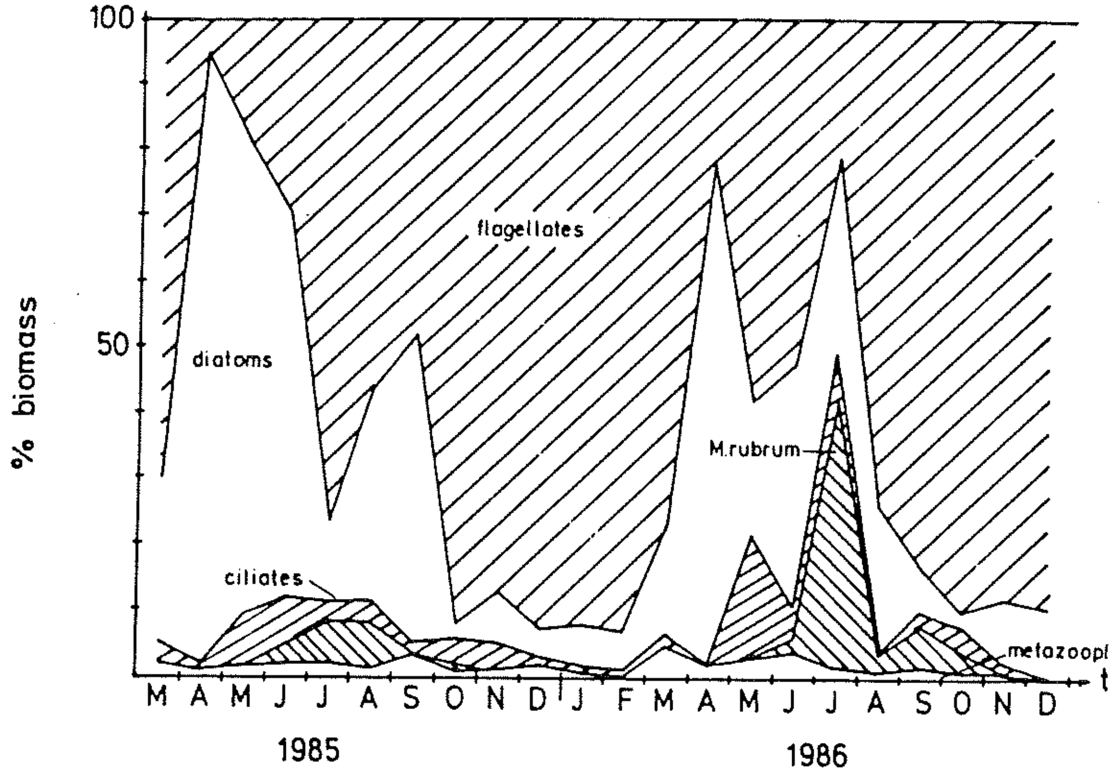
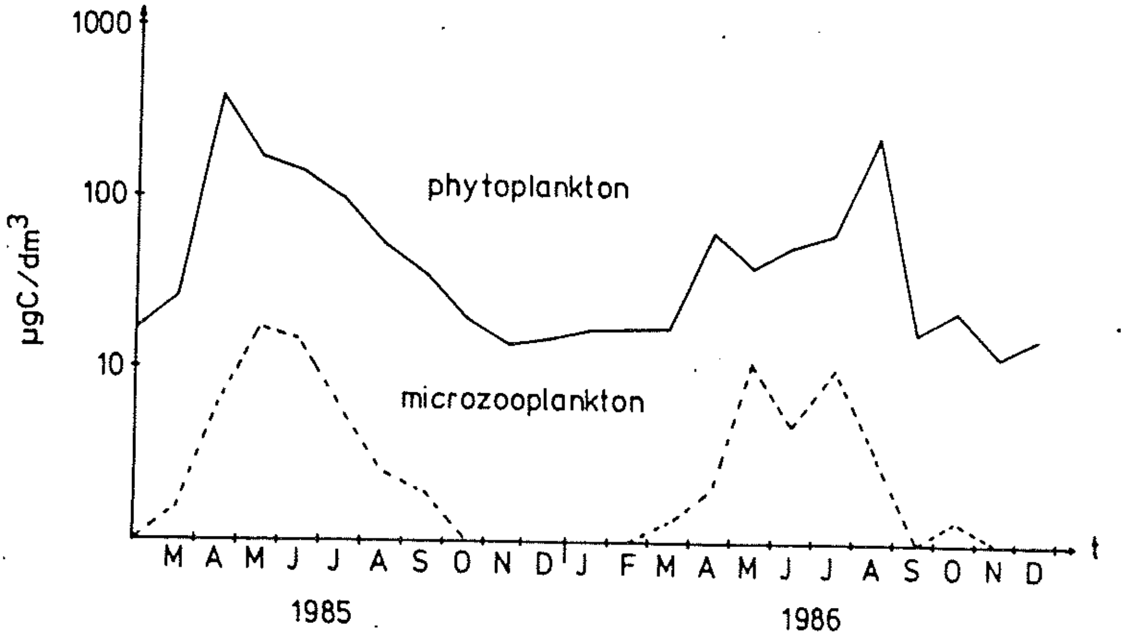


Fig. 3. ZISCH North Sea Survey, 02 May – 13 June 1986. Isogram of zooplankton dry weight (mg/m²)

Fig.III.1 ZISCH North Sea survey, 02 May - 13 June 1986. Isograms of zooplankton dry weight (a.: mg m^{-2} , b.: mg m^{-3}). (From KRAUSE & KNICKMEYER 1992).





Figs. III.2/3 Phyto- and microzooplankton biomass between March 1985 and December 1986 at Helgoland; mean monthly values. (From STEIFF 1988).

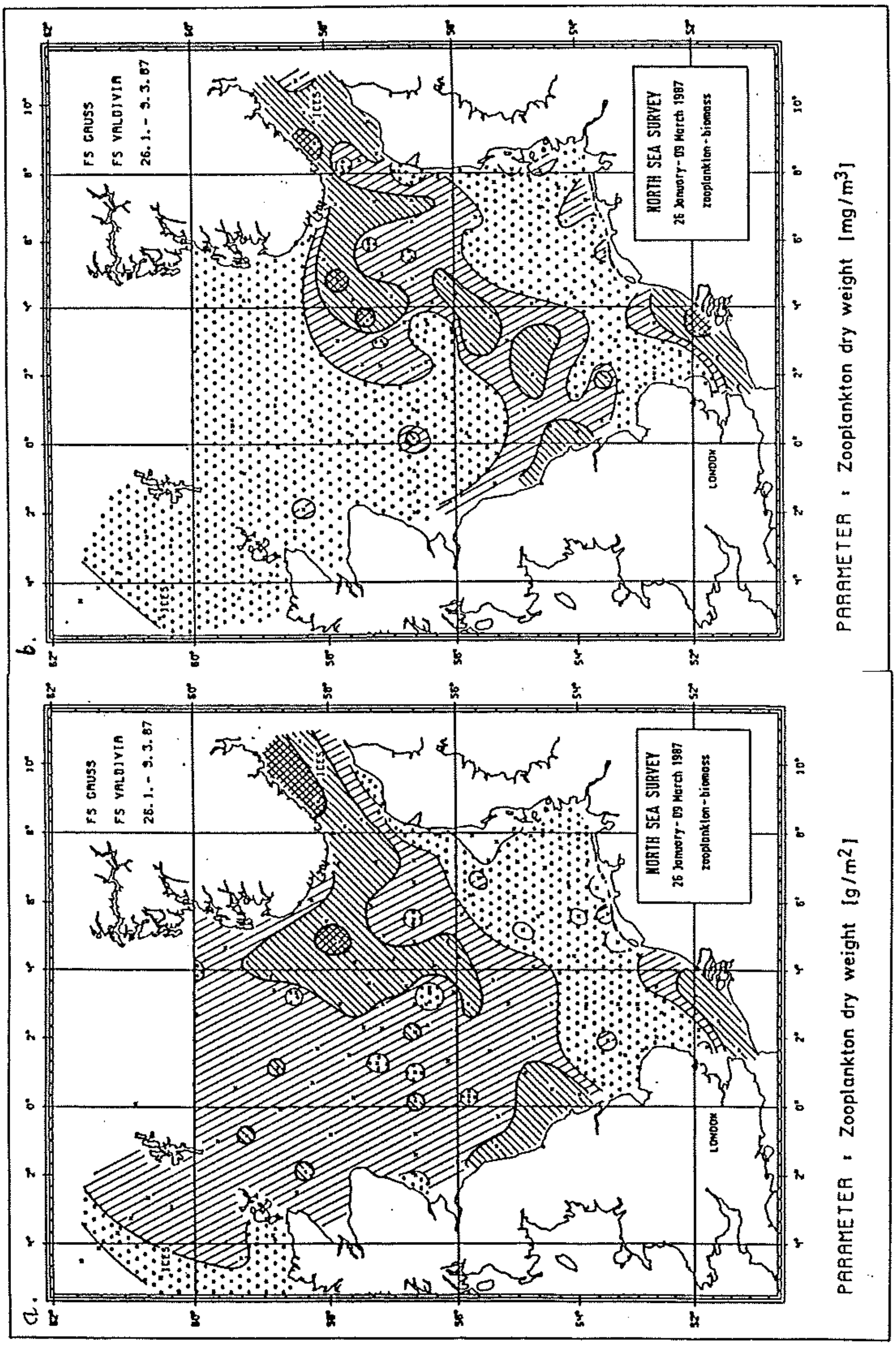


Fig. III.4 ZISCH North Sea survey, 26 January to 09 March 1986. Isograms of zooplankton dry weight (a.: mg m^{-2}, b.:mg m^{-3}). (From KRAUSE *et al.* in prep.).

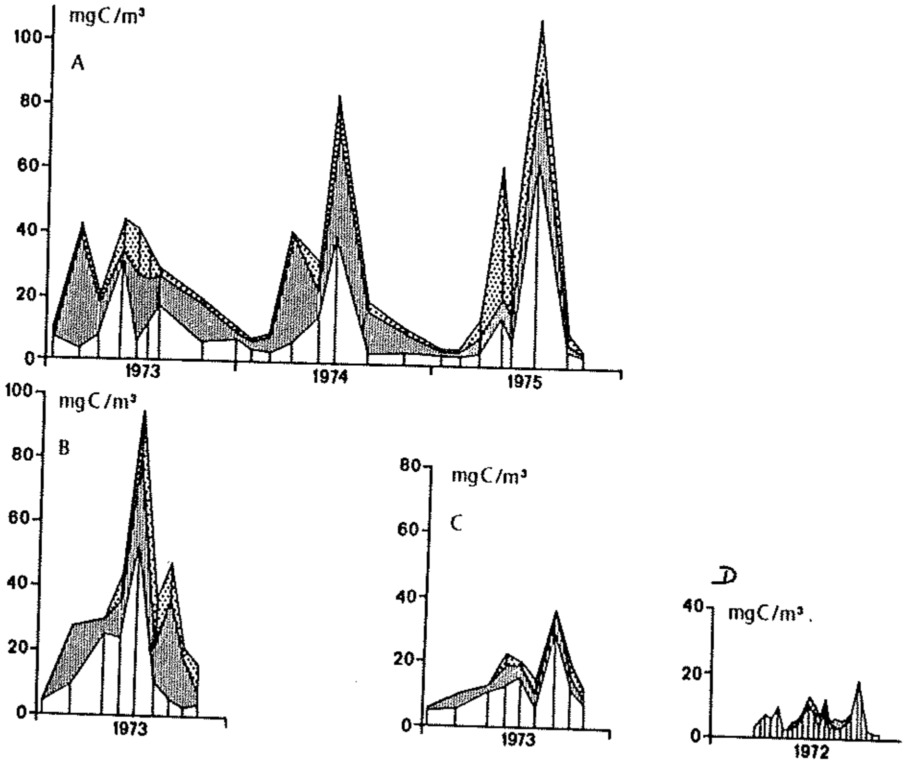


Fig. III.5 Biomass in mg carbon m^{-3} of copepods (white), polychaete larvae (hatched) and other herbivores (dotted). a. Mean values for the western Dutch Wadden Sea during three consecutive years 1973-1975; b. Mean values for a nearshore area of the North Sea between Vlissingen and Den Helder in 1973; c. Mean values for a more offshore area of the North Sea, beyond 30 km off the Dutch coast in 1973; d. Values for the North Frisian Wadden Sea near List at Sylt according to HICKEL (1975) in 1972. The vertical bars indicate sampling dates. (From FRANSZ 1980b).

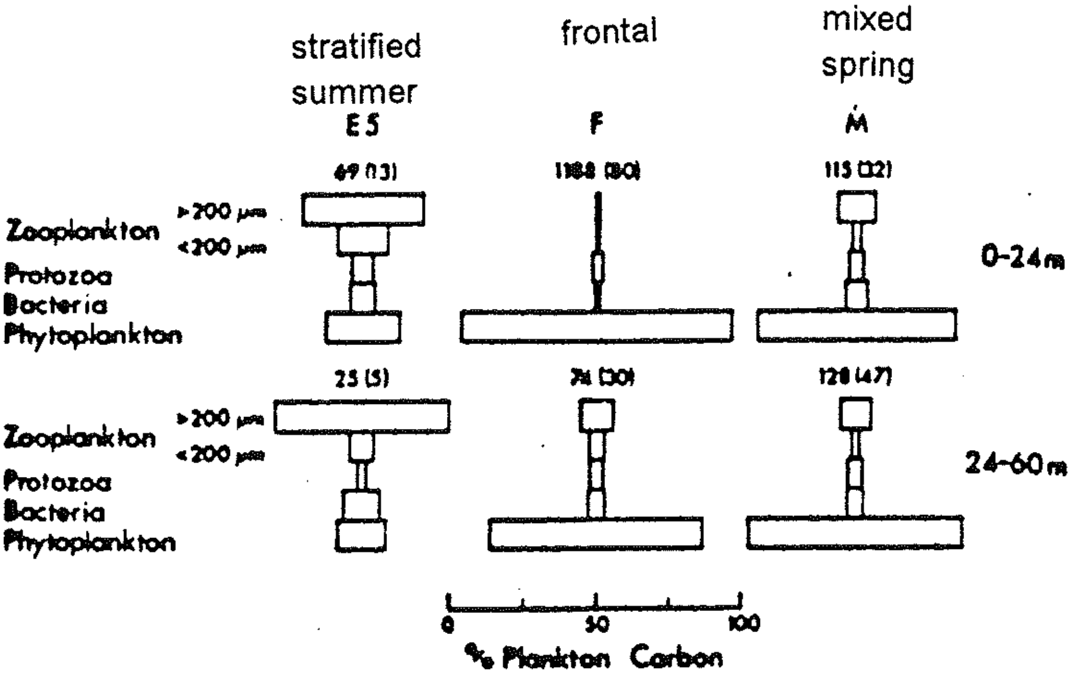


Fig. III.6 Relative distributions of organic carbon in zooplankton, protozoans, bacteria and phytoplankton in the 0-24m and 24-60 m layers at the stations E5 (stratified), F (frontal) and M (mixed) in the western English Channel. (From HOLLIGAN *et al.* 1984).

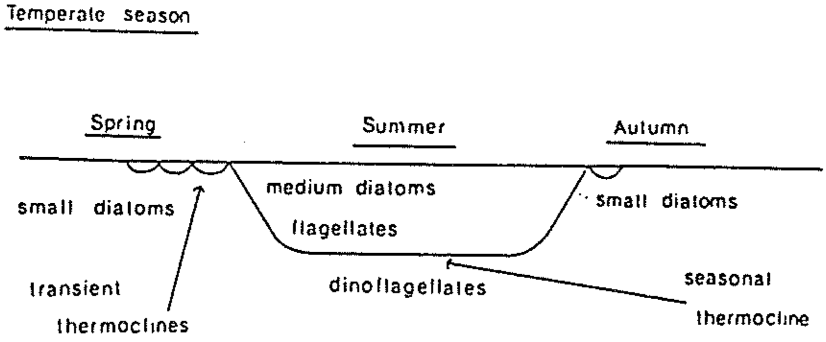


Fig. III.7 The seasonal production structure in temperate seas; production in spring and autum occurs in turbulent waters along the traditional food chain, production in summer is in a quasi-steady state, diversity is increased and the relationships in the food web more complex. (From CUSHING 1990).

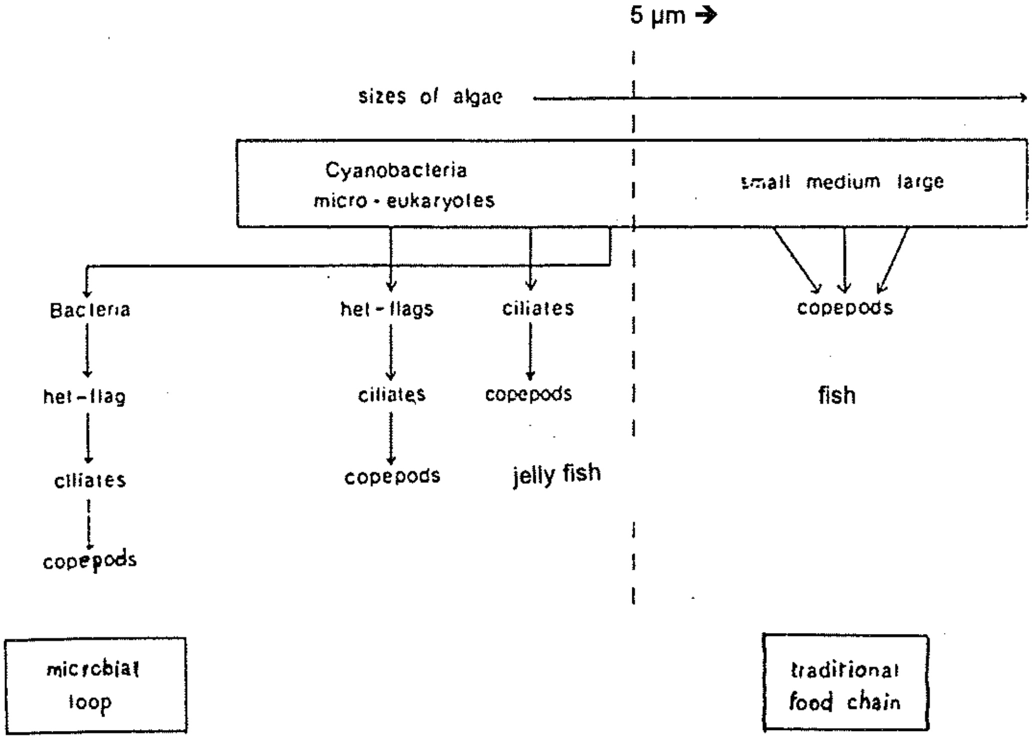
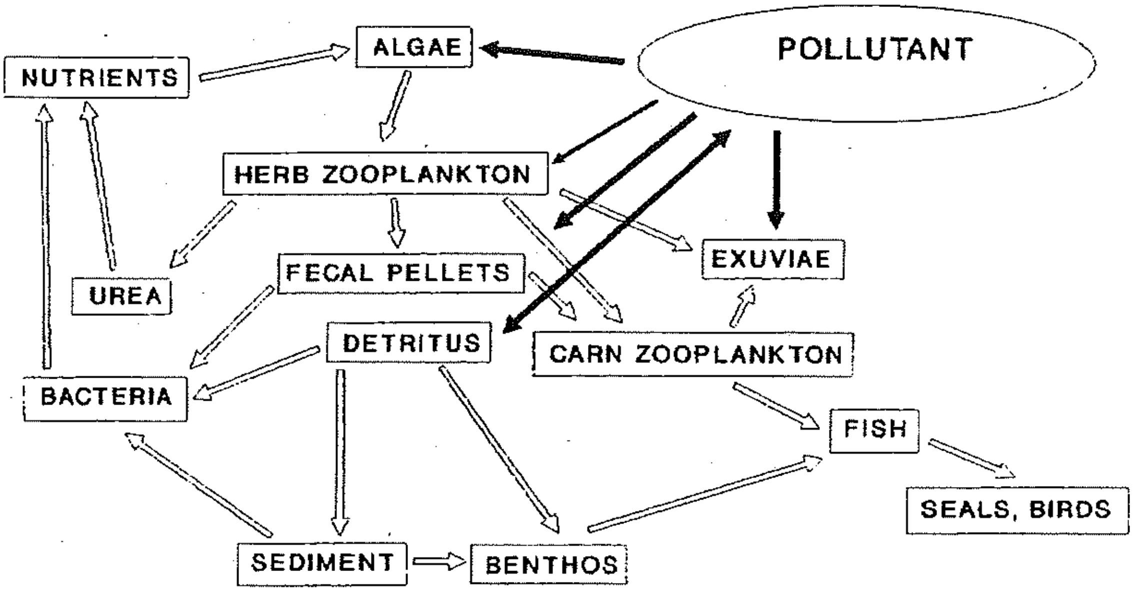


Fig. III.8 The structural difference between the microbial loop and the traditional food chain. (From CUSHING 1990).

THE MOST IMPORTANT PATHWAYS OF TRANSPORT OF CONTAMINANTS IN THE FOOD WEB



⇨ **indirect input**

➔ **direct input**

Fig. IV.1 Major pathways of contaminants in the marine food web.

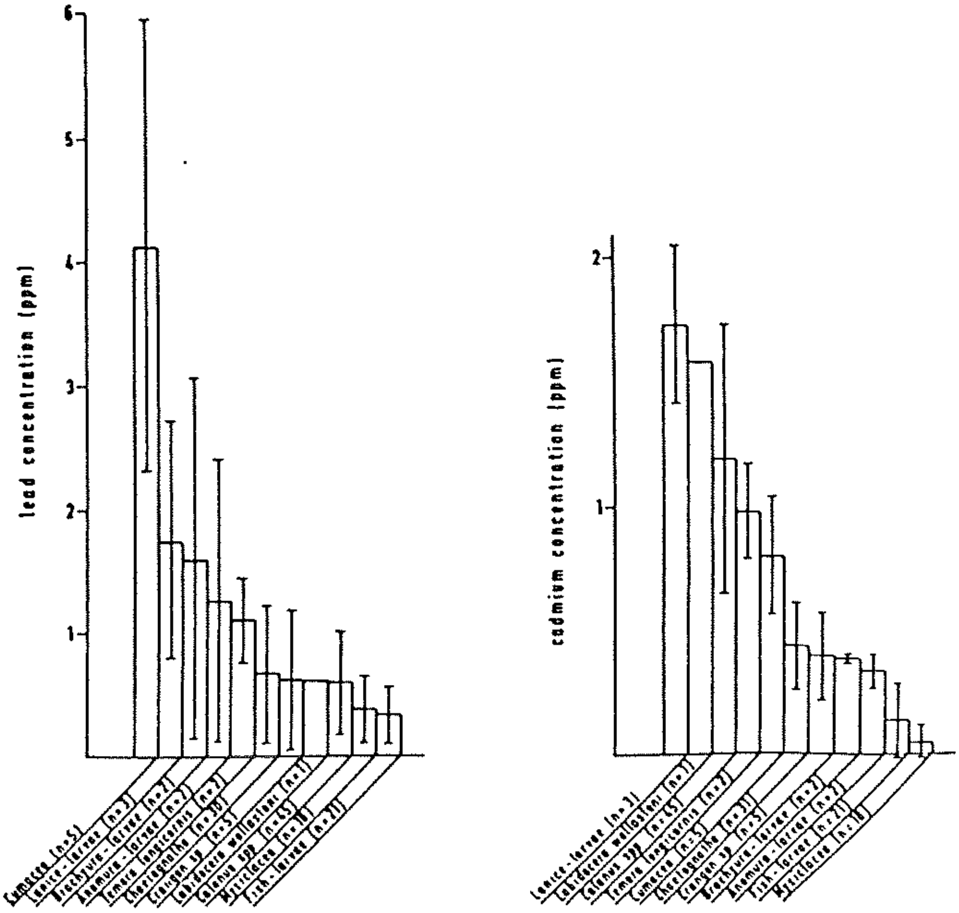


Fig. IV.2 Concentration of lead (left) and cadmium (right) in various zooplankton taxa, sampled in the German Bight between December 1988 and May 1989. Mean values and standard deviations (From HEYER et al. 1994).

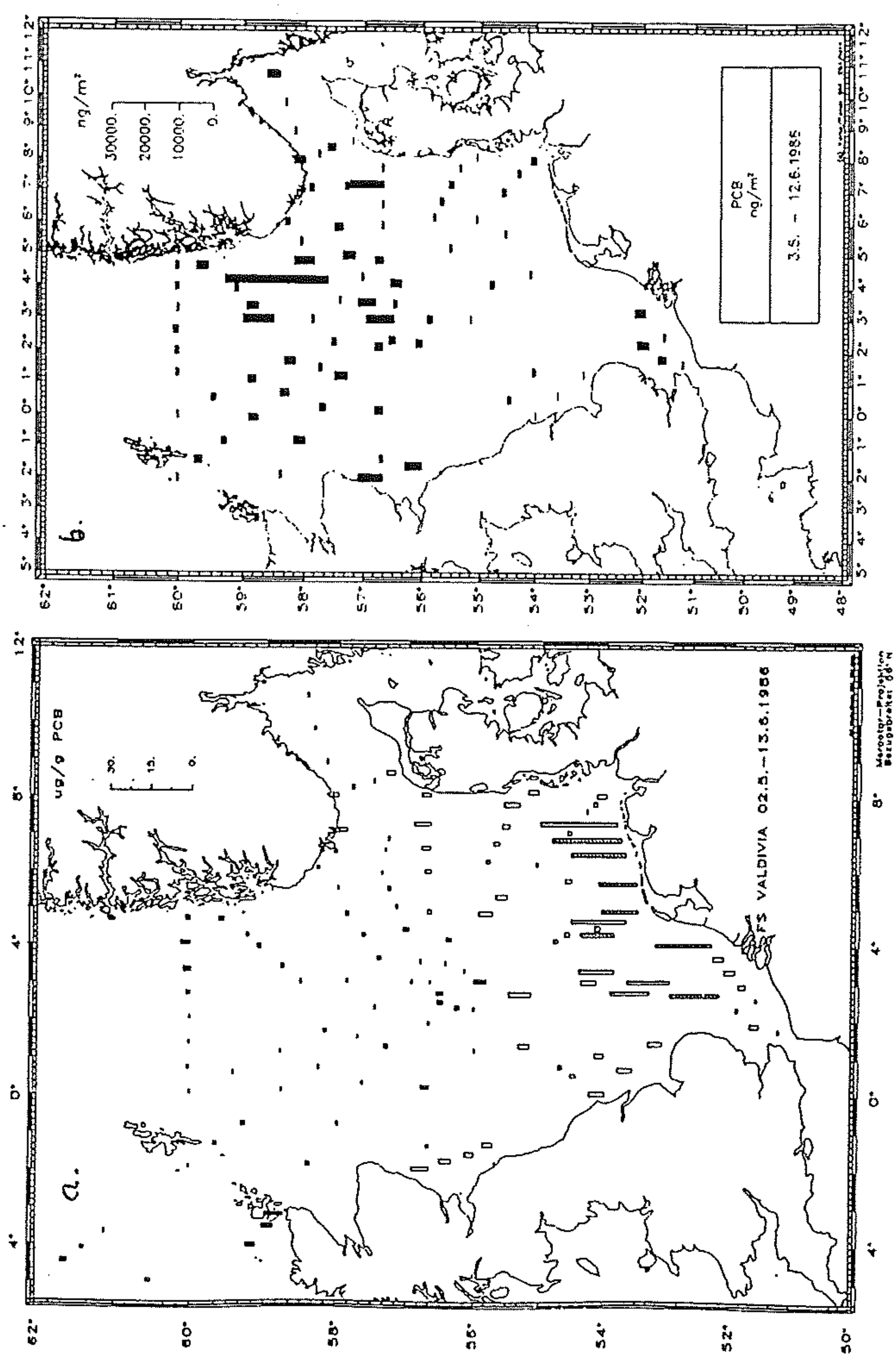


Fig. IV.3 Concentrations (a) and load (b) of ΣPCB in plankton of the North Sea: = samples dominated by *Calanus finmarchicus*, = samples dominated by *Temora longicornis*, ... = samples dominated by *Phaeocystis globosa*. Concentrations in ng g^{-1} n-hexane-extractable lipid, measured by the scale bar at top right of the chart (a: from KNICKMEYER & STEINHART 1989, b: from KRAUSE & KNICKMEYER 1992).

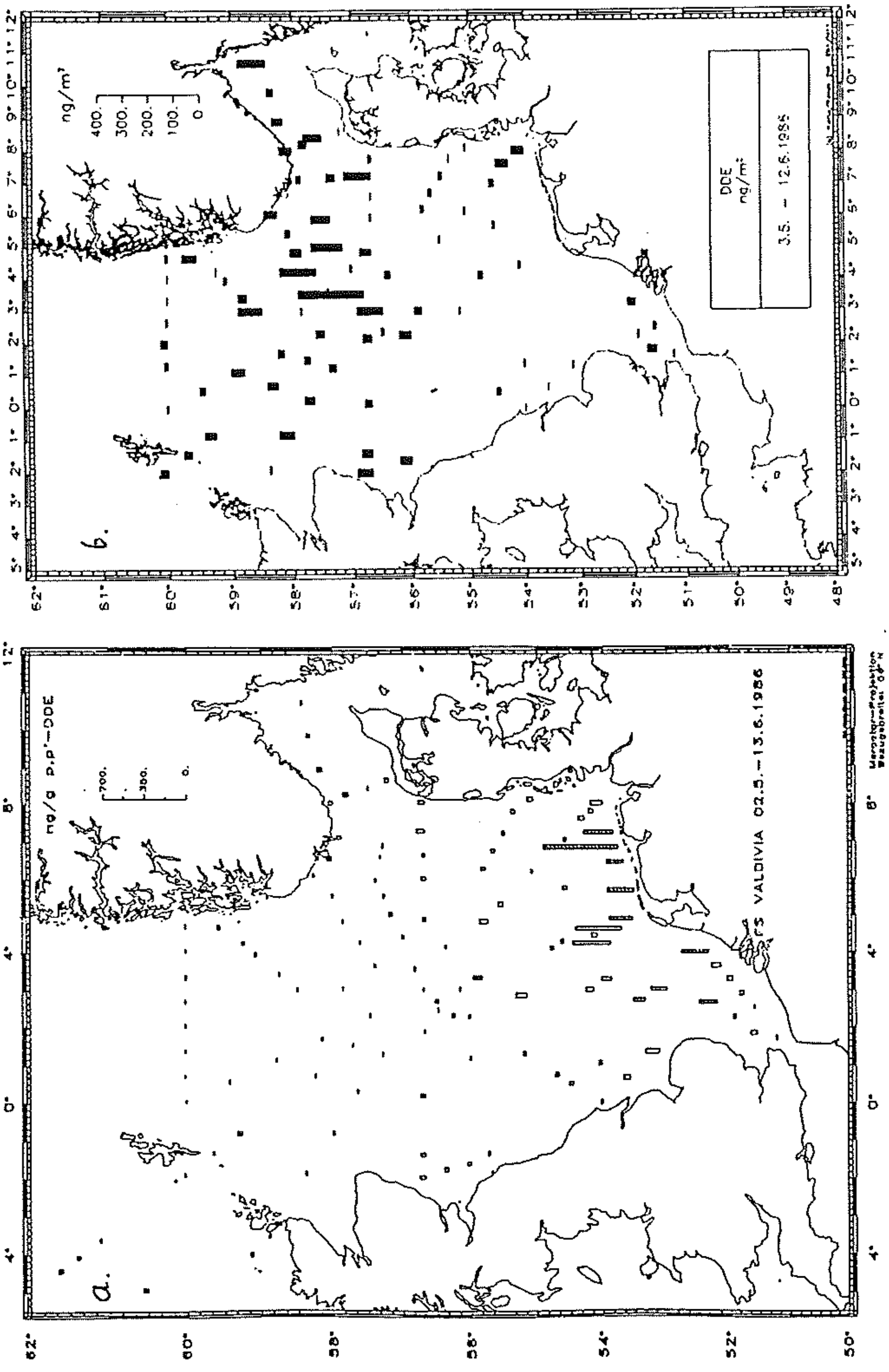


Fig. IV.4 Concentrations (a) and load (b) of p,p'-DDE in plankton of the North Sea: = samples dominated by *Calanus finmarchicus*, = samples dominated by *Temora longicornis*, ... = samples dominated by *Phaeocystis globosa*. Concentrations in ng g^{-1} n-hexane-extractable lipid, measured by the scale bar at top right of the chart (a: from KNICKMEYER & STEINHART 1989, b: from KRAUSE & KNICKMEYER 1992).

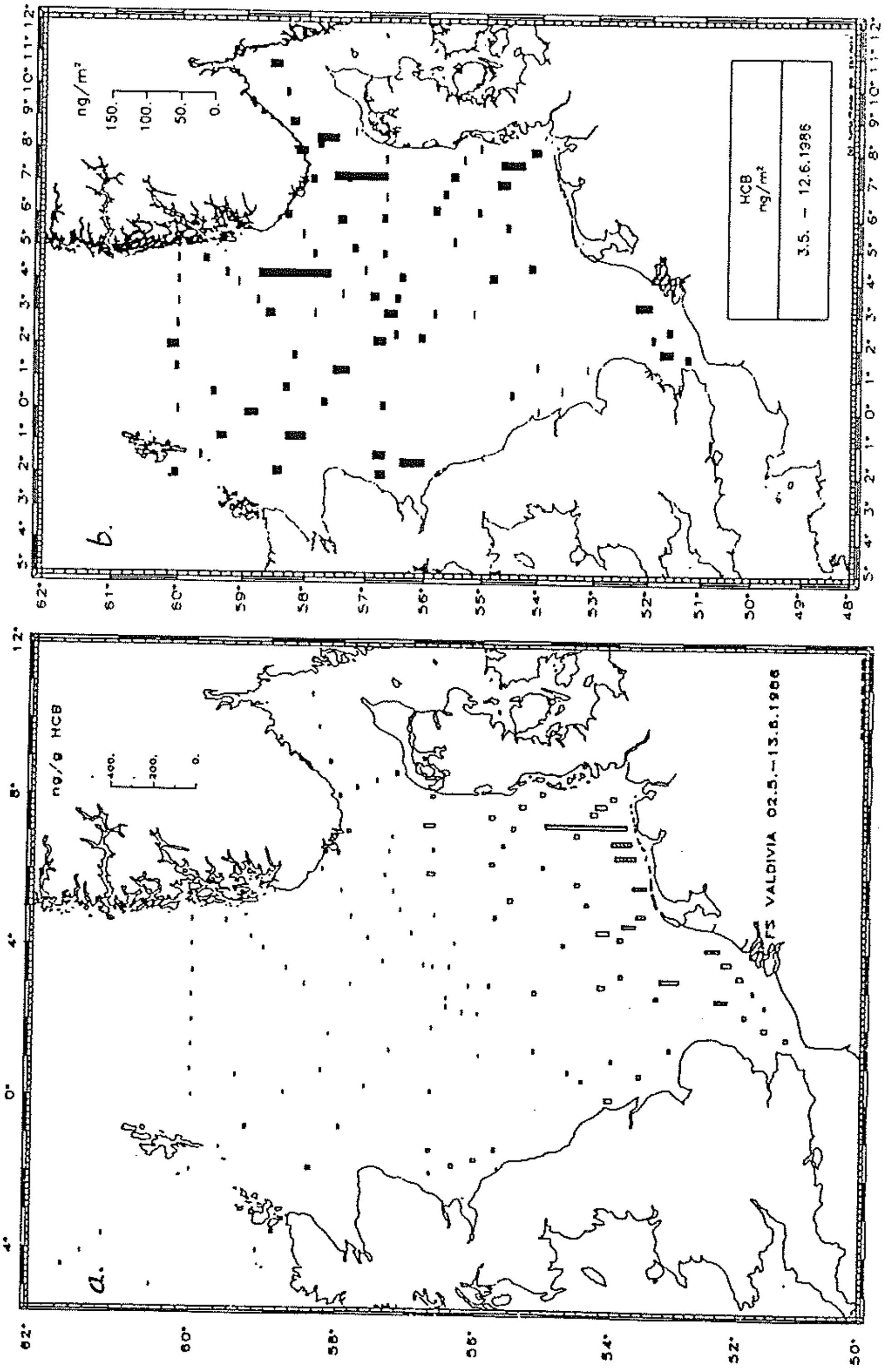


Fig. IV.5 Concentrations (a) and load (b) of HCB in plankton of the North Sea: = samples dominated by *Calanus finmarchicus*, = samples dominated by *Temora longicornis*, ... = samples dominated by *Phaeocystis globosa*. Concentrations in ng g^{-1} n-hexane-extractable lipid, measured by the scale bar at top right of the chart (a: from KNICKMEYER & STEINHART 1989, b: from KRAUSE & KNICKMEYER 1992).

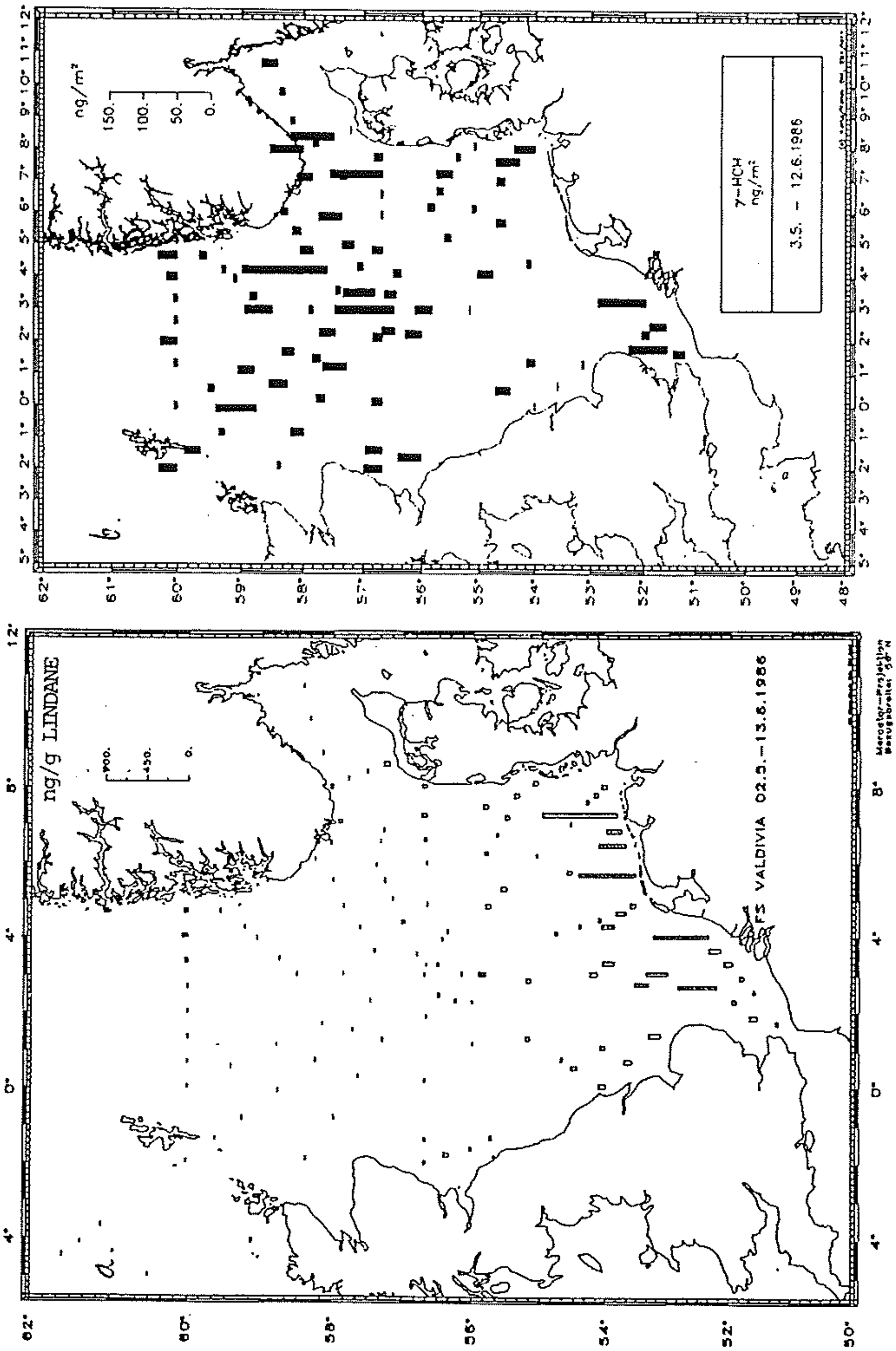


Fig. IV.6 Concentrations (a) and load (b) of Lindane in plankton of the North Sea: = samples dominated by *Calanus finmarchicus*, = samples dominated by *Temora longicornis*, ... = samples dominated by *Phaeocystis globosa*. Concentrations in ng g^{-1} n-hexane-extractable lipid, measured by the scale bar at top right of the chart (a: from KNICKMEYER & STEINHART 1989, b: from KRAUSE & KNICKMEYER 1992).

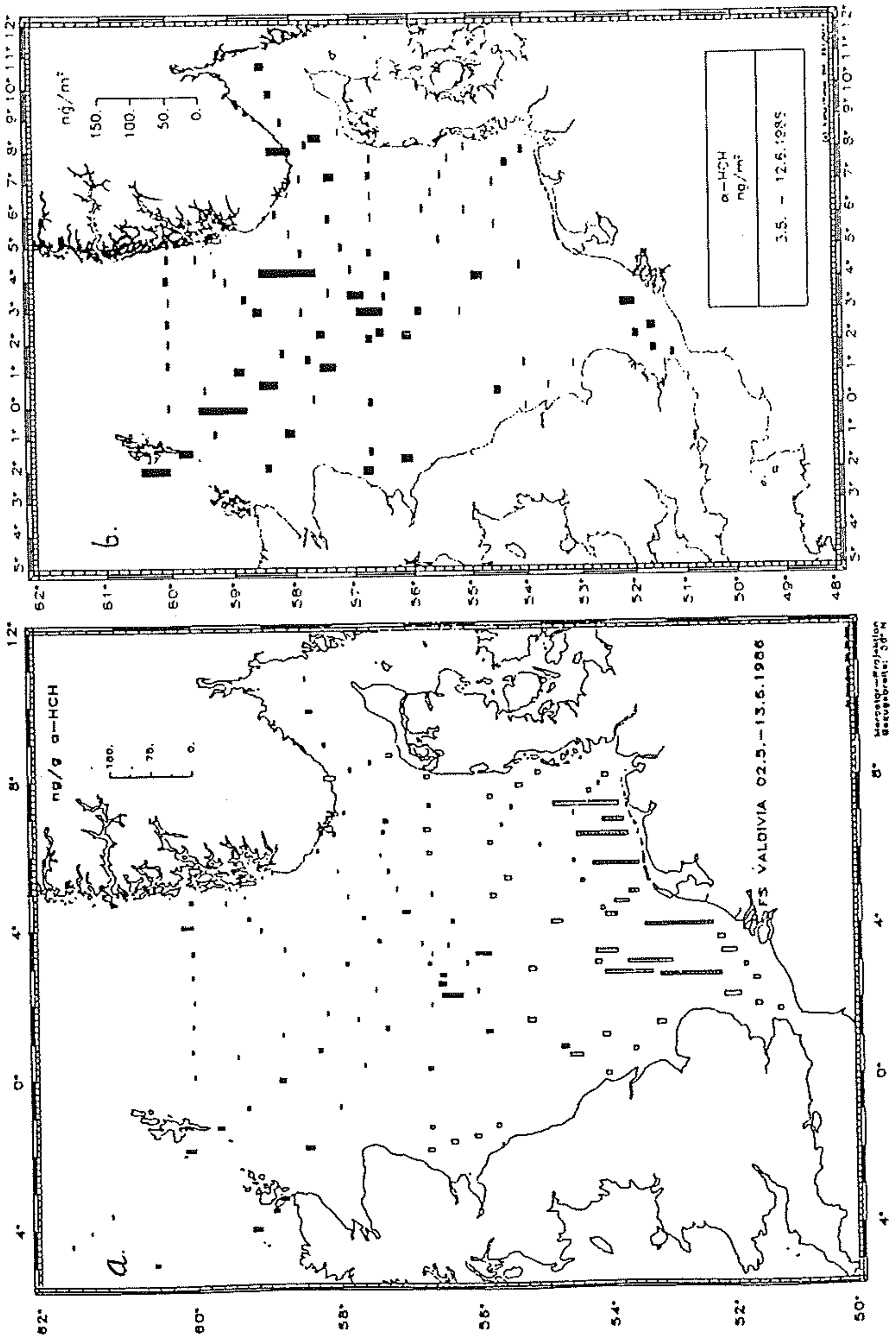


Fig. IV.7 Concentrations (a) and load (b) of alpha-HCH in plankton of the North Sea: = samples dominated by *Calanus finmarchicus*, = samples dominated by *Temora longicornis*, ... = samples dominated by *Phaeocystis globosa*. Concentrations in ng g^{-1} n-hexane-extractable lipid, measured by the scale bar at top right of the chart (a: from KNICKMEYER & STEINHART 1989, b: from KRAUSE & KNICKMEYER 1992).

GLOSSARY

AFDW	ash-free dry weight
allochtonous population	population which depends on advection for maintaining itself an area
autochtonous population	population which does not depend on advection for maintaining itself an area
autotrophs	primary producers, organisms capable of producing organic carbon from inorganic matter using light (phototrophs) or chemical energy (chemotrophs)
benthos	community of bottom-dwelling organisms
biomass	weight of living matter, usually in terms of carbon, dry weight, ash-free dry weight or wet weight
carbon	basic element of organic matter
CPRS	Continuous Plankton Recorder Survey
detritus	dead organic matter
DW	dry weight
eutrophic waters	waters rich in nutrients (contrast: oligotrophic, poor in nutrients)
eutrophication	nutrient enrichment of waters (mainly inorganic nitrogen and phosphorous, see p. 59)
front	boundary zone between two different water masses (see p. 3)
halocline	steep vertical salinity gradient
heterotrophs	organisms consuming the living or dead organic matter produced by autotrophs (secondary producers) or by higher trophic levels (tertiary producers)
holoplankton	organisms that spend all their life in the plankton
makroplankton	plankton size class 20 - 200 mm
meroplankton	benthic and nektonic organisms which spend part of their life cycle in the plankton
mesoplankton	plankton size class 0.2 - 20 mm
microplankton	plankton size class 0.02 - 0.2 mm
mixotrophs	organisms that may live alternatively as auto- or heterotrophs
nanoplankton	plankton size class 0.002 - 0.02 mm
nekton	pelagic organisms with own locomotion in relation to current speed

neritic	coastal, influenced by land, in particular riverine effluents
oceanic	as in the open sea
P/B ratio	production/biomass ratio (weight-specific production)
pelagos	community of organisms that live freely in the water column (plankton, nekton)
picoplankton	plankton size class 0.0002 - 0.002 mm
plankton	pelagic organisms without significant horizontal locomotion in relation to the currents
primary production	the amount of organic matter produced by autotrophs
pycnocline	steep vertical density gradient
stratification	horizontal layering of the water column in layers of different densities (determined by temperature and salinity)
thermocline	steep vertical temperature gradient

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WWF aims to conserve nature and ecological processes by preserving genetic, species and ecosystem diversity; by ensuring that the use of renewable natural resources is sustainable both now and in the longer term; and by promoting actions to reduce pollution and wasteful exploitation and consumption of resources.

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