Free University of Brussels
Ecology and Systematics Laboratory

Phytoplankton community structuring in some areas of the North Sea

by

M'harzi Ahmed

A thesis submitted for a Ph. D degree in Science

1999

Promotors: Profs. M. Tackx and M. H. Daro

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Dedication

To my lovely parents,

and all my teachers.

Author's Thesis Committee

Promotors: Profs. *M. Tackx* and *M. H. Daro*

Members of Jury:

Prof. N. Podoor (*Catholic University of Leuven* -KUL-)	Member
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A. M'harzi

Brussels, December 1999

Summary

Hydrographical, chemical and biological factors are known to affect seasonal and geographical variation in phytoplankton communities. This study analyses the phytoplankton species composition during late winter-early spring in two areas of the North Sea: the Belgian coastal zone and along a North-South transect covering the Dogger Bank, central and northern North Sea.

Spatial patterns in phytoplankton communities were analysed by Two-Way Indicator SPecies ANalysis (TWINSPAN), and their relationships with environmental factors by Canonical Correspondence Analysis (CCA).

A subsequant step analysed in how far distinct phytoplankton communities revealed on the basis of numerical species abundance, also resulted in differences in biomass (in terms of volume and carbon) and size structure of the phytoplankton community.

These features being important to the trophic transfer of phytoplankton to the zooplankton, the observed situtations were analysed in relation to the potential predation pressure exerted by the associated mesozooplankton communities using the model of Sheldon (1977).

An overview of the present knowledge on the spatial phytoplankton distribution in the North Sea is given in **chapter 1**. While, **chapter 2** explains the multivariate statistics used.

Chapter 3 and **4** report a spatial heterogeneity in phytoplankton community structure in late winter as observed in February 1994, 1995 and 1997 around some sandbanks along Belgian coastal zone. Based on species abundance, the offshore and nearshore areas are distinguished from each other. At a further

level, each sandbank is practically separated as a distinct area. This heterogeneity was explained by the variations in measured environmental factors. These can be explained by the fact that two water masses of different origin cover our study area: the Southern intrusion of Atlantic water from the English channel on the one hand and the coastal water on the other hand This heterogeneity was also observed, to some extend, in zooplankton community **(Chapter 3)**. The best explanation of the variance in phytoplankton community was obtained when nutrient concentrations were included in the CCA analysis **(Chapter 4)**. Differences in phytoplankton species composition also resulted in biomass and size structure between nearshore and offshore banks **(Chapter 4)**.

Chapter 5 reports a spatial heterogeneity in phytoplankton community structure, within a South-North transect in the North Sea. In early spring phytoplankton communities were discriminated between: (1) the shallow water of Dogger bank (DB) area and (2) deeper water of central/northern in which parallel subgroups could be distinguished. This pattern was related to the existing gradients in environmental factors. Phytoplankton biomass (in terms of volume or carbon concentration) showed a significant increase from central-northern North Sea towards the Dogger area: large diatom species were dominant (in term of volume or carbon concentration) in the Dogger Bank area. We noted the presence of non-diatoms mainly in the Dogger Bank area. This was explained by the fact that these microflagellates have an advantage to grow in a nutrient-limited environment. The variation in size-distribution of phytoplankton along the transect fits the expectation of dominance of large diatoms in shallow water of the Dogger Bank areas and small phytoplankton

species in the deeper stations of the central-northern North Sea. Moreover, each of the two zones (Dogger Bank and central-northern) was characterised by a rather equal phytoplankton volume and size structure. Besides the size differential control concept reported for both phytoplankton fractions (< 5 μm and > 5 μm) by Riegman et al., (1998), our results have shown that within, the > 5 μm size range, different contributions of cells < 10 μm may also provide a different trophic situation for the micro/meso-zooplankton.

The last purpose of this study was to evaluate if the observed spatial heterogeneity **(Chapter 3, 4 & 5)** in plankton also represented different situations regarding the potential energy transferred from phytoplankton to zooplankton. In **chapter 6**, we compared the neashore and offshore banks in the Belgian coastal zone on the one hand, and the shallower zone of the Dogger Bank and the deeper central-northern North Sea on the other hand. Normalised biomass spectra (dividing plankton volume concentration by width interval of each size class, Sprules and Munawar, 1986) followed a linear regression in all coastal banks examined in the Belgian coastal zone. The Stroombank, nearest to the coast, exhibited a significant different slope of the linear regression than the other banks. In general, the normalised spectra of the neashore banks showed a better fit to a polynomial than to a linear regression, indicating a different trophic situation in the plankton.

In the North Sea transect, no significant differences in slopes between the normalised spectra observed at each set of stations were formed over the entire study area, indicating a more homogenous standing stock relationship between

the phytoplankton and total mesozooplankton or the dominant zooplankton species, *Calanus finmarchicus*.

In general terms, the phytoplankton stock can support the carbon requirements of the dominant zooplankton during the early onset of growing season along the Belgian coastal zone in one hand, and both the dominant copepod *C. finmarchicus* and the total zooplankton in the North Sea transect during the early spring phytoplankton bloom, in other hand. This was reflected in the prediction of the Sheldon model that on a carbon or volume basis, the maximum potential consumption impact on the phytoplankton prey items does not exceed the prey's productivity. In the most nearshore banks of the Belgian coastal zone and in the Dogger Bank area, a quite important flux of energy is not channeled to holo-zooplankton and then to the higher trophic levels and will benefit the benthos, either as food for meroplanktonic larval stages or after sedimentation to the benthic system.

Samenvatting

Het is geweten dat hydrografische, chemische en biologische factoren de seizoensgebonden en geografische variatie in fytoplankton-gemeenschappen beïnvloeden. Deze studie analyseert de soortensamenstelling van het fytoplankton tijdens de late winter en vroege lente in twee zones van de Noordzee: de Belgische kustzone en langsheen een Zuid-Noord transect vanaf de Doggerbank langsheen de centrale en noordelijke Noordzee.

Ruimtelijke patronen in fytoplankton-gemeenschappen werden geanalyseerd door middel van 'Two Way INdicator SPecies ANalysis' (TWINSPAN), en hun relatie met de omgevingsfactoren met behulp van 'Canonical Correspondence Analysis' (CCA).

In een volgende stap werd geanalyseerd in welke mate verschillende fytoplankton-gemeenschappen die naar voor kwamen op basis van numerieke abondantie, ook resulteerden in verschillen in biomassa (in volume en in koolstof) en grootte-verdeling van de fytoplankton- gemeenschap.

Aangezien deze aspecten belangrijk zijn in de trofische transfer van fytoplankton naar zooplankton, werden de geobserveerde situaties geanalyseerd in relatie tot de potentiële predatie druk die er door het geassocieerde mesozooplankton kan worden op uitgeoefend. Dit werd gedaan met behulp van het model van Sheldon (1977).

Hoofdstuk 1 geeft een overzicht van de litteratuur betreffende de ruimtelijke verspreiding van (fyto)plankton in de Noordzzee, terwijl hoofdstuk 2 de gebruikte statistische technieken (TWINSPAN en CCA) nader toelicht.

Hoofdstuk 3 en Hoofdstuk 4 rapporteren een ruimtelijke heterogeniteit in de fytoplankton-gemeenschap die in de late winter (Februari 1994,1995 en 1997) werd geobserveerd rondom een aantal zandbanken in de Belgische kustzone. Op basis van soortenabundantie worden de kustzone en de meer zeewaarts gelegen zone van elkaar gescheiden. Op een lager niveau worden de meeste zandbanken van elkaar gescheiden. Deze heterogeniteit werd uigelegd door de variatie in omgevingsfactoren die werden gemeten in het studiegebied. Deze kunnen worden verklaard door het feit dat twee watermassa's van verschillende oorsprong voorkomen in het gebied : het Atlantisch water dat vanuit het zuiden (het Kannaal) binnnendringt enerzijds, en het kustwater anderzijds. Deze heterogeniteit werd, in enige mate, ook waargenomen in de zooplankton-gemeenschap (hoofdstuk 3).

De variabiliteit in fytoplankton samenstelling werd het best verklaard wanneer nutriënt-concentraties werden geïncorporeerd in de CCA analyse. Verschillen in fytoplankton soortensamenstelling resulteerden eveneens in verschillen in biomassa en grootte-verdeling tussen de kustzone en de zeewaartse zone (hoofdstuk 4).

Hoofdstuk 5 beschrijft een ruimtelijke heterogeniteit in de fytoplankton-gemeenschap, langsheen een zuid-noord traject in de Noordzee.Tijdens de vroege lente onderscheidden we verscheidene fytoplankton-gemeenschappen: (1) de ondiepe waters van de Dogger bank (DB) en (2) het diepere water van de

centrale en de noordelijke Noordzee, waarbinnen sub-gemeenschappen bestonden.

Dit patroon was gerelateerd aan gradiënten in omgevingsfactoren. De fytoplankton biomassa (in volume- en koolstof-concentratie) nam significant toe van de centrale-noordelijke Noordzee naar de Doggerbank: bij de Doggerbank waren grote diatomeeën dominant (in volume- en koolstof-concentratie). Niet-diatomeeën kwamen hoofdzakelijk bij de Doggerbank voor. Dit wordt verklaard doordat nutriënt gelimiteerde omstandigheden voordelig zijn voor de groei van microflagellaten. De variatie in groottte- verdeling van het fytoplankton langsheen het transect is in overeenstemming met de verwachting van grote diatomeeën in de ondiepe waters van de Dogger bank en kleine fytoplankton soorten in de diepere stations aan de centrale en noordelijke Noordzee. Bovendien werd elk van de twee zones (Doggerbank en centraal - noord) gekarakteriseerd door een vrij gelijkaardig fytoplankton-volume en grootte-structuur. Naast het 'size differential control' concept voor dit transect gerapporteerd door Riegman et al. (1998) voor de fracties < en > 5 mm, toonden onze resultaten aan dat verschillende bijdragen van cellen <10 mm eveneens verschillende trofische situaties voor het micro/mesozooplankton kunnen vertegenwoordigen.

Ee laatste objectief van deze studie was te evalueren of de geobserveerde ruimtelijke heterogeniteit in het plankton (hoofdstukken 3,4 en 5) ook verschillende situaties vertegenwoordigt voor de potentiële energie transfer van het fytoplankton naar het zooplankton. In hoofdstuk 6 vergeleken we de

kustzone met de zeewaarts gelegen zone voor de Belgische kustzone enerzijds, en de ondiepe zone van de Doggerbank met de diepere centrale- en noordelijke Noordzee anderzijds. Genormaliseerde spectra (waarin de volume concentratie van de plankton biomassa gedeeld wordt door de interval grootte van de verschillende grootte-klassen), Sprules en Munamar, 1986), vertoonden een lineaire regressie voor alle zandbanken bestudeerd in de Belgische kustzone. De Stroombank, die het dichtst bij de kust gelegen is, vertoonde een significant verschillende helling van de lineaire regressielijn dan de andere banken. In het algemeen vertoonden de zandbanken nabij de kust een betere fit met een polynomiale dan met een lineaire regressie, wat op een verschillende trofische situatie in het plankton tussen beide zones duidt.

In het Noordzee transect werden geen significante verschillen tussen de genormaliseerde spectra geobserveerd over de verschillende sets van stations verspreid over het gehele studiegebied, wat op een meer homogene trofische situatie wijst tussen de standing stocks van het fytoplankton en het mesozooplankton, of de dominante zooplankton soort, *Calanus finmarchicus*.

In het algemeen kan, bij de aanvang van het groeiseizoen, de fytoplankton-stock voldoen aan de koolstof behoeften van het dominante zooplankton in de Belgische kustzone. Hetzelfde geldt voor de relatie fytoplankton - totaal zooplankton alsook de dominante copepode

C. finmarchicus in het Noordzee transect gedurende de vroege lente. Dit bleek uit de resultaten van het Sheldon model, die aangeven dat, op koolstof basis, de maximale potentiële predatiedruk van het zooplankton nooit de fytoplankton productie overschreidt. Bij de meest kustwaarts gelegen banken in

de Belgische kustzone en in de Doggerbankzone, wordt een belangrijk deel van de energie niet doorheen het mesozooplankton naar de hogere trofische niveau's gesluisd, maar komt ten goede van het benthos, ofwel onder de vorm van voedsel voor meroplanktonische larven, ofwel na bezinking op de bodem.

Contents

Chapter I

INTRODUCTION

Content

1. General notes on phytoplankton, its diversity, size distribution and trophic interractions

1.1. Phytoplankton

Algae are photosynthetic organisms that occur in most aquatic habitats, ranging from marine to freshwater ecosystems. They vary from small, single-celled forms to complex multicellular forms (Kennish, 1990). They exhibit a wide range of reproductive strategies, from simple, asexual cell division to complex forms of sexual reproduction (Kennish, 1990). The sunlighted waters of the surface of the sea area containing microscopic, single-celled organisms which use energy from the sun and nutrients extracted from the water to make their own carbohydrates via a set of chemical reactions termed photosynthesis (equation 1) (Kennish, 1990). Collectively, they are referred to as phytoplankton (from the Greek words ***phytos*** = **plant** and ***planktos*** = **wanderer**).

$$nCO_2 + 2nH_2O \xrightarrow{\text{light}} n(CH_2O) + nO_2 + nH_2O \quad \textbf{(equation 1)}$$

The *phytoplankton* is comprised of a vast, diverse assemblage of organisms, which are united by their tiny size and drifting life mode. The names of the divisions and classes of algae often contain a reference to the colour of the organisms included in them: Cyanophyta, blue-green algae; Rhodophyta, red algae; Chrysophyceae, golden algae; Phaeophyceae, brown algae; Chlorophyta, green algae (in Van Den Hoek et al., 1997). Mainly the kinds and combinations of photosynthetic pigments present in the cell determine recent algal classification. A summary of these pigments and their

occurrence in different groups of algae is listed in Table 1.1. A detailed list is reported in Table 1.2, page 13 in Van Den Hoek et al., (1997).

The term diversity is used for the degree to which the total number N of individual organisms in a given ecosystem, area, community or trophic level is divided evenly over different species (Baretta-Bekker et al., 1998). Diversity can be expressed quantitatively by several diversity indexes (e.g. Margalef, Shannon-Weaver indexes). A community is defined as an assemblage of populations living in a given area with mutual interactions (Baretta-Bekker et al., 1998). Such communties are classified according to dominant species, indicator species, physical habitat, or type of community metabolism (e.g., based on rate and efficiency of production) (Baretta-Bekker et al., 1998).

Table 1.1. Algal pigments of major algal divisions and classes of marine phytoplankton (Parsons et al., 1977; Raymont, 1980; Williams and Claustre, 1991; Peeken, 1997; and Van Den Hoek et al., 1997)

	Pigments		
		Accessory pigments (carotenoids)	
Classes	Chl	carotene	Xanthophylls
Bacillariophyceae (Diatoms)	a & c	β	Fuco-, neofuco-, diadino-, and diato-Xantin
Dinophyceae (Dinoflagellates)	a & c	β	Peridinin, neoperidinin, diadino-, fuco-, and diato-Xanthin.
Haptophyceae (Prymnesiophyceae)	a & c	β	Fuco-, neofuco-, diadino-, diato-, 19'-butanoyloxyfuco-, and 19'-hexanoyloxyfuco-Xanthin
Chrysophyceae	a & c	β	Fuco-, neofuco-, diadino-, 19'-hexanoyloxyfuco- and 19'-nutanoyloxyfuco-Xanthin
Xanthophyceae	a & c	β	Fuco-, diadino-, diato-, and Viola-Xanthin
Cryptophyceae	a & c	α	Allo-, monodo-, croco-Xanthin, and Phycobillins
Chlorophyceae	a & b	β	Lutein, zea-, flavo-, viola-, nea-, and Siphono-Xanthin
Prasinophyceae	a & b	α, β &g	Lutein, zea-, and Viola-Xanthin

Compared to that of attached plants, species diversity of phytoplankton communities is labile and less predictable (Kennish, 1990). In general, planktonic component maintain high numbers of species, but from time to time, seasonally or episodically, the species diversity is greatly reduced (e.g. Leewis, 1985), with blooming of one or a few species (e.g. the bloom of *Phaeocystis* sp. in spring in the Belgian coastal zone). The classification of a phytoplankton species as neritic or oceanic provides only a general indication of its distribution with respect to distance from shore or to water depth. Smayda (1958) has recommended a more useful terminology, which relates habitat selection to life cycle. Meroplanktic refers to all those forms that either produce a resting spore or possess a sedentary stage or dormant pelagic phase and hence are pelagic only during part of their life cycle. Holoplanktic on the other hand refers to those species which do not produce resting spores and that are pelagic throughout their life cycle.

1.2. Cell size and sizes distributions

Based on cell size, phytoplankton communities can be divided into three major groups: picoplankton (0.2-2μm), nanoplankton (2-20 μm) and microplankton or net plankton (20-200 μm) (Malone, 1971; Siebruth et al., 1978; Fogg, 1991; Bouteiller et al., 1992). The variation of the biomass and taxonomic composition of these three groups, is related to the type of the environment and production regime.

The term size distribution is used to describe the distribution of the biomass of a phytoplankton population (usually expressed in terms of volume

per unit of water volume, e.g. ppm= $\mu m^3 x 10^6$ ml^{-1}) as a function of cell size. This latter is usually expressed as Spheric Equivalent Diameter (S.E.D, μm). The volume distribution of a phytoplankton community is evidently determined by the abundance and size of each constituting species. Both the total volume and the location of the size range of the bulk of this volume are relevant features in relation to the trophical role of the phytoplankton community (cf, Chapter 6).

In general, large phytoplankton species dominate in areas of high and variable nutrient levels, and smaller phytoplankton species dominate in areas with lower and stable nutrient levels (Varela 1987; Morris 1980; Kiørboe et al., 1990). Therefore, in open ocean conditions, smaller phytoplankton is usually prevalent, while in neritic waters, larger species make up a greater fraction of the phytoplankton population (Malone et al. 1973).

1.3. Trophic interractions

To understand trophic interractions and how the food web picture of the pelagic ecosystems is organised is important in relation to ecosystem management and assessing fish stocks of the ocean (Steele, 1965; Ryther, 1969; Parsons and Lebrasseur, 1970). As primary producer, phytoplankton forms a substantial basis for the marine and freshwater food webs. The efficiency of the energy flows from producers to zooplankton and to higher trophic levels depends mainly on the contrainst of the physical environment (Landry, 1977) (Figure. 1.1). This effect can be summurised as follows: in a high nutrient, and high turbulence environment a growth of large

phytoplankton cells is favoured (Landry, 1977; and Kiørboe, 1993) (Figure. 1.1b). While, small cells (e.g. microflagellates species, small herbivorous and microzooplankton) are dominating in a low nutrient and low turbulence environment) (Landry, 1977) (Figure 1.1a). Moreover, the suitability and the transfer efficiency of the primary production to zooplankton and then to higher trophic levels differs in both environments (explanation in Figure. 1.1).

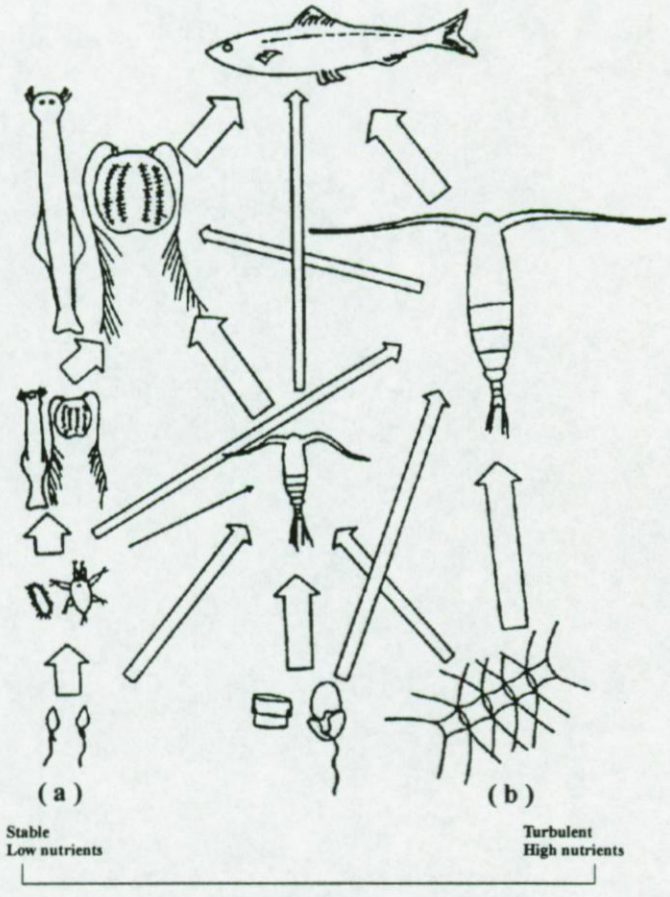

Figure 1.1. Trophic organisation in pelagic ecosystems, showing dominant pathways along which matter and energy are channeled in the ecosystem. Qualitatives differences in these pathways are illustrated by the widths of arrows. (a) Type of trophic structure organised in long pathways, where the energy tranfer is channeled is several intermediate levels before to be utilised by fich stocks. (b) Type of shorter structure, favoring greater transfer efficiency to larger herbivores and then to fish and invertebrates predators, (Landry, 1977).

2. The North Sea ecosystem

2.1 Topography and Hydrography

The North Sea, situated between 51°N and 61° and 4°W and 9°E, covers an area of about 525 000 km^2 and has a water volume of some 43000 km^3 (Zijlstra, 1988). Connexions with other sea areas throug which major water inflows into the North Sea occur, are illustrated in Figure 1.2. They can be summarised as followed: in the north, between Scotland and Norway, with the northern Atlantic; in the east with the Skagerrak; and finally in the south with the English channel (Figure. 1.2) (Zijlstra, 1988). The northern part - north of Dogger Bank- of the North Sea has an average depth of some 100 to 150m, and is relativelly little affected by fresh-water inflows (Zijlstra, 1988). South and southeast of the Dogger Bank, the average depth is around 30m (Zijlstra, 1988). This part -the Southern Bight of North Sea- receives inflow from some large continental rivers, as Rhine, Meuse, Scheldt, Weser, Elbe and Tames (Zijlstra, 1988).

2. 2 Waters masses

The hydrography of the North Sea shows a complex structure, where the Atlantic water intrusion, the dominant strong westerly winds, and strong tidal currents (specifically in the Southern Bight) play a major role (De Wilde et al., 1992). Indeed, water masses distribution can be divided into (a) The inflow of Atlantic water of high salinity from the north, and from the south through the Strait of Dover, and (b) the inflow from the Baltic, which is of

lower salinity (Lee, 1970 cited in Zijlstra, 1988). Moreover, 4 water masses can be

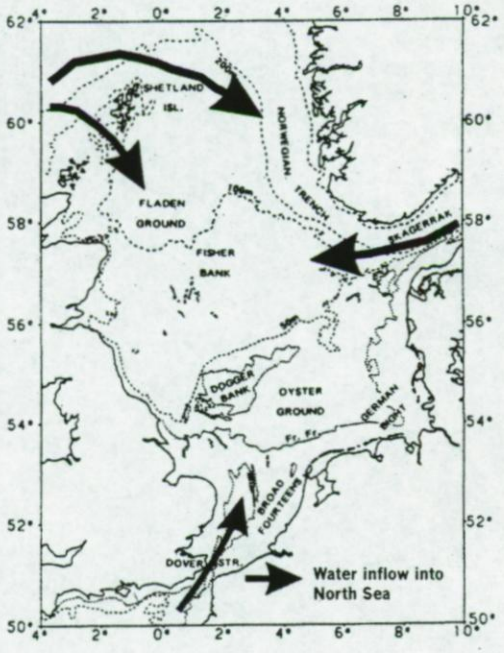

Figure 1.2. Map of the North Sea with depth contour lines of 50, 100, and 200m. (In De Wilde et al., 1992). Arrows indicate the three major inflows into North Sea.

distinguished in the North Sea. This division is based on the origin and the properties of the resident water: north Atlantic water (salinity > 35 ‰), coastal water (salinity < 34 ‰), Baltic water (salinity < 34 ‰) and mixed central North Sea water (salinity 34-35 ‰) (Otto et al., 1990; Fransz et al., 1991; and De Wilde et al., 1992) (Figure 1.3).

2. 3 Nutrients

Main nutrient concentrations (nitrate, phosphate and silicate) vary with season, depth and position (Zijlstra, 1988). Biological activity -the uptake by

algae and remineralisation by bacteria- affect nutrient concentration variations significantly (Zijlstra, 1988). The general trend for all three nutrients is similar: higher concentrations in the northern part of the North Sea, in the North Atlantic inflow and along the coasts, in particular in the southern and the southeastern North Sea (Brockmann et al., 1990). The central part of the North Sea shows low nutrients concentrations (Brockmann et al., 1990).

2. 4 Ecological subregions

Based on the depth countour lines of 50, 100 and 200-m, the North Sea can be subdivided into three regions (Southern, Central and Northern) (Figure. 4.1) (De Wilde et al., 1992). This subdivsion is also observed in the general distribution patterns of: phytoplankton (Reid et al., 1990); zooplankton distribution and production (Fransz et al., 1991); benthos levels ("étages") and faunal clusters (Glémarec, 1973; Basford et al., 1989; Künitzer et al., 1992); and fish distribution (Daan et al., 1990) (in De Wilde et al., 1992). Different ecological subareas can be superimposed on these major ecological regions. This was done based on a more detailed analysis of plankton and benthos components (e.g. Gieskes and Kraay, 1975; Duursma et al., 1988; Vincx, 1990; Fransz et al., 1991; and Duineveld et al., 1992; De Wilde et al., 1992).

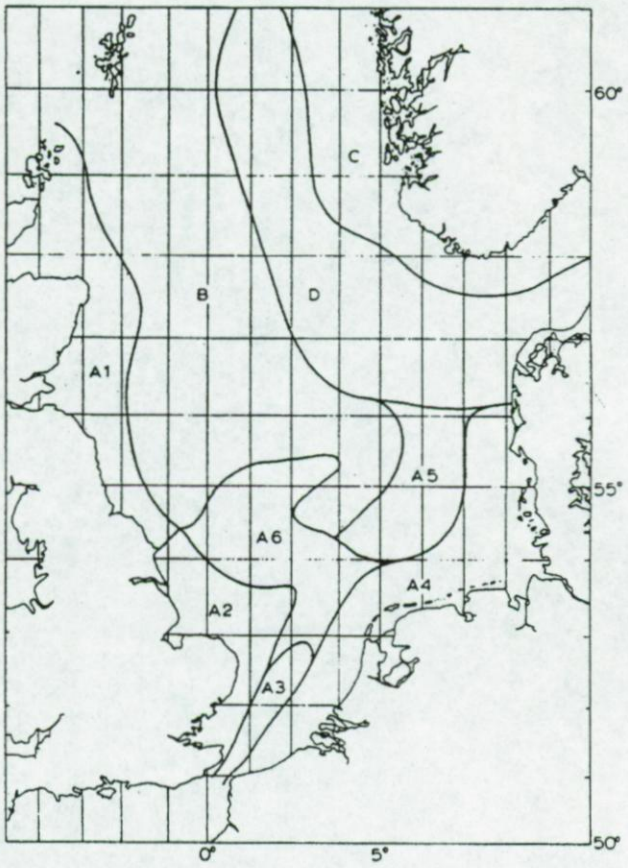

Figure 1.3. Hydrographical regions of the North Sea atfer Lee (1980). (In Otto et al., 1990)

2. 5 Biota

The biota of the North Sea are generally grouped as microorganisms, phyto- and zooplankton, benthos, and fish (Table 1.2). Other groups such as macroalgae, sea grass, birds and mammals are also found but their contribution to the functioning of the North Sea system as a whole, is small (De Wilde et al, 1992).

Table 1.2. Species richness of the differents components composed the Biota of the North Sea (in De Wilde et al., 1992).

	Number of species
Microorganisms & Protists species	unknown
Phytoplankton	500
Micro-and mesozooplankton	200
Macrozooplankton	100
Meiobenthos	1000
Macrobenthos	~1000
Fish	200
Bird	30
Mammals	10

Section 2.5.1 will specifically foccuss and discuss some aspects of the work on phytoplankton and zooplankton carried out in the North Sea.

2. 5 . 1 Phytoplankton

Information on phytoplankton in the North Sea has been obtained by two fundamentally different methods. The first one, by the Continuous Plankton Recorder Surveys (C.P.R.S) (using a mesh size of 270μm), providing the structure of net-phytoplankton (microplankton) in all seasons and in the whole area of the North Sea (e.g. Glover, 1967; Glover et al., 1974, Colebroock, 1984 and 1986; Reid et al., 1990; and Williams et al., 1993). While the second method focused on the functional properties of the plankton populations (Zijlstra, 1988). This was done by studying phytoplankton dynamics in relation to the environment (e.g. nutrients, light, hydrographical factors, zooplankton grazing, etc...) (Zijlstra, 1988). Examples of such studies are: in the Southern Bight of the North Sea (e.g. Mommaerts, 1973a, b;

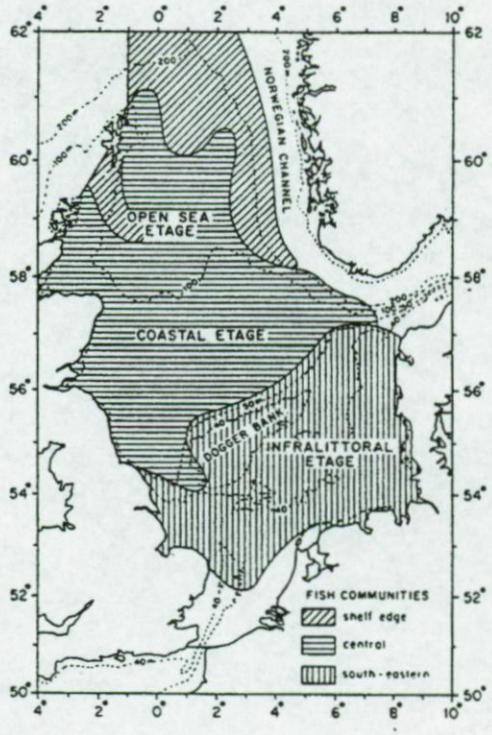

Figure 1.4. Subdivision of the North Sea into three ecological subareas: southern, central and northern North Sea. Partitioning is based on the 50, 100, and 300m depth contours and fish communities according to Daan et al., (1990). (In De Wilde et al., 1992).

Gieskes and Kraay, 1975, 1977; Joiris et al., 1982; Lancelot, 1983; Lancelot and Mathot, 1985 and 1987; Lancelot et al., 1987); in the German Bight (e.g. Hagmeier, 1978); in the central North Sea (e.g. Cushing et al., 1963) and in northern North Sea (e.g. Steele, 1956, 1957; Radach, 1982; Gamble 1978; and Daro 1980).

Several studies, carried out in the entire North Sea, report results on the seasonal variations in plankton biomass and production. Also, long-term changes within the phytoplankton (e.g. Reid et al., 1990), within the zooplankton (e.g. Fransz et al., 1991) and in the interrelation between

phytoplankton and zooplankton (e.g. Colebrook, 1984; Williams et al., 1993) are discussed.

2. 5. 2 Zooplankton

As for phytoplankton, North Sea zooplankton data are basically provided from 2 approaches. The first one was based on C.R.P.S, covering all North Sea areas, provided us long-term studies on species composition, distribution and seasonal variations (Zijlstra, 1988). The second source consist of special studies, on a small scale, with the aim to study the ecosystem dynamics (references, see section 2.5.1).

Both long and short term studies of several aspects of the zooplankton ecology can be summarised as followed: on zooplankton community structure and relationship to the environments (temperature, salinity and vertical water stability) (e.g. Colebroock 1964), on seasonal cycles (e.g. Colebroock and Robinson, 1965; Colebroock, 1979; Fransz, 1976 etc...), and vertical distribution and grazing activity (e.g. Daro, 1988). An important contribution was published by Fransz et al., (1991) with a review of the ecology of zooplankton in the North Sea. Indeed, this review concerns long-term studies on seasonal and temporal variations, trophic interractions, population dynamics and production of zooplankton. They reported also that the zooplankton distribution is related, as was mentioned above, to the hydrography, the origin of watermasses and the seasonal variation with respect to species, area, and communities structure in terms of herbivores, omnivores and carnivores (Fransz et al., 1991). Trophic interactions were also discussed and compared between north and south of the North Sea (Fransz et

al., 1991). Finally, they deal with population dynamics and production (e.g. reproduction and life strategy, growth and development, mortality, and secondary production) of the most important zooplankton species.

2. 6 Trophic levels and interractions

The present view of the food web structure of the North Sea differs from the earlier simple picture given by Steele (1974) (Zijlstra, 1988; and De Wilde et al., 1992). This latter presented an almost linear food chain where all primary production is controlled and channelled by herbivorous zooplankton to fishes (De Wilde et al., 1992). Herbivorous predators produced fecal pellets providing a food supplly to the benthic system (De Wilde et al., 1992). This linear transfer of energy did not satisfy the food requirements of the fish (Zijlstra, 1988). This is due to the considerations taken by Steele in his approach, the low estimation of primary production (90 g C m^{-2} yr^{-1}) and the assumption that all primary production is consumed only by the herbivorous zooplankton (Zijltsra, 1988). Later, Jones (1984) elaborated a more realistic picture, where other important processus were added (Figure 1.5). Thus, this picture considered a higher primary production of 130 g C m^{-2} yr^{-1}, a transfer efficiency of 15-20% between different components and finally a consumption 25% of primary production production by the benthos (Zijlstra, 1988). In this energy budget the food requirements of the fish stocks in the North Sea were satisfied (Figure 1.5a) (Jones, 1984).

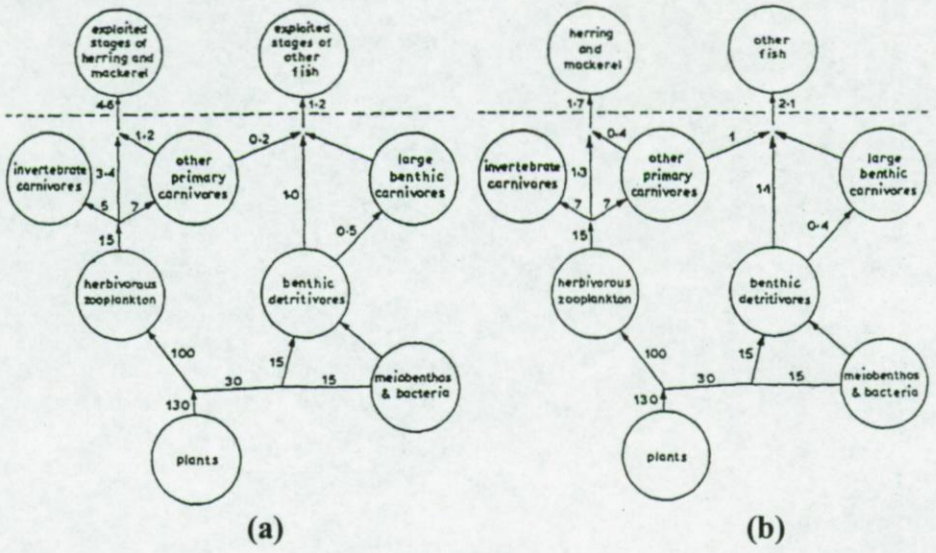

Figure 1.5. Estimations of the Energy-flow in g C m^{-2} yr^{-1}, based on a transfer efficiency of 20% to fish through 'other primary canivores' and 15% transfer efficiency through herbivorous zooplankton. (a) North Sea, early 1960's; (b) North Sea, late 1960's. (Adapted from Jones, 1984).

However, Jones (1984) showed that this budget is sensitive to changes occurring in the higher trophic level of the fish stock (such as the reduction of herring and mackerel stocks- after 1960). The response to this decreases was observed in the energy flow at the higher end of the food web "invertebrate carnivores" and others fish (Figure 1.5b) (Zijlstra, 1988). Such effect can be also observed in the food web structure in the shallower southern North Sea where benthic component has a more ecological role than just to be described (Zijsltra, 1988). Indeed, the carbon demand of benthic community decreased gradually from southern coastal area to deeper part on the northen North Sea (De Wilde et al., 1992.). Moreover, a high biomass of benthic species, and a higher transfer efficiency to the benthos can limit the flow of energy of the primary production to zooplankton in the shallow southern North Sea (Zijlstra

1988; and De Wilde et al., 1992). Within the Belgian coastal zone the meiofauna distribution differred from the neashore shallow waters with mean depth of 10m to the offshore waters with mean depth of 16m (Heip et al., 1990). Moreover, Joiris (1983) attributed the observed heterogeneity of Seabirds in the North to the ecological structure of the water masses. Atlantic water is characterised by a complete food web: phytoplankton-zooplankton-fish-Birds. This is found in the north of the North Sea where an intrusion of Atlantic water is penetrating with the Gulf Stream (Daro, 1980). While, in the Southern North Sea water, an important part of the primary prodcution (40%) is taken by the benthic component (Joiris et al., 1982).

3. Objectives

The natural or intrinsic variability of phytoplankton and zooplankton in relation to their environment is an important aspect of marine ecology. The knowledge of this variability is essential to understand the functioning and the possible human impact on plankton dynamics and behaviour. Moreover, the study of the spatial structure of the biological components plays an important role in ecological models (Legendre and Trousselier, 1993).

Specific statistical analysis are available from a dataset of species abundances- which subarea's in a given study area can be considered as bearing separate communities- (cf. Chapter 2).

Ecosystem functioning on the other hand is usually studied on a biomass stock and flux basis. In these studies, biota are usually considered in more 'functional' term such as the groups given in Table 1.2 (phytoplankton,

microzoplankton, etc...). this difference in approach raises the question in how far a distinction of area's or communities made on the basis of species composition corresponds to differences in functioning of 'pelagic' system in these areas.

This thesis will focus on the *Phytoplankton* community distributions of some coastal and open sea areas of the North Sea. In both cases the study was performed before or at the begening of the spring bloom. Therefore, the evaluation made considering mainly the 'starting position' within the phytoplankton in the different areas. These will be related, to some degree, to the *zooplankton* component and the prevailing environmental conditions. Although each chapter has its own specific objectives, we state the general objectives of this work as follows:

To describe the spatial and community structure of the plankton, in terms of number of species, volume and carbon content. To check whether differences (based on phytoplankton species composition) found within the spatial community structure of the plankton also, have a potential effect on the food web structure.

This thesis is organized into 7.chapters, this being the first one.

Chapters 2 deals in general with materials and methods, but the detailed methodology used is reported in each Chapter.

In **chapter 3** we report the first observations on the winter distribution of phytoplankton and zooplankton communities around some sandbanks along the Belgian coastal zone during February 1994.

In **Chapter 4** the observations on the distribution of phytoplankton around some Belgian sandbanks during February 1995 and 1997 are also investigated. The occuring spatial distribution of phytoplankton biomass (in terms of volume and carbon) and size fractions during the three sampling years, February 1994, 1995 and 1997 is also investigated.

Chapter 5 presents results on phytoplankton studies carried out along a North-South transect, during the early spring bloom, in the Open Sea of the North Sea. This chapter focusses on the spatial distribution and structure of phytoplankton communities, with emphasis on the biomass, and size structure.

Chapter 6 looks into the use of the size spectra approach to study the potential trophic relationships between phytoplankton and mesozooplankton within nearshore and offshore stations in the two study areas. It verifies if subareas distinguished as separate communities based on phytoplankton species composition also represent different situations to the potential trophic transfer of phyto- to mesozooplankton.

Chapter 7 summarises the main findings and results of the whole study.

Chapter II

MATERIALS AND METHODS

Content

1. Study area, sampling and laboratory analysis

In each of the chapters of this thesis, phytoplankton, and sometimes zooplankton were sampled in a number of stations spread over a geographic area and its abundance determined. Environmental factors such as temperature, salinity, turbidity and nutrient concentrations were determined at the same time.

Detailed descriptions of methods for the sampling and sample analysis will be given in each chapter.

It is however, necessary to give briefly the definitions and outline the interest of using multivariate analysis in marine biology as well as many applied ecological topics (e.g. ecological dynamics, ecological impacts, ecological management, ecotoxicology, etc...). The details on the application of these techniques to the specific datasets are given in chapters 3, 4 and 5.

2. Cluster analysis: TWINSPAN

Cluster analysis is a multivariate procedure commonly used for detecting natural "groupings" in ecological data (Gauch et al., 1981; Gauch, 1982; Pielou, 1984).

TWINSPAN is somewhat complex divisive clustering method originally devised by Hill for vegetation analysis but quite suitable for animal communities as well. The TWINSPAN program has been widely used by ecologists.

TWINSPAN (Two-Way Indicator SPecies ANalysis) is a development of a method already published under the name "indicator species analysis" (Hill et al., 1975). Its procedure and advantages are described by Hill, (1979) as: "*TWINSPAN is a program for classifying species and samples, producing an ordered two-way table of their occurrence. An interesting feature of TWINSPAN is that it forms what are termed pseudospecies. These are separate variables for the different levels of abundance of a species. Samples are ordinated using reciprocal averaging. A dichotomy is then made using the reciprocal averaging centroid line to divide the samples into two groups (negative and positive). This dichotomy is then refined using an iterative procedure. The clusters of samples obtained are then ordered so that similar clusters are near each other. This procedure continues in a hierarchical fashion to subdivide the groups until the minimum group size initially selected by the user is obtained. Species are then classified using the sample (quadrate) classification*". The final result is presented as a dendogram of stations.

3. Community, and species-environment relationships: CANOCO

A common problem in community ecology is to answer the question: how does a multitude of species responds to external factors such as environmental variables? To solve this problem, regression and ordination have been integrated into techniques of *multivariate* direct gradient analysis, called canonical ordination (Jongman et al., 1987; Ter Braak and Prentice, 1988). The Fortran program CANOCO (canonical community ordination, version 3.10) includes

canonical correspondence analysis (CCA), which escapes assumptions of linearity between species abundances and gradients (cf. Principal Components Analysis) and is able to detect unimodal relationships between species and "environmental" variables (Ter Braak 1986, 1987a, b and 1988).

The CCA option of CANOCO is used, for example to examine the relationship between the abundance of the x species entities trawled in the Sea, and relate the abundance/dominance of given species to the x selected geographical areas (localities). Presentation of an ordination diagram, with inclusion of species, sampling localities and environmental factors (t°, sal , etc...), allows one to search for relationships: species, which are arrayed close together, have similar species attributes. Species in close proximity to particular stations/localities will be more "dominant" (i.e. over-represented) than those further removed. The major points to be considered when interpreting the CCA plot in CANOCO are, as Ter Braak, (1986, 1988) mentions:

(1) Environmental factors with long " arrows" are better correlated with the axes than those with shorter "arrows", and accordingly more strongly related to the species pattern in the plot;

(2) "Arrows" point in the direction of maximal change of given environmental factors in the plot, and the length of the arrows is proportional with the degree of change (i.e. larger change reflected by long "arrows";

(3) Species can be projected relative to the "arrows", such that the ordering of species along the axis of the "arrow" is approximately the ranked, weighted median value of the species relative to the environmental factor;

(4) The absolute length of the "arrow" is immaterial; it is the relationship

between its length and direction that is important;

(5) The proximity of species plotted relative to localities denotes the degree of influence/dominance of the species at the localities.

Chapter III

WINTER DISTRIBUTION OF PHYTOPLANKTON AND ZOOPLANKTON AROUND SOME SANDBANKS OF THE BELGIAN COASTAL ZONE

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Key words: phytoplankton - zooplankton - Belgian coastal zone

Content

Abstract

Distribution of phytoplankton and zooplankton around 3 sandbanks (Gootebank, Westhinder and Buitenratel sandbank) of the Belgian Coast was investigated in February 1994.

The abundance of phytoplankton taxa was significantly different between the sandbanks. Community analysis using TWINSPAN resulted in a clear separation of clusters corresponding to the different sandbanks. The zooplankton community analysis, on the contrary, showed a rather undistinctive division of the sandbank stations. This was due to the omnipresence of three dominant copepod species *(Temora longicornis*, *Pseudocalanus elongatus* and *Centropages hamatus)*. When these species were excluded from the analysis, a clearer distinction between the different sandbanks was found.

The observed differences in phyto- and zooplankton species distribution could be explained by the position of the sandbanks. Westhinder is positioned further from the coast than Buitenratel, while Gootebank has an intermediate position. Buitenratel and Gootebank harbour typical coastal plankton communities, while the plankton community over Westhinder is clearly influenced by the Atlantic current penetrating the Southern North Sea from the English channel. More phyto-benthic species were found at Buitenratel than at Gootebank, probably because of its limited depth. Thus the Belgian coastal zone, which is considered as one box in most spatial descriptions of the North Sea plankton, in fact harbours heterogeneous plankton communities at the end of winter.

1. Introduction

In their respective reviews on phytoplankton and zooplankton studies in the North Sea, Reid et al. (1990) and Fransz et al. (1991) describe the distribution of plankton organisms as strongly linked to the hydrography of the North Sea, which is described in detail by Otto et al. (1990). Fransz et al. (1991) summarize the water bodies to be distinguished in relation to zooplankton distribution as follows:

"A large tongue of saline water from the Atlantic Ocean extends from the North into the North Sea between the Orkney islands and the Norwegian Trench, and in South-East direction towards the Dogger bank. The narrow tongue in the Southern Bight, which has the same salinity, is of considerably smaller extent corresponding to the smaller opening of the English Channel into the North Sea. In both areas the salinity reaches more than 35 psu. This water is called 'Atlantic water'. In coastal areas influenced by fresh water runoff salinities less than 34 psu are found. On the West and South-East coast this water is called 'coastal water'. The water masses in the central part of the North Sea, with salinities between 34 and 35 psu are called 'North Sea Water', and originate from the mixing of Atlantic and coastal waters (Böhnecke, 1922)".

The Belgian coastal zone, situated between 51° and 52° N in the Southern Bight of the North Sea (Figure 1), is defined, based on general circulation patterns, as the region limited by streamline 20 10^4 m^3 s^{-1} of the residual current entering from the Channel (Nihoul and Ronday, 1975; Joiris et al., 1982). Within this zone, which extends to about 40 km offshore and is influenced by terrestrial input from the Schelde estuary, salinity is usually less than 33 psu.

Mean depth in the coastal zone is 15 m and turbulence of the water column is so high that even during summer temperature stratification does not take place (Kuipers et al., 1991). Consequently the zone is generally considered as a homogeneous coastal area, to be distinguished from the adjacent open 'North Sea Water' area (Lancelot et al., 1980; Joiris et al., 1982). On a broader geographical scale, it falls within box 4 of the 'Flushing Times Group division of North Sea' (ICES, 1983).

Several sandbanks are situated in the Belgian coastal zone. They are either the result of sand accumulation or erosion and are situated approximately 10 km offshore and lie in the North-Eastern direction parallel to the residual transport (De Moor, 1985).

The observation of considerably higher abundances of piscivorous seabirds on the South-Western part of the Belgian coast, than on the North-Eastern part (Offringa et al., 1995) investigated, since 1994, a series of multidisciplinary ecological surveys to study the underlying trophic structure of the area, and possible differences herein between the various sandbanks.

Within this framework, this paper reports a first series of observations on the distribution of phytoplankton and zooplankton over the Buitenratel, Gootebank and Westhinder sandbank. Sampling took place in February 1994, and as such the results represent the starting conditions for the spring plankton bloom.

2. Materials and methods

2.1 Study area

Figure 3.1 shows the position of the Buitenratel, Gootebank and Westhinder sandbanks within the study area. Sampling stations on each sandbank are indicated in the enlargement.

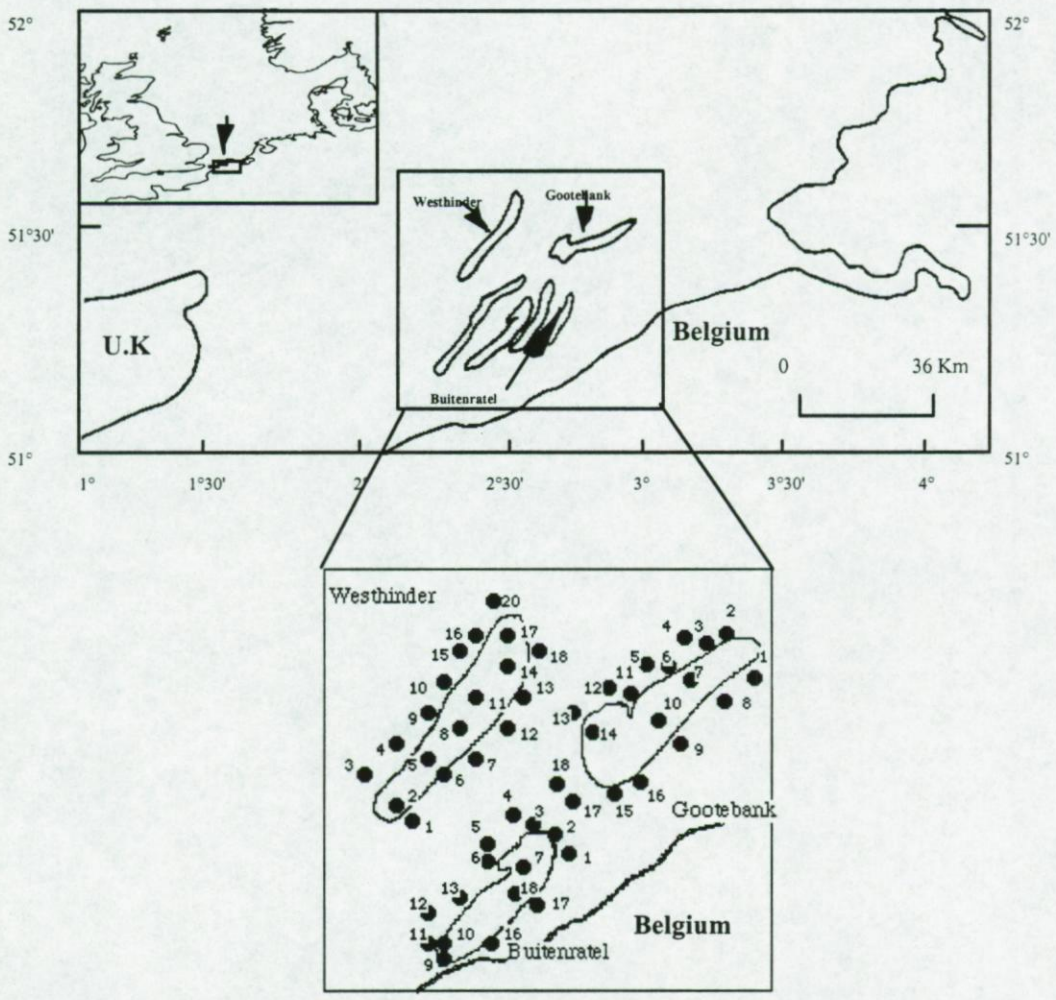

Figure 3.1 Map of Belgian continental Flat showing the sampling stations.

2.2 Sampling

Phytoplankton: Sampling was done on board of the R/V Belgica at twenty stations on each of the three sandbanks on 7 and 8 February 1994.

Water samples were collected with a Niskin bottle at 3 meter depth. Sub-samples of 250 ml were preserved with lugol's solution for phytoplankton counting.

Zooplankton: A plankton net with a mesh size of 300 μm was towed at 3 meter depth, the catch concentrated into a plastic sampling container (± 100 ml), and preserved in 4% formalin solution.

Each sample was given a letter designation followed by a number to represent sampling stations of the sandbanks as; **G** for **G**ootebank, **B** for **B**uitenratel and **W** for **W**esthinder bank. In the following, the sandbanks will be referred to as Gootebank, Buitenratel and Westhinder.

Environmental factors. Temperature, salinity and turbidity were determined with CTD, simultaneous with phytoplankton and zooplankton sampling at each sampling station.

2.3 Laboratory analysis

Phytoplankton: The preserved 250 ml samples were concentrated to 5 ml by decantation. Phytoplankton cells in the concentrated sample were counted with an inverted microscope at 10x20 and 10x40 magnification and species abundance expressed as cells per litre.

Keys and reference books used for identification were Van Heurck (1896); Schiller (1937); Cleve-Euler (1951); Butcher (1961); Hendey (1964); Drebes (1974); Hartley (1986); Pankow (1990) and Tomas (1993). Identification was done down to species or genus level.

Zooplankton: Preserved samples were concentrated to 20 ml by decantation. The concentrated samples were homogenised gently by a magnetic stirrer and 3 ml subsample was pipetted into a petri dish for counting. For some very abundant species, only one 3 ml subsample was counted. For all other organisms, the whole sample was counted. As the volume sampled was unknown species abundance was expressed as percentage of total abundance.

Identification keys used were: Lank (1948), Newell and Newell (1967); Rose (1970); Tattersal et al. (1976); Omori and Ikeda (1984), Klein Breteler (1992) and Gotto (1993). Identification was performed down to species level when possible. Copepod eggs and nauplii and fish eggs were also counted, but not identified.

2.4 Data analysis

Values measured for environmental factors on the 3 banks were compared using ANOVA. Phytoplankton absolute and relative abundances on the different banks were compared by Mann Whitney test.

'Two Way Indicator Species Analysis' (TWINSPAN) (Hill, 1979) was used to analyse the spatial distribution and community structure of phytoplankton and zooplankton over the study area. Species abundance was in both cases expressed as percentage and the default options of the TWINSPAN routine were used throughout the analysis.

Canonical Correspondence Analysis (CCA) using the CANOCO package (Ter Braak, 1987b and 1988) was used to determine the relation between zooplankton abundance and environmental variables. Phytoplankton data were

used as abundance and ln+1 transformed. Downweighing of rare species was performed. Zooplankton data were used in percentage and no transformation or downweighing was performed. Temperature, salinity and turbidity were used as environmental data in case of the phytoplankton analysis. For the zooplankton, CCA analysis, the relative abundance of the phytoplankton families was added to the file of environmental variables. A Monte Carlo test using 999 unrestricted permutations was performed to test the significance of the correlations.

3. Results

Environmental variables: Values of temperature, salinity and turbidity measured on the three sandbanks are given in Figure 3.2a-c. Westhinder showed the highest temperature values (7.66-7.75 °C), followed by Buitenratel (7.36 - 7.48) and Gootebank (7.19-7.30), each mean being significantly different from the other two (ANOVA, $p < 0.05$) (Figure 3.2a). Gootebank and Westhinder had similar salinity values (33.62 - 33.98 and 33.85-33.91 respectively), which were significantly higher than those of Buitenratel (Figure 3.2b). Turbidity values around Gootebank varied from 13 to 26 FTU, with one value being as low as 1 FTU and considered an erroneous reading. Turbidity reading around Westhinder varied between 18 and 20 FTU, with highest values occurring in stations 10-20 and was constant at 20 FTU at all Buitenratel stations (Figure 3.2c). Mean turbidity was higher at Buitenratel than at the two other banks, which did not differ significantly in turbidity.

Phytoplankton: The total of 123 phytoplankton taxa, which were identified, is listed in Table 3.1. Most of these species were typical neritic and pelagic species. Benthic species were rarely found. The results of a comparison of

absolute and relative numerical abundance of phytoplankton divisions between the sandbanks is shown in Table 3.2 and Figure 3.3 respectively.

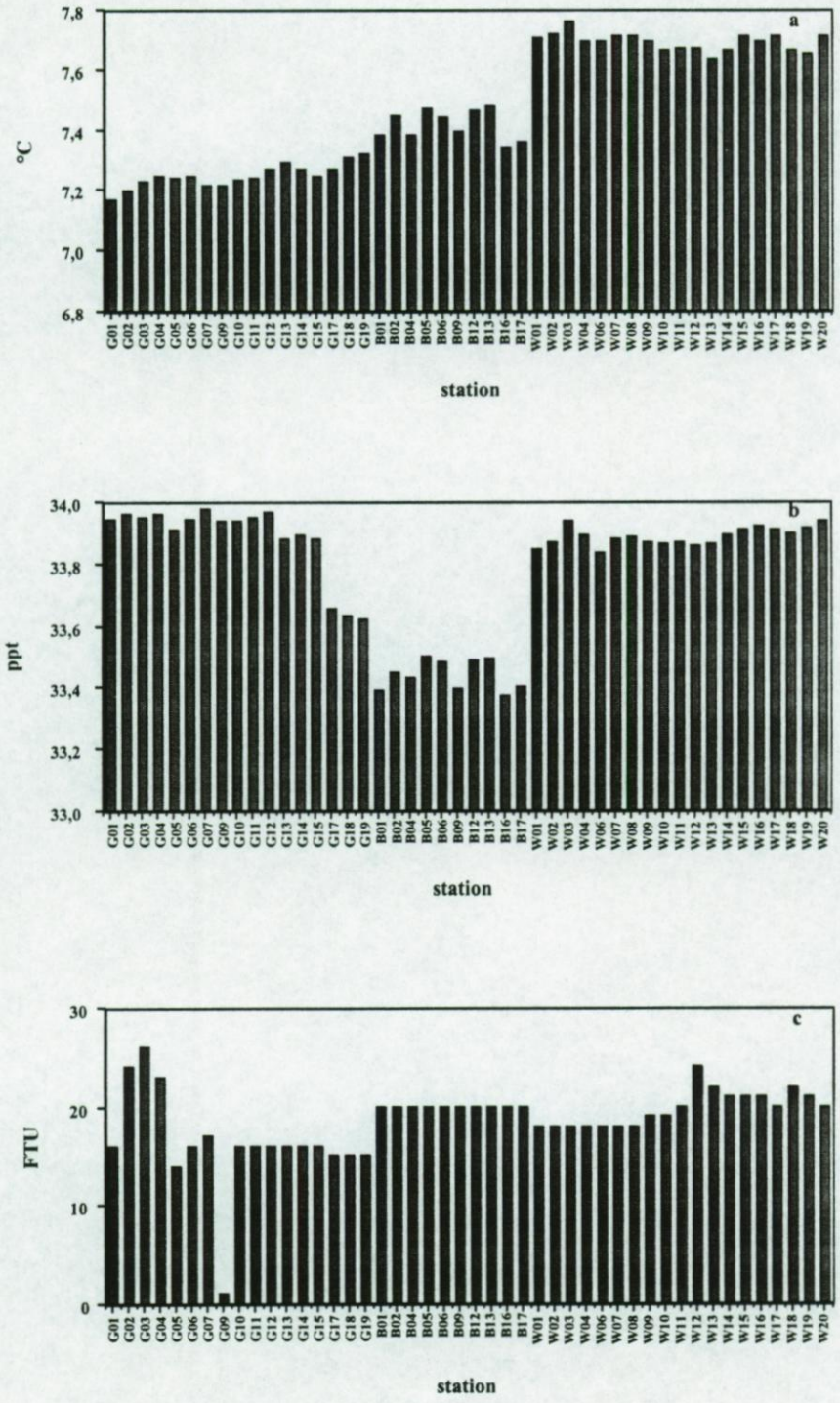

Figure 3.2 Environmental factors measured at the three sandbanks: (a) temperature; (b) salinity; (c) turbidity.

Table 3.1 List of phytoplankton species observed and abbreviation used in Figures 4.9, 4.10 and 4.11 (Chapter 4)

Division: Chrysophyta		
Class: Bacillariophyceae		
Order: Centrales		
Odontella	*aurita* (Lyngb.) Ag.	(Odo aur)
	granulata (Roper) R. Ross	(Odo gra)
	mobiliensis (Bail.) Grun.	(Odo mob)
	rhombus (Ehrenb.) Kütz.	(Odo rho)
	regia (Schiltze) Simonsen.	(Odo reg)
	sinensis (Grev.) Grun.	(Odo sin)
Paralia	*sulcata* (Ehrenb.) Cleve.	(Par sul)
Aulacoseira	*distans* (Ehrenb.) Simonsen.	(Aul dis)
	granulata (Ehrenb.) Simonsen.	(Aul gra)
Skeletonema	*costatum* (Grev.) Grun.	(Ske cos)
Cyclotella	*comta* (Ehrenb.) Kütz.	(Cyc com)
Stellarima	*stellaris* (Roper) Hasle & Sims.	(Cos ste)
Coscinodiscus	*radiatus* Ehrenb.	(Cos rad)
	centralis Ehrenb.	(Cos cen)
Psammodiscus	*nitidus* (Greg.) Round et Mann	(Psa nit)
Eucampia	*zoodiacus* Ehrenb.	(Euc zoo)
Thalassiosira	*leptopus* (Grun. in Van Heurck) Fryxell et Hasle	(Tha lep)
	eccentricus (Ehrenb.) Cleve	(Tha ecc)
	fallax Meunier.	(Tha fal)
	rotula Meunier.	(Tha rot)
Schroederella	*schroederi* (Bergon) Pavillard.	(Sch sch)
Ditylum	*brightwellii* (West.) Grunow.	(Dit bri)
Leptocylindrus	*danicus* Cleve.	(Lep dan)
	minimus Gran.	(Lep min)
Actinoptychus	*octonarius* Ehrenb.	(Act chr)
Actinocyclus	*octanorius* Ehrenb.	(Act oct)
Corethron	*criophilum* Castr..	(Cor cri)
Rhizosolenia	*delicatula* Cleve	(Rhi del)
	setigera Brightw.	(Rhi set)
	hebetata (Bail.) Gran.	(Rhi heb)
	shrubsolei	(Rhi shr)
	imbricata Brightw.	(Rhi imb)
Guinardia	striata (*stolterfoth*) Hasle.	(Gui sto)
	pungens Cleve-Euler.	(Rhi pun)
Proboscia	*alata* (Brightw.) Sundström.	(Pro ala)
Triceratium	*antediluvianum* (Ehrenb.) Grun.	(Tri alt)
	favus Ehrenb.	(Tri fav)
Chaetoceros	*danicus* Cleve.	(Cha dan)
	didymus Ehrenb.	(Cha did)
	crinitus Schutt.	(Cha cri)
	pseudosimilis Cleve	(Cha pse)
	fragilis Meunier	(Cha fra)
	compressus Lauder.	(Cha comp)
Order: Pennales		
Striatella	*unipunctata* (Lyngb.) Ag.	(Str uni)
Rhaphoneis	*amphiceros* Ehrenb.	(Rha amp)
	belgica Grun.	(Rha bel)
Delphineis	*surirella* (Ehrenb.) G. W. Andrews.	(Del sur)
Brockmanniella	*brockmannii* (Hust.) Hasle, Von Stosch & Syvertsen	(Bro bro)

Pleurosigma	*normanii* Ralfs in Pritchard.	(Ple nor)
	angulatum Hendey.	(Ple ang)
	nubecula W. Sm.	(Ple nub)
	var. intermedium (W. Sm.) Cleve	(Ple int)
	naviculaceum Bréb.	(Ple nav)
Ctenophra	*pulchella* (Ralfs ex Kütz.) Williams et Round	(Cte pul)
Synedra	*ulna* Ehrenb.	(Syn uln)
	acus Cleve after V. Heurck	(Syn acu)
	pelagica Cleve	(Syn pel)
Thalassionema	*nitzschioides* Grunow.	(Tha nit)
Asterionellopsis	*glacialis* (Castracane) Roundin Round al.	(Ast gla)
Asterionella	*kariana* Grun. in Cleve et Grun.	(Ast kar)
Achnanthes	*danica* (Flögel) Grun. in Cleve et Grun.	(Ach dan)
	parvula Kütz.	(Ach par)
Diploneis	*bombus* (Ehrenb.) Cleve	(Dip bom)
	didyma (Ehrenb.) Cleve	(Dip did)
	lineata (Donk.) Cleve	(Dip lin)
	oculata (Bréb.) Cleve	(Dip ocu)
Amphora	*alata* Per.	(Amp ala)
	proteus (Greg.) Cleve	(Amp pro)
Amphiprora	*alata* Ehrenb.	(Ampr ala)
Navicula	*distans* W. Sm. after Grunow.	(Nav dis)
	crytocephala Kütz.after Cleve.	(Nav cry)
	tripunctata (Müller.) Bory.	(Nav tri)
Navicula	*marina* Ralfs in Pritch	(Nav mar)
Pinnularia	*major* (Kütz.) W. Sm.	(Pin maj)
Haslea	*ostrearia* (Gaillon) Simonsen.	(Has ost)
Meuniera	*membranacea* (Cleve) Silva.	(Str mem)
Trachyneis	*aspera* (Ehrenb.) Cleve	(Tra asp)
Bacillaria	*paxillifer* (Müller.) Hendey	(Bac pax)
Nitzschia	*longissima* (Bréb.) Ralfs.	(Nit lon)
	dissipata (Kütz.) Grun.	(Nit dis)
	sigma (W. Sm.)	(Nit sig)
	tryblionella (Hantzsch.)	(Nit try)
	gracilis (Hantzsch.)	(Nit gra)
Pseudonitzschia	*seriata* (Cleve) H. et M. Perag.	(Nit ser)
	delicatissima (Cleve) Heiden in Heiden et Kolbe.	(Nit del)
Psammodictyon	*panduriforme* (Greg.) Mann	(Pse pan)
Class: Chrysophyceae		
Distephanus	*speculum* (Ehrenb.) Haeckel	(Dis spe)
Telonema	*subtilis* Griessmann 1913	(Tel sub)
Metromonas	*simplex* (Griessmann) Larsen & Patterson 1990	(Met sim)
Cafeteria	*minuta* (Ruinen) LARSEN & Patterson 1990.	(Caf min)
Pseudobodo	*tremulans* Griessmann 1913.	(Pse tre)
Bodo	*parvulus* Griessmann 1913.	(Bod pur)
Class: Haptophyceae		
Phaeocystis	*sp*	(Pha spe)
Imantonia	*rotunda* Reynolds 1974	(Ima rot)
Class: Rhaphidophyceae		
Oltmannsia	*viridis* Schiller 1925	(Olt vir)
Division: Pyrrophyta		
Class: Dinophyceae		
Order: Prorocentrales		

Prorocentrum (Pro mic)	*micans* Ehrenb.	
Exuviella	sp Ehrenberg	(Exu spe)
Order: Peridiniales		
Peridinium	*brevipes* (Pauls.) Lebour	(Per bre)
	punctulatum Paulsen	(Per pun)
	curvipes Ostenfeld	(Per cur)
Peridinium	sp. Drebes	(Per sp)
Pyrophacus	*horologium* Stein	(Pyr hor)
Amphidinium sp	Conrad & Kufferath, 1954	(Amp sp)
Diplopsalis	*minor* (Pauls.) Pavillard	(Dip min)
Dissodinium	*assymmetricum* (Mangin) Loeblich III	(Dis asy)
Maniscula	*bipes* (PAULS.) Lebour	(Man bip)
Gymnodinium	sp. Conrad & Kufferath, 1954	(Gym spe)
Ceratium	*lineatum* (Ehrenb.) Cleve.	(Cer lin)
Division: Crytophyta		
Class: Cryptophyceae		
Hemiselmis	*virescens* Droop 1955	(Hem vir)
Cryptomonas	sp.,Tomas	(Cry spe)
Chroomonas	*marina* (Buttner) Butcher 1967	(Chr mar)
Rhodomonas	sp. Karsten	(Rho spe)
Hillea	*fusiformis* (Schiller) Schiller1925	(Hil fus)
Hillea	*marina* Butcher 1925	(Hil mar)
Leucocryptos	*marina* (Braaud) Butcher 1976	(Leu mar)
Rhinomonas	*fulva* (Butcher) Hill & Wetherbee	(Rhi ful)
Teleaulax	*acuta* (Butcher) Hill 1991	(Tel acu)
Division: Euglenophyta		
Class: Euglenophyceae		
Eutreptia	*sp*, Tomas, 1973	(Eut spe)
Eutreptiella	*hirudoidea*, Butcher, 1961	(Eut hir)
	marina, da Cunha 1914	(Eut mar)
Euglena	*sp*. Butcher, 1961	(Eug spe)
Phacus	*triqueter* Butcher, 1961	(Pha tri)
Scenedesmus	*quadricauda* (Turpin) Bréb. Et Goday	(Sce qua)
Crucigenia	*tetrapedia* (Kirchner) W. et G. S. West	(Cru tet)
Division: Chlorophyta		
Class: Prasinophyceae		
Micromonas	*pusilla* (Butcher) Manton & Parke 1660	(Mic pus)
Pyramimonas	*sp*. Tomas, 1973	(Pyr spe))
Resultor	*mikron* (Throndsen) Moestrup 1991	(Res mik)
Tetraselmis	*suecica* (Kylin) Butcher.	(Tet sue)
Class: Chlorophyceae		
Chlamydomonas	*reginae* Ettl & Green 1973	(Chl reg)
	coccoides Butcher 1959	(Chl coc)
Dunaliella	*tertiolecta* Butcher 1959	(Dun ter)
Coccolithophorids		
Acanthoica	*aculeata* Kamptner	(Aca acu)
Crystallolithus	*hyalinus* Gaarder & Markali	(Cry hya)
Syracolithus	*dalmaticus* (Kamptner) Loeblich & Tappan	(Syr dal)

Table 3.2 The results of Mann Whitney-U test comparing abundance of main groups of phytoplankton on the Gootebank (G), Westhinder (W), and Buitenratel (B) (* p<0.05, ** p<0.01).

Groups	G & B	W & G	W & B
Chlorophyta	G > B**	W > G**	W > B**
Chrysophyta	no	W < G*	W < B*
Pyrrophyta	no	no	no
Cryptophyta	no	W > G*	W > B**
Euglenophyta	G < B*	W < G**	W < B**

Except for Pyrrophyta, the abundance of each of the phytoplankton groups was significantly different between Westhinder and the two other sandbanks (ANOVA, $p < 0.05$). Only Chlorophyta and Euglenophyta showed significant differences in abundance between Gootebank and Buitenratel (Table 3.2).

Euglenophyta and Chrysophyta (mainly composed of diatoms) had the highest relative abundance on all sandbanks (Figure 3.3). The dominance of Euglenophyta and to a smaller extent of Chrysophyta was somewhat reduced on Westhinder in comparison to the two other banks. On Westhinder Chlorophyta and Cryptophyta were relatively more important.

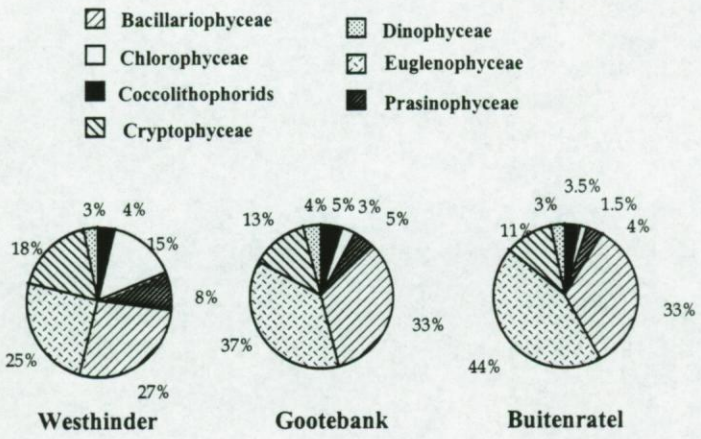

Figure 3.3. Percentage numerical abundance distribution of phytoplankton taxa at the three sandbanks.

The dendrogram for the TWINSPAN analysis of the phytoplankton abundance (Figure 3.4) showed a clear splitting, with a first division separating Westhinder from the 2 other sandbanks with indicator species *Chlamydomonas coccoides* (Chlorophyceae), *Metromonas simplex* (Chrysophyceae) and *Resultor mikron* (Prasinophyceae). The left hand split consisted of Gootebank and Buitenratel stations with *Rhizosolenia hebeteta* (Bacillariophyceae) as indicator species. A second division splitted Buitenratel-samples from those of Gootebank. Three Westhinder stations were included with the Gootebank cluster.

Zooplankton: 42 zooplankton taxa were identified most of which down to species or genus level, some at higher levels. The list of taxa is given in Table 3.3.

Copepods were strongly dominant constituting over 90% of numerical zooplankton abundance in all stations. At the species level dominant copepod species were *Temora longicornis* around

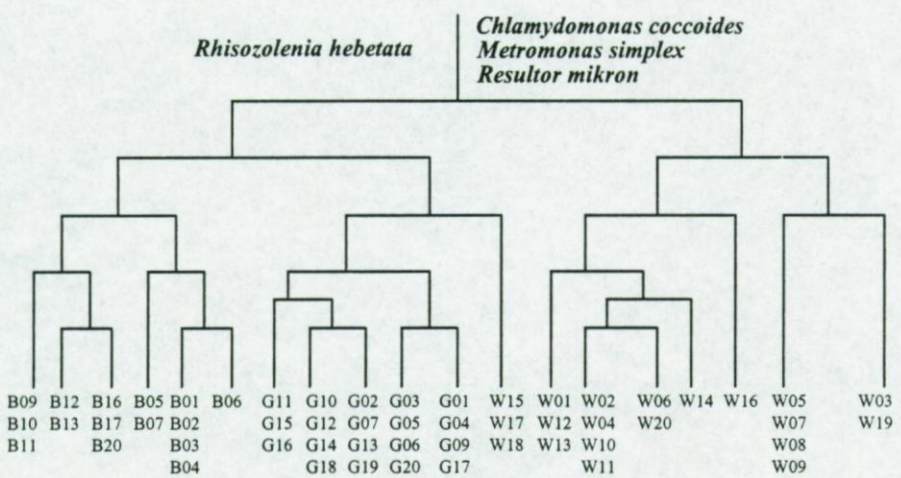

Fig 3.4 Twinspan analysis dendogram for phytoplankton on the Buitenratel, Gootebank and Westhinder stations.

Gootebank (72%), Buitenratel (59%) and Westhinder (54%). *Pseudocalanus elongatus* had the highest percentual abundance on Westhinder (41%) compared to Buitenratel (38%) and Gootebank (18%). *Centropages hamatus* contributed 6% to copepod abundance on Gootebank and only 2% on Westhinder and 1% on Buitenratel (Figure 3.5).

Other species that were regularly occurring around all sandbanks, but in smaller numbers, were: *Acartia clausi*, *Paracalanus parvus* and *Calanus helgolandicus*. *Centropages typicus* occurred only on Westhinder.

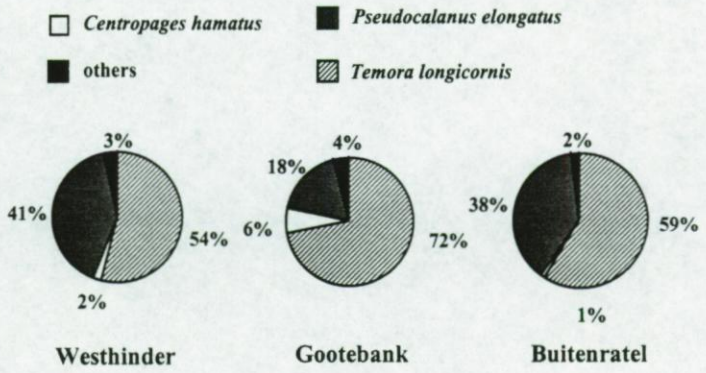

Figure 3.5 Percentage distribution of dominant copepods species at the three sandbanks. (Others: *Acartia clausi*, *Centropages hamatus* &*Pseudocalanus parvus*)

TWINSPAN analysis showed a quite undistinctive division of the three sandbanks (Figure 3.6). While there was a clear splitting in two clusters, stations of all banks occurred in both of these clusters.

The three dominant species, *T. longicornis*, *P. elongatus* and *C. hamatus*, which were abundant at all sandbanks, were excluded from the analysis to look for any specific patterns in the less abundant species. The original relative abundances of the remaining taxa were maintained because the relative abundance reflects the importance of a particular taxon in the study area.

Table 3.3 List of zooplankton taxa observed

Phylum: Cnidaria

Class: Hydrozoa

Order: Hydroida

3 unidentified species

Phylum: Ctenophora

Class: Tentaculata

Order: Cydippida

Pleurobrachia pileus O.F. Muller, 1776

Phylum: Annelida

Class: Polychaeta Grube, 1850

Order: Errantia Audouin & MILNE EDWARDS, 1832

Family: Syllidae Grube, 1850
Procerae cornuta (AGASSIZ, 1862)
Family: Spionidae G. O. Sars, 1872
Spionid sp.
Family: Polynoidae MALMGREN, 1867
Lepidonotus sp.
Family: Phyllodocidae WILLIAMS, 1852
Phyllodoce sp.
Family: Terebellidae MAMLGREN, 1865
Terebellia sp.

Phylum: Mollusca

Class: Bivalvia
Order: Anasomyaria

Family: Mytiladae
Mytilus edulis

Class Gastropoda

Order: Mesogastropoda

Family: Littorinidae
Littorina sp.

Phylum: Arthropoda

Sub Phylum: Crustacea
Class: Copepoda Edwards, 1840

Order: Calanoida Sars, 1903
Family: Acartiidae Sars, 1903
Acartia clausi Giesbrecht, 1889
Acartia longiremis Lilljeborg, 1853
Family: Temoridae Giesbrecht, 1892
Temora longicornis O. Fr. Muller, 1792
Family: Pseudocalanidae
Pseudocalanus elongatus Boeck, 1872
Family: Pseudocyclopidae Sars, 1902
Pseudocyclopsobtusatus (Brady & Robertson, 1873)
Family: Centropagidae Giesbrecht, 1892
Centropages hamatus Lilljeborg, 1853
Centropages typicus Kroyer, 1849
Family: Calanidae Dana, 1849
Calanus finmarchicus Gunner, 1765
Family: Paracalanidae Giesbrecht, 1892
Paracalanus parvus Claus, 1863

Order: Harpacticoida Sars, 1903

Family: Euterpinidae Boeck, 1864
Euterpina acutifrons Dana, 1852
Family: Longipediidae Brady, 1880
Longipedia helgolandica Klie, 1949

Order: Poecilostomatoida Thorell, 1859

Family: Corycaeidae Dana, 1852
Corycaeus ditrichocorycaeus anglicus Dana,1849
Family: Clausisiidae Giesbrecht, 1895
Hemicyclops purpureus Boeck, 1872

Order: Siphonostomoida Thorell, 1859

Family: Asterocheridae Giesbrecht, 1899
Acontiophorus scutatus Brady & Robertson, 1873

Order: Thoracica Darwin, 1854

Family: Balanidae LEACH, 1806
Balanus sp.

Class: Malacostraca LATREILLE, 1806

Order: Decapoda LATREILLE, 1803

Family: Crangonidae HAWORTH, 1825
Crangon crangon Sars, 1890
Family: Paguridae LATREILLE, 1803
Pagurus bernhardus (LINNAEUS, 1758)
Family: Portunidae RAFINESQUE, 1825
Portunus puber (LINNAEUS, 1758)

Order: Mysidacea BOAS, 1883

Family: Mysidae DANA, 1850
Sriella jaltensis Czerniavsky, 1868
Anchialina agilis (0.G. Sars, 1877)
Mesopodopsis slaberri (P.J. van Beneden, 1861)
Gastrosaccus spinnifer (Goes, 1864)
Schistomysis spiritus (Norman, 1860)

Order: Amphipoda LATREILLE, 1816

Family: Hyperiidae H. MILNE EDWARDS, 1830
Hyperia galba Montagu, 1815

Order: Cumacea KROYER, 1846

Family: Pseudocomatidae G.O. Sars, 1878
Pseudocoma longicornis Bate, 1858

Class: Branchiopoda LATREILLE, 1817

Order: CLADOCERA LATREILLE, 1829

Family: PODONIDAE MORDUKHAI-BOLTOVSKI, 1968
Evadne nordmani LOVEN, 1836

Phylum: Chaetognatha

Sagitta elegans Verrill, 1873
Spadella sp. J. Muller, 1847

Phylum: Chordata

Class: Appendiculata

Order: Appendicularia

Family: Oikopleuridae
Oikopleura sp. Lohman, 1896

Subphylum: Vertebrata

Class: Ostiechthyes

Order: Clupeiformes

Family: Clupeidae
Clupea harengus L. Kuffer, 1878
Clupea sprattus L. Hensen, 1883

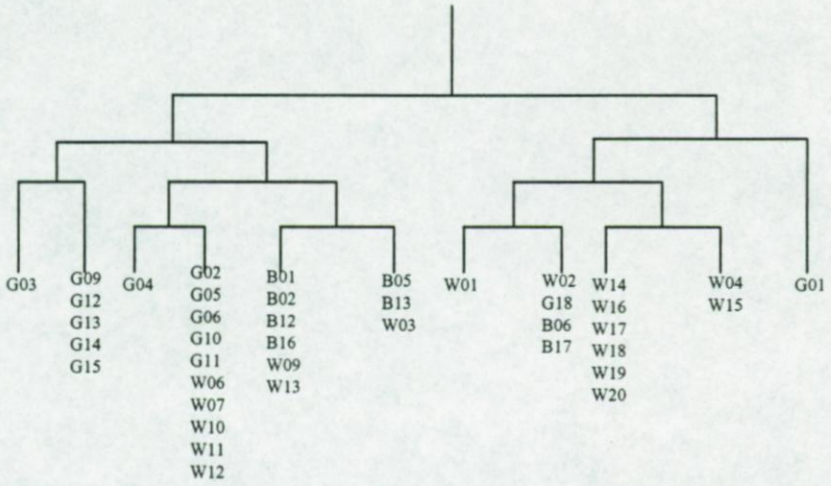

Figure 3.6 Twinspan analysis dendogram for all zooplankton species on the Buitenratel, Gootebank and Westhinder stations.

The dendrogram of TWINSPAN analysis for the remaining taxa showed a clearer split between three sandbanks (Figure 3.7). The right side cluster contained all stations from the Westhinder with *Clupea harengus* and *Sprattus sprattus* larvae as indicator species. The split on the left side of the diagram with *Paracalanus parvus* as indicator species consisted of two subclusters. The cluster on the left hand side with a medusa species and the ctenophore *Pleurobrachia pileus* as indicator species represented mostly Gootebank stations. The cluster on the right side mainly represented Buitenratel stations and the remainder of the Gootebank stations.

The plots for species and sample scores as a result of the CCA analysis on the total zooplankton dataset are shown respectively in Figure. 3.8a and 3.8b. Eigenvalues percentage explained variance and correlations coefficients with environmental factors for the first 4 axis are given in Table 3.4. Monte Carlo testing showed the variance in zooplankton species data to be explained in descending degree by temperature (9%, p= 0.01), Euglenophyceae abundance

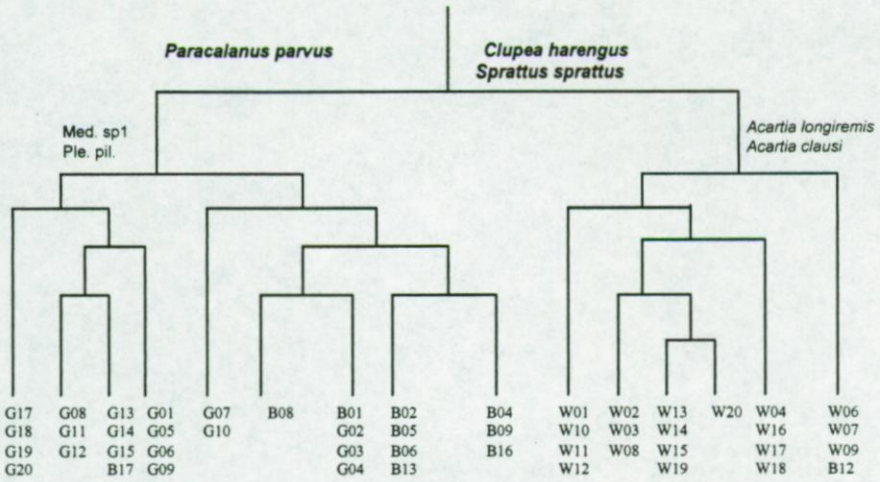

Figure 3.7 Dendogram from Twinspan analysis of zooplankton, excluding dominant species.

(3%, p= 0.01), salinity (2%, p= 0.02), and Chlorophyceae abundance (2%, p= 0.04). Temperature was highly correlated with axis 1, and salinity with axis 2. Gootebank stations were found on the left side of axis 2, with the majority of stations situated below axis 1. Westhinder stations were situated to the right of axis 2 while Buitenratel stations are distributed along the lower part of axis 2, in between Gootebank and Westhinder stations. Arrows for Euglenophyceae and diatoms point to the same direction, the lower left quadrant while Chlorophyceae, in the upper right quadrant, are associated with increasing salinity and temperature. Further details on the association between phytoplankton groups and physical environmental factors can be seen from the correlation matrix of environmental variables shown in Table 3.5. Figure 3.8b shows that the most dominant copepod species, *T. longicornis* and *C. hamatus* were found close to the centre of the plot, while *P. elongatus* was more associated with Gootebank stations. Also close to the centre of the plot, on the

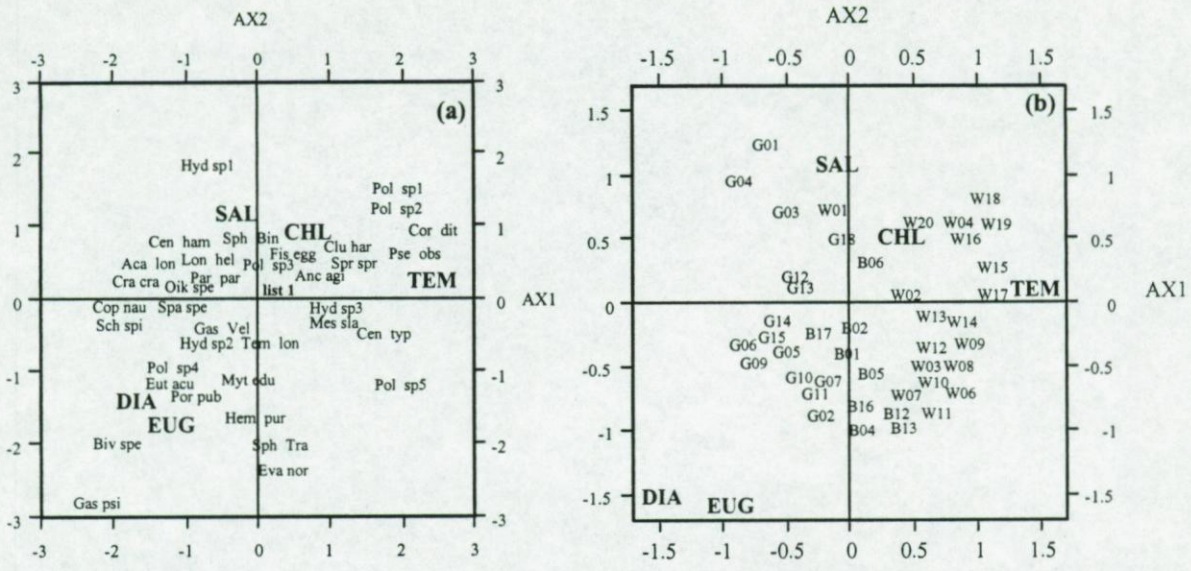

Figure 3.8 CCA analysis of zooplankton relative species abundance with respect to environmental factors: (a) Species biplot: List 1, including species which are close together: *Acartia clausi*, *Barnacle* larvae, *Calanus finmarchicus*, Copepod eggs, *Hyperia galba*, *Pagurus bernhardus*, *Lepidonotus*, *Proceraea cornuta*, *Pseudocalanus elongatus*, *Pseudocalanus longicornis*, *Sagitta elegans*, *Sirella jaltensis*, and Single species in the plot are, Aca lon = *Acartia longiremis*, Anc agi = *Anchialina agilis*, Biv spe = Clams, Cen ham = *Centropages hamatus*, Cen Typ = *Centropages typicus*, Clu har = *Clupea harengus*, Cop nau = Copepod nauplii, Cor dit = *Corycaeus ditrichocorycaeus angtlicus*, Cra cra = *Crangnon crangnon*, Eut acu = *Eutrepina acutifrons*, Eva nor = *Evadne nordmani*, Fis egg = Fish eggs, Gas psi = *Gastrosaccus spinnifer*, Gas Vel = Veliger larvae, Hem pur = *Hemicyclops purpureus*, Hyd sp1 = Hybocodon, Hyd sp2 = *Steenstrupia nutans*, Hyd sp3 = *Cladonema radiatum*, Lon hel = *Longipedia helgolandica*, Mes sla = *Mesopodosis slaberri*, Mut edu = *Mytilus edules*, Oik spe = *Oikopleura*, Par par = *Paracalanus parvus*, Pol sp1 = *Terebellia*, Pol sp2 = *Polychaete*, Pol sp3 = *glyceriid* larvae, Pol sp4 = Phyllodocidae, Pol sp5 = *Polychaete*, Por pub = *Portunus puber*, Pse obs = *Pseudocyclops obstusatus*, Tem lon = *Temora longicornis*, Sch spi = *Schistomysis spiritus*, Spa spe = *Spadella* species, Sph Bin = *Bolinopsis infundibulum*, Sph Tra = *Trachymedusae*, Spr spr = *Sprattus sprattus*, and Environmental factors are : CHL = Chlorophyceae, DIA = Diatoms, EUG = Euglenophyceae, SAL = Salinity, TEM = Temperature. (b) Stations biplot.

Westhinder side, was a list comprising the calanoid *C. typicus*, polychaete larvae, fish eggs and larvae of *C. harengus* and *S. sprattus*. More typically associated with Westhinder were Polychaete species, the calanoid *Pseudocyclops obtusatus* and the Poecilostomatoid *Corycaeus ditrichocorycaeus anglicus*.

Table 3.4 Weighed correlation matrix (inter-set correlation) showing relationship between zooplankton species axes and environmental variables: (1) CCA analysis with temperature, salinity, turbidity and phytoplankton taxa as environmental factors, (2) CCA analysis without phytoplankton taxa.

Axis	1	2	3	4
Eigenvalues:				
(1)	0.103	0.039	0.026	0.019
(2)	0.095	0.021	0.016	0.018
Cummulative pecentage variance of species-environment relation:				
(1)	72	88	100	0
(2)	71.8	87.9	100	0
Correlation coefficient:				
(1) Temperature	0.90	0.02	0.09	0.11
(1) Salinity	-0.024	0.32	0.05	0.69
(1) Euglenophyceae	-0.39	-0.48	0.3	-0.24
(1) Chlorophyceae	0.12	0.15	0.43	0.23

Table 3.5 Weighed correlation matrix (intra-set correlation) for environmental variables used in canonical correspondence analysis. DIA=Diatoms, DIN= Dinophyceae, CRS= Crysophyceae, CRP= Cryptophyceae, EUG= Euglenophyceae, PRA= Prasinophyceae, CHL= Chlorophyceae,RHA= Rhaphidophyceae, HAP= Haptophyceae, COCCOLIT= Coccolitophorids, Sal= Salinity, Tem= Temperature, and Tur= Turbidity.

DIA	1.0000												
DIN	.1642	1.0000											
CRS	-.3502	.1916	1.0000										
CRP	.0175	.3535	.4446	1.0000									
EUG	.6684	.0897	-.2908	-.0184	1.0000								
PRA	-.1389	.4193	.7747	.3531	-.0835	1.0000							
CHL	-.2483	.0766	.5948	.2971	-.1267	.5141	1.0000						
RHA	.1808	-.1067	-.2230	-.1610	.1290	-.0870	-.2087	1.0000					
HAP	.0345	.1368	.2895	.1789	-.2874	.1058	.0642	.0352	1.0000				
COCCOLIT	-.0672	.2682	.1123	.0806	-.0649	.2556	.0512	.2431	-.0530	1.0000			
Sal	-.3066	.1629	.3339	.1150	-.4814	.3936	.1804	.1789	.2709	.1597	1.0000		
Tem	-.5693	-.0301	.6229	.3001	-.4199	.4217	.4191	-.1087	.1302	.1761	.0476	1.0000	
Tur	-.2338	.0602	.0797	.0353	.0709	.0663	.0272	.1051	-.0552	.0484	-.1552	.3297	1.0000
	DIA	**DIN**	**CRS**	**CRP**	**EUG**	**PRA**	**CHL**	**RHA**	**HAP**	**COCC-OLIT**	**Sal**	**Tem**	**Tur**

4. Discussion

Most of the phytoplankton species reported in this study are common in the coastal waters of Atlantic Ocean (Reid et al., 1990) and have been mentioned before by previous investigators around the Belgian coastal zone (Louis et al., 1974; Louis and Smeets, 1981).

Louis and Smeets (1981) report phytoplankton cell numbers in the same area from February 1974 till 1978. They observe a considerable variation in species composition from year to year and find diatoms to be dominant and already blooming as early as February. Euglenophyceae are more abundant in November and Chlorophyceae in October and November (Louis et al., 1974). Lancelot and Mathot (1987), mention that diatoms are the dominant phytoplankton species in February in coastal waters of the Belgian coastal zone.

Our data show that, within the area covered by the three sandbanks studied, clear spatial heterogeneity in phytoplankton - and to a smaller extent zooplankton species composition occurred.

As shown by the subsequent splittings in the TWINSPAN analysis (Figure 3.4), the phytoplankton community of the Westhinder differed most strongly from that of the Gootebank and Buitenratel, which were nevertheless also different from each other. Although salinity, temperature and turbidity differences observed between the sandbanks were rather limited, these differences in environmental factors measured can explain the differences in species distribution and

abundance. Indeed, phytoplankton species distribution was shown to be significantly related to all three factors.

These differences in environmental conditions can be explained by the positioning of the banks. The Westhinder, positioned furthest from the coast, is obviously influenced by the Southern intrusion of Atlantic water, which explains the higher temperature and salinity values observed on this bank compared to values measured on the other banks positioned closer to the coast.

As shown in Figure 3.3, the main difference in phytoplankton composition -in general terms- was a predominance of Chrysophyta (with diatoms as strongly dominant family) and Euglenophyta at the coastal banks, which was partially replaced by Chlorophyta on the Westhinder bank. This could be due to the above mentioned environmental conditions, possibly combined with a number of other factors such as the amount of nutrients and pollution associated with the freshwater influence on the coastal zone (Leewis, 1985) as opposed to the Atlantic influenced Westhinder area.

Plankton samples from shallow, turbulent water, often contain benthic diatoms (most of them being pennate diatoms) which have been whirled up into the water (Newell and Newell, 1967). The Buitenratel area, with an average minimum depth of 4-7 m, is less deep than the Gootebank which has a water depth of 12 m at the centre of the bank (Lanckneus et al., 1993). Turbidity is quite high and constant at all Buitenratel stations, but more variable at Gootebank stations (Figure 2.3c). We compared the ratio of the centric diatoms to pennate diatoms in

Buitenratel and Gootebank samples. The ratio was significantly (Mann Whitney-U test, p=0.013) higher at Gootebank than at Buitenratel. Thus, the split between Buitenratel and Gootebank, is probably due to a more important contribution of benthic phytoplankton species in the shallower Buitenratel area.

Also the zooplankton species observed are known to be common species from the North Sea (reviewed by Franz et al., 1991; Hay et al., 1991; Hay, 1995) as well as from the Channel (Le Fèvre-Lehoërff et al., 1983; Brylinsky et al., 1988). The dominant species, the copepods *T. longicornis, Pseudocalanus elongatus* and *Centropages hamatus* were observed on all banks, resulting in a higher degree of mixing of stations of the various banks in the TWINSPAN analysis than was observed from the phytoplankton data. Williams et al. (1993), studied spatial patterns in phyto- and zooplankton data from continuous plankton records collected in the North Sea between 1984 and 1987, in the area between 44° N and 60° N. From their cluster analysis, they also report a higher similarity in zooplankton than in phytoplankton species composition.

Omitting the dominant species from the CCA analysis revealed a different zooplankton species composition between Westhinder and the two coastal banks. Herring and Sprat larvae were the indicator species for the Westhinder in the TWINSPAN dendogram. Herring spawn in the Central and Northern North Sea during August-September, and in the Southern Bight and the English Channel between November and January, and are carried towards the continental coast during the remainder of winter (Bartch et al., 1989 and references therein). Other species typically occurring at Westhinder were the calanoids *C. typicus*,

Pseudocyclops obtusatus polychaete larvae and the Poecilostomatoid *Corycaeus ditrichocorycaeus anglicus*. *C. typicus* is known to be an indicator of Atlantic temperate water, which can also be common more inshore (Fransz et al., 1991). Hay et al. (1991) describe the species as common in mixed coastal and oceanic waters. The presence of polychaete larvae and *Corycaeus ditrichocorycaeus anglicus*, a benthic-parasitic species, are consistent with the rather high turbidity values measured at stations 10 - 20 of Westhinder. Not considering the dominant copepods, Gootebank and Buitenratel zooplankton species composition also differed, although some degree of mixing remained to be observed in the positioning of the stations in the TWINSPAN dendogram. Species typically associated with Buitenratel were the cladoceran *E. nordmani,* a medusae species and mussel larvae.

The phytoplankton and zooplankton data presented here show that the different sandbanks studied harboured different planktonic populations at the end of winter 1994. Salinities measured at the three banks were all below 34 psu and as such the study area could be considered as 'coastal water'. Differences in salinity and temperature values observed were maximally 0.61 psu and 0.56 °C respectively. Nevertheless, the area studied apparently covered the bordering line or mixing zone of two water masses in which different planktonic communities were surviving. Westhinder was clearly within the Atlantic water influence, in contrast to the two coastal banks, Gootebank and Buitenratel. The latter nevertheless also differed from each other in both phytoplankton and zooplankton populations, probably because of the shallower depth at Buitenratel than at Gootebank. Running the CCA with only physical environmental variables reduced

the eigenvalue of the first axis from 0.103 to 0.095 and explained percentage variation in species data from 72.0 to 71.8 for the first 4 axis (Table 3.4). Thus the significant association of some phytoplankton groups with zooplankton species distribution can be considered a consequence of their covariation with the physical environmental factors. A similar separation of planktonic populations has been reported by Brylinsky (1986) and Brylinsky et al., (1988), who studied copepod species composition, abundance and size distribution of *T. longicornis* and *A. clausi* in a transect of the Channel between Boulogne-sur-mer and Dover. They demonstrate a discontinuity in copepod species abundance and distinct differences in developmental stage and size distribution of *T. longicornis* between the coastal waters on the one hand, and the open sea waters on the other. In their study however, the separation of the two communities is associated with an abrupt increase in salinity from below to above 34 psu, indicating poor mixing of the coastal and open sea water masses (Quisthoudt et al., 1987; Brylinsky et al., 1988). In front of the Belgian coast, stronger mixing of these two water bodies could be occurring because of the limited depth, presence of sandbanks and of the gyre circulation induced by the Schelde estuary (Joiris et al., 1982).

Apart from the detailed phytoplankton studies performed by Louis et al. (1974) and Louis and Smeets (1981), the spatial heterogeneity in plankton communities in front of the Belgian coast is little documented in open literature because most spatial studies consider the South-Eastern part of the North Sea as one compartment (e.g. box 4 of the 'Flushing Times Group division of North Sea' (ICES, 1983). Our early February observations represent the end of the over wintering season, during which feeding activity of the zooplankton is known to be

low or non existing. Nevertheless Hay et al. (1991; 1995), studying egg production of the dominant copepod species in the North Sea between 54° and 60 ° N, show that *C. typicus*, *T. longicornis*, *P. elongatus* and *P. parvus* all have a limited but continuous production during winter, the latter three species showing a substantial production in February, especially in the Southern part of their study area. Hay (1995) also demonstrates that production rates of copepods do not correlate with temperature or chlorophyll concentrations, suggesting that the relationship between primary and secondary production is complicated by copepod omnivory and selective feeding. Differences in phytoplankton species composition such as the stronger dominance of Euglenophyta in the coastal zone as opposed to a higher abundance of Chlorophyta and Prasinophyta in the Atlantic waters may represent a considerable difference in the feeding conditions to the zooplankton. The dominant copepod species are found at all three sandbanks and the continuous production during winter need not necessarily reflect active feeding during this period. Nevertheless our data suggest that within the area covered by the Belgian coastal sandbanks, 'starting positions' for the plankton spring bloom are considerably heterogeneous.

Acknowledgements

The authors are indebted to R. Vanthomme, J. Nijs and M. Bogaert for sampling under harsh winter conditions. H. Offringa and the personnel of MUMM provided us with environmental data. F. Fiers, J. Mees and X. Irigoien helped with identification of zooplankton. K. Sabbe helped with phytoplankton taxonomy.

Chapter IV

WINTER DISTRIBUTION OF PHYTOPLANKTON AROUND SOME SANDBANKS OF THE BELGIAN COASTAL ZONE

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Manuscript in preparation

Content

Abstract

Distribution of phytoplankton around several sandbanks of the Belgian Coast was investigated in February 1995 and 1997.The dendogram, for the 2 years, showed a clear separation of cluster correponding to different sandbanks. The nearshore banks phytoplankton community structure differed significantly in terms of species composition from the offshore Banks. Canonical Correspondence Analysis (CCA) of the phytoplankton data-set revealed, that beside temperature, salinity and turbidity nutrient concentration (NO_3^-) contributed substantially to explaining the variance in phytoplankton species. The observed differences in phytoplankton species distribution could be explained by the position of the sandbanks. Westhinder, OostDyck and Oosthinder are positioned further from the coast than Kwintebank, Middelkerke, and Stroombank, while the plankton community over Westhinder, Oostdyck, and Oosthinder are clearly influenced by the Atlantic current penetrating the southern North sea from the English channel. Thus, earlier reports difference in phytoplankton community exist in February 1994 within the study area (M'harzi et al. 1998; Journal of Plankton Research Vol.20 no.11 pp.2031-2052), were confirmed to be a regular feature at the end of winter.

1. Introduction

In 1994, a multidisciplinary ecological survey to study the underlying trophic structure and possible differences between the various sandbanks along Belgian coastal zone was performed. Primarily results of the distribution of phytoplankton and zooplankton in February 1994 are reported and discussed by M'harzi et al (1998). This study showed the existing spatial differences in phyto- and zooplankton communities between the nearshore and the offshore banks in the study area. These differences could be explained by the Atlantic water intrusion in the Southern Bight of the North Sea from the English Channel influencing the offshore banks. Several studies have reported the role of the hydrodynamic regime and meteorological conditions on the spatial structure and distribution of suspended particulate matter (e.g. Eisma & Kalf, 1979), nutrients (e.g. Van Bennekom A. J. & F. J. Wetsteijn, 1990), phytoplankton (e.g. Gieskes & Kraay, 1975, Louis et al., 1974; Louis & Smeets, 1981 etc...), zooplankton (e.g. Fransz et al., 1991 etc...), meroplankton (e.g. Belgrano et al., 1995; and Luczack et al., 1993) during winter in coastal areas of the Southern North Sea. Moreover, the spatial structure within higher trophic levels also showed a quite clear spatial heterogeneity of epibenthic fishes and invertebrates (Dalmas 1999), the meiofauna- nematodes and harpacticoid copepods- (Heip et al., 1990) and seabirds (Joiris, 1983) during winter in the Belgian coastal area.

This study verifies whether these 1994 observations are a regular feature at the end of winter. This paper reports observations on the distribution of phytoplankton over several sandbanks along the Belgian coastal zone, for February 1995 and 1997, in addition to the 1994 data. Beside the

phytoplankton communities analysis as carried out in Chapter 3, we also consider diversity, and analyse the phytoplankton biomass (expressed as volume and carbon) ad its size distribution as releavant feature to the potential trophic importance of the phytoplankton communities around the different sandbanks.

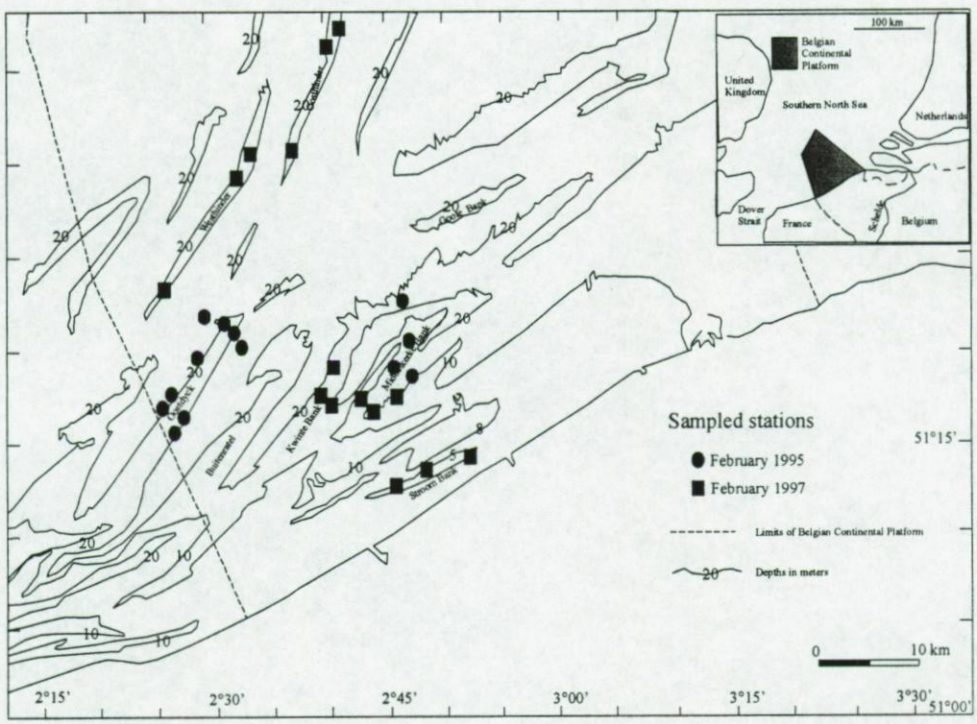


Figure 4.1. Location of the sampled sandbanks in the Belgian coastal zone. (The sampled stations for February 1994: See Figure 3.1, chapter 3)

2. Materials and methods

2.1 Study area

Figure 4.1 shows the position of the Stroombank, Buitenratel, Kwintebank, Middelkerke, Gootebank, Oost Dyck, Oosthinder and

Westhinder sandbanks within the study area. Sampling stations on each sandbank are also indicated.

2.2. Field sampling

Phytoplankton sampling. Sampling was performed on board of the R/V Belgica at several stations on the Buitenratel, Gootebank and Westhinder sandbanks on February 7 and 8 during 1994, on the Kwintebank, Middelkerke, and Oost Dyck sandbanks on February 7 and 8 during 1995; on the Stroombank, Kwintenbank, Middelkerke, Oostdyck, Oosthinder and Wethinder sandbanks on February 1, 3, 4, 5, 6, 10 and 12 during 1997.

Water samples were collected with a Niskin bottle at 3-meter depth. Sub-samples of 250 ml were preserved with lugol's solution for phytoplankton counting. (Detailed methodology in Chapter 3). 500-200 ml of water was filtered over GFC filter and stored in deep freeze for analysis of dry weight (DW), particulate total carbon concentration (PTC) and particulate inorganic carbon concentration (PIC).

Environmental factors. Temperature and salinity were determined by CTD, simultaneous with phytoplankton sampling at each sampling station. Methodology and results of the campaign 1994 are reported and discussed in Chapter 3. Turbidity measurements are missing for the campaign 1995 and 1997. Nutrient concentrations, dry weight, Particulate Organic Carbon and Chlorophyll a, which were missing for the 2 first campaigns 1994 and 1995, were measured in 1997. Water samples for nutrient analyses (nitrate, nitrite, ammonia, and silicate) were stored frozen and analyzed later with a Technicon AutoAnalyser™ II autoanalyser, following the procedure described in Elskens, (Pers. Comm.).

Each sample was given a letter designation followed by a number to represent sampling stations of the sandbanks as: W for Westhinder, G for Gootebank, O for Oost Dyck, OT for Oosthinder, B for Buitenratel, K for Kwintebank, M for Middelkerke and S for Stroombank.

2.3. Laboratory analysis

Phytoplankton

The preserved 250-ml samples were concentrated to 5 ml by decantation. Phytoplankton cells in the concentrated sample were counted with an inverted microscope at 10x20 and 10x40 magnification, and species abundance expressed as cells per liter (details see Chapter 3).

Keys and references books used for identification were Van Heurck (1896), Schiller (1937), Cleve-Euler (1951), Butcher (1961), Hendey (1964), Drebes (1974), Hartley (1986), Pankow (1990) and Tomas (1993).

Biomass and size structure

Cell volumes were calculated from cell dimensions of all phytoplankton species (length, diameter and width) using appropriate geometric formulae (Edler et al., 1979). Cell carbon (PCC) (C, pg. $cell^{-1}$), for diatoms and non-diatoms was estimated from cell volume (V, μm^3 $cell^{-1}$) using the conversion factor of Eppley et al. (1970) for phytoplankton:

$\log C = 0.76 \times (\log V) - 0.352$ for diatoms

$\log C = 0.94 \times (\log V) - 0.60$ for non-diatoms

Total phytoplankton volume (PV, ppm= 10^6 μm^3 ml^{-1}) and phytoplankton carbon (PC, pg. ml^{-1}) was then obtained by summing individual cell volume and cell carbon over abundance of all species respectively, for all species showing >1% of total numerical abundance. No attempt was made to distinguish between autotrophic and heterotrophic dinoflagellate species except for few well-known heterotrophic species. Phytoplankton volume (μm^{-3} cell $^{-1}$) was differentiated by size. From cell volume, spherical equivalent diameter (SED, μm) was calculated and this was used to allocate the species PV value into a given size class. The size classes used were logarithmic, corresponding to TA II Coulter size classes in the 5-100 μm size range (Tackx et al., 1991). PV values for each size class were averaged over each of the three stations situated at the same bank.

Chlorophyll (Chl a)

Chlorophyll a (Chla) concentration were determined using a high Performance Liquid Chromatography (HPLC) using 90% acetone as extractant. The extracted (Chla) in the samples was quantified by HPLC (using water C18 3.9 × 150-mm column, a waters Model 440 UV absorbance detector and a Waters 470 Scanning fluorescence detector). The solvent mixture used was 75% methanol, 22% acetone, 3% water. Calibration was done using commercial standards.

Dry Weight (DW)

The filters used for DW determination had previousely been dried at 60°C during 12h and weighed on a Mettler balance with sensitivity 0.1mg.

Particulate Organic Matter (POC)

Total particulate carbon (TPC) concentration and particulate inorganic carbon (PIC) concentration were measured on two replicate filters with Coulomat 702 (Stöhlein) using heating at 900°C and 8.5 % H3PO4 to convert respectively TPC and PIC to CO2, which was quantified by an automatic coulometric titration of a Ba(CIO4) solution. The coulomat was standardised with CaCO3. Particulate organic carbon concentration (POC, mg l^{-1}) was calculated as the difference between TPC and PIC.

2.4. Data analysis

Diversity in each station was calculated using the Shannon and Weaver (1963) index:

$$H = -\sum_{i=1}^{S} (p_i \times \ln p_i)$$

Where S is the number of species and pi is the proportion of the collection belonging to the i^{th} species.

Values measured for environmental factors on the all banks were compared using one way analysis of variance. Phytoplankton absolute abundances on the different banks were compared by Mann Whitney-U test.

Two Way Indicator Species Analysis (TWINSPAN) (Hill, 1979) was used to analyze the spatial distribution and community structure of

phytoplankton over the study area. Species abundance was expressed as percentage, and the default options of the TWINSPAN routine were used thoughtout the analysis.

Canonical Correspondence Analysis (CCA), using the CANOCO package program (Ter Braak, 1987b and 1988), was used to determine the relation between phytoplankton abundance and environmental variables. Phytoplankton data were used as abundance and ln+1 transformed. Downweighing of rare species was performed. Temperature, salinity, turbidity, and temperature, and salinity were used as environmental data in case of the phytoplankton analysis for the year 1994, and 1995 respectively. A Monte Carlo test using 999 unrestricted permutations was performed to test the significance of the relationships.

3. Results

3.1. Environmental variables

Values of temperature and salinity for the Campaign 1995, and of temperature, salinity and nutrient concentrations for the Campaign 1997 are shown in Figures 4.2a,b and 4.3a-g, respectively. Temperature ranged from 7,8 to 8,4°C in all stations in 1995, and Oostdyck values were significantly higher than those of Kwintebank and Middelkerk values (ANOVA, $p< 0,05$). Salinity varied between 33,698 psu and 34,233 psu during campaign 1995 (Figure 4.2a,b). The offshore banks showed generally high values of salinity and temperature during campaign 1997 (Figure 4.3a,b), except at the Stroombank stations where higher temperatures were registered (Figure

4.3b). Nutrient concentrations decreased significantly from the nearshore banks to the offshore banks (ANOVA, $p < 0.05$) (Figure 4.3c-g).

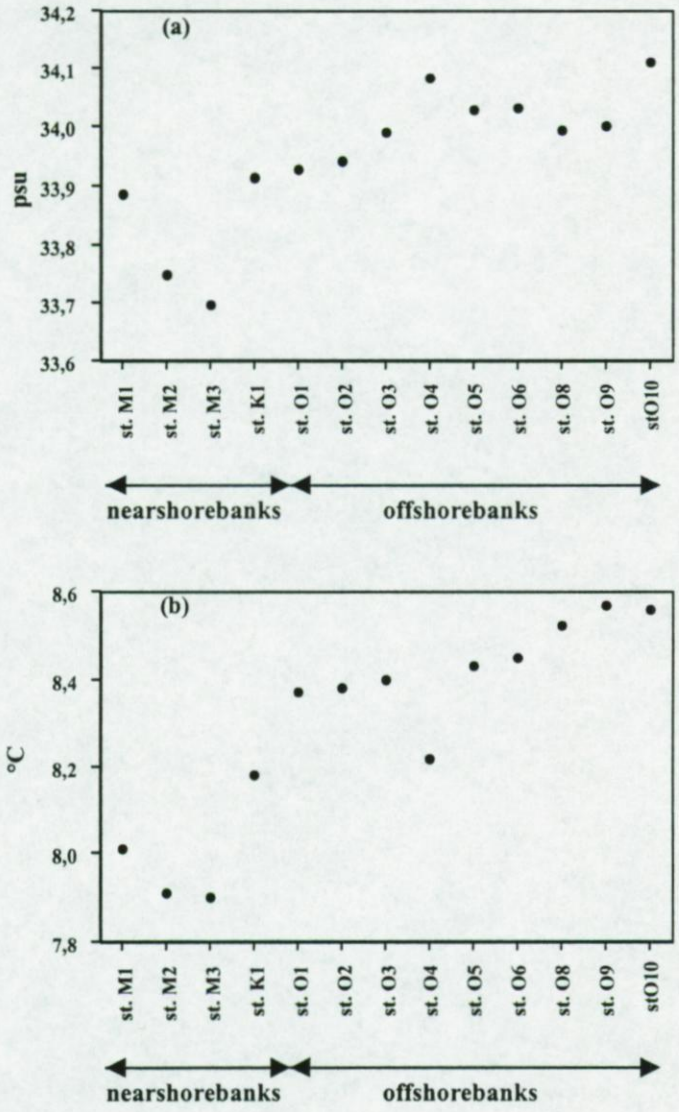


Figure 4.2. Environmental factors measured at the three sandbanks in February 1995: (a) Salinity, and (b) Temperature.

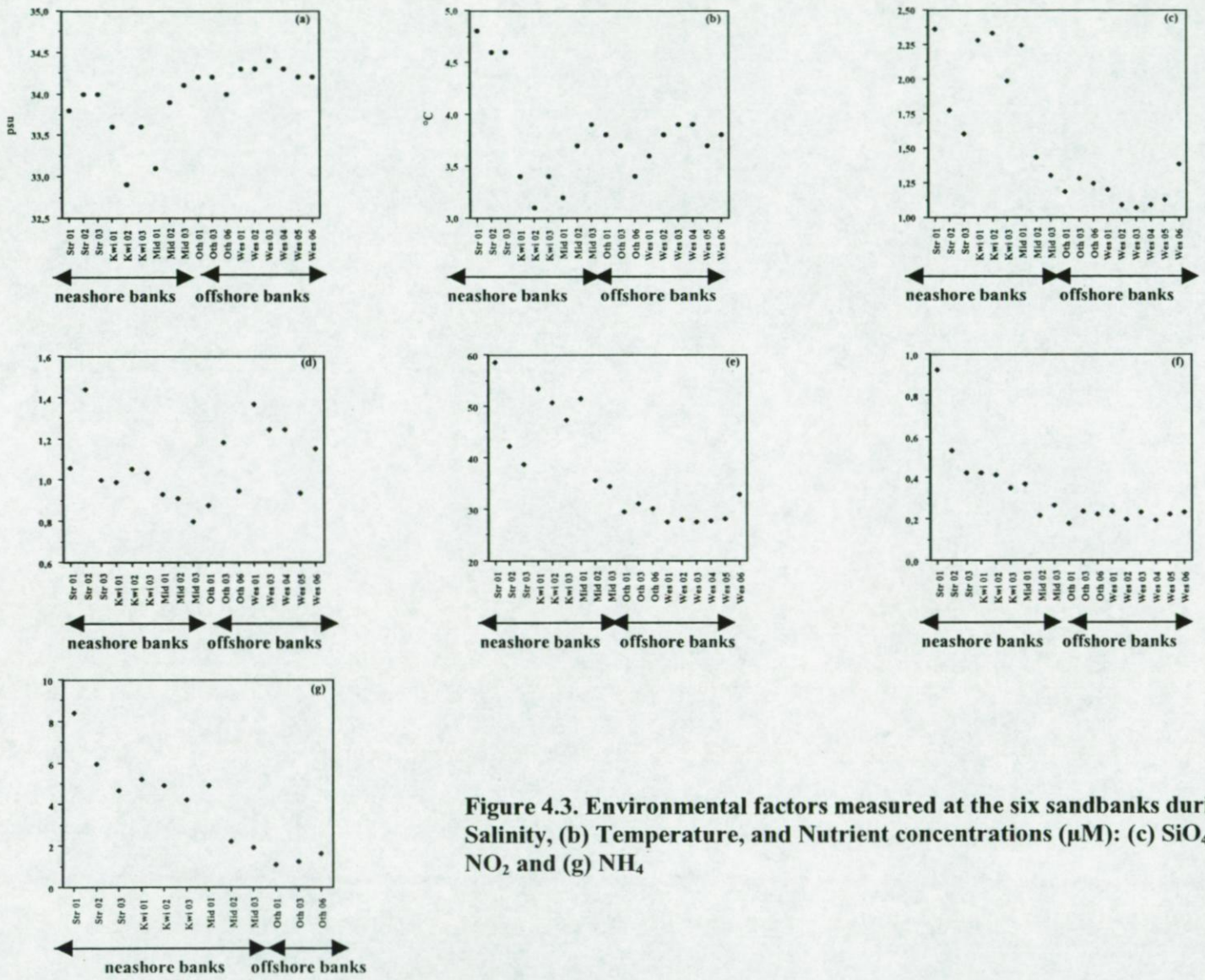


Figure 4.3. Environmental factors measured at the six sandbanks during February 1997: (a) Salinity, (b) Temperature, and Nutrient concentrations (µM): (c) SiO_4, (d) PO_4, (e) NO_3, (f) NO_2 and (g) NH_4

3.2. Phytoplankton abundance and diversity

Abundance

A total of 132 phytoplankton identified up to species or genus level are already reported by M'harzi et al., (1998) (See Table 3.1 in Chapter III). Few in these assemblages were resuspended benthic species.

A comparison of numerical abundance of phytoplankton taxa, for 2 years, between the sandbanks studied is shown in Table 4.1. Figures. 4.4, 4.5and 4.6 shows the detailed distribution gradients.

For campaign 1995, there was no significant difference in the phytoplankton taxa abundance between the sampled sandbanks, except that Chrysophyta abundance was significantly different between offshore and nearshore banks ($p < 0,05$).

The abundance of Chrysophyta (Bacillariophyceae), Cryptophyta (Cryptophyceae) and Chlorophyta (Chlorophyceae) was significantly lower at the offshore banks than at the nearshore banks ($p < 0,05$) during the Campaign 1997. Dinophyceae, Haptophyceae, Prasinophyceae (Chlorophyta), and Euglenophyceae showed no difference in abundance between the banks.

Table 4.1 Mann.Whitney *U*-test comparing the abundance of the main groups of phytoplankton on the offshorebanks (Westhinder, Oosthinder and Oostdyck) and the nearshorebanks (Stroombank, Middelkerke, and Kwintenbank). (*) significant at $p < 0.05$; *ns*, non-significant

Taxa	1995	1997
Chrysophyta	Offshore banks <nearshore*	Offshore banks <nearshore*
Cryptophyta	*ns*	Offshore banks <nearshore*
Pyrrophyta	*ns*	*ns*
Chlorophyta	*ns*	Offshore banks <nearshore*
Euglenophyta	*ns*	*ns*

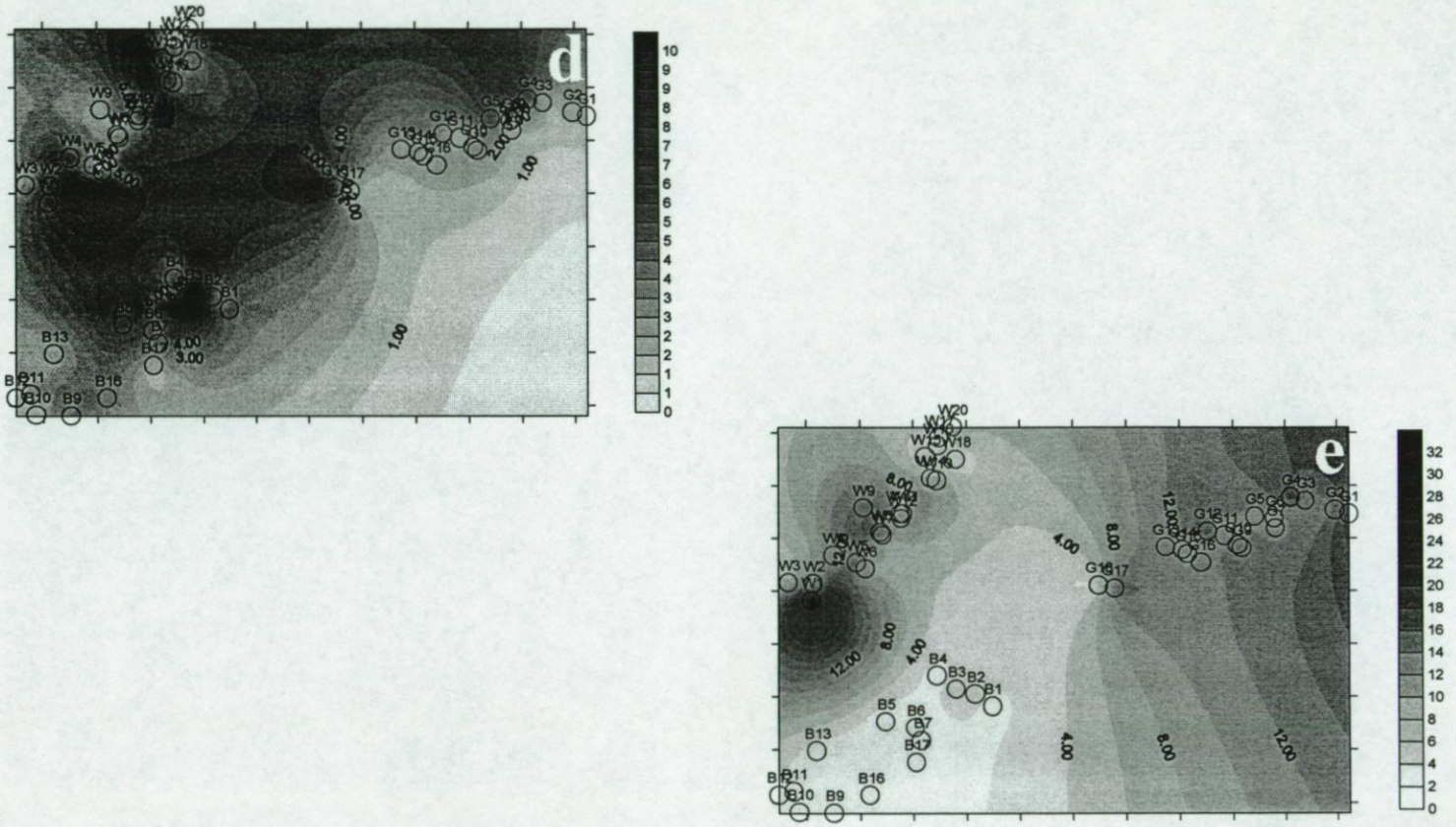


Figure 4.4. Distribution of total cell abundance of different taxa (*10^3 cells l^{-1}) in February 1994: (a) Diatoms, (b) Euglenophyceae, (c) Prasinophyceae, (d) Chlorophyceae, and (e) Cryptophyceae.

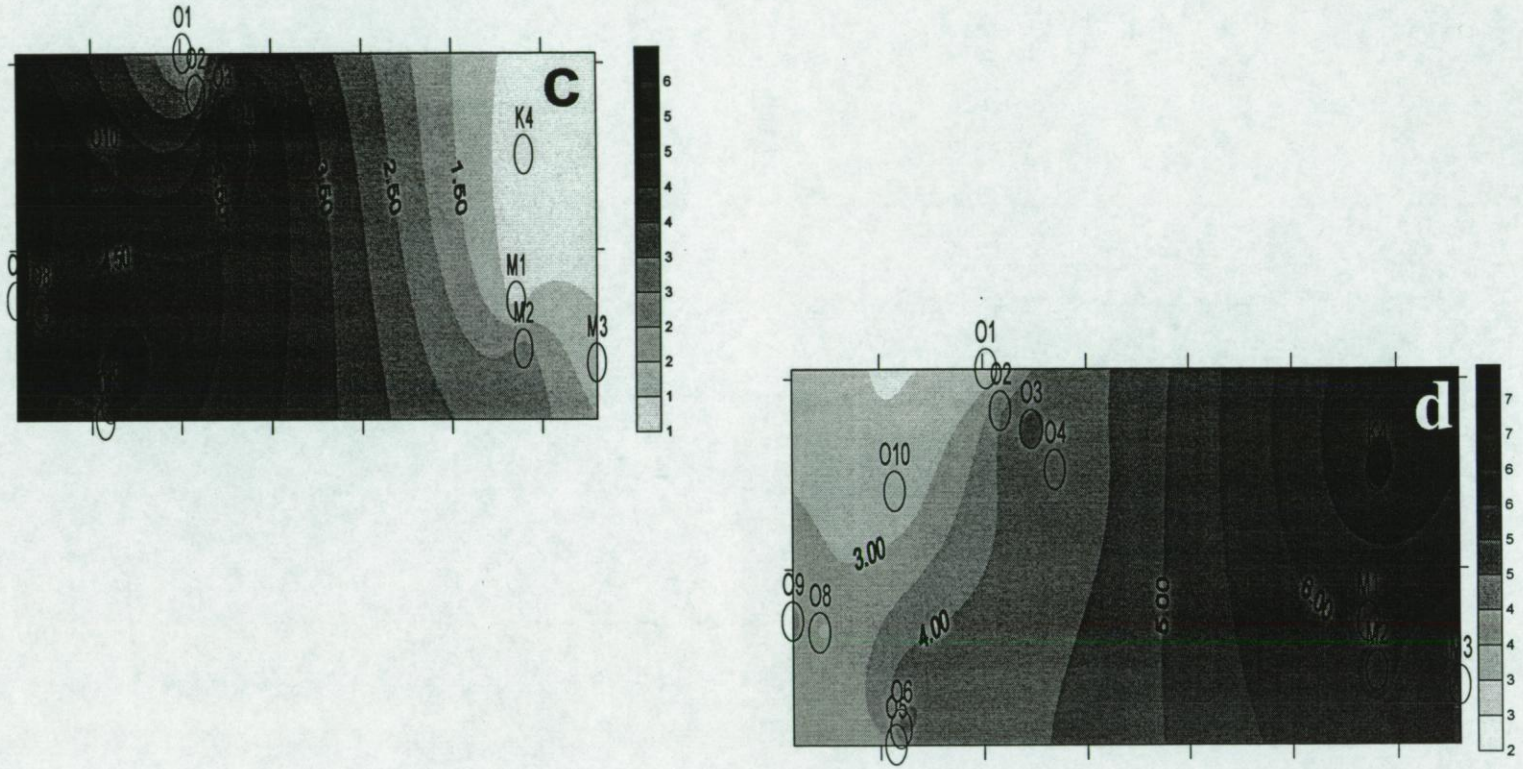


Figure 4.5. Distribution of total cell abundance of different taxa (*10^3 cells l^{-1}) in February 1995: (a) Diatoms, (b) Euglenophyceae, (c) Prasinophyceae, and (d) Chlorophyceae.

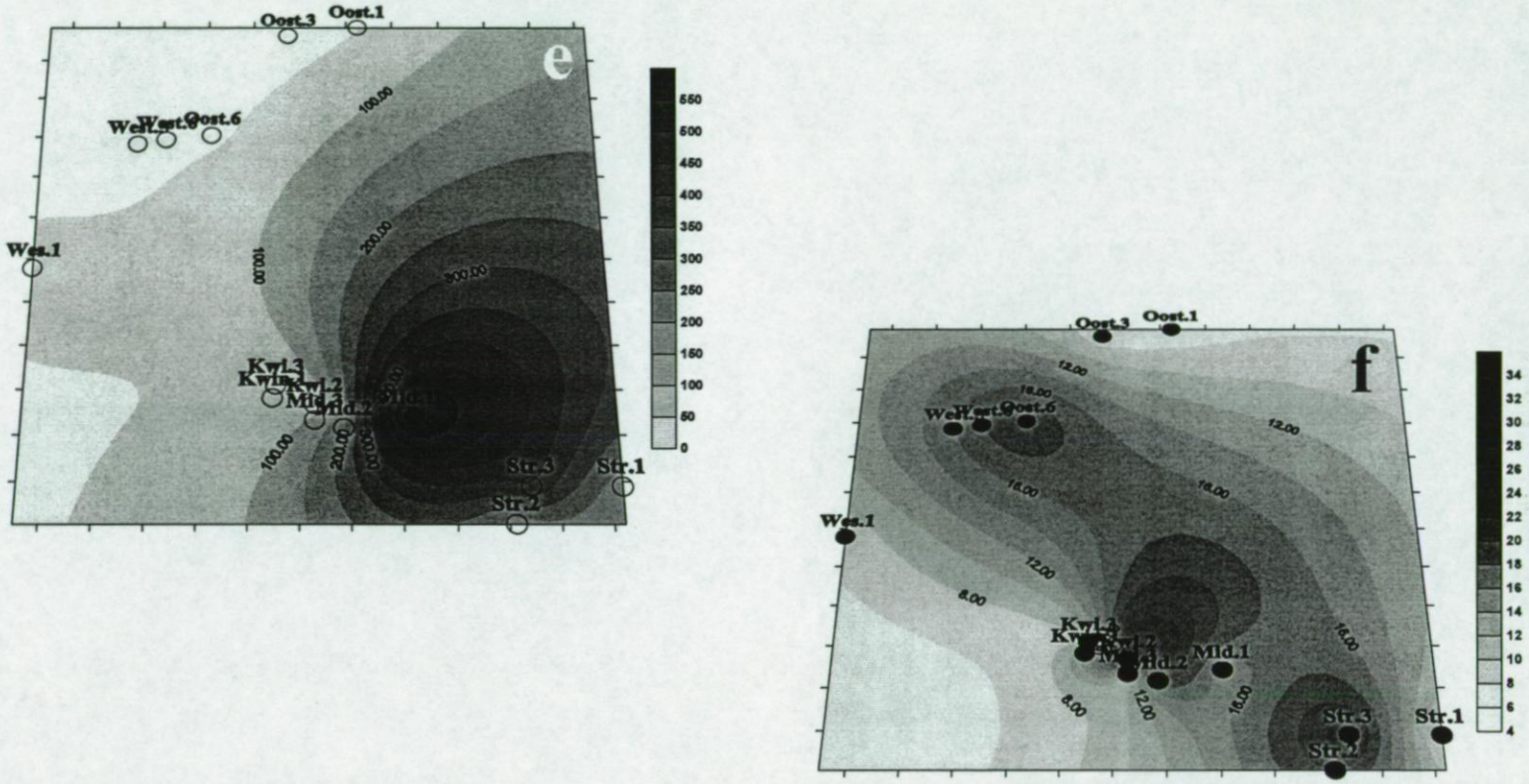


Figure 4.6. Distribution of total cell abundance of different taxa (*10^3 cells l^{-1}) in February 1997: (a) Diatoms, (c) Prasinophyceae, (d) Chlorophyceae, (e) Cryptophyceae and (f) Dinophyceae.

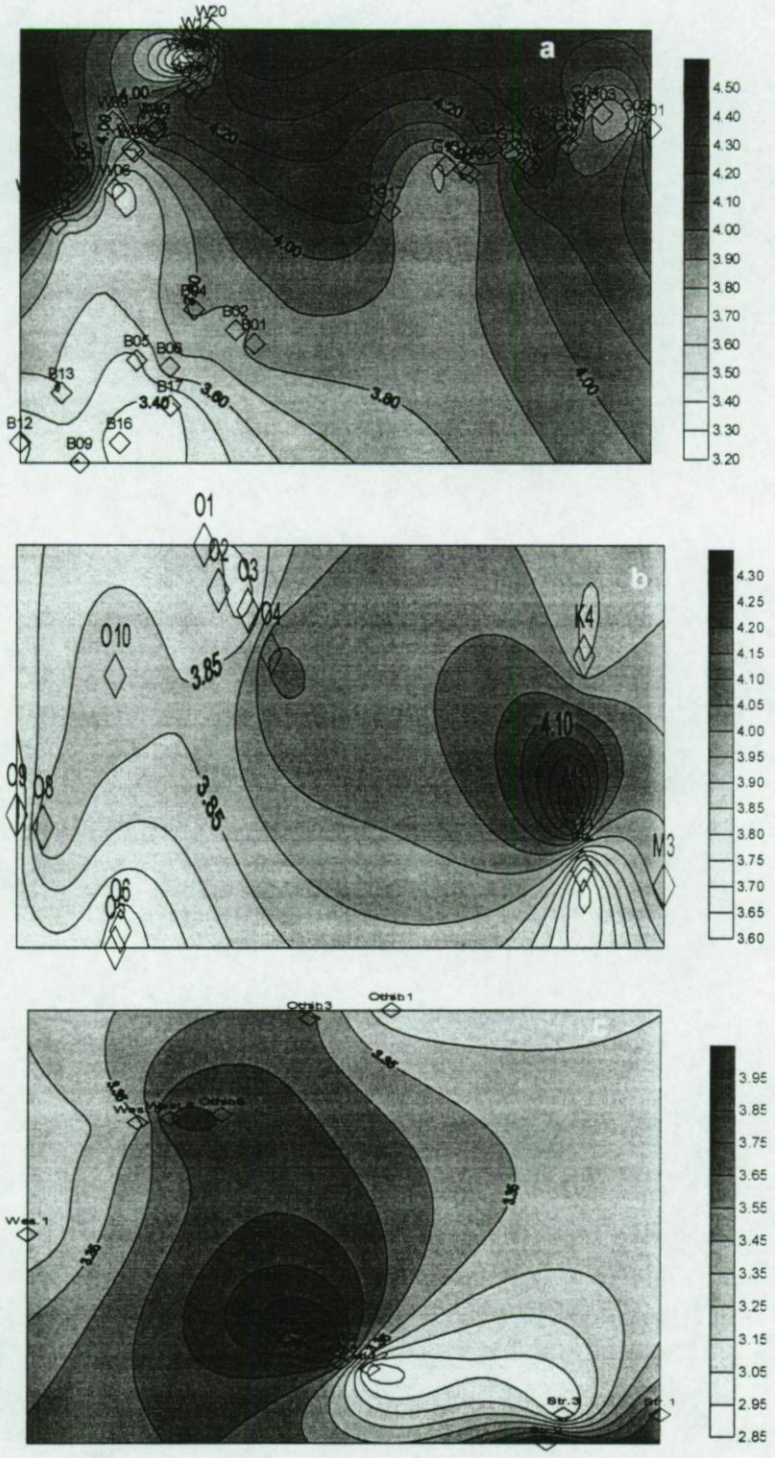


Figure 4.7 Shannon's diversity index (H') of phytoplankton during: (a) 1994, (b) 1995, and (c) 1997.

Diversity

The spatial pattern of the diversity (Shannon-Weaver index) in 1994, 1995 and 1997 are quite similar (Figure 4.7). Values of the index were high in most

sampled stations (>3) in the three years, except a few neashore stations in February 1997 with values between 1 to 2 and 2 to 3 (Figure 4.7c).

3.3. Twinspan analysis

Results of the Campaign 1994 were reported in detail in Chapter 3. For both the 1995 and 1997 campaigns (Figure 4.8a and b, respectively), the dendrogram for the TWINSPAN analysis of the phytoplankton abundance showed a clear splitting. For campaign 1995, a first split divided the data in cluster with samples from Oostdyck on the left side with *Micromonas pusilla* as indicator species and samples from Kwintebank and Middelkerke stations at the right side (Figure 4.8a). The dendrogram for the 1997 campaign also showed a clear split of the Westhinder, Oosthinder and Oostdyck stations in the left side, with *Odontella rhombus*, *Plagiogramma brockmanii* and *Rhodomonas* sp. as indicator species. While, in the left side cluster consisting on Stroombank stations, *Navicula fusiformis* was the indicator species (Figure 4.8b).

The nearshore banks phytoplankton community structure differed significantly in terms of composition from the offshore Banks. The 95 and 97 results confirm the observation of the campaign 1994 reported in the Chapter 3.

3.4. CCA analysis

Phytoplankton-environment relationships

CCA analysis was performed on the total phytoplankton numerical abundance dataset. The plots for species and sample scores combined with

environmental factors are shown in Figures 9.4, 10.4 and 11.4 for the 1994, 1995 and 1997 campaigns, respectively.

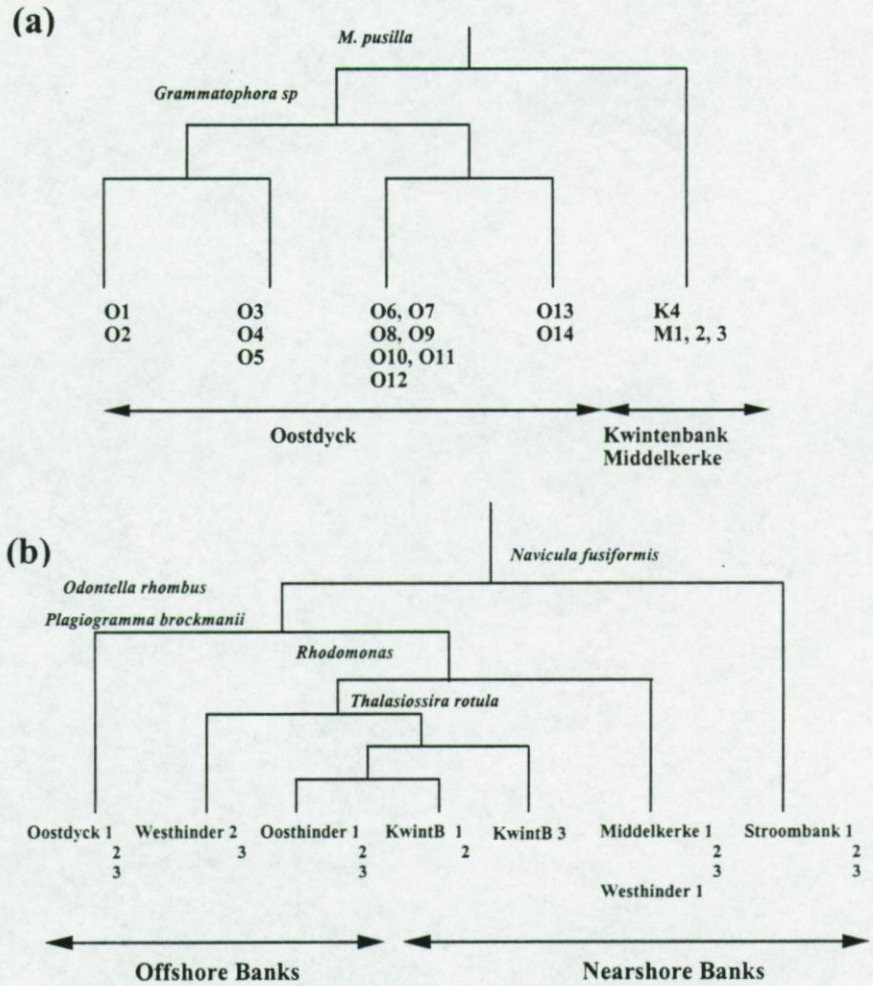


Figure 4. 8 Twinspan analysis dendograms for phytoplankton species s abundance on the: (a) February 1995 and (b) February 1997.

The axes 1 and 2 explained 53% and 30%, respectively, of the variance in the species-environmental biplot in 1994 (Figure 9.4), 64% and 46%, respectively, for Campaign 1995 (Figure 4.10) and 37% and 21 %, respectively, for Campaign

1997 (Figure 4.11). Eigenvalues, percentage explained variance and correlation coefficients with the environmental factors for the first 4 axes are given in Table 4.2. Monte Carlo test showed that the variance in phytoplankton species can be explained in ascending way by (a) temperature (3%, p= 0.01), salinity (3%, p= 0.01) and turbidity (3%, p= 0.01) for 1994; (b) temperature (10%, p= 0.01) for 1995, (c) temperature (17%, p= 0.01) and nitrate (13%, p= 0.01) for 1997 (Table 4.3). As shown in Figure 4.9b -campaign 1994-, Gootebank stations were found on the right side of axis 1, with the majority of stations situated under axis 1. Westhinder stations were situated to the left of axis 2 while Buitenratel stations were distributed along the lower part of axis 1. Arrows for temperature and salinity are in the lower quadrant, both point in opposite direction as turbidity. Figures 4.10a,b -campaign 1995- shows that samples from Oostdyck sandbank were located in the left side of the sample biplot, Kwintebank and Middelkerke stations on the right, confirming the clustering in the Twinspan. On the correlation biplot of the CCA (Figure 4.10b), the nearshore stations and the offshore stations each took different positions. Except for those of the Kwintenbank which were found together with the offshore stations in the lower left corner in the plot (Figure 4.11b). The nearshore banks stations were situated both in lower right corner and the higher part of the diagram and seemed to be correlated with temperature and nutrients (nitrate).

Diatoms (e.g. *Odontella* spp, *Rhizosolenia* spp, *Pleurosigma navicula*, *Diploneis didyma*) and Euglenophyceae (e.g. *Euglena* sp.) were the indicator taxa in the Buitenratel bank stations in the campaign 1994. All others groups had their maximal abundance in the offshore banks, Gootebank and Westhinder (Cryptophyceae, Prasinophyceae, and Dinophyceae) (Figure 4.9a). Figure 4.10a, shows also that diatom species (such as *Odontella* spp, *Rhizosolenia* spp,

Pleurosigma naviculaculaceum, *Diploneis didyma*) were the most important group in the nearshore stations, and *Euglena* sp. While, non diatoms species (e.g. *Maniscula bipes*, *Prorocentrum micans*, *Gymnodinium* spe, *Chlamydomonas reginae*, *Telonema subtilis*, *Cryptomonas* spe, *Eutreptia* spe, and *Eutreptiella hirudoidea*) reached their maximal abundance in the offshore banks stations (Oostdyck). Finally, diatom species such as *Odontella* spp, *Diploneis* spp, *Pleurosigma normanii*, *Rhizosolenia shrubsolei*, *Cylotella comta*, *Nitzschia* spp, and non-diatoms species such as *Eutreptiella hirudoidea*, *Micromonas pusilla* and *Crucergia tetrapedia* characterised the nearshore banks (Stroombank, and Middelkerke). Offshore bank stations (Kwintenbank and Oosthinder) were characterized mainly by some diatoms species (e.g. *Paralia sulcata*, *Odontella sinensis*, *Thalassionema nitzschoides*, Navicula *marina*, and *Rhaphoneis amphiceros*) and non-diatoms species such as *Rhodomonas* sp., *Eutreptia* sp., *Tetraselmis suecica*, *Leucocryptos marina*, *Cryptomonas* spe, *Amphidinium* sp., *Diplopsalis minor*, *Gymnodinium* spe and *Peridinium* sp. (Figure 4.11a).

Further details on the association between environmental factors can be seen from the correlation matrix of environmental variables shown in Table 4.4 The p values of the combined and individual environmental factors and their variance after subjection to the Monte Carlo Permutation test (99 unrestricted permutations) are given in Table 4.4.

Table 4.2 Weighed correlation matrix (inter-set correlation) showing relationship between phytoplankton species axes and environmental variables: (1) Campaign 1994, (2) Campaign 1995 and (3) Campaign 1997.

Axis	1	2	3	4
Eigenvalues:				
(1)	0.04	0.027	0.016	0.071
(2)	0.100	0.058	0.073	0.054
(3)	0.193	0.113	0.076	0.048
Cummulative pecentage variance of species-environment relation:				
(1)	52	82.8	100	0
(2)	63.3	100	0	0
(3)	36.5	57.9	72.3	81.4
Correlation coefficient:				
(1) Temperature	-0.422	-0.678	0.051	0.000
(1) Salinity	0.507	-0.335	0.517	0.000
(1) Turbidity	-0.604	0.105	0.513	0.000
(2) Temperature	-0.979	-0.080	0	0
(2) Salinity	-0.857	0.458	0	0
(3) Temperature	0.925	-.028	0.169	0.049
(3) Salinity	0.286	0.003	0.345	0.497
(3) Nitrite	0.708	-0.232	0.239	-0.537
(3) Nitrate	0.210	-.182	-.087	-.827
(3) Ammonium	0.639	-.229	-.081	-.597
(3) Silicate	0.133	-.229	-.188	-.771
(3) Phosphate	0.550	-.379	-.197	0.270

Table 4.3 p-values using Monte Carlo permutation tests from the CCA analysis, percentage variance explained by selected environmental variables for the 1994, 1995 and 1997 campaigns. N.S = non significant; (*) explained by each variable selected and (**) explained by all variables selected

Environmental factor	1994		1995		1997	
	% Variance (*)	p	% Variance (*)	p	% Variance (*)	p
Temperature	**03%**	**0.01**	**10%**	**0.01**	**17%**	**0.01**
Salinity	**03%**	**0.01**	**09%**	**N.S**	**08%**	**N.S**
Turbidity	**03%**	**0.01**	**xxxxxxxxxxxxxx**		**xxxxxxxxxxxxxx**	
Nitrate	**xxxxxxxxxxxxxx**		**xxxxxxxxxxxxxx**		**13%**	**0.01**
Ammonium	**xxxxxxxxxxxxxx**		**xxxxxxxxxxxxxx**		**09%**	**N.S**
Phosphate	**xxxxxxxxxxxxxx**		**xxxxxxxxxxxxxx**		**07%**	**N.S**
Silicates	**xxxxxxxxxxxxxx**		**xxxxxxxxxxxxxx**		**06%**	**N.S**
Variance (**)	9%		10%		49%	

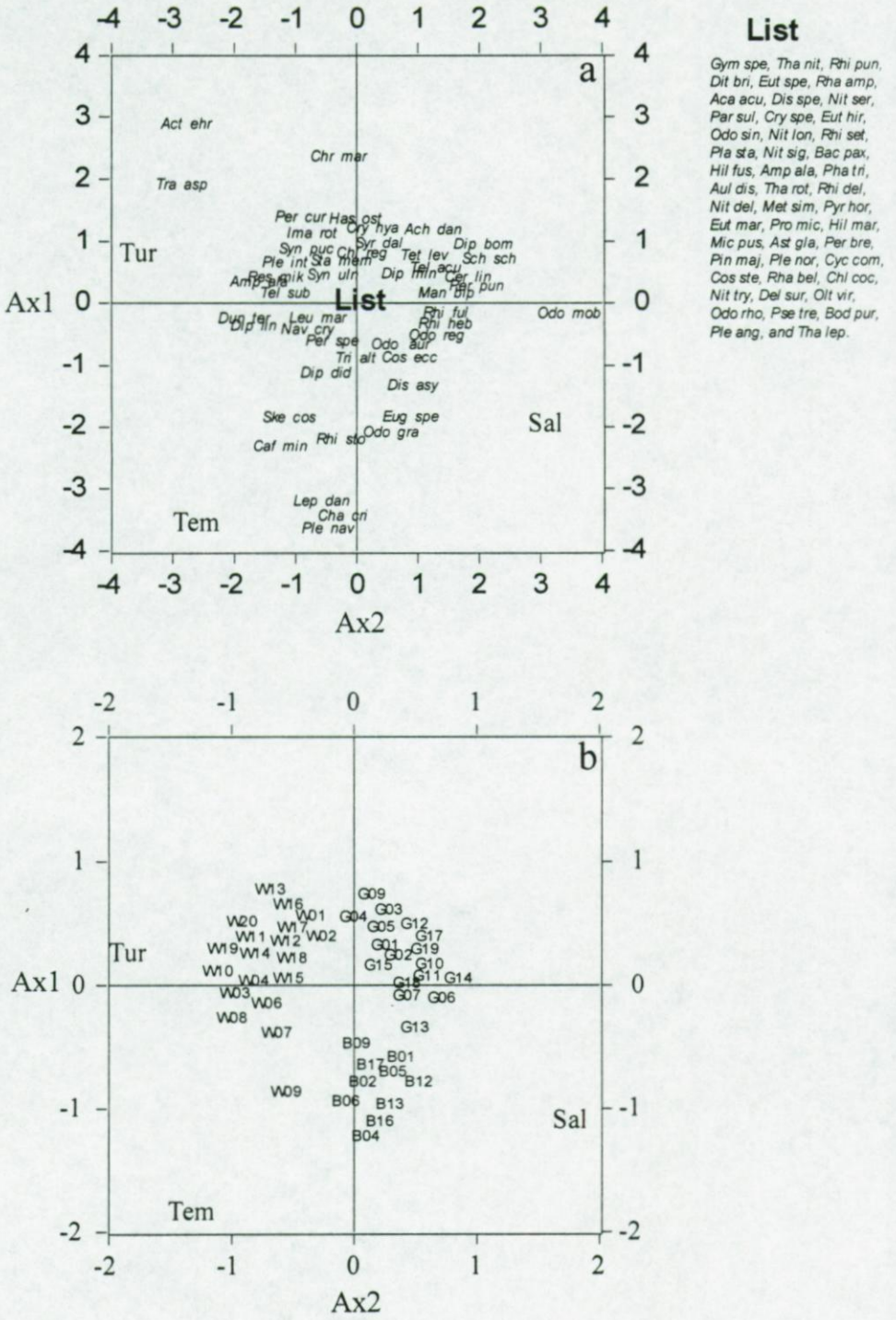
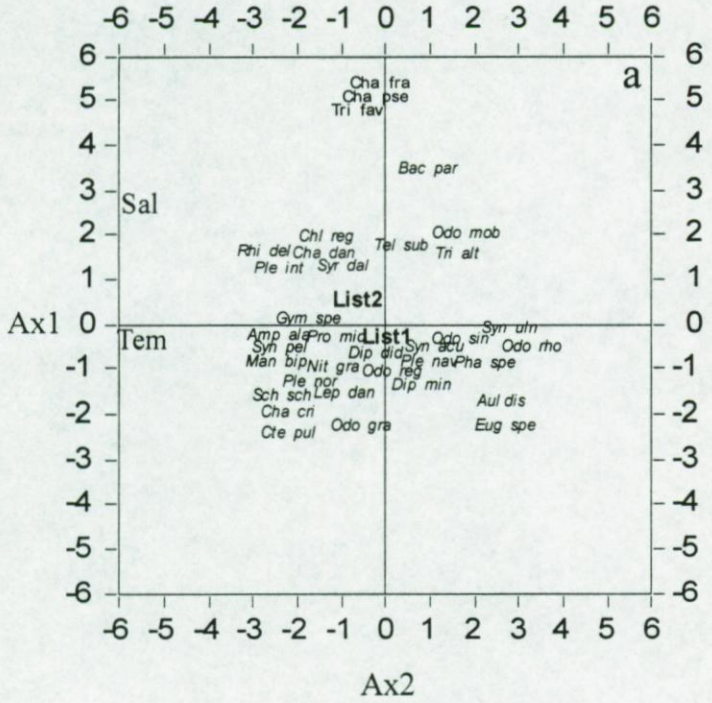


Figure 4.9 CCA analysis of phytoplankton species abundance with respect to environmental factors in 1994. (a) Species biplot: both, List (species, which are close together) and single species in the plot are reported in Table 3.1 in Chapter 3. Environmental factors are: Tur= turbidity, Tem= temperature, Sal= salinity. (b) Stations biplot: B= Buitenratel, G= Gootebank, W= Westhinder.



List1

Tra asp, Ple ang, Bro bro, Ast gla, Met sim, Cyc com, Rha amp, Nit ser, Del sur, Nit lon, Pha tri, Dis spe, Nit dis, Cha com, Cha did, Dis asy, Nit sig, Act chr, Aul gra, Nav cry, Tha nit, Par sul, Rhi set, Tha ecc, Tha rot, Cos ste, Ske cos, Dit bri, Cry spe, Eut spe, Etr hir.

List2

Tha fal, Dip bom, Cos rad, Gui str, Odo aur, Nit try, Per sp, Pro ala, Nit pan, Rha bel, Cos cen, Nit del, Pyr hor, Rhi pun, Mic pus, Chl coc, Lep min, Rhi heb, Hem vir, Ampr ala.

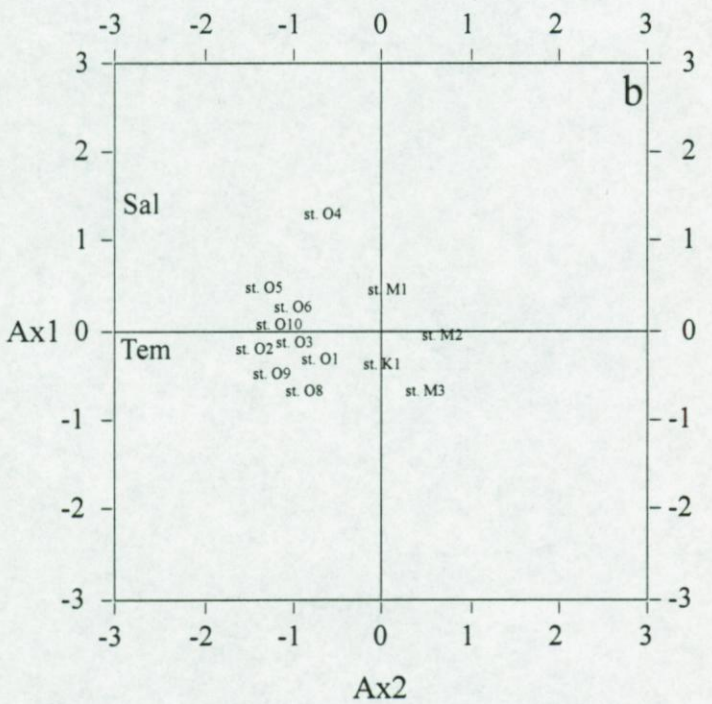


Figure 4.10 CCA analysis of phytoplankton species abundance with respect to environmental factors in 1995. (a) Species biplot: both List 1 and 2 (species, which are close together) and single species in the plot are reported in Table 3.1 in Chapter 3. Environmental factors are: Tem= temperature, Sal= salinity. (b) Stations biplot: M= Middelkerke, K= Kwintenbank, O= Oostdyck.

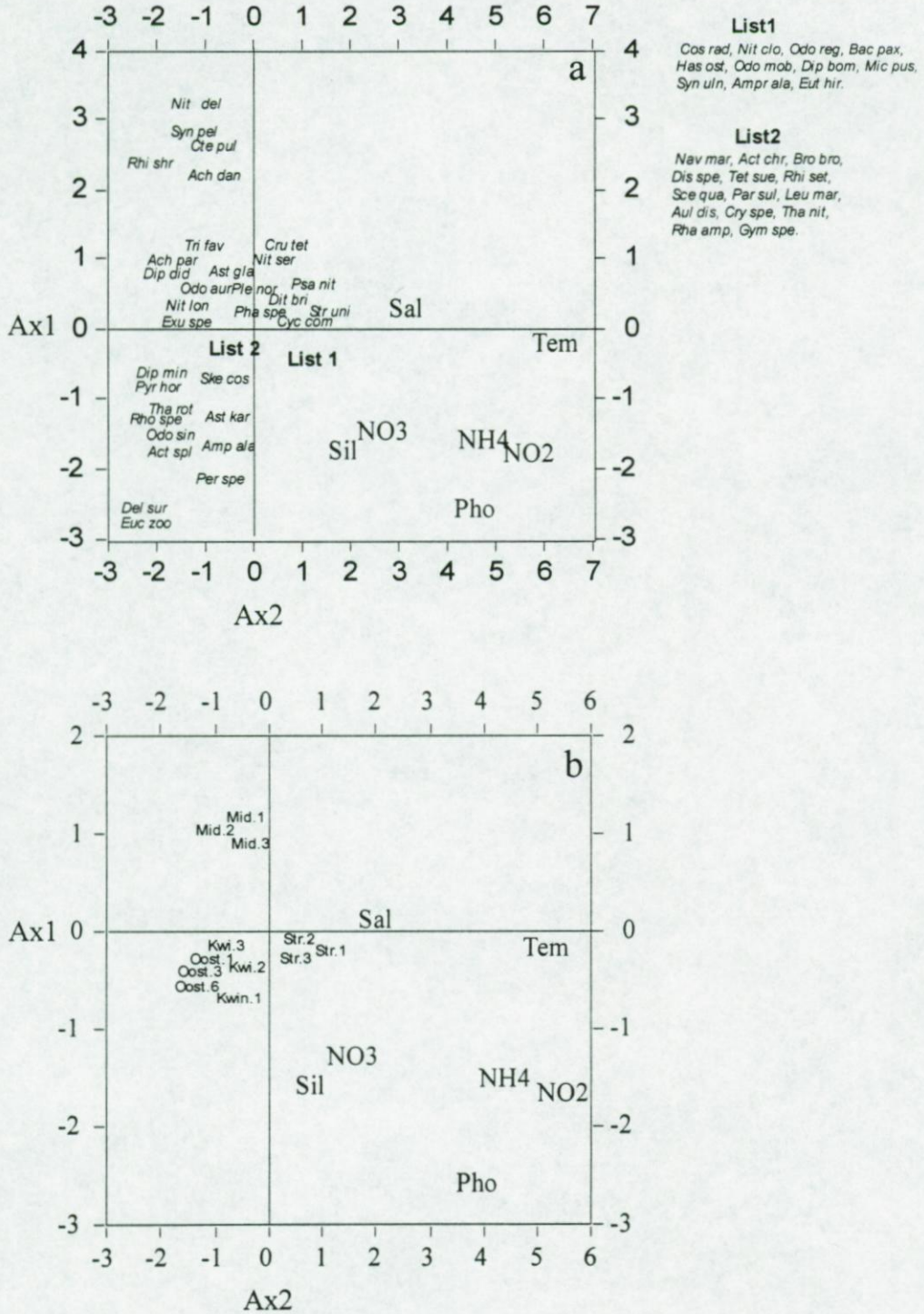


Figure 4.11 CCA analysis of phytoplankton abundance with respect to environmental factors in 1997. (a) Species biplot: both List1 and 2 (species, which are close together) and single species in the plot are reported in Table 3.1 in Chapter 3. Environmental factors are: Tem= temperature, Sal= salinity, Si= silicate, NO_3^-= nitrate, NO_2^-= nitrite, NH_4^+= ammonium, Pho= phosphate. (b) Stations biplot: Oost= Oosthinder, Kwin= Kwintenbank, Mid= Middelkerke, Str= Stroombank.

Table 4.4. Weighed correlation matrix (intra-set correlation) for environmental variables used in the Canonical Correspondence Analysis. SAL= Salinity, TEMP= Temperature, TUR= Turbidity, and nutrients (NO_2^-= nitrite, NO_3^-= nitrate, Si= silicate, PO_4= phosphate and NH_4^+= ammonium).

1994	TUR	SAL	TEMP	NO_2^-	NO_3^-	Si	PO_4	NH_4^+
TUR	1.0000							
SAL	0.0725	1.0000						
TEMP	.3209	-0.098	1.0000					
1995								
SAL		1.0000						
TEMP		0.8272	1.0000					
1997								
SAL		1.0000						
TEMP		0.5724	1.0000					
NO2			0.608	1.0000				
NO3			0.014	0.756	1.0000			
Si			-0.097	0.675	0.983	1.0000		
PO4			0.406	0.393	0.160	0.193	1.0000	
NH4			0.452	0.934	0.874	0.833	0.443	1.0000

3.5. Biomass and size structure

Spatial distribution of phytoplankton biomass (expressed as biovolume, ppm) ranged from 0.01 to 1.0 * 10^6 μm^3 ml^{-1}. In Figure 4.12 the phytoplankton volume distribution is presented for February 1994, 1995 and 1997. The gradual decrease in cell volume from nearshore banks towards offshore seems to be a characteristic pattern of the spatial phytoplankton volume distribution.

In February 1994 and 1995 cell carbon volumes were generally lower, <10 µg C l^{-1} (Figure 4.13a, b) than in February 1997 (Figure 4.13c). Carbon biomasses were higher at the nearshore banks and decreased towards the sea at the offshore banks for the three Campaigns (Figure 4.13a,b and c). Mean Carbon biomass of each bank ranged from 4 to 6 µg C l^{-1}, 2 to 6.5 µg C l^{-1} and 18 to 50 µg C l^{-1} for 1994, 1995 and 1997 respectively (Figure 4.13).

Carbon stocks were fractionated into <20 µm and >20 µm size fraction using spherical equivalent diameter (Table 4.5). The <20 µm fraction increased from the nearshore banks to offshore banks during 1994 and 1995. But is more or less constant in 1997 (Table 4.5).

The fraction > 20 µm was higher in the nearshore banks in 1994 and 1995, and equally distributed in 1997 (Table 4.5).

Diatom distribution showed a spatial variability for the three years (Table 4.5), with decreased contribution to total carbon during 1997, compared to the previous years 1994 and 1995. Crytophyceae biomass was slightly higher at the nearshore banks, while Prasinophyceae and Dinophyceae increased offshore in 1997 (Table 4.5).

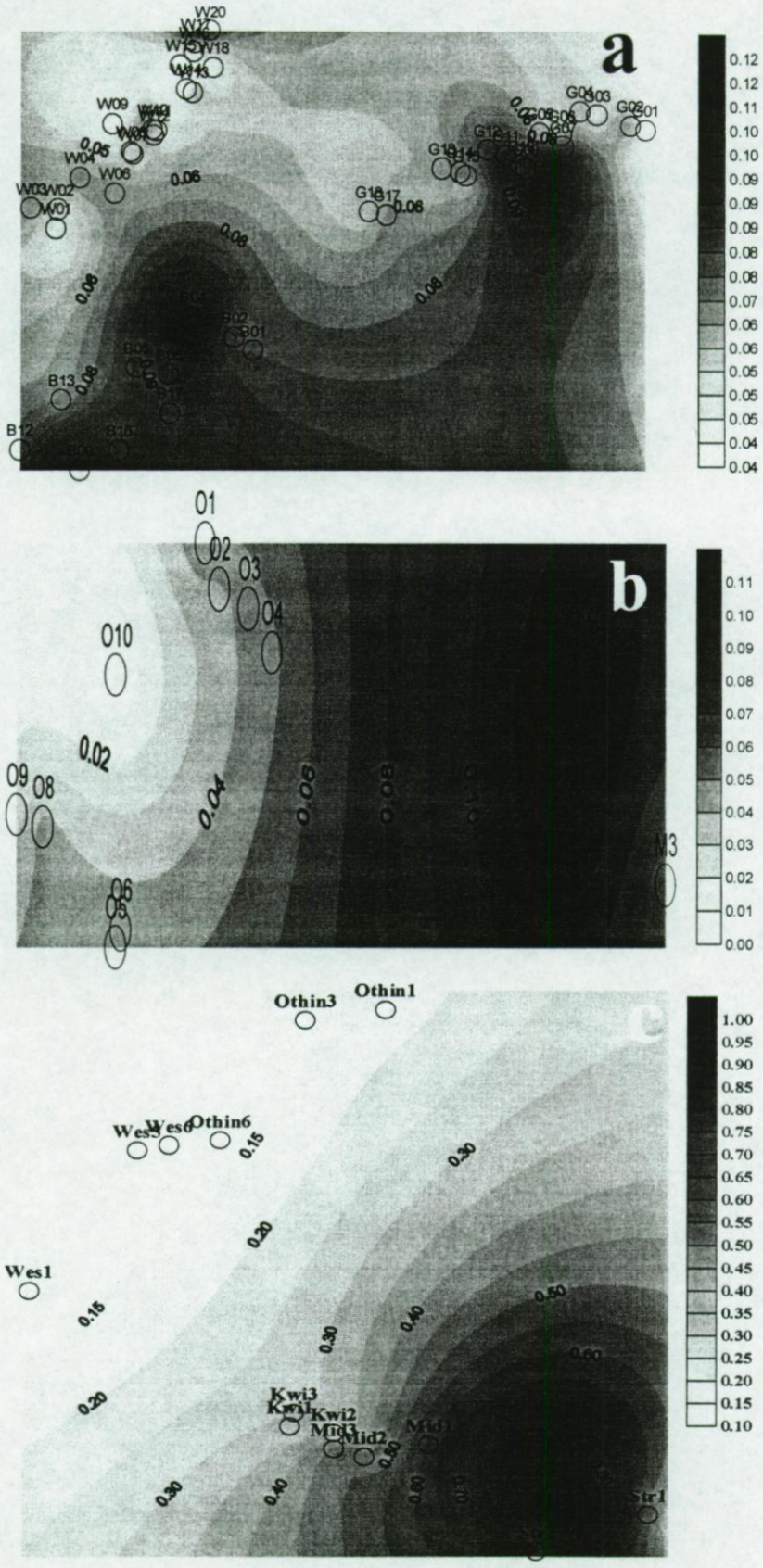


Figure 4.12 Distribution biovolume (ppm) of the total phytoplankton community in February: (a) 1994, (b) 1995 and (c) 1997.

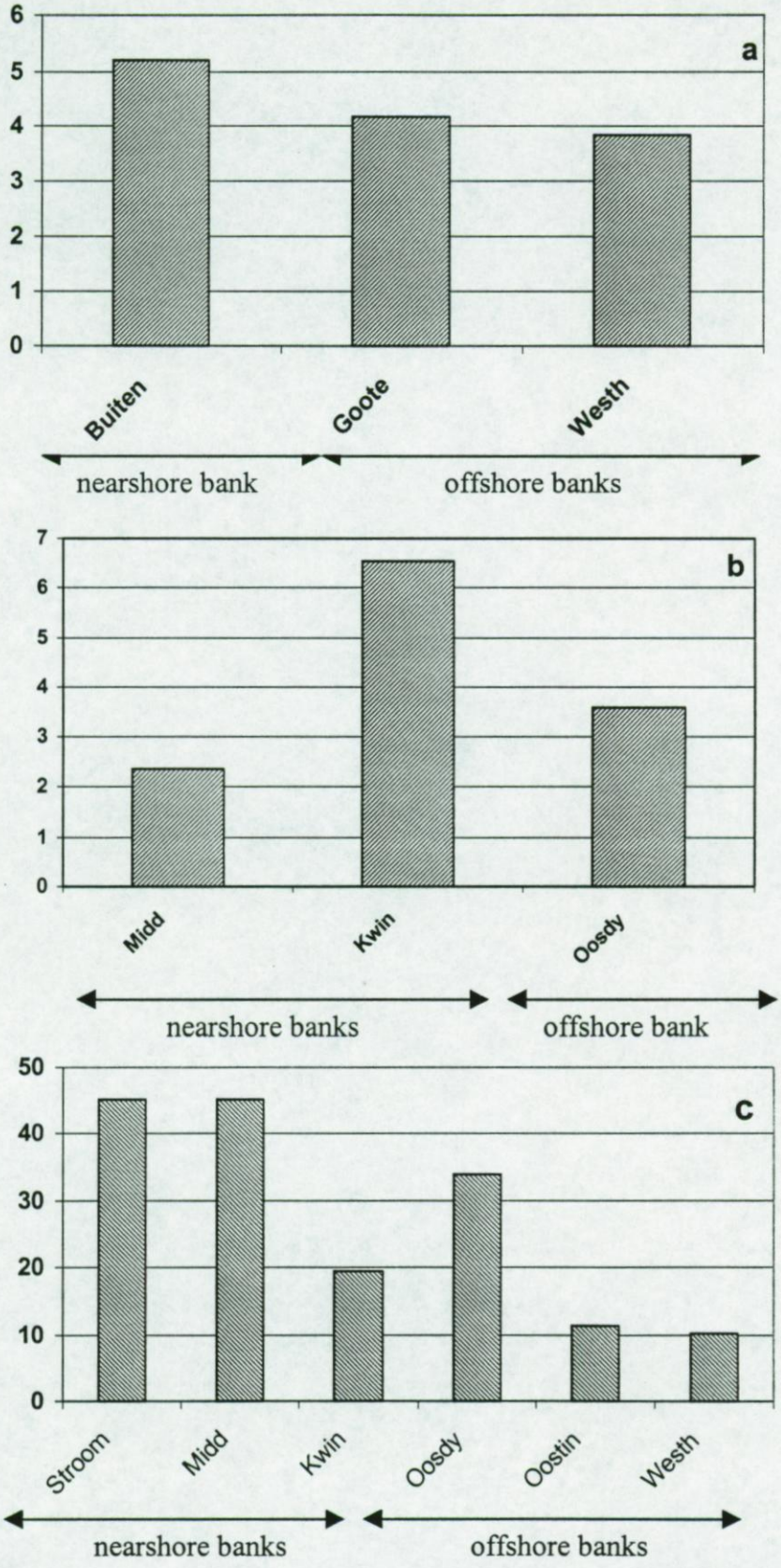


Figure 4.13 Carbon stocks of phytoplankton in February: (a) 1994, (b) 1995 and (c) 1997 at the different sandbanks. Stroom= Stroombank, Midd=Middelkerke, Kwin= Kwintenbank, Oosdy= Oostdyck, Oostin= Oosthinder and Westh= Westhinder.

Table 4.5 Carbon biomass and phytoplankton taxa on the different banks in February 1994, 1995 and 1997. Values between ( ) represent the percentage of the biomass of different size classes and taxa, on the nearshore and offshore area, respectively.

	1994		1995		1997	
	Carbon biomass (µg C l^{-1})					
	nearshore	offshore	nearshore	offshore	nearshore	offshore
Total carbon (PPC)	**5.21**	**4.0**	**4.44**	**3.58**	**35.42**	**18.23**
SED < 20 µm	**2.43**	**2.25**	**0.93**	**0.95**	**25.94**	**10.30**
(%)	(46.6)	(56.3)	(20.9)	(26.5)	(57.5)	(56.5)
SED > 20 µm	**2.78**	**1.75**	**3.51**	**2.63**	**9.48**	**7.93**
(%)	(53.4)	(43.7)	(79.1)	(73.5)	(42.5)	(43.5)
	Relative contribution (%) in terms of carbon biomass					
Bacillariophyceae	(89.6)	(78.3)	(94.7)	(91.8)	(63.1)	(71.5)
Dinophyceae	(4.0)	(6.0)	(2.0)	(2.3)	(2.5)	(4.5)
Prasinophyceae	(0.4)	(1.0)	(0.0)	(0.3)	(3.6)	(8.5)
Chlorophyceae	***	***	(0.4)	(0.5)	***	***
Euglenophyceae	(0.8)	(0.7)	(0.1)	(0.0)	(0.0)	(0.0)
Cryptophyceae	(5.0)	(13.5)	(2.2)	(3.6)	(30.0)	(15.2)
Chrysophyceae	***	***	***	***	(0.7)	(0.1)
Small unidentified Flagellates	***	***	***	***	(0.04)	(0.1)

3.6 Chlorophyll

Chlorophyll a stocks during February 1997 (Figure 4.14) varied from 0.31 to 4.55 µg l^{-1}. Spatial distribution had a similar pattern as was observed for biomass (Figure 4.13c), with high chlorophyll concentrations around the nearshore banks and decreasing towards sea.

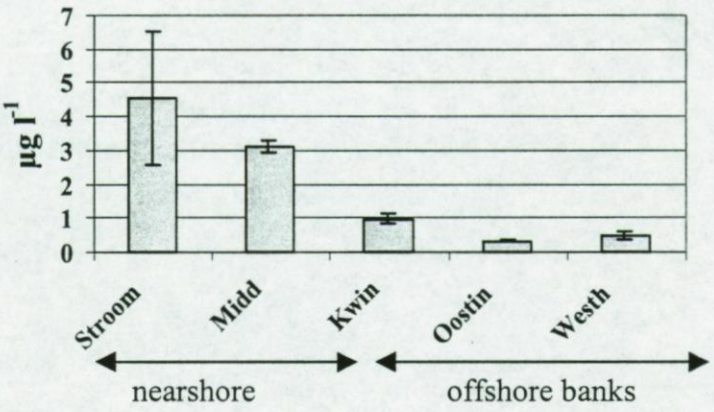


Figure 4.14 Distribution of chlorophyll a stocks in February 1997.

3.7. Dry Weight (DW) and Particulate Organic Carbon (POC)

Figures 4.15 and 4.16 show the concentration of DW and POC on all sandbanks during February 1997.

DW (Figure 4.15) fluctuated from the highest values (160 mg l^{-1}) at nearshore stations to the lowest (68 mg l^{-1}) offshore. POC (Figure 4.16) showed the same value gradient ranging 0.53 to 1.31. A significant correlation was observed between DW and POC ($r= 0.960$, $p= 0.0003$), but no significant correlation was observed between POC and Chla.

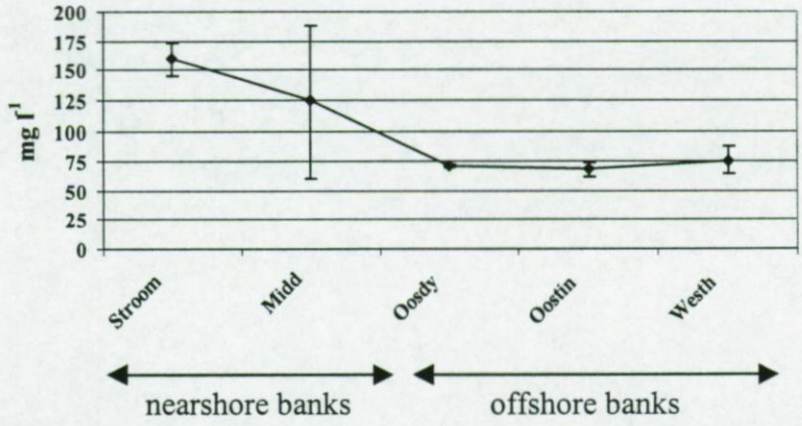


Figure 4.15 Mean dry weight concentrations (DW) around the Belgian sandbanks, during February 1997. Stroom= Stroombank, Midd= Middelkerke, Kwin= Kwintenbank, Oosdy= Oostdyck, Oostin= Oosthinder and Westh= Westhinder.

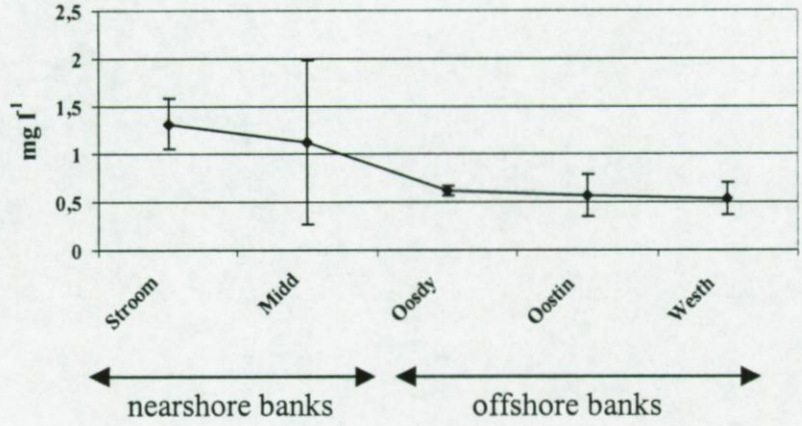


Figure 4.16 Mean Particulate Organic Matter concentrations (POC) around the Belgian sandbanks, during February 1997. Stroom= Stroombank, Midd= Middelkerke, Oosdy= Oostdyck, Oostin= Oosthinder and Westh= Westhinder.

Looking at the ratios, Chla:POC is generally higher on the nearshore banks than in the offshore banks (Figure 4.15a). POC:DW was highest at the nearshore bank Middelkerke and decreased slightly towards offshore banks (Figure 4.15b).

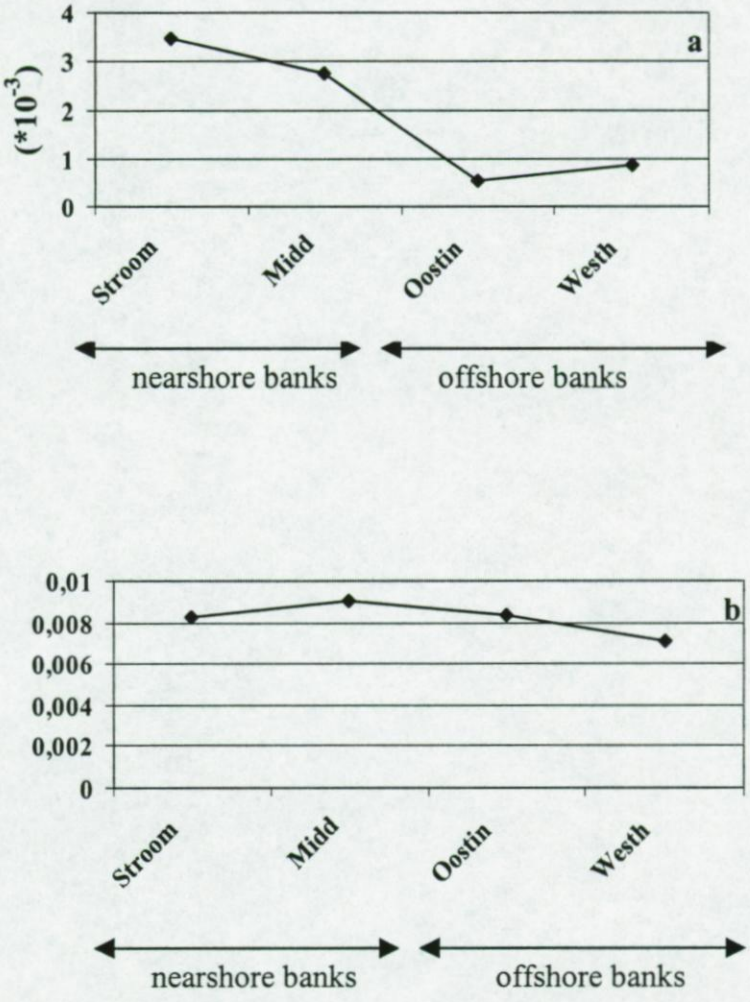


Figure 4.17 Variation of ratios: (a) Chla:POC and (b) POC:DW, in February 1997. Stroom= Stroombank, Midd= Middelkerke, Oostin= Oosthinder and Westh= Westhinder.

4. Discussion

Most of the phytoplankton species reported in this study are common in the coastal waters of Atlantic Ocean (Reid et al., 1990). They have been mentioned by previous investigations in the same area (e.g. Louis et al., 1974; Louis and Smeets, 1981, Gieskes and Kraay, 1975, Leewis, 1985, Novarino et al., 1997). Louis and Smeets (1981) report a considerable variation in phytoplankton species composition from year to year in the same area from February 1974 to 1978. They found the dominant species belonging to the Bacillariophyceae, while Euglenophyceae are more abundant in November and Chlorophyceae in October and November (Louis *et al.*, 1974). Moreover, several studies mention that diatoms are the dominant phytoplankton species in February in well-mixed coastal waters of the Southern North Sea (Gieskes and Kraay , 1975; Lancelot and Mathot, 1987, Reid *et al.*, 1990 etc...). Leewis (1985) reported also, in this area, the observation of 108 and 64 phytoplankton species during February 1974 and 1975, respectively. He observed no distinct species assemblages but only one *'association'* existing in the whole area, with only variations in species composition according to season, weather etc.... Leewis (1985) also reports high values of Shannon-Weaver index (H'= 3-4) in February 1974 in the Dutch coastal zone (See Figure 10 in Leewis, 1985). He concludes, based on yearly data, that the H' index can be useful to indicate the stage of a succession of the phytoplankton population (e.g. dominance of Phaeocystis pouchetii and micro-algae is illustrated by the lowest H' values) much better to predict the spatial pattern, in the Ducth coastal zone. While, Novarino et al. (1997) reported more than 84 pelagic flagellates species during the period 1988-89 in several sub-areas

in the Southern part of the North Sea. They report 52 dinoflagellates species, 6 cryptomonads, 5 green flagellates, one euglenoid, and one silicoflagellate.

Our results showed a clear spatial heterogeneity in phytoplankton occurs and for the three years, when data were expressed in terms of abundance. Thus, we confirmed our observations reported in Chapter 3. These showed, that in February 1994 an heterogeneity occurred in phytoplankton composition and to some extend in the zooplankton composition, between the offshore and the nearshore banks (M'harzi et al., 1998).

Twinspan analysis made clear that phytoplankton species composition was different between the areas covering the different sandbanks studied in the three years. Underlying differences in environmental conditions can be explained, as we already reported in Chapter 3, by the positioning of the banks. The Westhinder, Oostdyck, Oosthinder, and Kwintenbank positioned farest from the coast, and are obviously influenced by the southern intrusion of Atlantic water, which explains the higher temperature and salinity values observed on these bank, than on the other ones positioned closer to the coast. So in fact the neashore and offshore banks are positioned in two different water masses. As shown in Table 5 the main difference in phytoplankton composition- in general terms- was a predominance of Chrysophyta (represented by diatoms taxa) on the coastal banks, which was partially replaced by Dinophyceae and Cryptophyceae on the offshore banks, for the two first years. During 1997, Chrysophyta, Dinophyceae and Prasinophyceae taxa increased in contribution towards the Sea, while a quite high contribution of Cryptophyceae was observed on the coastal banks (Table 5). Leewis (1985) reported that the presence of phytoplankton species (e.g. *Ceratium* spp. and some small Dinophyceae species) originated from other North Sea floristic areas, linked to the tongue of oceanic water

coming from the English Channel. Leewis (1985) also found a quite different pattern of phytoplankton assemblage compared to the results reported by Giekes and Kraay (1975). Leewis (1985) explains this discrepancy by the fact that his results were expressed in terms of abundance whereas the results of Gieskes and Kraay (1975) were based on the biomass.

For the three years data, the first two CCA axes separated nearshore and offshore bank stations. The nearshore stations displayed a number of distinct characteristics when compared to the offshore ones. They have higher phytoplankton cells numbers and biomass (Table 1 and 5, Figures 4a, b and c) than the offshore and diversity is more variable than those in the offshore and does not differ significantly from year to year. Leewis (1985) found also a high diversity values (H' range 3-4) during February 1974 in the Dutch coastal zone. He noted that around the borderline of two sea areas, diversity could be high due to mixing of two water masses, which included different plankton communities.

This spatial phytoplankton heterogeneity can be due to the differences in the measured environmental factors. Salinity was found to be connected to a number of other factors with possible influence on phytoplankton distribution, such as nutrients associated with the freshwater flowing into the sea (Leewis, 1985). He found that salinity, temperature and wind are the important factors influencing significantly the phytoplankton distribution in the Dutch coastal zone, during summer and during the cold season, respectively. Van Bennekom and Wetsteijn, (1990) found that the winter distribution of nutrients in the eastern part of the Southern Bight of the North Sea is influenced by phytoplankton growth. They report that the NH_4-N is firstly used during the phytoplankton growth, and NO_3-N and NO_2-N were used when the NH_4-N is depleted. They conclude, also, that the NO_2 maxima could be used as indicators of the start of the phytoplankton

spring bloom, causing minima of Si, PO_4-P and NO_3-N. Van Bennekon A. J. and F. J. Wetsteijn, (1990) report an uptake of nutrients by phytoplankton in offshore waters (central part) in the Southern Bight of the North Sea, in February and already in January in some years. Gichuki (1997) found that an elevated ammonium concentration has a leading role in regulating the removal of nitrate and consequently, a reducing effect on the primary production in the southern Bight of the North Sea during spring 1997. The nutrient uptake regime in 1997 was characterized by high specific and absolute uptake rates of nitrate during the earliest stage of the growth season in the southern Bight (Gichuki, 1997). Moreover, the nitrate uptake rates values in 1997 were an order of magnitude higher than those measured at the same period -early growing season- of the previous year 1996 (Gichuki, 1997). This trend was maintained during the following days of the spring bloom (Gichuki, 1997). Based on culture and field experiments of nutrient assimilation by phytoplankton, it is well known, that the uptake and assimilation of NH_4^+ inhibits the uptake/assimilation of NO_3^- with complete inhibition of NO_3^- uptake occurring at NH_4^+ concentrations > 1 µM (Lomas and Glibert, 1999). Gichuki (1997) found high NO_3^- uptake rates during early March 1997, in the Belgian coastal zone, and this probably is a continuation of what happened the month before, during February 1997. Our study reports high NO_3^-, low NH_4+ concentrations (< 1 µM), and temperature values < 5°C. The positive correlation between NO_3^- and NH_4^+ (r^2= 0.87), NO_2^- and NH_4^+ (r^2= 0.93) and low temperature values had a significant effect on the phytoplankton distribution (Table 4). In the February 1997 multivariate analyses, nitrate concentrations contributed significantly to explain the variation in species composition. Thus, the inhibition of the NH_4^+ on the NO_3^-/NO_2^- uptake rates was not yet predominant during February 1997. However, the positive correlation

between NO_2^-/NO_3^- and NH_4^+, could be explained by nitrification by bacteria during autumn and winter in the Southern part of the North Sea (Nielsen and Stefels 1988).

The significant correlation between species composition and NO_3^- concentrations indicates that the differences in phytoplankton species composition, observed between nearshore and offshore banks, are not merely consequence of the presence of two phytoplankton communities in two distinct water masses of different origin. In this case nutrient data would not contribute to the explanation in phytoplankton species variability offered by the basic physical characteristics of the water masses: temperature and salinity. Differences in nutrient regime occurring within the study area seem to influence phytoplankton species composition.

Our studies showed also spatial variation in the different characteristics of measured SPM, DW, POC and Chla concentrations. Higher values of these factors were observed on the nearshore banks and then decreased seawards at the offshore banks. High POC concentrations (> 1 mg C l^{-1}) have been found in the shallow coastal zone of the North Sea (Cadée, 1982; Eisma et al., 1982a, 1982b; Ittekkot et al., 1982; Laane, 1982; Hickel, 1984) and in the Channel (0.1 - 0.7 mg C l^{-1}) (Banoub and Williams, 1973; Bos et al., 1987). This can be due to the riverine particulate matter trapped in the coastal zone gyre circulation (Nihoul and Ronday, 1975) and sedimentary organic matter originated from bottom erosion in this shallow area (Brockmann et al., 1990). Suspended particulate matter concentrations of more than 40 mg l^{-1} during February 1976 and January 1977, 1978 and 1980 were reported in the English/Scottish and continental coastal area of the southern North Sea (Figure 5b,e andg in Eisma and Kalf, 1979; and Figure 3 in Eisma and Kalf, 1987). A decrease towards sea was, also

observed in these studies. The strong tides, the supply of river water and erosion of coast of East Anglia mainly control the distribution of suspended matter in this area of the North Sea (Eisma and Kalf, 1987). POC and DW patterns seemed closely linked and this link was confirmed by significant correlation between the two measurements. Both showed consistent high values in the nearshore banks stations, and decreased towards Sea at the offshore banks. The spatial distribution of POC has similar pattern of the DW reported in the studies of Eisma and Kalf (1987). A high value is observed in most coastal stations of 1mg l^{-1} (Figure 3 in Eisma and Kalf, 1987), decreased towards sea to 0.5mg l^{-1} (Eisma and Kalf, 1987). They attributed the high concentrations of POC in the coastal water in the southern North Sea to the detritus. However, they report a low contribution of POC in the suspended matter (less <20%). Indeed, the resuspension of the bottom material can result in a high-suspended matter concentration, but with a low organic matter content (Eisma and Kalf, 1987). This is due to the consumption of the settled organic matter by bottom organims, including bacteria mineralization (Eisma and Kalf, 1987). Our studies showed a significant correlation between POC and DW, but with a very low contribution (maximally 1%) of POC to DW during winter 1997. The non-significant correlation between Chla and POC shows that the organic matter is mainly detritus. Using a Chla-POC conversion factor of 50, phytoplankton represents maximally 0.4% of the total POC.

Giekes and Kraay (1975) reported a high cell volume in the offshore areas of the Dutch coastal zone and in the French-Flemish Banks areas, during Winter-early spring 1974. Then the phytoplankton stock began to decrease gradually towards the sea in the Belgian coastal area during the same period of the year (Gieskes and Kraay, 1975). Our data showed the same scenario for the three

years, high concentrations in nearshore stations and a significant decrease towards Sea at the offshore stations. But, a very low phytoplankton standing stock was observed in February 1994 and 1995 compared to the high phytoplankton crops in February 1997. Such variation is also reported by several authors within the coastal area and the Southern part of the North Sea (Table 6), and is in a good agreement with the results given by Rousseau (1999, pers. comm) who reported a significant variation in phytoplankton stock from year to year (Table 6.4). Giekes and Kraay (1975) attributed the high observed phytoplankton stock in the Belgian banks to the potential fertilizing effect of the river waters (e.g. Schelde) which does not seem to be counterbalanced by the turbidity. While, the low phytoplankton standing stock in the nearshore stations of the Dutch coastal area is more influenced by the turbidity of Rhine (Giekes and Kraay, 1975).

During February 1994 and 1995 diatom biomass constituted a large fraction of the biomass in the < 20µm and > 20µm sizes classes (Table 5.4). However, a quite different pattern was observed during 1997. Cryptophyceae , together with diatoms, constituted a large fraction of the total carbon biomass and contributed significantly to the highly abundant small fraction (< 20 µm) on the nearshore banks (Table 5.4). Whereas, is attributed to the diatoms, Prasinophyceae and Dinophyceae in the offshore banks. The biomass of the fraction > 20 µm, was quite similar in both neashore and offshore banks. This can be explained by the fact that the decrease observed in Cryptophyceae taxa in the offshore banks was replaced by other small cell taxa belonging to Prasinophyceae and Dinophyceae, which hide the effect of the increase of diatoms. Gieskes and Kraay (1975) observed that diatoms were dominant and their cell volume (more than 95 %) consisted of a wide variety of species (e.g. *Biddulphia sinensis*, *B. regia*,

Lauderia borealis, *Thalassiosira* spp, *Coscinodiscus* spp., *Guinardia flaccida*, *Rhizosolenia imbricata*, *R. stolterfothii*, *R. hebetata*, *Bacillaria paradoxa*, *Melosira sulcata* and *Thalassionema*), during winter until April 1974. Also,

Table 6.4. Ranges in biomass values (μg C l^{-1}) of phytoplankton group taxa in the two main areas of the Belgian coastal zone, and some coastal zones along the North Sea ecosystem.

Taxa (Total μg C l-1)	Offshore areas	Nearshore areas	authors
Total biomass			
Feb 94	**4.44**	**5.21**	Our data
Feb 95	**3.58**	**4.44**	
Feb 97	**18.23**	**35.42**	
Bacillariophyceae	**26**	--	Mills et al., (1994)
Cryptophyceae	**0.76**	--	(Spring data)
Unidentified flagellates	**2.03**	--	
Phytoplankton (surface value)	**76**	--	
	5.5	--	
Protozoa (surface value)	**4.0**	--	Holligan et al.,
Microzooplankton	**16.3**	--	(1984)
Meosozooplankton	**3.76**	--	(Summer data)
Total particle Volume (ppm)	**0.14-0.21**	--	
Diatoms	--	**<20**	Peperzak et al.,
Autotrophic flagellates	--	**<20**	(1998)
			February
Total phytoplankton	**65**	--	Nielsen and Richardson,
Heterotr. Nanoflagellates	**0.09-0.10**	--	(1989)
			February/March
Total particle volume (ppm)	--	**0.2-2.6**	Richardson K.,
In the Danish coast			(1985)
			(spring data)
Total particle volume (ppm)	**1-5**	**0.1-1**	Gieskes and Kraay, (1975)
Danish coast and the Belgian coast	**0.2-0.5**	**1-5**	February 1974
Bacillariophyceae (Diatoms)			
Stn 330: Feb 90	**	**97.4**	Rousseau V., (pers. comm)
Feb 93	**	**24.1**	
Feb 94	**	**19.9**	
Feb 95	**	**5.3**	
Feb 96	**	**5.7**	
Feb 97	**	**37.9**	
Feb 98	**	**52.6**	

Stn, means station
Feb, means February.

Nielsen and Richardson, (1989) found that some diatom species (e.g. *Rhizosolenia* spp., *Plagiogramma brockmanii*) dominated the phytoplankton population (in terms of carbon) at the stations south of Dogger Bank in the North Sea - during February/March 1988 cruise. While, heterotrophic and autotrophic flagellates, and protozooplankton were present in low numbers before and during the spring bloom. Mills et al., (1994) reported also, in the shallow area of the South British coast, a dominance of diatom species (e.g. *Odontella sinensis*, *Rhizosolenia fragilissima*, *Stauroneins membranaceae*, *Coscinodiscus* sp. *Paralia sulcata*), other unidentified flagellates and *Cryptomonas acuta*.

As we already mentioned above, the early onset of the growing season of phytoplankton is well established during February 1997, but not with the same rate in the whole sampled area. Fact which is enhanced by the different developments in species composition (Leewis, 1985), which could explain the observed spatial trend within the phytoplankton size structure in the Belgian coastal zone.

5. Conclusion

We confirm in this study our first observations already reported in chapter 3. A spatial heterogeneity seems to be a general trend within the phytoplankton during winter around the Belgian sandbanks. The best explanation of the variance in phytoplankton community is obtained when nutrient concentration were included in the CCA analysis. This indicates that, besides the fact that the study are cover two water masses of different origin, variations in nutritional conditions also influence phytoplankton species composition. Differences in

phytoplankton species composition and taxa contribution also resulted in differences in biomass and size structure between nearshore and offshore banks. These may represent differences in the feeding conditions of the zooplankton. How this spatial heterogeneity affects the potential energy flux transfer from phytoplankton (considered as prey) to zooplankton (considered as predator) between the nearshore and offshore banks in the Belgian coastal area will be examined in detail in chapter 6.

Chapter V

SPRING PHYTOPLANKTON COMMUNITY STRUCTURE ALONG A NORTH SEA TRANSECT

Content

Spring phytoplankton community structure along a North Sea transect

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Abstract:

Phytoplankton samples were collected from 27 stations within a transect located between 60°56'86"N/1°01'81"W to 61°03'64"N/0°26'44"W and 55°12'10"N/3°00'88"E to 55°17'00"N/3°29'56"E (Dogger Bank area) in March/April 1994. Temperature, salinity and nutrient concentrations (SiO_4^{2-}, PO_4^{2-}, NO_3^-, NO_2^- and NH_4^+) were measured as environmental factors. A total of 100 species of phytoplankton were identified. The dominant taxa were Bacillariophyceae (*Coscinodiscus* spp, *Chaetoceros* spp, and *Rhizosolenia* spp.), Dinophyceae (*Ceratium* spp.) and flagellates (Prasinophyceae, Cryptophyceae, *Phaeocystis* sp. and some small unidentified flagellates). Phytoplankton concentration, decreased in terms of numerical abundance and biovolume, from the Dogger bank area (DB) to Central (cNS) and the Northern part of the North Sea (nNS). Twinspan analysis discriminated phytoplankton communities between: (1) the shallow water of Dogger bank (DB) area and (2) deeper water of Central (cNS)/northern (nNS) in which parallel subgroups could be distinguished. Canonical Correspondence Analysis (CCA) confirmed this pattern and indicated that the species distribution was significantly related to environmental factors, particularly to silicate, nitrate and nitrite concentration, temperature and salinity. Within the phytoplankton fraction > 5 µm a significant increase in biomass of species > µm was observed -both in terms of volume and carbon concentration- from the North to the South, big diatoms dominating in the Dogger Bank area. Although the biomass of cells < µm was higher in the Dogger Bank area than in the Central and Northern stations, their contribution to total phytoplankton biomass in the former was limited.

1. Introduction

The amount of information available on how hydrographical, chemical and biological factors affect the seasonal and geographical variation in phytoplankton communities in the North Sea has increased substantially over the past years. Phytoplankton and the environmental conditions that govern its production and abundance in the North Sea are, for example, extensively discussed by Reid et al. (1990) and reviewed by Brockmann et al. (1990) and Nelissen and Stefels (1988).

Ecosystem depth is known to have a structuring influence on the dominance of small versus large algal cells, and consequently on the food chain structure of the system (Cushing, 1989; Legendre, 1990; Legendre and Le Fèvre, 1989; Kiørboe, 1990). Indeed, large phytoplankton tend to dominate in neretic waters and areas of higher and variable nutrient levels, and smaller cells in open sea conditions and areas of stable nutrient levels (Varela, 1987; Morris, 1980; Kiørboe, 1990 and 1993). In addition to bottom-up forces such as turbulence and nutrient levels, top down control by grazing influences phytoplankton abundance and species composition (Kiørboe, 1993).

The concept of size differential control of phytoplankton biomass (Thingstad and Sakshaug, 1990) forms one of the theoretical frameworks for interpretation of observed phytoplankton communities. It states that, while biomass of small algae is mainly controlled by microzooplankton grazing, larger phytoplankton species are less subjected to predation and their abundance is mainly regulated by the balance between growth and sedimentation rates

(Riegman et al., 1993). This concept was successfully evaluated in several areas (e.g. for the North Atlantic by Taylor et al., 1993; Central North Sea and Mardsiep Sea by Riegman et al., 1993; a North Sea transect from the Dogger Bank to the Shetland islands by Riegman et al., 1998).

In this latter case, which considers the same study area as this paper, Riegman et al. (1998) consolidated this concept for the phytoplankton spring bloom, based on two size classes (< 5 μm and > 5 μm fractions). Riegman et al., (1998) showed that, on average over the entire transect, both carbon and nitrogen uptake rates based specific growth rates were significantly lower in the > 5 μm fraction than in the < 5 μm fraction. Nevertheless, in the Dogger Bank area, where the spring bloom had already started, 89 % of chla concentration was present in the > 5 μm fraction, while in the central North Sea and near the Shetland islands, 60 % of Chla was present in the > 5 μm fraction. Riegman et al., (1998) conclude that, in the Dogger Bank area, stronger grazing on small sized algae favored the biomass build up of large algal species, which were shown to be diatoms by qualitative microscopic observations. Kuipers and Whitte (1999) reported a higher microzooplankton grazing rate on the > 5 µm algal fraction in the Dogger Bank area than in the deeper stations during the same transect.

In this paper we report, for the same spring campaign of 1994, the results of detailed microscopical observations on phytoplankton species abundance and spatial distribution in the > 5 μm fraction. The principal aim of this study is to compare the phytoplankton community structure along a longitudinal transect in the Southern-Central North Sea and to assess the association between

phytoplankton communities and environmental factors. Secondly, we investigate in how far differentiation in phytoplankton species composition results in differentiation in the phytoplankton biomass and size distribution of the phytoplankton community.

The North Sea has been subdivided into a number of distinct areas by several authors (c.f. Williams et al. 1993). Parallel, several biological studies [e.g. microbial activity, Van Duyl et al. (1990); phytoplankton, Riegman et al. (1990); phytoplankton and zooplankton, Williams et al. (1993); zooplankton, Fransz et al. (1991 and 1998); macrobenthos, Duineveld et al. (1990) and fish, Daan et al. (1990)] have been carried out in the North Sea to identify the presence of floral and faunal assemblages which are associated with geographical boundaries. These studies generally report 3 main floral and faunal groups which are associated with: (1) a mixed shallow isothermal water (< 50 m depth); (2) frontal-central waters of the North Sea; and (3) stratified deeper waters, north of the Dogger Bank. Changes which are usually associated with the "front" occurring between different water masses within the North Sea are an elevation in terms of biomass, production and shift in community composition of the different biological components (Williams et al., 1993). Williams et al., (1993) described plankton assemblages and its dependence on physical and chemical factors covering North Sea Continuous Plankton Recorder (CPR) transects between 44 °N and 60°N. Their analysis was based on data from July 1984 to June 1987, using 36 phytoplankton taxa and species, which entities exceeded 10 % in the data tables and a spatial resolution of 1° latitude by 1° longitude. Our study was carried out along a North-South transect in the North

Sea with a spatial resolution of 1° latitude, from 61°N to 55°N latitude. A high number of phytoplankton taxa and species (44) were included in the analysis to identify possible phytoplankton assemblage and its geographical boundary in the North Sea.

2. Materials and methods

2.1 Sampling

Samples were collected in early spring (28 March to 12 April 1994) in the North Sea on board research vessel 'Pelagia'. A total of 21 station, distributed along three parallel transects were investigated (Figure 5.1). CTD profiles were obtained to provide information on temperature, light attenuation, turbidity and fluorescence.

Sampling was done with a 12 L Nansen bottle at 3 depths: 5, 10 and 40 m. 12 liters of sea water was filtered through a plankton net (30 μm) and concentrated to a volume of 100 ml or 200 ml. The samples were kept in glass bottles and preserved with Lugol's iodine solution.

2. 2 Laboratory analysis

For microscopic analysis, the samples were concentrated to 100 ml by decantation. 5 ml of concentrated sample was pipetted into a cuvette and allowed to stand for 20-30 minutes. Phytoplankton cells were identified and counted with an inverted microscope at 10x20 and 10x40 magnification, and species

abundance expressed as cells per liter. Keys and reference books used for identification were Van Heurck (1896), Schiller (1937), Cleve-Euler (1955), Butcher (1961), Hendey (1964), Drebes (1974), Hartley (1986), Pankow (1990), and Tomas (1993).

Cell volumes were calculated from cell dimensions (length, diameter and width) of all phytoplankton and microzooplankton species using appropriate geometric formulae (Edler et al., 1979). Cell carbon (PCC, pg. cell), for diatoms and non-diatoms was estimated from cell volume (V, μm^3 cell)

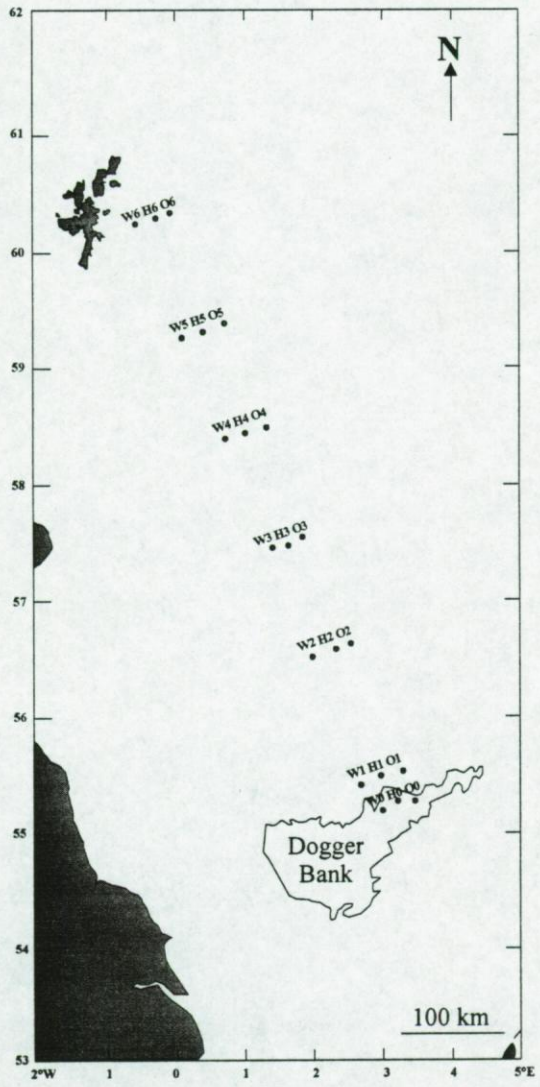

Figure 5.1 Map of study area showing the sampling stations along the transect.

using the formula of Eppley et al. (1970) for phytoplankton, and a conversion factor of 0.19 pg. C μm^{-3} for microzooplankton (Putt and Stoecker, 1989). Total phytoplankton volume (PV, ppm= 10^6 μm^3 ml^{-1}) and phytoplankton carbon (PC, pg C ml^{-1}) was then obtained by summing individual cell volume and cell carbon over abundance of all species respectively, for all species showing >1% of total numerical abundance. No attempt was made to distinguish between autotrophic and heterotrophic dinoflagellate species except for a few well-known heterotrophic species. Phytoplankton volume was differentiated by size (μm^{-3} cell $^{-1}$). From cell volume, spherical equivalent diameter (SED, μm) was calculated and this was used to allocate the species PV value into a given size class. The size classes used were logarithmic, corresponding to TA II Coulter size classes in the 5-100 μm SED range (Tackx et al., 1991). PV and PC values for each size class were averaged over each of the three stations situated at the same latitude.

Detailed results of ammonium, nitrate and urea concentrations along the same transect are reported by Riegman et al., (1998). In this paper, only the distribution of the environmental factors that came out as significant in relation to phytoplankton distribution by Monte-Carlo-testing (see data analysis), will be considered.

2.3 Data analysis

The main multivariate technique employed for the analysis of physico-chemical surface data was cluster analysis (joining tree clustering). Distance

metrics was Euclidean, employing the single linkage method (nearest neighbour). The data were previously standardized.

'Two Way Indicator Species Analysis' (TWINSPAN) (Hill, 1979) was performed on the abundance matrices to analyze the spatial distribution and community structure of phytoplankton over the study area. Taxa and species abundance (Table 1) were expressed as percentage and the default options of the TWINSPAN routine were used throughout the analysis.

Canonical Correspondence Analysis (CCA) using the CANOCO package (Ter Braak, 1987b and 1988) was used to determine the relation between phytoplankton species numerical abundance and environmental variables (temperature, salinity and nutrient concentrations). Species abundance data were ln+1 transformed. Downweighing of rare species was performed. Significance of the correlations between species distribution and environmental factors was tested by Monte Carlo using 99 unrestricted permutations.

3. Results

3.1 Environmental factors

Temperature, salinity and nutrient profiles revealed vertical homogeneity at all stations (see Riegman et al., 1998). Thus, the results reported here include

only surface water samples. Marked horizontal nutrient gradients were, however, observed.

Temperature in the investigated area ranged from 5.5 to 7.5°C with maximum values at the nNS stations (W_7, H_7, O_7, W_6, H_6, and O_6) and a decrease in the stations W_5, H_5, O_5, W_4, H_4, O_4, W_3, H_3, O_3, W_2, H_2 and O_2 (Figure 5.2a). Salinity values higher than 35 psu were observed in all stations except stations W_3, H_3 and O_3 (Figure 5.2b).

Surface nutrient concentrations were high in the north and decreased towards the south (DB). Silicate concentration was high at all stations with a maximum value of 4.4 μmol l^{-1}, except at the stations around the DB (W_1, H_1, O_1, W_0, H_0, and O_0), where a minimum value of 2.60 μmol l^{-1} was measured (Figure 5.2c). Nitrate+nitrite and phosphate concentrations (Figure 5.2d,e) were high at the nNS stations (11.72 and 0.76 μmol l^{-1} respectively), showing the inflow of the Atlantic at the northern boundary. They decreased towards the south (DB) to 0.10 μmol l^{-1} and 0.09 μmol l^{-1} respectively.

The cluster analysis for the environmental factors (temperature, salinity and nutrients) produced two well defined groups. The first group was composed of the shallow stations situated in the DB area. The second group was composed of the deeper stations of the cNS and nNS area. Within this group the central stations (W_2, H_2, *and* O_2) split from the rest of the northern stations. Within the first group, stations (W_0, H_0, O_0) in the DB area split from stations (W_1, H_1, O_1) which are situated in a transition zone between the deeper and shallower stations of the transect (Figure 5.3).

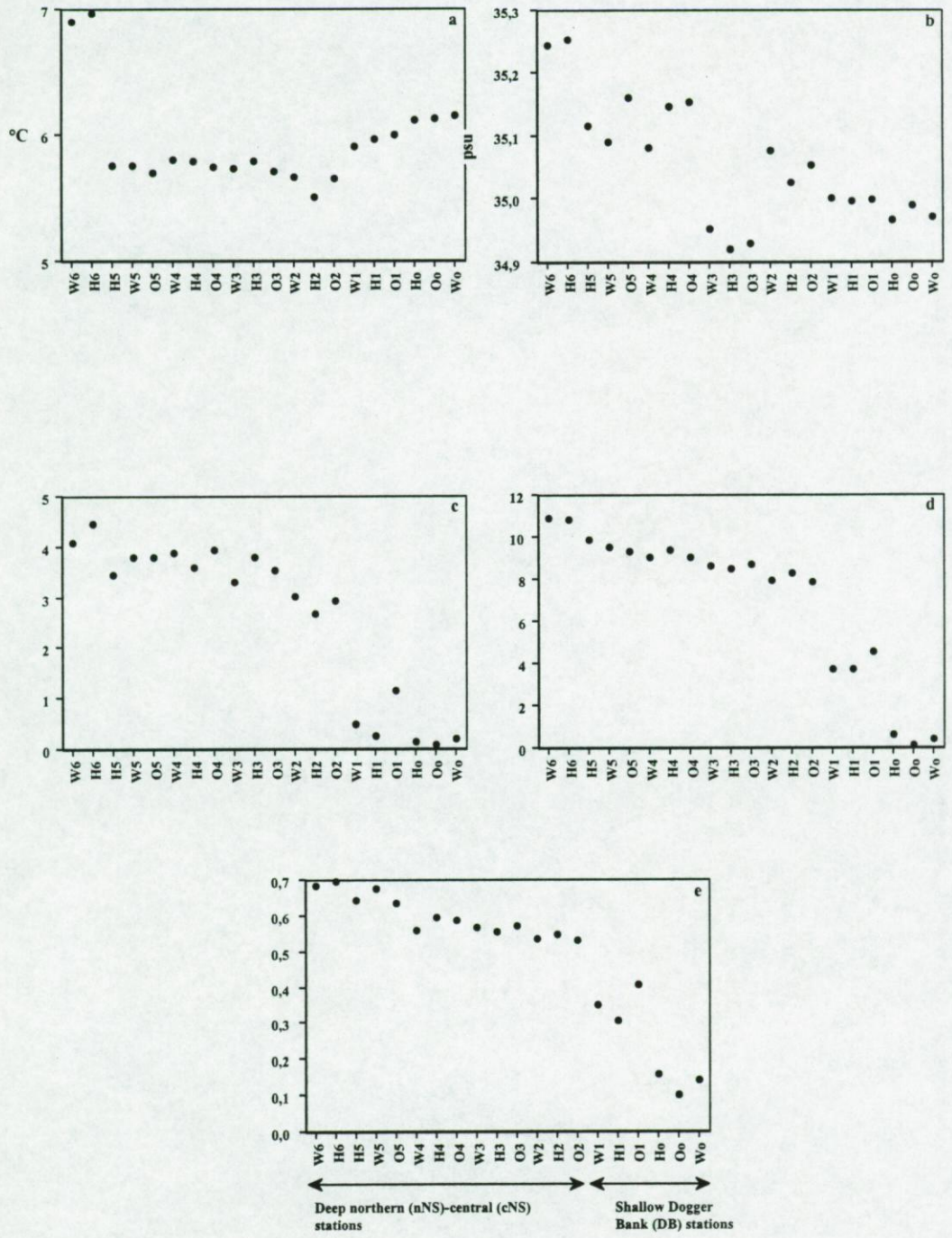

Figure 5.2 Environmental factors measured at all stations: (a) Temperature (°C) (b) Salinity (psu) and nutrients (μM l^{-1}): (c) Silicates (d) Nitrate+Nitrite and (e) Phosphate.

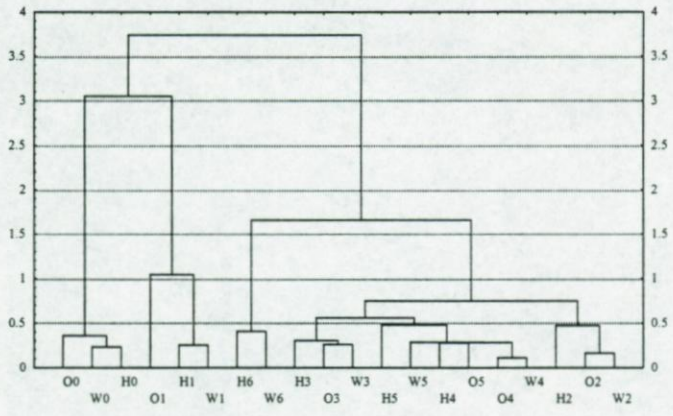

Figure 5.3 Cluster analysis of the stations based on the data-set of environmental factors.

3.2 Phytoplankton species abundance

A total of 100 species of phytoplankton and microzooplankton were identified (Table 4.1). Figure 5.4 shows the numerical abundance of the major taxonomic groups of phytoplankton. Bacillariophyceae (mostly diatom species) abundance was low in the Shetland area and Central North sea, and increased, by more than 5 times towards the Dogger Bank. Prasinophyceae + Chlorophyceae were restricted to stations W_1, H_1 and O_1, their abundance was similar to that of the Bacillariophyceae. Small-unidentified flagellates were also observed, in low abundance, at these stations only. Chrysophyceae and Dinophyceae occurred in all stations but in very low abundance compared to other classes. Haptophyceae were restricted to the Dogger Bank area (stations W_0, H_0, O_0) and occurred in a 20 times higher abundance than Bacillariophyceae in this area.

The contribution of Bacillariophyceae (diatoms) to total phytoplankton abundance was 92% in most of the northern and central stations (H_2, W_2, O_2, H_3, W_3, O_3, H_4, W_4, O_4, H_5, W_5, O_5, H_6 and W_6), and decreased to 54% in the transition zone (W_1, H_1, O_1) and to 4% in the Dogger Bank area (W_0, H_0, O_0). The contribution of Prasinophyceae and Cryptophyceae in stations W_1, H_1, O_1 and Haptophyceae in stations W_0, H_0 and O_0 was 48% and 96% respectively. Thus, diatoms dominated the phytoplankton community in terms of numerical abundance in all stations, except at the Dogger Bank stations, where the flagellate community was important.

Among the diatoms, *Thalassiosira* spp., was the dominant genus, with *T. rotula* (Meunier), *T. gravida* (Cleve) and *T. hyalina* (Grunow), as dominant species, contributing 21% of total phytoplankton abundance in the northern and central stations. It was accompanied by *Chaetoceros* spp. and *Nitzschia* spp., mainly *C. borealis* (Cleve), *C. diadema* (Cleve), *C. didymus* (Ehrenb.), Pseudo*Nitzschia. serriata* (Cleve) and *N. longissima* (Brèb. ex Kütz), with 13% and 38% respectively, of total phytoplankton abundance.

At stations H_2, W_2 and O_2, a large single celled diatom, *Coscinodiscus concinnus* (Smith) was dominant (21%). *Tetraselmis suecica* (Kylin) represented 37% of total abundance at stations W_1, H_1, O_1, accompanied by a small unidentified *Thalassiosira* sp. (20%) and *Rhodomonas (Karsten)* (9%), while *Phaeocystis* sp. (96%) was dominating at stations W_0, H_0 and O_0.

Table 5.1 Species List

Division: Chrysophyta
Class: Bacillariophyceae
Order: Centrales

Odontella	*aurita* (Lyngb.) Ag.
	regia (Schiltze) Simonsen
	sinensis (Grev.) Grun.
	mobiliensis (Bailey) Grunow
Paralia	*sulcata* (Ehrenb.) Cleve
Aulacoseira	*distans* (Ehrenb.) Simonsen
Aulacoseira	*granulata* (Ehrenb.) Simonsen
Skeletonema	*costatum* (Grev.) Grun.
Stellarima	*stellaris* (Repor) Hasle & Sims
	radiatus (Ehrenb.)
	centralis (Ehrenb.)
Thalassiosira	*eccentrica* (Ehrenb.) Cleve
	Antartica Comber
	rotula Meunier
	nordenskioeldii Cleve
	hyalina (Grun.) Gran
	subtilis (Ostenf.) Gran
	gravida Cleve
	sp. small unidentified species (S.E.D= 8 µm)
	leptopus (Grun. in Van Heurck) Fryxell et Hasle
Roperia	*tesselata* Grunow ex Pelletan
Ditylum	*brightwellii* (West.) Grunow
Leptocylindrus	*danicus* Cleve
	minimus Gran
Actinoptychus	*senarius* Ehrenberg
Corethron	*criophilum* Castr. 2387
Guinardia	*delicatula* (Cleve) Hasle G15883
	striata (Stolterfoth) Hasle
Rhizosolenia	*delicatula* Cleve
	setigera Brightwell
	hebatata (Bail.) Gran
	imbricata Brightw.
	pungens Cleve
Bacteriastrum	*hyalinum* Laud. 2866
Chaetoceros	*danicus* Cleve
	densus Cleve
	didymus Ehrenb.
	socialis Lauder
	borealis (Bail.)
	teres Cleve
	decipiens Cleve
	similis Cleve
	diadema (Ehrenb.) Gran
	compressus Laud.
Eucampia	*zodiacus* Ehrenb. 2733

Guinardia	*flaccida* (Castr.) H. Perag.
Lauderia	*annulata* Cleve 2533
Order: Pennales	
Fragilaria sp	Lyngb.
Gyrosigma sp	Hass. 4692
Brockmanniella	*brockmannii* (Hust.) Hasle, Von Stosch & Syvertsen
Plagiogrammopsis	*vanheurckii* (Grun.) Hasle, Von Stosch & Syvertsen
Pleurosigma	*normanii* Ralfs in Pritchard
	sp.
? *Ctenophora*	*pulchella* (Ralfs ex Kütz.) Williams et Round
Thalassionema	*nitzschioides* Grunow
Asterionellopsis	*glacialis* (Castracane) Round in Round al. 615890
Amphiprora	*alata* Ehrenb. 4680
Navicula	*distans* W. Sm. after Grunow
	sp
Meuniera 615897	*membranacea* (Cleve) Silva 615896
Trachyneis 4547	*aspera* (Ehrenb.) Cleve 4548
Bacillaria	*paxillifer* (Müller.) Hendey
Rhabdonema	*sp.*
Nitzschia	*longissima* (Bréb.) Ralfs
	sp
Pseudonitzschia	*seriata* (Cleve) H. Peragallo
Pseudonitzschia	*delicatissima* (Cleve) Heiden
Cylindrotheca	*closterium* (Ehrenb.) Reiman et Lewin
Pennates diatom	*sp*
Triceratium	*spinosum* J. W. Bail.
Class: Chrysophyceae	
Distephanus	*speculum* (Ehrenb.) Haeckel
Class: Prasinophyceae	
Tetraselmis	*suecica* (Kylin) *Butcher.*
Class: Cryptophyceae	
Rhodomonas	*sp.* Karsten
Class: Haptophyceae	
Phaeocystis	*sp.*
Division: Pyrrophyta	
Class: Dinophyceae	
Order: Prorocentrales	
Prorocentrum	*micans* (Ehrenb.)
Mesoporos	*perforatus* (Gran) Lillick

Order: Peridiniales	
Dinophysis	*acumunita* Clap. et Lachm.
	ovum Schütt
Amphidinium	sp.
Gymnodinium	*fissum* Levander
	splendens Lebour
Gymnodinium	*sp.* Conrad & Kufferath, 1954.
Noctiluca	*scintillans* (Macartney) Kof.
Pyrophacus	*sp.* Stein
Diplopeltopsis	*minor* (Pauls.) Pavillard
Dissodium	*assymmetricum* (Mangin) Loeblich III
Protoperidinium	*claudicans* (Paulsen) Balech
	leonis (Pavillard) Balech
Peridinium	*sp* Drebes
	ovatum (Pouchet) Schütt
Gonyaulax	*grindleyi* Reinecke
Ceratium	*lineatum* (Ehrenb.) Cleve
	arietinum Cleve
	macroceros (Ehrenberg) Vanhöffer
	tripos (O. F. Müller) Nitzsch
	horridum (Cleve) Gran
	longipes (Bailey) Gran
	furca (Ehrenberg) Clap. et Lachm.
	fusus (Ehrenberg) Duj.
	sp.
Microzooplankton:	
Hemicostonella	sp.
Tintinnopsis	sp.

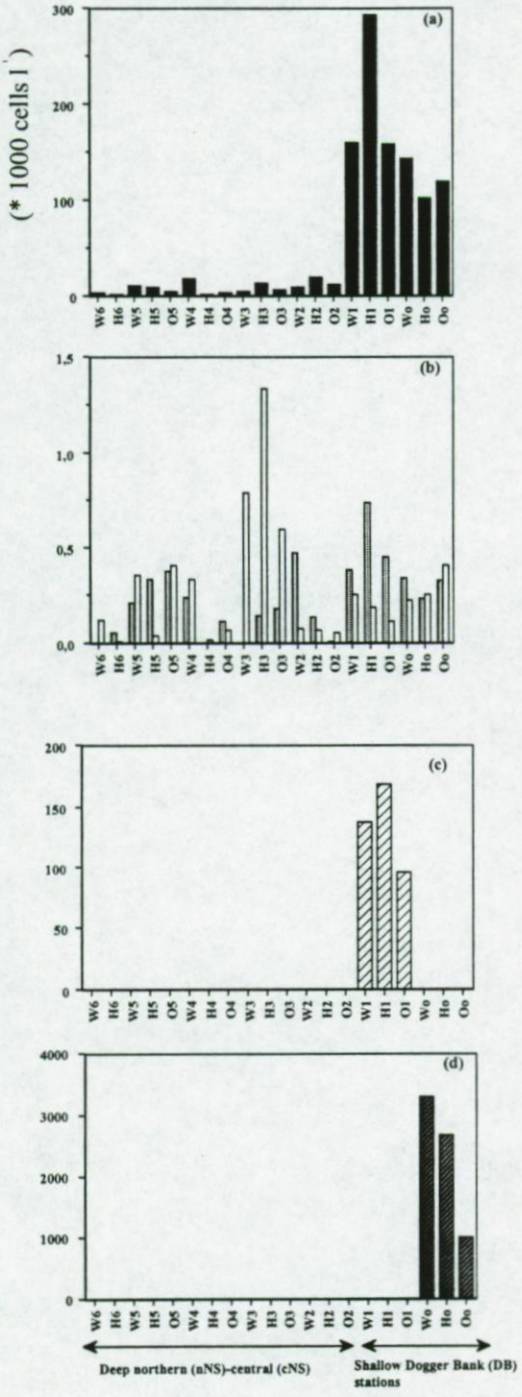

Figure 5.4 Abundances (in *10^{3}cells. l^{-1}) of the differents phytoplankton taxa along the transect.

Bacillariophyceae, Dinophyceae, Chrysophyceae, Haptophyceae and, Prasinophyceae + Cryptophyceae

3.3 Phytoplankton community analysis

The TWINSPAN results (Figure 5.5) showed a clear splitting, separating the Dogger Bank area, with indicator species *Navicula* spp. from the central and northern stations of the transect, with *Thalassionema nitzschioides* as indicator species. Within the left group a split of stations just North of the Dogger Bank (H_1, O_1 and W_1) from those situated in the Dogger Bank area ($W_0H_0O_0$) occured, the latter having *Odontella* spp. as indicator species.

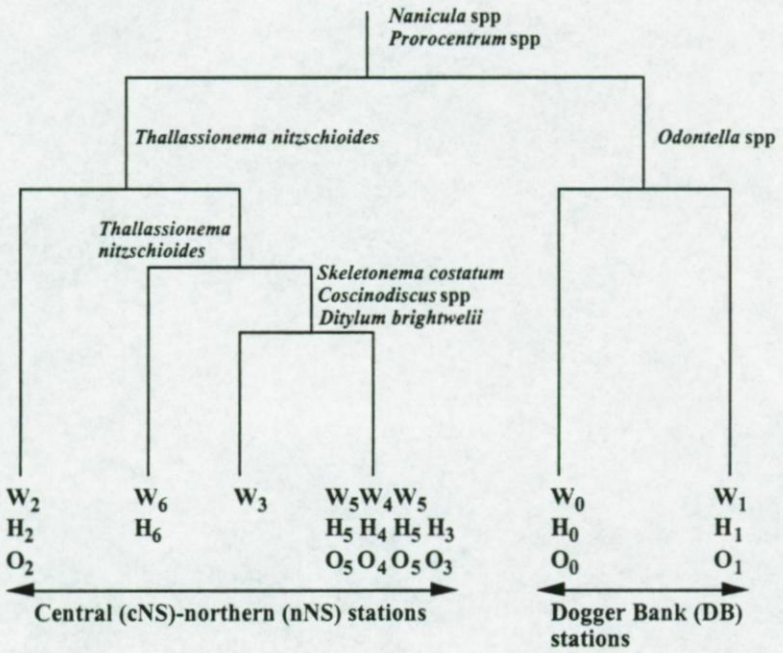

Figure 5.5 Twinspan analysis dendogram for phytoplankton along the transect.

The plots for sample and taxa - species and scores as a result of a combination of environmental factors are shown in Figure 5.6 a and b, respectively. CCA axis 1 and 2 explained 37% and 33%, of the variance in the species - environmental biplot (Figure 5.6a). Axes 3 and 4 explained 18% and

7% of the variance. For axis 1, axis 2, axis 3 and axis 4, the eigenvalues were 0.380, 0.338, 0.190 and 0.073, respectively. Correlations between ordination axes and environmental variables (Table 5.2) showed that silicate, nitrate and nitrite concentrations and salinity were correlated with axis 1, temperature with axis 2 and axis 4. The station biplot showed a clear split along the transect between the Northern and central area and the Dogger bank area. Axis 1 had a high correlation with silicate, nitrate and nitrite concentrations and salinity (r = 0.886, 0.737, 0.425 and 0.434 respectively) which ordered stations and taxa along nutrient and salinity gradients (Table 5.3). Stations $W_6H_6O_6$, $W_5H_5O_5$, $W_4H_4O_4$, $W_3H_3O_3$ and $W_2H_2O_2$ were found on the right side of axis 1, with generally higher salinity, and silicate, nitrate and nitrite concentrations (Figure 5.6b). The Dogger Bank stations $W_0H_0O_0$ were situated higher on axis 2, associated with higher values of temperature, and low nutrient concentrations. Stations $W_1H_1O_1$ took up an intermediate position on the left side of axis 2. Taxa with high positive correlation with axis 1 were those occurring in the majority of the stations (except stations $W_1H_1O_1$ and $W_0H_0O_0$). Axis 2 and 4 were positively correlated with temperature (r= 0.358 and 0.464 respectively). Taxa with the highest positive correlations with Axis 2 and 4 were *Phaeocystis* sp., *Tetraselmis* sp, *Rhodomonas* sp., *Thalassiosira* sp., *Rhizosolenia* spp, *Paralia* sp, *Staurauneis membranaceae*, *Guinardia flaccida*, *Pleurossigma* spp, *Bacteriastrum hyalinum*, and microzooplankters They exhibited maximum abundance in the Dogger Bank area.

Forward selection by Monte-Carlo testing in the CCA showed that the variance in phytoplankton species data were explained in descending degree by

the silicate concentration (37%, p = 0.01), concentration of nitrate (28%, p = 0.01), salinity (18%, p = 0.01), temperature (8%, p = 0.01) and nitrite concentration (7%, p = 0.01). 95% of the variance in phytoplankton taxa was explained by the entire set of environmental factors tested. The p-value of the test of significance of the first canonical axis was 0.01.

Table 5.2 Summary of CCA results on phytoplankton data.

	p-values	Variance explained by the variables selected
Silicate	0.01	37%
Nitrate	0.01	28%
Salinity	0.01	18%
Temperature	0.01	8%
Nitrite	0.01	7%
Test of significance of first canonical axis	0.01	

	Axis			
	1	2	3	4
Silicate	0.886	-0.381	-0.007	0.006
Nitrate	0.737	-0.609	-0.077	-0.003
Salinity	0.434	-0.253	-0.585	-0.081
Temperature	-0.159	0.358	-0.446	0.464
Nitrite	0.425	-0.776	-0.032	0.005

Table 5.3 Weighed correlation matrix (intra-set correlation) for environmental variables used in canonical correspondence analysis. SIL=Silicates, PO_4= Phosphate, NO_3= Nitrate, NO_2= Nitrite, NH_4= Ammonium, and URE= Urea.

SAL	1.0000							
TEM	.2449	1.0000						
SIL	.5293	-.2885	1.0000					
PO4	.5717	-.3130	.8771	1.0000				
NO2	.5006	-.3583	.7690	.8545	1.0000			
NO3	.5980	-.3102	.9465	.9390	.8694	1.0000		
NH4	-.0886	.4154	-.2791	-.3391	-.2795	-.3554	1.0000	
URE	-.1502	-.0449	.0648	.0006	-.0273	.0115	.2467	1.0000
	SAL	TEM	SIL	PO4	NO2	NO3	NH4	URE

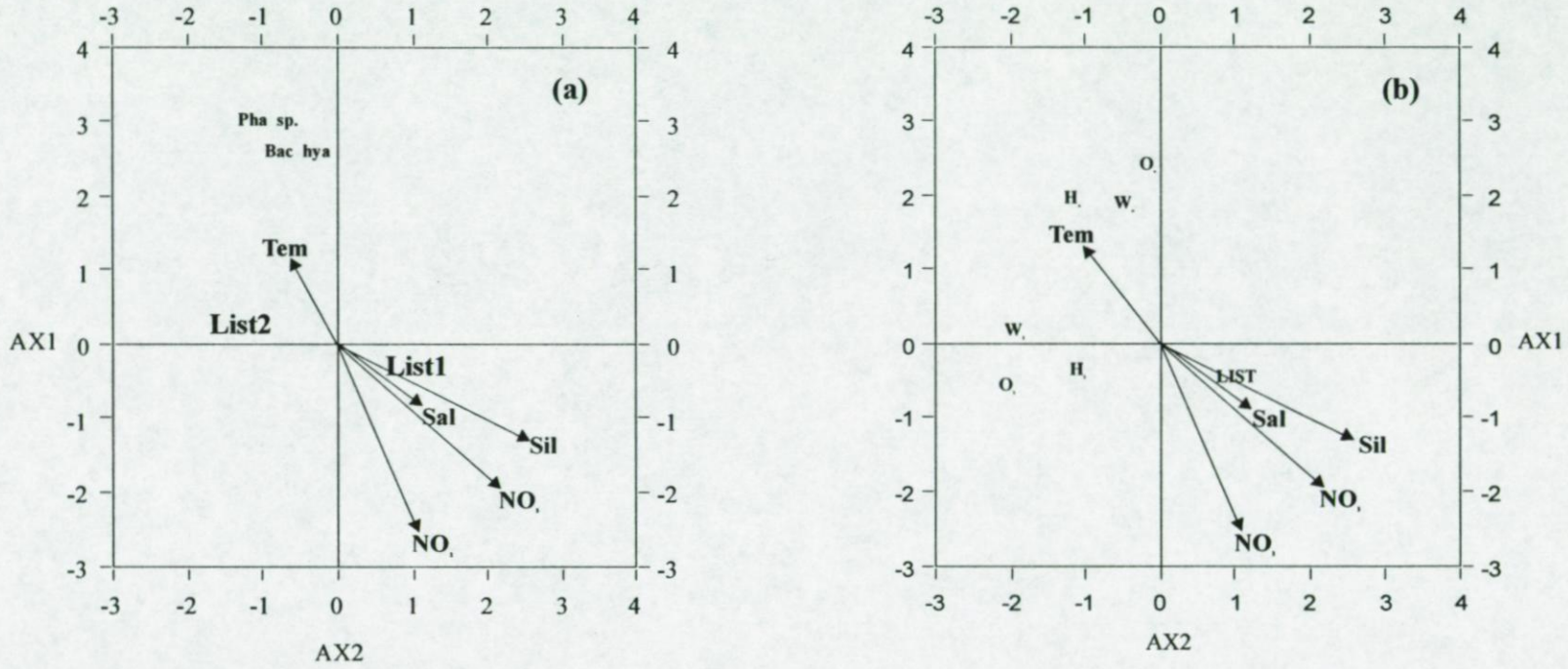

Figure 5.6. CCA analysis of phytoplankton species abundance with respect to environmental factors: (a) Species biplot: List1, including species which are close together: *Skeletonema costatum*, *Thalassionema nitzschoides*, *Thalassiosira* spp, *Chaetoceros* spp, *Coscinodiscus* spp, *Ditylum brigtwellii*, *Asterionellopsis glacialis*, *Bacillaria paxillifer*, *Eucampia zoodiacus*, Pennates diatom, *Corethron criphilum*, *Roperia tesselata*, *Triceratium spinosum*, *Leptocylindrus* spp, *Distephanus speculum*, *Gymnodinium* spp, *Ceratium* spp, *Gonyaulax grindleyi*, *Diplopeltopsis minor*, *Dinophysis* spp; **List 2**, *Rhodomonas* sp, *Tetraselmis suecica*, *Thalassiosira* sp. (SED= 8µm), *Paralia* spp, *Rhizosolenia* spp, *Guinardia flaccida*, *Pleurosigma* spp, *Odontella* spp, *Fragilaria* sp., *Amphiprora* sp, *Brockmaniella brockmannii*, *Plagiogrammopsis vanheurckii*, Navicula spp, *Meuniera membranacea*, *Nitzshia* spp, *Lauderia borealis*, *Actinoptychus senarius*, *Gyrosigma* sp., *Prorocentrum micans*, *Mesoporos perforatus*, *Peridinium* spp, and Microzooplankton spp; and environmental factors are: **Tem= temperature, Sal= salinity, Sil= silicates, NO3= nitrate, and NO2= nitrite. (b) Stations biplot: LIST=** H_6, W_6, W_5, H_5, O_5, W_4, H_4, O_4, W_3, H_3, O_3, W_2, H_2 and O_2.

3.4 Phytoplankton size distribution

Figure 5.7 shows the PV distributions observed as average at each groups of stations situated at the same altitude in the transect. In the northern and central stations, one, two or three volume peaks occurred in the 20 to 50 μm size range, which generally showed concentrations < 0.04 ppm (Figure 5.7 a, b, c, and d). At stations $W_2H_2O_2$ (Figure 5.7e) and in the Dogger Bank area ($W_1H_1O_1$ and $W_0H_0O_0$) (Figure 5.7 f, g) peak volumes were over an order of magnitude higher than in the northern and central part of the transect. A typical pronounced peak around 100 μm SED occurred in stations $W_2H_2O_2$ and in the Dogger Bank area ($W_1H_1O_1$ and $W_0H_0O_0$), where it was associated with a few smaller peaks of smaller sized species. The particle-size spectrum was dominated by the large diatom *Coscinodiscus concinnus* (66 % of PV and > 62 % of PC) at $W_2H_2O_2$ and *Rhizosolenia* spp. (53 % of PV and > 25 % of PC) in the Dogger Bank area ($W_1H_1O_1$ and $W_0H_0O_0$). Total phytoplankton biomass showed high values around Dogger Bank, compared to the central and northern stations of the transect where significantly lower values were found (Table 5.4).

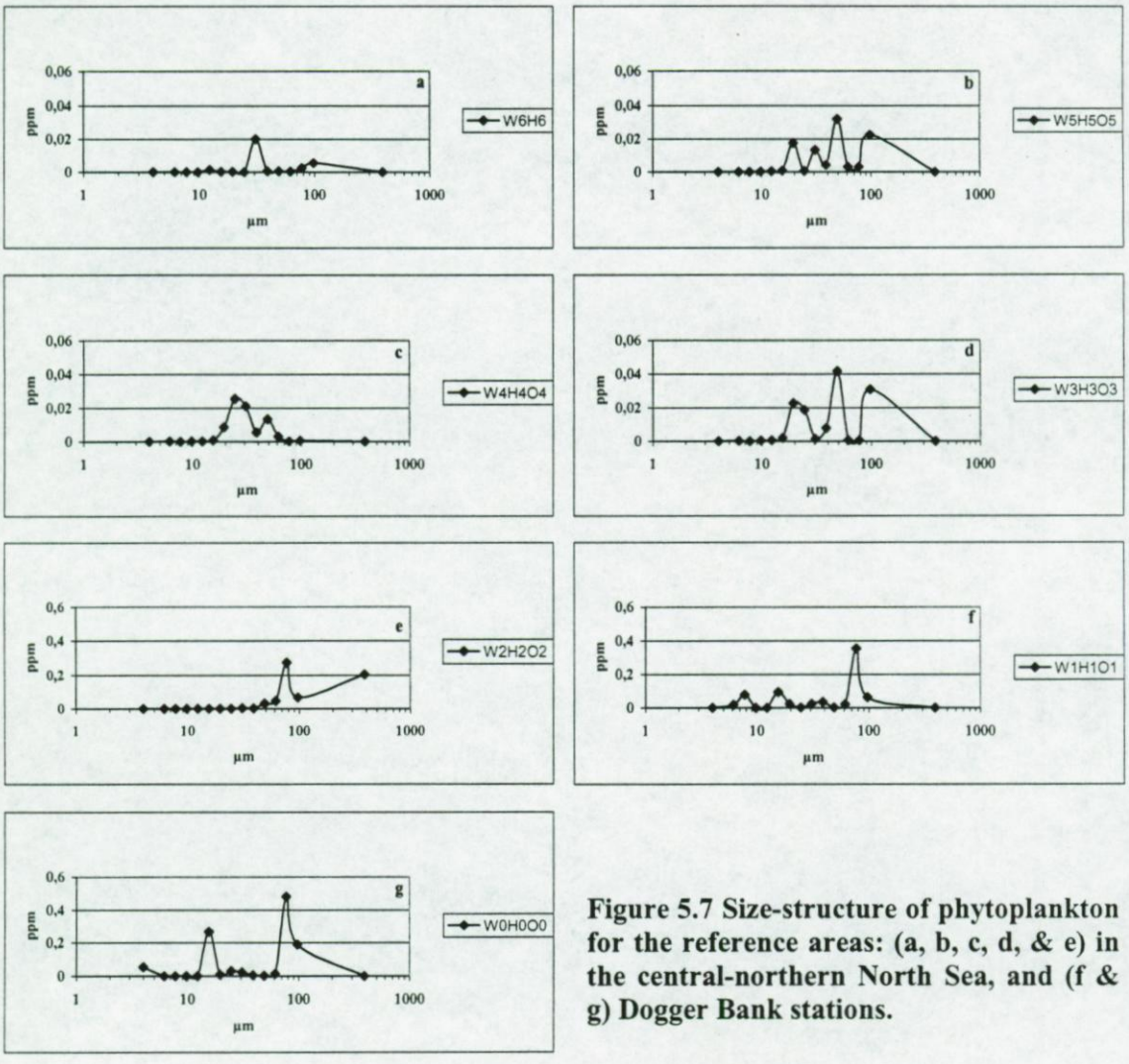

Figure 5.7 Size-structure of phytoplankton for the reference areas: (a, b, c, d, & e) in the central-northern North Sea, and (f & g) Dogger Bank stations.

4 Discussion

The non-significant differences between different depths of one station and between stations on the same latitude for the prevailing environmental factors and phytoplankton species abundance revealed homogeneity in the water column during the spring bloom period. Rather homogeneous vertical and horizontal conditions in the FLEX box at end of March 1976 (Svanson, 1980) and a vertical homogeneity in temperature and salinity were also observed in various regions of the North Sea during February-March cruise by Nielsen and Richardson (1989).

As shown by the subsequent splitting in the TWINSPAN analysis (Figure 5.5), the phytoplankton communities of the central and northern stations differed substantially from that around Dogger Bank, and were also different from each other. CCA analysis showed that about 95% of the variability in the phytoplankton species could be explained by the selected physical-chemical variables. The transect showed distinct communities along a nutrient-salinity-temperature gradient: a low abundance of phytoplankton in the Central and Northern zone, where North Atlantic water mass intrusion provides high nutrient concentrations and salinity, and a high abundance in Dogger Bank area with low nutrient concentrations and relatively high temperature (Figure 5.6b, and Table 5.2). This corroborates the general picture of the early onset of the spring bloom in the shallow Dogger Bank due to the relative increase in irradiance, homogeneity of the water column, the availability of the nutrients during spring 1994 (Riegman et al., 1998). While, in the Central and Northern North Sea, low

incident irradiance in combination with deep mixing provides light limitation for the phytoplankton (Williams and Lindley, 1980; Reid et al., 1990; Nielsen and Richardson, 1989).

During our sampling campaign, the spring bloom had clearly already started in the Dogger bank area, leading to substantially higher phytoplankton stocks than in the central and northern North Sea, both in terms of numerical (Figure 5.4), volumetric (Figure 5.5) and carbon (Table 5.4) concentrations. Indeed, the high abundance of microflagellates (Prasinophyceae, and Chlorophyceae) and *Phaeocystis* sp. in the Dogger Bank area is due to the advantage of the non-diatoms species for growth in a nutrient-limited environment after exhaustion of nutrients (mainly silicate) by diatoms (Bauerfeind et al., 1990). This was confiremd by our CCA analysis where these microflagellates taxa were positioned in the Dogger Bank stations and in the opposite direction of the nutrient concentrations (Figure 5.6a). Nevertheless, some large diatoms, such as *Rhizosolenia* spp. were found to be associated with these microflagellate taxa, in the silictae-depleted environment in the Dogger Bank area (Figure 5.6a). The contribution of large diatoms to total biomass, expressed in term of biovolume or carbon content, exceeded that of the microflagellates taxa (Table 5.4). The apparent contradiction of a high stock of diatom species occurring at low silicate concentrations, can be explained if we consider the following: (a) the onset of spring bloom started already in the course of February or early March in the Dogger bank area (e.g. Richardson et al., 1998), while the Dogger Bank stations were sampled in the mid of April (12 and 13) during our cruise; (b) *Rhizosolenia* spp. are often observed together with *Phaeocystis* and are known to grow under

lower silicate concentrations than other diatom species (Lancelot et al., 1998; Rousseau and Lancelot, in prep.). Mills et al., (1994) also, reported a dominance of some diatom species such as some *Rhizosolenia* spp, *Paralia sulcata* and *Thalassiosira eccentrica*, in terms of volume, during April 1989. These were observed in stations associated with a 40m-depth coutour and situated at the latitude of 55°N in the central North Sea (station CT, in Mills et al., 1994). During our campaign, the large diatom species *Coscinodiscus concinnus*, however was observed in the $W_2H_2O_2$ stations related to high silicate concentrations (List 1 in Figure 5.6a). This species contributed a major fraction of the phytoplankton biomass in these stations. A high contribution of *Coscinodiscus concinnus* of more than 60 % of total phytoplankton biomass was also noted during the spring diatom bloom -April 1985- in the southeastern part of the North Sea (Bauerfeind et al., 1990). Indeed, the high biomass produced during the course of the spring bloom is due to the capacity of some phytoplankton species to grow and exploit the initial high winter nutrient concentrations (Harris, 1986; Bauerfeind et al., 1990).

The non-diatom species, mainly *Rhodomonas*, *Tetraselmis*, *Phaeocystis* found only in the Dogger Bank stations (List 2, Figure 5.6a) also are positioned in the opposite direction of maximum nutrient concentrations (Figure 5.6a). Indeed, the non-diatoms species are found to grow in Si-depleted environment (Bauerfeind et al., 1990), if the nitrogen pool is sufficient, and a quick tunover of phosphorus is assumed (Bauerfeind et al., 1990). In our study, CCA analysis showed that the variance in species distribution is explained significantly by nitrate and nitrite concentrations (Table 5.2), but this is not the case for

phosphorus concentration. Kuipers and Witte (1999) report, for the same transect, that the ammonium uptake is not negligible for the total phytoplankton fraction in the Dogger bank. After the early spring diatom bloom a non-diatomous phytoplankton bloom of mainly *Phaeocystis* and other flagellates- increases in terms of biomass and this is due to Si and or P limitation (Bauerfeind et al., 1990) and to nitrogen, phosphorus and silicon limitation (Riegman et al. 1990).

In general terms, distinct early spring phytoplankton communities revealed in this study confirm a distinction between the northern deeper and southern shallower water zones in the North Sea. Such distinction was also reported by several studies as was mentioned in the beginning of this paper (e.g. Williams et al., 1993). Indeed, Williams et al. (1993) and Fransz et al., (1991) reported that the distribution of the pelagic biota in the North Sea, is affected by the bathymetry and hydrography. Thus the northern-central deeper water is more influenced by the oceanic species which were carried with the inflow of the North Atlantic Ocean (Fransz et al., 1991). While, the contribution of benthic biota - meroplankton and supra benthis species- to the community observed in the water column increased in the shallower water of the Dogger Bank and towards the south of the southern North Sea (Williams et al., 1993).

The variation in size-distribution of phytoplankton along the transect fits the expectation of dominance of large diatoms in shallow water of the Dogger Bank areas and small phytoplankton species in the deeper stations of the central and northern the North Sea. The concept of size-differential control of phytoplankton communities demonstrated by Riegman et al., 1998 for the same transect was

based on two fractions < 5μm and > 5 μm. Our results consider essentially cells fractions bigger than 5 μm along this transect. Within this fraction, a high biomass were observed in the Dogger Bank area while decreasing towards North in the deeper stations of the transect (Figure 5.7). The contribution of the lower or the upper end of the spectrum (ca ranges between 5-10µm and 50-100µm SED, respectively) were high in the Dogger Bank (Figure 5.7 f and g). The size classes in between (10-50µm, SED) were dominant in the central- northern area of the North Sea (Figure 5.7a, b, c, d and e). In the Dogger Bank area, a phytoplankton volume peak in the size range 5-10 µm was observed (Figure 5.7 f and g) which was absent in the Central and Northern stations. It is known that

Table 5.5 Ranges in biomass values (μg C l^{-1}) of phytoplankton classes in the two main areas of the North Sea (DB= Dogger Bank area, CNS+NNS= central and northern North Sea.

Taxa (Total μg C l-1)	Range NNS+CNS	Range DB	authors
Bacillariophyceae (Diatoms)	1,062-9,411	23-39	
Dinophyceae	0,7-16,001	1,8-7,08	
Haptophyceae	0	0-11.22	Our data
Prasinophyceae	0	8.92	
Chlorophyceae	0	0.9	
Microzooplankton	0	0.1	
Bacillariophyceae		93	
Dinophyceae		24.31	
Haptophyceae		1.52	Mills et al., (1994)
Unidentified Prasinophyceae		1.71	(Spring data)
Unidentified flagellates		16.58	
Cyanophyceae		0.25	
Autotr. Nanoflagellates (without Phaeocystis)	xxxx	1-175	Van Duyl et al., (1990)
Phaeocystis-like cells	xxxx	1-26	(Summer data)
Heterotr. nanoflagellates	xxxx	4-287	
Algae < 5μm	10	12.5	Riegman et al., (1998)
Algae > 5 μm	25	125.0	In Fransz et al., (1998)
Total phytoplankton	15.8	42.5	Nielsen and Richardson,
Heterotr. Nanoflagellates	0.06-0.15	0.08-0.26	(1989)
Total phytoplankton	xxxx	50-100	Bauerfeind et al., (1990)
Bauefreind			(spring data)
Phytoplankton > 11μm	123	83	Nielsen et al., (1993)
Phytoplankton < 11 μm	994	438	(Summer Data)

small cells may have competitive advantage over larger sized species in nutrient-depleted and stratified environment (Fenchel, 1988, Kiørboe, 1993). This can also explain the presence of the observed microzooplankton stock in the Dogger Bank area (List 2 in Figure 5.6a and Table 5.4. The stock of cells size at the lower end spectrum (fraction between 5-10 μm in Figure 5.7 f and g), which approach the lower limit of the food size spectra for adult copepods (e.g. Berggreen et al., 1988; Nielsen et al., 1993), probably does not constitute an optimal size to be grazed by mesozooplankton in the Dogger Bank area. It could however, provide adequate prey for microzooplankton. Indeed, Kuipers and Witte (1999) reported a relatively high grazing rate of the microzooplankton, within the fraction of > 5μm, in the Dogger Bank area compared to the deeper stations.

Besides the size differential control concept reported for both fractions (< -5 μm and > 5 μm) by Riegman et al., (1998), our results showed that within the > 5 μm size range different contribution of cells < 10 μm may also provide different trophic situation for the micro/meso-zooplankton.

Our results also showed that, despite a substantial species variety along the transect, there was not much variety in the dominant species within each zone (central-northern and Dogger Bank). Also, each of the two zones was characterised by a rather typical phytoplankton volume and size structure. The consequences of this to the trophical chain structure will be discussed in the next chapter and in a further paper.

Acknowledgement: A. M'harzi thanks H. S. Fransz, B. Kuipers and R. Riegman for the opportunity to join their March/April Shetland cruise with the R.V. Pelagia (NIOZ, Texel, nl). The authors thank the cruise leader for the cruise-report and the permission to use measured environmental factors as temperature, salinity and nutrients. K. Sabbe helped with phytoplankton taxonomy.

Chapter VI

Plankton size distribution and predator-Prey relationship in the North Sea

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Manuscript in preparation

Content

1. Introduction

1. 1. Size and trophic relationships in the plankton: prey size and copepod feeding

Copepods being dominant zooplankters in most marine ecosystems, their feeding activity is subject to intensive research. In relation to the construction of C-cycling models, the feeding activity of copepods has to be analysed as a function of food concentration. Ingestion rates (I; e.g. µg C ind.$^{-1}$ hr^{-1}) of dominant copepods in most marine system are known to follow a saturation type curve as a function of prey concentration (Fig 6.1) (Frost, 1972, Mullin et al., 1975). Increases with prey concentration up to a maximum, which is reached at the incipient limiting concentration (ILC). Feeding does not occur at prey concentrations below the low treshold concetration (LTC).

A second important aspect to correctly evaluate the role of zooplankton in an ecosystem, is to know which of the potential prey items within the suspended particulate matter are eaten in what degree. While in principle all suspended particulate matter between a few and around 100 µm can be taken up by copepods, many studies show that, withing a certain size spectrum of prey (particles) biomass distribution, copepods select larger particles, often those forming the peak of the volume distribution (Poulet, 1973; 1974; Allan et al., 1977). Such selective feeding

behaviour is evidenced by enhanced clearance rates (F; ml ind^{-1} hr^{-1}) (=predation pressure) on these prey type (Fig 6.2).

Many investigations on copepod feeding show selective feeding on phytoplankton and/or microzooplankton in the field (Gamble 1978; Tackx et al., 1989; Gasparini and Castel, 1997). Within phytoplankton assembleges, certain sizes are sometimes selected (Paffenhöfer, 1984; Paffenhöfer and Van Sant, 1985). This selective feeding behaviour can be explained by the superior food quality of phyto- and microzooplankton in comparison to other suspended particles, such as detritus (Stoecker and Cappuzo, 1990). Indeed, recent studies, both from laboratory and field experiments, show the important role of food quality on the copepod production (e.g. StØttrup and Jensen, 1990; Jónasdóttir, 1994; Jónasdóttir et al., 1995; Pond et al., 1996 and Meyer-Harms et al., 1999).

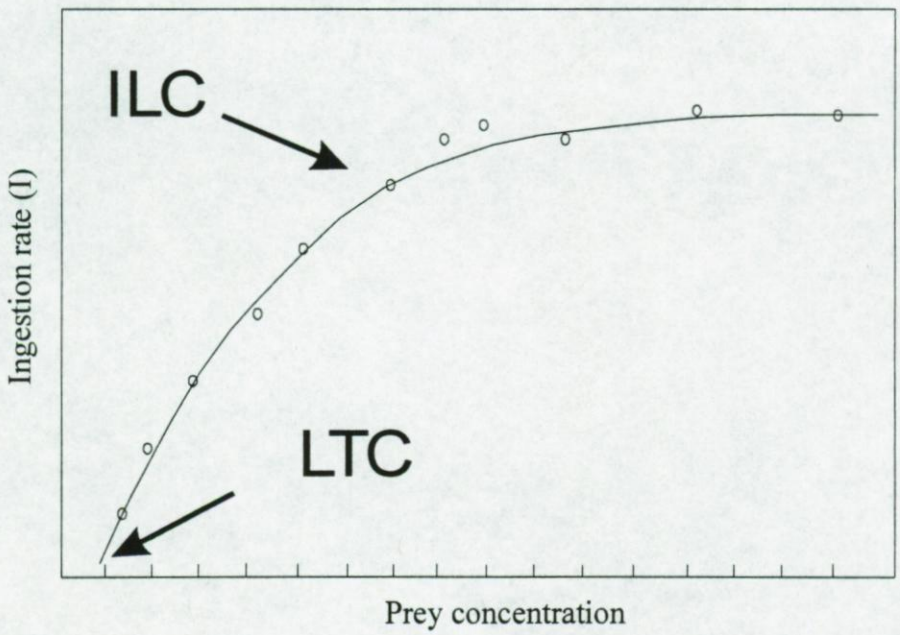


Figure 6. 1. The curvilinear curve describing the feeding activity of copepods (after Mullin et al., 1975). ILC= incipient limiting concentration; LTC= low threshold concentration.

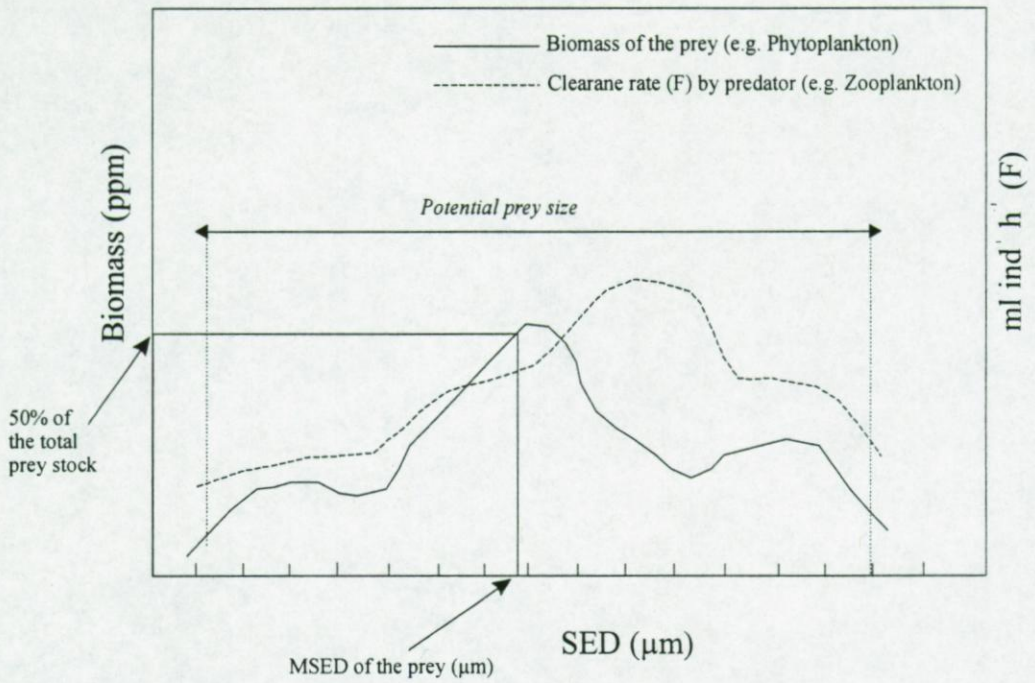


Figure 6. 2. Example of Clearance rates (F) as a function of prey volume distribution. MSED= median SED (µm) at which half of total prey stock is reached.

1. 2. Size distribution of particles in the pelagic system

The biomass size spectrum in an aquatic ecosystem is the distribution of living biomass across the range of organism size (Sprules et al., 1991). Predation, in aquatic ecosystems, is defined as the consumption of one organism (the prey), by another organism (the predator) (in Baretta-Bekker et al., 1998).

Several researches have supported and confirmed the usefulness of size to classification of and ecological studies on marine organisms (e.g. Fenchel 1974; Kerr, 1974; Platt and Denman, 1977, 1978; Silvert and Platt 1978, 1980; Platt and Silvert 1981; Schwinghamer 1981; Sprules and Munawar 1986; Gasol et al., 1991).

Sheldon et al., (1972) showed that phytoplankton, zooplankton and fish reach about equal biomass in marine ecosystems and developed a prey- predator model which allows to predict stocks of one trophic level based on stock data of the previous trophic level. This new approach to predict fish biomass in the ocean was soon used in several studies. Thus, large data-sets were collected in marine and freshwater environments, confirming and providing further evidence of patterns in biomass-size spectra (e.g., Schwinghamer 1981; Sprules and Munawar 1986; Ahrens and Peters 1991; Cattaneo 1993). The models were also applied, successfully, to predict dynamic variables such as, fish production (Borgmann 1982; Sprules et al., 1991 Cyr and Peters, 1996) and contaminant cycling (Griesbach et al. 1982; Borgmann and Whittle 1983)

As stated by (Sprules and Munawar, 1986; Cyr and Peters, 1996), major supporting factors for the usefullness of the biomass spectrum appraoch can be summarized as followed: (1) The structure of the biomass spectrum is characteristic of the environment, (2) The slope of the biomass spectrum is an indicator of the state and productivity of the ecosystem, (3) Predation can easily be described on the basis of size, (4) based on the size spectrum, models can be easily developed.

1. 3. Sheldon model

In order to test the Sheldon model (Eq. 1), data on the standing stock (Sc and Sp) and sizes (Dc and Dp) of the predator(s) and prey(s), respectively, are necessary. The

growth efficiency and predation impact of predators on a certain prey can be calculated as follows:

$$Sc/Sp = (Dc/Dp)^{0.72}\, Ge.Ce \qquad \textbf{(Eq. 1)}$$

Where
Sc= the standing stock of the predator
Sp= the standing stock of the prey
Dc= the mean size of the predator
Dp= the mean size of the prey
Ge= the growth efficiency, which is the quantity of tissue formed relative to the amount of prey ingested. A Ge values of 15% is generally assumed for zooplankton (Sheldon et al., 1977)
Ce= the fraction of prey production taken by the predator

In our datasets, all elements were known except *Ce*. We apply the model to calculate *Ce* values for each zone, in order to verify the transfer rate of phytoplankton primary production that would need to occur if the observed zooplankton stock lives on phytoplankton as sole prey.

1. 4. Trophic structure in the North Sea

Intensive research carried has been caried out in the North Sea in order to gain information on the food chain structure and its relationship with fisheries (Tett and Mills, 1991). In Sheldon et al.'s model (1977), transfer efficiencies from one trophic level to the next are considered to be in principal ~100%. This is the case of the open

oceanic systems, where zooplankton consumes up to 100% of the primary production (Joiris et al., 1982). In the simple food-chain of Steele (1974), about one third of the North Sea primary production goes to the benthos, and the other two-thirds are eaten by herbivorous zooplankton (Table 6.1). The results of Fransz and Gieskes (1984) and Smetecek (1984) suggest that the transfer is less efficient during blooms -Spring and early summer- (<10% of the primary production) and more efficient during the 'regenerated' primary production period -later in the season-. Gamble (1978) compared the grazing rates of larger (*Calanus finmarchicus*) and smaller (*Acartia clausii*, *Pseudocalanus elongatus*) copepods during a declining spring phytoplankton bloom in the northern North Sea, and found that grazing activity of the copepods is phytoplankton size depended.

In coastal areas of the Southern Bight of the North Sea, the flux of new primary production to zooplankton is less than 50% (Joiris et al., 1982; Billen et al., 1990), due to an inportant role of the microbial food web (Kuipers et al., 1981) and benthos (Peinert et al., 1982; Smetacek, 1984). The main explanation is sumarized by De Wilde et al., (1992) as: (1) zooplankton stock is at low levels in early spring and thus can not utilize the excess food supply (e.g. Fransz and Gieskes, 1984; Smetacek, 1984). (2) The abundance of non-favorable food items for copepods, represented by the well-known blooming algal species in the coastal zone (i.e. *Phaeocystis globosa*) (Lancelot et al., 1998).

Table 6. 1. Zooplankton grazing as percentage of phytoplankton primary production in the North Sea (in Tett and Mills, 1991).

	Grazing in %	References
Northern North Sea	60-100	Steele (1974); Gamble (1978); Daro (1980); Radach (1980); Hay et al (1991).
Southern North Sea	10-50	Dagg et al. (1982); Joiris et al (1982); Nicolajsen et al. (1983); Baars and Fransz (1984); and Hay et al. (1991).

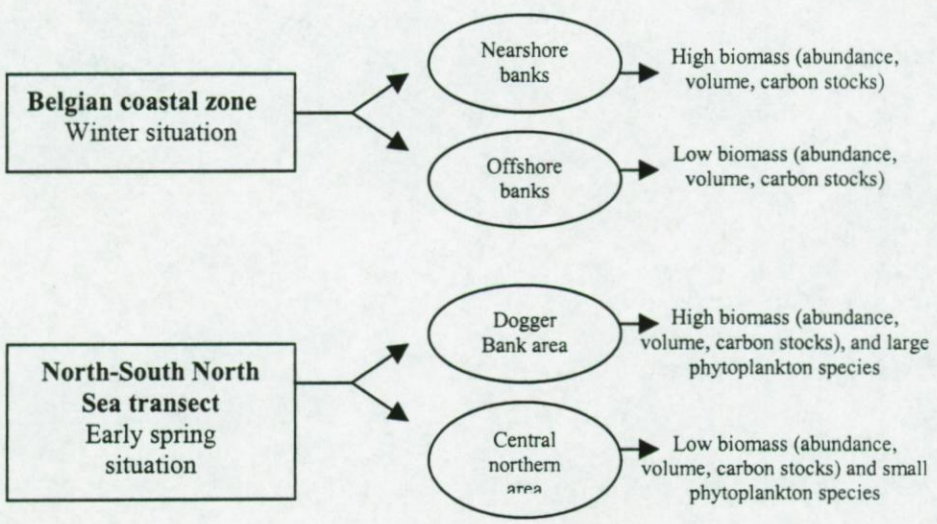
A few studies, carried out over large areas in the North Sea, give comprehensive information on the seasonal distribution of the plankton, including the winter period (e.g. Rae, 1952; Glover, 1967; Colebrook, 1972, 1985, 1986; Nielsen and Richardson, 1989; Hay et al., 1991 and Fransz et al., 1991). These studies report higher copepod production in the South than in the northern North Sea, during winter. Indeed, Hay et al., (1991) report that, during winter 1988, *Temora longicornis*, *Acartia clausi*, *Centropages typicus*, *Pseudocalanus elongatus*, *Paracalanus parvus* and copepod nauplii, maintained substantial productivity in the southeastern part of the North Sea. Thus, the winter survival of herring larvae and other predators in this area is supported by this herbivorous production. At the same time, in the north of the North Sea, low zooplankton production influences predator survival negatively (Hay et al., 1991). Bathmann et al., (1990) studied the response of the grazing of copepods to increasing phytoplankton growth, during late winter 1987 in the Norwegian Sea. They concluded that copepods actively grazing in

surface layers (0 to 200m) have important consequences on the whole pelagic biological regime in early spring (Bathmann et al., 1990).

1. 5. Aim

As was explained in section 1.1 and 1.2, the size structure and food quality of a given phytoplankton population influence the grazing activity and feeding behavior of zooplankton. In reverse, selective feeding by zooplankton potentially governs the composition of the phytoplankton community (Levinton, 1982; Kennish, 1990).

In the two studies reported here (Belgian coastal zone and North Sea transect) we have two adjacent areas which, based on phytoplankton species composition, are illustrated to contain two seperate subareas (and possible further subdivisions) by statistical 'cluster' analysis (TWINSPAN). In each case, the two main subareas have been shown in chapter 3, 4, and 5 to harbour, besides differences in phytoplankton species composition, different phytoplankton biomasses and size distribution characteristics, which can be summarized as follows:



In the Belgian coastal zone, the two areas differ in phytoplankton biomass which is, a factor 2 higher in the neashore than in the offshore area (Fig 4.13c, Chapter 4). As to size distribution, both areas are characterised by several volume peaks spread over the 4 to 61 µm SED size range. This was accompanied by clear differences in phytoplankton community structure where contribution of the phytoplankton group taxa differed from neashore to offshore banks differed significantly (Table 4.5, Chapter 4).

In the North Sea transect the phytoplankton volume is a factor 20 higher in the Dogger Bank than in the central-northern area. The size distribution clearly differs from Dogger Bank to central-northern areas with a dominance of large phytoplankton species in the Dogger Bank area and small ones in the deeper stations of the central and northern the North Sea.

The aim of this chapter is to analyse if these subzones, separated on the basis of phytoplankton community composition, also represent various situations in relation to food web structure. This will be analysed using Sheldon's (1977) model. This model is constructed to analyse trophic transfer on a year or growth season basis. In our application, we apply it to the situation in the planktonic community occuring at the end of winter and early spring respectively for the Belgian coastal zone and the North Sea transect. As such it simply serves to evaluate the potential for trophic transfer in the various subareas.

2. Materials and Methods

2. 1. Sampling

The samples and sampling strategy in this chapter are the same as those of chapter 4 and 5.

2. 2. Phytoplankton and zooplankton measurements

2. 2. 1 Belgian coastal zone

Phytoplankton

Calculations of cell volume and cell carbon content was done following the procedure described in Chapter 4. Phytoplankton standing stock (expressed as µg C l^{-1}) per bank for the 3 stations were pooled and averaged for each size class.

Zooplankton

Abundance of developmental stages of dominant mesozooplankton species (*Temora longicornis*, *Pseudocalus elongatus*, *Centropages typicus*, *Paracalanus parvus*, and *Acartia clausii*), stages (CI, II, III, IV, V and Nauplii) were determined from the microscopic counts.

Dry weight of the zooplankton species and stage-groups were calculated from length and width measurements using the following formula given in litterature (Omori, 1978; Fransz and van Arkel, 1980 and Diel , 1991):

Dry Weight (mg) = a * L (mm) ^{b} (Eq.2)

L, standard lengths
(a), regression coefficient
(b), exponent for the length (mm).

For each copepod species and stage-groups, convertions from DW (µg) into Wet Weight (WW, µg), volume ($\mu m^3 * 10^6$) and carbon weight (µg C) was done using the following conversion factors:

10^6 μm^3 body volume ~ 1 µg wet weight (Omori and Ikeda, 1984).
Dry weight ~ 20 % wet weight (Gifford and Dagg, 1988) and references therein.
Carbon weight ~ 45% dry weight (Heinle et al., 1977; Sautour and Castel, 1995).

For all species (*Temora longicornis*, *Pseudocalus elongatus*, *Centropages typicus*, *Paracalanus parvus*, and *Acartia clausi*) and stages (CI, II, III, IV, V and Nauplii), standard lengths and regression coefficient (a) and exponent (b) were obtained from Hay et al., (1991) (Tables 6.2A, 6.3A, 6.4A, 6.5A, 6.6A). Dry weight was then calculated for all species and stages by substituting lengths for equation 2 (Eq. 2). The mean lengths for stages (CI/II, CIII/IV, CV and nauplii) were determined using standard lengths from Hay et al., (1991) (See Table 2 in Hay et al., 1991) by adding individual stages CI and CII, CIII and CIV, and Nauplii for all dominant species considered for the present study. The standard weights which was then calculated by substituting these mean lengths for differents copepodites stage-groups ($C_{I/II}$, $C_{III/IV}$ and C_V) and Nauplii in eqaution 2, were expressed as percentage of the dry weight of adults male and female of each copepod species, also given in Hay et al., (1991) (Tables 6.2A, 6.3A, 6.4A, 6.5A, 6.6A). These percentages were then multiplied by values of the dry weight of adults male and female, respectively, of copepods species given in Van Gijsegem (1979) and Daro and Van Gijsegem (1988) (Tables 6.2B,

6.3B, 6.4B, 6.5B, 6.6B) to provide an estimation of the dry weight for each copepodite stage-groups ($C_{I/II}$, $C_{III/IV}$ and C_V) and nauplii. Mean dry weight, wet weight and carbon weight for all copepod species and stage-groups (CI/II, CIII/IV, CV and nauplii) were then calculated (Tables 6.2C, 6.3C, 6.4C, 6.5C, 6.6C).

Finally, obtained values were multiplied by species and stage-groups abundances (derived from microscopic count) to calculate total zooplankton biomass (in terms of volume and carbon).

Total average volume concentration (standing stock) values for phytoplankton and zooplankton were calculated by summing the mean average values over all size classes in which each component occurred. All standing stock values are expressed in ppm, equivalent to $\mu m^3\ 10^6.ml^{-1}$.

2. 2. 2. North-South transect

Phytoplankton

Calculations of cell volume and cell carbon content was done following the procedure described in Chapter 5. Phytoplankton standing stock (expressed as $\mu gC\ l^{-1}$) per 3 stations, situated at the same latitude, were pooled and averaged for each size class (details in Chapter 5).

Zooplankton

Abundance of the dominant mesozooplankton species, *Calanus finmarchicus*, was determined from microscopic counts (Fransz, pers. comm.). Dry Weight (DW) calculation is given in Fransz et al., (1998). Data of the the total DW ($\mu g\ l^{-1}$) of *Calanus finmarchicus* was provided by NIOZ (Fransz, pers. comm.). Total volume

(ppm), and total carbon weight (μg C l^{-1}) of *Calanus finmarchicus* in all stations was calculated following the same procedure given in the above section. Data on total biomass of all mesozooplankton species was provided by Fransz (pers. comm.) and also converted into carbon (μg C l^{-1}) and volume (ppm). Then, the total volume (ppm) and total carbon content of all mesozooplankton species (including *C. finmarchicus*) and only for *C. finmarchicus* were averaged per 3 stations situated at the same latitude.

Table 6. 2. Dry weight (µg), volume (ppm) and Carbon weight (µg) for , *Temora longicornis* adult and stage-groups in the Belgian coastal zone (C), derived from the standard lengths at stage, regression coefficients (a) and exponents (b) for the major copepod species given in Hay et al., (1991) (A), and applied to Dry weight data set on adults given in Van Gijsegem (1979) and Daro and Van Gijsegem (1988) (B).

A	*Temora longicornis*	L (mm)	a	b	DW (µg)	% of DW/ ♂	% of DW/ ♀
	N1-6	0,23	0,009	2,17	0,3	1,5	1,1
	C_I/C_{II}	0,38	0,0313	3,06	1,6	6,9	5,0
	C_{III}/C_{IV}	0,53	0,0313	3,06	4,7	20,3	14,7
	C_V	0,75	0,0313	3,06	12,9	55,3	40,2
	♂	0,91	0,0313	3,06	23,4		
	♀	1,01	0,0313	3,06	32,2		

B	*Temora longicornis*	DW (µg) / ♂	DW (µg)/ ♀	Mean DW (µg)
	N1-6	0,23	0,16	0,20
	C_I/C_{II}	1,04	0,71	0,88
	C_{III}/C_{IV}	3,05	2,0	2,57
	C_V	8,30	5,71	7,00
	♂			15
	♀			14,2

C	*Temora longicornis*	Mean DW (µg)	WW =DW*100/20 (µg)	Carbon Weight (µg C)	Body volume *$10^{(6)}$ µm^3	Size class (SED, µm)	Size class (µm^3)
	N1-6	0,20	1,00	0,09	0,50	97	243418
	C_I/C_{II}	0,88	4,41	0,39	2,20	154	967128
	C_{III}/C_{IV}	2,57	12,87	1,15	6,43	194	1931345
	C_V	7,00	35,03	3,15	17,51	309	7725595
	♂	15	75	6,75	37,5	389	15451189
	♀	14,2	71	6,39	35,5	389	15451189

Table 6. 3. Dry weight (µg), volume (ppm) and Carbon weight (µg) for, *Pseudocalanus elongatus* adults and stage-groups in the Belgian coastal zone (C), derived from the standard lengths at stage, regression coefficients (a) and exponents (b) for the major copepod species given in Hay et al., (1991) (A), and applied to Dry weight data set on adults given in Van Gijsegem (1979) and Daro and Van Gijsegem (1988) (B).

A	*Pseudocalanus elongatus*	L (mm)	a	b	DW (µg)	% of DW/ ♂	% of DW/ ♀
	N1-6	0,3	0,017	2,27	1,1	14,5	9,2
	C_I/C_{II}	0,42	0,019	2,73	1,8	23,2	14,7
	C_{III}/C_{IV}	0,58	0,019	2,73	4,3	56,3	35,8
	C_V	0,73	0,019	2,73	8,0	103,8	66,0
	♂	0,72	0,019	2,73	7,7		
	♀	0,85	0,019	2,73	12,1		

B	*Pseudocalanus elongatus*	DW (µg) / ♂	DW (µg)/ ♀	DW (µg)
	N1-6	14,51	9,22	1,13
	C_I/C_{II}	23,23	14,76	1,81
	C_{III}/C_{IV}	56,38	35,84	4,40
	C_V	103,83	66,00	8,11
	♂			7,74
	♀			12,4

C	*Pseudocalanus elongatus*	Mean DW (µg)	WW =DW*100/20 (µg)	Carbon Weight (µg C)	Body volume $*10^{(6)}$ µm^3	Size class (SED, µm)	Size class (µm^3)
	N1-6	1,13	5,67	0,51	2,83	154	968128
	C_I/C_{II}	1,81	9,08	0,81	4,54	194	1931345
	C_{III}/C_{IV}	4,40	22,03	1,98	11,01	245	3852724
	C_V	8,11	40,57	3,65	20,28	309	7725595
	♂	7,74	38,74	3,48	19,37	309	7725595
	♀	12,4	62	5,58	31	389	15451189

Table 6. 4. Dry weight (µg), volume (ppm) and Carbon weight (µg) for , *Paracalanus parvus* adult and stage-groups in the Belgian coastal zone (C), derived from the standard lengths at stage, regression coefficients (a) and exponents (b) for the major copepod species given in Hay et al., (1991) (A), and applied to Dry weight data set on adults given in Van Gijsegem (1979) and Daro and Van Gijsegem (1988) (B).

A	*Paracalanus parvus*	L (mm)	a	b	DW (µg)	% of DW/ ♂	% of DW/ ♀
	N1-6	0,19	0,0077	2,28	0,1	2,3	2,2
	C_I/C_{II}	0,27	0,0191	2,74	0,6	8,1	7,8
	C_{III}/C_{IV}	0,51	0,0191	2,74	3,0	40,9	39,4
	C_V	0,65	0,0191	2,74	5,8	78,5	75,5
	♂	0,71	0,0191	2,74	7,4		
	♀	0,72	0,0191	2,74	7,7		

B	*Paracalanus parvus*	DW (µg) / ♂	DW (µg)/ ♀	DW (µg)
	N1-6	2,33	2,24	0,18
	C_I/C_{II}	8,14	7,83	0,65
	C_{III}/C_{IV}	40,98	39,44	3,30
	C_V	78,51	75,55	6,33
	♂			7,47
	♀			9

C	*Paracalanus parvus*	Mean DW (µg)	WW =DW*100/20 (µg)	Carbon Weight (µg C)	Body volume $*10^{(6)}$ µm^3	Size class (SED, µm)	Size class (µm^3)
	N1-6	0,18	0,94	0,08	0,47	77,59	121950
	C_I/C_{II}	0,65	3,28	0,29	1,64	122,96	485402
	C_{III}/C_{IV}	3,30	16,53	1,48	8,26	245,27	3852724
	C_V	6,33	31,66	2,85	15,83	309,02	7725595
	♂	7,47	37,36	3,36	18,68	309,02	7725595
	♀	9	45	4,05	22,5	309,02	7725595

Table 6. 5. Dry weight (µg), volume (ppm) and Carbon weight (µg) for , *Centropages hamatus* adult and stage-groups in the Belgian coastal zone (C), derived from the standard lengths at stage, regression coefficients (a) and exponents (b) for the major copepod species given in Hay et al., (1991) (A), and applied to Dry weight data set on adults given in Van Gijsegem (1979) and Daro and Van Gijsegem (1988) (B).

A	*Centropages hamatus*	L (mm)	a	b	DW (µg)	% of DW/ ♂	% of DW/ ♀
	N1-6	0,22	0,0145	2,24	0,4	1,7	1,3
	C_I/C_{II}	0,38	0,0178	2,45	1,7	6,3	5,1
	C_{III}/C_{IV}	0,66	0,0178	2,45	6,5	23,2	18,7
	C_V	0,99	0,0178	2,45	17,3	61,1	49,4
	♂	1,21	0,0178	2,45	28,3		
	♀	1,32	0,0178	2,45	35,1		

B	*Centropages hamatus*	DW (µg) / ♂	DW (µg)/ ♀	DW (µg)
	N1-6	1,71	1,38	0,22
	C_I/C_{II}	6,31	5,10	0,82
	C_{III}/C_{IV}	23,24	18,77	3,02
	C_V	61,16	49,41	7,97
	♂			13,3
	♀			15,8

C	*Centropages hamatus*	Mean DW (µg)	WW =DW*100/20 (µg)	Carbon Weight (µg C)	Body volume $*10^{(6)}$ µm^3	Size class (SED, µm)	Size class (µm^3)
	. N1-6	0,22	1,11	0,10	0,55	97	243418
	C_I/C_{II}	0,82	4,11	0,37	2,05	154	968128
	C_{III}/C_{IV}	3,02	15,14	1,36	7,57	194	1931345
	C_V	7,97	39,85	3,58	19,92	309	7725595
	♂	13,3	66,5	5,98	33,25	389	15451189
	♀	15,8	79	7,11	39,5	389	15451189

Table 6. 6. Dry weight (µg), volume (ppm) and Carbon weight (µg) for , *Acatia clausi* adult and stage-groups in the Belgian coastal zone (C), derived from the standard lengths at stage, regression coefficients (a) and exponents (b) for the major copepod species given in Hay et al., (1991) (A), and applied to Dry weight data set on adults given in Van Gijsegem (1979) and Daro and Van Gijsegem (1988) (B).

A	*Acartia clausi*	L (mm)	a	b	DW (µg)	% of DW/ ♂	% of DW/ ♀
	N1-6	0,19	0,096	3,21	0,4	5,5	4,7
	C_I/C_{II}	0,515	0,0152	2,97	2,2	27,1	23,5
	C_{III}/C_{IV}	0,54	0,0152	2,97	2,5	29,9	26,0
	C_V	0,69	0,0152	2,97	5,0	59,8	51,9
	♂	0,82	0,0152	2,97	8,4		
	♀	0,86	0,0152	2,97	9,7		

B	*Acartia clausi*	DW (µg) / ♂	DW (µg)/ ♀	DW (µg)
	N1-6	5,51	4,78	0,39
	C_I/C_{II}	27,12	23,54	1,92
	C_{III}/C_{IV}	29,96	26,01	2,12
	C_V	59,89	51,99	4,24
	♂			7,54
	♀			7,66

C	*Acartia clausi*	Mean DW (µg)	WW =DW*100/20 (µg)	Carbon Weight (µg C)	Body volume $*10^{(6)}$ µm^3	Size class (SED, µm)	Size class (µm^3)
	N1-6	0,39	1,95	0,17	0,97	122	485402
	C_I/C_{II}	1,92	9,62	0,86	4,81	194	1931345
	C_{III}/C_{IV}	2,12	10,62	0,95	5,31	194	1931345
	C_V	4,24	21,24	1,91	10,62	245	3852724
	♂	7,54	37,7	3,39	18,85	309	7725595
	♀	7,66	38,3	3,44	19,15	309	7725595

Table 6. 7. Median spheric equivalent diameter (MSED, µm) and size range (min-max) of phytoplankton and zooplankton was used as (Dp) and (Dc), respectivelly. MSED is the size class (in µm) which corresponds to 50% of the total biomass. Str= Stroombank, Midd= Middelkerke, Kwint= Kwintenbank, Oosdy= Oostdyck, Oosthi= Oosthinder and Westh= Westhinder. Min-max: size range of phyto- and zooplankton (µm)

	str			Midd			Kwin			Oosdy			Oosthi			Westh		
	MSED	min	max	MSED	min	max	MSED	min	max	MSED	min	max	MSED	min	max	MSED	min	max
Phytoplankton	24,55	3,89	61,64	15,49	3,89	48,97	24,55	4,9	61,64	24,55	3,89	61,64	15,49	4,9	61,64	15,49	3,89	48,97
Zooplankton	490	194	490	389	122	490	389	122	490	490	194	490	389	122	490	389	122	490

2. 3. Biomass size distribution, normalisation and Sheldon Model

Description of how biomass of phytoplankton and zooplankton, was differenciated by volume and then allocated into size classes (SED, μm) is reported in Chapter 4. Normalisation of the size spectra was done by dividing the volumetric of each size class by the width interval of each size class (Annex 1) (Sprules and Munawar, 1986). The size classes and size intervals are shown in Annex 1. The normalized biomass distribution is then plotted against the size classes, both in log scales. For a pelagic community confirming to the theoretical steady state, the normalized spectrum will be linear with a slope close to -1 (Kerr 1974; Sheldon et al., 1977; Platt and Denman 1978). The slope of such spectra, and the pattern of residual variation around the line, can thus serve both to characterize the size structure of the community and indicate the degree of deparature from the theoretical steady state (e.g. Sprules and Munawar, 1986 and Gasol et al., 1991).

The size distributions, obtained for each of the cases, were fitted with linear and polynomial functions. ANCOVA significance test was used to compare the goodness of linear fit of the functions (Sokal and Rohlf, 1981).

2. 3. 1 Belgian coastal zone

Standing stock measurements were measured as described above and averaged per 3 stations of each sandbank. Standing stocks were expressed in volumetric concentrations and in carbon units.

Mean sizes of phytoplankton group taxa and zooplankton are based on the dimensions measured as was explained above. The Dp (μm) and Dc (μm) values for phytoplankton and zooplankton taxa, respectively, were taken as the median spheric equivalent diameter (MSED) as was explained and reported in Table 6.7.

2. 3. 2 North-South transect

Standing stock of phytoplankton and *Calanus finmarchicus* or total zooplankton was measured and averaged per 3 stations, situated at the same latitude, as is described in chapter 5. The stock was measured and averaged per 3 stations situated at the same latitude along the transect. Standing stocks were expressed in volumetric concentrations and in carbon content units.

The mean sizes of phytoplankton group taxa are based on the dimensions measured as was explained in the section 2.3. The Dp values for phytoplankton were taken as the median of the Dp of the different size classes of phytoplankton species (Table 6. 8). When we considered only zooplankton species *Calanus finmarchicus* as a potential predator, we considered only one S.E.D of 618.04 μm, which represented the Dc of the predator (Table 6. 9). Dc for total zooplankton was considered as 300 μm in correspondence with values of the mixed population measured in the Belgian coastal zone.

Table 6. 8. The median spheric equivalent diameter (MSED, µm) of phytoplankton was used as (Dp). MSED is the size class (in µm) which correspond to 50% of the total biomass. Min-max: size range of phytoplankton (µm)

	W6H6			W5H5O5			W4H4O4			W3H3O3			W2H2O2			W1H1O1			W0H0O0		
	MSED	**min**	**max**	**MSED**	**min**	**max**	**MSED**	**min**	**max**	**MSED**	**min**	**max**	**MSED**	**min**	**max**	**MSED**	**min**	**max**	**MSED**	**min**	**max**
Phyto-plankton	30,9	6,17	97,68	48,97	6,17	97,68	30,9	6,17	97,68	48,97	6,17	97,17	77,59	6,17	389	77,59	6,17	97,68	77,59	4,99	77,59

Table 6. 9. Spherical Equivalent Diameter (S.E.D) and the size interval calculated for *Calanus finmarchicus* based on the Dry weight (DW) derived from : [(1)] the standard lengths provided by Fransz et al., (Pers. Comm.); [(2)] regression coefficients (a) and exponents (b) given in Fransz et al., (1998).

	L (mm) [(1)]	a[(2)]	b[(2)]	DW (µg)[(1)]	WW= DW*100/20 (µg)	Body volume *10[(6)] µm^3	Size class (SED, µm)	Size class (µm^3)
Calanus finmarchicus	1.345	13.2	3.26	34.690	173.4517087	173.45	618.04	61804756

3. Results

3. 1. Biomass size spectra

3. 1. 1 Belgian coastal zone

Fig 6.3 shows the typical size distributions of the plankton on the 6 sandbanks along Belgian coastal zone, expressed in volumetric concentrations. In summary, volume concentrations were highest on the nearshore banks (Stroombank, Middelkerke) and Oostdyck with several peaks reaching up to 0.01ppm (Figure 6.3). Concentrations did not exceed values of 0.005ppm for the whole size spectrum on the Oosthinder and Westhinder banks within the range 4 to 100µm representing the phytoplankton. However, the size range > 100µm showed high concentrations, more than 0.01ppm on the Westhinder, and Kwintenbank. Oostdyck exhibited a high peak (0.04ppm) around 30µm size class (Figure 6.3).

The normalized size distributions of the plankton are shown in Fig 6.4. The data were also tested for linear fit as well as for polynomial fit of second degree (Fig 6.4 and Table 6.10). The slopes (b) and x^2 coefficients (b') of the fitted equations are tabulated in Table 6.8. b and b' values are normally taken as absolute values with the sign '-' mainly used as indication of where the line is directed. Per sandbank, b values ranged from -2.42 to -3.43. b' values ranged from 0.3 to -1.05 with the neashore banks (Stroombank and Middelkerke) and

Oostdyck having the highest values and the offshore banks (Oosthinder and Westhinder) and Kwintenbank having the lowest values.

Significance tests showed that both linear and polynomial functions fit the data significantly for all banks, but with a tendence of a better polynomial than linear fit on the most nearshore bank, Stroombank (Fig 6.4 and Table 6.10).

ANCOVA *test* showed that only the slope of the linear fit of the Stroombank differed significantly ($p < 0.05$) from that of all other banks (Table 6.11).

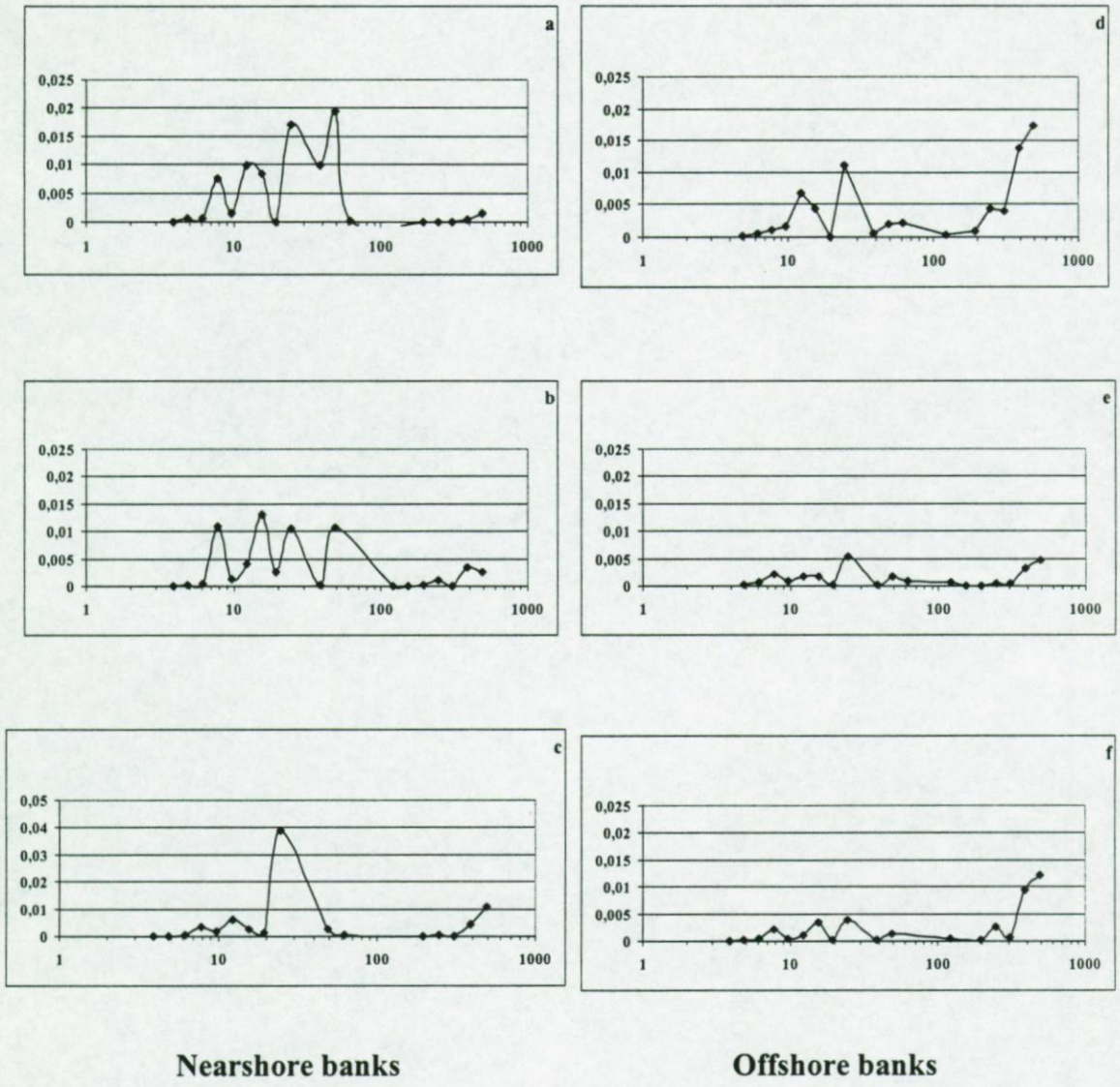
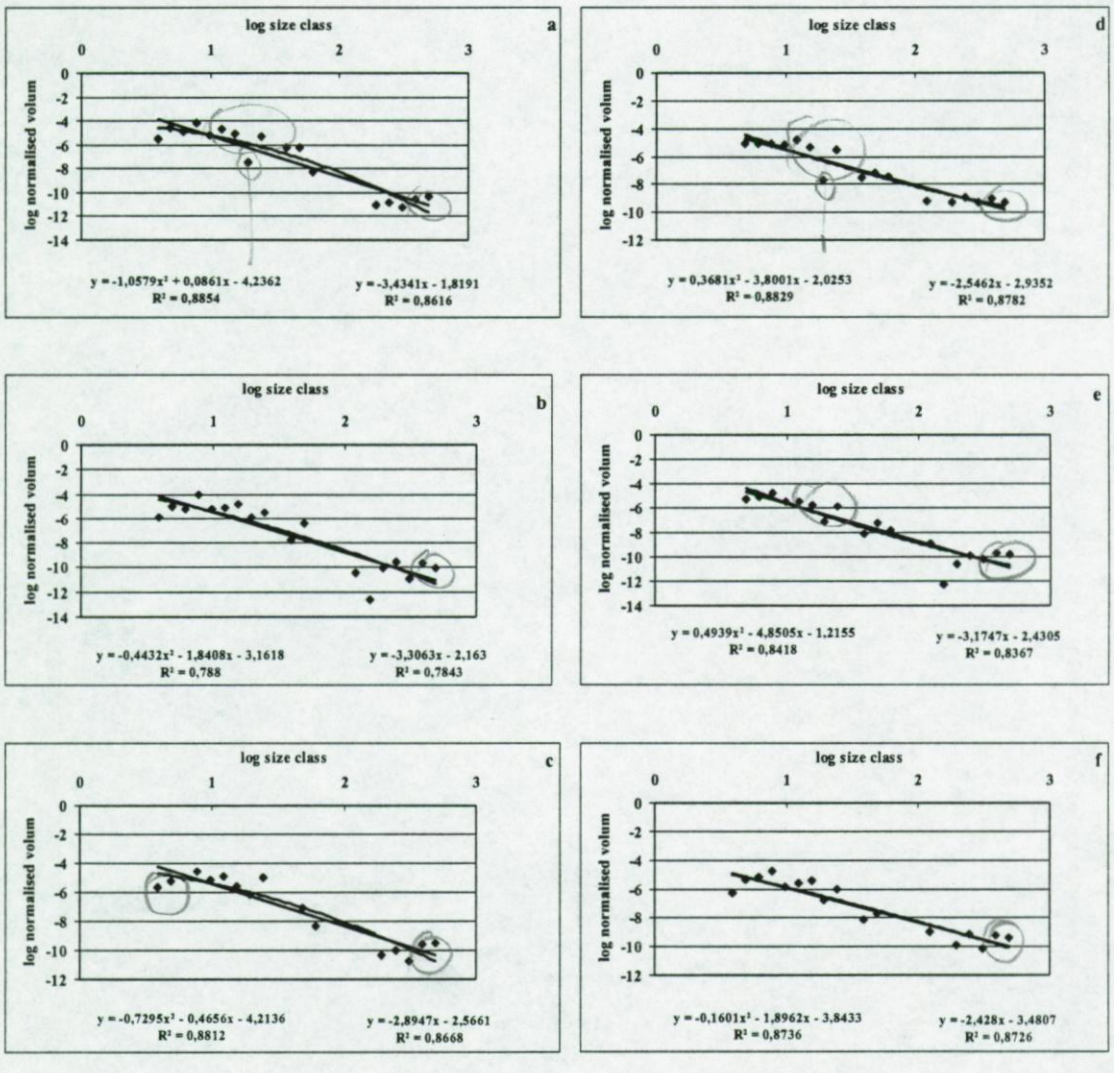


Fig 6. 3. Size distributions of phytoplankton and zooplankton in the Belgian coastal zone for 6 sandbanks (averaged over 3 stations) expressed in volumetric concentration (ppm= $*10^6$ μm^3 ml^{-1}): (a) Stroombank, (b) Middelkerke, (c) Oostdyck, (d) Kwintenbank, (e) Oosthinder and (f) Westhinder.



Nearshore banks **Offshore banks**

Fig 6. 4. Normalised mean size distributions of plankton in the Belgian coatal zone for 6 sandbanks (averaged over 3 stations) expressed in volumetric concentrations fitted with linear and polynomial equations: (a) Stroombank, (b) Middelkerke, (c) Oostdyck, (d) Kwintenbank, (e) Oosthinder and (f) Westhinder.

Table 6. 10. Belgian costal zone: Slopes (b) of the linear equations and (b') coefficients of the second degree polynomial equations fitted on the normalized size distributions averaged per bank. r^2 = regression coefficient of the fitted equations, n = number of samples, R= correlation coefficient.

Bank	*n*	*b*	r^2	*R*	*p*	*b'*	r^2	*R*	*p*
Str	17	-3.43	0.84	0.920	<0.0001	-1.05	0.88	0.934	<0.0001
Midd	17	-3.30	0.84	0.916	<0.0001	-0.44	0.87	0.927	<0.0001
Kwint	17	-2.5	0.89	0.933	<0.0001	0.3	0.89	0.935	<0.0001
Oostdyck	16	-2.89	0.85	0.922	<0.0001	-0.72	0.88	0.931	<0.0001
Oosthin	17	-3.17	0.92	0.957	<0.0001	0.4	0.92	0.957	<0.0001
Westhin	17	-2.42	0.87	0.927	<0.0001	-0.16	0.88	0.928	<0.0001

Str= Stroombank; Midd= Middelkerke; Kwint= Kwintenbank; Oosthin= Oosthinder; Westhin= Westhinder

Table 6. 11. Belgian coastal zone: Fs values calculated by Ancova testing for significant differences between the slopes of the linear functions fitted to the normalized spectrum between differents banks. (*) significant at 5%; ns= non significant

	Str	Midd	Kwint	Oostdyck	Oosthin	Westhin
Str	xxxx	5.144*	5.144*	1.37	2.287*	4.59*
Midd	xxxx	xxxx	ns	ns	ns	ns
Kwint	xxxx	xxxx	xxxx	2.151	1.32	ns
Oostdyck	xxxx	xxxx	xxxx	xxxx	ns	1.69
Oosthin	xxxx	xxxx	xxxx	xxxx	xxxx	ns
Westhin	xxxx	xxxx	xxxx	xxxx	xxxx	xxx

Str= Stroombank; Midd= Middelkerke; Kwint= Kwintenbank; Oosthin= Oosthinder and Westhin= Westhinder

3. 1. 2 North-South transect

The size distributions of the plankton on the different stations along a North-South transect expressed in volumetric concentrations are reported and discussed in Chapter 5.

The normalised size distributions (including phytoplankton and *C. finmarchicus*) are shown in Fig 6.5. The data were also tested for linear fit as well as for polynomial fit of the second degree (Fig 6.5 and Table 6.12). The slopes (b) and x2 coefficients (b') of the fitted equations are tabulated in Table 6.10. Per 3 stations, situated at the same latitude, b values ranged from -1.44 to -2.71. b' values ranged from 0.42 to -0.77 with the Dogger Bank stations having the highest values and the central-northern stations of the North Sea having the lowest values. Significance tests showed that both linear and polynomial regression fit the data significantly for all stations (Table 6.12).

While, the normalised size distributions (including phytoplankton and all dominant mesozooplankton species) were calculated. The data were also tested for linear fit as well as for polynomial fit of the second degree. The slopes (b) and x2 coefficients (b') of the fitted equations are tabulated in Table 6.13.

ANCOVA *test* showed -in both cases- that there were no significant differences between the slopes of the linear functions, fitted to the normalized spectrum, between the different groups of averaged stations.

Table 6. 12. The different slopes (b) of the linear equations and coefficients (b') of the second degree polynomial equations fitted on the normalized size distributions averaged per three stations situated at the same latitude. r^2 = regression coefficients of the fitted equations, n = number of samples, R= correlation coefficient.

stations	*N*	*b*	r^2	*R*	*p*	*b'*	r^2	*R*	*p*
W_6H_6	12	-1.65	0.70	0.83	<0.0007	-0.22	0.70	0.84	<0.003
$W_5H_5O_5$	13	-1.99	0.73	0.85	<0.0002	-0.71	0.78	0.88	<0.0005
$W_4H_4O_4$	12	-2.13	0.67	0.82	<0.001	-0.45	0.68	0.82	<0.005
$W_3H_3O_3$	13	-1.80	0.58	0.76	<0.002	-0.77	0.64	0.80	<0.005
$W_2H_2O_2$	12	-1.44	0.53	0.73	<0.006	-0.49	0.56	0.75	<0.02
$W_1H_1O_1$	14	-2.71	0.79	0.89	<0.0001	0.42	0.80	0.89	<0.0001
$W_0H_0O_0$	13	-2.64	0.78	0.88	<0.0001	0.03	0.78	0.88	<0.0005

Table 6.13. The different slopes (b) of the linear equations and coefficients (b') of the second degree polynomial equations fitted on the normalized size distributions averaged per three stations situated at the same latitude. r^2 = regression coefficients of the fitted equations, n = number of samples, R= correlation coefficient.

stations	*n*	*b*	r^2	*R*	*p*	*b'*	r^2	*R*	*p*
W_6H_6	12	-1.31	0.53	0.72	<0.007	0.30	0.53	0.73	<0.03
$W_5H_5O_5$	13	-1.70	0.64	0.80	<0.001	-0.60	0.66	0.81	<0.004
$W_4H_4O_4$	12	-1.95	0.56	0.75	<0.004	-0.64	0.58	0.76	<0.01
$W_3H_3O_3$	13	-1.64	0.44	0.66	<0.01	-0.64	0.47	0.68	<0.04
$W_2H_2O_2$	12	-1.45	0.49	0.70	<0.01	-0.60	0.52	0.72	<0.03
$W_1H_1O_1$	14	-2.74	0.75	0.87	<0.0001	0.80	0.77	0.88	<0.0003
$W_0H_0O_0$	13	-2.22	0.66	0.81	<0.0007	0.86	0.70	0.83	<0.002

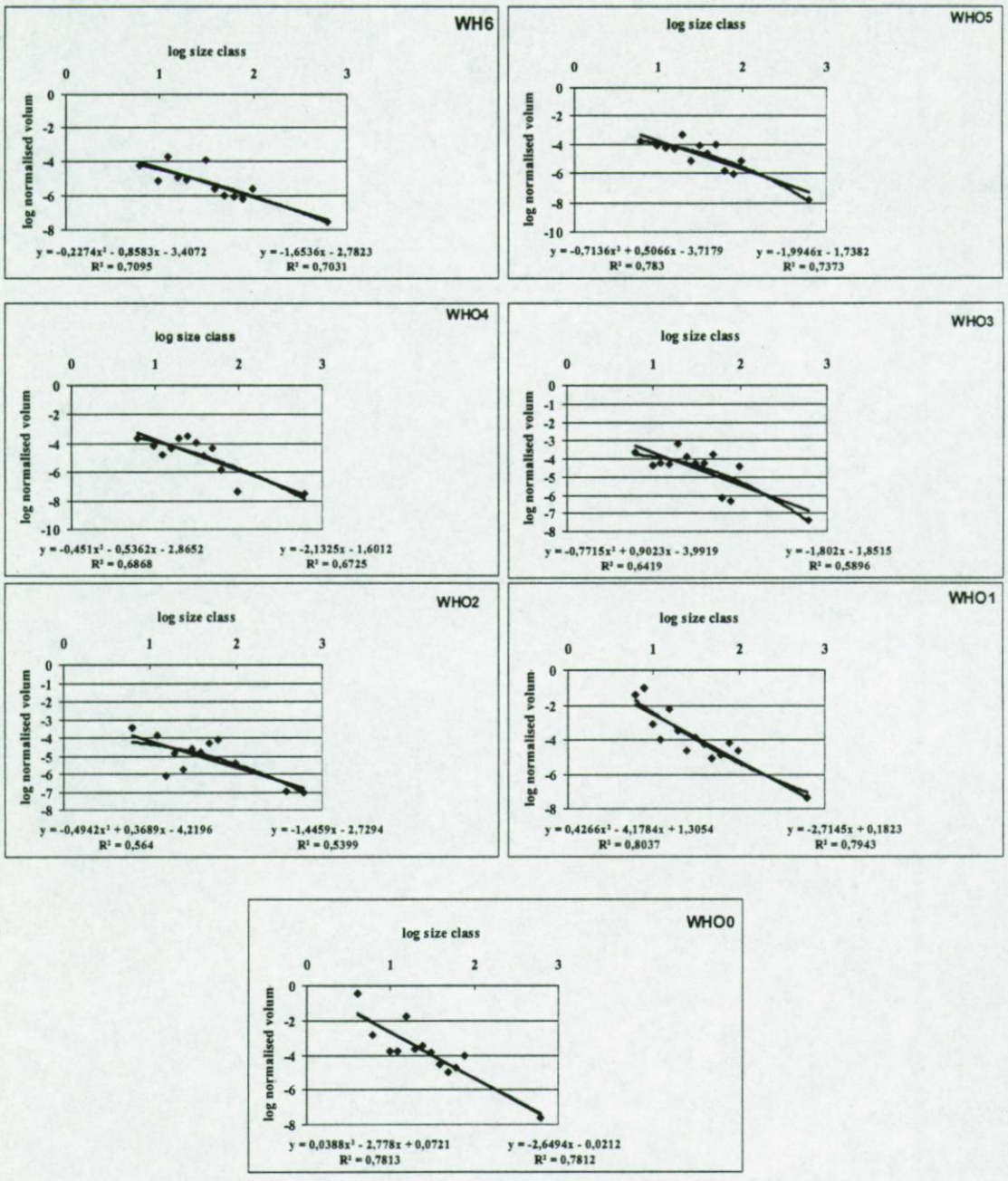


Fig 6. 5. Normalised mean size distributions of plankton (phytoplankton + *Calanus finmarchicus*) along the spring North-South transect covering Dogger Bank central-northern North Sea (averaged over 3 stations) expressed in volume concentration fitted with linear and polynomial equations: W_6H_6, $W_5H_5O_5$, $W_4H_4O_4$, $W_3H_3O_3$, $W_2H_2O_2$, represented central-northern part; and $W_1H_1O_1$, and $W_0H_0O_0$ represented the Dogger Bank area.

3. 2. The Sheldon model applied

3. 2. 1. Belgian coastal zone

Considering all abundant zooplankton species as predator preying on phytoplankton stock, Sc/Sp values ranged from 0.02 to 2.00 and Dc/Dp ranged from 19 to 25 (in terms of volumetric concentrations), Ge*Ce values ranged from 0.003 to 0.19 (Table 6.14). Sc/Sp values, using carbon biomass, ranged from 0.004 to 0.23 and were generally lower than those calculated in volumetric concentrations. As a consequence, Ge*Ce values ranging from 0.0005 to 0.02 were lower than those calculted in volumetric concentrations (Table 6.15).

Ce values ranged from 0.02 to 1.31 and from 0.003 to 0.15, based on volumetric and carbon calculations, respectivelly.

3. 2. 2 North-South transect

Considering only the dominant zooplankton species, *Calanus finmarchicus*, as a potential predator preying on phytoplankton stock, Sc/Sp values ranged from 0.01 to 0.63 and Dc/Dp ranged from 7.96 to 20.00 (in terms of volumetric concentrations), Ge*Ce values ranged from 0.004 to 0.06 (Table 6.16). Sc/Sp values, using carbon biomass, ranged from 0.03 to 1.003 were generally higher than those calculated in volumetric concentrations. As consequence, Ge*Ce values were higher than those calculated in volmetric concentrations (0.008-0.10) (Table 6.17).

Ce values ranged from 0.03 to 0.70 and from 0.05 to 0.70, based on volumetric and carbon calculations, respectivelly.

Considering all abundant zooplankton species as predator preying on phytoplankton stock, Sc/Sp values ranged from 0.19 to 1.90 and Dc/Dp ranged from 3.8 to 9.7 (in terms of volumetric concentrations), Ge*Ce values ranged from 0.08 to 0.40 (Table 6.18). Ce values ranged from 0.53 to 2.69 based on volumetric calculations.

Table 6. 14. Belgian coastal zone: the different values used in the Sheldon model wherein all dominant zooplankton (copepods) is taken as the predator and phytoplankton as prey. Standing stocks (Sc and Sp) are in terms of mean volumetric concentrations. The mean size of copepods (Dc) was taken as mean diameter dc from Table 6.7. The mean size of phytoplankton (Dp) is the median spheric equivalent diameter of the differents size classes given in Table 6.7.

Bank name	Sc (ppm)	Sp (ppm)	Dc (µm)	Dp (µm)	Sc/Sp	Dc/Dp	$(Dc/Dp)^{0,72}$	Ge*Ce	Ce
Stroombank	0,002	0,075	490	24,55	0,03	19,96	0,12	0,003	0,02
Middelkerke	0,008	0,054	389	15,49	0,14	25,11	0,10	0,014	0,09
Kwintenbank	0,041	0,030	490	24,55	1,34	19,96	0,12	0,156	1,04
Oostdyck	0,015	0,057	389	24,55	0,27	15,85	0,14	0,037	0,24
Oosthinder	0,009	0,015	389	15,49	0,61	25,11	0,10	0,060	0,40
Westhinder	0,026	0,013	389	15,49	2,01	25,11	0,10	0,197	1,31

Table 6. 15. Belgian coastal zone:the different values used in the Sheldon model wherein all dominant copepods are considered a predator and total phytoplankton as prey. Standing stock biomass (Sc and Sp) are in terms of mean carbon concentrations. The median sizes (Dc and Dp) are the same as in Table 6.7.

Bank name	Sc ($\mu g\ C\ l^{-1}$)	Sp ($\mu g\ C\ l^{-1}$)	Dc (μm)	Dp (μm)	Sc/Sp	Dc/Dp	$(Dc/Dp)^{0,72}$	Ge*Ce	Ce
Stroombank	0,19	45,30	490	24,55	0,004	19,96	0,12	0,0005	0,003
Middelkerke	0,68	45,15	389	15,49	0,015	25,11	0,10	0,0015	0,010
Kwintenbank	3,71	19,58	490	24,55	0,190	19,96	0,12	0,0220	0,147
Oostdyck	1,37	33,89	389	24,55	0,041	15,85	0,14	0,0055	0,037
Oosthinder	0,92	11,23	389	15,49	0,082	25,11	0,10	0,0080	0,054
Westhinder	2,36	10,17	389	15,49	0,232	25,11	0,10	0,0228	0,152

Table 6. 16. North Sea Transect: the different values used in the Sheldon model wherein *Calanus finmarchicus* is considered a predator and total phytoplankton as prey. Standing stock biomass (Sc andSp) are in terms of mean volume concentrations. The median sizes (Dc and Dp) are the same as in Tables 6.8 and 6.9.

stations	Sc (ppm)	Sp (ppm)	Dc (µm)	Dp (µm)	Sc/Sp	Dc/Dp	$(Dc/Dp)^{0,72}$	Ge*Ce	Ce
W_6H_6	0,02	0,03	618,04	30,9	0,638	20,001	0,102	0,065	0,437
$W_5H_5O_5$	0,01	0,09	618,04	48,97	0,111	12,620	0,162	0,018	0,121
$W_4H_4O_4$	0,02	0,07	618,04	30,9	0,284	20,001	0,102	0,029	0,194
$W_3H_3O_3$	0,02	0,18	618,04	48,97	0,155	12,620	0,162	0,025	0,168
$W_2H_2O_2$	0,06	0,62	618,04	77,59	0,103	7,965	0,257	0,026	0,178
$W_1H_1O_1$	0,03	0,69	618,04	77,59	0,044	7,965	0,257	0,011	0,076
$W_0H_0O_0$	0,01	0,88	618,04	77,59	0,019	7,965	0,257	0,004	0,033

Table 6. 17. North Sea Transect: the different values used in the Sheldon model wherein *Calanus finmarchicus* is considered a predator and total phytoplankton as prey. Standing stock biomass (Sc andSp) are in terms of mean carbon concentrations. The median sizes (Dc and Dp) are the same as in Tables 6.8 and 6.9.

stations	Sc ($\mu g\ C\ l^{-1}$)	Sp ($\mu g\ C\ l^{-1}$)	Dc (μm)	Dp (μm)	Sc/Sp	Dc/Dp	$(Dc/Dp)^{0,72}$	Ge*Ce	Ce
W_6H_6	1,81	1,80	618,04	30,9	1,003	20,001	0,102	0,103	0,687
$W_5H_5O_5$	0,98	6,76	618,04	48,97	0,145	12,620	0,162	0,023	0,157
$W_4H_4O_4$	2,02	4,59	618,04	30,9	0,440	20,001	0,102	0,045	0,301
$W_3H_3O_3$	2,55	17,87	618,04	48,97	0,142	12,620	0,162	0,023	0,154
$W_2H_2O_2$	5,83	14,20	618,04	77,59	0,411	7,965	0,257	0,106	0,707
$W_1H_1O_1$	2,79	38,70	618,04	77,59	0,072	7,965	0,257	0,018	0,124
$W_0H_0O_0$	1,53	44,46	618,04	77,59	0,034	7,965	0,257	0,008	0,059

Table 6. 18. North Sea Transect: the different values used in the Sheldon model wherein all dominant zooplankton species are considered a predator and total phytoplankton as prey. Standing stock biomass (Sc andSp) are in terms of mean volume concentrations. The median size (Dp) is the same as in Table 6.8.

stations	Sc (ppm)	Sp (ppm)	Dc (µm)	Dp (µm)	Sc/Sp	Dc/Dp	$(Dc/Dp)^{0,72}$	Ge*Ce	Ce
W_6H_6	0,06	0,03	300	30,9	1,91	9,71	0,21	0,40	2,69
$W_5H_5O_5$	0,02	0,10	300	48,97	0,24	6,13	0,34	0,08	0,54
$W_4H_4O_4$	0,04	0,08	300	30,9	0,46	9,71	0,21	0,10	0,65
$W_3H_3O_3$	0,07	0,18	300	48,97	0,37	6,13	0,34	0,12	0,83
$W_2H_2O_2$	0,12	0,63	300	77,59	0,20	3,87	0,53	0,10	0,70
$W_1H_1O_1$	0,14	0,69	300	77,59	0,19	3,87	0,53	0,10	0,69
$W_0H_0O_0$	0,20	0,88	300	77,59	0,23	3,87	0,53	0,12	0,80

4. Discussion

4. 1. Plankton size distribution spectrum

4. 1. 1 Belgian coastal zone

In the Belgian Coastal zone, both linear and polynomial regression fitted the dataset for all banks. The regression coefficients of the linear regression were somewhat lower for the nearshore than for the offshore banks (Table 6.10). In fact, for most nearshore banks, there was a tendency for a better fit of the polynomial than the linear regression. This reflects a tendency for plankton in the lower or the upper end of the spectrum to have lower biomass compared to the size classes in between (Fig 6.1a, b and c).

A significantly higher slope (b) was found for the most nearshore bank (Stroombank) than for all the other banks.

As our data describe only a momentary situation, we can merely interpret these differences in the fitting to the linear model as a descriptor of a different trophic situation between the phytoplankton and the zooplankton considered in the model. This differences can again be explained by the fact that the stations located in the proximity of the coast, are influenced by strong mesoscale currents produced by the presence of a residual gyre along the Belgian coastal zone off Zeebrugge (Belgrano et al., 1995). As the depth in this area is limited (< 8m) both benthic and littoral influence (import from the Scheldt estuary) are

considerable. Enhanced concentrations of non-phytoplankton particulate matter can hamper the feeding activity of the zooplankton on phytoplankton (Sherk, et al., 1974; Tackx et al., 1995; Gasparini et al., 1997). As a consequence, zooplankton survival or production in such areas can be limited.

Several studies have confirmed the trends towards polynomial fit in many size distributions of living organisms, in lakes (e.g. Peters, 1983; Gasol et al., 1991; Sprules et al., 1983; Sprules and Munawar, 1986, Hansen et al., 1989; Ahrens and Peters, 1991; Gaedke, 1992) and North Atlantic and Southern Ocean (e.g. Wells and Goldberg, 1994). Gasol et al (1991) observed that the polynomial fit is more pronounced in winter spectra in Lake Cisó. Billones (1998) found a better polynomial fit in size spectra in the downstream stations of the Scheldt river than in the upstream ones during the year 1997.

Sprules and Munawar, (1986) explained a good fit of the normalized size distribution to the linear regression observed in the open Pacific Ocean as a minimal influence of benthic or neashore processes on the major predator-prey interactions and the isolation of the offshore community due to the great depth and large surface area of the large oligotrophic Lake Superior.

4. 1. 2 North-South transect

The normalized size distributions averaged per 3 stations situated at the same latitude, in the open North Sea case, also fitted both the linear and the polynomial regression significantly. The Dogger Bank area showed the highest b

values of all the observed stations (Tables 6.12 and 6.13). This can be explained, as was already reported in the chapter 5, by an earlier onset of phytoplankton bloom around the shallow Dogger Bank area which is already established days before the one in the deeper central-northern stations, resulting in a higher biomass in the phytoplankton range of the spectrum. However, the size distributions did not exhibit a significant difference in the slope of the linear fit between the Dogger Bank stations and the central-northern stations. This can perhaps be explained by the fact that the biomass size spectra in our study included only phytoplankton and one zooplankton species (*C. finmarchicus*) or all dominant mesozooplankton species. Other components such as bacteria, benthos, and fish were not considered.

4. 2. Predator-prey relationship (Sheldon model)

This study uses the Sheldon model to evaluate the potential trophic transfer between phytoplankton and mesozooplankton, including all abundant copepods in the Belgian coastal zone. In the North-South transect phytoplankton and only the dominant zooplankter, *Calanus finmarchicus* are considered.

4. 2. 1 Belgian coastal zone

The observed ratio of zooplankton to phytoplankton standing stock (Sc/Sp), based on volume and carbon biomass, falls within the range of values calculated

by the model of Sheldon et al. (1977; 0.300-2.000) and Tackx et al. (1994; 0.070-0.280), for all banks except the most neashore one (0.004), where the standing stock ratio is rather low, indicating a very high prey standing stocks relative to its predator. Dc/Dp ratios found are within the range given by Sheldon et al., (1997; 5-25). The values of Ce must, theoretically, be ≤ 1, meaning that the predator eats only the production of its prey. Based on volume, Ce values are above 1 was calculated for the most offshore bank Westhinder, and also for the Kwintenbank. This means that, on these banks, copepods would have to consume more than > 100% of phytoplankton production to have a growth efficiency of 15%. On the nearshore banks, Ce values were < 1, the lowest value (0.02) being found for the Stroombank.

Based on carbon values, the required consumption of the prey production by the predator, to have a growth efficiency of 15%, was only 14%, 5%, and 17% in the Kwintenbank, Oosthinder and Westhinder, respectively. On the nearshore banks maximally 3.6% (on Oostdijk) would be required. So, Ce values based on carbon were ≤ 1, on all banks, indicating that in most cases, phytoplankton could be sufficient as the sole food source for the dominant copepods.

A discrepancy between the outcome of the model when calculated on a volume or a carbon basis was also found by Billiones (1998). Its evaluation is subject to a future paper (Tackx et al., in prep.).

However, both calculations revealed the same differences in trophic potential between the nearshore and the offshore banks: the potential predation impact of the copepods on the phytoplankton is higher in the offshore area that

in the nearshore area. This is caused by both lower Sc and higher Sp values in the nearshore than in the offshore area.

As explained before, a hindrance of the (selective) feeding by copepods on phytoplankton by high abundance of non phytoplankton suspended matter could explain the low development of zooplankton in the nearshore area, resulting in smaller standing stocks of zooplankton than in the offshore area, although phytoplankton stocks are significantly (Mann Whitney, $p< 0.05$) higher in the former (Table 6.14).

As in the offshore areas, concentration of non phytoplankton potential food items such as detritus is also lower than in the nearshore area (DW: Chapter.4). Consequently, the presence of substantial zooplankton standing stocks in the offshore areas supposes a substantial transfer of phytoplankton (or microzooplankton) to zooplankton.

Differences in phytoplankton species composition and size spectra from the neashore banks to the offshore might provide an explanation for this. The high phytoplankton stock on the neashore banks consisted of a co-dominance of Cryptophyceae and diatoms. On the offshore banks, diatoms dominated the low phytoplankton stock, but motile taxa such as Dinoflagellates and Prasinophyceae also contributed considerably to this stock (Table 5. 5, in Chapter 5) (Table 4.5, Chapter 4). This could also favour the predation on living prey and the development of copepods species in these areas.

Hay et al., (1991) showed that several copepod species have a substantial production during winter, supposing active feeding even at low temperatures and phytoplankton concentrations. As explained in the introduction, many copepods

tend to select the bigger phytoplankton species within a certain size range, and the diatoms within the 10 to 50μm size range could provide a highly favored food source for the copepods in the offshore areas.

Recent studies concerning selective feeding of calanoid copepods have shown that the motility of the prey can also influence their feeding behavior when phytoplankton stock is low (e.g., Saiz 1994; Saiz and Kiørboe 1995; Kiørboe et al., 1996; Kleppel et al., 1996; and Meyer-Harms et al., 1999). This was due to the switching feeding mode exerted by the copepods (Kiørboe and Saiz, 1995). Thus, copepods were found in laboratory as well as field experiments, to switch from suspension to ambush feeding prefering motile prey, such as dinoflagellates (e.g. Bellingshausen Sea, Atkinson 1995; Norwegian Sea, Meyer-Harms et al., 1999) or both dinoflagellates and ciliates (e.g. Kiørboe et al., 1996; Kiørboe and Saiz, 1995; and Saiz and Kiørboe 1995) when phytoplankton concentration is low. Laboratory experiments also showed that for *Acartia tonsa*, the ambush-mode feeding is much more dependent than suspension-mode feeding on turbulence (Saiz and Kiørboe, 1995).

Thus, in the less turbulent offshore banks, the phytoplankton community consisting of big diatoms and motile species, probably provides a food source on which the dominant copepod species can feed more efficiently than the nearshore phytoplankton communtiy.

Similarly, Gowen et al., (1999), studying zooplankton feeding in the Irish Sea, report a higher grazing efficiency (22%) of copepods (copepodites, and adults of *Pseudocalanus* and *Temora)* in the offshore western Irish Sea stations,

than in neashore stations (17%) during spring 1997. They attributed this pattern to the difference in populations size occurring during the spring bloom.

In chapter 4, the question was raised: 'How does this spatial difference (in phytoplankton species composition) between nearshore and offshore banks affect the potential energy flux from phytoplankton to zooplankton?'

Our data show that indeed, a difference exists in potential trophic transfer between phytoplankton and zooplankton. The high phytoplankton stock on the nearshore banks is underexploited by the zooplankton, while higher trophic transfers between phyto- and zooplankton must occur on the offshore banks. In terms of volumes, the phytoplankton seems to be even insufficient to support copepod production at some of the offshore banks at the time of our sampling. As to development conditions for the spring bloom, which is about to start shortly after the February situation analysed here, this suggest an 'advantage' for the nearshore zooplankton populations. However, considering the high concentrations of non-phytoplankton particulate matter in the nearshore environment, it is dubious that zooplankton development can really profit from this potential food resource.

4. 2. 2 North-South transect

The ratio of *Calanus finmarchicus* stock to phytoplankton standing stock (Sc/Sp), based on volume (Table 6.16), falls within the range of values given by Sheldon et al. (1977; 0.300-2.000) and Tackx et al. (1994; 0.070-0.280). This is also the case for the ratio, based on carbon content, except in the most northern

stations (W_6H_6) and in the central stations ($W_2H_2O_2$) where values were quite high. Dc/Dp ratios found in our calculations are within the range given by Sheldon et al., (1977; 5-25).

Except in the Dogger Bank area, the Ce values were quite higher, both in terms of volume and carbon stocks (Table 6. 16 and Table 6. 17). Highest Ce values (0.70) -but < 1- were calculated for the northern (W_6H_6) and central stations. This was however, expected if we consider that winter conditions were still prevailing in the northern North Sea. This can be said also in the case of the central stations where the potential feeding pressure of *C. finmarchicus* on phytoplankton stock was quite high, but still < 100%.

Substantially lower Ce values were calculated for the Dogger Bank area ($W_0H_0O_0$) and the stations just above the Dogger Bank ($W_1H_1O_1$) than for the other stations. So, the earlier onset of the phytoplankton bloom in the Dogger Bank area, seems to provide sufficient phytoplankton food to meet the energy demand of the *C. finmarchicus* population in that area (Ce values are lower than < 1, both in terms of carbon and volume calculations; Tables 6. 16 and 6. 17). The *C. finmarchicus* population had to consume only between 3 % to 12 % of the phytoplankton stock to have a growth efficiency of 15%. While, a quite important phytoplankton stock is taken (69% to 80%, Table 6.18) by all dominant mesozooplankton species (Ce values is lower than < 1, but higher than Ce values reported in Table 6.16). So, there is a quite important flux of energy, which will be available to other primary consumers, such as other dominant zooplankters species (*Oikapleura dioica* and some meroplanktonic benthic species such as Lamellibranchidea) which were dominant in the Dogger Bank

area (Figure 6.6), but also to the benthos. Indeed, it is well known that in the shallower southern North Sea (depth is less than 40m in the Dogger bank area) the benthos also consumes a substantial fraction of the primary production (see also Joiris et al., 1982; Jones et al., 1984; Zijlstra, 1988; and De Wilde et al., 1992).

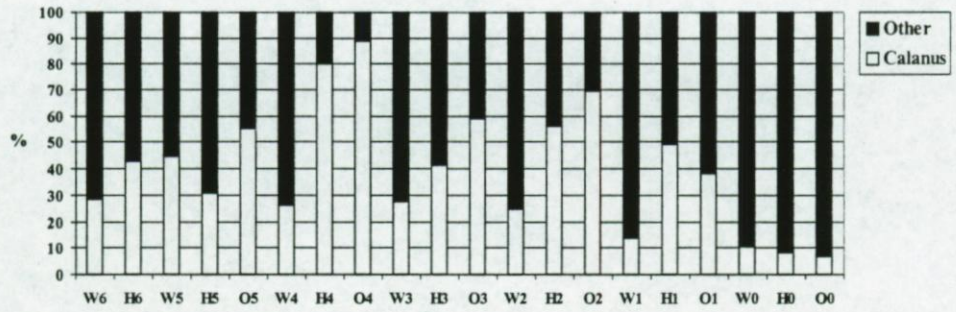


Fig 6.6 Percentage contribution of *Calanus finmarchicus* and the rest of zooplankton species (other) to total zooplankton biomass. (data provided by NIOZ (Fransz, pers. Comm.)

Despite, a high phytoplankton stock at stations ($W_2H_2O_2$), a rather high potential *C. finmarchicus* pressure on phytoplankton stock was obtained (17.8 and 70% based on volume and carbon respectively, Table 6.16 and Table 6.17). This was mainly due to the fact that a maximum Sc values (0.06) was observed at these stations. *Calanus sp.* are able to eat larger preys than most other (smaller) copepod species in the North sea (Irigoien, pers. comm.). Perhaps the association between the maximum of the *C. finmarchicus* population and the dominance of the large diatom *Coscinodiscus concinnus* (See Chapter 5) is not a coincidence.

Richardson et al., (1998) report that copepod ingestion exceeds the primary production in May 1992 in the Central North Sea (north of Dogger Bank). Thus, they suggested that the copepods are exploiting either the protozooplankton production in addition to phytoplankton in order to satisfy their energy requirements. However, they reported lower copepod ingestion (less than 100%) on the primary production, during May 1992 in the Dogger Bank area. They explained that by the fact that the *Calanus* spp. stock contributed only as a small part of the total zooplankton stock at the stations less than 40m depth (Richardson et al., 1998). This was the case of the Dogger Bank area, in our study, where a small fraction of the phytoplankton stock seems to be sufficient to meet the energy demand of *C. finmarchicus*. The contribution of *C. finmarchicus* to the total zooplankton stock in this area is, however, reduced (Figure 6.6).

As in the Belgian coastal zone, the subareas, which were separated, based on phytoplankton species composition, also display a different situation with regard to the potential trophic transfer between phytoplankton and zooplankton. In the North- South transect, the phytopankton stock seems sufficient as sole food source to the zooplankton over the entire study area.

5. Conclusions

Our results indicate a clear pattern in the biomass size spectrum of plankton community, during winter in the Belgian coastal zone, and during an early spring bloom in the North-South transect in the North Sea. Recognition of these trends is possible because the slope of the normalized biomass size spectrum is a quantitative index of the system structure. The application of the Sheldon model is limited to plankton communities and does not provide information on seasonal variability or benthic-pelagic coupling. Nevertheless, the trends we have noted are likely correct on a first approximation and are of sufficient general importance to warrant further investigation. A spatial heterogeneity was also observed in the Flemish banks along Belgian coastal zone: within the epibenthic fishes and invertebrates at the same area during winter 1997 and 1998 (Dalmas, 1999) on the one hand; and of seabirds in the early eighties (Joiris, 1983) on the other hand.

Moreover, this spatial heterogeneity was also observed within bacteria biomass in February-March 1988, with low stock in the northern stations (north of Dogger Bank) and an increased stock towards the Dogger Bank area (Nielsen and Richardson, 1989). Heterotrophic nanoflagellates (S.E.D= 3.5 μm) also showed a spatial heterogeneity (Nielsen and Richardson, 1989), as well as protozooplankton production along a May transect of 1992, between the Dogger Bank area and central north Sea (Richardson et al., 1998). Morover, a spatial heterogeneity within the heterotrophics protists, with a proncounced high stock in the Dogger Bank area compared to the low one in the deeper northern stations (Kuipers and Witte, 1999), and a 4 discernable latitudinal zones based on the

metazoan plankton distribution (Fransz et al., 1998), were observed for the same transect reported in our study.

Chapter VII

General conclusions

A spatial heterogeneity seems to be a general trend within the phytoplankton and -to some extend- in zooplankton during winter around some sandbanks of the Belgian coastal zone. This could be due to the differences observed in environmental conditions (salinity, temperature, turbidity and nutrient concentrations) and can be explained by the positioning of the banks. The offshore banks (e.g. Oosthinder, Westhinder, and Oosdyck) positioned furthest from the coast, are obviously influenced by the Southern intrusion of Atlantic water. The best explanation of the variance in phytoplankton community was obtained when nutrient concentrations were included in the analysis. This indicates that, besides the fact that the study area covers two water masses of different origin, variations in nutritional conditions also influence phytoplankton species composition. Differences in phytoplankton species composition and taxa contribution also resulted in differences in biomass (in terms of volume and carbon concentrations) and size structure between nearshore and offshore banks.

Our studies along a North Sea transect, showed large variations in phytoplankton community, biomass (in terms of volume and carbon concentrations) and size structure during early spring phytoplankton bloom. This was explained by the variations -along the transect- of the environmental factors such as temperature, salinity and nutrient concentrations (mainly silicate and nitrate concentrations). Results obtained, corroborate the general picture of the early onset of the spring bloom with higher phytoplankton stocks in the shallow Dogger bank area and lower in the deeper central and northern North Sea areas, both in terms of numerical, volumetric, and carbon concentrations. The high abundance of microflagellates (Prasinophyceae and Chlorophyceae) and

Phaeocystis sp. in the Dogger Bank area is explained by the advantage of the non-diatom species for growth in a nutrient-limited environment after exhaustion of nutrients (mainly silicate) by diatoms. Nevertheless, the contribution of large diatoms (e.g. *Rhizosolenia* spp.) to total biomass, expressed in term of biovolume or carbon content, exceeded that of the microflagellates taxa in the Dogger Bank area. This shows that the onset of spring bloom started already in the course of February or early March in the Dogger bank area, and illustrates the fact that some large diatoms (e.g. *Rhizosolenia* spp.) are often observed together with *Phaeocystis* and are known to grow under lower silicate concentrations than other diatom species.

In general terms, distinct early spring phytoplankton communities revealed in this study confirm a distinction between the northern deeper and southern shallower water zones in the North Sea, and seem to be affected by the bathymetry and hydrography. The variation in size-distribution of phytoplankton along the transect fits the expectation of dominance of large diatoms in shallow water of the Dogger Bank areas and small phytoplankton species in the deeper stations of the central and northern the North Sea. Also, each of the two zones was characterised by a rather typical phytoplankton volume and size structure.

Moreover, our results showed that within the > 5 μm size range different contribution of cells < 10 μm may also provide different trophic situation for the micro/meso-zooplankton.

The last purpose of this study was to evaluate if the difference observed in phytoplankton communities (Chapters 3, 4 and 5) represented different situations to the potential trophic transfer phytoplankton-mesozooplankton, and

as such provided different structuring conditions at the onset of the spring bloom. Evaluation of the potential predation pressure exerted by the associated mesozooplankton communities, using the model of Sheldon et al., (1977) shows that indeed differences in potential trophic transfer are found between the subareas.

In the Belgian coastal zone, different normalised size spectra are observed reflecting a different trophic structure between the nearshore and offshore banks. In the North-South transect, the size distributions did not exhibit a significant difference in the slope of the linear fit between the Dogger Bank area and the central-northern stations. However, the Dogger Bank area showed the highest b values of all the observed stations (Tables 6.12 and 6.13). This can be explained, by an earlier onset of phytoplankton bloom around the shallow Dogger Bank area days before the one in the deeper central-northern stations, resulting in a higher biomass in the phytoplankton range of the spectrum.

In general term, the phytoplankton stock can support the carbon requirements of the dominant neretic copepod during the early onset of growing season along the Belgian coastal zone in one hand, and the dominant *Calanus finmarchicus* or total mesozooplankton along a North-South transect in the North Sea during the early spring phytoplankton bloom, in other hand. The maximum potential consumption impact (Ce $\leq$ 15% and 70% in the sandbanks in the Belgian coast and in the open North Sea system, respectively) on the phytoplankton prey items does not exceed the prey's productivity. However, the dominant neretic copepods in the Belgian coastal zone and the *Calanus finmarchicus* in the North-South transect in the North Sea seem to be using only a small part of the high phytoplankton stock

(Ce ≤ 02% and 05% in the shallow stations of the Belgian coastal zone -e.g. in the Stroombank and Middelkerke- and in the Dogger Bank area, respectively). A quite important flux of energy is not channeled to holo-zooplanktoners and then to the higher trophic levels and will benefit to the benthos, either as food for meroplanktonic larval stages or after sedimentation to the benthic system (Figure 1.7a). While, in the deeper stations of the Belgian coastal zone (e.g. in the Westhinder, Oosthinder, Oosdyck, and Kwintenbank) and the deeper central-northern areas of the North Sea, a quite important carbon stock is channeled to the holo-zooplankton (Figure 1.7b). Based on these different considerations and the information available in literature, we draw here a diagram (Figure 7.1a,b) to illustrate our finding in chapter 6.

Finally, our results from different parts of the North Sea indicate that the spatial phytoplankton community structuring, in the North Sea, is not only limited to the 'blooming' period of the year, as was intensively reported during spring time (e.g. Gamble, 1978; Smetacek et al., 1978; Richardson, 1985; Nielsen and Richardson, 1989; Mills et al., 1994, Bauerfeiund et al., 1990; Kuipers and Witte, 1999; and Meyer-Harms et al., 1999) or summer time (e.g.; Daro, 1980; Holligan et al., 1984, Kiorboe et al., 1990; Nielsen et al., 1993; Riegman et al., 1998; Richardson et al., 1998; Kuipers and Witte, 1999). Interactions between phytoplankton community structure and environmental factors, on the one hand, and to higher trophic level (mesozooplankton), on the other hand, can start already earlier in the year -late winter/early spring- (e.g. Nielsen and Richardson, 1989; Bathmann et al., 1990; M'harzi et al., 1998) and constitute an important factor affecting the pelagic biological regime later in the year in the North Sea.

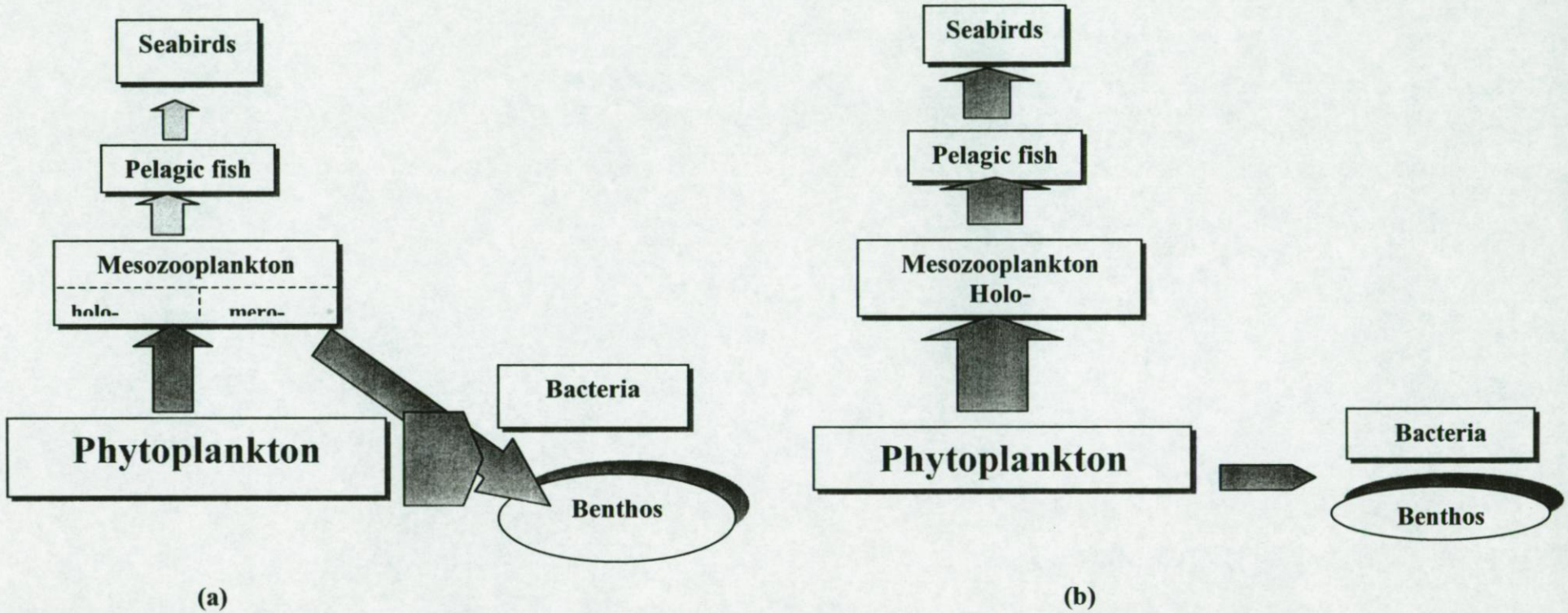


Figure 7.1. Simplified representation of dominant pathways along which matter and energy are channeled in the: (a) Shallow water of the neashore banks of the Belgian coastal zone and in the Dogger Bank area and (b) deeper offshore banks of the Belgian coastal zone and in the Central-northern area of the North Sea. Quantitatives differences in these pathways are illustrated by the widths of the arrows based on literature and our observations.

VIII. References

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IX. Appendices

Appendix 1

The different logarithmic size classes of particles (base 2), the spheric equivalent diameters (SED) and the size intervals. (After Sheldon et al., 1972).

Size class	Volume (μm^3)	SED (μm)	interval
1	0,25	0,78	
2	0,49	0,98	0,24
3	0,97	1,23	0,48
4	1,95	1,55	0,98
5	3,88	1,95	1,93
6	7,79	2,46	3,91
7	15,45	3,09	7,66
8	30,82	3,89	15,37
9	61,60	4,90	30,78
10	122,99	6,17	61,39
11	245,62	7,77	122,63
12	489,80	9,78	244,18
13	976,73	12,31	486,93
14	1946,05	15,49	969,32
15	3882,42	19,50	1936,37
16	7747,35	24,55	3864,93
17	15448,06	30,90	7700,71
18	30821,05	38,90	15372,99
19	61487,80	48,97	30666,75
20	122627,00	61,64	61139,20
21	244577,15	77,59	121950,15
22	487995,23	97,68	243418,08
23	973397,41	122,96	485402,18
24	1941525,70	154,78	968128,29
25	3872870,60	194,84	1931344,90
26	7725594,60	245,27	3852724,00
27	15451189,20	309,02	7725594,60
28	30902378,40	389,34	15451189,20
29	61804756,80	490,54	30902378,40
30	123609513,60	618,04	61804756,80
31	247219027,20	778,68	123609513,60

Appendix 2

Scientific reports and publications:

Below is a list of publications and reports wherein the author and his research study has contributed into:

- ✓ H. Lung'ayia; **A. M'harzi**; J. W. Gichuki; M. Tackx; & J. J. Symoens (1999): Phytoplankton community structure in relation to environmental factors in Lake Victoria (Kenyan Part). *Freshwater Biology*: (Accepted, In press).

- ✓ **M'harzi A.**; M. Tackx; M. H. Daro; I. Kesaulya and R. Caturao (1998): Winter distribution of phytoplankton and zooplankton around some sandbanks of the Belgian coastal zone: *Journal of Plankton Research*, Vol.20, Issue 11 pp. 2031-2052.

- ✓ G. Torres; Jerry Landivar; Q. L. Burgos; **A. M'harzi**; M. Osore; X. Irigoien; M. Tackx and N. Daro (1998): Phytoplankton and zooplankton community structure in the Guayaquil estuary and the Estero Salado during August 1996 (Ecuador).

- ✓ **M'harzi A** (1998): A report on the distribution of phytoplankton and zooplankton around Buitenratel, Gootebank and Westhinder sandbanks of the Belgian coastal zone.Project: Advanced Modelling and Research on Eutrophication (*AMORE*).Programme "Gestion Durable de la Mer du Nord". Service du Premier Ministre, Services Fédéraux des Affaires Scientifiques, Techniques et Culturelles. February 1998.

- ✓ G. Torres; Jerry Landivar; Q. L. Burgos; **A. M'harzi**; M. Osore; X. Irigoien; M. Tackx and N. Daro (1998): Phytoplankton and zooplankton community structure in the Guayaquil estuary and the Estero Salado during August 1996 (Ecuador). Proceeding Volume of the *ICES* International Symposium On Brackish Water Ecosystems. Helsinki, Finland. (25-28 August 1998). Page 48.

- ✓ H. Lung'ayia, **A. M'harzi**, J. Gichuki & J. J. Symoens (1998): Relationships between chlorophyll a and environmental factors in Lake Victoria (Kenyan part). Proceeding volume of the XXVII SIL Limnological Congress, Dublin Ireland, (August, 9-14 August 1998).

- ✓ **M'harzi A**, J. H. Vosjan; M. Tackx and N. Daro (1997): Changing phytplankton Community Structure along a North Sea transect (spring, 28 March to 15 April). Proceeding Volume of the 3RD LOICZ open science meeting on Global Change Science In The Coastal Zone. Leeuwenhorst Conference Centre, Noordwijkerhout, The Netherlands (October 10-13, 1997). No. 29; page 82.

- ✓ **M'harzi A**; M. Tackx; M. H. Daro; I. Kesaulya and R. Caturao (1997): Winter distribution of phytoplankton and zooplankton around some sandbanks of the Belgian coastal zone. Proceeding Volume of the 32ND European Marine Biology Symposium (EMBS), August 1997 Lysekil Sweden. page 119.

- ✓ Landivar, M. K. Osore, **A. M'harzi**, M. Tackx, and N. Daro (1997): A Report on Comparative Analysis of Zooplankton collected from two Tropical Estuarine Ecosystems- Estero Salado/Rio Guayas in Ecuador and Tudor Creek/Gazi Bay in Kenya.

- ✓ G. Torres, **A. M'harzi**, M. Tackx, and N. Daro (1997): A Report on Comparative Analysis of phytoplankton collected from two transect in Guayaquil estuary (Ecuador).

- ✓ H. Lung'ayia; **A. M'harzi**; J. W. Gichuki; M. Tackx; & J. J. Symoens (1997): Phytoplankton community structure in relation to environmental factors in Lake Victoria (Kenyan Part). *Phycologia*: *Journal* of the *International Phycological Society*.July 1997, Vol.36 No.4; page 67.

- ✓ **M'harzi A**, M. Tackx, N. Daro and J. H. Vosjan (1996): Changing Plankton Community Structure along a North Sea Transect. Workshop of Progress in Belgian Oceanographic Research Brussels. page: 139-141. January 8-9 1996.

- ✓ Tackx, N. Daro and **A. M'harzi** (1994): Characterization of particulate matter and quantification of particulate matterzooplankton interactions. IGBP and "Global Change" Related Research in Belgium II, 1994. page: 142-143

- ✓ **M'harzi A**, M. Tackx and C. Bakker (1993): Changes in the summer succession of phytoplankton induced by the storm-surge barrier in the Oosterschelde (S.W.Netherlands).

Appendix 3

Participation in International Scientific Activities:

- **First international conference on biodiversity and renewable natural resources preservation**. Al AKHAWAYN University, Ifrane, Morocco. (May 13-15, 1999).

- Third Annual Meeting of the North Sea project ***"AMORE"***. Ecology and Systematic laboratory Free University of Brussels (V.U.B) Brussels Belgium (February 11, 1999).

- Annual meeting of the **Causal factors of Biodiversity project**: Community structure, phylogeny and biogeography. **(1996-2000)** Coordinator: Prof. M. Vincx, Marine biology section, Zoological Institute. University of Gent, Belgium (December 3, 1998).

- **ICES INTERNATIONAL SYMPOSIUM ON BRACKISH WATER ECOSYSTEMS.** University of Helsinki, Porthania, Yliopistonkatu 3, Helsinki, Finland (August, 25-28, 1998).

- **XXVII SIL of Limnology Congress.** University of Dublin, Dublin, Ireland (August, 9-14 August 1998)

- Second Annual Meeting of the North Sea project ***"AMORE"***. Laboratoire de Microbiologie des Milieux Aquatiques, Université Libre de Bruxelles (U.L.B), Bruxelles Belgium (February 5, 1998).

- Seminar **"General introduction to the Schelde and the North Sea Project"**. at the Ecology and Systematics Laboratory, Free University Brussels (V.U.B), Brussels Belgium (January 12, 1998).

- Seminar:**"Phytoplankton"** at the Ecology and Sytematics Laboratory, Free University Brussels (V.U.B) Belgium (November 10, 1997).

- **3RD Loicz open science meeting on Global Change Science In The Coastal Zone**. Leeuwenhorst Conference Centre, Noordwijkerhout, The Netherlands (October 10-13, 1997).

- European Marine Biology Symposium. **32nd European Marine Biology Symposium (EMBS)**. Lysekil, Zweden, (August16-22, 1997).

- **The Sixth International Phycological Congress**. Pieterskerk- Leiden The Netherlands. (August.09-16, 1997).

- **ENISMA** Workshop, organized by the Free Univeristy Of Brussels (V.U.B) Belgium (May 29-31, 1997).

- Workshop **"Zandbanken-Sandbanks"**, organized by the Belgian Marine Scientific Research Institute **(IZWO)**.in Brugge, 14 Mai 1997.

- Workshop **(IZWO)** organized by the International Marine Research supported by the European Commission. Brugge, 15 Mai 1996.

- Workshop **"Progress in Belgian Oceanographic Research"**, organized by the Royal Academy of Belgium & National Committee of Oceanology, in Brussels from 08 to 09 of January 1996.