Vakgroep Mariene Biologie
KL Ledeganckstraat 35
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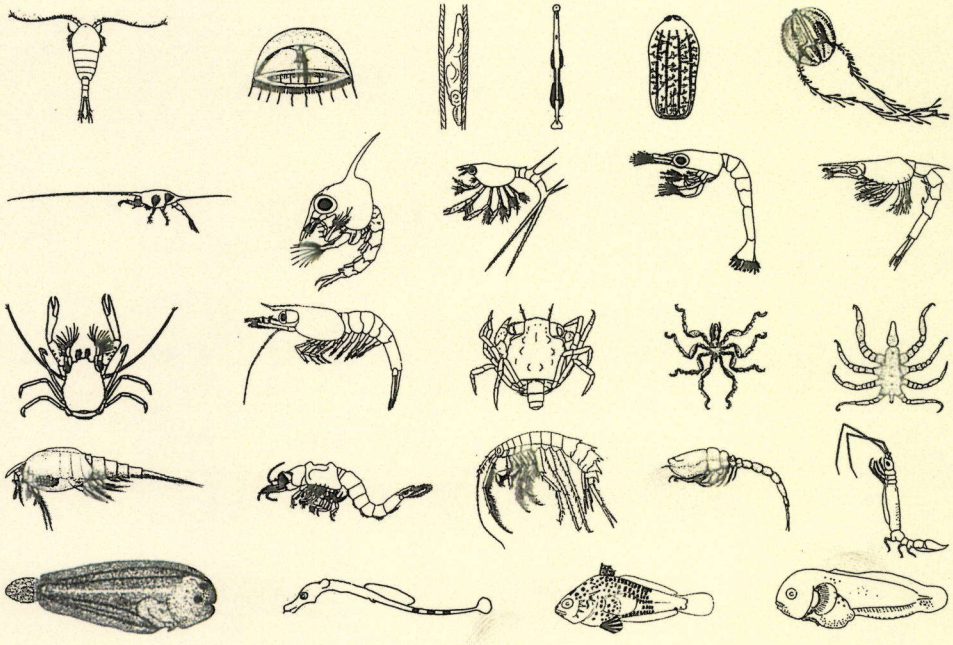
UNIVERSITEIT GENT
Faculteit der Wetenschappen
Academiejaar 2001 - 2002

Hyperbenthic communities of the North Sea

De hyperbenthische gemeenschappen van de Noordzee

Ann Dewicke



Promotor: Prof. Dr. M. Vincx
Co-promotor: Dr. J. Mees

Proefschrift ingediend tot het
behalen van de graad van Doctor
in de Wetenschappen (Biologie)

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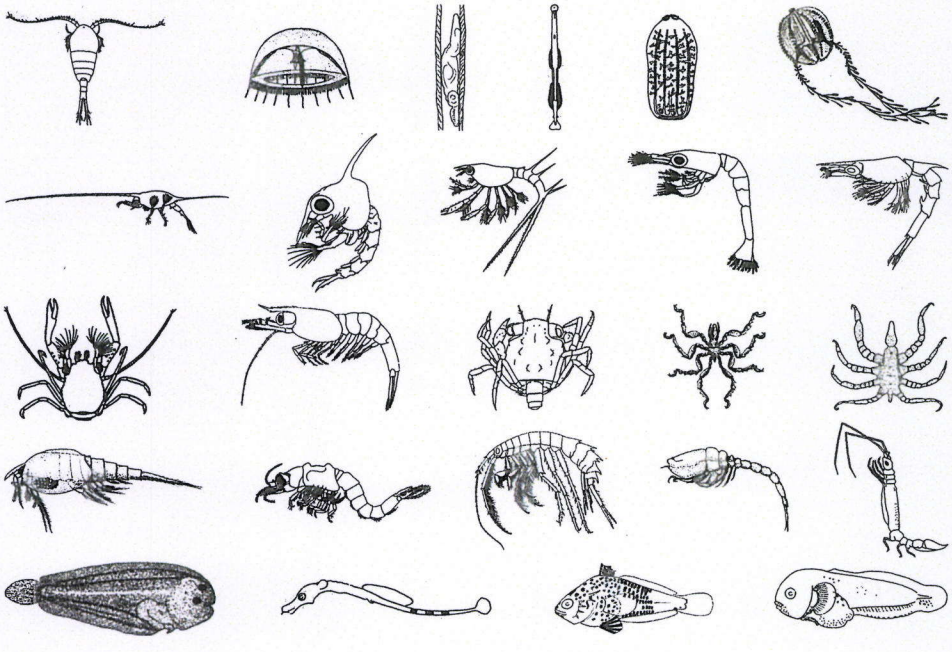

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« ... Le seule fait de rêver est déja très important. Je vous souhaite des rêves à n'en plus finir et l'envie furieuse d'en réaliser quelques-uns. Je vous souhaite d'aimer ce qu'il faut aimer et d'oublier ce qu'il faut oublier. Je vous souhaite des silences. Je vous souhaite des chants d'oiseaux au réveil, des rires d'enfants. Je vous souhaite de résister a l'enlisement, à l'endifférence, aux vertus négatives dans le monde. Je vous souhaite surtout d' être vous. »

Jacques Brel

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Ann,
Gent, 3 November 2001

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Introduction

Challenge

The North Sea is one of the environmentally most diverse regions in the NE Atlantic (Glémarec 1973; Lee 1980) and one of the most productive oceanic regions in the world (Backhaus 1980). It has a long history of multiple uses by people from many nations and its watershed covers highly developed industrial and agricultural areas. This involves strong pressure on the health of the North Sea ecosystem, a major environmental issue for many decades. Fisheries (removal of target species, seabed disturbances, effects of discards and mortality of non-target species), inputs of trace organic contaminants (from land and shipping) and nutrients input from land are known as the severest human impact at the end of the 20th century (OSPAR Commission 2000). Coastal areas in particular are under pressure of numerous activities and conflicting uses, leading to habitat changes and loss (Ducrotoy *et al.* 2000). Since the last decade, major changes are taking place in approaching the protection of the marine environment. There is now an awareness of the need to safeguard the marine ecosystem and to achieve sustainability in respect to human use (OSPAR Commission 2000). The international context is evolving constantly and since the 1990s legislation is under development in order to address threats to the biodiversity of the North Sea ecosystem (e.g. OSPAR Convention, Ramsar Convention, Wild Birds Directive, Habitats Directive) (see Ducrotoy *et al.* 2000). Despite the fact that scientific research has been intense in the North Sea region, there is still a lack of knowledge of its biodiversity (Cripps & Christiansen 2001, website). Additional data is needed in order to properly manage the area (Ducrotoy *et al.* 2000).

Data on species distributions of the North Sea's plankton is delivered by Continuous Plankton Recorders (CPR Survey Team 1992), regularly be deployed since 1946 (Warner & Hays 1994). The provision of this long-term data series has therefore revealed a well-known phyto- and zooplankton community of the area (e.g. Colebrook 1982; Lindley 1987; Reid *et al.* 1990; Fransz *et al.* 1991; Williams *et al.* 1993). Endobenthic communities of the North Sea have been recognized from the twentieth century (e.g. Gilson 1907; Petersen 1914, 1918), and a synoptic survey has been undertaken in 1986 characterizing the meio- and macrobenthic communities it harbours (e.g. Huys *et al.* 1990; Künitzer *et al.* 1992; Heip *et al.* 1992; Heip & Craymeersch 1995). Epibenthic communities (both free-living and attached species) were described by Dyer *et al.* (1983) and more recently by Jennings *et al.* (1999) and Rees *et al.* (1999). Approximately 230 species of fish are known to inhabit the North Sea of which 13 are the main targets of major commercial fisheries (OSPAR Commission 2000). The ecology of North Sea fish has been reviewed by Daan *et al.* (1990), and a characterization of demersal fish communities is given by Rogers *et al.* (1998). From top-predators in the North Sea ecosystem, it is known that seabirds represent substantial proportions of the world population (OSPAR Commission 2000), whereas less quantitative information exists for mammals. The first detailed survey of small cetacean populations in the North Sea was only carried out in 1994 (Hammond *et al.* 1995).

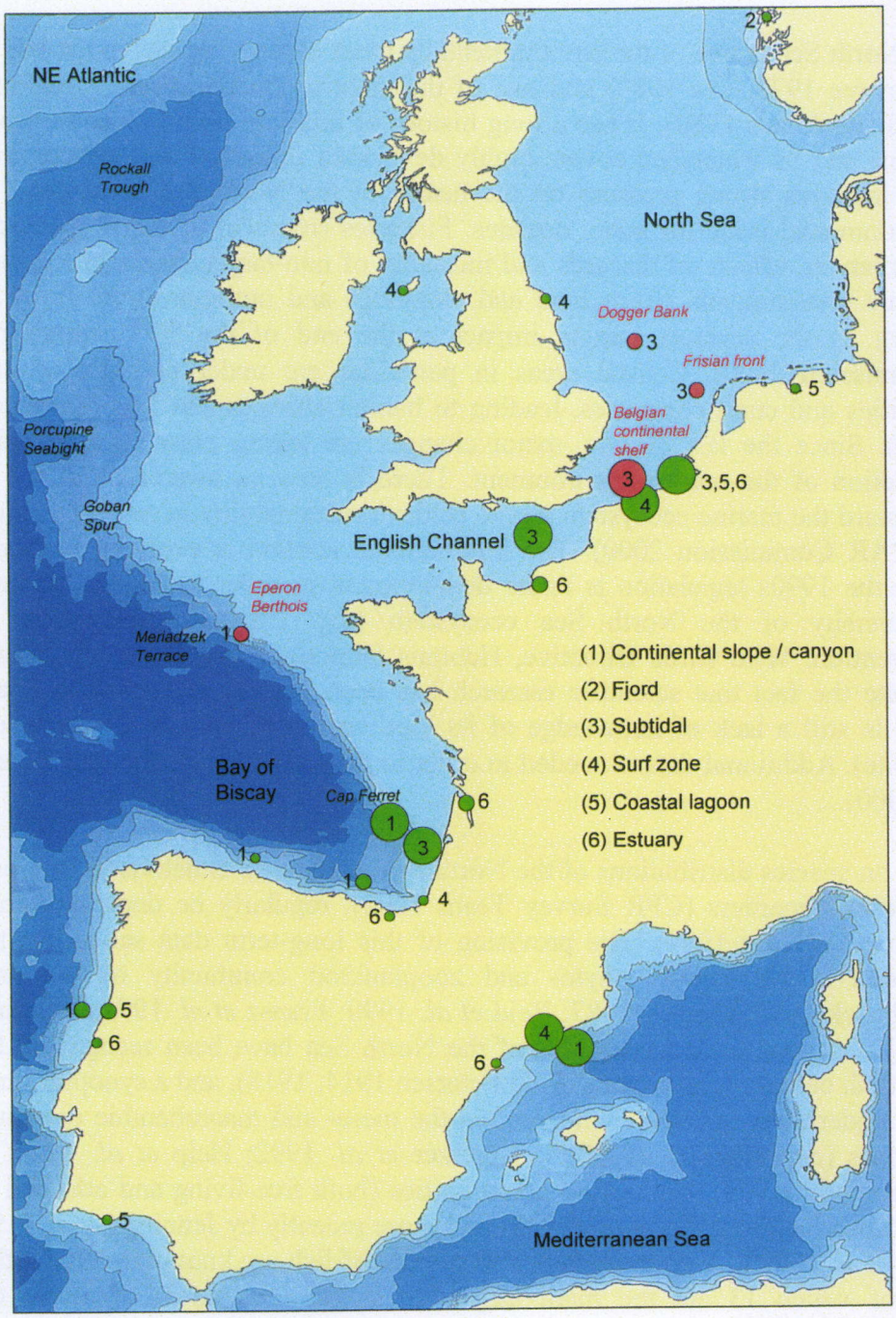

Fig. 1. Overview of research sites for the hyperbenthos on the European continental shelf (see Table 1). Sources from literature are indicated in green, selected working areas for this study are indicated in red. Dots are roughly sized according to the quantity of available data.

Until now however, the hyperbenthic fauna (the association of small animals living in the water layer close to the seabed) has been poorly examined and even baseline data on hyperbenthic community structure are virtually unknown for most parts of the North Sea (see Fig.1). This has been attributed to the only recent development (since the last 2 decades) of suitable sampling gear required for quantitative research to catch this motile fauna in the vicinity of the bottom (Mees & Jones 1997). Still, few scientific research teams concentrate on the hyperbenthic fauna involving the information gathered remains quite locally restricted and is concentrated to vast working areas, mainly in W Europe. In the southern North Sea, the hyperbenthos has intensively been studied in the shallow Dutch delta area (papers by Mees) and in the surf zone of the Belgian coast (papers by Beyst). Further southwards, detailed information is available on this fauna thriving in the English Channel and the Seine estuary (papers by Dauvin). Elaborated research on the continental shelf and slope in the Bay of Biscay has started already in the 1980's and is still going (papers by Sorbe). In Portugal, this fauna has been studied at the shelf break and in a coastal lagoon (papers by Cunha). Studies in the Mediterranean have mainly been concentrating on surf zones (papers by Vicente and Munilla) and on the continental slope (papers by Cartes). Research outside Europe is most extensively for polar regions (papers by Brandt) (see Table 1 for an overview of literature by the mentioned authors).

Despite the scattered knowledge on hyperbenthos communities, evidence of their potential function through carbon fluxes has often been emphasized. The potential role of the hyperbenthic fauna in marine ecosystems can be summarized as follows:

(1) *Flux to higher trophic levels.* The role of the hyperbenthos as a food source for juvenile demersal fish and adult shrimp is well documented for shallow coastal areas and estuaries (e.g. Mauchline 1980; Mees & Jones 1997; Hostens & Mees 1999; Beyst *et al.* 1999a; Pedersen 1999; Oh *et al.* 2001) and more recently for the deep sea as well (Mauchline 1986; Cartes 1998; Bjelland *et al.* 2000). Also coelenterates, cephalopods, birds and mammals were identified as potential predators on hyperbenthos (Mees & Jones 1997).

(2) *Consumption of detritus, zooplankton and phytoplankton.* Hyperbenthic species are omnivorous or detritivorous, though trophic guilds of strictly herbivores or carnivores may be present too (Mees & Jones 1997). They are believed to contribute to the conversion and recycling of organic matter as several species were indicated to feed on non-refractory detrital matter (Kost & Knight 1975; Jansen 1985; Fockedey & Mees 1999). Mysids can selectively feed on specific zooplankton species and size groups, thus potentially structuring zooplankton communities (Fulton 1982; Rudstam *et al.* 1989). Particularly for the deep sea, scavenging amphipods and isopods might be of specific importance for the flux of organic matter to the sea floor (Thurston 1979; Lampitt *et al.* 1993; Kaïm-Malka 1997). Certain asellote isopod families have been shown to feed mainly on benthic foraminifers moreover (Svavarsson *et al.* 1993; Gudmundsson *et al.* 2000), suggesting an important link in deep-sea food webs.

(3) *Modification and transport of organic matter.* The swimming activities of he hyperbenthos might also contribute to the fragmentation of organic matter or marine snow in the water column, as was indicated for euphausiids (Dilling & Alldredge 2000; Graham *et al.* 2000). Disaggregation of marine snow alters the availability and size distribution of particles possibly leading to a change in the rate of particulate carbon utilization and overall microbial activity in the water column

(Dilling & Alldredge 2000). The vertical migration behaviour coupled with organic material turnover activity also affects the energy transfer between the pelagic and benthic realm (Lampitt *et al.* 1993). Finally, the motility and behaviour of the hyperbenthos at the sea floor / water column interface might contribute to bioresuspension and biodeposition processes, increasing the particle flux as evidenced for other benthic organisms (Graf & Rosenberg 1997).

Further, most of the benthic organisms spend a certain time of their life history in the water column as larvae. After a dispersal phase, they migrate from the pelagic to the benthic realm during ontogenetic development. Pre-settlement stages can be seen as transitional and exert characteristic behaviour, often coinciding with strong morphological metamorphosis (Shanks 1995). Recruitment to adult populations is strongly affected by pre- and post-settlement processes in the benthic boundary layer showing large variations on diverse temporal and spatial scales (Butman 1987; Roughgarden *et al.* 1988). Baseline data are thus important to evaluate hypotheses in the study of successions of benthic communities, leading to a better understanding of short and long term stability.

The **primary aim of this study is to provide a baseline study of the species composition and spatio-temporal distribution of the hyperbenthic communities of the North Sea.** The challenge was to contribute to filling the gap in knowledge on hyperbenthic biodiversity in the North Sea. The approach was to selectively examine well-chosen areas within the vast North Sea and then focusing on species composition, density and diversity of the hyperbenthos.

Table 1. (next pages) Overview of literature providing quantitative data on hyperbenthic communities or on separate hyperbenthic taxa. As the development of sampling gear involved quality improvement of effective sampling, only recent studies performed by sledge sampling are listed. Literature on studies applying other sampling devices has been assemblaged by Mees & Jones (1997); for a literature review of Mysidacea (strictly hyperbenthic taxon) is referred to Mauchline (1980). Geographical regions are ordered according to (1) ecological biomes in oceanography as classified by Longhurst (1998) and (2) per habitat (see Appendex 1). The information given in the respective papers is tabulated as mainly providing spatial or temporal data. For temporal data, a distinction was made between monthly / bimonthly data (i.e. in general temporal succeeding data of 6 or more months a year), seasonal data (data of 2 to 5 months a year) and circum-diurnal data (with focus on tidal or day / night difference). The most common hyperbenthic taxa or listed (see Fig. 3 and Table 3). (4) Decapoda and Polychaeta may comprise larvae, juveniles or adults; Pisces are mostly dealing with larval stages (see the respective papers). As a remark, the deep-sea waters of the Bay of Biscay rather belong to the Atlantic Westerly Wind Biome (see Longhurst 1998).

Regio	Habitat	Study site	Source	Spatial	Monthly / bimonthly	Seasonal	Circum-diurnal	Hydromedusa	Ctenophora	Polychaeta	Chaetognatha	Copepoda	Nebaliacea	Euphausiacea	Decapoda	Mysidacea	Cumacea	Amphipoda	Isopoda	Tanaidacea	Pycnogonida	Pisces
ATLANTIC POLAR BIOME																						
Siberian Arctic																						
	shelf / slope / deep sea	Laptev Sea	Sirenko *et al.* (1996)	*				*		*	*	*		*	*	*	*	*	*	*	*	*
Greenland Sea																						
	shelf	Westwind Trough	Brandt (1995)	*												*	*	*	*	*		
	shelf / slope	off E Greenland	Brandt (1997a, b)	*												*	*	*	*	*		
	deep sea		Svavarsson *et al.* (1990)	*															*			
Iceland Sea																						
	ridge / slope	Kolbeinsey Ridge	Brandt (1993), Brandt & Piepenburg (1994)	*												*	*	*	*	*		
Norwegian Sea																						
	slope / deep sea		Svavarsson *et al.* (1990)	*															*			
	fjords / shelf	off Norway	Buhl-Jensen (1991)	*														*				
ATLANTIC COASTAL BIOME																						
E Atlantic																						
Northern North Sea																						
	fjords	Norway	Fosså & Brattegard (1990)	*												*						
Skagerrak																						
	fjords	Sweden	Buhl-Jensen & Fosså (1991)	*	*										*	*		*				
Baltic Sea																						
	coastal	Kieler Bucht	Hesthagen (1973)			*	*	*			*	*		*	*	*	*	*	*		*	*
Central North Sea																						
	surf zone	Robin Hood's Bay	Colman & Segrove (1955)				*			*		*			*	*	*	*	*		*	
	shelf	Dogger Bank	this study (Chapter 1)	*				*	*	*	*	*	*	*	*	*	*	*	*		*	*
Southern North Sea																						
	estuary	Eems	Mees *et al.* (1995)	*							*				*	*		*	*			*
		Westerschelde	Mees *et al.* (1993b)	*		*				*	*	*			*	*	*	*	*		*	*
			Mees *et al.* (1993a)	*	*											*						
			Cattrijsse *et al.* (1993)	*	*														*	*		
			Mees & Hamerlynck (1992)	*											*	*	*	*	*			
			Mees *et al.* (1995)	*							*				*	*		*	*		*	*
			Beyst *et al.* (1999b)	*	*																	*
			this study (Chapter 4)	*				*	*		*	*			*	*		*	*		*	*
	lagoon	Oosterschelde	Mees & Hamerlynck (1992)	*											*	*						
	surf zone	Belgian beaches	Lock *et al.* (1999)				*	*	*	*	*	*			*	*	*	*	*			*
			Beyst *et al.* (in press a)	*	*			*	*	*	*	*		*	*	*	*	*	*		*	*
			Beyst & Mees (submitted)	*				*	*	*	*	*		*	*	*	*	*	*		*	*
			Beyst *et al.* (in press c)				*	*	*	*	*	*		*	*	*	*	*	*		*	*
	coastal	Voordelta	Hamerlynck & Mees (1991)	*	*					*	*	*		*	*	*	*	*	*		*	*
			Mees & Hamerlynck (1992)	*							*	*			*	*	*	*	*		*	
			Mees *et al.* (1993a)	*	*									*		*						
			Cattrijsse *et al.* (1993)	*	*														*	*		
			Beyst *et al.* (1999b)	*	*																	*
	coastal	off Zeeland	this study (Chapter 4)	*				*	*	*	*	*			*	*	*	*	*			*
	coastal / shelf	Frisian front	this study (Chapter 2)	*		*		*	*	*	*	*	*	*	*	*	*	*	*		*	*
	coastal / shelf	Belgian sandbanks	this study (Chapter 4)	*				*	*	*	*	*		*	*	*	*	*	*		*	*
			this study (Chapters 5 and 6)	*	*			*	*	*	*	*	*	*	*	*	*	*	*		*	*
			unpublished data (A. Dewicke)	*			*	*	*	*	*	*		*	*	*	*	*	*		*	*
English Channel																						
	estuary	Seine	Mouny *et al.* (1996)	*		*		*	*	*	*	*			*	*	*	*	*			*
			Mouny *et al.* (2000)	*	*				*		*					*	*	*	*			*
			Dauvin *et al.* (2000)	*	*		*								*	*	*	*	*			*
	coastal / shelf	N France	Dauvin *et al.* (1994)		*		*						*		*	*	*	*	*		*	
			Vallet & Dauvin (1998)	*			*				*	*	*	*	*	*	*	*	*			*
			Vallet & Dauvin (1999)		*			*			*	*		*	*	*	*	*	*			*
			Zouhiri *et al.* (1998)	*	*		*									*						
			Vallet & Dauvin (1995)	*			*											*				
			Wang & Dauvin (1994)				*								*	*	*	*	*		*	
			Dauvin & Zouhiri (1996)	*			*						*		*	*	*	*	*			
			Wang *et al.* (1994)				*		*	*	*	*			*							*
			Dauvin *et al.* (2000)	*	*		*						*		*	*	*	*	*			*

Regio Habitat	Study site	Source	Spatial	Monthly / bimonthly	Seasonal	Circum-diurnal	Hydromedusa	Ctenophora	Polychaeta	Chaetognatha	Copepoda	Nebaliacea	Euphausiacea	Decapoda	Mysidacea	Cumacea	Amphipoda	Isopoda	Tanaidacea	Pycnogonida	Pisces
Irish Sea																					
surf zone	off Isle of Man	Fincham (1970)		*		*											*				
Bay of Biscay (5)																					
estuary	Gironde	Mees *et al.* (1995)	*							*				*	*		*	*			*
estuary	Guipuzcoa estuaries	San Vicente *et al.* (1993)	*											*	*	*	*	*			*
surf zone	S France	San Vicente & Sorbe (1993)	*											*	*	*	*	*	*		
		San Vicente & Sorbe (in press)		*								*	*	*	*	*	*	*	*	*	
coastal / shelf	S France	Sorbe (1982)	*										*	*	*	*	*	*		*	
		Sorbe (1989)	*	*								*	*	*	*	*	*	*		*	
		Cornet *et al.* (1983)	*										*	*	*	*	*	*		*	
coastal / shelf / slope	N Spain	Anadón (1993)	*												*						
shelf break / slope	Eperon Berthois	this study (Chapter 3)	*				*			*	*	*	*	*	*	*	*	*	*	*	*
slope	Cap Ferret area	Elizalde *et al.* (1993)	*											*	*	*	*	*	*	*	*
		Dauvin & Sorbe (1995)	*														*				
		Elizalde *et al.* (1991)	*												*						
		Sorbe & Weber (1995)	*									*	*	*	*	*	*	*	*	*	
slope / canyon	Cap Ferret area	Dauvin *et al.* (1995)	*										*	*	*	*	*	*	*	*	*
canyon	Cap Ferret canyon	Sorbe (1999)	*		*							*	*	*	*	*	*	*	*	*	*
slope / canyon	Cabreton area	Corbari & Sorbe (2001)	*										*	*	*	*	*	*	*	*	*
canyon	Cabreton canyon	Marquiegui & Sorbe (1999)	*										*	*	*	*	*	*	*		
NE Atlantic Ocean (off Portugal)																					
estuary	Mondego	Azeiteiro & Marques (1999)	*	*										*	*		*	*			*
lagoon	Ria de Aveiro	Cunha *et al.* (1999)	*	*											*	*	*	*	*		
lagoon	Ria Formosa	Lock & Mees (1999)	*											*	*	*	*	*	*		*
shelf / shelf break	off N Portugal	Cunha *et al.* (1997)	*									*	*	*	*	*	*	*	*	*	*
W ATLANTIC																					
NW Atlantic																					
shelf	Browns Bank	Wildish *et al.* 1992	*				*			*	*		*	*	*	*	*	*	*		
shelf	Bay of Fundy, Gulf of St. Lawrence	Chevrier *et al.* 1991	*	*		*							*	*	*	*	*	*	*		
shelf	Gulf of St. Lawrence	Sainte-Marie & Brunel 1985	*	*		*											*				
SW Atlantic																					
lagoon	Cananeia lagoon (Brazil)	Tararam *et al.* (1996)	*	*										*	*	*	*	*	*		*
ATLANTIC WESTERLY WINDS BIOME																					
Meditterranean																					
surf zone	Catalan Sea	San Vicente & Sorbe (1993)	*								*		*	*	*	*	*	*	*	*	
		Munilla & Corrales (1995)	*				*				*			*	*	*	*	*			
		Munilla *et al.* (1998)	*								*		*	*	*	*	*	*	*	*	*
		San Vicente & Sorbe (1999)		*									*	*	*	*	*	*	*	*	
		San Vicente & Munilla (2000)	*												*						
		Munilla & San Vicente (2000)	*	*																*	
		San Vicente & Sorbe (in press)		*								*	*	*	*	*	*	*	*	*	
slope / canyon	Catalan Sea and La Merenguera Canyon	Cartes (1998)	*		*		*		*	*	*	*	*	*	*	*	*			*	*
		Cartes *et al.* (1994)	*		*								*	*							
		Cartes & Sorbe (1997)	*		*											*					
		Cartes & Sorbe (1996)	*	*												*					
		Cartes & Sorbe (1995)	*		*										*						
		Cartes & Sorbe (1999)	*		*												*				
ANTARCTIC WESTERLY WINDS BIOME AND ANTARCTIC POLAR BIOME																					
Beagle Channel (Patagonia)																					
shelf		Brandt *et al.* (1997)	*												*	*	*	*	*		
South Shetland Islands & Bransfield Strait																					
shelf		San Vicente *et al.* (1997)	*									*	*	*	*	*	*	*	*	*	

Study area

The North Sea is a relatively shallow (average depth of 90 m) semi-enclosed sea and has a temperate climate (Ducrotoy *et al.* 2000). The water of this shallow North Sea consists of a varying mixture of North Atlantic water and fresh-water runoff (Fig. 2A). The southern North Sea is influenced by a combination of water masses: (1) warmer waters originating from the Channel; (2) an inflow from the region between the Shetland and Orkney Islands (Fair Isle Current), with one branch running southwards and then east along the 100 m contour (Dooley Current); (3) a second southerly flowing branch, to the south of this 100 meter contour, along the English coast which meets the Channel inflow water (Lee 1980). Summer temperature stratification is established over large areas of the North Sea (Tomczak & Goedecke 1964). The water is vertically well mixed all year round, especially along the continental coast but to a certain extent also across the Dogger Bank (Tomczak & Goedecke 1964). At the boundary between well-mixed and stratified waters, tidal fronts occur, running in a series of almost fixed geographical locations and characteristic for the summer regime on the northwest European continental shelf (Simpson *et al.* 1978; Bowers & Simpson 1987; van Aken *et al.* 1987; Bo Pedersen 1994; Tett & Walne 1995) (Fig. 2B). Fronts are important because they may restrict horizontal dispersion and are believed to conspicuously enhance biological activity in their environs (Nielsen *et al.* 1993; Bo Pedersen 1994; Richardson & Bo Pedersen 1998; Richardson *et al.* 1998).

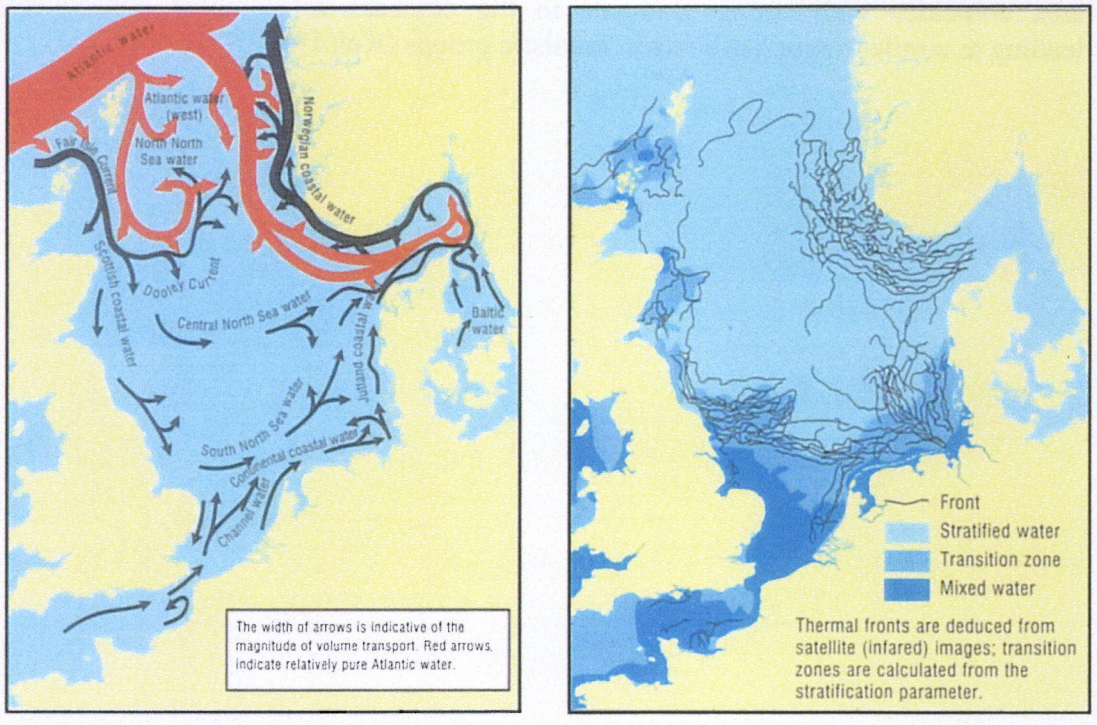

Fig. 2. (A) Schematic diagram of general circulation in the North Sea (source: after Turrell (1992), in OSPAR Commission 2000). **(B)** Transition zones between mixed and stratified water in the North Sea (source: after Becker (1990), in OSPAR Commission 2000).

This southern North Sea was the focus of the present study (see Fig. 1). Two working areas were selected at the transition between mixed and stratified water masses in order to cover this frontal boundary area. Although the **Dogger Bank** is located in the central North Sea it borders the southern North Sea to the north. This vast, submerged sandbank is regarded as a special ecological region (Kröncke & Knust 1995). Phytoplankton production is nearly continuous throughout the year related with near-stable abundances for macrofauna and fish. The Dogger Bank (between 18 and 40 m depth) has a significant impact on the circulation in the central and southern North Sea and is an important fishing area moreover (OSPAR Commission 2000). The **Frisian front** (located off the northwest Dutch coast at the boundary between the Southern Bight and the Oyster Ground) approximately coincides with the position of the summer tidal mixing front and has very particular characteristics regarding its benthic community (Creutzberg 1985). High sedimentation of organic matter occurs in the area leading to an enriched bottom fauna (Baars *et al.* 1991).

The main working area for this study however was the **Belgian continental shelf**. This area is characterised by numerous linear subtidal sandbanks, reflected as sets of parallel groups. Their close position to the coastline and the shallowness of the area make them unique, both from an ecological as well as from a geological point of view. The continuous interaction between morpho- and hydrodynamics results in a complex heterogeneous structure, generating a variety of habitats for marine life. It has additionally often been hypothesized that the protective character of these sandbank systems possibly sustains a nursery function for several fish and crustacean species (Dyer & Huntley 1999).

Towards the south, the hyperbenthos was studied along the **shelf break and upper continental slope** delineating the continental shelf from the deep sea. This area coincides with strong gradients in the physical environment consequently leading to similar major gradients in faunistic groups (Rex 1981).

Objectives

The hyperbenthic community of the Dogger Bank is dealt with in **Chapter 1**. This chapter aimed to describe the hyperbenthic fauna along a south-to-north transect across the Dogger Bank by considering species composition, density, biomass, and diversity. The following topics are discussed: (1) the presence of a distinct fauna in the hyperbenthal zone with its endemics, and a particular transition from the benthic to the pelagic realm; (2) the distribution of the fauna in relation to the environment on a small and large spatial scale; (3) the possible influence of the North Sea tidal mixing front during summer.

The Frisian front hyperbenthos was sampled twice, during August 1994 and April 1996 (**Chapter 2**). The aims of this study were (1) to describe the hyperbenthic fauna of the Frisian front during an early spring and summer situation in terms of species composition, density, biomass, and diversity; (2) to investigate structural characteristics of the hyperbenthic community along a cross-frontal gradient in order to discover a possible shift in community structure at the Frisian front.

The hyperbenthic community at the shelf break and upper continental slope is discussed in **Chapter 3**. For this aim, the northern edge of the Bay of Biscay (Eperon Berthois) was selected as working site. Taxonomic composition, density, biomass and species diversity were examined. It is obvious that this approach focuses on hyperbenthic community structure in relation to the bathymetric gradient.

To provide a baseline study for the characterisation of the hyperbenthic communities inhabiting the subtidal waters of the Belgian continental shelf, an extensive spatial study (62 sites) was performed in September 1993. A depth-integrated sampling was carried out, covering the main sandbank sets in the area: the Coastal Banks, the Flemish Banks, the Hinder Banks, and the Zeeland Banks. Also included in the sampling design were the marine and brackish waters of the Westerschelde estuary, and the part of the Zeeland Banks, extending on the Dutch continental shelf. An elaborate ecological description of the hyperbenthic communities thriving in the area is given and their major structuring gradients are discussed (**Chapter 4**). The following questions were addressed in this chapter: (1) What species are present in the hyperbenthal zone?; (2) What about the spatial structure of the hyperbenthic community in terms of species composition, density, biomass, and diversity?; (3) Is there a relationship between community structure and the identified environmental gradients on the Belgian continental shelf?

Chapter 5 focuses on the temporal occurrence of holo- and merohyperbenthic taxa in the Belgian coastal area. Monthly sampling was carried out from September 1994 until December 1995. Besides a temporal description, emphasis is specifically laid on different biotopes of the studied area. The presented data is unique in the sense that the sites covered an onshore-offshore gradient and an alongshore gradient (related to estuarine outflow). The final discussion goes beyond the studied area focusing on remarkable differences with the hyperbenthos of surrounding biotopes such as the shallow Dutch delta area, the adjacent surf zone, and the Westerschelde estuary, including its salt marshes.

The relation between the spatio-temporal community structure of the hyperbenthos and the environmental characteristics in the Belgian coastal area, are the scope of **Chapter 6**. Special emphasis has here been put on the particular relation with the prevailing hydrodynamic characteristics of the area, such as tidal and residual currents. Respons to physico-chemical variables has mainly been discussed in Chapter 4, but are considered here as well.

Approach

Working definition

The benthic boundary layer relates to the immediate physical environment of the benthos, a term applied for the entire bottom community (McCave 1976). Its fauna consists of endobenthic (living in the bottom), epibenthic (living on the bottom), and hyperbenthic organisms, classified according to their position relative to the sea floor (Pearson & Rosenberg 1987; Mees & Jones 1997). The hyperbenthos is defined as the association of small animals living in the water layer close to the seabed (Mees & Jones 1997). It includes endemic species, planktonic species derived from downwards extensions, and endo-or epibenthic species that emerge into the water column (Mees & Jones 1997). This study's approach is to assess the fauna of the hyperbenthal zone (i.e. the zone occupied by the hyperbenthos) as an ecological entity at the interface between the benthic and pelagic realm. Thus, rather than to focus on specific taxa, the entire hyperbenthic community is considered, i.e. all small animals swimming in the vicinity of the seabed.

The applied study's working definition therefore categorizes the hyperbenthos as all animals caught with the Sorbe-hyperbenthic sledge (see further), with a size range between 1 and 20 mm (Fig. 3). The **holohyperbenthos** consists of small animals that spend variable periods of their adult life in the hyperbenthal zone (Mees & Jones 1997). Most abundant holohyperbenthic taxa are mysids, amphipods, isopods, copepods, and chaetognaths. The term **merohyperbenthos** is applied for the early life history stages of species that subsequently recruit to the nekton, epibenthos, and endobenthos communities (Mees & Hamerlynck 1991). Caridean shrimps, brachyuran crabs, postlarval fish and polychaete larvae are most common.

As a general rule, all animals larger than approximately 20 mm (see Table 2 for details) and animals manifestly belonging to the endo- or epibenthos (attached organisms and animals being strictly buried in, or sitting onto the bottom) were considered as non-hyperbenthos (see Table 2). Most of these animals were rather occasionally caught and were removed from all analyses. For juvenile and adult polychaetes it was more difficult to decide upon, as they are generally burrowing, but might spend some time swimming in the water column. Yet, they were poorly caught, except in few cases when the catch was slightly contaminated by touching a sand ripple or some mud from the bottom. These catches could be distinguished, as we experienced the presence of other endobenthic organisms. Therefore, it was decided to exclude all polychaetes (apart form larval stages or real planktonic taxa).

To avoid confusion in ecological terminology, definitions as applied through the text of this study are listed in Appendix 1. The reader is also referred to this Appendix for the applied definitions of (1) marine biotic communities (2) the delineation of marine depth zones and classification of habitats.

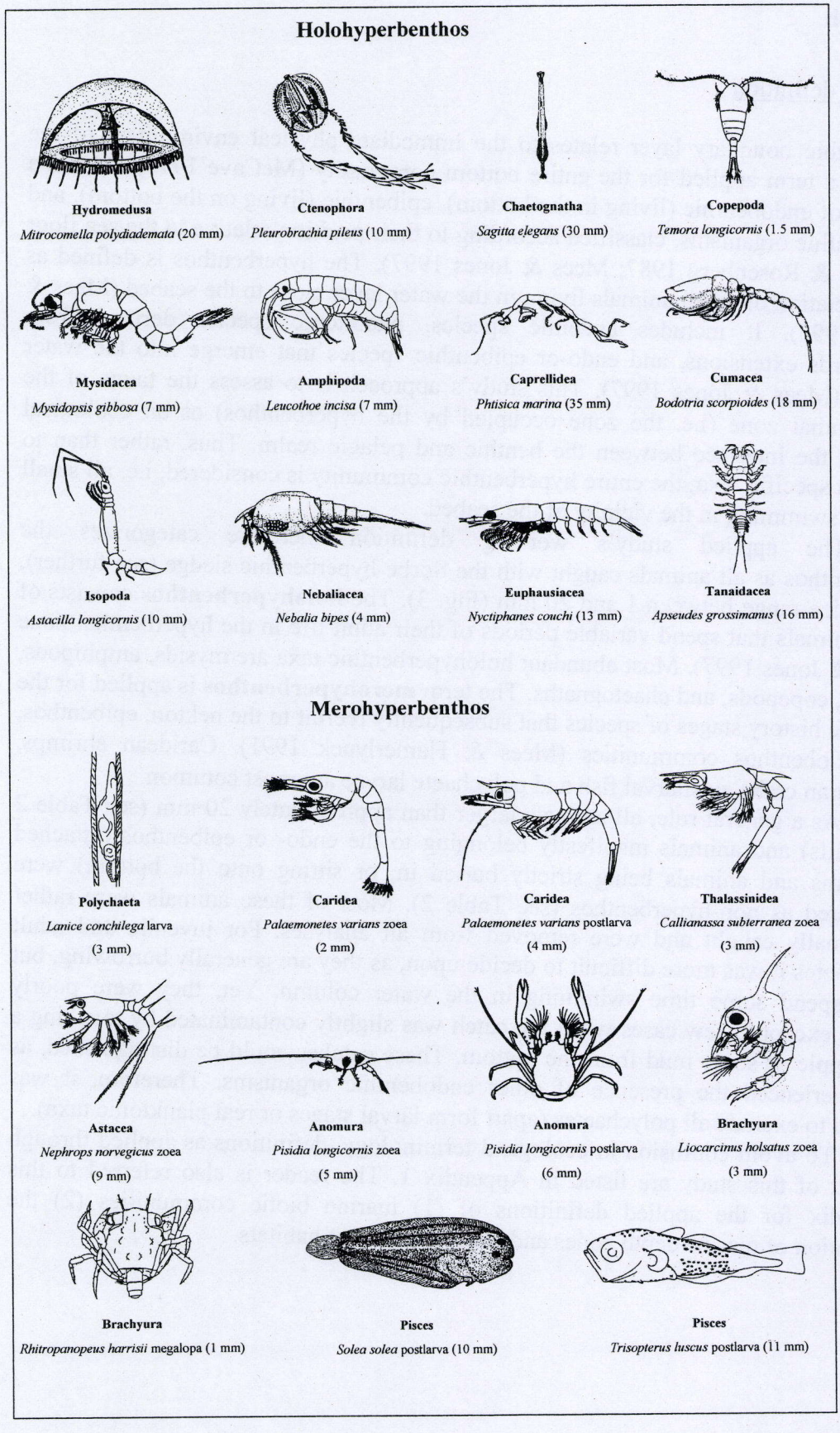

Fig. 3. Illustration of the major taxonomic groups belonging to the holohyperbenthos (top) and merohyperbenthos (bottom), most of the presented species were commonly encountered during this study.

Table 2. List of all major taxa caught during this study with details for their different life history stages. Indication of holohyperbenthos (H), merohyperbenthos (M) and taxa considered as non-hyperbenthos (N). The frequency of occurrence (F) of non-hyperbenthic taxa is classified as common (C), occasional (O) or rare (R).

Systematic taxon	Life stage	H	M	N	F	Common name
Phylum Porifera	adult			N	R	sponge
Phylum Cnidaria						
Subphylum Anthozoaria						
Superclassis Anthozoa	polyp			N	R	coral, sea anemone
Subphylum Medusozoa						
Superclassis Scyphozoa	medusa			N	R	jellyfish
Superclassis Hydrozoa						
Classis Siphonophora	colony			N	R	
Classis Hydroidomedusae	hydromedusa	H				hydromedusa
	polyp			N	O	
Phylum Ctenophora	juvenile, adult	H				comb jelly
Phylum Echinodermata						
Classis Asteroidea	juvenile, adult			N	O	sea star
Classis Ophiuroidea	juvenile, adult			N	O	brittle star
Classis Echinoidea	juvenile, adult			N	R	sea urchin
Classis Holothuroidea	juvenile, adult			N	R	sea cucumber
Classis Crinoidea	juvenile, adult			N	R	feather star
Phylum Nematoda	adult			N	R	roundworm
Phylum Nemertinea	adult			N	R	ribbonworm
Phylum Annelida						
Classis Polychaeta	larva		M			
	juvenile, adult			N	O	
	exception: Tomopteridae (planktonic)	H				
Classis Oligochaeta	adult			N	R	
Classis Hirudinea	adult			N	R	leech
Phylum Chaetognatha	juvenile, adult		H			arrowworm
Phylum Brachiopoda	adult			N	R	lamp shell
Phylum Bryozoa	stolon			N	R	moss animal
Phylum Mollusca						
Classis Gastropoda						snail
Subclassis Prosobranchia	juvenile, adult			N	O	
Subclassis Opisthobranchia						
Ordo Gymnosomata	adult	H				naked pteropod
Ordo Nudibranchia	juvenile, adult	H				sea slug
Classis Bivalvia	juvenile, adult			N	O	
Classis Cephalopoda	juvenile (< 1 cm)		M			
	adult (> 1 cm)			N	R	
	exception: *Sepiola atlantica* (adult < 3 cm)	H				
Phylum Arthropoda						
Subphylum Crustacea						
Classis Copepoda						
Ordo Calanoida	adult	H				
Ordo Siphonostomatoida	adult (Caligidae)			N	O	
Classis Cirripedia	adult			N	R	barnacle
Classis Malacostraca						
Subclassis Phyllocarida						
Ordo Nebaliacea	juvenile, adult	H				
Subclassis Eumalacostraca						
Superordo Eucarida						
Ordo Euphausiacea	juvenile, adult	H				krill
Ordo Decapoda						
Infraordo Penaeidea	zoea	M				prawn

Systematic taxon	Life stage	H	M	N	F	Common name
	postlarva (< 10 mm)	M				
	juvenile, adult (> 10 mm)			N	R	
Infraordo Caridea	zoea		M			shrimp
	postlarva (< 10 mm)		M			
	juvenile, adult (> 10 mm)			N	C	
Infraordo Astacidea	zoea		M			lobster
	postlarva (< 10 mm)		M			
	juvenile, adult (> 10 mm)			N	R	
Infraordo Thalassinidea	zoea		M			
	postlarva		M			
	juvenile, adult			N	R	
Infraordo Anomura	zoea		M			hermit crab, porcelain
	postlarva		M			
	juvenile, adult			N	O	
Infraordo Brachyura	zoea		M			true crab
	megalopa		M			
	juvenile, adult			N	O	
Superordo Peracarida						
Ordo Mysidacea	juvenile, adult	H				mysid, opossum shrimp
Ordo Cumacea	juvenile, adult	H				
Ordo Amphipoda	juvenile, adult	H				
Ordo Isopoda	juvenile, adult	H				
	exception: *Prodajus ostendensis*, Cymothoidae (parasites)			N		
Ordo Tanaidacea	juvenile, adult	H				
Subphylum Chelicerata						
Classis Pycnogonida	juvenile, adult	H				sea spider
Phylum Hemichordata						
Classis Enteropneusta	larva		M			acorn worm
Phylum Chordata						
Subphylum Urochordata						
Classis Ascidiacea	adult			N	R	sea squirt
Classis Thaliacea	adult			N	R	salp
Subphylum Vertebrata						
Classis Actinopterygii (Pisces)	fish egg			N		
	in general: postlarva (< 20 mm)		M			
	others: postlarvae of Ammodytidae (< 60 mm), Clupeidae (< 40 mm), Syngnathidae (< 70 mm)		M			
	juvenile, adult (>20 mm) (mainly gobies)			N	C	
	exception: *Diplecogaster bimaculata* (adult < 40 mm)	H				

Methodology

Sampling methodology was standardised by daytime sampling and by consistently using the same gear for each field campaign. Spatial patterns for each study area were assessed during a late-summer sampling. Sampling was always carried out from the *RV* Belgica.

A modified hyperbenthic sledge after Sorbe (1983) was used, designed to collect the fauna of the lower 100 cm of the water column (Fig. 4). The sledge is 301 cm long, 169 cm wide, and 137 cm high; total weight is approximately 500 kg. The floats on top of the sledge keep it in an upright position. Although slightly curved, the sloping slide in front of the sledge, is as close as possible in contact with the bottom, therefore permitting sampling of the lowermost water stratum adjacent to the sea floor. Two pairs of nets (3 m long) were mounted next to each other. Mesh sizes of the two superimposed nets to the left were 1 mm, while only 0.5 mm to the right.

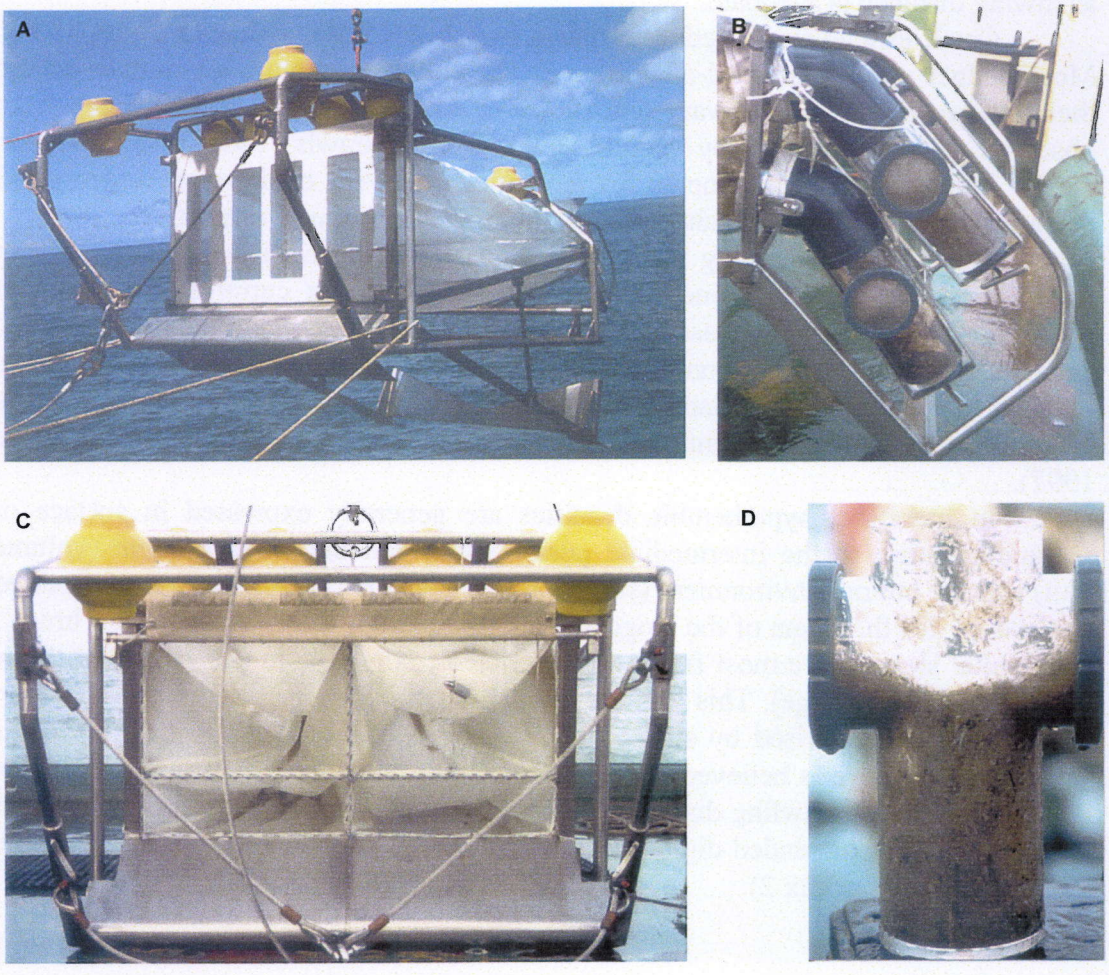

Fig. 4. The hyperbenthic sledge (Sorbe 1983). **(A)** Closed blind when floating in the water column; **(B)** the collectors mounted to each net; **(C)** the sledge with open blind when in contact with the bottom; **(D)** collector with catch (see text for explanation).

The lower nets sample the hyperbenthal zone from 0 to 50 cm above the sea floor while the upper nets cover the adjacent stratum from 50 to 100 cm. The collector (provided with lateral openings covered with a 0.5 mm gaze) of each net is fixed onto the sledge's frame along an angle of 45 ° (Fig. 4B). This prevents the collected fauna to escape (by swimming back) or to get damaged by the strong flow. An opening mechanism automatically operates when touching the bottom, preventing contamination by upper water strata (Fig. 4A and 4C). An odometer (registering the towing distance) and a flow meter (for calculating the volume of water filtered through the nets) were also installed.

The hyperbenthic sledge was consistently towed at an average ship speed of 1.5 knot relative to the sea floor and against the current (except at the shelf break sites). Towing duration was standardized to 5 minutes, yet for certain campaigns asking high sampling effort (Bay of Biscay, Dogger Bank) or when catches were poor (Frisian front in April 1996), sampling duration was doubled to 10 minutes.

No replicate sampling was performed. Replicability of hyperbenthic sledges was tested by different authors (Hesthagen & Gjermunsen 1978; Schnack 1978; Brattegard & Fosså 1991) concluding that samples are highly representative as long as towing distance is adequate.

Catch efficiency of sledges remains largely unknown (Mees & Jones 1997). Most sledges are at best semi-quantitative. The ability to capture all animals within their sweep, might largely vary among taxa. As an example, mysids have been observed to avoid capture by swimming in front of trawls (Lasenby & Sherman 1991). Therefore, no adjustments for net efficiency were made. Consequently, all densities and biomass values should be considered as minimum estimates.

Standardized sampling for hyperbenthos is mostly carried out with 0.5 mm mesh size nets (Mees & Jones 1997). Due to the strong currents and turbulent conditions in the Belgian coast however, the 0.5 mm nets were regularly detached during sampling. The additional high load of suspended matter in the area may have resulted in reduced filter capacity. It was therefore decided on to only examine the samples derived from the 1 mm net, being acceptable in such cases (Mees & Jones 1997).

In literature, hyperbenthic densities are generally expressed in surface or volume, relating to the intermediate position between the water column (volume unit) and the bottom environment (surface unit). Densities in this study are expressed per 100 m^2 for the fauna of the Dogger Bank, the Frisian front, and the shelf break / continental slope, since most fauna was restricted to the bottom (i.e. caught with the lower nets of the sledge). This was not as such for the Belgian coast fauna however. This area is characterised by strong tidal variations in current strength in space as well as in time; it was believed to be more accurate to express densities per volume unit. Still, both the trawling distance as the volume of water filtered through the nets is included in the appended digital database, allowing conversion from one unit into the other (see Appendix 2).

Chapter 1. The hyperbenthos of the Dogger Bank (North Sea)

Ann Dewicke, Jan Mees & Magda Vincx

Summary

Despite intensive research carried out on the North Sea, the hyperbenthos (the fauna living in the near-bottom water layer) has rarely been examined. This study therefore aims to describe the hyperbenthic community structure of the Dogger Bank - an offshore North Sea area - along a south-to-north transect, covering water masses on the most shallow part of the sandbank itself and from its deeper surroundings. Nine stations were sampled with a sledge in August 1994. The hyperbenthal zone (the lower 100 cm above the sea floor) was shown to harbour a diverse and characteristic fauna. A total of 158 species was caught, belonging to at least 28 orders. Amphipods and mysids were the most abundant taxa.

The total density of the holohyperbenthos (small animals occurring as adults in the hyperbenthal zone) ranged from 47 to 3681 ind. 100 m^{-2} and peaked in the deepest areas. Highly motile species such as the mysids *Schistomysis ornata* and *Erythrops elegans* reached highest densities on muddy substrata, supposedly due to a benefit in food supply. These species dominated the community both to the north as well as to the south of the Dogger Bank, together with a number of detritivorous amphipods and cumaceans. North of the Dogger Bank, the fauna was much more diverse and species composition differed drastically, mainly due to the appearance of boreal species.

Merohyperbenthic species (mainly larval decapods and postlarval fish) attained prominent density peaks (maximum of 1350 ind. 100 m^{-2}) at the northern shallow part of the Dogger Bank itself, except for postlarval Caridea. Brachyura larvae were the most abundant. This increase in density coincided with a drop in surface temperature and salinity, presumably due to the intrusion of a water mass from coastal origin. A possible relationship between the observed pattern in community structure of the hyperbenthos and the summer tidal mixing front occurring in the area, is discussed.

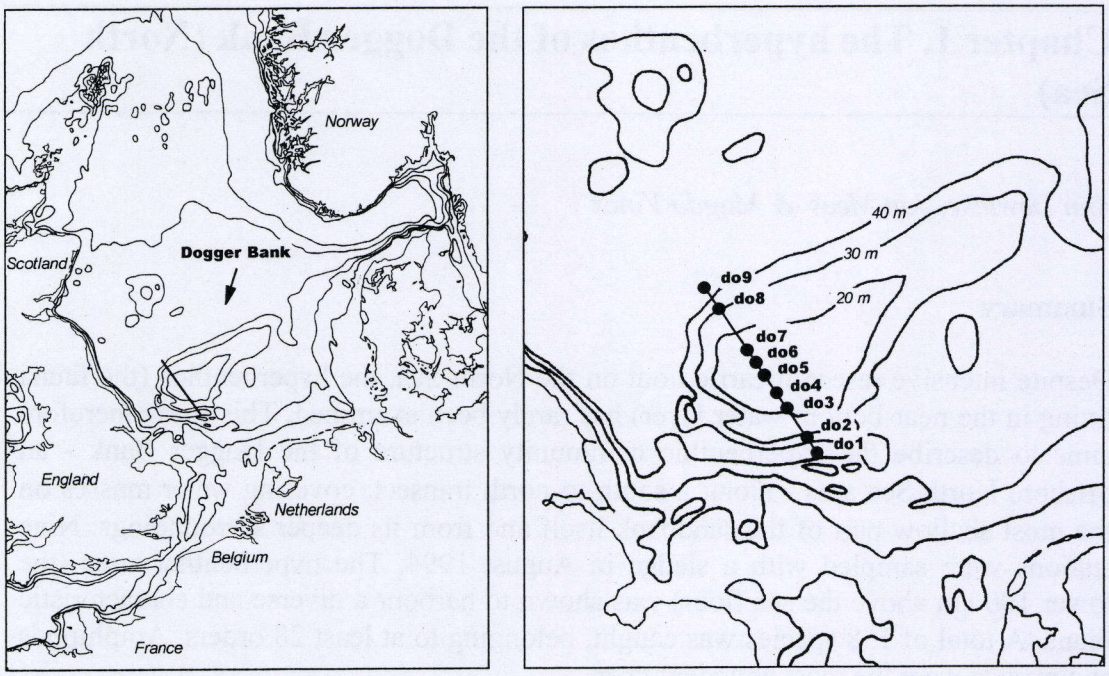

Fig. 1. Study area and position of sampling sites along the transect across the Dogger Bank.

Site	do1	do2	do3	do4	do5	do6	do7	do8	do9
Longitude E	2° 35'	2° 27'	2° 17'	2° 08'	2° 00'	1° 54'	1° 47'	1° 35'	1° 15'
Latitude N	54° 09'	54°16'	54° 28'	54° 35'	54° 43'	54° 49'	54° 55'	55° 12'	55° 22
Distance from do1 (km)	0	12	35	47	61	71	81	113	130
Distance trawled (m)	410	408	446	292	388	407	395	352	341
Volume filtered (m^3)	154	153	168	162	159	134	139	117	98
Depth (m)	58	27	15	20	32	28	26	37	70
Surface temperature (°C)	16.87	16.62	16.57	16.6	16.25	16.03	15.53	14.66	15.26
Surface salinity (psu)	34.79	34.76	34.75	34.75	34.7	34.67	34.58	34.5	34.65
Median grain size (µm)	97	201	177	331	217	170	188	204	185
Mud (%)	24.3	2.1	0.0	1.3	4.1	3.9	0.0	0.0	21.1
Very fine sand (%)	50.1	5.2	12.1	4.1	14.0	12.5	8.9	3.8	15.7
Fine sand (%)	19.7	69.0	72.2	26.6	38.7	73.1	71.8	71.4	26.3
Medium sand (%)	4.3	22.9	14.9	38.7	27.0	10.3	18.6	22.9	32.8
Coarse sand (%)	1.6	0.7	0.8	29.3	16.2	0.2	0.7	1.8	4.1

Table 1. Geographical coordinates and values of the measured environmental variables for each site.

Introduction

The Dogger Bank is a shallow region in the southern central North Sea and used to be dry land during the last glaciation (8000 years ago). This shallow area now extends over 300 km with a depth between 18 and 40 m. Kröncke & Knust (1995) reviewed the current knowledge about the Dogger Bank and emphasized the special ecological character of the region. The biology of this shallow system is in many ways quite different from other North Sea areas, such as the nearly continuous phytoplankton production throughout the year, connected with a low periodicity in macrofaunal abundance. Additionally, the Dogger Bank seems to be affected by eutrophication and pollution levels that are exceptional for offshore regions (Kröncke & Knust 1995).

The hydrography of the area is characterized by a complex regime of currents and eddies, forced by the counter clockwise residual currents of the North Sea (Kröncke & Knust 1995). During summer, the Dogger Bank is influenced by mixed water masses from the south (through the Channel) and by stratified water masses from the north, both meeting and mixing in this area (Nielsen *et al.* 1993; Bo Pedersen 1994). At the boundary between well mixed and stratified waters, bottom fronts develop off the Dogger Bank as a part of an extended frontal zone running from west to east across the North Sea (i.e. the North Sea tidal mixing front) (Simpson *et al.* 1978; Bowers & Simpson 1987; van Aken *et al.* 1987; Bo Pedersen 1994; Tett & Walne 1995). These fronts enhance new production (Nielsen *et al.* 1993; Richardson & Bo Pedersen 1998; Richardson *et al.* 1998) supposedly driving the productive fisheries in the Dogger Bank area (e.g. Nielsen *et al.* 1993; Nielsen & Sabatini 1996).

Because of its outstanding features and its importance for fisheries the area has been put forward as a potential location for the establishment of a Marine Protected Area within the OSPAR framework (Berry 1999).

Although several studies have already contributed to the ecological knowledge of the Dogger Bank, the hyperbenthos is still largely unknown, except for some early collections in the search to describe new species. The hyperbenthos is the association of small animals living in the water layer close to the seabed (Mees & Jones 1997). They are carnivorous, herbivorous or omnivorous feeders and are consumed by a variety of organisms (Mees & Jones 1997). Their importance in the diet of juvenile demersal fish and adult shrimp has been emphasized by several authors (Mauchline 1980; Hamerlynck & Hostens 1993; Mees & Jones 1997; Beyst *et al.* 1999a; Hostens & Mees 1999; Pedersen 1999; Oh *et al.* 2001). This study is the first to consider the hyperbenthic community for an offshore North Sea region and contributes to fill the gap in knowledge on the biodiversity of the area.

The aims of the present study are to describe the hyperbenthic fauna along a south-to-north transect across the Dogger Bank by considering species composition, density, biomass and diversity. The following topics will be discussed: (1) the presence of a distinct fauna in the hyperbenthal zone with its endemics, and a transition between the benthic and pelagic realm; (2) the distribution of the fauna in relation to the environment on a small and large spatial scale; (3) the possible influence of the North Sea tidal mixing front occurring during summer in the Dogger Bank area.

Material and methods

Sampling

The hyperbenthos of the Dogger Bank area was sampled on 31 August 1994. Nine sites were selected (do1 to do9) along a south-to-north transect across the Dogger Bank, covering water masses from the most shallow area of the sandbank and its deeper surroundings. Sampling sites were more or less evenly spread over a total distance of 130 km. Their geographical position is shown in Fig. 1, geographical coordinates are listed in Table 1. Sampling was done from the *RV* Belgica with a modified hyperbenthic sledge after Sorbe (1983). Two superimposed nets (1 mm mesh size, 3 m long, 71 cm wide) were fixed on the sledge and sampled the water layer from 0 to 50 cm (lower net) and from 50 to 100 cm (upper net) above the sea-floor. The sledge was equipped with an opening-closing mechanism and an odometer (for details see Sorbe 1983). A flow meter (*Hydrobios 438-110*) was fixed in the upper net. All sampling was carried out during daytime. Towing lasted for 10 minutes, at an average ship speed of 1.5 knots relative to the sea floor and against the current. Average towing distance was 382 ± 15.4 m; the water volume filtered per net amounted to 143 ± 7.7 m^3.

The catches from the upper and lower net were rinsed separately over a 1 mm mesh size sieve and preserved in a buffered formaldehyde solution (7 % final concentration). The following environmental variables were continuously registered during the cruise: water depth, surface temperature and salinity (thermosalinograph *Sea-Bird SBE21*). Additionally, a box corer (*Reineck*) was lowered at each site and the upper 2 cm of the sediment were sampled for grain fraction analysis (particle size analyser *Coulter LS 100*) (Wentworth scale, Buchanan 1984). Median grain size and percentage mud (<63 µm, considered as the organic and inorganic fraction superimposed) were calculated for each site.

Data acquisition

After sorting out, all organisms were identified - if possible - to species level. For certain taxa, further classification was done based on the life history stage, such as zoea and megalopa or postlarva stage of decapods. All animals were counted on species and stage level. Certain specimens were reported on a higher taxonomic level (noted as 'spp.'); these taxa are further also called 'species'. *Calanus helgolandicus* and *C. finmarchicus* were lumped together as *Calanus* spp. Larval Processidae were probably exclusively a mixture of *Processa modica* and *P. nouveli* subsp. *holthuisi*. All Crangonidae zoeae, mainly being representatives of *Philocheras bispinosus* were reported on the family level. Only certain typical zoeae of Brachyura were identified, all other specimens were lumped as Brachyura spp. zoea, the majority belonging to the genus *Liocarcinus*.

Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans and from the tip of the lower jaw to the end of the notochord for fish larvae) and their biomass was derived from regressions relating standard length to Ash free Dry Weight (ADW). ADW was determined as the difference between dry weight (60 °C for 5 days) and ash weight (650 °C for 2 hours) for representative size distributions of the various species. For species caught in discrete life stages or occurring with a particular

length, an average biomass value was assigned per stage or per species. This value was determined by measuring the ADW of batches of animals belonging to a certain stage. Both the regressions and the assigned biomass values were partly determined using animals from this study and from previous research (Beyst *et al.* 1999a; A. Dewicke unpubl. data).

After identification and measurement, non-hyperbenthos representatives were removed from the 'catch-dataset' (i.e. all animals that were caught by the Sorbe-hyperbenthic sledge and which were retained on a 1 mm sieve). Juvenile and adult decapods and fish, polychaetes (except the planktonic Tomopteridae), scyphozoans, echinoderms, fish eggs and all strictly sedentary organisms were excluded (see Introduction). The holohyperbenthos comprises a group of taxa with a rather small adult habitus (generally smaller than 20 mm), like several peracarid orders (mysids, amhipods, cumaceans, isopods), copepods, chaetognaths and hydromedusae. The merohyperbenthos mainly consists of early life history stages of larger animals and is dominated by decapod larvae (< 10 mm) and fish larvae (< 20 mm). The resulting species list of all hyperbenthos is presented in Addendum. Density (see Addendum) and biomass data were calculated as numbers of individuals and as mg ADW per 100 m^{-2}.

Numerical analysis

Structural community characteristics from south to north were investigated by graphic presentations of total densities and biomasses and densities per taxon. Hill's diversity numbers N_0, N_1 and N_2 were calculated (Hill 1973). N_0 is equal to the number of species of the sample, N_1 is the inverted natural logarithm of the Shannon-Wiener diversity index and N_2 is the reciprocal of Simpson's dominance index. Hurlbert's modification of Sanders' rarefaction curves (Hurlbert 1971) was used to calculate diversity for standardized sample size: $E(S_{100})$ determines the expected number of species present in a sample of 100 individuals. Species reported on a higher taxon level were considered as 'a single species' if no other representative of the same taxon level was present or if they were distinctly different. Thus, diversity is considered as a minimum estimate.

The vertical distribution of organisms in the hyperbenthal layer was investigated by calculating the Bottom Association (BA) index: numbers of individuals caught in the lower net (0 to 50 cm stratum) divided by the total caught number (0 to 100 cm stratum) (modified after Elizalde *et al.* 1991). A high BA index means that organisms were mainly present in the lower net and thus indicates a closer association to the sea floor.

Additionally, raw density data (without species reduction) were fourth root transformed (Field *et al.* 1982; Legendre & Legendre 1998) and ordination techniques were performed, using the software package CANOCO 4 (ter Braak & Smilauer 1998). An exploratory Detrended Correspondence Analysis (DCA) was performed for estimating the gradient length of species turnover, which was 2.224 and 1.526 standard deviation units for holo- and merohyperbenthos, respectively. Linear methods were chosen for further analysis (see ter Braak & Prentice 1988; Van Wijngaarden *et al.* 1995). An indirect technique, Principal Components Analysis (PCA) was applied for detecting spatial trends in community structure for both datasets. Some ecologically meaningful environmental variables were passively added in the analyses. Furthermore, cluster analyses on the species densities were performed using the Bray-Curtis dissimilarity index (Bray & Curtis 1957), and

according to a group-average sorting algorithm (PC-ORD 4, McCune & Mefford 1999).

The non-parametric Mann-Whitney U-test and Kruskal-Wallis test were applied (Sokal & Rohlf 1995). Moreover, Spearman rank's correlation coefficient, r_s, was calculated between some variables (after transformation) and linear regression analysis was performed using an adjusted coefficient of determination (R^2_{adj}), as an index of fit (Sokal & Rohlf 1995).

Results

Species composition of the total hyperbenthos

A total of 158 species was recorded (Addendum), mainly representatives of the peracarid crustaceans (91 species). Amphipods (61 species) were the most diverse peracarid order. Other species rich orders among the Peracarida were the mysids and the cumaceans (both 14 species). Decapods were represented by 28 species and 14 postlarval fish were recorded. The high heterogeneity in the faunal composition of the hyperbenthos is illustrated in Table 2. At least 28 orders were present, belonging to 8 phyla.

Phylum	Classis	Ordo	# species
Cnidaria	Hydroidomedusae	Filifera	≤ 2
		(subclassis Leptomedusae)	≤ 2
		(subclassis Trachymedusae)	1
		(not identified)	1
Ctenophora	Tentaculata	Cydippida	1
Annelida	Polychaeta	Phyllodocida	≤ 1
		(not identified)	≤ 1
Chaetognatha	Sagittoidea	Monophragmophora	1
		Aphragmophora	1
Mollusca	Gastropoda	Nudibranchia	1
	Cephalopoda	Sepiida	1
		Teuthida	1
Arthropoda	Copepoda	Calanoida	≤ 6
	Malacostraca	Nebaliacea	1
		Euphausiacea	2
		Decapoda	≤ 28
		Mysidacea	14
		Cumacea	14
		Amphipoda	≤ 61
		Isopoda	2
	Pycnogonida		1
Hemichordata	Enteropneusta		≤ 1
Chordata	Actinopterygii	Clupeiformes	≤ 1
		Gadiformes	1
		Gasterosteiformes	≤ 1
		Scorpaeniformes	1
		Perciformes	≤ 6
		Pleuronectiformes	4

Table 2. Numbers of species caught per major taxonomic group, according to taxonomic hierarchy.

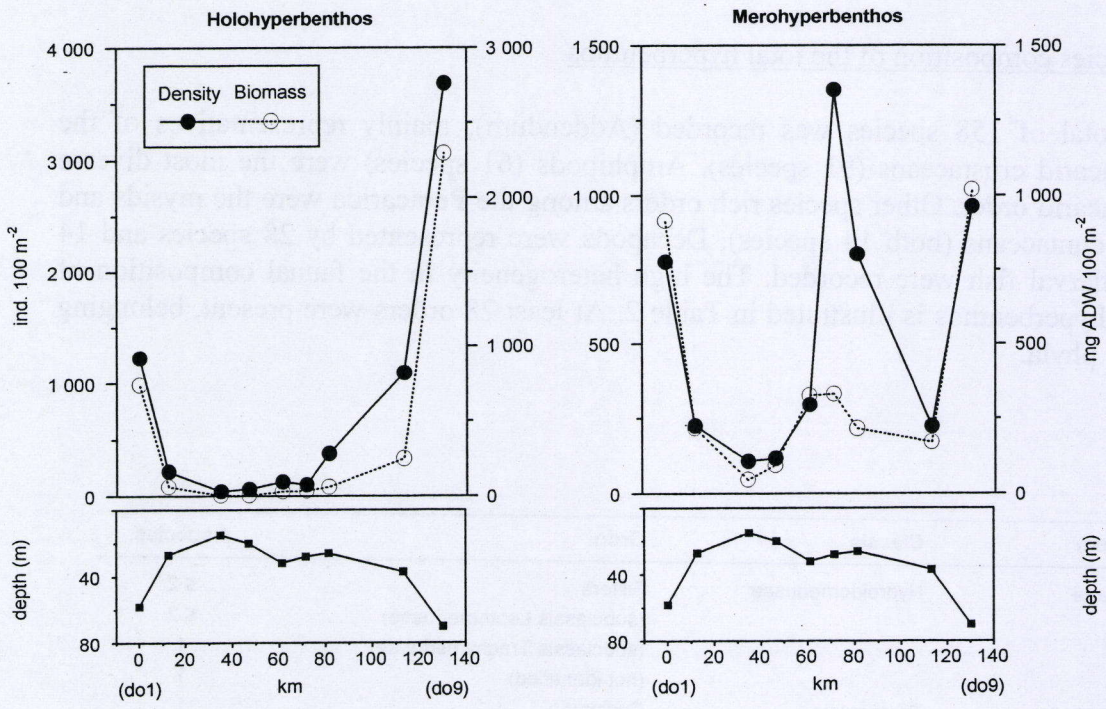

Fig 2. Absolute density (left axis) and biomass (right axis) for holohyperbenthos (left) and merohyperbenthos (right) along the sampled transect and presentation of the depth profile (bottom).

	do1	do2	do3	do4	do5	do6	do7	do8	do9
Holohyperbenthos									
N_0	55	37	27	28	34	29	38	40	82
N_1	14.9	15.3	15.1	7.7	8.1	18.2	12.0	4.9	25.1
N_2	9.9	9.4	10.6	3.4	3.7	13.1	7.4	2.3	15.5
$E(S_{100})$	20.9	22.1	23.1	19.0	20.8	23.2	19.1	13.9	29.1
Merohyperbenthos									
N_0	25	23	18	17	23	27	25	24	29
N_1	6.3	5.3	6.5	6.7	8.1	3.0	7.0	11.4	5.8
N_2	3.6	3.3	3.8	4.5	4.8	1.8	5.1	8.5	3.6
$E(S_{100})$	12.8	12.1	13.3	12.8	14.9	10.0	11.6	15.8	12.7

Table. 3. Hill's diversity numbers N_0, N_1 and N_2 and Hurlbert's expected number of species $E(S_{100})$ per site for holohyperbenthos **(top)** and merohyperbenthos **(bottom).**

Distribution along the south - to - north gradient

Total density, biomass and diversity

Total density (all hyperbenthos) per site ranged from 156 to 4644 ind. 100 m^{-2}. The density distribution along the transect for holo- and merohyperbenthos differed conspicuously (Fig. 2). Highest density for holohyperbenthos was reached at the deepest sites and reached its maximum north of the Dogger Bank (3681 ind. 100 m^{-2} at site do9). Abundances were very low (between 47 and 382 ind. 100 m^{-2}) at the sandbank itself (site do3 to do7). Linear regression analysis on the total holohyperbenthos density as a function of depth predicted 81 % (R^2_{adj} = 0.81, $p < 0.001$) of the observed variability (Fig. 3). A density incline with depth was also obvious for the merohyperbenthos (Fig. 2). This hyperbenthal fraction showed a more striking increase in density at the northern part of the sandbank itself and reached a maximum at site do6 (1350 ind. 100 m^{-2}).

Total biomass ranged from 55 to 3319 mg ADW 100 m^{-2} along the transect. Holohyperbenthos showed a similar biomass pattern as shown for its density and peaked at the deepest sites with a maximum value of 2299 mg ADW 100 m^{-2} at site do9 (Fig. 2). Highest biomasses did not coincide with highest densities for the merohyperbenthos, but were - as indicated for the holohyperbenthos - considerably higher at the deeper sites (max. 1020 mg ADW 100 m^{-2} at site do9).

In general, the holohyperbenthic fauna of the Dogger Bank was much more diverse than the merohyperbenthos. Average values for $E(S_{100})$ were 21.3 ± 1.37 and 12.9 ± 0.58, respectively (Table 3). Species richness (N_0) for holohyperbenthos peaked at the deepest sites and was especially high at site do9 (82 species). N_1 and N_2 varied considerably along the gradient. Unlike the first Hill number (N_0), the other diversity indices for site do1 were comparable to those reported for the sandbank itself. This was not the case for the most northern site (do9), which was more diverse than all other stations, judging from all diversity indices calculated. Such trend was not observed for the merohyperbenthos: species richness and diversity varied only slightly along the transect (Table 3).

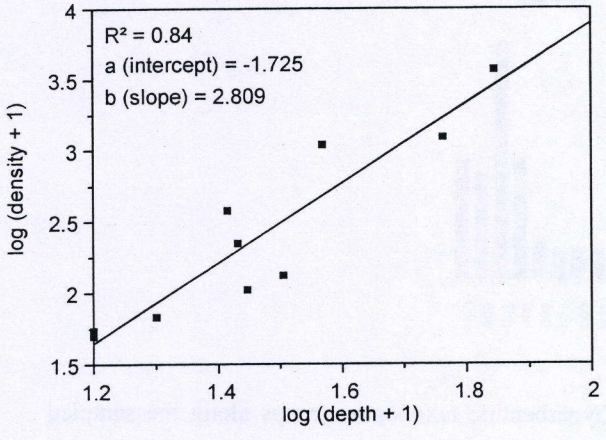

Fig. 3. Linear regression analysis of holohyperbenthos density versus depth (density expressed as ind. 100 m^{-2}, depth in m)

Distribution of major taxonomic groups

The density increase at the deeper sites was a general feature for the amphipods, mysids, cumaceans, chaetognaths, copepods, nudibranchs and euphausiids (Fig. 5). Amphipods and mysids dominated the holohyperbenthos in terms of density, with their highest values at the northernmost sites: 1519 ind. 100 m^{-2} at site do9 for amphipods and 810 ind. 100 m^{-2} at site do8 for mysids. Cumaceans were very abundant at site do9 (888 ind. 100 m^{-2}). These three together accounted for 83 % of the mean holohyperbenthic density. Nudibranchs and isopods were rather restricted to the northernmost sites. The abundance of hydromedusae and ctenophores was not related to depth. Hydromedusae were more frequently caught at the southernmost sites, whereas ctenophores were more abundant at the northern sites.

Total density distribution for the major merohyperbenthic taxa resulted from two distinct patterns (Fig. 4). The Caridea (mainly composed of postlarvae) were responsible for the high densities at the deepest sites (max. 762 ind. 100 m^{-2} at site do9). Brachyura, Thalassinidea, Anomura and Pisces on the other hand attained highest densities at the northern part of the Dogger Bank itself. Brachyurans dominated the merohyperbenthic fauna and a density peak of 1179 ind. 100 m^{-2} was recorded at site do6. Densities for the other taxa were much lower (always < 180 ind. 100 m^{-2} for each taxon). Thalassinidea and Anomura showed the same pattern and were most abundant at site do6, similarly as for Brachyura. Highest density for fish larvae was observed at site do5.

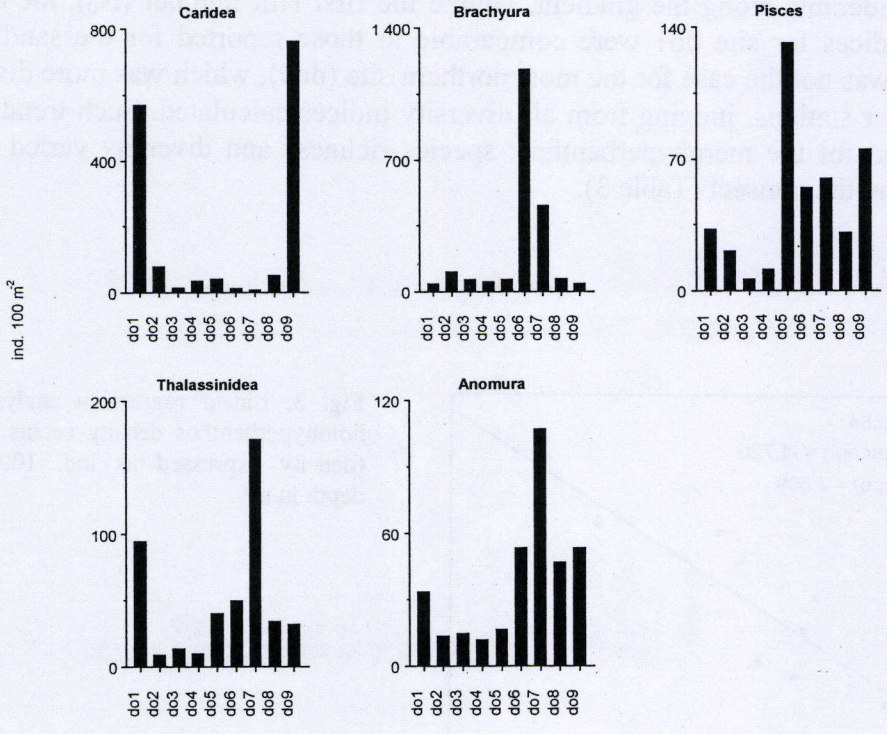

Fig. 4. Distribution patterns for the major merohyperbenthic taxonomic groups along the sampled transect.

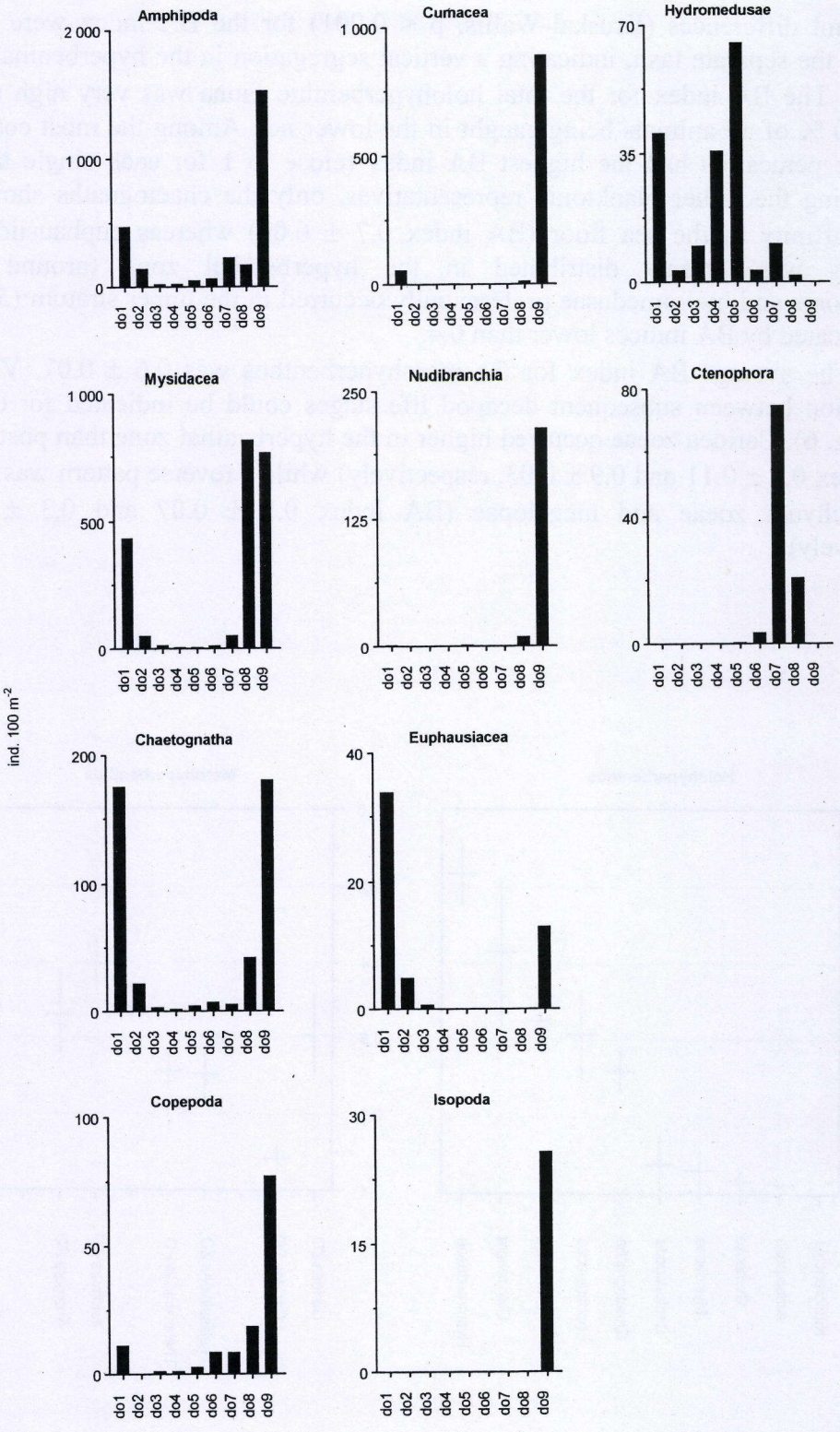

Fig. 5. Distribution patterns for the major holohyperbenthic taxonomic groups along the sampled transect.

Association with the sea floor

Significant differences (Kruskal-Wallis, $p < 0.001$) for the BA index were found between the separate taxa, indicating a vertical segregation in the hyperbenthal zone (Fig. 6). The BA index for the total holohyperbenthic fauna was very high (0.9 ± 0.02), 90 % of all animals being caught in the lower net. Among the most common taxa, the peracarids had the highest BA index (close to 1 for each single taxon). Concerning the rather planktonic representatives, only the chaetognaths showed a certain affinity to the sea floor (BA index 0.7 ± 0.06) whereas euphausiids and copepods were evenly distributed in the hyperbenthal zone (around 0.5). Ctenophores and hydromedusae preferentially occurred in the upper stratum (50-100 cm) indicated by BA indices lower than 0.4.

The average BA index for the merohyperbenthos was 0.6 ± 0.07. Vertical segregation between subsequent decapod life stages could be indicated for certain taxa (Fig. 6). Caridea zoeae occurred higher in the hyperbenthal zone than postlarvae (BA index 0.6 ± 0.11 and 0.9 ± 0.03, respectively) while a reverse pattern was found for Brachyura zoeae and megalopae (BA index 0.5 ± 0.07 and 0.3 ± 0.05, respectively).

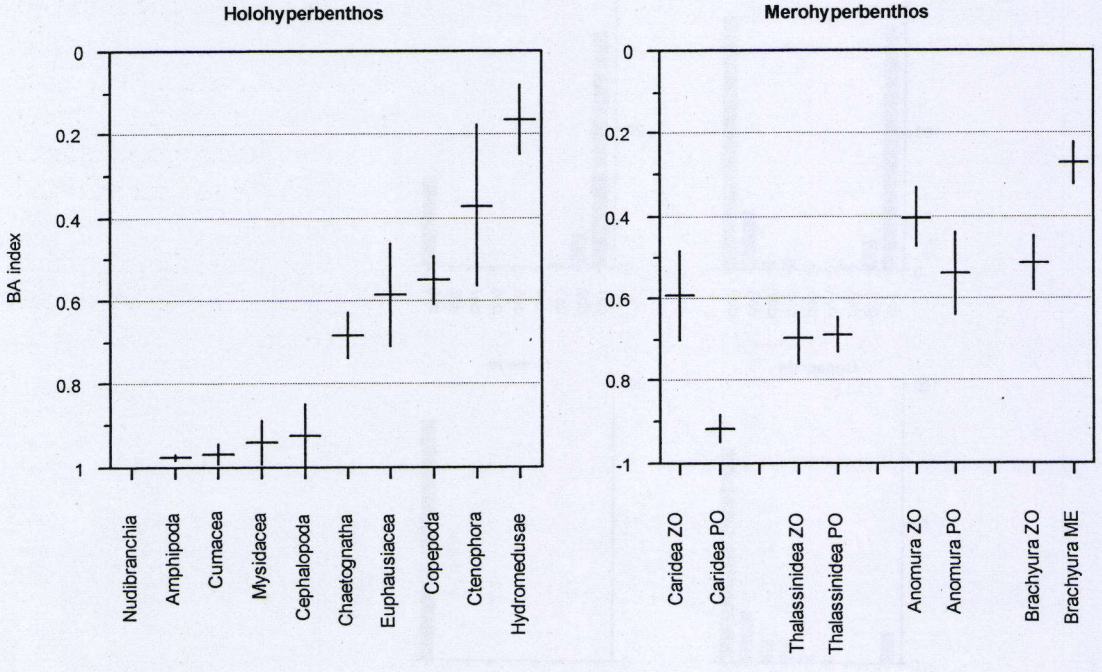

Fig. 6. Average BA index with standard error for the major holohyperbenthic taxonomic groups **(left)** and for the zoea (ZO), postlarva (PO) or megalopa (ME) life stages for some decapod taxa **(right).**

Community structure

Holohyperbenthos

The eigenvalues for the PCA performed on the holohyperbenthos densities were 0.465 and 0.180 for the first and second axis, respectively (Fig. 7A). The main variation is to be found along the first axis, representing 46.5 % of the variance in the species data. An additional 8.0 % is displayed along the second axis. The ordination diagram shows that the Dogger Bank itself harbours a rather uniform community, whose structure changes towards greater depths (sites do3 to do7 are closer together, the other sites are more dispersed over the diagram). More muddy sediments characterize the deeper sites, whereas the sediments of the shallow sites are coarser. Site do9 is aberrant and has a much higher sample score on the first axis than site do1, reflecting a sharp change in community structure southwards and northwards of the Dogger Bank.

The dendrogram for the cluster analysis illustrates the dissimilarity for station do9 and the other sites (Fig. 7C); site do1 is quite similar to the other sites at the southern part of the transect.

Merohyperbenthos

The correlation biplot composed by the first and second axis (eigenvalues 0.325 and 0.244, resp.) for the PCA applied on the merohyperbenthos data should be interpreted along both axes, given their subequal importance (Fig. 7B). The first two axes together display 57.0 % of the species variance. The deepest sites (do1 and do9) reach a comparable score on the first axis and thus are not as distinct from each other as compared to the holohyperbenthos result. The succeeding sites along the transect are additionally spread in a circular shape with respect to their geographical distribution. Temperature and salinity are highly correlated with the second axis and indicate lowest values for the northern part of the Dogger Bank itself.

Site do1 and do9 are grouped together in the cluster dendrogram that generally conforms to the result of the PCA (Fig. 7D). The successive sites along the transect from do5 up to do8 have a fairly high similarity moreover.

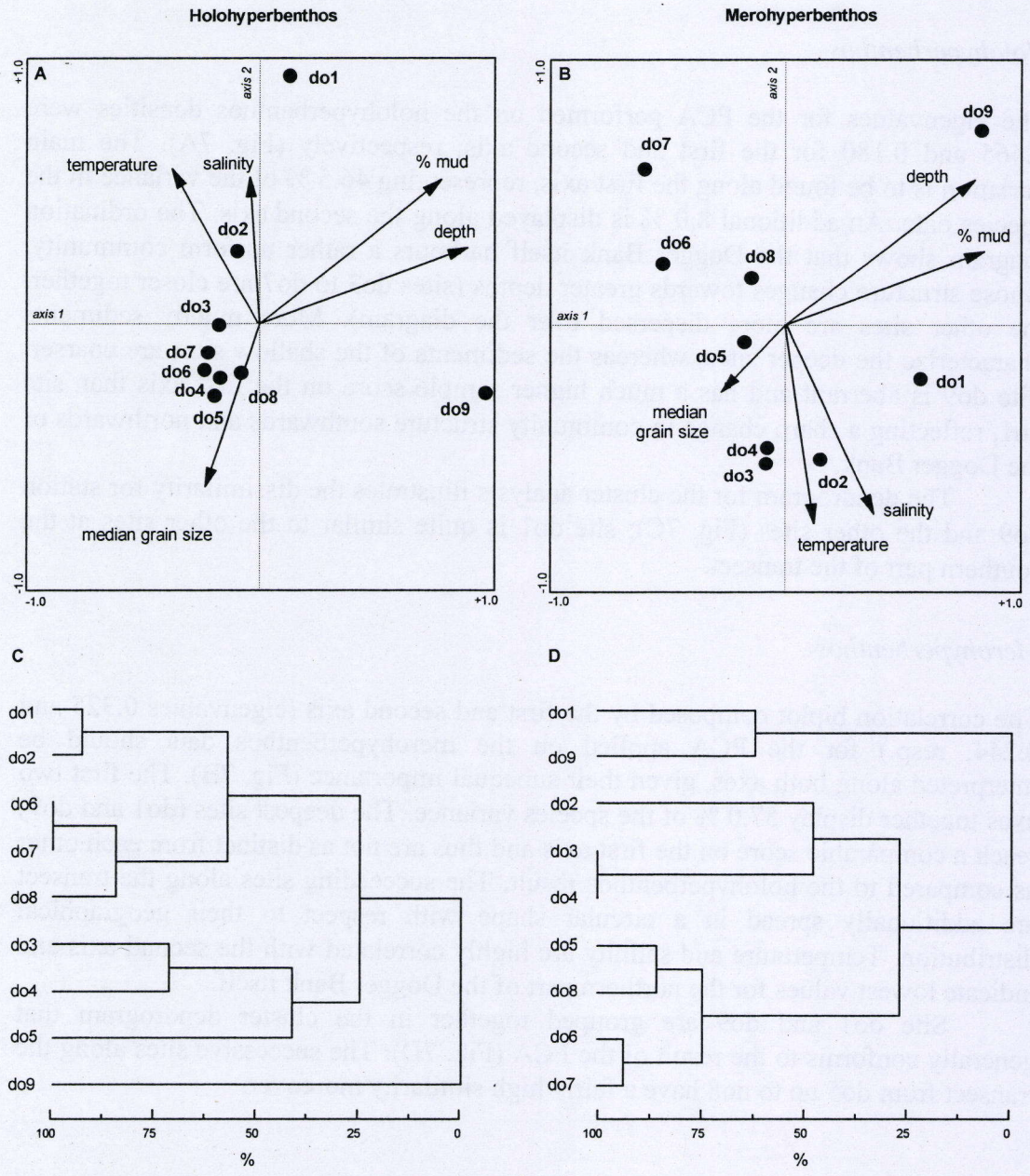

Fig. 7. Correlation biplots for the PCA analysis of **(A)** holohyperbenthos species densities (eigenvalues for the first three axis: 0.465, 0.180 and 0.114) and **(B)** merohyperbenthos species densities (eigenvalues for the first three axis: 0.325, 0.244 and 0.16). Sample scores (black dots) are displayed along the first and second axis. Some meaningful environmental variables were passively added and are presented as arrows. Cluster analysis dendrogram for **(C)** holohyperbenthos and **(D)** merohyperbenthos. The horizontal scale represents the relative similarity among sites.

Discussion

The hyperbenthal zone

The hyperbenthal is the transitional zone between the characteristic environments of the sea floor and the water column and harbours organisms from a wide range of taxa, as illustrated by the comprehensive species list (158 species belonging to at least 28 orders) (Table 2 and Addendum). This heterogeneity results from the gathering of planktonic species derived from their downward extensions, endo- and epibenthic species emerging into the water column and endemic species living in the hyperbenthal zone (Mees & Jones 1997).

Typical hyperbenthic representatives

Mysids are often quoted as being the classic example of a hyperbenthic taxon, i.e. of endemic hyperbenthal species. During daytime they mainly aggregate in the near-bottom water layers, as revealed by multi-level sledge results (Elizalde *et al.* 1991; Dauvin *et al.* 1994; Wang & Dauvin 1994; Cartes & Sorbe 1995; Dauvin *et al.* 1995; Zouhiri *et al.* 1998; Dauvin *et al.* 2000). Their high BA index (0.9 ± 0.05, Fig. 6) strongly supports these findings. Being good swimmers, many species perform daily vertical migrations with dispersion into the water column at night (Mauchline 1980; Wang & Dauvin 1994; Zouhiri *et al.* 1998). Mysids are nevertheless poorly caught by plankton nets or pumps (Mees & Jones 1997). A few burrowing species (as within the genus *Gastrosaccus*) are known from bottom grabs or box corer sampling. Most observations for offshore waters in the North Sea however date from the early taxonomic studies (compiled by Tattersall & Tattersall 1951) and the majority of species has never been recorded for the area since. This gap of knowledge, even for the well-studied North Sea, has often been attributed to the lack of suitable sampling devices. Remote collections of these motile animals require particular sampling gear such as sledges, certainly for quantitative research purposes (Mees & Jones 1997).

Endo- and epibenthic representatives

Data on the occurrence of amphipods and cumaceans in the Dogger Bank area are mainly obtained in the frame of macrobenthos research (Kröncke 1990, 1992; Heip *et al.* 1992; Künitzer *et al.* 1992; Heip & Craeymeersch 1995; Kröncke & Knust 1995), i.e. derived from grab or box corer sampling. Amphipods however were the most dominant taxon during this study, with a maximum density of 1519 ind. 100 m^{-2} and occurred with a high species variety (61 species).

In order to evaluate the occurrence of amphipods in the hyperbenthal zone, we compared our data with data obtained by endobenthic sampling at the Dogger Bank (28 sites covering the whole Dogger Bank area, August data, Kröncke & Knust 1995) and the 1986 ICES North Sea Benthos Survey (224 sites, April data, Heip *et al.* 1992; Künitzer *et al.* 1992).

Though a possible temporal effect must be taken into account, a rough comparison of the taxonomic composition on the family level can be meaningful. As illustrated in Fig. 8A, the endobenthic amphipod fauna of the Dogger Bank seems to be dominated by one family for more than 70 %, i.e. the Pontoporeidae. For the

remaining families, only the Urothoidae, the Oedicerotidae and the Ampeliscidae contribute for more than 3 % (Kröncke & Knust 1995). These families together with the Phoxocephalidae and Lysianassidae dominate the endobenthos of the entire North Sea (between 51° - 61° N and 0° - 8° E), as revealed by the ICES North Sea Benthos Survey (Heip *et al.* 1992; Künitzer *et al.* 1992). The family composition of the amphipod fauna in the hyperbenthal zone differs from that of the endobenthos with clearly a higher diversity; Oedicerotidae, Phtisicidae and Lysianassidae accounted together for more than 50 % of the average density (Fig. 8B).

An analogous pattern with regard to the composition and diversity between the endobenthos and hyperbenthos might probably exist for cumaceans on the genus level (Fig. 8C and 8D). It must be stated however that several cumacean species were only caught at site do9, being known for its high cumacean density, and the average composition may therefore not be very representative.

Two explanations for the indicated differences can be formulated. The first one deals with advantages and disadvantages of sampling gear while the second points to ecological traits.

Firstly, the large surface area sampled by sledges may cover a wide heterogeneity in habitats and therefore definitely contributes to the higher diversity in he hyperbenthal zone. This is illustrated by the presence of only 11 families in more than 10 % of the endobenthic samples (224 in total) collected for the ICES North Sea Benthos Survey (Heip *et al.* 1992), whereas for this study, each sample (9 in total) consisted of representatives of at least 10 families (except for site do3). A disadvantage of sledges is the difficult evaluation of the sampling efficiency believed to largely underestimate the densities. It has also often been criticized that sledge samples may be seriously contaminated by endobenthic representatives through disturbances and resuspension, leading to sampling bias. This indeed occurs on muddy substrata in particular, and cannot be avoided. The faunistic composition of the endobenthos versus hyperbenthos as above discussed, argues however for a distinction between both. Similar differences in composition and diversity for sledge versus grab or box corer samples were also noted by Sainte-Marie & Brunel (1985), Dauvin *et al.* (1994) and Dauvin *et al.* (1995).

In addition, the Amphipoda are a very diverse order that has widely varying ecological preferences and occupies a broad range of niches (Lincoln 1979; Ruppert & Barnes 1994). Their swimming behaviour has been assessed by several authors (e.g. Macquart-Moulin 1984, 1985, 1993; Kaartvedt 1986) and is also obvious from multi-level sledge results (e.g. Dauvin *et al.* 1994; Wang & Dauvin 1994; Vallet & Dauvin 1995; Dauvin *et al.* 2000). As Sainte-Marie & Brunel (1985) concluded, one might expect a complete continuum. This continuum consists of fully planktonic forms approaching the bottom during the day; it gradually extends to increasing bottom-dependent species making shorter or fewer, upward swimming excursions; and it eventually switches to endobenthic species swimming or crawling from their burrows or tubes during very short daily periods. Cumaceans are often burrowing and emerge from the bottom at night, yet the onset of diurnal swimming activity varies seasonally and with depth (Kaardvedt 1986).

The ecological importance of these vertical migrations by amphipods and cumaceans in the hyperbenthal zone must be viewed in relation to trophic fluxes. Sorbe (1981) pointed out that availability for fish predation is higher when individuals occur in the hyperbenthal rather than being buried in the sediment. Although only a very small

fraction of the population of endobenthic species may be present in the hyperbenthal, this fraction is thus more vulnerable for potential predators, and might therefore end up more significantly in their diet (Highes 1988; Essink *et al.* 1989).

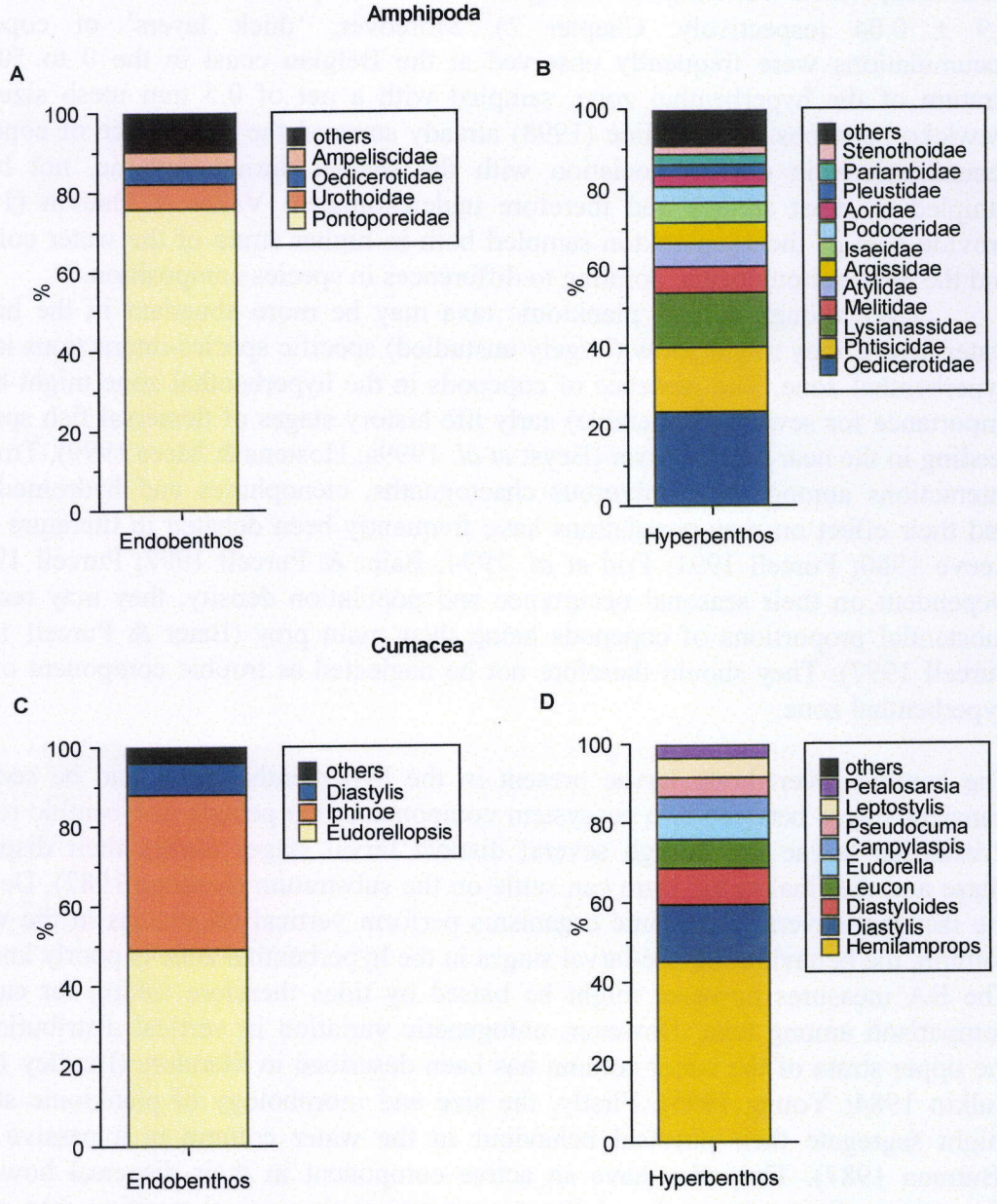

Fig. 8. The relative mean abundance of amphipod families **(A)** for the endobenthos data collected by Kröncke & Knust (1995) and, **(B)** for the hyperbenthos from this study. Similar for cumacean genera:, **(C)** endobenthos collected by Kröncke & Knust (1995). **(D)** hyperbenthos from this study The endobenthos data derive from 28 samples (spatial grid, 20 - 61 m depth), collected in August 1986.

Planktonic representatives

Euphausiids, chaetognaths, copepods, ctenophores and hydromedusae are fully planktonic forms reaching the lower limit of their vertical migration in the hyperbenthal zone. Chaetognaths showed a certain affinity to the bottom (BA index 0.7 ± 0.06, Fig. 6), while the other taxa were evenly distributed or occurred in the upper hyperbenthal layer (50 to 100 cm stratum). Chaetognaths and copepods were however found to occur in high numbers and very close to the sea floor in the Frisian front area, which was sampled during the same survey (BA indices 0.9 ± 0.06 and 0.9 ± 0.04 respectively, Chapter 2). Moreover, 'thick layers' of copepod accumulations were frequently observed at the Belgian coast in the 0 to 50 cm stratum of the hyperbenthal zone, sampled with a net of 0.5 mm mesh size (A. Dewicke pers. obs.). Mauchline (1998) already stressed the importance of copepod accumulations in close association with the seabed during daytime, not being sampled in most studies and therefore underestimated. Vallet & Dauvin (1999) provide data of the zooplankton sampled both in higher strata of the water column and the near-bottom layers, pointing to differences in species composition.

Even though several planktonic taxa may be more abundant in the higher water layers, they might show (largely unstudied) specific species-interactions in the hyperbenthal zone. The presence of copepods in the hyperbenthal zone might be of importance for several (vulnerable) early life history stages of demersal fish species feeding in the near-bottom layer (Beyst *et al.* 1999a; Hostens & Mees 1999). Trophic interactions among the carnivorous chaetognaths, ctenophores and hydromedusae and their effect on prey populations have frequently been debated in literature (e.g. Reeve 1980; Purcell 1991; Frid *et al.* 1994; Baier & Purcell 1997; Purcell 1997). Dependent on their seasonal occurrence and population density, they may remove substantial proportions of copepods being their main prey (Baier & Purcell 1997; Purcell 1997). They should therefore not be neglected as trophic component of the hyperbenthal zone.

The benthic invertebrate larvae present in the hyperbenthal layer can be seen as transient stages between two ecosystem components, the pelagic and benthic realm. Crustacean larvae go through several distinct larval stages during their dispersal phase and the final larval form can settle on the substratum (Butman 1987). Despite the fact that several planktonic organisms perform vertical migrations in the water column, the behaviour of late-larval stages in the hyperbenthal zone is poorly known. The BA measures however might be biased by tides therefore asking for careful comparison among taxa. However, ontogenetic variation in vertical distribution in the upper strata of the water column has been described in literature (Lindley 1986; Sulkin 1984; Young 1995). Firstly, the size and morphology of planktonic stages might segregate their physical behaviour in the water column in a passive way (Butman 1987). They also have an active component in their dispersal however, since they often possess the ability to regulate their vertical position into water masses (e.g. Mileikovsky 1973; Sulkin 1984; Butman 1987; Young 1995). The behaviour of early stages often exists in order to promote movement towards surface waters, leading to dispersal (Sulkin 1984). Later stages might possess tactic traits and high precision in depth regulation, contributing to the selection of favourable adult habitats (Sulkin 1984).

Hyperbenthos communities of the North Sea

Small-scale patterns

Holohyperbenthos

Total density of holohyperbenthos along the examined transect was most distinct between the shallow part of the Dogger Bank itself and its deeper surroundings and was positively correlated with depth. The deepest sites were characterized by a fairly high percentage of mud (> 20 %, see Table 1) in the upper bottom layer. The holohyperbenthic fauna actively searches for food (Vallet & Dauvin 1998) and feeds on material in suspension or deposited on the bottom (Mauchline 1980). Muddy sediments generally have higher carbon content than sandy sediments (Snelgrove & Butman 1994). This may become available for the holohyperbenthos when resuspended. In addition, the macro-endobenthos is also very abundant at the deeper parts of the Dogger Bank (Kröncke 1992) and very high densities were reported for *Amphiura filiformis* (Ophiuroidea, Echinodermata, epibenthos) at the southern edge (Duineveld *et al.* 1987). A further feeding benefit may thus be induced by incorporation of organic matter through secondary benthic production and subsequent degradation and resuspension processes. This most likely explains the high densities at the deepest sites of the mysids *Schistomysis ornata* and *Erythrops elegans*, feeding on the surface layers of the bottom (Mauchline 1968, 1970a), and the scavenging amphipod *Orchomenella nana* (Fig. 9, Addendum). All of them attained densities at least 10 times higher at site do1 or do9 as compared to the Dogger Bank itself. The remaining species that contributed to the density increase were the carnivorous chaetognath *Sagitta elegans* and caprellid *Phtisica marina*, and several detritus feeding amphipods (e.g. *Perioculodes longimanus, Westwoodilla caecula*) and cumaceans (e.g. *Hemilamprops rosea*) (Fig. 9, Addendum). High densities and biomasses of holohyperbenthos in food-enriched environments have been reported by several authors (Cunha *et al.* 1997; Mees & Jones 1997; Cunha *et al.* 1999; Dauvin *et al.* 2000).

The sediment on the Dogger Bank itself consists of fine to medium sand, sometimes with a small amount of gravel and fragmented shells (Table 1, Kröncke 1992; Langston *et al.* 1999). From a trophic point of view, coarser sediments generally provide more food for grazing, predating and suspension feeding fauna (Biernbaum 1979). The carnivore *Mysidopsis gibbosa* (Mauchline 1970b) was the most abundant mysid species and is also fairly common on similar sediments in the English Channel (Zouhiri *et al.* 1998) and in Belgian coastal waters (Chapter 5). Furthermore, a number of epifaunal amphipods were caught, such as *Microprotopus maculatus* and *Aora gracilis* that are often reported as being associated with hydroids or bryozoans (Lincoln 1979; Conradi & López-Gonzalez 1999). The presence of gravel or shell fragments on the Dogger Bank itself might support the growth of attached fauna creating microhabitat structures for a variety of holohyperbenthic species.

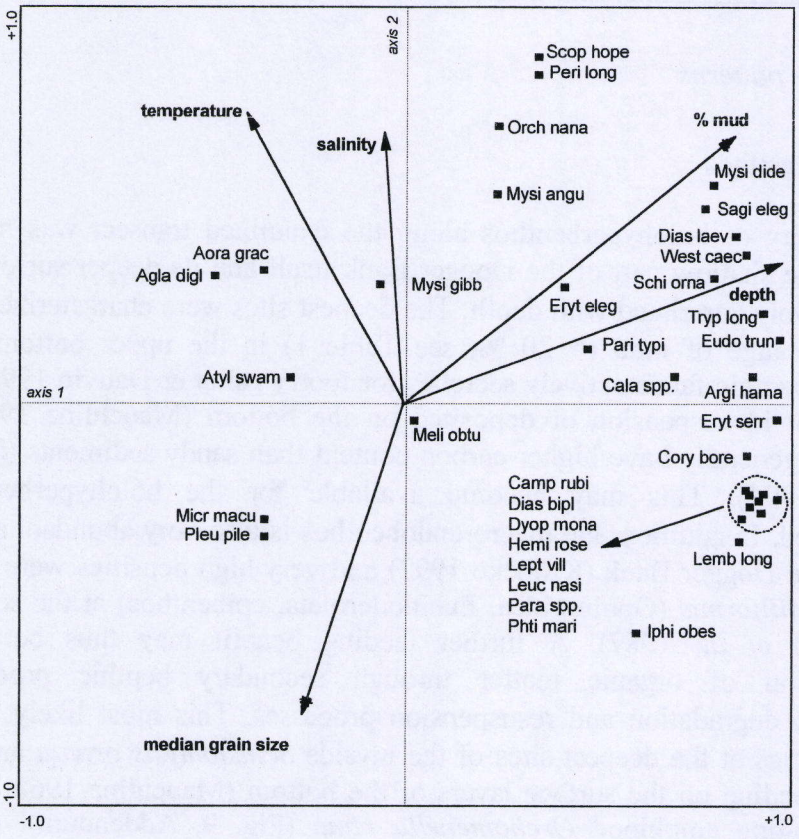

Fig. 9. Species scores for the most abundant holohyperbenthos species (together accounting for more than 90 % of the total average density) displayed in the plane of the first two axes of the PCA correlation biplot (i.e. Fig. 7A). Abbreviations of species names: *Aglantha digitale* (Agla digl), *Aora gracilis* (Aora grac), *Argissa hamatipes* (Argi hama), *Calanus* spp. (Cala spp.), *Campylaspis rubicanda* (Camp rubi), *Coryphella borealis* (Cory bore), *Diastylis laevis* (Dias laev), *Diastyloides biplicata* (Dias bipl), *Dyopedos monacantha* (Dyop mona), *Erythrops elegans* (Eryt eleg), *Erythrops serrata* (Eryt serr), *Eudorella truncatulla* (Eudo trun), *Hemilamprops rosea* (Hemi rose), *Iphimedia obesa* (Iphi obes), *Lembos longipes* (Lemb long), *Leptostylis villosa* (Lept vill), *Leucon nasica* (Leuc nasi), *Melita obtusata* (Meli obtu), *Microprotopus maculatus* (Micr macu), *Mysidopsis angusta* (Mysi angu), *Mysidopsis didelphys* (Mysi dide), *Mysidopsis gibbosa* (Mysi gibb), *Orchomenella nana* (Orch nana, *Paradulichia* spp. (Para spp.), *Pariambus typicus* (Pari typi), *Perioculodes longimarinus* (Peri long), *Phtisica marina* (Phti mari), *Pleurobrachia pileus* (Pleu pile), *Sagitta elegans* (Sagi eleg), *Schistomysis ornate* (Schi orna), *Scopelocheirus hopei* (Scop hope), *Tryphosites longipes* (Tryp long), *Westwoodilla caecula* (West caec).

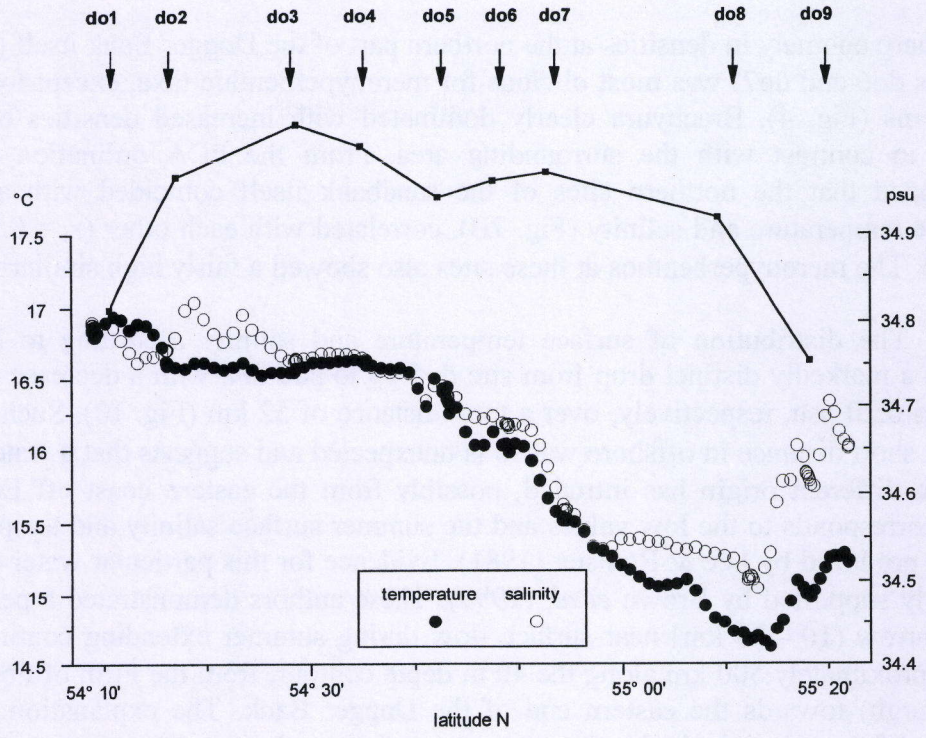

Fig. 10. Distribution of surface temperature (left axis) and salinity (right axis) according to latitude along the sampled transect. The depth profile is indicated as a full line with black squares for the respective sites.

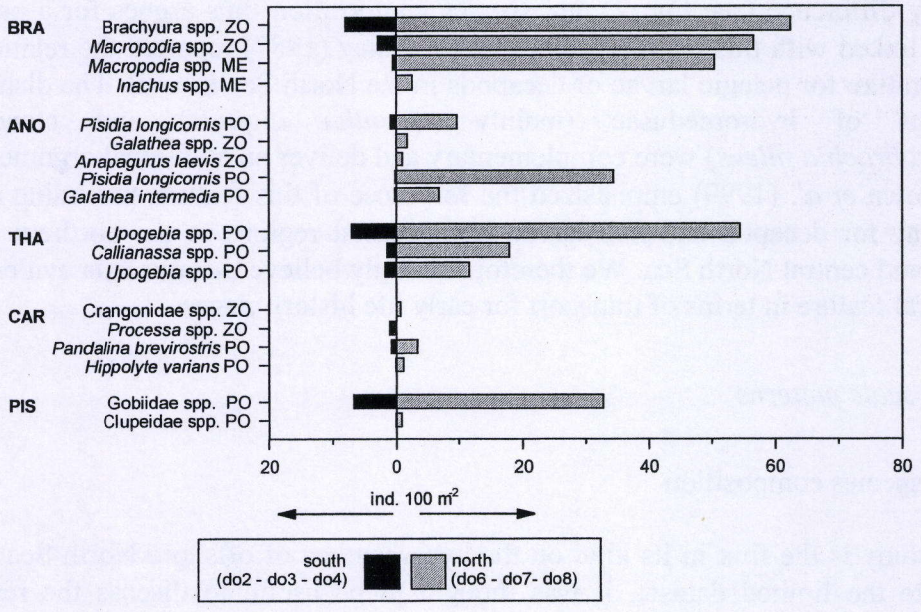

Fig. 11. Average density of all merohyperbenthic species for whom a significant difference was found between the southern (sites do2, do3 and do4) and northern part (sites do5, do7 and do8) of the Dogger Bank itself. Anomura (ANO), Brachyura (BRA), Caridea (CAR), Pisces (PIS), Thalassinidae (THA); zoea (ZO), postlarva (PO), megalopa (ME).

Merohyperbenthos

The sharp anomaly in densities at the northern part of the Dogger Bank itself (mainly at sites do6 and do7) was most obvious for merohyperbenthic taxa, except for larval carideans (Fig. 4). Brachyura clearly dominated with increased densities of > 10 times in contrast with the surrounding area. From the PCA ordination can be concluded that the northern sites of the sandbank itself coincided with a lower surface temperature and salinity (Fig. 7B), correlated with each other ($r_s = 0.98$, $p < 0.001$). The merohyperbenthos at these sites also showed a fairly high similarity (Fig. 7D).

The distribution of surface temperature and salinity according to latitude shows a markedly distinct drop from site do5 up to site do8 with a decrease of 1.59 °C and 0.20 psu, respectively, over a total distance of 52 km (Fig. 10). Such a drop over a short distance in offshore waters is unexpected and suggests that a water mass from a different origin has intruded, possibly from the eastern coast off England. This corresponds to the low values and the summer surface salinity and temperature charts produced by Lee & Ramster (1981). Evidence for this particular water mass is strongly supported by Brown *et al.* (1999). These authors demonstrated a persistent and narrow (10 - 15 km) near-surface flow during summer extending continuously for approximately 500 km along the 40 m depth contour, from the Firth of Forth (off Edinburgh) towards the eastern end of the Dogger Bank. The explanation of this physical feature is linked with the occurrence of strong bottom fronts between mixed and stratified waters (Brown *et al.* 1999).

In order to further examine this feature, the mean abundances of all merohyperbenthic species between the southern (sites do2, do3 and do4) and northern part (sites do5, do7 and do8) of the Dogger Bank itself were compared (Mann-Whitney U-test, $p < 0.05$). Merohyperbenthic species that attained significantly higher densities at the northern part of the Dogger Bank, accounted for 44 % of the total merohyperbenthos density in this area (Fig. 11). The pronounced density difference (see Fig. 2) and species composition thus argues for a particular fauna linked with this distinct water mass. Lindley (1987) reported the relation with temperature for pelagic larvae of decapods in the North Sea as well. The distribution patterns of hydromedusae (mainly *Aglantha digitale*) and ctenophores (*Pleurobrachia pileus*) were complementary and deliver an additional argument (Fig. 5). Brown *et al.* (1999) emphasized the relevance of this feature, providing a direct pathway for decapod and fish larvae from coastal regions to the northern Dogger Bank and central North Sea. We therefore strongly believe that our data evidence this physical feature in terms of transport for early life history stages.

Large scale patterns

Total species composition

This study is the first in its kind on the hyperbenthos of offshore North Sea waters. Despite the limited dataset, it was thought to be useful to discuss the results in relation with the current knowledge on the geographical distribution of the North Sea's communities. The area north of the Dogger Bank has often been mentioned as being the main transition area between southern and northern communities for several biota, as there are zooplankton (Williams *et al.* 1993), endobenthos (Künitzer *et al.* 1992; Heip & Craymeersch 1995) and epibenthos (Dyer *et al.* 1983;

Frauenheim *et al.* 1989; Duineveld & Van Noort 1990; Jennings *et al.* 1999; Rees *et al.* 1999). This hypothesis might also hold true for holohyperbenthos, since some evidence arises from the multivariate analyses when focusing on the two outermost sites, south and north of the Dogger Bank (do1 and do9, resp.).

The northernmost site harboured a richer fauna in terms of density and biomass (Fig. 2). The most conspicuous difference though was its diversity since all calculated diversity indices were higher at do9 compared to do1 (Table 3). Species composition also changed south and north of the Dogger Bank: *Schistomysis ornata* was dominating at both sites, but subdominant species were strongly different (see Addendum). The percentage of species common for both sites was 44 % (42 species), while 14 % (13 species) was limited to site do1 and 42 % (40 species) was uniquely reported for site do9 (Table 4). Moreover, 37 % of the total density at site do9 was accounted for by species that did not occur at site do1. The species, either confined to the southern or to the northern area of the Dogger Bank, were mainly peracarid crustaceans (Table 4). The above mentioned density increase of cumaceans at site do9 was also due to appearance of boreal representatives such as *Hemilamprops rosea*, *Diastyloides biplicata*, *Leucon nasica* and *Campylaspis rubicanda* (Jones 1976). A reverse pattern was found for mysids: 5 species were unique for the southern area. *Erythrops serrata* was restricted to the northern edge of the Dogger Bank. This is the southernmost latitude of the North Sea this species was ever reported for. It is well known however from Scandinavian fjords (Buhl-Jensen 1986; Fosså & Brattegard 1990; Buhl-Jensen & Fosså 1991) and from the north of Scotland (Mauchline 1968).

Boreal species were also found for other taxa such as for Nudibranchia. *Coryphella borealis* occurred with enormous densities (213 ind. 100 m^{-2}) at the northern edge of the Dogger Bank, while never being rediscovered since 1939 off the coast of Norway (Odhner 1939; J. Evertsen pers. comm.).

		Only at do1			Only at do9			At both sites
		# spec	Abs dens	% dens	# spec	Abs dens	% dens	# spec
Holohyperbenthos		13	76	6	40	1370	37	42
Peracarida	Amphipoda	5	21	4	24	613	40	23
	Mysidacea	5	3	<1	1	< 1	< 1	8
	Cumacea	0	0	0	8	716	81	6
	Isopoda	0	0	0	2	26	100	0

Table 4. Comparison of the total number of holohyperbenthic species and the numbers per major peracarid order between site do1 and do9. The numbers of species that were present at site do1 and absent at site do9 are reported (only at do1) and vice versa (only at do9); the numbers of species reported from both sites are given in the last column (at both sites). Their absolute (ind. 100 m^{-2}) and relative (%) density (as a fraction of the total holohyperbenthos density) are also tabulated.

Biogeographical elements

Further comparison on a latitudinal scale was done with the hyperbenthic amphipod fauna of the Belgian continental shelf (data from 12 sites sampled in September 1994, Chapter 5). Amphipods were grouped according to the major biogeographical assemblages occurring around the British Isles based on the classification given by Lincoln (1979). Lincoln (1979) considered four groups in the area: arctic-boreal, cold-temperate, temperate and warm-temperate elements (see Lincoln 1979 for definitions).

In terms of species numbers, most species of the three areas were temperate representatives (Table 5). Only two cold-temperate species were found at the Belgian continental shelf, arctic-boreal species were absent in this area as for site do1. The relative abundance of the faunal elements gives an even stronger indication of a biogeographical transition north of the Dogger Bank: 60 % of the total amphipod density at site do9 (55.5° N) was represented by arctic-boreal and cold-temperate species. In contrast, more than 80 % of the amphipod abundance at site do1 (54° N) and at the Belgian continental shelf (51° N) was delivered by temperate elements (Table 5).

This strongly presumes that the amphipod fauna of the Belgian continental shelf and the area south of the Dogger Bank (332 km distance between both) have more affinity in relation to biogeography, as compared to the fauna north of the Dogger Bank (130 km between do1 and do9). Site do9 may thus be situated in a transition zone between northern and southern faunal elements, harbouring species of both. This is strongly supported by Künitzer *et al.* (1992) who concluded that the northern elements of the bottom fauna of the North Sea do not extend further south than the north of the Dogger Bank, while southern elements are believed not to go any further north than the 100 m contour.

Such an overlap in biogeographic elements might partly explain the higher diversity as reported for site do9. Still, the northern fauna *in se* has been found to be more diverse for several ecosystem compartments such as endofauna (Heip *et al.* 1992; Heip & Craeymeersch 1995) and epifauna (Jennings *et al.* 1999).

	Belgian continental shelf			Site do1			Site do9		
	# spec	Abs dens	% dens	# spec	Abs dens	% dens	# spec	Abs dens	% dens
Arctic-boreal	0	0	0	0	0	0	5	159	14
Cold-temperate	2	2	6	5	64	14	9	540	46
Temperate	15	37	84	16	373	82	23	199	17
Warm-temperate	3	5	11	1	6	1	1	2	10
Total (*)	20	44	100	22	443	100	38	900	100
Total (**)	21	44		25	452		43	1166	

Table 5. Comparison of the numbers of amphipod species caught at the Belgian continental shelf (12 sites, September 1994, Chapter 5) and at site do1 and do2, according to the biogeographical classification by Lincoln (1979). Total (*) concerns the species from whom the classification could be made (taxa reported as 'spp.' could not be classified); total (**) deals with all amphipods caught. The absolute (ind. 100 m^{-2}) and relative density (%) for each biogeographical assemblage is also given. Relative densities were calculated as a fraction of the total amphipod density for whom the biogeography is reported, i.e. Total (**).

Structuring environmental factors

The hydrography and bathymetry of the North Sea, characterized by sharp gradients north of the Dogger Bank, have often been put forward as the main structuring force for different ecosystem components. The 100 m depth contour is believed to separate two different hydrographic zones (Basford *et al.* 1993). North of this contour Atlantic water enters the North Sea from between the Orkney and the Shetland Islands, running southwards and then east along the 100 m contour. To the south of the 100 meter contour there is a residual southerly flow along the English coast which meets the Channel inflow water and then flows further north-east, finally leaving the North Sea via the Norwegian Trough (Lee 1980; Basford *et al.* 1993).

Firstly, the origin of water masses as such might determine the distribution of the motile hyperbenthic communities, i.e. a direct relation through transport and consequent dispersion of organisms. The depth gradient and current pattern (combined with winds and tides) of the North Sea indirectly determines different regimes of temperature and temperature variation, which might be important factors for species' physiology. In the deeper areas north of the Dogger Bank, the water column is thermally stratified throughout the summer (Lee 1980) and the bottom temperature remains below 7° C. The annual variation in temperature is much more pronounced south of the Dogger Bank (5 - 15° C), since this area is homothermal all year round (Lee 1980). A hydrographically more stable environment often supports a more diverse fauna in contrast to areas with a high seasonality, as discussed for the hyperbenthos by Chevrier *et al.* (1991) and Dauvin *et al.* (2000).

Stratification has also an impact on primary production cycles and food web structure (e.g. Nielsen *et al.* 1993; Fransz *et al.* 1998; Richardson & Bo Pedersen 1998; Richardson *et al.* 1998; Kiørboe 1993) and might therefore also determine the food supply for the hyperbenthos as was already suggested for endobenthos (Heip *et al.* 1992; Künitzer *et al.* 1992; Heip & Craeymeersch 1995).

Finally, the difference in community structure between southern and northern fauna might be discussed from a geological point-of-view. According to Heip *et al.* (1992) it is conceivable that the colonization of the North Sea both from the north and the south after the last Ice Age, is still reflected in latitudinal patterns of species occurrence. They argued that the southern element of the North Sea, which penetrated through the Channel, is still quite young (4000 years). It therefore might not have stabilized or reached its final diversity yet (Heip *et al.* 1992).

The North Sea tidal mixing front

The transition area between mixed and stratified water masses in the North Sea runs from west to east along the 40 m depth contour and is often referred to as the 'North Sea tidal mixing front' (Tett & Walne 1995). Strong bottom fronts have been reported at the northern edge of the Dogger Bank and to a lesser extent at its southern edge by different authors (Van Aken *et al.* 1987; Riegman *et al.* 1990; Baars *et al.* 1991; Nielsen *et al.* 1993; Bo Pedersen 1994; Munk & Nielsen 1994; Nielsen & Munk 1998; Richardson & Bo Pedersen 1998; Richardson *et al.* 1998; Tett & Walne 1995). The distribution of the merohyperbenthos was already supposed to be related to an intruding water mass, which is on itself the result of the occurrence of bottom fronts (see Brown *et al.* 1999). Since fronts are often highly productive areas though (Le Fèvre 1986; Kiørboe 1993), one should not exclude an even more important impact on both the holo- and merohyperbenthic communities surrounding the front.

Richardson & Bo Pedersen (1998) predicted that 20 % of the new production in the North Sea during summer months could be associated with these fronts. Maximum phytoplankton biomass and production rates are observed at the pycnocline of the stratified waters around the Dogger Bank (Nielsen *et al.* 1993). Efficient energy transfer to higher trophic levels and accumulations of pelagic feeders (fish and larvae) are expected in such areas (Richardson *et al.* 1998).

Evidence is given by Munk & Nielsen (1994) who found peak abundances for zooplankton at all trophic levels at the front north of the Dogger Bank. For this study, fish larvae were also most abundant in the northern part of the transect. Several studies have demonstrated that the distribution of fish larvae is often related to such fronts locally enhancing feeding and growth (Kiørboe 1993). This has been documented for the western part of the tidal mixing front in the North Sea (Kiørboe & Johansen 1986; Richardson *et al.* 1986; Kiørboe *et al.* 1988) as well as for the eastern part (Munk 1993; Nielsen & Munk 1998; Munk *et al.* 1999).

The motile and omnivorous nature of the holohyperbenthos also benefits from such enriched areas, turning its capability to rapidly respond to food supply or escape from changing unfavourable conditions. It might therefore not be excluded that the increased densities at the deeper parts of the Dogger Bank result from front-associating processes.

The North Sea tidal mixing front might also be related to the biogeographical transition reported for the holohyperbenthos. Concerning ecological geography, Longhurst (1998) already identified subdivisions of the Northeast Atlantic Shelves Province based on the predictable location of tidal fronts. It was pointed out that the concept of ecotones as introduced by Odum (1971), i.e. the transition zone between two ecological communities, holds partly true for tidal fronts as well (Longhurst 1998). Tidal fronts may play an important role in the advection and / or retention of organisms, e.g. as for the holoplankton and larval dispersal stages (Le Fèvre 1986; Kiørboe *et al.* 1988; Kiørboe 1993; Longhurst 1998). Bailey (1997) presumed that the North Sea fronts might act as barrier for the larval dispersion of flatfish populations, thus inhibiting gene flow and population mixing. A transition in species assemblages at the front north of the Dogger Bank was found for fish larvae (Munk & Nielsen 1994). Moreover, a clear association of species composition with water-mass properties - being mixed, stratified and transitional - was also reported for phyto- and zooplankton assemblages in the North Sea (Williams *et al.* 1993; Lindley & Williams 1994).

Final remarks

The transition zone between the planktonic and benthic environment harbours a fauna closely related to the sea floor, although interactions between the environmental compartments occur by organisms performing vertical migration. Due to the high number of hyperbenthic species, this study contributes to the knowledge of the biodiversity of the Dogger Bank ecosystem. Unfortunately, biological interactions and processes occurring in the hyperbenthic layer are poorly known. Still, the hyperbenthos might play a role in transfer of organic matter to benthic communities through performing vertical migrations and as food source for many postlarval and juvenile demersal fish. Frontal zones have often been mentioned as being biological 'hot spots' (Nielsen & Munk 1998). Within short distance, not only the productivity, but also the structure and the trophic diversity of the communities

may change significantly. It is hypothesized that such areas might in particular be attractive for the holohyperbenthos, through their motility and omnivorous behaviour.

Furthermore, the occurrence of early life history stages in the hyperbenthal might bring up some indications to generate hypotheses concerning larval supply to an offshore area such as the Dogger Bank. Larval transport mechanisms are to a certain extent controlling community structure of benthic organisms, in addition to larval supply and settlement success (Giangrande *et al.* 1994). Heip (1992) and Heip & Craeymeersch (1995) already stressed the need to include the planktonic phase of benthic macro-invertebrates and recruitment processes in ecological models. As the Dogger Bank is very special regarding its current regime, research should focus on the transport of decapod and fish larvae in this area and their behaviour in tidal flow. The tidal mixing front and associated physical mechanisms north of the Dogger Bank might be of significance for transport towards suitable nurseries, as also suggested by Brown *et al.* (1999).

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	H/M	do1	do2	do3	do4	do5	do6	do7	do8	do9
Phylum Cnidaria										
Subphylum Medusozoa										
Superclassis Hydrozoa										
Classis Hydroidomedusae										
Subclassis Anthomedusae										
Ordo Filifera										
Subordo Margelina										
Bougainvillia spp. HM	H	0.0	0.0	0.0	0.5	0.0	0.0	0.4	0.0	0.0
Subordo Tiarida										
Leuckartiara spp. HM	H	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0	0.0
Subclassis Leptomedusae										
Eutonina indicans HM	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0
Mitrocomella spp. HM	H	0.0	0.0	1.3	0.0	1.5	0.0	2.1	0.0	0.0
Subclassis Trachymedusae										
Aglantha digitale HM	H	40.5	3.1	8.5	35.2	63.2	3.1	4.6	0.0	0.0
Hydroidomedusae species 1 HM	H	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Phylum Ctenophora										
Classis Tentaculata										
Ordo Cydippida										
Pleurobrachia pileus	H	0.0	0.0	0.0	0.0	0.4	3.5	74.5	20.4	0.0
Phylum Annelida										
Classis Polychaeta										
Ordo Phyllodocida										
(not identified subordo)										
Tomopteridae spp.	H	9.3	2.4	0.0	0.0	2.9	5.9	2.5	0.8	0.0
Polychaeta spp. LA	M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Phylum Chaetognatha										
Classis Sagittoidea										
Subclassis Chorismogonata										
Ordo Monophragmophora										
Spadella cephaloptera	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.0
Ordo Aphragmophora										
Sagitta elegans	H	174.9	21.7	2.8	1.4	4.0	6.9	5.0	41.6	172.6
Phylum Mollusca										
Classis Gastropoda										
Subclassis Opisthobranchia										
Ordo Nudibranchia										
Subordo Aeolidacea										
Coryphella borealis	H	1.0	0.3	0.0	0.0	1.5	0.0	0.4	9.2	212.3
Classis Cephalopoda										
Subclassis Coleoidea										
Ordo Sepiida										
Subordo Sepiina										
Sepiola atlantica	H	0.0	0.0	0.0	0.0	2.2	2.1	1.4	0.8	0.0
Ordo Teuthida										
Subordo Myopsida										
Loligo forbesii JU	M	1.4	0.3	0.6	0.5	5.1	1.4	0.0	0.0	0.0
Phylum Arthropoda										
Subphylum Crustacea										
Classis Copepoda										
Ordo Calanoida										
Anomalocera patersoni	H	0.0	0.0	0.3	0.5	0.0	0.7	1.4	2.4	1.2
Calanus spp.	H	11.0	0.0	0.0	0.0	0.0	1.4	6.4	15.6	74.8
Centropages typicus	H	0.0	0.0	0.3	0.5	1.1	6.2	0.4	0.0	0.8
Labidocera wollastoni	H	0.0	0.0	0.3	0.0	0.7	0.0	0.0	0.4	0.0
Temora longicornis	H	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Calanoida species 1	H	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Classis Malacostraca										
Subclassis Phyllocarida										
Ordo Nebaliacea										
Nebalia bipes	H	2.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subclassis Eumalacostraca										
Superordo Eucarida										
Ordo Euphausiacea										
Nyctiphanes couchi	H	26.1	4.1	0.6	0.0	0.0	0.0	0.0	0.0	0.8
Thysanoëssa raschi	H	7.6	0.7	0.0	0.0	0.0	0.0	0.0	0.0	12.0
Ordo Decapoda										
Subordo Pleocyemata										
Infraordo Caridea										
Crangon allmanni PO	M	78.0	1.7	0.3	0.0	0.0	0.0	0.4	0.0	313.5
Crangonidae spp. ZO	M	0.3	0.0	0.0	0.0	0.4	0.7	0.7	0.8	1.7
Hippolyte varians PO	M	0.3	0.3	0.0	0.0	6.5	1.0	1.8	0.8	3.3
Hippolyte varians ZO	M	0.0	0.0	0.0	0.0	0.0	0.3	0.4	0.0	0.0
Pandalina brevirostris PO	M	12.7	1.0	0.3	1.0	3.6	2.4	2.1	6.0	42.5
Pandalina brevirostris ZO	M	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
Philocheras bispinosus PO	M	378.9	65.9	9.2	32.3	28.3	6.2	0.0	44.0	391.1
Philocheras trispinosus PO	M	0.0	0.0	2.5	0.0	0.7	0.7	2.1	0.0	0.0
Pontophilus spinosus PO	M	3.4	0.3	0.0	0.0	0.0	0.3	0.0	0.0	6.6
Processa spp. PO	M	95.8	6.6	0.6	0.0	0.0	0.0	0.0	0.0	0.8
Processa spp. ZO	M	1.0	1.7	0.9	0.5	0.0	0.3	0.0	0.0	0.0
Thoralus cranchii PO	M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1
Infraordo Astacidea										
Nephrops norvegicus PO	M	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nephrops norvegicus ZO	M	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Addendum. Species list and density (ind. 100 m^{-2}) per site with indication of holohyperbenthos (H) and merohyperbenthos (M); hydromedusa (HM), juvenile (JU), larva (LA), megalopa (ME), postlarva (PO), zoea (ZO).

	H/M	do1	do2	do3	do4	do5	do6	do7	do8	do9
Infraordo Thalassinidea										
Callianassa spp. PO	M	30.9	1.0	0.0	0.0	1.5	0.0	1.4	0.0	3.7
Callianassa spp. ZO	M	40.5	2.8	0.6	1.0	9.4	8.3	32.1	13.6	17.8
Upogebia spp. PO	M	16.8	2.1	1.3	1.9	4.4	17.3	13.5	4.4	6.6
Upogebia spp. ZO	M	6.2	2.8	11.4	6.8	24.3	23.9	124.1	15.6	3.3
Infraordo Anomura										
Anapagurus laevis ZO	M	0.0	0.0	0.0	0.0	0.4	1.7	1.1	0.4	0.4
Galathea dispersa PO	M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7
Galathea spp. ZO	M	0.0	0.0	0.0	0.0	0.0	0.3	3.6	1.6	0.0
Galathea intermedia PO	M	2.7	0.7	0.0	0.0	1.5	3.5	5.0	12.4	3.7
Paguridae spp. PO	M	12.0	2.1	2.2	1.9	1.5	5.2	3.2	1.6	35.9
Pagurus bernhardus ZO	M	13.1	9.3	10.4	7.2	5.4	12.1	7.5	7.6	6.2
Pagurus prideauxi ZO	M	0.0	1.4	0.9	0.0	0.0	2.4	4.3	0.8	0.0
Pisidia longicornis PO	M	5.5	0.0	0.6	0.0	3.6	14.2	69.9	19.2	4.1
Pisidia longicornis ZO	M	0.0	0.0	0.3	2.4	4.0	13.8	12.5	3.2	1.2
Infraordo Brachyura										
Cancer pagurus ME	M	1.4	0.3	7.3	2.4	5.4	32.2	16.4	3.2	9.5
Carcinus maenas ME	M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Corystes cassivelaunus ME	M	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ebalia spp. ME	M	8.6	1.4	0.0	0.0	0.4	0.0	1.8	4.0	2.9
Hyas spp. ZO	M	0.0	0.0	0.0	0.5	0.4	0.0	0.4	1.6	0.0
Inachus spp. ME	M	0.0	0.0	0.0	0.0	0.0	0.7	6.4	0.8	0.0
Inachus spp. ZO	M	0.0	0.0	0.0	0.0	0.0	1.0	1.1	0.0	0.0
Liocarcinus holsatus ME	M	30.6	101.5	44.8	28.0	37.4	923.6	182.2	18.0	5.0
Macropodia spp. ME	M	0.0	0.3	0.3	1.0	12.0	70.2	78.1	3.2	0.8
Macropodia spp. ZO	M	0.0	0.0	1.9	6.8	2.5	67.8	92.7	9.6	0.0
Pilumnus hirtellus ME	M	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Thia scutellata ME	M	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brachyura species 1 ME	M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Brachyura species 2 ZO	M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Brachyura spp. ZO	M	1.0	2.1	6.6	15.0	6.9	83.7	77.0	26.8	22.3
Superordo Peracarida										
Ordo Mysidacea										
Subordo Mysida										
Acanthomysis longicornis	H	1.4	0.3	0.6	0.0	0.7	0.7	0.7	0.4	0.0
Anchialina agilis	H	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Erythrops elegans	H	149.8	20.0	3.2	0.5	0.0	0.7	11.8	704.2	100.4
Erythrops serrata	H	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	90.5
Gastrosaccus spinifer	H	0.7	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.4
Heteromysis norvegica	H	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Leptomysis gracilis	H	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9
Leptomysis lingvura	H	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mesopodopsis slabberi	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8
Mysidopsis angusta	H	46.7	6.2	0.3	0.5	0.4	1.7	15.7	35.6	7.0
Mysidopsis didelphys	H	22.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	27.7
Mysidopsis gibbosa	H	4.5	5.9	5.7	5.3	1.5	3.8	6.8	0.8	3.3
Schistomysis kervillei	H	0.7	2.8	2.2	0.0	1.5	2.4	13.2	0.0	0.0
Schistomysis ornata	H	204.7	13.1	0.6	0.0	1.5	1.4	1.4	69.2	527.9
Ordo Cumacea										
Campylaspis costata	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.9
Campylaspis rubicanda	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	38.0
Diastylis laevis	H	26.1	1.4	0.3	0.0	0.0	0.0	0.0	0.0	92.1
Diastylis lucifera	H	9.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Diastylis rugosa	H	5.2	0.0	0.0	0.5	0.7	0.0	0.0	0.4	1.2
Diastyloides biplicata	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	88.8
Eudorella truncatulla	H	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	54.5
Hemilamprops rosea	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	430.4
Iphinoe trispinosa	H	0.0	0.0	0.0	0.5	0.4	0.3	0.0	0.4	0.4
Leptostylis villosa	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	46.7
Leucon nasica	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	70.2
Petalosarsia declivis	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	31.4
Pseudocuma longicornis	H	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	4.1
Pseudocuma similis	H	2.4	0.0	0.3	0.5	0.0	0.0	1.1	8.8	19.0
Ordo Amphipoda										
Subordo Caprellidea										
Caprella linearis	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.5
Pariambus typicus	H	4.5	2.4	0.0	0.0	0.0	3.5	1.8	30.4	14.0
Phtisica marina	H	9.6	4.1	1.9	1.9	3.3	8.3	13.2	37.6	305.6
Pseudoprotella phasma	H	0.0	0.0	0.0	0.0	0.0	0.3	0.4	2.0	0.0
Subordo Gammaridea										
Acidostoma nodiferum	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.4
Acidostoma obesum	H	0.0	1.7	0.0	0.0	0.0	0.0	0.0	1.2	6.6
Ampelisca brevicornis	H	3.1	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Ampelisca tenuicornis	H	3.4	0.0	0.0	0.0	3.6	0.0	0.0	0.0	11.6
Amphilochus neapolitanus	H	0.0	0.0	0.0	0.5	0.0	4.8	0.0	0.4	0.0
Aora gracilis	H	10.6	5.9	0.0	1.4	0.0	9.3	32.1	12.0	0.0
Apherusa bispinosa	H	0.0	0.0	0.0	1.4	0.0	0.0	0.4	1.6	15.3
Apherusa ovalipes	H	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Argissa hamatipes	H	3.4	0.7	0.0	1.9	0.0	0.0	0.0	0.4	118.1
Atylus falcatus	H	0.0	0.7	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Atylus swammerdami	H	2.7	24.5	7.6	2.4	1.1	2.4	86.3	6.4	1.7
Atylus vedlomensis	H	0.3	0.0	0.0	0.5	0.0	0.0	0.0	0.0	4.1
Bathyporeia spp.	H	1.7	0.3	0.0	0.5	0.0	0.0	0.0	0.4	0.4
Cheirocratus sundevallii	H	0.0	0.0	0.0	0.5	2.5	0.0	0.0	0.0	1.7
Dyopedos monacantha	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	93.8
Dyopedos porrectus	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3
Gammaropsis nitida	H	0.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0
Gammaropsis palmata	H	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.0	8.7
Harpinia antennaria	H	13.4	1.4	0.0	0.0	0.0	0.0	0.0	0.0	4.1

Addendum. (continued).

	H/M	do1	do2	do3	do4	do5	do6	do7	do8	do9
Harpinia crenulata	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.5
Hippomedon denticulatus	H	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.1
Iphimedia minuta	H	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.4	0.0
Iphimedia obesa	H	0.0	0.0	0.0	0.0	2.2	1.0	0.4	4.4	25.6
Jassa pusilla	H	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.8	6.6
Lembos longipes	H	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	70.2
Lepidepecreum longicorne	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Leucothoe incisa	H	0.0	0.0	0.3	0.0	0.0	0.0	0.4	0.0	0.8
Maera othonis	H	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0
Megaluropus agilis	H	5.8	0.7	1.3	1.0	0.0	1.4	5.7	4.8	0.0
Megamphopus cornutus	H	0.0	0.0	0.0	0.5	2.9	0.0	0.0	0.8	10.3
Melita obtusata	H	0.3	56.3	2.2	0.5	0.0	19.7	7.5	62.8	5.4
Melphidippella macra	H	1.7	0.0	0.0	0.0	0.0	0.0	0.0	1.2	7.0
Metopa alderi	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1
Metopella nasuta	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.7
Microjassa cumbrensis	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7
Microprotopus maculatus	H	0.0	0.0	0.0	0.5	0.0	5.5	67.0	2.0	0.0
Monoculodes carinatus	H	0.0	0.0	0.0	5.8	0.0	0.0	0.0	0.0	0.0
Orchomenella nana	H	159.7	11.4	0.6	1.0	25.8	0.0	0.0	0.0	3.3
Paradulichia spp.	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	233.4
Paramphilochoides intermedius	H	7.2	0.7	0.0	0.0	0.0	0.0	0.0	0.0	5.0
Parapleustes assimilis	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	32.6
Parapleustes bicuspis	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	27.3
Perioculodes longimanus	H	146.3	13.8	2.8	0.0	0.7	0.0	3.6	1.2	7.4
Photis longicaudata	H	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	11.6
Pontocrates altamarinus	H	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	1.7
Pontocrates arenarius	H	0.0	0.0	0.0	0.5	0.0	0.0	0.7	0.0	0.0
Scopelocheirus hopei	H	35.0	6.6	1.3	0.0	0.0	0.0	6.1	0.0	2.5
Siphonoecetes striatus	H	0.0	1.7	0.0	0.0	0.0	5.9	1.8	0.8	5.0
Stenothoe marina	H	4.1	0.7	0.0	0.0	0.4	0.3	0.0	0.0	6.2
Stenula rubrovittata	H	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.9
Synchelidium haplocheles	H	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	15.3
Tmetonyx cicada	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8
Tryphosites longipes	H	2.7	0.3	0.0	0.0	0.0	0.0	0.0	0.0	47.5
Unciola crenatipalma	H	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Westwoodilla caecula	H	46.7	5.2	0.6	0.0	0.0	0.0	0.0	0.0	310.6
Gammaridea species 1	H	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subordo Hyperiidea										
Hyperia galba	H	0.7	0.3	0.0	0.0	0.0	0.3	0.0	0.0	12.0
Ordo Isopoda										
Subordo Valvifera										
Arcturella dilatata	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.4
Astacilla longicornis	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2
Subphylum Chelicerata										
Classis Pycnogonida										
Anoplodactylus petiolatus	H	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0
Phylum Hemichordata										
Classis Enteropneusta										
Enteropneusta spp.	M	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.2	0.0
Phylum Chordata										
Subphylum Vertebrata										
Superclassis Gnathostomata										
Classis Actinopterygii										
Subclassis Neopterygii										
Ordo Clupeiformes										
Subordo Clupeoidei										
Clupeidae spp. PO	M	5.8	0.3	0.0	0.0	0.0	0.7	0.4	1.6	34.7
Superordo Paracanthopterygii										
Ordo Gadiformes										
Merlangius merlangus PO	M	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Superordo Acanthopterygii										
Ordo Gasterosteiformes										
Subordo Syngnathoidei										
Infraordo Syngnata										
Syngnathinae spp. PO	M	0.0	0.7	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Ordo Scorpaeniformes										
Subordo Cottoidei										
Agonus cataphractus PO	M	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Ordo Perciformes										
Subordo Percoidei										
Trachurus trachurus PO	M	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subordo Trachinoidei										
Ammodytidae spp. PO	M	1.0	0.0	0.0	0.5	2.9	3.8	3.2	0.0	0.0
Echiichthys vipera PO	M	0.3	1.0	3.5	2.9	4.7	7.3	2.1	0.8	0.0
Subordo Gobiesocoidae										
Diplecogaster bimaculata	H	0.0	0.0	0.0	0.5	1.5	0.7	0.4	7.2	0.4
Subordo Callionymoidei										
Callionymus reticulatus PO	M	3.8	0.7	0.9	1.0	1.5	4.8	0.0	0.4	3.7
Subordo Gobioidei										
Gobiidae spp. PO	M	13.1	13.5	0.6	5.8	118.0	28.4	51.0	18.8	10.7
Ordo Pleuronectiformes										
Subordo Pleuronectoidei										
Arnoglossus laterna PO	M	8.2	3.1	0.9	0.5	2.5	8.3	2.1	1.6	0.4
Buglossidium luteum PO	M	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
Limanda limanda PO	M	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	24.4
Microstomus kitt PO	M	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0

Addendum. (continued).

Chapter 2. Evidence for an enriched hyperbenthic fauna in the Frisian front (North Sea)

Ann Dewicke, Veerle Rottiers, Jan Mees & Magda Vincx

Summary

The hyperbenthos of the Frisian front, i.e. an enriched benthic area of the southern North Sea, and surrounding waters was investigated along two cross-frontal transects in August 1994 and April 1996. A total of 111 species was recorded, mainly peracarid crustaceans and decapods. On average, *Calanus* spp. (Copepoda), *Schistomysis ornata* (Mysidacea) and *Scopelocheirus hopei* (Amphipoda) represented more than 40 % of the total density, while *S. ornata* dominated the biomass for 30 %. Community structure differed strongly between both months, as shown by the species composition and the fact that densities and biomasses were much lower in April.

In August, the density of the holohyperbenthos fraction reached quite pronounced peaks in the area coinciding with the Frisian front: densities for chaetognaths, copepods, amphipods and mysids were one order of magnitude higher compared to the surrounding waters. Diversity was also highest at the Frisian front. The high abundances might be explained by active migration and/or by passive transport to the food-enriched area. Merohyperbenthic species showed a less distinct increase in density in the front zone, but a clear south-to-north change in community structure was observed. These species are more heavily subjected to the prevailing tidal flow. The Frisian front fauna seems to be transitional between two merohyperbenthic communities established in late summer, belonging to the environmentally different sandy Southern Bight to the south and the silty Oyster Ground to the north.

In spring, no such hyperbenthic enrichment over the Frisian front was observed. This is most probably due to the strong seasonality of the hyperbenthic fauna and the low water temperature suggesting that production and subsequent recruitment does not have started yet. Alternatively, winter storms could have resuspended particulate organic matter, followed by a rapid reaction of the motile hyperbenthos to more northern depositional areas and thus leading to a temporal density decline. In conclusion, the Frisian front is an enriched area for the hyperbenthos at the end of summer, as was already reported for the benthic system below.

Introduction

The hydrodynamic regime of the North Sea is to a large extent reflected in its sediment granulometry, with a marked discontinuity between the sandy shallow Southern Bight and the silty deeper Oyster Ground. At this boundary, tidal current velocity drops below a critical value, enabling fine-grained material to settle from the water column (Creutzberg & Postma 1979; Creutzberg *et al.* 1984). Favourable conditions generate a vigorous spring phytoplankton bloom and a locally stronger primary production during summer (Baars *et al.* 1991), resulting in high sedimentation of organic matter and leading to an enriched bottom fauna. This enriched benthic zone is referred to as the 'Frisian front' and is located between the -30 and -40 m isobaths, as first reported by Creutzberg *et al.* (1984). The area has been found to act as a boundary between northern and southern communities, as described for macrobenthos and epibenthos (Baars *et al.* 1991). More recently, focus has been put on the quality and quantity of the near-bottom particulate organic matter and its degradation and incorporation into the sediment (Boon & Duineveld 1996, 1998; Boon *et al.* 1998; Dauwe & Middelburg 1998; Dauwe *et al.* 1998, 1999).

Additionally, the Frisian front approximately coincides with the transition between the permanently mixed southern North Sea and the stratified water masses of the central North Sea during summer (Creutzberg 1985). Tidal fronts occur at these boundary areas in a series of near to fixed geographical locations and are characteristic for the summer regime on the northwestern European continental shelf (Simpson *et al.* 1978; Bowers & Simpson 1987; Brown *et al.* 1999).

To date, no information is available on the hyperbenthos of the Frisian front. The hyperbenthos is the faunal element of the benthic boundary layer, i.e. the fauna living in the lower strata of the water column and dependent on the proximity of the bottom (Mees & Jones 1997). Hyperbenthic animals possibly signify a major link in coastal food webs as consumers of detritus, algae and zooplankton and as prey for demersal fish (in particular for postlarval and juvenile life stages) and adult shrimp (Mauchline 1980; Mees & Jones 1997; Beyst *et al.* 1999a; Hostens & Mees 1999; Pedersen 1999; Oh *et al.* 2001). The highly motile hyperbenthic organisms (mainly peracarid crustaceans and early life history stages) often reach high densities in regions with a strong input of organic matter to the bottom environment (Sorbe 1984; Buhl-Jensen & Fosså 1991; Dauvin *et al.* 1994; Mees & Jones 1997). The elevated carbon flux at the Frisian front can thus be expected to attract hyperbenthic species, resulting in an increased density and biomass as compared to surrounding waters.

The aims of this study were (1) to describe the hyperbenthic fauna of the Frisian front during a spring and summer situation in terms of species composition, density, biomass and diversity; (2) to investigate structural characteristics of the hyperbenthic community along a cross-frontal gradient in order to discover a possible shift in community structure at the Frisian front.

Material and methods

Sampling

The Frisian front (15 km wide) is approximately located between 53° 30' N - 4° E and 54° N - 5° E and between the -30 and -40 m isobaths (Baars *et al.* 1991). Sampling was done along two parallel south-to-north transects (transects A and B) perpendicular to the isobaths and covering the front and the surrounding waters. Six sites were selected along transect A (from site A1 to A6); only four sites were sampled along the shorter transect B (from site B1 to B4). According to the geographic position of the Frisian front, four sites were situated in the front zone, three to the south and three to the north. All sites were sampled on two occasions: in August 1994 (the 30th) and in April 1996 (the 16th, except site B1 and B4 which were both sampled on the 25th). In April 1996, two additional sites (site A7 and B5) north of the study area were sampled. A total of 22 samples were assessed; the geographical position of the sampling sites is presented in Fig. 1.

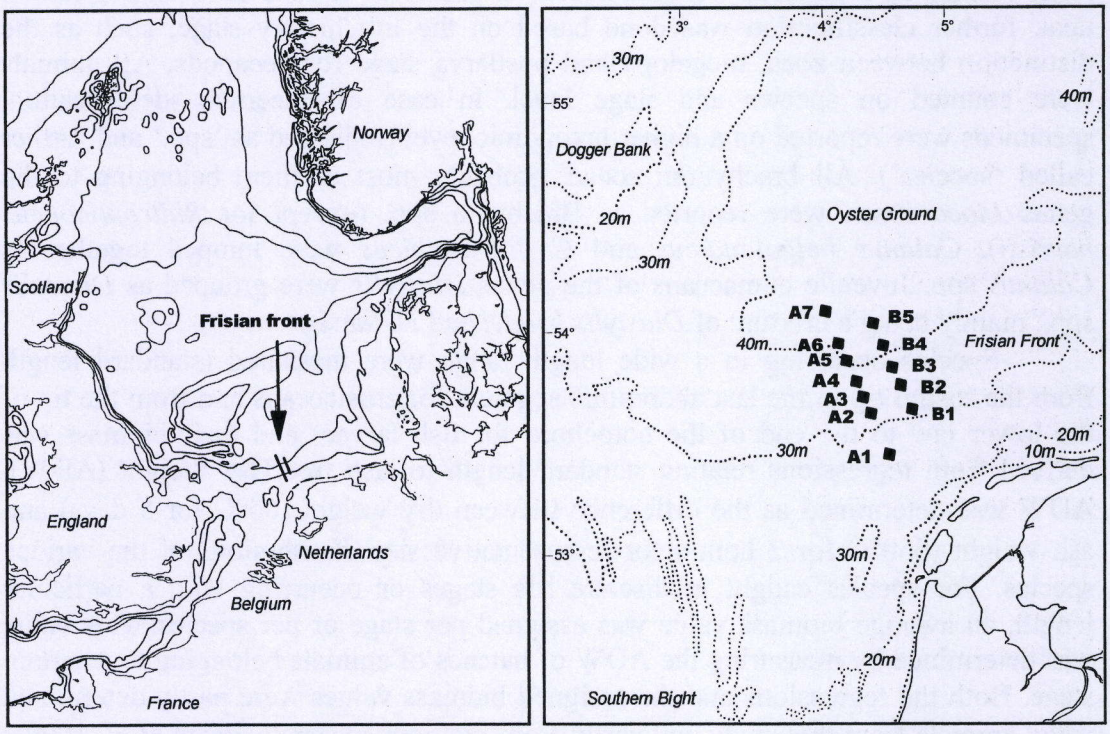

Fig. 1. Study area and position of the transects A and B with indication of sampling sites.

Sampling was done from the *RV* Belgica with a modified hyperbenthic sledge after Sorbe (1983). Two superimposed nets (1 mm mesh size, 3 m long, 71 cm wide) were fixed on the sledge and sampled the water layer from 0 to 50 cm (lower net) and from 50 to 100 cm (upper net) above the sea floor. The sledge was equipped with an opening-closing mechanism and an odometer (for details see Sorbe 1983). A flow meter (*Hydrobios 438-110*) was fixed in the upper net. All sampling was carried out during daytime, against the current and at an average ship speed of 1.5 knot relative to the bottom. Towing lasted 5 minutes for the August samples; in April towing duration was doubled (10') because of poor catches. Average towing distance was 258 ± 16.0 m in August and 503 ± 27.0 m in April; the volume filtered per net amounted to 100 ± 5.3 m^3 and 184 ± 17.8 m^3, respectively. The catches from the upper and lower net were rinsed separately over a 1 mm mesh size sieve and preserved in a buffered formaldehyde solution (7 % final concentration).

Surface temperature and salinity (thermosalinograph *Sea-bird SBE21*) and *in situ* depth were registered. Additionally - only for the August campaign - a box corer (*Reineck*) was lowered at each site, the upper 2 cm of the sediment being sampled for grain fraction analysis (particle size analyser *Coulter LS 100*). Median grain size and percentage mud (<63 µm, considered as the organic and inorganic fraction superimposed) were calculated for each site.

Data acquisition

After sorting, all organisms were identified - if possible - to species level. For certain taxa, further classification was done based on the life history stage, such as the distinction between zoea, megalopa and postlarva stage for decapods. All animals were counted on species and stage level. In case of uncertain identification, specimens were reported on a higher taxonomic level (indicated as 'spp.' and further called 'species'). All brachyuran zoeae, probably most of them belonging to the genus *Liocarcinus*, were reported as Brachyura spp. (except for *Rhitropanopeus harrisii*). *Calanus helgolandicus* and *C. finmarchicus* were lumped together as *Calanus* spp. Juvenile cumaceans of the genus *Diastylis* were grouped as *Diastylis* spp., mainly being a mixture of *Diastylis bradyi* and *D. laevis*.

Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans and from the tip of the lower jaw to the end of the notochord for fish larvae) and their biomass was derived from regressions relating standard length to Ash free Dry Weight (ADW). ADW was determined as the difference between dry weight (60°C for 5 days) and ash weight (650°C for 2 hours) for representative size distributions of the various species. For species caught in discrete life stages or occurring with a particular length, an average biomass value was assigned per stage or per species. This value was determined by measuring the ADW of batches of animals belonging to a certain stage. Both the regressions and the assigned biomass values were partly determined using animals from this study and partly from previous research (Beyst *et al.* 1999a; A. Dewicke unpubl. data).

After finishing all identification, non-hyperbenthic species were removed from the 'catch-dataset', i.e. all animals that were caught by the Sorbe-hyperbenthic sledge and which were retained on a 1 mm sieve. This way, juvenile and adult decapods and fish, polychaetes (except Tomopteridae), scyphozoans, echinoderms, fish eggs and all sedentary organisms were excluded (see Introduction). Additionally, the hyperbenthos was divided into its holo- and merohyperbenthic representatives.

Holohyperbenthos is defined as animals that spend variable periods of their adult life in the hyperbenthal zone (Mees & Jones 1997). It comprises a group of taxa with a rather small adult habitus (generally < 20 mm), such as all peracarids, copepods, chaetognaths and hydromedusae. The merohyperbenthos consists of early life history stages, generally originating from larger animals, and is mainly represented by decapod larvae (< 10 mm) and postlarval fish (< 20 mm) (modified after Mees & Jones 1997). The resulting species list of all hyperbenthos is presented in the Addendum. Density and biomass data were calculated as numbers of individuals and mg ADW per 100 m^{-2}. Since catch efficiency of sledges remains largely unknown (Mees & Jones 1997), all densities and biomass values are considered as minimum estimates.

Data analysis

Seasonal differences and spatial trends along the cross-frontal gradient were investigated. The two extra April samples north of the study area were omitted from the dataset, except for examining the total species composition. Holo- and merohyperbenthos were considered separately for describing species composition, density, biomass and diversity. Hill's diversity numbers N_0, N_1 and N_2 were calculated per sample (Hill 1973). N_0 is equal to the number of species, N_1 is the inverted natural logarithm of the Shannon-Wiener diversity index and N_2 is the reciprocal of Simpson's dominance index. Hurlbert's modification of Sanders' rarefaction curves (Hurlbert 1971) was used to calculate diversity for standardized sample size, allowing comparison between different sites and seasons: $E(S_{100})$ determines the expected number of species present in a sample of 100 individuals. Species reported on a higher taxon level were considered as a single species if no other representative of the same taxon level was present or if they were distinctly different. Thus, diversity is considered as a minimum estimate.

Additionally, raw density data were fourth root transformed (Field *et al.* 1982; Legendre & Legendre 1998) and ordination techniques were performed, using the program package CANOCO 4 (ter Braak & Smilauer 1998). First, an exploratory Detrended Correspondence Analysis (DCA) was performed for estimating the gradient length (g.l.) of species turnover in standard deviation units (s.d.), which gives an indication of the expected underlying model for species response curves (unimodal or linear) (ter Braak & Prentice 1988; Van Wijngaarden *et al.* 1995). Indirect techniques were further applied to detect any gradients in community structure. Principal Components Analysis (PCA) (linear method) was applied on the holohyperbenthos data (g.l. 2.370 s.d.) and Correspondence Analysis (CA) (unimodal method) was used for merohyperbenthos (g.l. 3.283 s.d.). Spearman rank's correlation coefficient (r_s) (Sokal & Rohlf 1995) was calculated between the abundance of the most common species and some environmental variables.

Results

The Frisian front is considered as the area between the -30 and -40 m isobaths, with geographical coordinates as described by Baars *et al.* (1991). The median grain size ranged from 99 to 296 µm. Along both transects, medium sandy sediments in the south were gradually displaced by very fine sands towards the north. Total mud fraction increased with depth from 0 up to nearly 40 % (see Fig. 5); *in situ* depth is shown in the same figure. Surface temperature was on average 17.4 ± 0.12 °C in August and 5.4 ± 0.20 °C in April; mean values for surface salinity were 34.2 ± 0.08 psu and 34.2 ± 0.15 psu, respectively.

Seasonality

The number of species encountered in the hyperbenthal zone was slightly higher for August (84 species) compared to April (70 species); 111 species were recorded in total (see Addendum). The holohyperbenthos showed a strong overlap in species composition between both months, except for hydromedusae (Table 1). Amphipods were the most diverse group: 36 species were recorded in total. Other species mainly belonged to the Mysidacea (9 species), the Cumacea (6 species) and the Copepoda (6 species). The merohyperbenthos community was much poorer in species numbers in April (14 species) than in August (30 species). Nearly all decapod species caught in April (8 species), were also present in August (21 species). This was not so for fish larvae for whom only postlarval Ammodytidae were reported in both months.

	Only in August	Only in April	In both months	In total		Only in August	Only in April	In both months	In total
Holohyperbenthos					**Merohyperbenthos**				
Hydromedusae	3	7	1	9	Polychaeta	0	1	0	1
Ctenophora	1	1	1	1	Cephalopoda	1	0	0	1
Polychaeta	1	0	0	1	Caridea	8	2	2	8
Chaetognatha	2	2	2	2	Thalassinidea	2	2	2	2
Copepoda	5	3	2	6	Anomura	5	3	2	6
Nebaliacea	1	1	1	1	Brachyura	6	1	1	6
Euphausiacea	1	1	1	1	Pisces	8	5	1	12
Mysidacea	8	7	6	9					
Cumacea	6	5	5	6					
Amphipoda	24	28	15	36					
Isopoda	2	0	0	2					
Pycnogonida	0	1	0	1					
Total	54	56	34	75	Total	30	14	8	36

Table 1. The number of species recorded per taxonomic group. A distinction is made between species numbers that were only reported in August, only reported in April and encountered in both months. T0he last column refers to the total number of species per taxonomomic group.

In August, average total density and biomass for holohyperbenthos amounted to 1019 ± 303.4 ind. 100 m^{-2} and 195 ± 55.3 mg ADW 100 m^{-2}, respectively. Hydromedusae (mainly *Mitrocomella* spp.) were numerically dominating (40 %) (Fig. 2A). Subdominant taxa, i.e. amphipods, chaetognaths, mysids and copepods, each contributed for approximately 15 % (or 150 ind. 100 m^{-2}) of the total density. The gravimetrical composition of the total biomass was quite different, yet more than 62 % was accounted for by the mysid fauna alone (mainly *Schistomysis ornata*). Density and biomass mean values for merohyperbenthos were much lower (152 ± 29.6 ind. 100 m^{-2} and 139 ± 35.5 mg ADW 100 m^{-2}, respectively). The merohyperbenthos consisted for nearly 90 % of decapod larvae in August (mainly postlarval Processidae). Yet, its biomass was dominated by fish larvae (66 %) with postlarval gobies as main representatives.

Average density and biomass of the holohyperbenthos were nearly one order of magnitude lower in April (132 ± 23.3 ind. 100 m^{-2} and 30 ± 4.6 mg ADW 100 m^{-2}, respectively). Dominance among major taxonomic groups also changed (Fig. 2B). The dominant taxa in terms of density were the ctenophores (39 %), the copepods (29 %) and the mysids (15 %). As in August, mysids dominated the total biomass (70 %), but the highest contribution was delivered by *Schistomysis spiritus* in this month. Also for the merohyperbenthos, much lower density (19 ± 2.8 ind. 100 m^{-2}) and biomass values (8 ± 1.4 mg ADW 100 m^{-2}) were reported in April. Fish larvae (mainly postlarvae of *Merlangius merlangus* and Ammodytidae) were the most important taxa, both for density as for biomass. Decapod abundance was low in April and most individuals were still in the zoea stage.

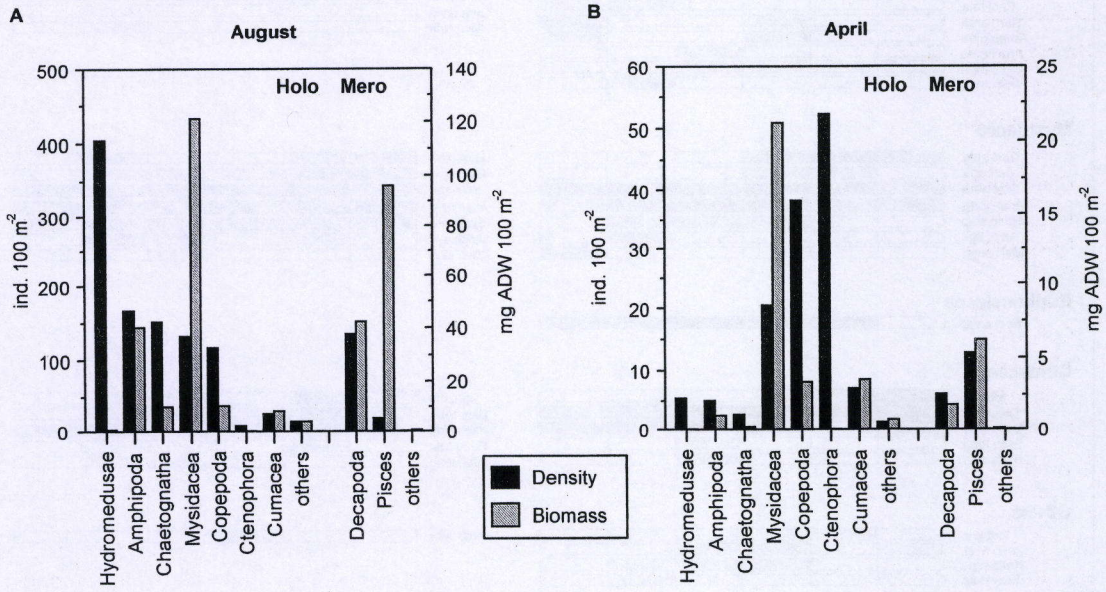

Fig. 2. Mean density and biomass for the major taxonomic groups in **(A)** August, **(B)** April; holohyperbenthos (holo), merohyperbenthos (mero).

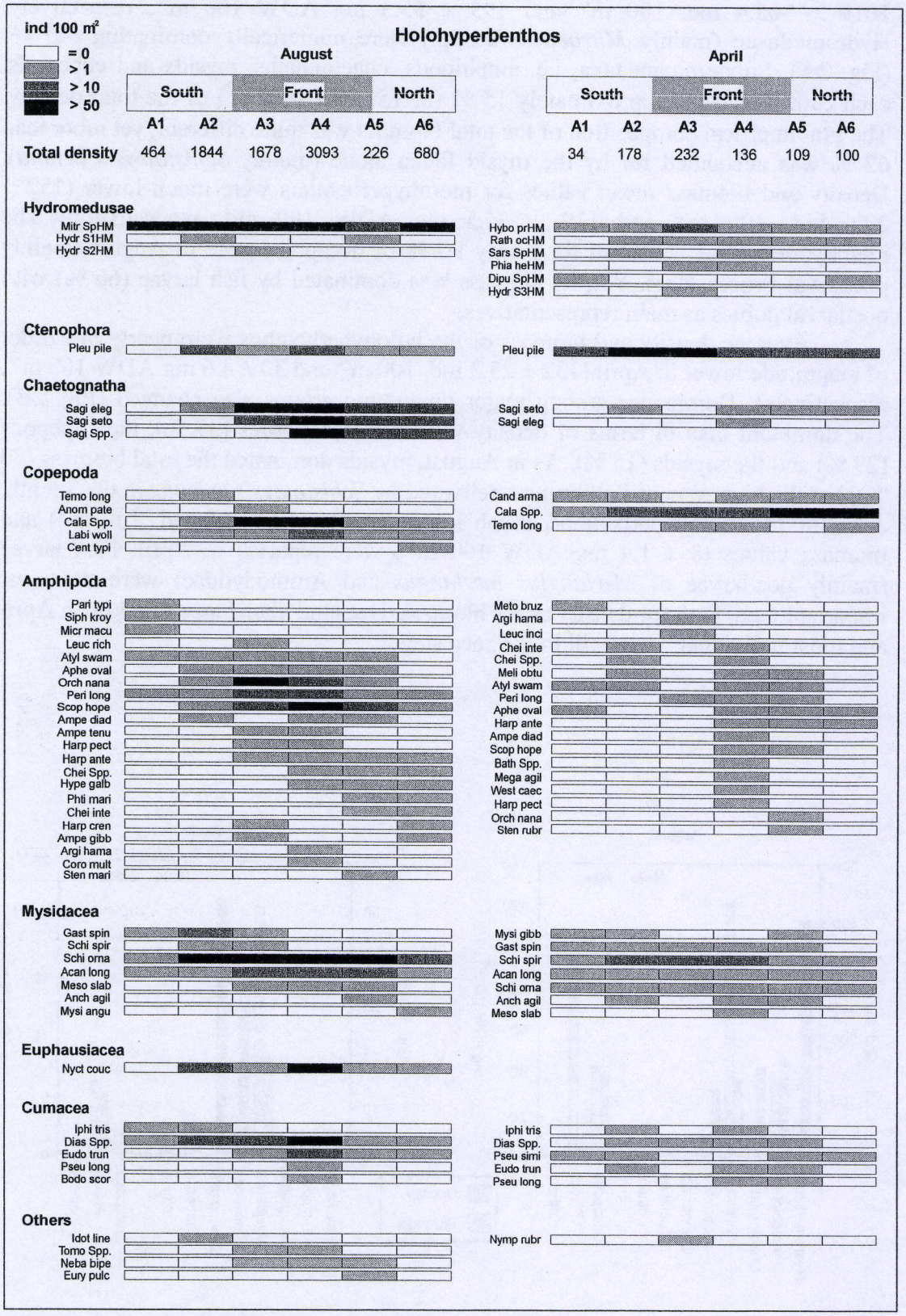

Fig. 3. Distribution patterns for all holohyperbenthic species along transect A in August **(left)** and April **(right)**, representing gross density classes; total density is expressed as ind. 100 m^{-2}. Abbreviations of species names are given in the Addendum.

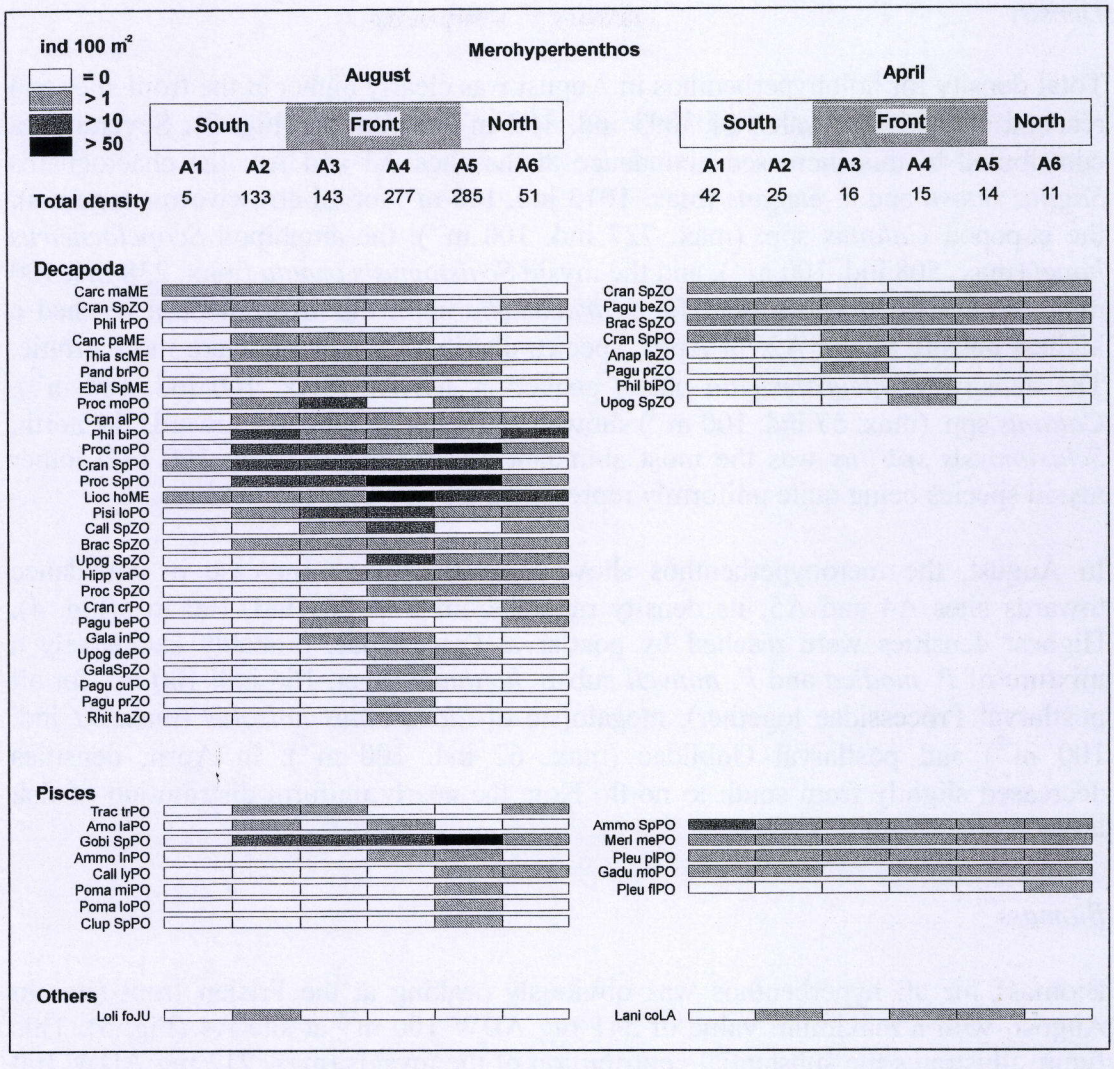

Fig. 4. Distribution patterns for all merohyperbenthic species along transect A in August **(left)** and April **(right)**, representing gross density classes; total density is expressed as ind. 100 m^{-2}. Abbreviations of species names are given in the Addendum.

Community structure along the south-to-north gradient

Density

Total density for holohyperbenthos in August was clearly higher at the front sites and reached a maximum value of 3093 ind. 100 m^{-2} at site A4 (Fig. 3). Several taxa contributed to this increased abundance at the sites A3 and A4: the chaetognaths *Sagitta setosa* and *S. elegans* (max. 1013 ind. 100 m^{-2} for all arrowworms together), the copepod *Calanus* spp. (max. 727 ind. 100 m^{-2}), the amphipod *Scopelocheirus hopei* (max. 508 ind. 100 m^{-2}), and the mysid *Schistomysis ornata* (max. 238 ind. 100 m^{-2}). Such a trend was absent for *Mitrocomella* spp.; this hydromedusa reached a highest density at site A2. In April, species distribution patterns were more erratic. The density of *Pleurobrachia pileus* peaked at site A3 (max. 160 ind. 100 m^{-2}), *Calanus* spp. (max. 57 ind. 100 m^{-2}) showed an incline in numbers towards the north. *Schistomysis spiritus* was the most abundant mysid (max. 37 ind. 100 m^{-2}), other mysid species being quite uniformly represented although in low numbers.

In August, the merohyperbenthos showed a rather weak increase in abundance towards sites A4 and A5; its density ranged from 5 to 285 ind. 100 m^{-2} (Fig. 4). Highest densities were reached by postlarval Processidae, probably exclusively a mixture of *P. modica* and *P. nouveli* subsp. *holthuisi* (max. 160 ind. 100 m^{-2} for all postlarval Processidae together), megalopae of *Liocarcinus holsatus* (max. 92 ind. 100 m^{-2}) and postlarval Gobiidae (max. 62 ind. 100 m^{-2}). In April, densities decreased slightly from south to north. Note the nearly uniform distribution of fish larvae.

Biomass

Biomass for all hyperbenthos was obviously peaking at the Frisian front sites in August, with a maximum value of 541 mg ADW 100 m^{-2} at site A4 (Fig. 5). This figure illustrates the substantial contribution of the mysids (max. 212 mg ADW 100 m^{-2}) to the total biomass at the Frisian front area. Smaller organisms such as amphipods, copepods and chaetognaths attained biomass values, which were often one order of magnitude higher at the Frisian front as compared to the surrounding waters (max. 179 mg ADW 100 m^{-2}, 68 mg ADW 100 m^{-2} and 67 mg ADW 100 m^{-2}, respectively). A different trend was found for merohyperbenthic taxa. The biomass for decapod larvae was only slightly higher at the front sites (max. 80 mg ADW 100 m^{-2}), highest biomass for fish larvae was reached at site A5 (330 mg ADW 100 m^{-2}). In April, the total biomass varied between 18 and 68 mg ADW 100 m^{-2} without any conspicuous changes along the transect (not figured).

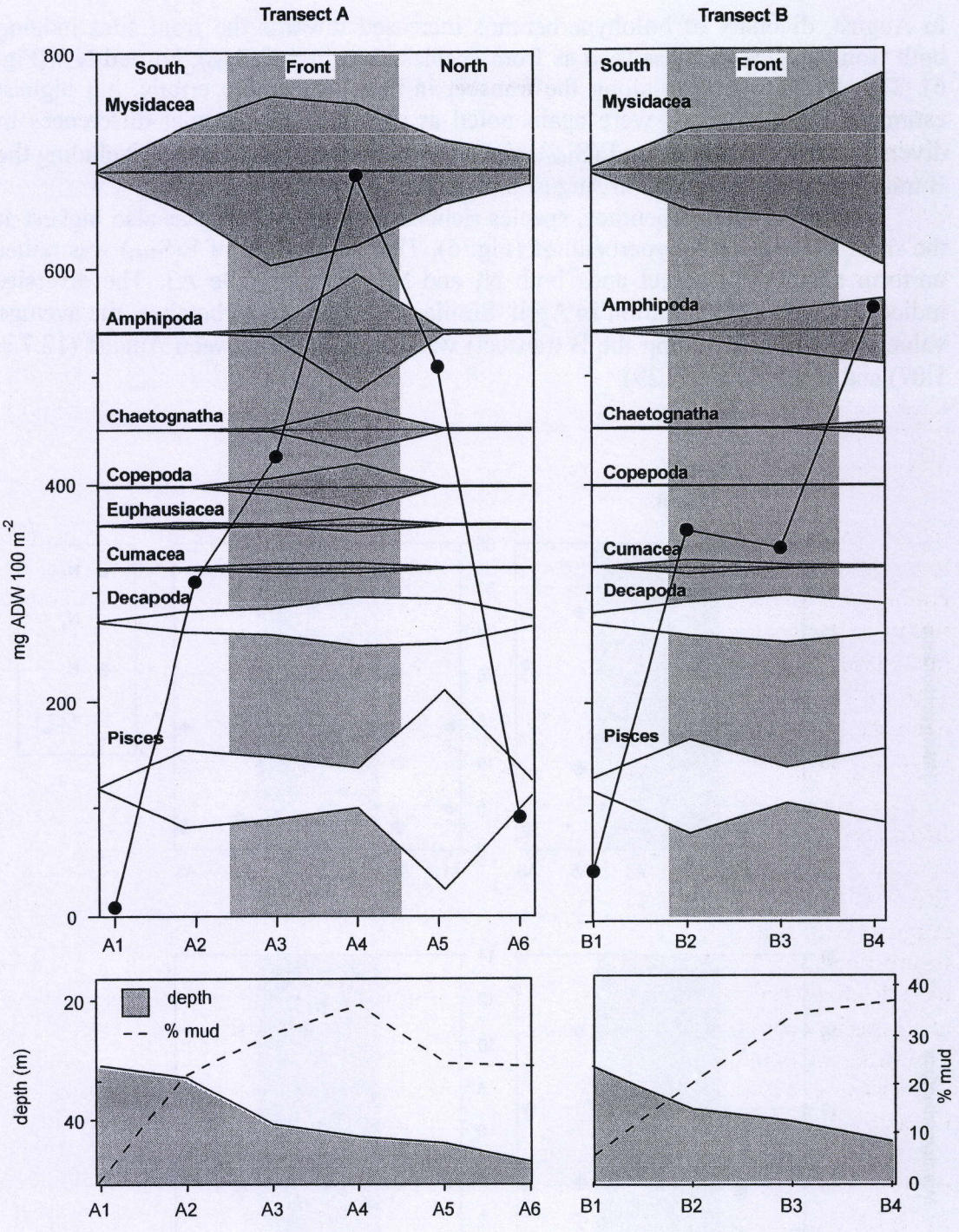

Fig. 5. The August biomass distribution along transect A **(left)** and B **(right)** for the total hyperbenthos and for the main taxonomic groups, together accounting for > 97 % of the total biomass. Total biomass corresponds with the y-axis and is represented by dots connected with a full line. Biomass per taxonomic group is shown as kite diagrams; the same scale was used for all taxa, for absolute values is referred to the text. The shaded area represents the geographical position of the Frisian front between the -30 and -40 m isobaths. *In situ* Depth (left axis) and % mud (< 63 µm) (right axis) along both transects are also figured **(bottom)**.

Diversity

In August, diversity of holohyperbenthos increased towards the front sites judging both from species richness (N_0) as from species diversity ($E(S_{100})$, N_1 and N_2) (Fig. 6). The diversity pattern along the transect in April was more erratic, but highest estimates for all indices were again noted at site A4. No seasonal differences in diversity existed considering $E(S_{100})$, since the mean value for all sites (including the B transect) was 10.6 ± 1.28 in August and 11.7 ± 1.03 in April.

As for holohyperbenthos, species richness (N_0) in August was also highest at the front sites for merohyperbenthos (Fig. 6). The distribution of $E(S_{100})$ was rather uniform along the transect and both N_1 and N_2 peaked at site A3. The diversity indices showed little variation in April. Similar as for holohyperbenthos, the average value of $E(S_{100})$ (including the B transect) was comparable between August (12.7 ± 1.07) and April (11.6 ± 0.29).

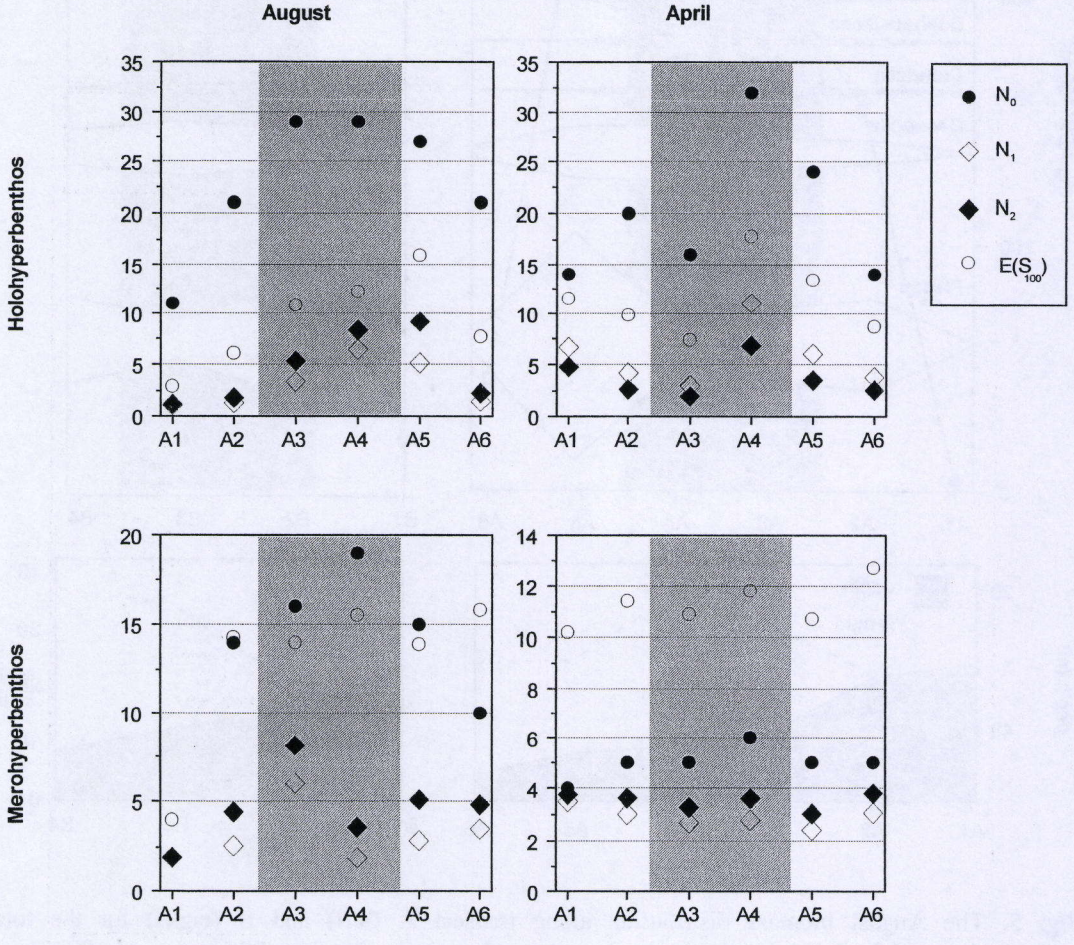

Fig. 6. Hill's diversity numbers N_0, N_1 and N_2 and the expected numbers of species $E(S_{100})$ along transect A, for holo- **(top)** and merohyperbenthos **(bottom)**, separately presented for August **(left)** and April **(right)**. The shaded area represents the geographical position of the Frisian front between the -30 and -40 m isobaths.

Ordination

Eigenvalues for the PCA analysis performed on the holohyperbenthos density data were 0.489 for the first axis and 0.150 for the second axis. They display together 63.9 % of the species variance (Fig. 7). Seasonal patterns appear along the first axis since the April samples (left) are separated from the August samples (right). However, the August samples situated south to the Frisian front (A1 and A2) have a comparable score on the first axis as the April samples. They therefore show a high resemblance.

Axis one (eigenvalue 0.719) and axis two (eigenvalue 0.183) of the CA analysis applied on merohyperbenthos densities represent together 49.3 % of the species variance (Fig. 7). Judging from the much higher eigenvalue of the first axis compared to the other axes, the seasonal separation shown in Fig. 7 is strong. Yet, a distinct and meaningful pattern did appear along the second axis. The August samples are spread according to their geographical position from south to north. No such pattern was found for April since all samples are rather lumped together.

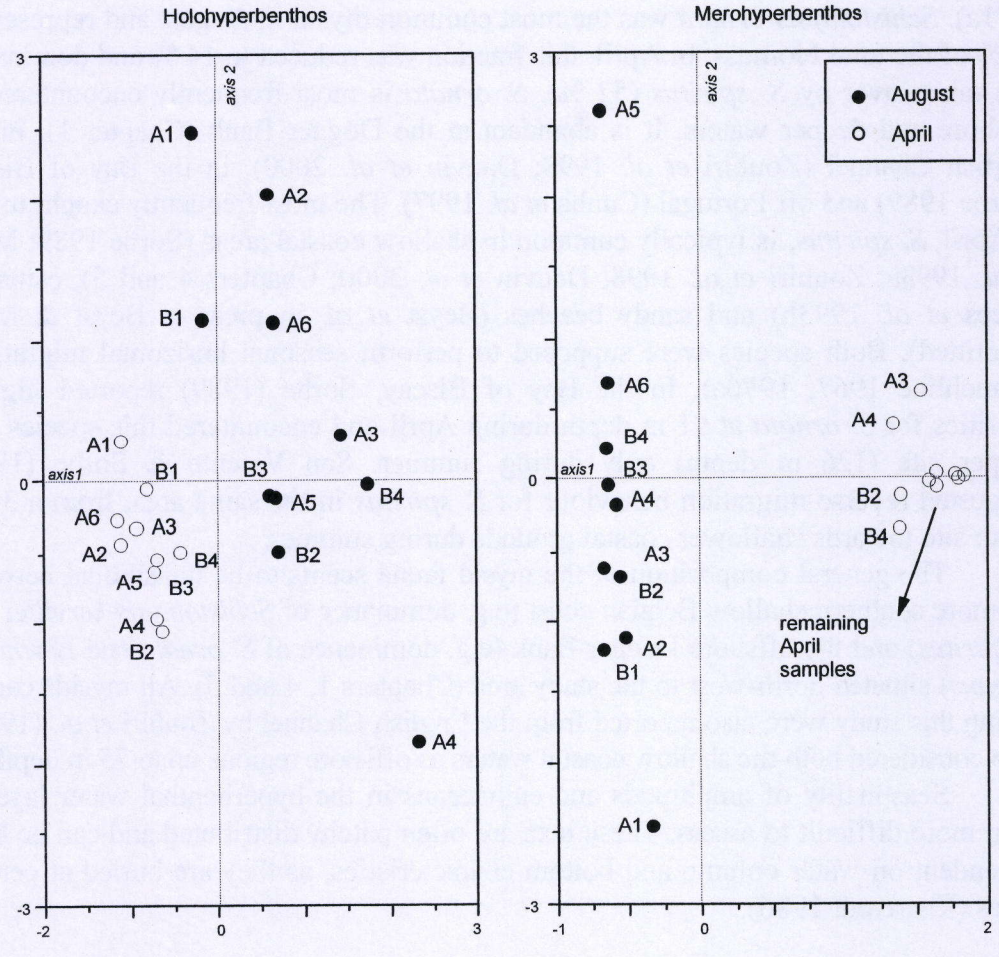

Fig. 7. Ordination diagrams resulting from the multivariate techniques performed on the holohyperbenthos **(left)** and merohyperbenthos **(right)** species densities. Eigenvalues for the PCA analysis on holohyperbenthos are 0.489, 0.150 and 0.183 for the first to third axis, respectively. Axis one and two represent together 63.9 % of the species variance. CA analysis on merohyperbenthos has eigenvalues of 0.719 (axis one), 0.183 (axis two) and 0.173 (axis three). The diagram formed by the first and second axis represents 49.3 % of the species variance.

Discussion

Seasonality

The April hyperbenthos differed structurally from August. Species composition altered, densities and biomasses were much lower and south - north related patterns were not prominently present. It is important to stress that both surveys were not conducted during the same year. The August samples were taken in 1994 and the April ones two years later (in 1996). The hyperbenthos is often characterized by a strong seasonality in community structure, particularly in shallow waters (Sorbe 1989; Mees & Jones 1997; Cunha *et al.* 1999; Vallet & Dauvin 1999; Beyst *et al.* in press a, Chapters 5 and 6). The change in species composition was mainly due to the seasonal occurrence of planktonic representatives, like hydromedusae and fish larvae (Table 1).

Temporal density fluctuations of mysids can be real, i.e. through recruitment, or apparent, i.e. caused by their migration and aggregation behaviour (Mauchline 1971a). *Schistomysis ornata* was the most common mysid in August and represented 59 % of the total biomass. In April, this fraction was reduced to 14 % and dominance was taken over by *S. spiritus* (52 %). *S. ornata* is most frequently encountered in offshore and deeper waters. It is abundant at the Dogger Bank (Chapter 1), in the English Channel (Zouhiri *et al.* 1998; Dauvin *et al.* 2000), in the Bay of Biscay (Sorbe 1989) and off Portugal (Cunha *et al.* 1997). The most frequently caught mysid in April, *S. spiritus*, is typically common in shallow coastal areas (Sorbe 1989; Mees *et al.* 1993a; Zouhiri *et al.* 1998; Dauvin *et al.* 2000; Chapters 4 and 5), estuaries (Mees *et al.* 1993b) and sandy beaches (Beyst *et al.* in press a; Beyst & Mees submitted). Both species were supposed to perform seasonal horizontal migrations (Mauchline 1967, 1970a). In the Bay of Biscay, Sorbe (1989) reported highest densities for *S. ornata* at 91 m depth during April and encountered this species at a deeper site (126 m depth) only during summer. San Vicente & Sorbe (1995) suggested reverse migration behaviour for *S. spiritus* in the same area, from a 30 m depth site towards shallower coastal grounds during summer.

The general composition of the mysid fauna seems to be transitional between the more southern shallow Belgian coast (e.g. dominance of *Schistomysis kervillei* and *S. spiritus*) and the offshore Dogger Bank (e.g. dominance of *S. ornata* and *Erythrops elegans*) situated north-west to the study area (Chapters 1, 4 and 5). All mysids caught during this study were also reported from the English Channel by Zouhiri *et al.* (1998), who considered both the shallow coastal waters as offshore regions up to 75 m depth.

Seasonality of amphipods and cumaceans in the hyperbenthal water layer is even more difficult to assess. These taxa are often patchy distributed and can be both dependent on water column and bottom characteristics, as they are buried at certain times (Kaartvedt 1986).

According to Lindley (1987, 1998), seasonal occurrence of decapod larvae is much more related to temperature than are seasonal cycles of holoplankton (e.g. copepods, chaetognaths). Data from the continuous plankton records in the North Sea revealed an increase in species numbers of decapod larvae through the year from January (no larvae) to August (30 species) (Lindley 1998). Average temperature recorded in April at the Frisian front was only 5.4 °C, which is probably still too low to start

reproduction and subsequent larval recruitment for most decapod species. This therefore most likely explains their low densities.

Larval Processidae were the most common decapods encountered in August. This taxon is less common in the nearby S Dutch and Belgian coastal waters, where *Crangon crangon* larvae are dominant (Hamerlynck & Mees 1991, Chapters 4 and 5). Larvae of *Philocheras bispinosus* are dominant around the Dogger Bank at that time of the year (Chapter 1).

Markedly, fish larvae were much more abundant at the Frisian front during summer, compared to the Belgian coast and the Dogger Bank; postlarval gobies were the dominant fish for these three mentioned areas (Chapters 1 and 4). Temporal distribution of fish larvae is often sharply restricted to a certain period of the year, which is species-specific and mostly very short (Beyst *et al.* 1999b; Beyst *et al.* in press a, Chapter 5). This is illustrated in this study by the strong difference in species composition for fish larvae between August and April.

Thus, it is postulated that the observed seasonal pattern results from a complex variety in species-specific ecology and life history traits of the hyperbenthic fauna, in addition to density fluctuations caused by generating offspring.

August

Holohyperbenthos

The summer holohyperbenthos showed some drastic changes in community structure at the Frisian front area. Several species attained maximum densities between the -30 and -40 m isobaths, which were often one order of magnitude higher than those recorded for surrounding waters. Increased abundances were mainly caused by holohyperbenthic species as concluded from their distribution along the transect; only the hydromedusae of the genus *Mitrocomella* showed a reverse pattern (Fig 3). The Frisian front thus seems to attract a variety of species that most probably take advantage of the increased food supply. The bottom enrichment of the Frisian front that was first described by Creutzberg (1985) was still a fact in August 1994, as confirmed by Boon & Duineveld (1996), Dauwe & Middelburg (1998) and Dauwe *et al.* (1998), who conducted field campaigns in the this month. High sedimentation of particulate organic matter at the Frisian front did occur and the incorporation of chlorophyll *a* into the sediment was > 10 times higher compared to the Broad Forteens (located south of the Frisian front) (Dauwe *et al.* 1998). Macrofauna biomass was also reported to be 7 times higher (Dauwe & Middelburg 1998).

The abundance of several species was significantly correlated with the percentage of mud in the sediment, as indicated for the mysid *Schistomysis ornata* (r_s = 0.85, $p < 0.005$). As mysids are good swimmers and omnivores (Mauchline 1980), it is suggested that *S. ornata* actively migrates to the food-enriched area. This species reached also highest abundances at the more muddy sites of the Dogger Bank (Chapter 1). Likewise, the high densities reported for the lysianassid amphipods *Scopelocheirus hopei* (r_s = 0.84, $p < 0.005$, for density vs. % mud) and *Orchomenella nana* (r_s = 0.68, $p < 0.05$, for density vs. % mud) - typical scavengers and less dependent on burrowing into the sediment (Vallet & Dauvin 1998) - may be linked with their motile behaviour. Mysids and amphipods delivered the major part (83 %) of the total biomass at the Frisian front. Most mysids utilize organic detritus to a considerable extent (Kost & Knight 1975; Jansen 1985; Fockedey & Mees 1999) and

therefore they might add to the remineralisation of refractory organic matter. Since they often contribute substantially to the diet of juvenile demersal fish (Mees & Jones 1997), their presence might be of significance for sustaining the rich fauna at the Frisian front system.

The density of the planktonic taxa *Sagitta* spp. and *Calanus* spp. was also significantly correlated with the mud content of the bottom ($r_s = 0.85$, $p < 0.005$ and $r_s = 0.78$, $p < 0.01$, respectively). For both taxa, a striking increase in density at the front sites was noted, being 22 and 85 times higher compared to the surrounding sites, respectively. Despite having a planktonic behaviour, copepods can maintain themselves within topographic locations by tide related vertical migration (Wooldridge & Erasmus 1980; Kimmerer & McKinnon 1987; Hough & Nayler 1991). They may respond to the elevated summer primary production at the Frisian front as previously reported by Kuipers *et al.* (1991) and/or to the enhanced carbon flux. Chaetognaths are strictly carnivorous, mainly feeding on copepods (Stuart & Verheye 1991; Alvarez-Cadena 1993; Frid *et al.* 1994; Baier & Purcell 1997; Froneman *et al.* 1998). Hourly sampling data revealed that their vertical migration closely follows that of large calanoid copepods (Stuart & Verheye 1991).

A response of the hyperbenthic fauna to increased inputs of organic matter to the bottom environment was already mentioned by several authors (e.g. Sorbe 1984; Buhl-Jensen & Fosså, 1991; Dauvin *et al.* 1994; Mees & Jones 1997), but the particular relation with primary production and/or degraded organic matter remains often unclear. This is mainly due to the lack of knowledge on trophic structure for the fauna thriving in the hyperbenthal zone. Chevrier *et al.* (1991) found highest densities for hyperbenthic amphipods in areas of high primary production, but scavengers and predators had a similar success in less productive areas. According to Vallet & Dauvin (1998), peracarids and decapods occurring in the hyperbenthos are relatively independent of primary production, reaching highest biomasses in eutrophic conditions. Hamerlynck & Mees (1991) also noted highest densities in sheltered areas where organic matter may settle. It should be clear that having a high swimming ability facilitates an efficient foraging behaviour (Mees & Jones 1997; Vallet & Dauvin 1998) and therefore fastens the response to available food sources in competition with other benthic animals. Rapid reaction to the extensive food supply at the Frisian front was also suggested for *Amphiura filiformis* (Ophiuroidea) being a suspension feeder and to a lesser extent, a deposit feeder (Duineveld & van Noort 1986).

Merohyperbenthos

The merohyperbenthos showed a smoother density increase along the transects with highest values at the northern part of the Frisian front. This fauna has a more planktonic lifestyle and is thus more vulnerable to the prevailing currents. The gradually changing community structure along the south-to-north gradient, judging from the ordination analysis, was conspicuous (Fig. 7). This indicates that the Frisian front harbours a transitional community between the two communities established in late summer in the environmentally different Southern Bight (south of the Frisian front) on the one hand and the Oyster Ground (north of the area) on the other. A similar trend was observed for macrobenthic communities in the studied area. Holtmann *et al.* (1996) identified three macrobenthos communities: a Frisian front

community, an Oyster Ground community and a Southern Bight community, with the Frisian front community characterized by highest densities and biomasses. Benthic species showed even a marked zonation from south to north corresponding with a succession in feeding types (Creutzberg *et al.* 1984). A change in species composition was also found for the epibenthos (Baars *et al.* 1991). Less evidence is available for the pelagic surroundings. Only Boon *et al.* (1998) mentioned a shift in algal families south and north of the Frisian front.

Additionally, hydrodynamic processes as associated with tidal mixing fronts - a summer phenomenon occurring in the study area (Simpson *et al.* 1978; Bowers & Simpson 1987; van Aken *et al.* 1987; Bo Pedersen 1994; Tett & Walne 1995) - might affect the distribution of planktonic organisms. In this view, two different water masses, each characterized by a distinct merohyperbenthic community, might meet at the approximate location of the Frisian front. Such a community transition has been reported for the tidal front off the east coast of England by Lindley & Williams (1994). These authors found a close relation between the position of the tidal front and the geographical division between plankton assemblages. Data from this study are too scarce to assess this complex phenomenon though. Yet, such fronts are known to act as community boundaries (Longhurst 1998) and are suggested to be biological 'hot spots', with a significant change in productivity, structure and diversity at the higher trophic levels in the pelagic food web (Nielsen & Munk 1998).

Early spring situation

Several hypotheses can be put forward to explain the temporary disappearance of the above discussed summer enrichment, i.e. the spatial pattern across the Frisian front. They might even act in concert. First of all, the low April temperature suggests that the benthic area will still be low in production and biological activity. Food supply for the holohyperbenthos is therefore believed to be much more pronounced during summer. The absence of a south-north related structure for the merohyperbenthos is most probably due to its poor development early in the year. Another possible explanation appears after considering the two extra sites (site A7 and B5) sampled in April, north of the study area (Fig. 1). The holohyperbenthos reached a density peak of more than 600 ind. 100 m^{-2} at site A7, and a less distinct density peak of 230 ind. 100 m^{-2} at site B5 while more southern densities were on average 75 ± 10.9 ind. 100 m^{-2}. The abundances at these northern sites were in the same order as the ones reported in August for the waters surrounding the Frisian front. Enhanced abundance was not due to a sudden incline for one or a few species, but was an overall feature. The most abundant species at site A7 were *Calanus* spp. (242 ind. 100 m^{-2}), *Schistomysis ornata* (99 ind. 100 m^{-2}) and *Diastylis* spp. (84 ind. 100 m^{-2}), which were all frequently caught during the August campaign. Apart from seasonal migration patterns as discussed for *Schistomysis ornata* and *S. spiritus*, one might suppose that the enrichment in the hyperbenthal layer has temporally shifted to a more northern position. The motile hyperbenthos might respond quickly to local variations in food supply, by active migration to more favourable feeding areas or alternatively by being transported with the prevailing current to deposition areas of suspended matter. In fact, sedimentation processes in the area have a seasonal character as mentioned by van Raaphorst *et al.* (1998). Suspended matter originates from the turbidity plume from SE England and is transported by the residual current into a north-eastwards direction, settling in the calmer waters of the Frisian front during spring and summer. Resuspension processes occur during autumn and winter

and the material is ultimately deposited in the Skagerrak and Norwegian Channel area (Eisma & Kalf 1987; van Raaphorst *et al.* 1998). And finally - although the sampling interval of this study was less than two years - one might not want to exclude the possibility of a long-term decline such as recorded for the macrobenthos community of the area during the nineties (Frisian front 1999).

Conclusions

During summer, the Frisian front harbours an enriched fauna in the hyperbenthal zone, both in densities as in species. Hyperbenthic motile species might be attracted by and therefore actively migrate to the organically enriched area. The advantage of the motility of the hyperbenthos as compared with endofauna is that they are less vulnerable to spatial or temporal variations of organic deposition. They are able to simply move to more tempting feeding areas. In times of scarce food supply to the surrounding areas, the flux of organic matter to the sediment at the Frisian front might therefore be of benefit during their quest for food. Besides active migration, additional entrapment and passive transport to the depositional area could contribute to hyperbenthic enrichment as well. Furthermore, hyperbenthos is known to be an important prey for juvenile demersal fish. Therefore, the Frisian front is likely to act as a favourable feeding ground for these life stages and to contribute considerably to the migration of larger predators into the area.

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Species	H/M	Abbreviation
Phylum Cnidaria		
Subphylum Medusozoa		
Classis Hydroidomedusae		
Rathkea octopunctata HM	H	Rath ocHM
Dipurena spp. HM	H	Dipu SpHM
Sarsia tubulosa HM	H	Sars tuHM
Hybocodon prolifer HM	H	Hybo prHM
Mitrocomella spp. HM	H	Mitr SpHM
Phialidium hemisphaericum HM	H	Phia heHM
Hydroidomedusae species 1 HM	H	Hydr S1HM
Hydroidomedusae species 2 HM	H	Hydr S2HM
Hydroidomedusae species 3 HM	H	Hydr S3HM
Phylum Ctenophora		
Pleurobrachia pileus	H	Pleu pile
Phylum Annelida		
Classis Polychaeta		
Tomopteridae spp.	H	Tomo Spde
Lanice conchilega LA	M	Lani coLA
Phylum Chaetognatha		
Sagitta elegans	H	Sagi eleg
Sagitta setosa	H	Sagi seto
Sagitta spp.	H	Sagi Spp.
Phylum Mollusca		
Classis Cephalopoda		
Loligo forbesii JU	M	Loli foJU
Phylum Arthropoda		
Subphylum Crustacea		
Classis Copepoda		
Ordo Calanoida		
Candacia armata	H	Cand arma
Centropages typicus	H	Cent typi
Anomalocera patersoni	H	Anom pate
Labidocera wollastoni	H	Labi woll
Temora longicornis	H	Temo long
Calanus spp.	H	Cala Spp.
Classis Malacostraca		
Subclassis Phyllocarida		
Ordo Nebaliacea		
Nebalia bipes	H	Neba bipe
Subclassis Eumalacostraca		
Superordo Eucarida		
Ordo Euphausiacea		
Nyctiphanes couchi	H	Nyct couc
Ordo Decapoda		
Subordo Pleocyemata		
Infraordo Caridea		
Hippolyte varians PO	M	Hipp vaPO
Processa modica PO	M	Proc moPO
Processa nouveli subsp. *holthuisi* PO	M	Proc noPO
Processa spp. PO	M	Proc SpPO
Processa spp. ZO	M	Proc SpZO
Pandalina brevirostris PO	M	Pand brPO
Crangon allmanni PO	M	Cran alPO
Crangon crangon PO	M	Cran crPO
Crangon spp. PO	M	Cran SpPO
Philocheras bispinosus PO	M	Phil biPO
Philocheras trispinosus PO	M	Phil trPO
Crangonidae spp. ZO	M	Cran SpZO
Infraordo Thalassinidea		
Callianassa tyrrhena PO	M	Call tyPO
Callianassa spp. ZO	M	Call SpZO
Upogebia deltaura PO	M	Upog dePO
Upogebia spp. ZO	M	Upog SpZO
Infraordo Anomura		
Galathea intermedia PO	M	Gala inPO
Galathea spp. ZO	M	Gala SpZO
Pisidia longicornis PO	M	Pisi loPO
Anapagurus laevis ZO	M	Anap laZO
Pagurus bernhardus PO	M	Pagu bePO
Pagurus bernhardus ZO	M	Pagu beZO
Pagurus cuanensis PO	M	Pagu cuPO
Pagurus prideauxi ZO	M	Pagu prZO
Paguridae spp. PO	M	Pagu SpPO
Infraordo Brachyura		
Thia scutellata ME	M	Thia scME
Cancer pagurus ME	M	Canc paME
Liocarcinus holsatus ME	M	Lioc hoME
Carcinus maenas ME	M	Carc maME
Rhithropanopeus harrisii ZO	M	Rhit haZO
Ebalia spp. ME	M	Ebal SpME
Brachyura spp. ZO	M	Brac SpZO

Species	H/M	Abbreviation
Superordo Peracarida		
Ordo Mysidacea		
Subordo Mysida		
Anchialina agilis	H	Anch agil
Gastrosaccus spinifer	H	Gast spin
Mysidopsis angusta	H	Mysi angu
Mysidopsis gibbosa	H	Mysi gibb
Acanthomysis longicornis	H	Acan long
Mesopodopsis slabberi	H	Meso slab
Schistomysis ornata	H	Schi orna
Schistomysis spiritus	H	Schi spir
Heteromysis microps	H	Hete micr
Ordo Cumacea		
Bodotria scorpioides	H	Bodo scor
Iphinoe trispinosa	H	Iphi tris
Eudorella truncatulla	H	Eudo trun
Pseudocuma longicornis	H	Pseu long
Pseudocuma similis	H	Pseu simi
Diastylis spp.	H	Dias Spp.
Ordo Amphipoda		
Subordo Caprellidea		
Pariambus typicus	H	Pari typi
Phtisica marina	H	Phti mari
Subordo Gammaridea		
Ampelisca diadema	H	Ampe diad
Ampelisca gibba	H	Ampe gibb
Ampelisca tenuicornis	H	Ampe tenu
Aoridae spp.	H	Aori Spp.
Argissa hamatipes	H	Argi hama
Atylus swammerdami	H	Atyl swam
Apherusa ovalipes	H	Aphe oval
Corophium multisetosum	H	Coro mult
Siphonoecetes kroyeranus	H	Siph kroy
Microprotopus maculatus	H	Micr macu
Photis longicaudata	H	Phot long
Leucothoe incisa	H	Leuc inci
Leucothoe lilljeborgi	H	Leuc lill
Leucothoe procera	H	Leuc proc
Orchomenella nana	H	Orch nana
Scopelocheirus hopei	H	Scop hope
Tryphosites longipes	H	Tryp long
Megaluropus agilis	H	Mega agil
Cheirocratus intermedius	H	Chei inte
Cheirocratus spp.	H	Chei Spp.
Melita obtusata	H	Meli obtu
Monoculodes carinatus	H	Mono cari
Perioculodes longimanus	H	Peri long
Pontocrates altamarinus	H	Pont alta
Westwoodilla caecula	H	West caec
Harpinia antennaria	H	Harp ante
Harpinia crenulata	H	Harp cren
Harpinia pectinata	H	Harp pect
Dyopedos monacantha	H	Dyop mona
Bathyporeia spp.	H	Bath Spp.
Metopa bruzelii	H	Meto bruz
Stenothoe marina	H	Sten mari
Stenula rubrovittata	H	Sten rubr
Urothoe elegans	H	Urot eleg
Subordo Hyperiidea		
Hyperia galba	H	Hype galb
Ordo Isopoda		
Subordo Flabellifera		
Eurydice pulchra	H	Eury pulc
Subordo Valvifera		
Idotea linearis	H	Idot line
Subphylum Chelicerata		
Classis Pycnogonida		
Nymphon rubrum	H	Nymp rubr
Phylum Chordata		
Subphylum Vertebrata		
Classis Actinopterygii		
Clupeidae spp. PO	M	Clup SpPO
Gadus morhua PO	M	Gadu moPO
Merlangius merlangus PO	M	Merl mePO
Trachurus trachurus PO	M	Trac trPO
Ammodytidae spp. PO	M	Ammo SpPO
Callionymus lyra PO	M	Call lyPO
Pomatoschistus lozanoi PO	M	Poma loPO
Pomatoschistus microps PO	M	Poma miPO
Gobiidae spp. PO	M	Gobi SpPO
Arnoglossus laterna PO	M	Arno laPO
Limanda limanda PO	M	Lima liPO
Pleuronectes platessa PO	M	Pleu plPO
Pleuronectes flesus PO	M	Pleu flPO

Addendum. Species list of all hyperbenthos caught with indication of holo- (H) and merohyperbenthos (M), and with abbreviation of species names; hydromedusa (HM), juvenile (JU), larva (LA), megalopa (ME), postlarva (PO), zoea (ZO).

Chapter 3. Hyperbenthic communities inhabiting the benthic boundary layer of the shelf break and the upper continental slope at the northern edge of the Bay of Biscay (NE Atlantic)

Ann Dewicke, Véronique Vanquickelberghe, Jean-Claude Sorbe, Ann Vanreusel & Jan Mees

Summary

Community structure, density and diversity of the hyperbenthos in the benthic boundary layer of the shelf break and the upper slope of the northern margin of the Bay of Biscay (Eperon Berthois) were investigated for 6 stations between 200 and 700 m depth. A total of 214 species were caught and a pronounced shift in community structure between the shelf break (250 - 300 m depth) and the upper slope (600 - 700 m depth) was present.

The shelf-break hyperbenthos (862 ind. 100 m^{-2}) mainly consisted of mysids (33 %), amphipods (28 %) and euphausiids (19 %). Densities at the upper slope were slightly higher (959 ind. 100 m^{-2}) and amphipods represented 45 % of the total community; subdominant taxa were cumaceans (26 %) and isopods (13 %). Estimates of species richness and species diversity indicated a more diverse fauna at the deeper stratum. Hurlberts' $E(S_{100})$ for the total hyperbenthos was on average 21.6 ± 1.16 for the shelf break and 36.8 ± 0.27 for the upper slope. The high diversity of the upper slope hyperbenthos was mainly due to high species numbers of isopods and cumaceans (as for the asellote isopod families and Cumacea of the family Nannastacidae) and an increase in the number of copepod species. The amphipod assemblage was only slightly more diverse at the upper slope than at the shelf break, but a clear transition in family composition was observed. Similarly, a change in the mysid assemblage was observed at the genus level. The Mysidacea was the only peracarid taxon for which species richness was observed to decrease with depth.

The bathymetric distribution of mysids, euphausiids and decapods (good swimmers) is believed to be rather related to properties of the water column (light transmission, suspended matter concentration,…), than to sediment characteristics. The increase at the upper slope of bottom-dependent taxa such as amphipods, cumaceans and isopods, is suggested to be more related to a change in sediment structure, in addition to variations in organic particle transport in the benthic boundary layer.

Source	Sledge and mesh size	Depth range	Fauna	Major patterns
NE Atlantic - temperate waters				
Norwegian Sea and fjords				
Fosså & Brattegard (1990)	RP 0.5 mm	32 - 1260 m	Mysidacea S	Highest density at depths less than 200 m; decrease in diversity below 400 m depth
Buhl-Jensen (1986)	RP 0.5 mm	147 - 550 m	Amphipoda S	Distibution related to bathymetry and sediment
Cap Ferret area (SE Bay of Biscay)				
Dauvin *et al.* (1995)	MG 0.5 mm	346 – 3070 m	Hyperbenthos T	Highest density at 500 - 700 m, further decrease with depth
Elizalde *et al.* (1993)	MG 0.5 mm	425 – 1043 m	Hyperbenthos S	Diversity increase with depth
Elizalde *et al.* (1991)	MG 0.5 mm	346 – 1099 m	Mysidacea S	Three bathymetric communities: at 350 - 500m, 520 - 925m and below 1000 m
Dauvin & Sorbe (1995)	MG 0.5 mm	346 – 1099 m	Amphipoda S	Highest density at 425 - 924 m; increase of species richness with depth
Sorbe & Weber (1995)	SS 0.5 mm	392 - 717 m	Hyperbenthos S	Density and species richness decrease with increasing distance above the sea bed; diversity increase with depth
Sorbe (1999)	MG 0.5 mm	2400, 3000 m	Hyperbenthos S	Temporal fluctuations in community composition, probably linked to seasonal carbon flux; dominance of Isopoda
Capbreton canyon (SE Bay of Biscay)				
Marquiegui & Sorbe (1999)	SH 0.5 mm	1000 m	Hyperbenthos S	Strong dominance of three 'canyon indicator species'
Corbari & Sorbe (2001)	MG 0.5 mm	162 - 987 m	Hyperbenthos S	Different communities in the canyon than at the slope; presence of 'canyon indicator species'
Portuguese continental margin (off Aveiro)				
Cunha *et al.* (1997)	SS 0.5 mm	21 - 299 m	Hyperbenthos S	Increase of diversity with depth; dominance of mysids and amphipods
Catalan Sea (NW Mediterranean)				
Cartes & Sorbe (1995)	MG 0.5 mm	385 – 1859 m	Mysidacea S	Highest density at 549 - 601 m; diversity decrease with depth
Cartes & Sorbe (1996)	MG 0.5 mm	389 – 1808 m	Cumacea S	Recruitment for species at 549 - 1355 m depth possibly related to phytodetritus peak, wider reproductive periods for species living at shallower depths
Cartes & Sorbe (1997)	MG 0.5 mm	389 – 1859 m	Cumacea S	Highest density at 549 - 601 m; highest diversity at 1250 - 1355 m
Cartes & Sorbe (1999)	MG 0.5 mm	389 – 1859 m	Amphipoda S	Highest density at 392 - 601 m; highest diversity at 549 - 601 m, further decrease with depth
Cartes *et al.* (1994)	MG 0.5 mm	389 – 1859 m	Euphausiacea S	Lowest density at 393 - 450 m

Source	Sledge and mesh size	Depth range	Fauna	Major patterns
Cartes (1998)	MG 0.5 mm	389 - 1859 m	Hyperbenthos S	Hyperbenthos as important prey for megafaunal decapods; dominance of Copepoda and Peracarida
Northern (sub)polar regions				
Laptev Sea (Siberian Arctic)				
Sirenko *et al.* (1996)	BS 0.4 mm	51- 3042 m	Hyperbenthos S	Most common taxa: Cnidaria, Polychaeta, Copepoda, Mysidacea and Gammaridea
Westwind Trough (off NE Greenland)				
Brandt (1995)	BB 0.3 mm	45 - 517 m	Peracarida S	No bathymetric related gradient in community structure; dominance of Cumacea; Amphipoda most diverse
Off E Greenland				
Brandt (1997a,b)	BB 0.3 mm	197- 2681 m	Peracarida S	Highest density at 1525 m depth; highest diversity at shallow depths up to 800 m; dominance of Isopoda
Kolbeinsey Ridge (off N Iceland)				
Brandt (1993), Brandt & Piepenburg (1994)	BB 0.3 mm	830 - 1100 m	Peracarida S	Composition, density and diversity differ at both sides of the ridge, presumably related to food supply and sediment composition; Isopoda and Amphipoda are most common
Norwegian and Greenland Seas				
Svavarsson *et al.* (1990)	WH and RP 0.5 mm	794 - 3709 m	Isopoda S	Highest diversity at 800 m, further decrease with depth
Southern (sub)polar regions				
South Shetland Islands & Bransfield Strait (Antarctic Peninsula)				
San Vicente *et al.* (1997)	MG 0.5 mm	45 - 650 m	Hyperbenthos T	Commonest taxa: Amphipoda, Mysidacea, Isopoda, Cumacea and Euphausiacea; dominance of Amphipoda
Beagle Channel (Patagonia)				
Brandt *et al.* (1997)	BB 0.3 mm	40 - 665 m	Peracarida S	Community composition seems to be related to sediment composition and hydrographical characteristics; dominance of amphipods

Table 1. Overview of recent literature reporting on the hyperbenthos (or on hyperbenthic taxa) occurring at depth strata below 200 m. Identification was performed at the species (S) or at higher taxon level (T). All studies applied sledges for sampling; BB: Brandt-sledge (Brandt & Barthel 1995), BS: benthopelagic sampler attached to Agassiz trawl (see Sirenko *et al.* 1996), MG: Macer-GIROQ sledge (Dauvin & Lorgeré 1989), RP: Rothlisberg & Pearcy sledge (Rothlisberg & Pearcy 1977), SH: Sanders & Hessler sledge (see Marquiegui & Sorbe 1999), SS: Sorbe-sledge (Sorbe 1983), WH: Woods Hole epibenthic sledge (Svavarsson *et al.* 1990). As a remark, not all studies listed deal with continental margins, but they all consider depth strata greater than 200 m and were therefore added to extend the information.

Introduction

The deep-sea benthic boundary layer (BBL) is enriched in biomass and numbers of species, relative to the overlying water column (Wishner 1980; Angel 1990; Cartes 1998; Christiansen *et al.* 1999). It is inhabited by (1) pelagic species whose ranges are truncated by the seabed, (2) benthic species using this zone as a refuge, for dispersal and for locating their food and (3) species from a wide variety of taxonomic groups that seem to be specialized to the benthopelagic environment (Angel 1990).

This study deals with the hyperbenthic component of the BBL fauna, defined as the small (1 - 20 mm) animals that swim in the vicinity of the seabed (Mees & Jones 1997). The main representatives of the hyperbenthos are peracarid crustaceans, a group that shows a rich diversification in the deep sea often reaching high abundances (Gage & Tyler 1996). Since the last decade, evidence of their potential function in deep-sea trophic webs is growing. Vertical migration behaviour may affect the energy transfer between the pelagic and benthic realm, either in the form of gut contents or as a result of predation (Angel 1989; Longhurst & Harrison 1989). Swimming activities might also contribute to the fragmentation of marine snow in the water column, as was indicated for euphausiids (Dilling & Alldredge 2000; Graham *et al.* 2000). Extremely high feeding rates were reported for scavenging amphipods, which are numerous in the deep-sea BBL (Angel 1990). Recently, certain asellote isopods have been shown to feed predominantly on benthic foraminifers, suggesting an important trophic link (Svavarsson *et al.* 1993; Gudmundsson *et al.* 2000). Several hyperbenthic crustaceans constitute an important part of the food exploited by megafaunal decapods (Cartes 1998) and demersal fish (Mauchline 1982; Gordon & Mauchline 1991). Cartes (1998) could even indicate a link in seasonal abundance of the hyperbenthos and megafaunal decapods.

Specific hyperbenthos studies at greater depths than the shelf (appr. 200 m depth) in the NE Atlantic, have been performed along the continental slope and adjacent canyons in the southeastern Bay of Biscay (Elizalde *et al.* 1993; Dauvin *et al.* 1995; Sorbe & Weber 1995; Sorbe 1999; Marquiegui & Sorbe 1999; Corbari & Sorbe 2001), in the Catalan Sea (Cartes 1998) and at the shelf break off Portugal (Cunha *et al.* 1997). The hyperbenthos of polar areas has been studied in Antarctic regions (around the South Shetland Islands and in the Bransfield Strait, San Vicente *et al.* 1997) and in Arctic waters (the Laptev Sea, Sirenko *et al.* 1996). Other studies again focused on the entire peracarid community of the BBL or concentrated on separate orders such as the Amphipoda, Isopoda, Cumacea, Mysidacea or Euphausiacea. An overview of the recent relevant literature is given in Table 1.

In this study, the hyperbenthos inhabiting the BBL (lower one meter stratum of the water column) of the shelf break and the upper slope, at the northern edge of the Bay of Biscay, was investigated. The entire hyperbenthic community present at the shelf break (250 - 300m) is compared with the upper slope community (600 - 700 m) in terms of taxonomic composition, density, biomass and species diversity. Possible causes for differences in community structure between both bathymetric zones are discussed.

Material and methods

The study area, the Eperon Berthois (between 47° 53' - 47° 44' N and 7° 47' - 8° W), is situated at the continental edge bordering the Bay of Biscay (NE Atlantic) to the north (Fig. 1). Six sampling stations were selected within a depth range of 200 to 700 m. One site was located at the continental shelf (cs200), two sites were located around the shelf break (sb250, sb300) while the three remaining sites were situated at the upper continental slope (us600, us650 and us700). Sampling was done in September 1995 from the *RV* Belgica with a hyperbenthic sledge modified after Sorbe (1983). Two superimposed nets (1 mm mesh size, 3 m long, 71 cm wide) were fixed on the sledge and sampled the water layer within 0 to 50 cm (lower net) and within 50 to 100 cm (upper net) above the sea floor. The sledge was equipped with an opening-closing mechanism and an odometer (for details see Sorbe 1983). A flow meter (*Hydrobios 438-110*) was fixed in the upper net. All sampling was carried out during daytime and towing lasted 10 minutes at an average ship speed of 1.5 knot relative to the bottom. Sampling was done parallel to the isobaths. After each tow, the exact towing distance was registered (701 ± 73.7 m) and the sampled water volume calculated (365 ± 45.4 m^3). The catches from the upper and lower net were rinsed separately over a 1 mm mesh size sieve and preserved in a buffered formaldehyde solution (7 % final concentration). The water column depth was registered and the bottom temperature, salinity and oxygen concentration were obtained from vertical profiles (Sea-Bird SBE09*plus*). A box corer (*Reineck*) was additionally lowered at each station (except for station us700). The upper 2 cm of the sediment were sampled for grain fraction analysis (particle size analyser *Coulter LS 100*). Some characteristics for each sampling site are listed in Table 2.

Data acquisition

All organisms were identified to species level. Certain morpho-species (being distinctly different from other specimens within the same taxon and / or not yet being described in literature) were defined and are tabulated as 'species x'. If characteristics for diagnostics were lacking, specimens were pooled at a higher taxonomic level (reported as 'spp.' and called species). For certain taxa, further classification was done based on the life history, such as zoea, megalopa and postlarva stage for decapods. All animals were counted on species and stage level.

Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans and from the tip of the lower jaw to the end of the notochord for fish larvae) and their biomass was derived from regressions relating standard length to Ash free Dry Weight (ADW). ADW was determined as the difference between dry weight (60°C for 5 days) and ash weight (650°C for 2 hours) for representative size distributions of the various species. For species caught in discrete life stages or occurring with a particular length, an average biomass value was assigned per stage or per species. This value was determined by measuring the ADW of batches of animals belonging to a certain stage. Both the regressions and the assigned biomass values were partly determined using animals from this study and from previous research (Beyst *et al.* 1999a; A. Dewicke unpubl. data).

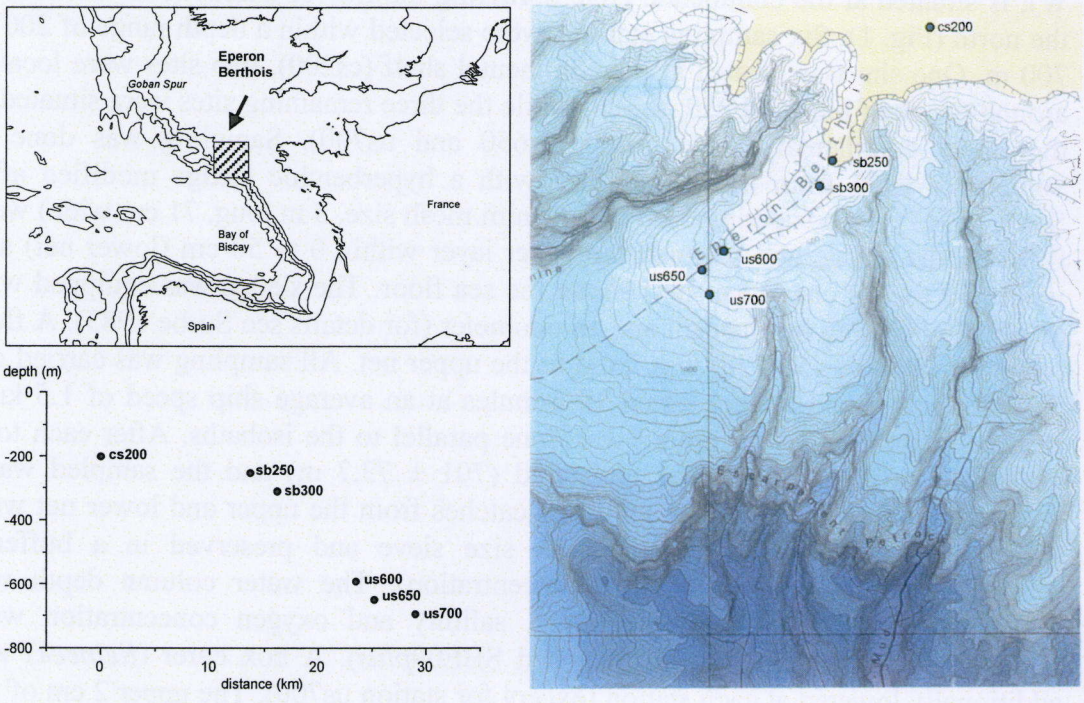


Fig. 1. Location and depth profile of the study area with indication of sampling sites; continental shelf site (cs200), shelf-break sites (sb250, sb300) and upper slope sites (us600, us650, us700).

Station	cs200	sb250	sb300	us600	us650	us700
Sampling date	23/09/95	24/09/95	24/09/95	25/09/95	24/09/95	25/09/95
Longitude W	7° 47.94'	7° 50.95'	7° 53.34'	8° 0.96'	8° 01.43'	8° 0.48'
Latitude N	47° 59.53'	47° 52.34'	47° 51.17'	47° 47.82'	47° 46.94'	47° 44.79'
Distance from cs200 (km)	0	14	16	24	25	29
Distance trawled (m)	543	894	846	825	454	643
Volume filtered (m^3)	239	493	348	508	285	315
Depth (m)	201	253	312	592	650	695
Temperature (°C)	11.65	11.18	11.11	10.13	(na)	10.15
Salinity (psu)	35.55	35.55	35.55	35.55	(na)	35.55
Dissolved oxygen (µmol/kg)	244	244	244	216	(na)	218
Median grain size (µm)	268	210	206	147	165	(na)
Mud (%)	1.9	4.1	4.1	16.6	10.9	(na)

Table 2. Some characteristics of the sampling sites; not analysed (na).

After identification and measuring, non-hyperbenthic representatives were removed from the 'catch-dataset' (i.e. all animals that were caught by the Sorbe-sledge and which were retained on a 1 mm sieve). The hyperbenthos (generally < 20 mm) mainly comprises several peracarid orders (mysids, amphipods, isopods, cumaceans, tanaids), euphausiids and copepods, and early life history stages from decapod larvae and fish larvae. Rejected taxa were all siphonophores, polychaetes, juvenile and adult decapods, echinoderms, and all sedentary organisms (see Introduction). Density and biomass data were expressed as numbers of individuals and mg ADW per 100 m^{-2}. Since the catch efficiency of sledges is largely unknown (Mees & Jones 1997), densities and biomasses were reported as such and should be considered as minimum values. The full species list is listed in the Addendum.

After fourth root transformation of the raw density data (Field *et al.* 1982; Legendre & Legendre 1998), Detrended Correspondence Analysis (DCA) was performed in order to estimate the gradient length of species turnover, which was 3.103 standard deviation units. A predominance of unimodal response curves could therefore be expected (see ter Braak & Prentice 1988; Van Wijngaarden *et al.* 1995) and Correspondence Analysis (CA) was further applied to visualise the variance in the species data (using the software package CANOCO 4, ter Braak & Smilauer 1998). Furthermore, cluster analysis on the species densities were performed using the Bray-Curtis dissimilarity index (Bray & Curtis 1957) and according to a group-average sorting algorithm (PC-ORD 4, McCune & Mefford 1999).

In order to estimate species diversity, Hill's diversity numbers N_0, N_1 and N_2 were calculated (Hill 1973). The first Hill number, N_0, estimates the species richness (equal to the number of species of the sample). N_1 is the inversed natural logarithm of the Shannon-Wiener diversity index and N_2 is the reciprocal of the Simpson's dominance index. Hurlbert's modification of Sanders' rarefaction curves (Hurlbert 1971) was used to calculate diversity for a standardised sample size: $E(S_{100})$ determines the expected number of species present in a sample of 100 individuals. Since individuals could not always be identified to species level, the calculated diversity indices represent minimum values.

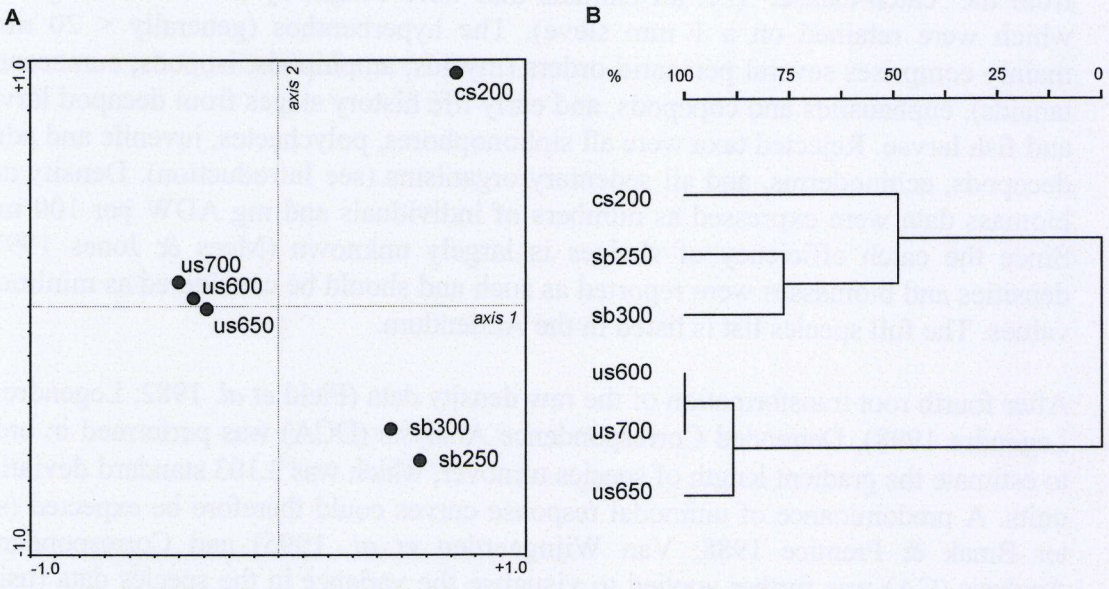


Fig. 2. (A) Ordination diagram of the CA performed on the species density data. Samples scores are represented along axis one (eigenvalue 0.630) and axis two (eigenvalue 0.352); the first axis represents 42.4 % of the total species variance and the second axis an additional 23.6 %. **(B)** Cluster analysis dendrogram. The horizontal scale represents relative similarity.

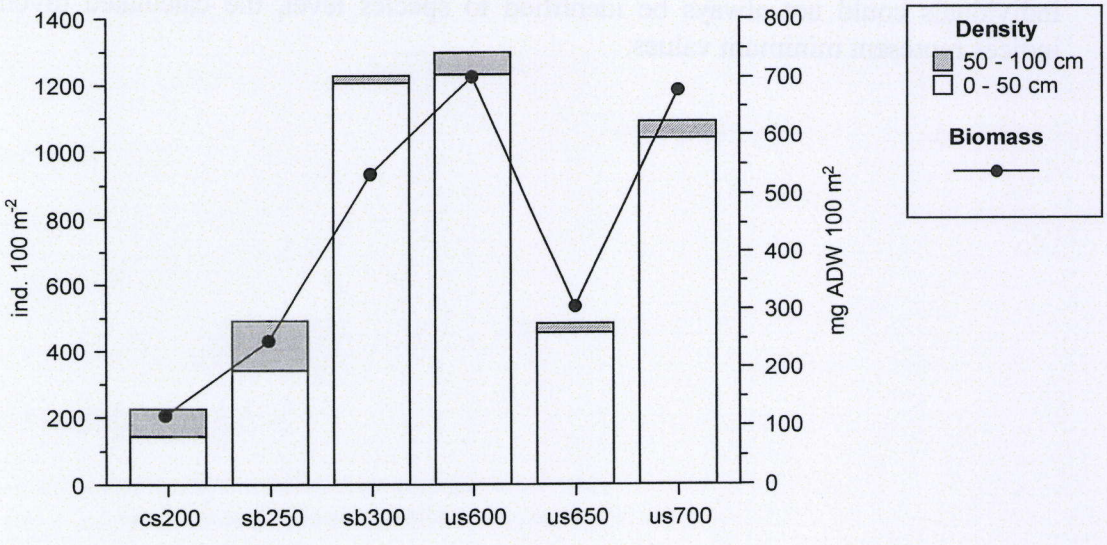


Fig. 3. Total density (left axis) of the hyperbenthos per site presented as the sum of the density of the lower (0 – 50 cm) and upper net (50 – 100 cm) of the sledge. Total biomass (right axis) is shown for the full water stratum sampled (0 - 100 cm).

Results

A total of 25558 individuals were caught, belonging to 214 species. The peracarid crustaceans represented more than 80 % of the total hyperbenthos. Amphipods were the most diverse group with 84 species. Other species rich taxa were the copepods (28 species), the mysids (23 species), the isopods (22 species), the decapods (12 species) and the cumaceans (16 species) (see Addendum).

Environmental variables

Median grain size decreased with depth (Table 2). The sediment at station cs200 consisted of medium sand, fine sands were dominant at the other sites. The upper slope stations contained more than 10 % up to 17 % mud. Bottom salinity was identical for all sites (33.55 psu). Temperature showed a decline of approximately 1.2 °C from the shelf break to the upper slope, dissolved oxygen was also lower for the deeper sites.

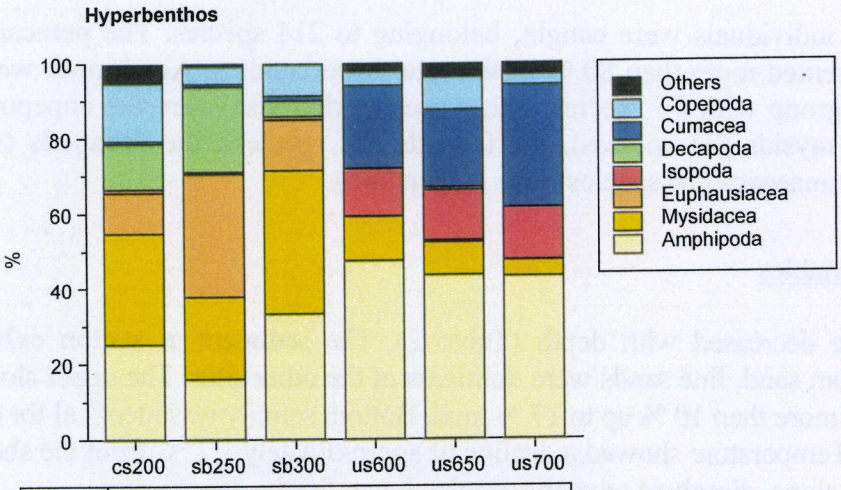
Multivariate analyses

The CA ordination diagram shows a pronounced distinction between the two depth strata (200 - 300 m depth versus 600 - 700 m depth) along the first axis (eigenvalue 0.630) (Fig. 2A). The second axis (eigenvalue 0.352) separates station cs200 (continental shelf site) from the two shelf-break sites (sb250 and sb300). A similar result was obtained by the cluster analysis, as depicted in Fig. 2B. Further description of results focuses on this shift in hyperbenthic community structure between the 200 - 300 m depth stratum (continental shelf site and the shelf-break sites) versus the 600 – 700 m stratum (the upper slope).

Density, biomass and diversity

Total hyperbenthic density is presented in Fig. 3, as the sum of the abundance derived from the lower (0 - 50 cm) and the upper nets (50 - 100 cm) of the sledge. Total density varied between 226 and 1300 ind. 100 m^{-2}. The abundance was lowest at the continental shelf (cs200) and increased with depth along the shelf break (sb250, sb300). Densities at the upper slope sites us600 and us700 were comparable with these at sb300. Much lower abundance was recorded at site us650. Fig. 3 also illustrates that most animals were found in the 0 - 50 cm water stratum above the bottom, i.e. in the lower net. Biomass varied from 99 to 683 mg ADW 100 m^{-2} and showed a similar pattern as the total density.

The taxonomic composition of the hyperbenthos differed considerably between both depth zones (Fig. 4). The Amphipoda was the only taxon that accounted for a substantial fraction (> 20 %) of total hyperbenthic density at all sites. They were particularly abundant at the upper slope with a mean density of 433 ± 118.6 ind. 100 m^{-2} (45 % of the total density). Mysids and amphipods were of equal importance at the shelf break (33 and 28 %, resp.); absolute densities amounted to 288 ± 180.6 ind. 100 m^{-2} (Mysidacea) and 224 ± 165.0 ind. 100 m^{-2} (Amphipoda). Euphausiids, decapods and copepods were also considerably present at this depth stratum (163 ± 2.9 ind. 100 m^{-2}, 82 ± 30.0 ind. 100 m^{-2} and 63 ± 40.2 ind. 100 m^{-2}, resp.). Cumaceans and isopods



	cs200	sb250	sb300	us600	us650	us700
N_0	76	67	72	110	94	108
N_1	31	12	17	37	37	38
N_2	20	6	11	25	23	24
$E(S_{100})$	33	20	23	36	37	37

Fig. 4. Taxonomic composition, Hill's diversity numbers N_0, N_1 and N_2 and Hurlbert's $E(S_{100})$ of the total hyperbenthos per site.

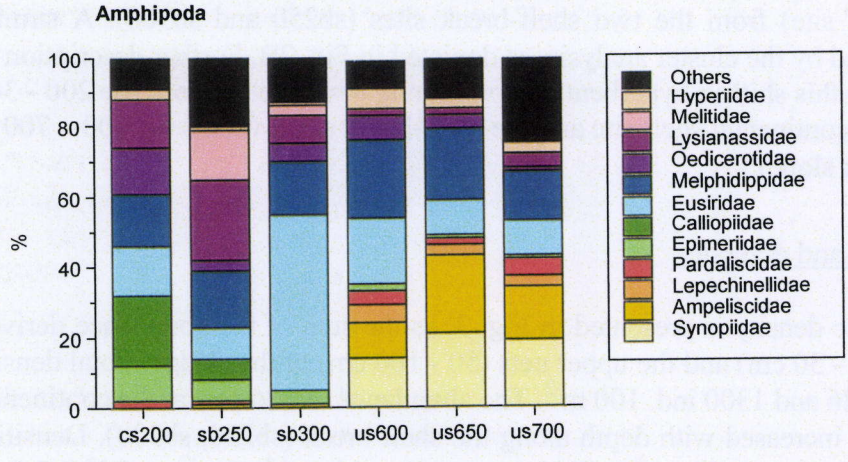


Fig. 5. Relative composition of the amphipod fauna (family level) per site.

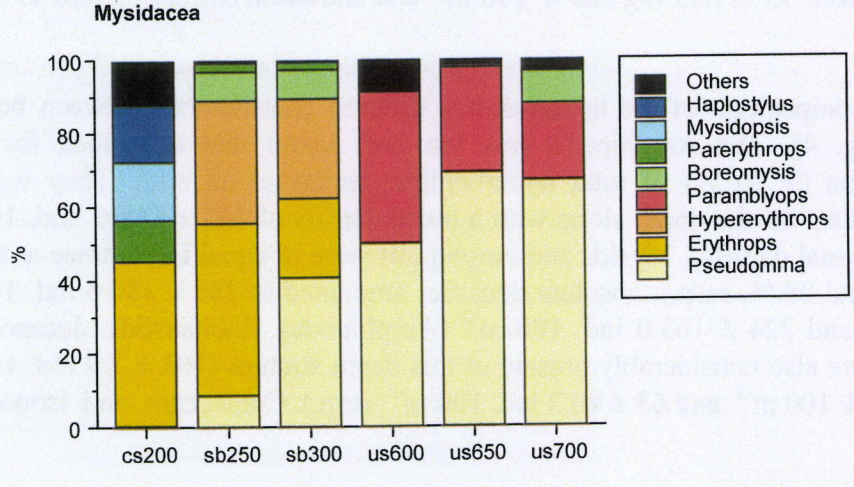


Fig. 6. Relative composition of the mysid fauna (genus level) per site.

were more abundant at the upper slope stations with mean densities of 248 ± 76.6 ind. 100 m^{-2} (26 %) and 125 ± 30.9 ind. 100 m^{-2} (13 %) respectively. Euphausiids and decapods were nearly absent at the upper slope and pycnogonids, chaetognaths and tanaids appeared at these deeper sites in low numbers (< 15 ind. 100 m^{-2}).

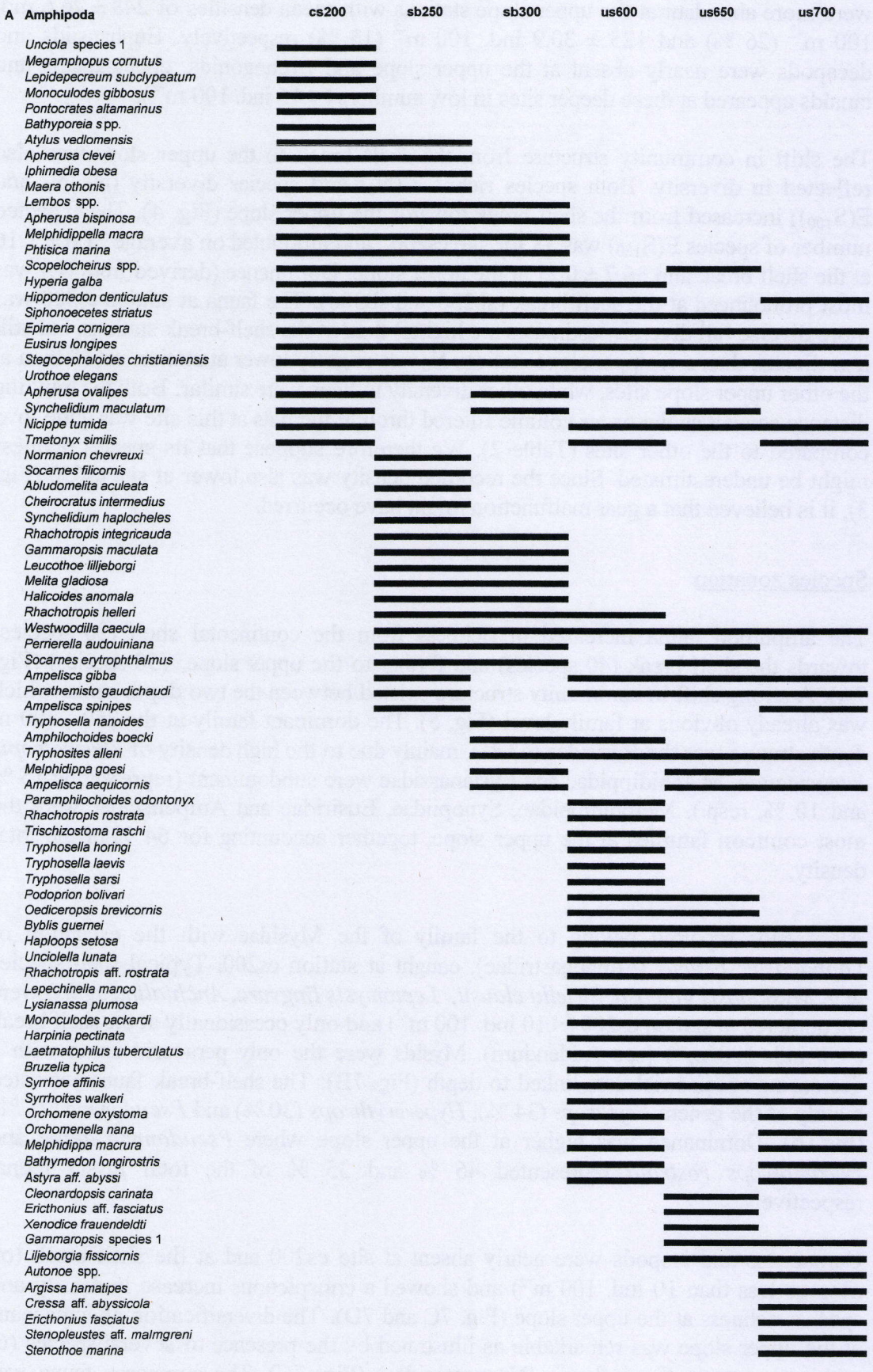
The shift in community structure from the shelf break to the upper slope was also reflected in diversity. Both species richness (N_0) and species diversity (N_1, N_2 and $E(S_{100})$) increased from the shelf break towards the upper slope (Fig. 4). The expected number of species $E(S_{100})$ was 33 for site cs200, and amounted on average 21.6 ± 1.16 at the shelf break and 36.7 ± 0.27 at the upper slope. Dominance (derived from N_2) was most pronounced at the shelf break (sb250 and sb300). The fauna at station cs200 was more diverse (all diversity estimates are higher) than at the shelf-break stations, but still less diverse than any upper slope station. N_0 was slightly lower at station us650 than at the other upper slope sites, while other diversity indices were similar. Both the trawling distance as well as the water volume filtered through the nets at this site was quite low, compared to the other sites (Table 2). We therefore suppose that its species richness might be underestimated. Since the recorded density was also lower at site us650 (Fig. 3), it is believed that a gear malfunction might have occurred.

Species zonation

The amphipod fauna increased in richness from the continental shelf (26 species) towards the shelf break (40 species) and further to the upper slope (58 species) (Fig. 7A). A strong shift in community structure existed between the two depth strata, which was already obvious at family level (Fig. 5). The dominant family at the 250 - 300 m depth stratum was the Eusiridae (43 %), mainly due to the high density of *Rhachotropis integricauda*. Melphidippidae and Lysianassidae were subdominant (representing 15 % and 10 %, resp.). Melphidippidae, Synopiidae, Eusiridae and Ampeliscidae were the most common families at the upper slope, together accounting for 64 % of the total density.

All mysids reported belong to the family of the Mysidae with the exception of *Lophogaster typicus* (Lophogastridae), caught at station cs200. Typical shelf species (e.g. *Mysidopsis gibbosa*, *Siriella clausii*, *Leptomysis lingvura*, *Anchialina agilis*) were encountered at station cs200 (< 10 ind. 100 m^{-2}) and only occasionally at the shelf break (< 1 ind. 100 m^{-2}) (see Addendum). Mysids were the only peracarid taxon with a decreasing species richness linked to depth (Fig. 7B). The shelf-break fauna consisted mainly of the genera *Erythrops* (34 %), *Hypererythrops* (30 %) and *Pseudomma* (25 %) (Fig. 6). Dominance was higher at the upper slope where *Pseudomma affine* and *Paramblyops rostrata* represented 46 % and 35 % of the total mysid fauna, respectively.

Cumaceans and isopods were nearly absent at site cs200 and at the shelf break (on average less than 10 ind. 100 m^{-2}) and showed a conspicuous increase in density and species richness at the upper slope (Fig. 7C and 7D). The diversification of cumaceans at the upper slope was remarkable as illustrated by the presence of several species (6) within the genus *Campylaspis* (Nannastacidae) (Fig. 7C). The cumacean fauna was numerically dominated by representatives of the Lampropidae such as *Hemilamprops uniplicata* (19 %) and *Platysympus typicus* (18 %) and of the Diastylidae like *Makrokylindrus josephinae* (17 %).


A Amphipoda
cs200
sb250
sb300
us600
us650
us700
Unciola species 1
Megamphopus cornutus
Lepidepecreum subclypeatum
Monoculodes gibbosus
Pontocrates altamarinus
Bathyporeia s pp.
Atylus vedlomensis
Apherusa clevei
Iphimedia obesa
Maera othonis
Lembos spp.
Apherusa bispinosa
Melphidippella macra
Phtisica marina
Scopelocheirus spp.
Hyperia galba
Hippomedon denticulatus
Siphonoecetes striatus
Epimeria cornigera
Eusirus longipes
Stegocephaloides christianiensis
Urothoe elegans
Apherusa ovalipes
Synchelidium maculatum
Nicippe tumida
Tmetonyx similis
Normanion chevreuxi
Socarnes filicornis
Abludomelita aculeata
Cheirocratus intermedius
Synchelidium haplocheles
Rhachotropis integricauda
Gammaropsis maculata
Leucothoe lilljeborgi
Melita gladiosa
Halicoides anomala
Rhachotropis helleri
Westwoodilla caecula
Perrierella audouiniana
Socarnes erytrophthalmus
Ampelisca gibba
Parathemisto gaudichaudi
Ampelisca spinipes
Tryphosella nanoides
Amphilochoides boecki
Tryphosites alleni
Melphidippa goesi
Ampelisca aequicornis
Paramphilochoides odontonyx
Rhachotropis rostrata
Trischizostoma raschi
Tryphosella horingi
Tryphosella laevis
Tryphosella sarsi
Podoprion bolivari
Oediceropsis brevicornis
Byblis guernei
Haploops setosa
Unciolella lunata
Rhachotropis aff. rostrata
Lepechinella manco
Lysianassa plumosa
Monoculodes packardi
Harpinia pectinata
Laetmatophilus tuberculatus
Bruzelia typica
Syrrhoe affinis
Syrrhoites walkeri
Orchomene oxystoma
Orchomenella nana
Melphidippa macrura
Bathymedon longirostris
Astyra aff. abyssi
Cleonardopsis carinata
Ericthonius aff. fasciatus
Xenodice frauendeldti
Gammaropsis species 1
Liljeborgia fissicornis
Autonoe spp.
Argissa hamatipes
Cressa aff. abyssicola
Ericthonius fasciatus
Stenopleustes aff. malmgreni
Stenothoe marina

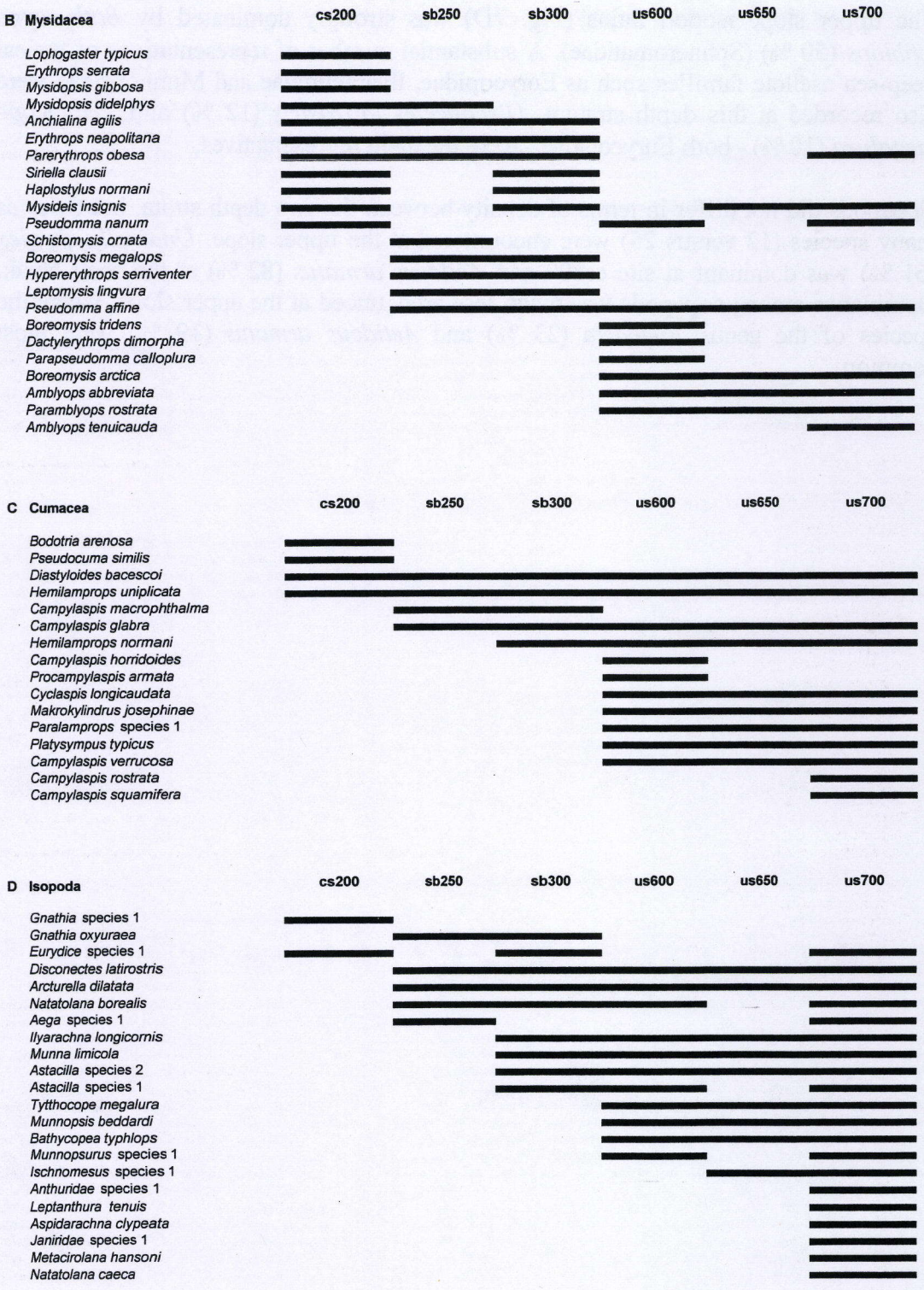


Fig. 7. Species occurrences with depth for **(A) (left page)** amphipods, **(B)** mysids, **(C)** cumaceans and **(D)** isopods.

The upper slope isopod fauna (Fig. 7D) was strongly dominated by *Bathycopea typhlops* (50 %) (Sphaeromatidae). A substantial number of representatives of typical deep-sea asellote families such as Eurycopidae, Ilyarachnidae and Munnopsidae were also recorded at this depth stratum. *Disconectes latirostris* (12 %) and *Tytthocope megalura* (10 %) - both Eurycopidae - were the main representatives.

Copepods did not differ in terms of density between the two depth strata, but twice as many species (12 versus 25) were encountered at the upper slope. *Undinella simplex* (61 %) was dominant at site cs200 and *Aetideus armatus* (82 %) at the shelf break. Dominance among copepods was much less pronounced at the upper slope, where the species of the genus *Euchaeta* (23 %) and *Aetideus armatus* (19 %) were most common.

Discussion

Zonation, diversity and community structure

Few studies on hyperbenthic communities have considered the transition between the continental shelf and slope. This area nevertheless coincides with strong gradients in the physical environment and it is characterised by a very pronounced transition in fauna, as was already reported for the macro-endobenthic and mega-epibenthic fauna (Rex 1981; Flach & Thomsen 1998; Duineveld *et al.* 1997; Flach & de Bruin 1999). This study revealed an obvious shift in community structure between the hyperbenthos inhabiting the shelf break (250 – 300 m depth) and the upper slope (600 – 700 m depth), and a sharp increase in species number with depth. On average $E(S_{100})$ increased with 70 % from the shelf break to the upper slope. The pronounced community transition at the boundary between the shelf and the deep sea is generally attributed to differential adaptation to the gradient of increasing environmental predictability with depth around the upper slope (Rex 1981). Zonation control however can be explained by a wide variety of depth related gradients including (1) physical factors like temperature, topography, sedimentology, deep boundary currents and (2) biological factors like resource-availability, interspecific competition and predator-prey relationships (Rex 1981). It still remains poorly understood which factor causes species replacement, with regard to the zonation of hyperbenthic species.

The higher diversity (Fig. 4) at station cs200 compared to the shelf-break sites is due to the presence of both typical shelf and upper slope species. At least 30 % of all reported species at this site are known to occur in the English Channel (Zouhiri *et al.* 1998; Dauvin 1999; Dauvin *et al.* 2000). Another 30 % did also occur at the deepest site (us700). Site cs200 is therefore believed to be the lower depth distribution limit of the shelf species and the upper bathymetric range for the deep-sea species.

Mysids

The hyperbenthos at the 250 - 300 m depth stratum was numerically dominated by mysids. They were far less abundant at the upper slope sites. In the southeastern part of the Bay of Biscay (Elizalde *et al.* 1991) and in the Catalan Sea (Cartes & Sorbe 1995), this taxon was most abundant around 500 - 600 m depth, i.e. the bathymetric range in-between the depths sampled during this study. Both studies revealed a further decrease with depth. Sorbe (1999) reported on very low mysid densities for abyssal strata (2400 - 3000 m depth, Cap-Ferret canyon, SE Bay of Biscay), accounting for only 3 % of the total hyperbenthic community. The mysids were the only peracarid taxon that were less diverse in species numbers at the upper slope as compared to the shelf break. This correlation was also observed by Cartes & Sorbe (1995) (Table 1).

Bathymetric zonation of benthopelagic mysids has been illustrated by several authors (e.g. Fosså & Brattegard 1990; Elizalde *et al.* 1991; Cartes & Sorbe 1995; Cunha *et al.* 1997) and is, at genus level, often quite similar for different geographical areas. The dominant species at the upper slope in this study, *Paramblyops rostrata* and *Pseudomma affine*, were also abundant in the southeastern part of the Bay of Biscay (Elizalde *et al.* 1993) and in the Catalan Sea (Cartes & Sorbe 1995), and also occur in the Rockall Trough (off Ireland) (Mauchline 1986).

In an investigation of the mysid fauna of the continental slope (400 to 2900 m depth) of the Rockall Trough (Mauchline 1986), data were collected with a Rectangular Midwater Trawl (RMT) but also originated from the stomachs of demersal and benthopelagic fish. The mysid fauna caught with the RMT (mainly pelagic species) differed strongly from the species encountered during this study. The mysids from the fish stomachs however (mainly benthopelagic species) showed a strong overlap in species composition with our data. This observation illustrates the segregation between pelagic and hyperbenthic (= benthopelagic) mysid species and stresses the importance of the hyperbenthic mysid species as a food source for higher trophic levels (Mauchline 1982).

According to Mauchline (1980), light might be the most important factor affecting the distribution of mysids. Lindström (2000) found a relation between the eye spectral sensitivity of several mysid species in the Baltic Sea and the light transmittance in their respective habitat. The eyes of mysids have a wide range of shapes, from semi-globular to dorso-ventrally flattened in shelf species to reduced plate-like eyes without cornea in deep-sea species (Tattersall & Tattersall 1951). All genera found at station cs200 have well-developed eyes. Species with quite rudimentary eyes (or without visual elements) occurred more frequently at deeper sites (mainly the genera *Pseudomma* and *Paramblyops*) and were dominant at the upper slope. These results support the idea that light plays a key role in the zonation of mysids along a sharp depth gradient such as the continental slope, where light is rapidly attenuated with depth.

Amphipods, cumaceans and isopods

Grain size distribution of the sediment has often been put forward as being a structuring factor for hyperbenthic (bentho-pelagic) amphipods (Buhl-Jensen 1986; Marques & Bellan-Santini 1993; Dauvin & Sorbe 1995), isopods (Svavarsson 1990) and cumaceans (Roccatagliata 1991). The increased density and diversity for amphipods, cumaceans and isopods at the upper slope coincided with a decrease in median grain size and a higher mud content of the sediment. It is important to mention that the catch by the Sorbe-sledge may have been slightly contaminated by the fauna present in the upper centimetre of the bottom triggered by disturbances and resuspension. This might be particularly true for soft-bottom substrata.

Amphipods numerically dominated the hyperbenthos at the upper slope, and densities were in the same order of magnitude as the ones reported by Dauvin *et al.* (1995) around 425 - 924 m depth in the Cape-Ferret area (Table 1). The amphipod fauna was only slightly richer in species numbers at the upper slope as compared to the shelf break, though the species composition had distinctly changed. In terms of the dominant families (Eusiridae, Melphidippidae and Lysianassidae) the shelf break corresponded well with adjacent areas. *Rhachotropis integricauda* (Eusiridae) was, as for this study, dominant at similar depths off Portugal (Cunha *et al.* 1997). Dauvin & Sorbe (1995) also found a dominance of Eusiridae and Lysianassidae at the southern margin of the Bay of Biscay. Eusiridae are generally encountered in the upper nets of multi-level sledges, pointing to their swimming ability (Dauvin *et al.* 1994; Dauvin & Sorbe 1995). The Melphidippidae (e.g. *Apherusa*) are often very abundant in areas characterised by strong currents (Vallet & Dauvin 1998, 1999).

At the upper slope, the Eusiridae were still important. For the other dominant families some geographical differences were noted: Synopiidae - strictly mud

dwellers (Ruffo 1998) – accounted for 17 % of the total density in this study, while the Stegocephalidae dominated at the southern Bay of Biscay (Dauvin & Sorbe 1995). A shift in the amphipod composition at 500 m depth was found for this area with the sediment composition suggested as main structuring factor.

Cumaceans showed a strong diversification at the upper slope. Important species mainly belonged to the Nannastacidae, in particular within the genus *Campylaspis*. Several species of this family were also reported for the Portuguese continental margin at a depth of 300 m (Cunha *et al.* 1997). According to Jones & Sanders (1972), cumaceans have narrow and discrete depth ranges resulting in a sharp bathymetric zonation. The latter authors reported 32 species at a 2900 m deep site in an area south of New England. Important geographical differences exist in cumacean assemblages even at a very local level (Jones 1990). These are probably associated with changes in water masses or sediment type, to which cumaceans are most sensitive (Roccatagliata 1991; Cartes & Sorbe 1997). According to Cartes & Sorbe (1997), the succession of dominant species with depth in the Catalan Sea was related to trophic differences, judging from their mouthparts structure.

As for cumaceans, isopods were nearly absent at the shelf break and tended to expand at the upper slope. At bathyal depths of the Cap-Ferret canyon, isopods accounted for more than 40 % of the total hyperbenthos density (Sorbe 2000). The genus *Bathycopea* (Sphaeromatidae) clearly dominated at the upper slope, followed by the family Eurycopidae (mainly *Disconectes latirostris* and *Tytthocope megalura*). The latter family was co-dominant with the Ilyarachnidae at the upper slope in the Bay of Biscay (Sorbe & Weber 1995) and off the Portuguese coast (Cunha *et al.* 1997). Asellote isopods like *Disconectes latirostris* and *Tytthocope megalura* are well adapted for swimming (Hessler *et al.* 1979). Svavarsson *et al.* (1990) reported a rapid species replacement for isopods with depth and a maximum diversity at 800 m in the deep Norwegian and Greenland Seas. The authors also related diversity patterns with the heterogeneity of the sediment (Svavarsson *et al.* 1990). Hult (1941) mentioned that isopods show a conspicuous diversity in their ability to burrow in sediments of different grain sizes.

Comparison with the endobenthos

The endofauna along the Goban Spur slope, which is situated adjacent to our study area (Flach & Thomsen 1998) (see Fig. 1), was also reported with a low crustacean fraction at the shelf break (in summer and at a depth of 231 m). The main representatives were decapods and amphipods. At the upper slope (693 m depth), decapods were nearly absent, amphipods had increased in density, and cumaceans and isopods had reappeared as well (Flach & Thomsen 1998). The main distribution trends for the common taxa in the latter study were thus remarkably similar to the ones found for the hyperbenthos. In addition, the total macrobenthic community was characterised by lower species richness and a higher dominance at the shelf break as compared with deeper strata (Flach & de Bruin 1999). Also this trend was confirmed for the hyperbenthos in this study. Highest numbers and species diversity for endobenthic crustaceans were reported at the mid-slope (1425 - 2210 m depth) (Flach & Thomsen 1998; Flach & de Bruin 1999). We therefore might expect the fauna to get more diverse at deeper sites. This was obvious for the hyperbenthos at the upper slope level showing an increasing diversity with depth (Fig. 4 and 7).

Functioning in the BBL

The shelf-break hyperbenthos was for more than 60 % composed of mysids, euphausiids and decapods. These organisms are known to be good swimmers and are often filterfeeding or hunting their prey (Mauchline 1980, 1984; Ruppert & Barnes 1994). *Rhachotropis integricaudata* (Eusiridae) dominated the amphipod fauna at these sites and has a high swimming ability as well (Dauvin *et al.* 1994; Dauvin & Sorbe 1995). The motility of these animals allows them to reach food sources faster than more bottom-dependent animals, an advantage for thriving in areas with turbulent conditions and little net deposition. For the Goban Spur, it was suggested that the sediment has a low nutritive value at the shelf break, the water column offering the main food source (Flach & Thomsen 1998). Pingree & Le Cann (1990) reported a much higher current velocity (11.5 cm s^{-1} at 500 m depth, 6 m off the bottom) for our study area compared to similar depth strata at the Goban Spur. Moreover, median grain size for this study approached 228 ± 20.2 µm around 250 m depth and 156 ± 8.8 µm around 650 m depth (Table 2); values for the Goban Spur were much lower (94 ± 1.6 µm and 55 ± 3.5 µm, resp.) (Flach *et al.* 1999). Thus, we therefore believe that settling of suspended matter might rather be poor at the shelf-break sites of this study. This might explain the low densities of animals depending on surface-bottom matter for their food supply, as suggested for several amphipods, cumaceans and isopods.

In addition to their motility, the visual perception capacities of the dominant fauna at the shelf break may also play a role in food resource partitioning. It was already mentioned that the mysid species occurring at the shelf break mostly have well-developed eyes. Company & Sardà (1998) suggested that shrimps at shallow sites are likely to rely more on visual predation as compared to deeper living species, as suggested by their higher metabolic rate.

The hyperbenthos at the upper slope was characterised by the increase of amphipod, isopod and cumacean densities. These peracarid crustaceans are often generalised as having a free-living epibenthic or hyperbenthic lifestyle and eating detritus (Vinogradov 1995; Gage & Tyler 1996). Cumacean species of the genus *Campylaspis*, that suddenly appeared at the upper slope, have piercing mouthparts probably adapted to feed on forams (Jones 1976). Also, Gudmundsson *et al.* (2000) recently pointed out that certain asellote isopods mainly eat benthic foraminifers. Specialization in foraminifer species or genera may even exist (Gudmundsson *et al.* 2000). Despite this scattered and only recently growing knowledge on the feeding ecology of deep-sea peracarid species, it presumes that trophic structure of the hyperbenthos had changed as compared to the community of the shelf break. Similarly, the feeding guild dominance in the macro- and megafauna communities of the Goban Spur, shifted from suspension feeders towards deposit feeding animals at 670 m depths (Flach *et al.* 1998). These authors report on a succession of feeding types along the continental margin, related to transport of food particles in the BBL (Flach *et al.* 1998; Thomsen 1999; Thomsen 1999; Thomsen & van Weering 1998).

Conclusions

The transition between shelf and deep sea is characterised by strong gradients in the physical properties of the bottom and the water column. Mysids, euphausiids and decapods - taxa with high swimming abilities and therefore less confined to the sea floor - seem to be able to withstand the often unstable conditions at the shelf break and dominate the BBL hyperbenthos at this depth stratum. The bathymetric distribution of mysids, euphausiids and decapods is believed to be rather related to physical properties of the water column (e.g. light transmission, suspended matter concentration), than to sediment characteristics. The increase of more bottom-dependent taxa, such as amphipods, cumaceans and isopods, at the upper slope however, is suggested to be related to a change in sediment structure and to variations in organic particle transport in the BBL (e.g. deposition and resuspension events). Biological factors (e.g. competition for food) nevertheless might also contribute to this shift in community structure.

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	H/M	cs	sb	us
Phylum Cnidaria				
Subphylum Medusozoa				
Superclassis Hydrozoa				
Classis Hydroidomedusae				
Subclassis Trachymedusae				
Familia Rhopalonematidae				
Hydroidomedusae species 1 HM	H	8.6	0.0	0.2
Hydroidomedusae species 2 HM	H	0.3	0.9	0.0
Phylum Chaetognatha				
Classis Sagittoidea				
Subclassis Chorismogonata				
Ordo Monophragmophora				
Familia Eukrohniidae				
Eukrohnia fowleri	H	0.3	1.7	3.7
Eukrohnia spp.	H	0.0	0.0	0.4
Ordo Aphragmophora				
Familia Sagittidae				
Sagitta aff. *tasmanica*	H	0.3	0.0	0.3
Sagitta spp.	H	0.0	0.0	0.9
Chaetognatha spp.	H	0.0	0.1	2.3
Phylum Mollusca				
Classis Gastropoda				
Subclassis Opisthobranchia				
Ordo Gymnosomata				
Gymnosomata species 1	H	0.5	0.0	1.5
Classis Cephalopoda				
Subclassis Coleoidea				
Ordo Teuthida				
Subordo Myopsida				
Familia Loliginidae				
Loligo species 1 JU	M	0.0	0.0	0.1
Phylum Arthropoda				
Subphylum Crustacea				
Classis Copepoda				
Ordo Calanoida				
Superfamilia Aritelloidea				
Familia Heterorhabdidae				
Heterorhabdus papilliger	H	0.3	0.0	3.7
Familia Metridinidae				
Metridia species 1	H	0.0	0.0	0.1
Pleuromamma robusta	H	0.0	0.0	2.4
Pleuromamma spp.	H	1.0	0.8	2.7
Familia Phyllopodidae				
Phyllopus bidentatus	H	0.0	0.0	0.4
Superfamilia Centropagoidea				
Familia Candaciidae				
Candacia armata	H	1.6	0.0	0.0
Familia Centropagidae				
Centropages hamatus	H	0.0	0.6	0.1
Centropages typicus	H	1.0	0.1	0.1
Familia Temoridae				
Temora longicornis	H	0.0	0.2	0.0
Superfamilia Megacalanoidea				
Familia Calanidae				
Calanidae spp.	H	1.0	1.6	0.5
Familia Megacalanidae				
Megacalanus longicornis	H	0.0	0.0	0.3
Superfamilia Eucalanoidea				
Familia Eucalanidae				
Eucalanus crassus	H	0.5	0.1	1.0
Rhincalanus nasutus	H	0.0	0.1	1.1
Superfamilia Clausocalanoidea				
Familia Aetideidae				
Aetideus armatus	H	0.5	55.5	7.9
Chiridius armatus	H	0.0	0.0	3.7
Gaetanus kruppi	H	0.0	0.0	0.7
Gaetanus latifrons	H	0.0	0.0	0.2
Gaetanus pileatus	H	0.0	0.0	0.3
Familia Euchaetidae				
Euchaeta spp.	H	7.5	0.3	9.3
Familia Phaennidae				
Brachycalanus atlanticus	H	0.0	0.0	0.2
Oothrix bidentata	H	0.0	0.0	0.2
Familia Scolecitrichidae				
Lophothrix frontalis	H	0.0	0.0	1.1
Familia Tharybidae				
Undinella simplex	H	21.5	4.1	0.0
Calanoida species 1	H	0.0	0.0	0.3
Calanoida species 2	H	0.0	0.0	1.9
Calanoida species 3	H	0.0	0.0	0.1
Calanoida species 4	H	0.0	0.0	0.1
Calanoida species 5	H	0.0	0.0	2.9
Calanoida species 6	H	0.0	0.0	0.1
Classis Malacostraca				
Subclassis Phyllocarida				
Ordo Nebaliacea				
Nebaliacea spp.	H	1.0	0.0	0.0
Subclassis Eumalacostraca				
Superordo Eucarida				
Ordo Euphausiacea				
Familia Euphausiidae				
Euphausia krohni	H	0.0	0.9	0.9
Meganyctiphanes norvegica	H	0.0	0.0	0.1
Nyctiphanes couchi	H	23.9	162.4	0.0
Thysanoëssa inermis	H	0.3	0.0	0.5
Ordo Decapoda				
Subordo Dendrobranchiata				
Infraordo Penaeidea				
Superfamilia Penaeoidea				
Familia Penaeidae				
Penaeidae spp. PO	M	0.3	0.3	0.4
Penaeidae spp. ZO	M	0.0	0.0	0.1
Superfamilia Sergestoidea				
Familia Sergestidae				
Sergestidae spp. PO	M	1.3	0.0	0.0
Subordo Pleocyemata				
Infraordo Caridea				
Familia Hippolytidae				
Caridion gordoni PO	M	0.3	0.0	0.0
Hippolyte holthuisi PO	M	0.3	15.6	0.0
Hippolytidae spp. PO	M	0.0	0.4	0.0
Familia Processidae				
Processa nouveli subsp. *holthuisi* I	M	5.2	3.1	0.2
Familia Pandalidae				
Pandalina profunda PO	M	0.0	21.4	0.3
Pandalidae spp. PO	M	6.0	38.9	0.3
Familia Crangonidae				
Philocheras bispinosus PO	M	11.9	0.0	0.0
Philocheras echinulatus PO	M	0.3	1.5	0.0
Crangonidae spp. ZO	M	1.0	0.0	0.0
Caridea spp. PO	M	0.0	0.2	0.5
Infraordo Anomura				
Superfamilia Paguroidea				
Familia Paguridae				
Anapagurus laevis ZO	M	0.3	0.0	0.0
Paguridae spp. ZO	M	0.0	0.0	0.1
Anomura spp. ZO	M	0.3	0.1	0.0
Infraordo Brachyura				
Section Oxystomata				
Superfamilia Leucosoidea				
Familia Leucosiidae				
Subfamilia Ebaliinae				
Brachyura aff. *Liocarcinus* ZO	M	0.5	0.1	0.5
Brachyura spp. ME	M	0.0	0.5	0.0
Decapoda species 1 PO	M	0.0	0.0	0.1
Decapoda species 2 PO	M	0.0	0.2	0.1

Addendum. Full species list with the noted densities (ind. 100 m^{-2}) for the continental shelf (cs) (i.e. cs200), mean densities for the shelf break sites (sb) (i.e. sb250 and sb300) and mean densities for the upper slope sites (us) (i.e. us600, us650 and us700); holohyperbenthos (H), merohyperbenthos (M); hydromedusa (HM), juvenile (JU), megalopa (ME), postlarva (PO), zoea (ZO).

	H/M	cs	sb	us
Superordo Peracarida				
Ordo Mysidacea				
Subordo Lophogastrida				
Familia Lophogastridae				
Lophogaster typicus	H	1.3	0.0	0.0
Subordo Mysida				
Familia Mysidae				
Subfamilia Boreomysinae				
Boreomysis arctica	H	0.0	0.0	1.6
Boreomysis megalops	H	0.0	22.9	0.0
Boreomysis tridens	H	0.0	0.0	0.1
Boreomysis spp.	H	0.0	0.1	0.0
Subfamilia Siriellinae				
Siriella clausii	H	1.0	0.2	0.0
Subfamilia Gastrosaccinae				
Anchialina agilis	H	5.4	0.7	0.0
Haplostylus normani	H	10.4	0.2	0.0
Subfamilia Mysinae				
Tribus Erythropini				
Amblyops abbreviata	H	0.0	0.0	1.0
Amblyops tenuicauda	H	0.0	0.0	0.1
Dactylerythrops dimorpha	H	0.0	0.0	0.4
Erythrops neapolitana	H	21.5	75.8	0.0
Erythrops serrata	H	7.8	0.0	0.0
Erythrops spp.	H	0.8	0.1	0.0
Hypererythrops serriventer	H	0.0	81.3	0.0
Paramblyops rostrata	H	0.0	0.0	28.1
Parapseudomma calloplura	H	0.0	0.0	3.3
Parerythrops obesa	H	7.5	6.3	0.1
Pseudomma affine	H	0.0	99.7	36.6
Pseudomma nanum	H	0.3	0.0	0.9
Pseudomma spp.	H	0.0	0.1	8.0
Tribus Leptomysini				
Leptomysis lingvura	H	0.0	0.2	0.0
Mysideis insignis	H	0.3	0.2	0.2
Mysidopsis didelphys	H	7.5	0.2	0.0
Mysidopsis gibbosa	H	3.1	0.0	0.0
Tribus Mysini				
Schistomysis ornata	H	0.0	0.1	0.0
Ordo Cumacea				
Familia Bodotriidae				
Subfamilia Bodotriinae				
Bodotria arenosa	H	0.3	0.0	0.0
Cyclaspis longicaudata	H	0.0	0.0	21.1
Familia Nannastacidae				
Campylaspis glabra	H	0.0	0.2	21.0
Campylaspis horridoides	H	0.0	0.0	0.1
Campylaspis macrophthalma	H	0.0	1.3	0.0
Campylaspis rostrata	H	0.0	0.0	0.4
Campylaspis squamifera	H	0.0	0.0	0.1
Campylaspis verrucosa	H	0.0	0.0	15.0
Procampylaspis armata	H	0.0	0.0	3.4
Familia Pseudocumatidae				
Pseudocuma similis	H	0.3	0.0	0.0
Familia Lampropidae				
Hemilamprops normani	H	0.0	2.8	11.8
Hemilamprops uniplicata	H	0.3	3.7	48.2
Paralamprops species 1	H	0.0	0.0	28.6
Platysympus typicus	H	0.0	0.0	45.8
Familia Diastylidae				
Diastyloides bacescoi	H	0.8	2.9	10.7
Makrokylindrus josephinae	H	0.0	0.0	42.1
Ordo Amphipoda				
Subordo Caprellidea				
Familia Phtisicidae				
Phtisica marina	H	0.3	4.6	0.0
Subordo Gammaridea				
Familia Ampeliscidae				
Ampelisca aequicornis	H	0.0	1.3	2.5
Ampelisca gibba	H	0.0	0.1	42.8
Ampelisca spinipes	H	0.0	0.5	0.2
Ampelisca spp.	H	0.0	0.0	2.3
Byblis guernei	H	0.0	0.0	10.7
Haploops setosa	H	0.0	0.0	1.3
Familia Amphilochidae				
Amphilochoides boecki	H	0.0	4.2	0.7
Paramphilochoides odontonyx	H	0.0	0.0	0.1
Familia Aoridae				
Autonoe spp.	H	0.0	0.0	0.1
Lembos spp.	H	0.8	4.5	0.0
Unciola species 1	H	0.3	0.0	0.0
Unciolella lunata	H	0.0	0.0	4.5
Familia Argissidae				
Argissa hamatipes	H	0.0	0.0	1.7
Familia Astyridae				
Astyra aff. *abyssi*	H	0.0	0.0	1.0
Familia Atylidae				
Atylus vedlomensis	H	0.8	0.2	0.0
Familia Calliopiidae				
Apherusa bispinosa	H	4.9	2.8	0.0
Apherusa clevei	H	0.8	0.1	0.0
Apherusa ovalipes	H	5.2	0.1	0.0
Apherusa spp.	H	0.3	0.0	0.0
Familia Corophiidae				
Siphonoecetes striatus	H	1.3	6.6	0.5
Familia Cressidae				
Cressa aff. *abyssicola*	H	0.0	0.0	3.8
Familia Epimeriidae				
Epimeria cornigera	H	5.7	11.4	6.1
Epimeria spp.	H	0.0	0.0	0.0
Familia Eusiridae				
Cleonardopsis carinata	H	0.0	0.0	0.1
Eusirus longipes	H	7.8	2.4	9.1
Rhachotropis helleri	H	0.0	8.1	0.1
Rhachotropis integricauda	H	0.0	94.8	0.0
Rhachotropis rostrata	H	0.0	0.0	0.1
Rhachotropis aff. *rostrata*	H	0.0	0.0	53.1
Familia Iphimediidae				
Iphimedia obesa	H	0.3	0.1	0.0
Familia Isaeidae				
Gammaropsis maculata	H	0.0	2.6	0.0
Gammaropsis species 1	H	0.0	0.0	1.5
Megamphopus comutus	H	0.8	0.0	0.0
Familia Ischyroceridae				
Ericthonius fasciatus	H	0.0	0.0	10.5
Ericthonius aff. *fasciatus*	H	0.0	0.0	0.6
Ericthonius spp.	H	0.0	0.0	5.7
Familia Lepechinellidae				
Lepechinella manco	H	0.0	0.0	17.5
Familia Leucothoidae				
Leucothoe lilljeborgi	H	0.0	1.6	0.0
Familia Liljeborgiidae				
Liljeborgia fissicornis	H	0.0	0.0	5.7
Familia Lysianassidae				
Hippomedon denticulatus	H	5.2	18.7	0.4
Hippomedon spp.	H	0.0	0.0	0.1
Lepidepecreum subclypeatum	H	0.3	0.0	0.0
Lysianassa plumosa	H	0.0	0.0	3.2
Normanion chevreuxi	H	0.0	0.1	0.0
Orchomene oxystoma	H	0.0	0.0	1.4
Orchomenella nana	H	0.0	0.0	0.8
Perrierella audouiniana	H	0.0	0.3	0.2
Podoprion bolivari	H	0.0	0.0	0.3
Scopelocheirus spp.	H	0.0	0.0	0.1
Socarnes erytrophthalmus	H	0.0	0.3	0.1
Socarnes filicornis	H	0.0	4.5	0.0
Tmetonyx similis	H	0.8	0.0	0.1
Trischizostoma raschi	H	0.0	0.0	0.1
Tryphosella horingi	H	0.0	0.0	0.1
Tryphosella laevis	H	0.0	0.0	0.3
Tryphosella nanoides	H	0.0	0.4	0.0
Tryphosella sarsi	H	0.0	0.0	0.1
Tryphosites alleni	H	0.0	0.2	4.6
Lysianassidae spp.	H	0.0	0.0	0.1

Addendum. (continued)

	H/M	cs	sb	us
Familia Melitidae				
Abludomelita aculeata	H	0.0	0.4	0.0
Cheirocratus intermedius	H	0.0	3.2	0.0
Maera othonis	H	0.3	0.1	0.0
Melita gladiosa	H	0.0	7.3	0.0
Familia Melphidippidae				
Melphidippa goesi	H	0.0	13.9	13.9
Melphidippa macrura	H	0.0	0.0	2.1
Melphidippella macra	H	8.6	22.8	0.0
Melphidippidae spp.	H	0.0	0.0	65.0
Familia Oedicerotidae				
Bathymedon longirostris	H	0.0	0.0	4.6
Monoculodes gibbosus	H	0.8	0.0	0.0
Monoculodes packardi	H	0.0	0.0	8.4
Oediceropsis brevicornis	H	0.0	0.0	1.5
Pontocrates altamarinus	H	0.3	0.0	0.0
Synchelidium haplocheles	H	0.0	0.2	0.0
Synchelidium maculatum	H	5.7	1.8	0.1
Westwoodilla caecula	H	0.0	10.2	4.4
Oedicerotidae spp.	H	0.8	0.1	0.0
Familia Pardaliscidae				
Halicoides anomala	H	0.0	0.7	0.0
Nicippe tumida	H	1.0	0.0	17.2
Pardaliscidae spp.	H	0.0	0.0	0.0
Familia Phoxocephalidae				
Harpinia pectinata	H	0.0	0.0	1.1
Familia Pleustidae				
Stenopleustes aff. *malmgreni*	H	0.0	0.0	0.1
Familia Podoceridae				
Laetmatophilus tuberculatus	H	0.0	0.0	6.2
Xenodice frauendeldti	H	0.0	0.0	0.3
Familia Pontoporeidae				
Bathyporeia spp.	H	0.3	0.0	0.0
Familia Stegocephalidae				
Stegocephaloides christianiensis	H	0.3	9.0	16.2
Familia Stenothoidae				
Stenothoe marina	H	0.0	0.0	1.8
Familia Synopiidae				
Bruzelia typica	H	0.0	0.0	9.4
Syrrhoe affinis	H	0.0	0.0	48.6
Syrrhoites walkeri	H	0.0	0.0	15.6
Familia Urothoidae				
Urothoe elegans	H	0.3	1.6	2.0
Gammaridea spp.	H	0.3	0.0	0.0
Subordo Hyperiidea				
Familia Hyperiidae				
Hyperia galba	H	1.6	1.6	0.1
Parathemisto gaudichaudi	H	0.0	0.1	19.9
Ordo Isopoda				
Subordo Gnathiidae				
Familia Gnathiidae				
Gnathia oxyuraea	H	0.5	1.7	0.0
Gnathia species 1	H	0.3	0.0	0.0
Gnathia spp.	H	0.0	0.0	1.0
Subordo Flabellifera				
Familia Aegidae				
Aega species 1	H	0.0	0.1	0.2
Familia Anthuridae				
Anthuridae species 1	H	0.0	0.0	0.2
Familia Cirolanidae				
Eurydice species 1	H	1.6	0.1	3.2
Metacirolana hanseni	H	0.0	0.0	0.3
Natatolana borealis	H	0.0	0.6	3.3
Natatolana caeca	H	0.0	0.0	0.4
Familia Paranthuridae				
Leptanthura tenuis	H	0.0	0.0	0.1
Familia Sphaeromatidae				
Bathycopea typhlops	H	0.0	0.0	62.2
Subordo Valvifera				
Familia Arcturidae				
Arcturella dilatata	H	0.0	0.2	6.3
Astacilla species 1	H	0.0	0.1	0.3
Astacilla species 2	H	0.0	0.2	10.2
Astacilla spp.	H	0.0	0.0	0.5
Subordo Asellota				
Familia Eurycopidae				
Disconectes latirostris	H	0.0	4.2	15.3
Munnopsurus species 1	H	0.0	0.0	0.4
Tytthocope megalura	H	0.0	0.0	12.9
Familia Ilyarachnidae				
Aspidarachna clypeata	H	0.0	0.0	0.2
Ilyarachna longicornis	H	0.0	0.1	4.7
Familia Ischnomesidae				
Ischnomesus species 1	H	0.0	0.0	0.5
Familia Janiridae				
Janiridae species 1	H	0.0	0.0	0.4
Familia Munnidae				
Munna limicola	H	0.0	0.1	0.7
Familia Munnopsidae				
Munnopsis beddardi	H	0.0	0.0	1.9
Ordo Tanaidacea				
Subordo Apseudomorpha				
Familia Apseudidae				
Apseudes grossimanus	H	0.0	0.0	0.1
Apseudes spinosus	H	0.0	0.0	0.3
Subordo Tanaidomorpha				
Familia Leptognathiidae				
Typhlotanais aequiremis	H	0.0	0.0	1.9
Subphylum Chelicerata				
Classis Pycnogonida				
Familia Nymphonidae				
Nymphon gracile	H	0.0	0.0	0.1
Nymphonidae species 1	H	0.0	0.1	0.5
Familia Ammotheidae				
Ammotheidae species 1	H	0.0	0.2	0.0
Ammotheidae species 2	H	0.0	0.0	7.1
Ammotheidae species 3	H	0.0	0.1	0.0
Familia Callipallenidae				
Callipallene phantoma	H	0.0	0.0	0.5
Pycnogonida species 1	H	0.0	0.0	6.7
Phylum Chordata				
Subphylum Vertebrata				
Superclassis Gnathostomata				
Classis Actinopterygii				
Subclassis Neopterygii				
Division Teleostei				
Subdivision Euteleostei				
Superordo Protacanthopterygii				
Ordo Osmeriformes				
Subordo Argentinoidei				
Superfamilia Argentinoidea				
Familia Argentinidae				
Argentinidae species 1 PO	M	0.3	0.0	0.0
Superordo Acanthopterygii				
Series Percomorpha				
Ordo Perciformes				
Subordo Callionymoidei				
Familia Callionymidae				
Callionymus reticulatus PO	M	0.3	0.0	0.0
Subordo Gobioidei				
Familia Gobiidae				
Subfamilia Gobiinae				
Gobiidae species 1 PO	M	0.3	0.0	0.0
Pisces species 1 PO	M	0.0	0.1	0.0
Pisces species 2 PO	M	0.0	0.0	0.1
Pisces species 3 PO	M	0.0	0.0	0.1
Pisces species 4 PO	M	0.0	0.0	0.1
Pisces species 5 PO	M	0.0	0.0	0.1

Addendum. (continued)

Chapter 4. Structuring patterns of the hyperbenthos communities of the Belgian and Zeeland subtidal sandbanks (North Sea)

Ann Dewicke, André Cattrijsse, Jan Mees & Magda Vincx

Summary

The hyperbenthos of the Belgian continental shelf, the Dutch continental shelf off Zeeland and the Westerschelde estuary was sampled within a two-week period at 62 locations in the summer of 1993. A total of 109 taxa were recorded, half of which were amphipods and decapods. Mysids were the most important taxon in terms of density and biomass. In all, seven hyperbenthic communities were identified. Their geographical occurrence was correlated with the presence of isolated sandbank systems in the area. The community in the mesohaline reaches of the Westerschelde estuary was different from the shelf hyperbenthos and was characterized by the highest density and biomass and lowest diversity. Two gradients in community structure were detected on the continental shelf: the principal onshore-offshore gradient perpendicular to the coastline and a less pronounced east-west gradient parallel to the coastline. The first gradient mainly indicated differences in density and biomass, while the second reflected species richness and diversity.

The most diverse communities were found at the Flemish and Zeeland Banks. The holohyperbenthos (i.e. animals that spend variable periods of their adult life in the hyperbenthal zone) reached high densities at the Coastal Banks and consisted nearly exclusively of mysids; *Schistomysis spiritus* and *S. kervillei* were the most common species. The high levels of suspended matter and mud in this onshore area probably advantage this motile fauna in terms of food. Community composition altered with distance from the shore and planktonic species gained in abundance. Outflow from the Westerschelde estuary may cause a decline of species richness at the East Coast, but favours high densities of resistent species.

The merohyperbenthos (early life history stages) was most abundant at the Flemish and Zeeland Banks and was mainly composed of a variety of larval decapods. Biomass peaked at the Coastal Banks with a dominance of postlarval gobies. A strong diversity gradient was found for the merohyperbenthos with a richer fauna off the Belgian coast as compared to the Zeeland offshore waters. Habitat heterogeneity and water mass flow characteristics are believed to be the most important structuring environmental factors.

Introduction

The southern North Sea is characterized by numerous subtidal sandbanks, being grouped in a parallel pattern. They are elongated sedimentary bodies, typically tens of kilometres long, a few kilometres wide and several tens of metres high (Trentesaux *et al.* 1999). Four sets of sandbanks cover a large part of the Belgian continental shelf: the Coastal Banks, the Flemish Banks, the Zeeland Banks and the Hinder Banks (Fig. 1). Their close position to the coastline and the shallowness of the area make them unique, both from an ecological and geological point of view. Nearshore coastal sandbanks dissipate energy from incoming waves and are very effective in protecting the coast (Carter & Balsillie 1983). The continuous interaction between morpho- and hydrodynamics results in a complex heterogeneous structure of the coastal area. This generates a variety of habitats for marine sea life showing patches of varying organic entrapment and shelter. In addition, it has often been hypothesized that the protective functioning of these sandbank systems might sustain nursery areas for several fish and crustacean species (Dyer & Huntley 1999). It has recently been shown that the sandbank system in the Belgian coastal area acts as an internationally important resting and foraging area for various seabird species (Maes *et al.* 2000; Cattrijsse & Vincx 2001). Part of the area has therefore been designated as a Belgian Marine Wetland of International Importance under the Ramsar Convention (Maes *et al.* 2000).

The vulnerable area experiences heavy human mediation such as nutrient enrichment, dredging activities and dumping of dredged material, sand and gravel extraction, ship traffic and oil pollution (Maes *et al.* 2000; Volckaert *et al.* 2000). In all, fisheries have been categorized as exerting the strongest pressure on the North Sea ecosystem (OSPAR Commission 2000). The project 'Structural and functional biodiversity of North Sea ecosystems: species and their habitats as indicators for a sustainable development of the Belgian continental shelf' aims to assess the factors that determine and influence the marine biodiversity of the area. The present study deals with the hyperbenthic biodiversity of the area.

The hyperbenthos is the association of small animals living in the water layer close to the seabed (Mees & Jones 1997). This faunistic group has not yet been studied in the Belgian coastal area. The only literature on some typical representatives of the hyperbenthos of the Belgian coast dates from the nineteenth century (Van Beneden 1860). Few typical hyperbenthic species appear in species lists (often in grey literature) from plankton or macrobenthos research and they are often classified as occasional or rare catches. This is mainly attributed to the lack of a specialized sampling device to catch this motile fauna. This kind of device has only been well developed and deployed during the last two decades (Mees & Jones 1997).

As knowledge on the hyperbenthos is accumulating, its importance in shallow coastal and estuarine food webs becomes well established (Mees & Jones 1997). Crustaceans, especially mysids, often dominate the hyperbenthos in shallow areas (Mees & Jones 1997). These omnivores feed on detritus, algae or zooplankton (Mauchline 1980) and can contribute substantially to the diet of fish (Beyst *et al.* 1999a; Hostens & Mees 1999; Pedersen 1999) and shrimp (Oh *et al.* 2001; Hostens unpubl. data). Up to now, hyperbenthic communities of the NE Atlantic coasts have been investigated in the Scandinavian fjords (Buhl-Jensen & Fosså 1991), the Dutch Voordelta (Hamerlynck & Mees 1991; Mees & Hamerlynck 1992), the English Channel (Dauvin *et al.* 1994; Wang & Dauvin 1994; Wang *et al.* 1994; Dauvin &

Zouhiri 1996; Zouhiri & Dauvin 1996; Vallet & Dauvin 1998; Vallet & Dauvin 1999; Dauvin *et al.* 2000), the Bay of Biscay (Sorbe 1982, 1989; Cornet *et al.* 1983) and off Portugal (Cunha *et al.* 1997).

This chapter presents the first data on the biodiversity of the hyperbenthos inhabiting the subtidal waters on the Belgian continental shelf. The following questions were addressed: (1) What species are present in the hyperbenthal zone? (2) Is the hyperbenthic community spatially structured in characteristics such as species composition, density, biomass and diversity? (3) Is there a relationship between community structure and the known environmental gradients on the Belgian continental shelf? Seasonal patterns in community structure will be dealt with in Chapter 5.

Material and methods

Study area

The Belgian continental shelf (on average 30 m deep) has a maximum seaward width of 87 km and is bordered by a rectilinear 70 km long sandy coastline that merges eastwards into the Westerschelde estuary (Maes *et al.* 2000). A saline (33.5-34.5 psu) Channel water mass enters the area by the NE directed residual current and meets the SW oriented Westerschelde outflow (Nihoul & Hecq 1984; Djenidi *et al.* 1996; Baeyens *et al.* 1998). The current regime is macro-tidal and keeps the water column well mixed. Tidal amplitude is 4 m and the depth-average current velocity exceeds 1 m s^{-1} during spring tide (Beheerseenheid Mathematisch Model Noordzee 1996).

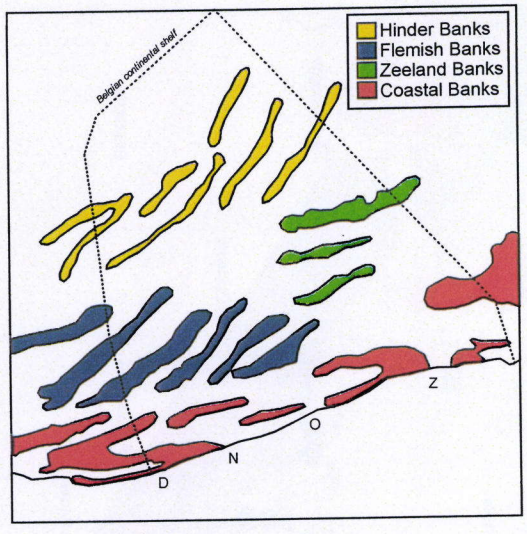

Fig. 1. The sandbank sets occurring in the study area

The Coastal Banks (max. 20 km long and 1 km wide) are stretched out parallel along the coastline within a distance of 10 km from the shore; the crests are situated 2–3 m below MLLWS (Mean Lowest Low Water Spring Level). To the west of Oostende and at 10-30 km from the shore, the Flemish Banks (max. 15-25 km long and 3-6 km wide) occur. They are NE oriented with crests some 4 m below MLLWS. The Zeeland Banks are located to the east of Oostende, partly situated in Belgian and further extending in Dutch waters. As the Coastal Banks, their orientation is parallel to the shore (at a distance of 15-30 km), but they have crests below 10 m MLLWS. The Hinder Banks are located further offshore in the deepest part of the Belgian continental shelf. Their distance to the coast is 35-60 km and their crests are at the same depth as the Zeeland Banks. For a detailed description of the sandbank system we refer to Bastin (1974).

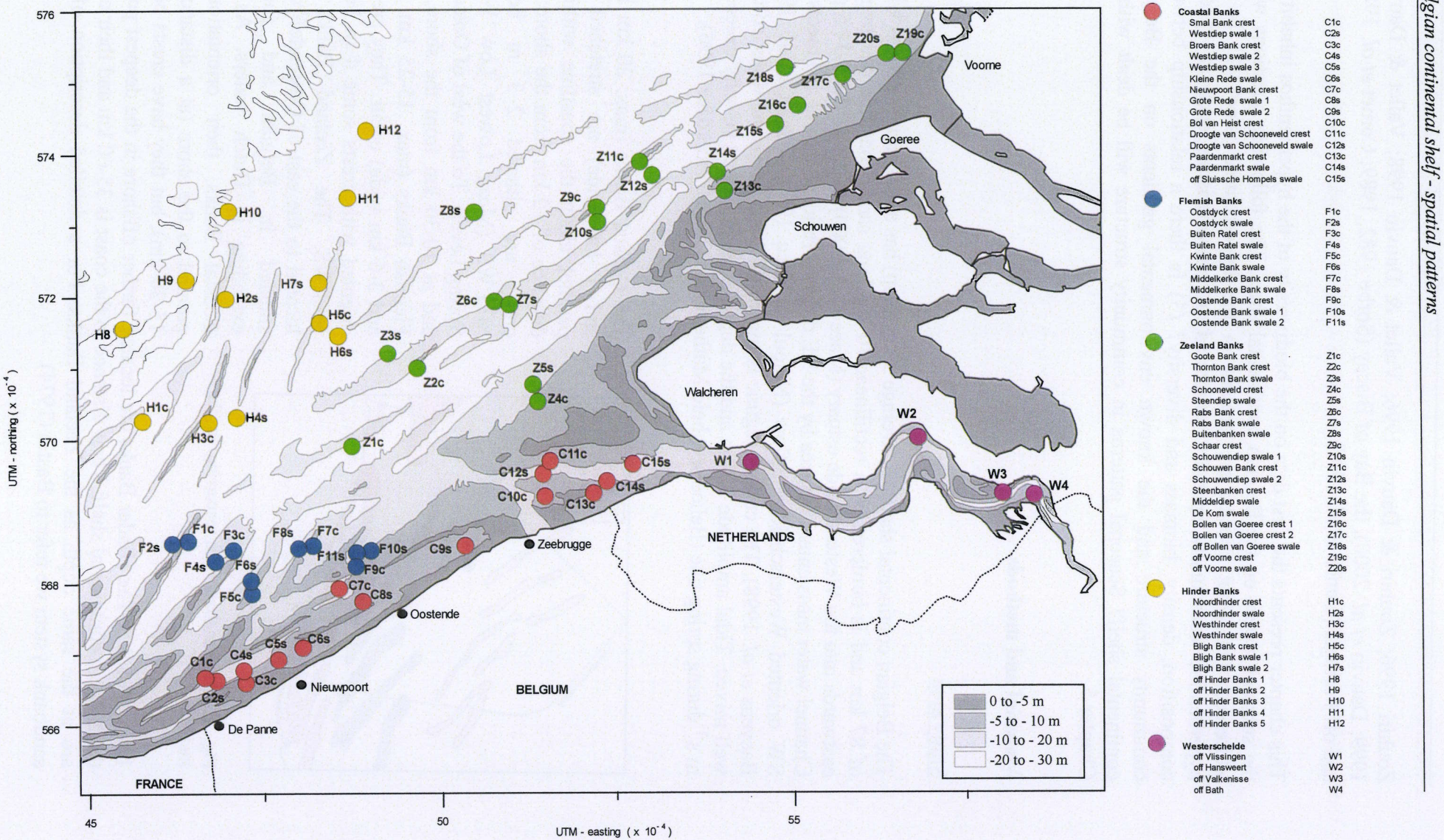

Fig. 2. Map of the study area showing the location of the sampling sites. Symbols refer to the sandbank complexes. The sandbanks dealt with are listed for each sandbank complex in the table above.

Sampling

The hyperbenthos of the Belgian continental shelf (42 sites), the Dutch coastal area off Zeeland (16 sites), and the Westerschelde estuary (4 sites), was sampled in September 1993, during a two-week period. Sampling sites were chosen in order to cover all major sandbanks and gullies in the area. Sites located on a sandbank were always chosen as shallow as possible on its crest (sample named after the sandbank set with extension 'c') and the sites in the swales in-between at their deepest part (sample name with extension 's'). The northernmost sites are located off the sandbank system (sample name without extension). Depth of the sampling sites ranged from 7 to 39 m. (See Fig. 2 for the full list of sandbanks and swales dealt with.)

A total of 62 samples were collected, sampling sites are shown in Fig. 2. All sampling was done from the *RV* Belgica with a modified hyperbenthic sledge after Sorbe (1983). Two superimposed nets (1 mm mesh size, 3 m long, 71 cm wide) were fixed on the sledge and sampled the water layer from 0 to 50 cm (lower net) and from 50 to 100 cm (upper net) above the sea floor. The sledge was equipped with an opening-closing mechanism and an odometer (for details see Sorbe 1983). A flow meter (*General Oceanics* 2030R) was fixed in the upper net. All sampling was carried out during daytime; towing was done against the current for five minutes at an average ship speed of 1.5 knot relative to the bottom. Towing distance was 146 ± 14.4 m and a volume of 101 ± 9.3 m^3 was filtered through the nets.

The catches from the upper and lower net were rinsed separately over a 1 mm mesh size sieve and preserved in a buffered formaldehyde solution (7 % final concentration). Before each tow, surface temperature and salinity (thermosalinograph *Sea-bird SBE21*), and Secchi depth were registered. Depth was standardized to the local MLLWS level. Additional sediment samples were taken with a multi-corer (*Bowers-Connelly*). The upper 2 cm of the sediment was sampled for grain fraction analysis (particle size analyser *Coulter LS 100*). The near-bottom water collected with the multi-corer was drained. A volume of 1000 ml was pushed through Whatman glass-fibre filters (GF/C) for pigment analysis (chlorophyll *a* and fucoxanthin) and immediately deep-frozen. An extraction with aceton (90 %) was performed prior to a chromatography, with a HPLC-chain (High-Performance Liquid Chromatography *Gilson*), according to the method of Mantoura & Llewellyn (1983).

Data acquisition

In the laboratory, all organisms were sorted out, identified, if possible to species level and counted. For certain taxa, further classification was done based on the life history stage of the organism, such as the distinction between zoea, megalopa and postlarva stages for decapods. In case of uncertain identification, specimens were reported on a higher taxomomic level (reported as 'spp.' and further called 'species').

Species occurring in a wide length range were measured (standard length from the rostral tip to the last abdominal segment for crustaceans and from the tip of the lower jaw to the end of the notochord for fish larvae) and their biomass was derived from regressions relating standard length to Ash free Dry Weight (ADW). ADW was determined as the difference between dry weight (60°C for 5 days) and ash weight (650°C for 2 hours) for representative size distributions of the various species. For species caught in discrete life stages or occurring with a particular

length, an average biomass value was assigned per stage or per species. This value was determined by measuring the ADW of batches of animals belonging to a certain stage. Both the regressions and the assigned biomass values were partly determined using animals from this study and from previous research (Beyst *et al.* 1999a; A. Dewicke unpubl. data).

The resulting dataset (i.e. all animals that were caught by the Sorbe-hyperbenthic sledge and which were retained on a 1 mm sieve) was reduced. Non-hyperbenthic species, like all juvenile and adult decapods and fish, polychaetes, scyphozoans, fish eggs, sedentary and ectoparasitic organisms, were removed (see Introduction). Further, the hyperbenthos was divided into its holo- and merohyperbenthic components. Holohyperbenthos is defined as animals that spend variable periods of their adult life in the hyperbenthal zone (Mees & Jones 1997). It comprises a group of taxa with a rather small adult habitus (generally less than 20 mm), such as all peracarids, copepods, chaetognaths, pycnogonids and hydromedusae. The merohyperbenthos consists of early life history stages, frequently from larger animals, and is mainly represented by decapod larvae (< 10 mm), postlarval fish (generally < 20 mm) and larval polychaetes (modified after Mees & Jones 1997). The resulting species list of all hyperbenthos is listed in Addendum. Density and biomass data were calculated as numbers of individuals and mg ADW per 100 m^{-3}. Since catch efficiency of sledges remains largely unknown (Mees & Jones 1997), all densities and biomass values are considered as minimum estimates.

Numerical analysis

Raw density data were fourth root transformed (Field *et al.* 1982; Legendre & Legendre 1998) and subjected to multivariate statistical analyses; hydromedusae and ctenophores were omitted because they heavily skewed the analysis. The classification program TWINSPAN (Hill 1979) was applied in order to identify communities. This analysis was complemented with ordination techniques, using the program package CANOCO 4 (ter Braak & Smilauer 1998). After a first analysis of the full datamatrix, it was further subdivided. This allowed for more detailed ordination techniques, thus optimizing the visualization of the spatial species variance into a two-dimensional plane (see Results). For the full dataset and each subset, an exploratory Detrended Correspondence Analysis (DCA) was first performed, in order to estimate the gradient length (g.l.) in standard deviation (s.d.) units giving an indication of the expected underlying model for the species response curves (unimodal or linear) (see ter Braak & Prentice 1988; Van Wijngaarden *et al.* 1995). Indirect techniques, both CA (Correspondance Analysis, unimodal technique) and PCA (Principal Components Analysis, linear technique) were further applied to determine the relative amount of variation in the species dataset along the main structuring axes.

Selection of environmental variables

The following environmental variables were considered for the ordination analyses: depth, temperature, salinity, Secchi depth, chlorophyll *a*, fucoxanthin, mean and median grain size, all granulometric fractions between 0 and 1000 according to the Wentworth scale (Buchanan 1984) and the percentage of mud (< 63 µm, the sum of organic and inorganic fractions). Sediment fractions were arcsine transformed; all

other variables were log(x+1) transformed in order to obtain a normal distribution (Legendre & Legendre 1998). The independent contribution of each single variable in explaining the total variation was assessed by performing preliminary constrained analyses, i.e. CCA (Canonical Correspondance Analysis, unimodal technique) and RDA (Redundancy Analysis, linear technique) in which each environmental variable in turn was used as a single constrained variable. Only these variables that independently explained a significant amount of variation (Monte Carlo permutation test (Manly 1997), 999 unrestricted permutations, $p<0.01$) in the dataset were selected for further analysis (Økland & Eilertsen 1994).

Relation with the environment

The forward selection procedure followed by Monte Carlo permutation tests was applied to generate a 'minimal set' of environmental variables (for each sub-dataset separately) which independently and significantly ($p<0.01$) explained the variation in the species data as well as the full set (ter Braak & Verdonschot 1995). Special attention was paid to highly multi-colinear variables, since these may destabilize the final ordination. This was done by checking the inflation factor being always lower than 5 for the final analysis (see ter Braak & Smilauer 1998). These minimal sets were eventually used to assess the fraction of species variance explained by the explanatory variables as recommended by Økland (1996). Since no *a priori* hypothesis was postulated, ordination diagrams aimed to visualize the major gradients in community structure, and thus derive from unconstrained techniques.

Community characteristics

Species richness was estimated by Hill's diversity number N_0, which is equal to the number of species in a sample (Hill 1973). The expected number of species for a sample of 100 individuals $E(S_{100})$ (Hurlbert 1971) and the Hill diversity numbers N_1 and N_2, were calculated to estimate species diversity. N_1 is the inversed natural logarithm of the Shannon-Wiener diversity index and N_2 is the reciprocal of Simpson's dominance index (Hill 1973). Species reported on a higher taxon level were considered as a single species if no other representative of the same taxon level was present or if they were distinctly different. Diversity is thus considered as a minimum estimate.

Differences between communities were assessed using ANOVA and subsequent *post-hoc* comparisons (parametric) for densities and biomasses (both log(x+1) transformed). The environmental variables and diversity estimates did not meet the assumptions for ANOVA. Therefore, a non-parametric Kruskal-Wallis test followed by multiple comparisons according to Conover (1971) was used.

	# sp	abs den	% den	abs bio	% bio		% freq	abs den	% den	max den	abs bio	% bio	max bio
Phylum Cnidaria	2	70	7	0	0	*Mitrocomella polydiademata* HM	60	69	7	804	0	0	2
Phylum Ctenophora	3	110	5	0	0	*Pleurobrachia pileus*	65	109	5	2538	0	0	0
Phylum Annelida													
Classis Polychaeta	2	17	2	1	0	*Lanice conchilega* LA	73	17	2	165	1	0	5
Phylum Chaetognatha	1	68	5	5	1	*Sagitta elegans*	92	68	5	936	5	1	62
Phylum Mollusca	2	0	0	2	1	*Sepiola atlantica* *	26	0	0	4	2	0	27
Phylum Arthropoda													
Subphylum Crustacea													
Classis Copepoda	3	12	1	1	0	*Calanus helgolandicus* *	61	11	1	198	1	0	18
Classis Malacostraca													
Superordo Eucarida													
Ordo Euphausiacea	1	0	0	0	0	*Nyctiphanes couchi* *	3	0	0	1	0	0	1
Ordo Decapoda													
Infraordo Caridea	9	172	13	49	14	*Crangon crangon* PO	90	69	3	580	21	3	176
						Crangonidae spp. ZO	95	66	5	401	15	5	91
						Philocheras trispinosus PO	84	19	2	122	8	3	50
						Hippolyte varians PO	89	11	1	208	4	1	70
InfraordoThalassinidea	2	1	0	1	0	*Upogebia* spp. ZO *	13	1	0	12	0	0	8
Infraordo Anomura	5	24	4	16	8	*Pisidia longicornis* ME	84	15	2	108	10	5	72
						Pisidia longicornis ZO	66	4	0	58	2	1	36
						Galathea intermedia ME	36	3	1	45	2	2	30
Infraordo Brachyura	9	281	23	43	16	*Liocarcinus* spp. ME	92	139	10	1652	26	9	312
						Liocarcinus spp. ZO	89	66	6	536	10	4	81
						Pilumnus hirtellus ME	92	24	2	185	2	1	15
						Carcinus maenas ME	82	20	1	232	2	1	19
						Carcinus maenas ZO	69	13	1	118	1	0	6
Superordo Peracarida													
Ordo Mysidacea	10	1837	33	1946	46	*Mesopodopsis slabberi*	61	921	5	51977	615	5	34606
						Schistomysis spiritus	63	369	10	4514	538	11	8339
						Schistomysis kervillei	65	335	10	3901	455	13	6017
						Gastrosaccus spinifer	97	126	7	1204	112	14	951
Ordo Cumacea	7	9	1	4	0	*Diastylis bradyi* *	71	6	0	73	2	0	28
Ordo Amphipoda	30	125	6	28	5	*Atylus swammerdami*	97	52	5	690	13	4	258
Ordo Isopoda	3	5	0	2	0	*Idotea linearis* *	13	5	0	312	2	0	123
Subphylum Chelicerata													
Classis Pycnogonida	4	0	0	0	0	*Endeis laevis* *	2	0	0	4	0	0	0
Phylum Chordata													
Subphylum Vertebrata													
Classis Actinopterygii	16	30	1	113	8	*Pomatoschistus* spp. PO	94	26	1	239	95	5	1456
						Hyperoplus lanceolatus PO	10	0	0	3	7	2	304

	# sp	mean ± se den	mean ± se bio	max den	min dens	max bio	min bio
Total hyperbenthos	109	2761± 914	2210 ± 826	56235	60	47870	22

Table 1. Summary of some ecological characteristics of all major taxonomic groups belonging to the hyperbenthos and of their most common representatives. For each taxonomic group, total species numbers is given (# sp) and all species accounting for more than 1 % to the total density or biomass are listed. Some taxonomic groups were only poorly represented. In this case, their most abundant species seldom met the 1 % criterion and is indicated with '*'. Mean absolute and relative densities (abs den and % den) and biomass (abs bio and % bio) over all samples are tabulated. 'max den' and 'max bio' refer to the maximum values for density and biomass reported at a single site. The relative occurrence over all samples is presented (% freq). Density is expressed as ind. 100 m^{-3} and biomass as mg ADW 100 m^{-3}. Developmental stages of decapods are treated as a separate taxa. Hydromedusa (HM), larva (LA), zoea (ZO), postlarva (PO), megalopa (ME).

Results

Hyperbenthos species richness, density and biomass

A total of 109 species was observed (see Addendum). Some ecological characteristics per higher taxonomic level guided by a selection of the most important representatives, are presented in Table 1 (see legend for selection criteria). Total density per site ranged from 60 to 56235 ind. 100 m^{-3} and total biomass varied between 22 and 47869 mg ADW 100 m^{-3}. Highest values were reached in the brackish part of the Westerschelde estuary (sites W2, W3 and W4). After exclusion of these stations, average density and biomass were 1827 ± 266 ind. 100 m^{-3} and 1406 ± 358 mg ADW 100 m^{-3}, respectively. Three major groups were found to be important for community characteristics like species number, abundance or biomass: peracarids (mainly gammaridean amphipods and mysids), larval decapods and postlarval fish. Amphipods had the highest species richness (30 species). *Atylus swammerdami* was the most abundant species and it was very common, as it was nearly caught at each station. Mysids contributed for 33 % to total density and for 46 % to the total biomass. *Mesopodopsis slabberi* reached the highest average density. This was due to the very high values recorded in the brackish part of the Westerschelde estuary. *Schistomysis spiritus* and *S. kervillei* were the dominant mysid species on the continental shelf, mostly occurring in shallow, nearshore waters. They each contributed more than 10 % to total biomass. The same counts for the mysid *Gastrosaccus spinifer*.

A high variety of early life history stages of decapods was encountered (25 species) and often in high abundances. The Crangonidae were the dominant family of shrimp. They were mainly represented by *Crangon crangon*, and to a lesser extent by *Philocheras trispinosus*. From other shrimp families, only *Hippolyte varians* (Hippolytidae) was recorded in appreciable numbers. The Brachyura were also a very abundant taxon (23 % of the total density and 16 % of the total biomass). Highest values were reached in offshore waters. Swimming crab *Liocarcinus* spp. (probably almost exclusively *L. holsatus*) was the most dominant species. Other common species were the shore crab *Carcinus maenas* and hairy crab *Pilumnus hirtellus*. Postlarval fish were on average not so abundant, but they attained a high biomass (8 % of the total biomass); a total of 16 fish species were encountered. The larvae of gobies of the genus *Pomatoschistus* (probably mainly *P. lozanoi*) dominated and were recorded at nearly all stations.

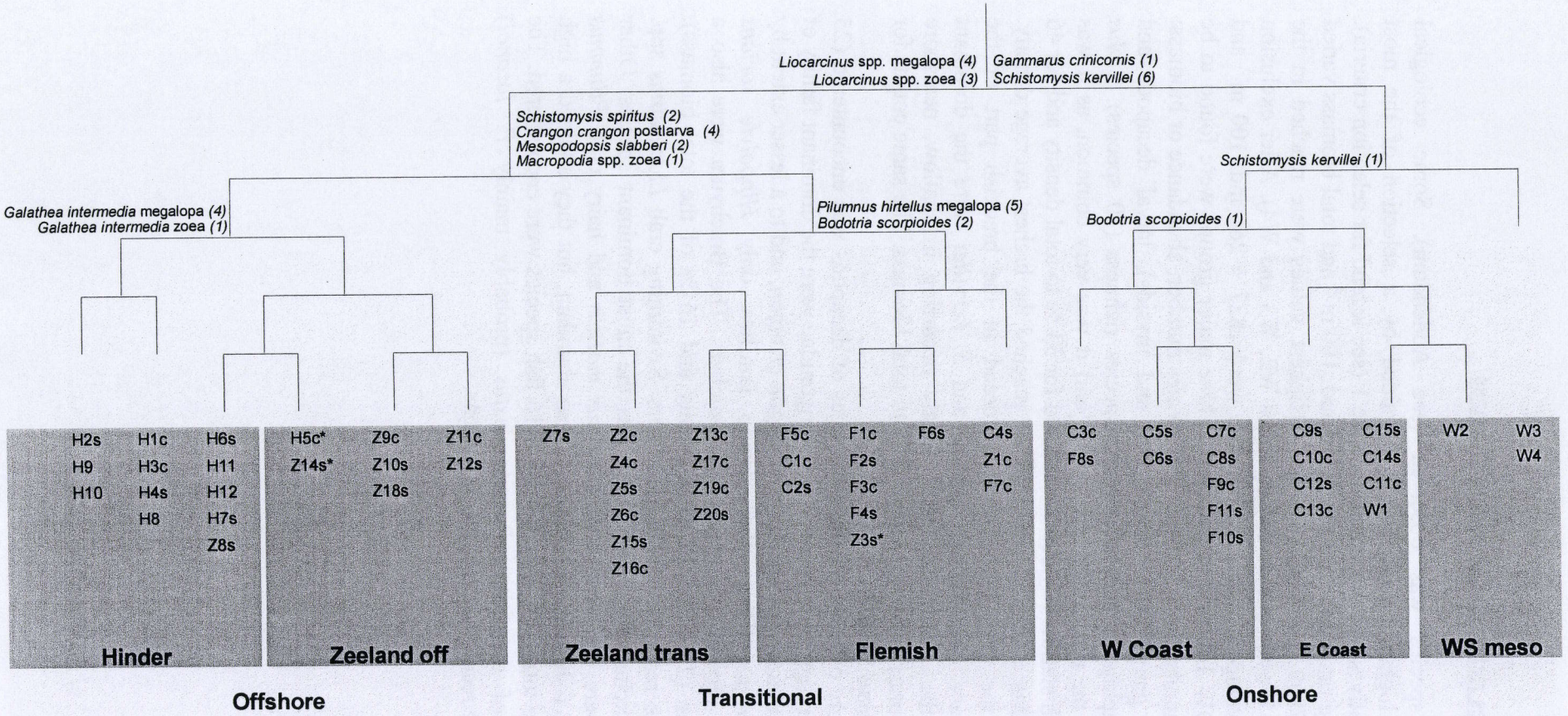

Fig. 3. TWINSPAN dendrogram based on species density data. Indicator species are show together with their cutlevel class; cutlevels used were 0, 1.03, 1.29, 1.67, 2.31 and 2.96. The final identified communities are indicated. Some minor differences exist with the output from the ordination techniques (see Fig. 4, 5 and 6), such as the classification of the sites indicated with '*'. These samples were mostly recognized as being misclassified or borderlines by the TWINSPAN program, therefore their final classification into the biotic communities was based on the ordination output shown in Fig. 4, 5 and 6.

Multivariate analyses

TWINSPAN

The dendrogram generated by the TWINSPAN analysis performed on the full density matrix is depicted in Fig. 3. The first two division levels separate the mesohaline sites of the Westerschelde estuary and project the continental shelf sites along an onshore-offshore gradient. An onshore, a transitional and an offshore cluster of stations can be identified. At the following division levels, each cluster is further divided into a western and an eastern group (see below).

Ordination

Unimodal techniques were applied on the full density dataset, as the gradient length determined by an explanatory DCA was 3.542 s.d. units. The first axis of the CA has an eigenvalue (e.v.) of 0.405 and represents 19.2 % of the variation in the species data (Fig. 4). The three stations from the mesohaline reaches of the Westerschelde are widely spread along this axis, while the sample scores for the shelf stations show little variability. The second axis has a much lower eigenvalue (0. 247) and shows an additional 11.6 % of the total variation. Salinity, Secchi depth and depth (minimal set) together explain 28.9 % of the species variation. Salinity explains 16.5 % on its own and is highly correlated with the first axis, indicating a gradient for the mesohaline Westerschelde sites with lowest salinity at W3 and W4. The correlation with the second axis is highest for Secchi depth, which explains an additional 7.1 % of the total species variance. Fig. 4 shows that the second axis reflects an onshore-offshore gradient, the onshore sites (upper part of the diagram) being characterized by the highest turbidity.

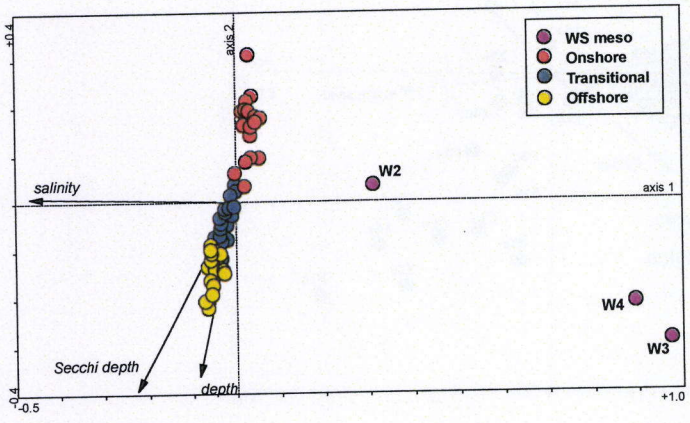

Fig. 4. Ordination diagram for the CA analysis of the full density datamatrix. The first (e.v. 0.405) and second axis (e.v. 0.247) are presented and display 30.8 % of the species variance. Eigenvalues for axis 3 and 4 are 0.136 and 0.111, resp. The environmental variables shown (minimal set), together explain 28.9 % of the species variance (derived from CCA). Sites are labelled according to the final identified communities.

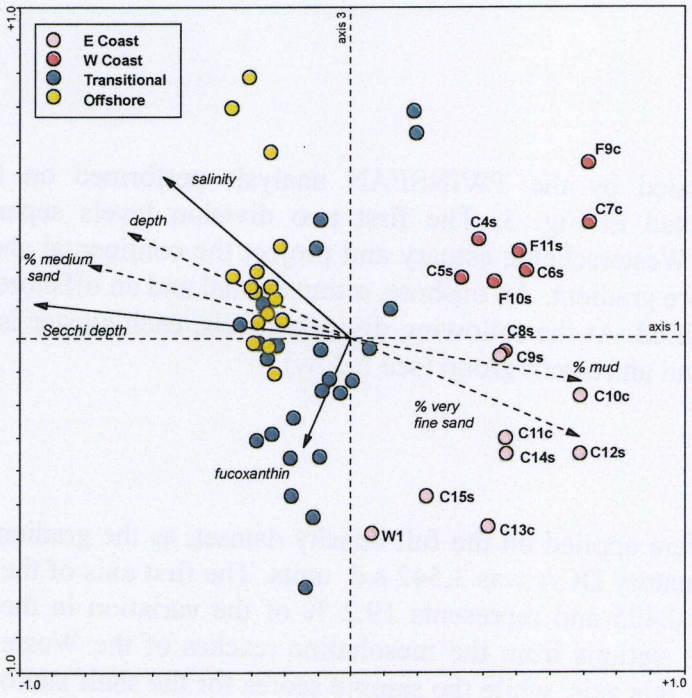

Fig. 5. Correlation biplot for the PCA analysis of the species density data after exclusion of W2, W3 and W4. The first (e.v. 0.381) and third axis (e.v. 0.062) are represented and display 44.3 % of the total variation. Eigenvalues for axis two and four are 0.153 and 0.058, resp. The environmental variables indicated with a full line (minimal set) explain together 43.1 % of the species variance (derived by RDA). Broken lines present some other meaningful variables, which were selected for independent and significant influence on the ordination. Sites are labelled according to the final identified communities.

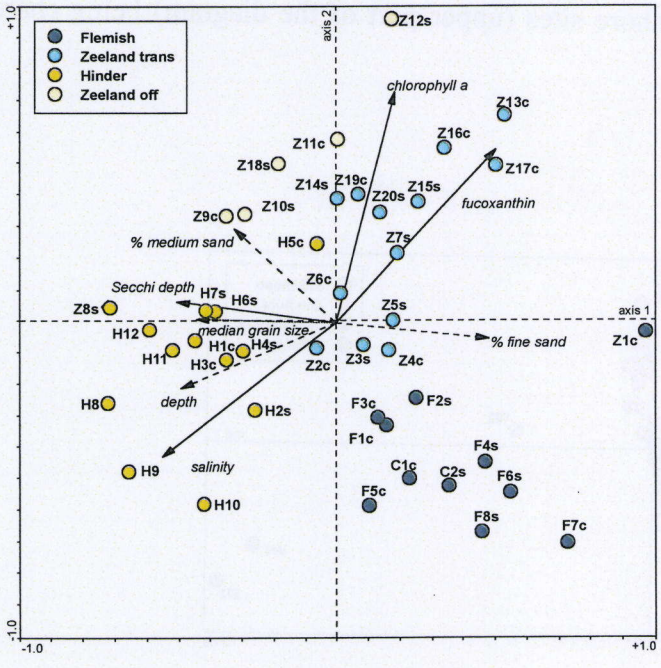

Fig. 6. Correlation biplot for the PCA of the species density data after exclusion of the onshore and the Westerschelde sites. Axis one (e.v. 0.276) and axis two (e.v. 0.109) represent 38.5 % of the species variance. Eigenvalues of axis three and axis four are 0.105 and 0.095, respectively. The environmental variables indicated with a full line (minimal set) together explain 35.5 % of the species variance (derived by RDA). Broken lines represent some other meaningful variables, which were selected for independent and significant influence on the ordination. Sites are labelled according to the final identified communities.

The mesohaline Westerschelde stations (W2, W3 and W4) were excluded from further analysis to assess the community structure on the continental shelf more comprehensively. The remaining dataset showed a gradient length of 2.105 s.d. units (explanatory DCA); one outlier site (C3c) was omitted. It was chosen as subject to a subsequent PCA analysis. Eigenvalues for the first three axes of the PCA are 0.381, 0.153 and 0.062, respectively (Fig. 5). The structure in the species data is shown as the correlation biplot formed by the first and third axis, which together display 44.3 % of the total variation. The onshore-offshore gradient from the previous analysis (Fig. 4) now appears along the first axis. The samples situated on the left (offshore and transitional) and the right (onshore) in the biplot roughly correspond to the first division in TWINSPAN (Fig. 3). The third axis reveals an east-west gradient for the onshore stations: the sites located between De Panne and Oostende (i.e. the West Coast) are grouped in the upper right part and the sites around Zeebrugge (i.e. the East Coast) in the lower right part of Fig. 5. This separation of the onshore sites again corresponds with the TWINSPAN results (third division, Fig. 3). Three variables together explain 43.1 % of the species variance: Secchi depth, fucoxanthin and salinity (minimal set). Secchi depth alone explains 34.0 % and is strongly correlated with the first axis, indicating a higher turbidity in the onshore sites - as illustrated in Fig. 5. This pattern follows a major gradient in sediment composition, with coarser sediments offshore. The east-west gradient along the third axis shows that all West Coast sites (upper part of the diagram) correspond with a higher salinity and lower fucoxanthin levels.

Eventually, a dataset with the offshore and transitional sites (situated on the left side in Fig. 5) was analysed separately. Gradient length was 1.703 s.d. units (exploratory DCA) and consequently, a PCA was performed. Sample scores along the first (e.v. 0.276) and second (e.v. 0.109) axis are presented in Fig. 6, displaying 38.5 % of the species variance. Sample scores along the first axis are related to the sites' distance from the coast and an east-west gradient is evident along the second axis. This again is in agreement with the results of TWINSPAN (Fig 3). The Flemish Bank sites are located in the lower right part of the diagram, the Hinder Bank stations in the lower left part. The upper section of the diagram includes all Zeeland Bank sites. The latter are also spread along the first axis, reflecting their distance to the coast. A set of four variables together explains 35.5 % of the species variation: salinity, Secchi depth, fucoxanthin and chlorophyll *a* (minimal set). With the exception of chlorophyll *a* (8 %), they all explain more than 11 % on their own. Figure 5 shows that the above-mentioned onshore-offshore gradient in turbidity further extends to the transitional and offshore sites. The sediment in the more turbid transitional sites is finer as compared with the offshore sediments. The east-west gradient along the second axis indicates highest pigment levels at the Zeeland Banks. High salinity is characteristic for the Hinder Banks.

Characterisation of the hyperbenthic communities and their habitat

The multivariate analyses revealed two structuring gradients in the hyperbenthic fauna on the continental shelf: a quite pronounced onshore-offshore gradient and a less distinctive east-west gradient. The mesohaline zone of the Westerschelde estuary harboured a distinct community, quite different from those found on the continental shelf. Based upon the result of TWINSPAN and ordinations, seven hyperbenthic communities were identified for the study area; they are indicated on the TWINSPAN dendrogram (Fig. 3) and on the ordination diagrams (Fig. 4, 5 and 6). Differences in habitat- and biotic characteristics were tested among communities; some results are summarized in Table 2 and 3. The sites from the mesohaline reaches of the Westerschelde estuary were omitted from the statistical analyses.

Geographical location

The 'WS meso' community occurred in the upstream reaches (mesohaline zone) of the Westerschelde estuary. Two 'onshore' communities, the 'W Coast' (from de Panne to Oostende) and 'E Coast' (around Zeebrugge) communities, were thriving on the Coastal Banks (Fig. 7). The 'E Coast' community includes also the fauna from the mouth of the Westerschelde estuary. Further away from the coast, the Flemish Banks harboured the 'Flemish' community and the 'Zeeland trans' community was living at the most onshore part of the Zeeland Banks; these are further called the 'transitional' communities. In the most offshore part of the continental shelf the Hinder Bank complex was characterized by the 'Hinder' community and the 'Zeeland off' community corresponded to the fauna of the most offshore Zeeland Banks' stations (the two 'offshore' communities).

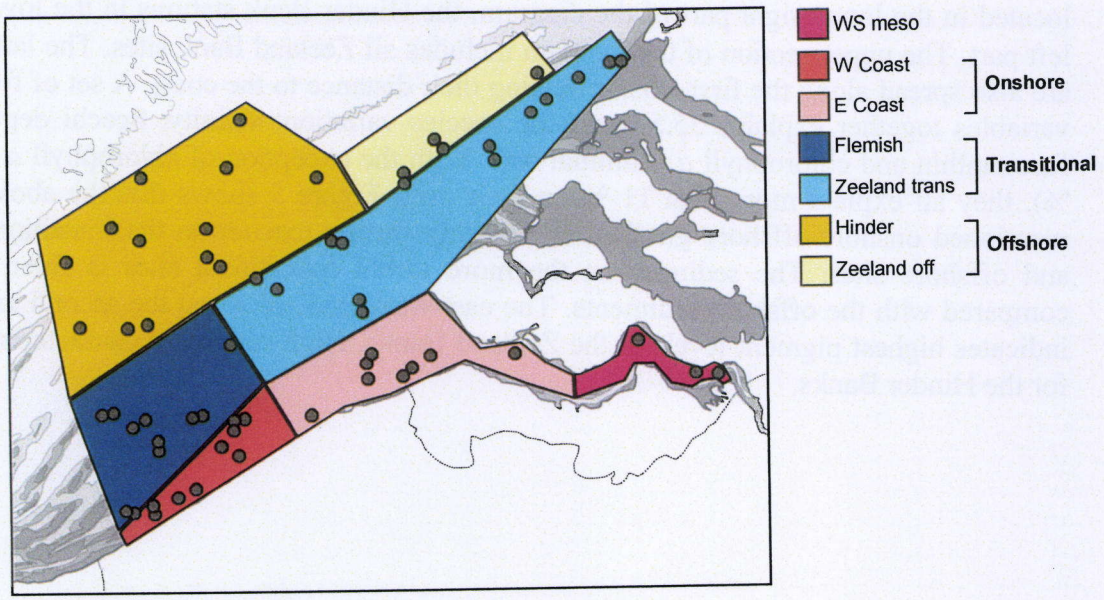

Fig. 7. Geographical position of the identified biotic communities.

Habitat characteristics

Salinity increased from onshore to offshore and decreased from west to east (Fig. 8). Turbidity was the most distinctive variable measured for the onshore-offshore gradient: Secchi depth was clearly lower at the Coastal Banks (the 'onshore' communities) compared to the remaining sites. The east-west gradient was largely reflected in chlorophyll *a*, being clearly higher in the eastern part of the study area. Generally, sediments mainly consisted of fine to medium sands in the whole area. The separate sediment fractions show the dominance of finer fractions in the Coastal Banks area. The 'E Coast' community was characterized by a high percentage of mud and the 'W Coast' by fine sands. The remaining communities were dominated by medium sand and, to a lesser extent, by fine sand, except for the 'Hinder' community, where quite some coarse sand was encountered. Though within-variability was slightly present, habitat characteristics between communities were indicated to significantly differ from one another (Table 2).

	1st Analysis (onshore - offshore)				2nd Analysis (east - west)			
	Main effect	Onshore vs Transitional	Onshore vs Offshore	Transitional vs Offshore	Main effect	E Coast vs W Coast	Flemish vs Zeeland trans	Hinder vs Zeeland off
Depth	***	ns	*	**	***	***	ns	ns
Temperature	***	**	***	***	**	***	ns	ns
Salinity	***	***	***	***	***	***	**	*
Secchi depth	***	***	***	***	***	ns	ns	*
Chlorophyll *a*	ns				***	***	***	***
Fucoxanthin	*	ns	ns	*	***	***	***	***
Mean grain size	***	**	***	***	***	***	ns	ns
Median grain size	***	**	***	***	***	***	ns	ns
% mud	***	**	***	*	***	***	ns	ns
% very fine sand	***	**	***	**	***	***	ns	ns
% fine sand	**	*	***	**	**	***	ns	ns
% medium sand	***	**	***	***	***	***	ns	ns
% coarse sand	***	**	***	*	***	***	ns	*

Table 2. Summary of the results of the Kruskal-Wallis test and subsequent multiple comparisons ('WS meso' was omitted) performed for some environmental variables of the shelf communities, The 'onshore', 'transitional' and 'offshore' communities were compared in a first analysis. Further, the 6 communities were dealt with in a second analysis, for which only the results for the corresponding eastern and western communities are presented; $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), not significant (ns).

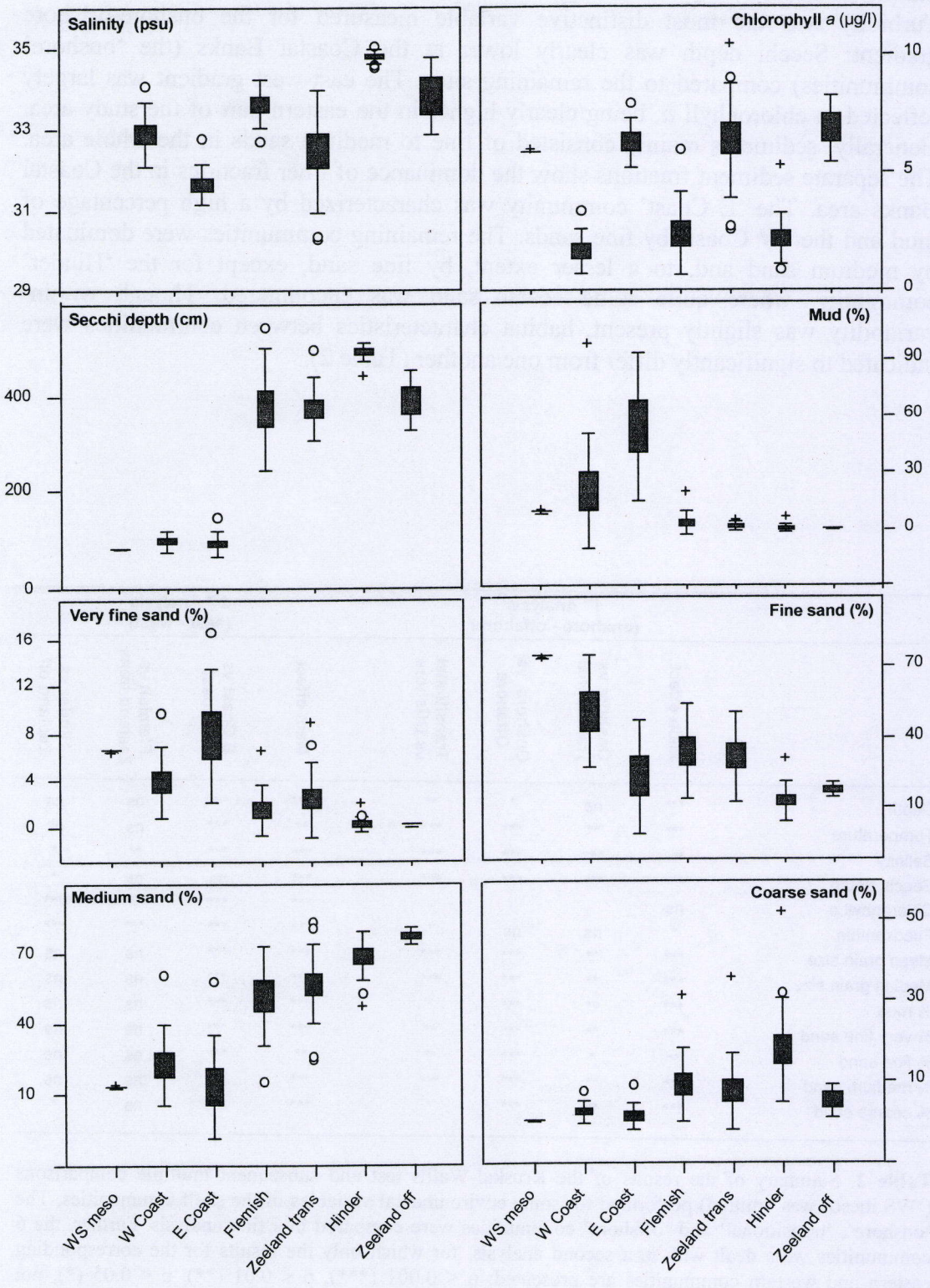

Fig. 8. Spatial variability for some environmental characteristics per community. Boxes represent mean values with standard error and whiskers indicate standard deviation; outliers (o) and extremes (+) are also shown. Salinity for the 'WS meso' community is not presented (17.81 ± 0.32 psu).

Community characteristics of the holohyperbenthos

The 'WS meso' community attained very high densities and consisted nearly exclusively of mysids (Fig. 10A). *Mesopodopsis slabberi* was dominant and represented 92 % of the total density, a much smaller fraction was accounted for by *Neomysis integer* (7 %). Mysids also dominated the hyperbenthos of the two 'onshore' communities, both in terms of density and biomass (Table 4). The most characteristic species for these communities were *Schistomysis spiritus* and *S. kervillei*, together accounting for more than 70 % of the total density on the Coastal Banks. The first species was dominant in the 'W Coast' community; while the latter dominated the 'E Coast' community. The holohyperbenthos community changed in taxonomic composition in a seaward direction and density as well as biomass decreased. Mean density was significantly different between the 'onshore' and 'transitional' communities, and even between the 'transitional' and the 'offshore' communities (Table 3). Mysids decreased in density and planktonic representatives such as hydromedusae, ctenophores and chaetognaths gained in abundance (Fig.10A). The total biomass of these communities was still dominated by mysids (always more than 60 %). No significant differences for density or biomass related to the east-west gradient on the continental shelf were found.

Apart from the 'WS meso' community, species richness (N_0) was significantly lowest in the 'offshore' communities (Fig. 9 and Table 3) Species diversity increased significantly in a direction perpendicular to the coast, as judged from N_1 and $E(S_{100})$. An east-west change in species richness (N_0) was observed for the 'onshore' communities, N_0 was significantly higher for the 'W Coast' than for the 'E Coast' community. The offshore community was less diverse at the Hinder Banks as compared to the 'Zeeland off' community.

Community characteristics of the merohyperbenthos

The merohyperbenthos attained significantly higher densities in the 'transitional' communities (Fig. 10B, Table 3) and was mainly composed of larval Brachyura and, to a lesser extent, larval stages of Caridea. *Liocarcinus* spp. and Crangonidae (mainly *Crangon crangon*) were the dominant taxa (Table 4). Still, total biomass peaked in the 'onshore' communities, due to the occurrence of postlarval gobies. Nevertheless, the Caridea was the most abundant taxon for the onshore communities. The total density for 'WS meso' was low. A change from west to east was noted in taxonomic composition at the species level. The 'Zeeland trans' and 'Zeeland off' communities were dominated by *Liocarcinus* larvae, whereas these taxa were relatively less important at the Flemish and Hinder communities, which consisted of a higher number of species being evenly presented (e.g. *Pilumnus hirtellus*, *Pisidia longicornis*) (Table 4).

Both species richness (N_0) and species diversity (N_1 and $E(S_{100})$) of the merohyperbenthos increased in a seaward direction, with significant differences between the 'onshore' community on the one hand and the 'transitional' and 'offshore' communities on the other hand (Fig. 9, Table 3). Lowest values were calculated for the 'WS meso' community. A quite strong east-west gradient for species diversity existed as well. N_1, N_2 and $E(S_{100})$ were significantly higher for the 'Flemish' community than for 'Zeeland trans' and also for the 'Hinder' community as compared with 'Zeeland off'.

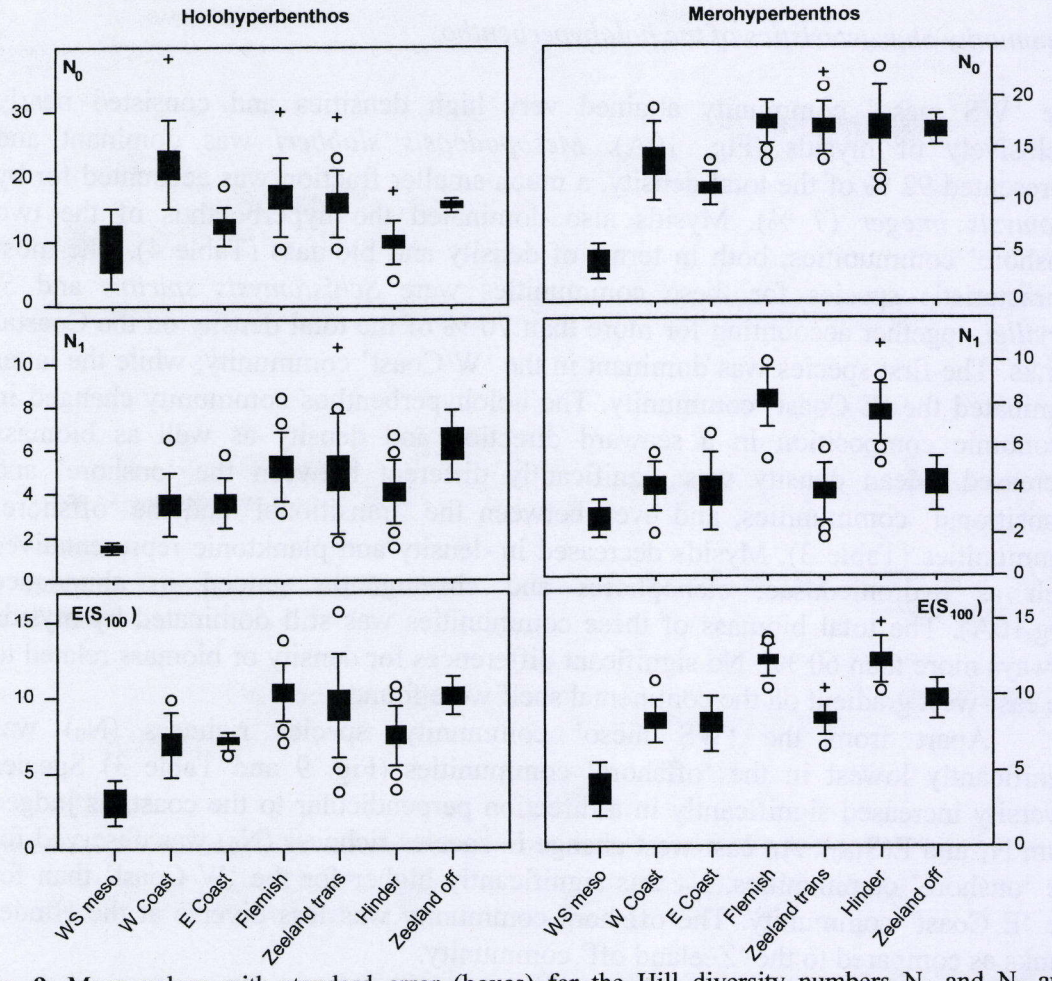

Fig. 9. Mean values with standard error (boxes) for the Hill diversity numbers N_0 and N_1 and Hurlbert's $E(S_{100})$. N_2 is not figured since it showed very similar trends as N_1. Data are presented per community for holo- **(left)** and merohyperbenthos **(right)**. Whiskers indicate standard deviation; outliers (o) and extremes (+) are also shown.

		1st Analysis (onshore - offshore)				2nd Analysis (east - west)			
		Main effect	Onshore vs Transitional	Onshore vs Offshore	Transitional vs Offshore	Main effect	E Coast vs W Coast	Flemish vs Zeeland trans	Hinder vs Zeeland off
Holohyperbenthos									
Density	(1)	***	***	***	**	***	ns	ns	ns
Biomass	(1)	***	***	***	ns	***	ns	ns	ns
N_0	(2)	**	ns	**	*	***	***	ns	*
N_1	(2)	*	**	*	ns	*	ns	ns	ns
N_2	(2)	ns				ns			
$E(S_{100})$	(2)	**	***	*	***	**	ns	ns	*
Merohyperbenthos									
Density	(1)	***	*	ns	***	***	ns	ns	ns
Biomass	(1)	***	ns	**	*	***	ns	ns	ns
N_0	(2)	***	***	***	ns	**	ns	ns	ns
N_1	(2)	**	***	***	ns	***	ns	**	**
N_2	(2)	*	***	**	ns	***	ns	**	**
$E(S_{100})$	(2)	***	**	***	*	***	ns	***	**

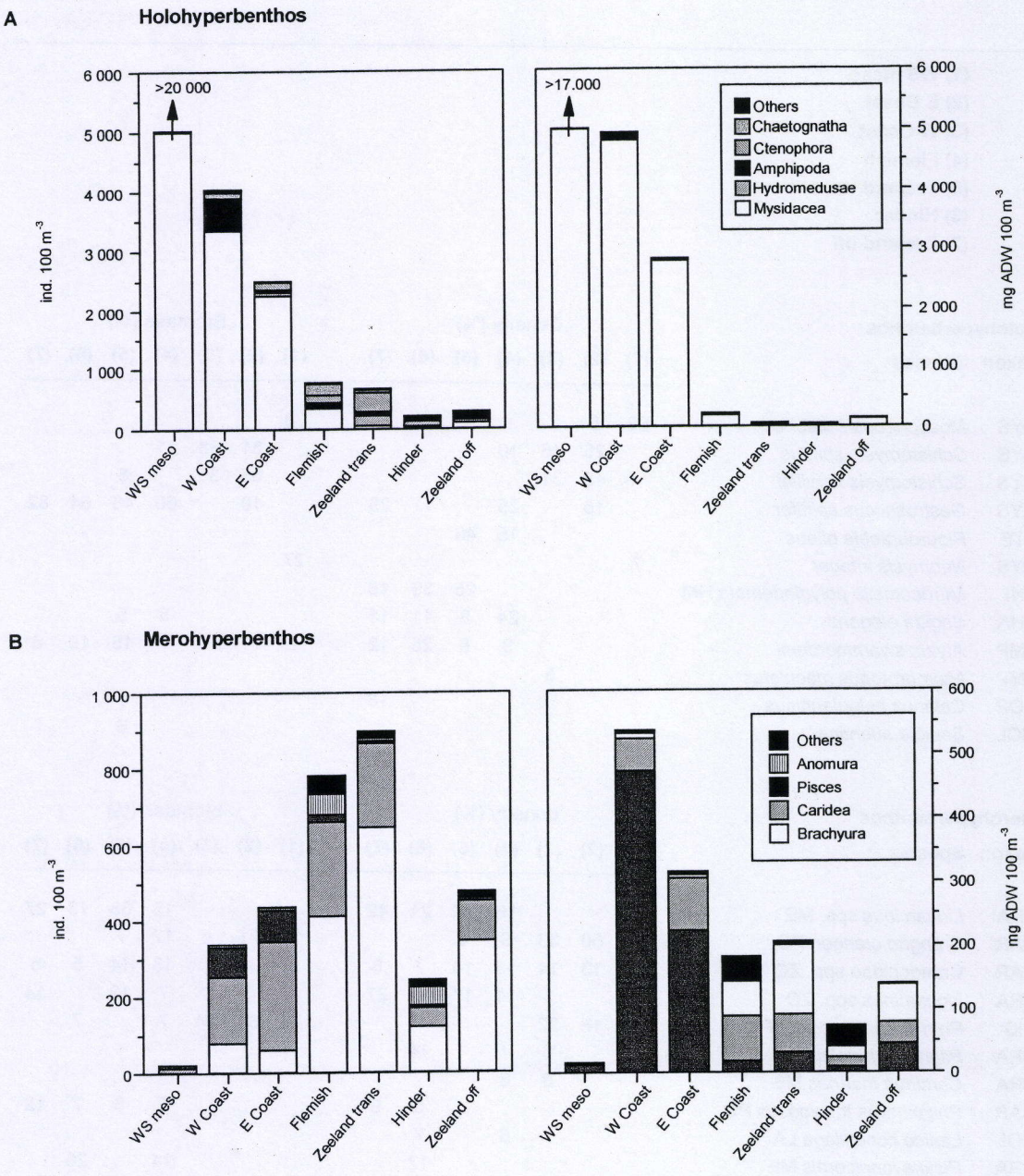

Fig. 10. Mean total density (left) and biomass (right) per community and per major taxonomic group for **(A)** holohyperbenthos and **(B)** merohyperbenthos.

Table 3. (left page) Summary of statistical differences for some ecological characteristics among the shelf communities. The 'onshore', 'transitional' and 'offshore' communities were compared in a first analysis ('WS meso' was omitted). Further, the 6 communities were compared in a second analysis, for which only the results for the corresponding eastern and western community are presented; (1) one-way ANOVA and *post-hoc* comparisons, (2) Kruskal-Wallis test and subsequent multiple comparisons; $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), not significant (ns).

(1) WS meso
(2) E Coast
(3) W Coast
(4) Flemish
(5) Zeeland trans
(6) Hinder
(7) Zeeland off

Holohyperbenthos		Density (%)							Biomass (%)						
Taxon	Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(1)	(2)	(3)	(4)	(5)	(6)	(7)
MYS	*Mesopodopsis slabberi*	92	5						73						
MYS	*Schistomysis spiritus*		25	46	10					31	58	11			
MYS	*Schistomysis kervillei*		45	31						55	35		8		
MYS	*Gastrosaccus spinifer*		15		25		11	29		10		60	48	64	82
CTE	*Pleurobrachia pileus*				15	46									
MYS	*Neomysis integer*	7							27						
CNI	*Mitrocomella polydiademata* HM					25	39	18							
CHA	*Sagitta elegans*				24	8	11	11				5	5		
AMP	*Atylus swammerdami*				9	8	25	12				7	15	19	6
AMP	*Microprotopus maculatus*			5											
COP	*Calanus helgolandicus*							16							
MOL	*Sepiola atlantica*												6		

Merohyperbenthos		density (%)							biomass (%)						
Taxon	Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(1)	(2)	(3)	(4)	(5)	(6)	(7)
BRA	*Liocarcinus* spp. ME				16	46	21	42				13	38	13	27
CAR	*Crangon crangon* PO	44	50	33	9	5			19	21	6	12	7		
CAR	Crangonidae spp. ZO	6	13	14	13	14	7	8				13	14	5	6
BRA	*Liocarcinus* spp. ZO				11	17	10	27				7	12		14
PIS	*Pomatoschistus* spp. PO	40	18	22					76	60	84	7		7	
BRA	*Pilumnus hirtellus* ME			8	7		14								
BRA	*Carcinus maenas* ME			8	6										
CAR	*Philocheras trispinosus* PO						5	9				6	6	7	12
POL	*Lanice conchilega* LA				6		7								
BRA	*Pisidia longicornis* ME						12					14		26	
CAR	*Hippolyte varians* PO											7			
ANO	*Galathea intermedia* ME						5							12	
PIS	Syngnathidae spp. PO														
CAR	Palaemonidae spp. ZO	6													
PIS	Clupeidae spp. PO									6					
PIS	*Hyperoplus lanceolatus* PO												12		17
PIS	Ammodytidae spp. PO														10

Table 4. Relative density and biomass for the most common (accounting for more than 5 %) taxa of each community. Taxa are sorted according to highest mean abundance over all communities. Amphipoda (AMP), Anomura (ANO), Brachyura (BRA), Caridea (CAR), Chaetognatha (CHA), Cnidaria (CNI), Copepoda (COP), Ctenophora (CTE), Mollusca (MOL), Mysidacea (MYS), Pisces (PIS), Polychaeta (POL). Developmental stages of decapods are treated as a separate taxon; hydromedusa (HM), larva (LA), zoea (ZO), postlarva (PO), megalopa (ME).

Discussion

Species composition

The hyperbenthal zone of the study area harbours a high variety of peracarid crustaceans and early life history stages of macrocrustaceans and fish. Data on the occurrence of species of the most typical hyperbenthic taxon, i.e. the Mysidacea, is compared with other subtidal (up to 200 m depth) and intertidal areas along the European coast in Table 5. Certain rather sporadic species were only encountered during the temporal survey performed in the area (Chapter 5) and were added to complete the comparison.

Although *Neomysis integer* typifies the brackish water community of the Westerschelde (Mees 1994), a strong dominance of *Mesopodopsis slabberi* was noted in this study. This has been reported previously during summer (Mees *et al.* 1993b; Mees 1994). This euryhaline species (Mauchline 1980) is one of the most common mysids along the European coasts and is often present with high numbers in strongly fluctuating environments (e.g. brackish waters, coastal lagoons, sandy beaches) and even in fully marine conditions (Table 5).

The dominant species of the onshore communities, i.e. *Schistomysis kervillei* and *S. spiritus*, occur in similar habitats although never very abundant in low salinity reaches (Table 5). A number of species that are quite common in adjacent areas are rare in the study area, e.g. *Schistomysis ornata* (only one specimen caught) and *Anchialina agilis* (Table 5). Moreover, some species thriving in the Atlantic water masses along the southern European coasts up to the Western English Channel (e.g. *Erythrops elegans*, *Mysidopsis angusta*) are completely absent from Belgian waters (Sorbe 1989; Cunha *et al.* 1997; Zouhiri *et al.* 1998). This is most probably attributed to the shallowness and / or typical shelf characteristics of the study area with the influence of continental water. These species often re-appear in deeper waters north of the study area, such as the Dogger Bank (Chapter 1) and the Scandinavian fjords (Fosså & Brattegard 1990; Buhl-Jensen & Fosså 1991). Their distribution thus seems to be related to Atlantic water masses that enter the North Sea both from the south via the Channel and from the north via the Shetlands (Lee 1980; Ducrotoy *et al.* 2000). This is probably not true for the genus *Haplostylus*, which is numerically dominant in the English Channel (Dauvin *et al.* 2000) but it has not been recorded in our study nor in more northern waters (Fosså & Brattegard 1990; Buhl-Jensen & Fosså 1991; Chapter 1). Another pronounced distinction with the nearby Channel is the very diverse amphipod fauna in the latter which has been attributed to the co-occurrence of several biogeographical traits (Dauvin *et al.* 2000).

The most remarkable finding was *Paramysis bacescoi*, a littoral species (Mauchline 1980) that has only poorly been reported in the NE Atlantic, which might be due to confusion with congeneric species (Labat 1953). It has been reported from sandy beaches (Labat 1953; San Vicente & Sorbe in press) and was even dominant in an estuarine environment (Cunha *et al.* 1999). Despite the comprehensive current knowledge of the adjacent intertidal areas (Beyst *et al.* in press a; Beyst & Mees submitted) and the subtidal of the English Channel (Zouhiri *et al.* 1998; Dauvin *et al.* 2000), *P. bacescoi* was not reported by these authors. A few numbers of this species were regularly caught during winter at a site close to the Belgian-French border during the temporal survey (Chapter 5). We therefore suppose that it may have been washed out from a shallow habitat around this area or that it is very local in occurrence.

Habitat	Area	*Acanthomysis longicornis*	*Anchialina agilis*	*Gastrosaccus spinifer*	*Leptomysis lingvura*	*Mesopodopsis slabberi*	*Mysidopsis gibbosa*	*Neomysis integer*	*Paramysis arenosa*	*Paramysis bacescoi*	*Praunus flexuosus*	*Schistomysis kervillei*	*Schistomysis ornata*	*Schistomysis spiritus*	*Siriella armata*	*Siriella clausii*	*Siriella jaltensis*	Source
Fjord																		
Northern North Sea	W Norway				*		*	*			*		C	*				Fosså & Brattegard (1990)
Skagerrak	W Sweden			*		*	*						C	*				Buhl-Jensen & Fosså (1991)
Subtidal																		
Baltic Sea	Kieler Bucht			*			*	*			*			*				Hesthagen (1973)
Central North Sea	Dogger Bank	*	*	*	*	*	*					C	*					Chapter 1
Southern North Sea	Frisian front (N Netherlands)	*	*	*		*	*						C	*				Chapter 2
Southern North Sea	off Zeeland (S Netherlands)	*		C		C	*		*		*	C		C	*			Mees *et al.* (1993a), this study
Southern North Sea	Belgium	*	*	C	*	C	*	*	*	*	*	C	*	C	*	*	*	Chapter 5, this study
E English Channel	N France	C	C	C	*	*	*	*				*	*	*	*	*	*	Zouhiri *et al.* (1998), Dauvin *et al.* (2000)
W English Channel	N France	*	C	*	*		*	*					*	*	*	C	*	Zouhiri *et al.* (1998), Dauvin *et al.* (2000)
Celtic Sea	Bristol Channel (England)		*	*		*		*	*		*	*	*	C		*		Williams & Collins (1984)
N Bay of Biscay	Eperon Berthois		*		*		*						*			*		Chapter 3
SE Bay of Biscay	off Arcachon, off Hendaya (S France)	*	C	*	*	*	*		*	*		*	*	*	*			Sorbe (1982), Cornet *et al.* (1983), San Vicente & Sorbe (in press)
S Bay of Biscay	N Spain		C		*								*				*	Anadón (1993)
NE Atlantic	off Aveiro (Portugal)	*	C	*		C	*					*	*	*				Cunha *et al.* (1997)
NW Meditterranean	N Spain	C	C		*	C	*		*						*			San Vicente & Munilla (2000)
Surf zone																		
Central North Sea	off E England			*	C	*					*			C	*		*	Colman & Segrove (1955)
Southern North Sea	Belgium		*	*		C	*	*			*	C		C	*	*	*	Lock *et al.* (1999), Beyst *et al.* (in press a), Beyst & Mees (submitted)
SE Bay of Biscay	off Hendaya (S France)	*	*	*		C	*		*	C				C	*			San Vicente & Sorbe (in press)
NW Meditterranean	N Spain			*	C	C			*						*		*	San Vicente & Sorbe (1993), San Vicente & Munilla (2000), San Vicente & Sorbe (1999)
Coastal lagoon																		
Southern North Sea	Oosterschelde (S Netherlands)			*		C					*	*		*				Mees & Hamerlynck (1992), Mees (1994)
NE Atlantic	Ria de Aveiro (Portugal)		*	*	*	C		C		C	*			*	*	*	*	Cunha *et al.* (1999)
NE Atlantic	Ria Formosa (S Portugal)					C										*		Lock & Mees (1999)
NW Meditterranean	Ebro delta (Spain)					C												Delgado *et al.* (1997)
Estuary																		
Southern North Sea	Eems (N Germany)			*		C		C			*	C		*				Mees *et al.* (1995)
Southern North Sea	Westerschelde (S Netherlands)	*		*		C		C			*	*		*				Mees *et al.* (1993a), this study
Eastern English Channel	Seine (N France)	*	*	*		C	*	C					*			*	*	Wang & Dauvin (1994), Dauvin *et al.* (2000), Mouny *et al.* (1996), Mouny *et al.* (2000)
SE Bay of Biscay	Gironde (S France)			*		C		C				*		*				Sorbe (1981), Mees *et al.* (1995)
S Bay of Biscay	Guipuzcoa estuaries (N Spain)			C	*	C	*	C			*			C	C			San Vicente *et al.* (1993)
NE Atlantic	Mondego (Portugal)			*		C				*	*			C		*		Azeiteiro & Marques (1999)
Salt Marsh																		
Southern North Sea	Saefthinge, Waarde (S Netherlands)					C		C			*	*		*				Mees *et al.* (1993a)

Table 5. Occurrence of mysid species (up to 200 m depth) in the hyperbenthos of the NE Atlantic, sorted per biotope and according to the geographical gradient from Norway to Portugal. The most common species for each area is indicated with 'C'.

	Netherlands			Belgium		English Channel		Bay of Biscay		off Portugal	
	Frisian front	Zeeland	Voordelta	Offshore	Onshore	East	West	Deep	Shallow	Deep	Shallow
	(1)	(2)	(3)	(2)	(2)	(4)	(4)	(5)	(5)	(6)	(6)
Sampling period	Aug	Sep	AM	Sep	Sep	May/Jun	May/Jun	AM	AM	Jul/Aug	Jul/Aug
Depth (m)	39	19	10	26	12	28	61	91	31	91	21
# stations	10	18	24	24	17	3	3	1	1	1	1
Mesh size (mm)	1.0	1.0	1.0	1.0	1.0	0.5	0.5	0.5	0.5	0.5	0.5
Sledge	A	A	C	A	A	B	B	A	A	A	A
Species numbers											
Absolute											
Mysidacea	8	7	7	7	7	9	10	15	8	9	5
Cumacea	6	5	10	5	6	5	5	14	7	3	6
Isopoda		1	4	1	2	4	5	7	4	2	0
Amphipoda	25	14	36	23	18	46	56	52	25	19	13
Euphausiacea	1	0	1	1	0	1	2	1	1	1	0
Pycnogonida	0	0	5	0	4	3	3	1	1	0	0
Relative (%)											
Mysidacea	20	26	11	19	19	13	12	17	17	26	21
Cumacea	15	19	16	14	16	8	6	16	15	9	25
Isopoda	0	4	6	3	5	6	7	8	9	6	0
Amphipoda	63	52	57	62	49	67	68	58	54	56	54
Euphausiacea	3	0	2	3	0	2	2	1	2	3	0
Pycnogonida	0	0	8	0	11	4	4	1	2	0	0
Density											
Absolute											
Mysidacea	131	72	20	181	2829	138	54	1590	2514	1992	490
Cumacea	26	5	0	6	18	58	10	199	122	27	43
Isopoda	0	0	0	0	19	5	5	36	9	5	0
Amphipoda	166	57	4	71	295	169	141	985	5927	174	142
Euphausiacea	14	0	0	0	0	2	317	359	61	2094	0
Pycnogonida	0	0	0	0	0	1	1	<3.6	<8.7	0	0
Relative (%)											
Mysidacea	39	54	82	70	89	37	10	50	29	46	73
Cumacea	8	3	2	2	1	15	2	6	1	1	6
Isopoda	0	0	0	0	1	1	1	1	0	0	0
Amphipoda	49	43	16	28	9	45	27	31	69	4	21
Euphausiacea	4	0	0	0	0	1	60	11	1	49	0
Pycnogonida	0	0	0	0	0	0	0	0	0	0	0

Table 6. Species numbers and densities for the main taxonomic groups belonging to the holohyperbenthos recorded in subtidal waters (5 - 100 m depth) of the NE Atlantic. As sampling effort widely differs between the presented studies, species numbers per taxon were also tabulated as a percentage of the total numbers of species listed. Similarly, density for each taxon is given absolutely and relatively (as a percentage of the total density of the presented taxa). Data are gathered from (1) Chapter 2, (2) this study, (3) Hamerlynck & Mees (1991), (4) Vallet & Dauvin (1998), (5) Sorbe (1989), (6) Cunha *et al.* (1997). Except for the Channel hyperbenthos, all data derive from day-time sampling and species numbers were cumulatively calculated. For the E and W Channel, 5 hauls were performed at 3 stations, spread over day and night. In this case, species numbers were cumulatively calculated for one station and averaged over the three stations. Some data are annual mean values (AM), the sampling period is indicated in the other case. All densities are expressed as ind. 100 m^{-3}, except for the Frisian front and the Voordelta (expressed as ind. 100 m^{-2}). Type of sledge: (A) Sorbe-sledge (Sorbe 1983), (B) Macer-Giroq (Dauvin & Lorgeré 1989), (C) sledge applied by Hamerlynck & Mees (1991).

Community structure

Care should be taken when comparing the literature on the structure of hyperbenthic communities. Bias may occur according to the type of sampling gear used (efficiency of sledges in different habitats and the mesh size of the mounted nets). The hyperbenthos also consists of a wide variety of taxa and different authors often use a different definition, i.e. handle other criteria to omit or include certain - often abundant - taxa. Therefore, a comparison of data obtained by this study with literature from subtidal waters in the NE Atlantic was restricted to the most common taxa belonging to the holohyperbenthos (Table 6). The absolute and relative densities for each taxon are given (as a percentage of the total density of the presented taxa). As sampling effort differs widely between the presented studies, species numbers per taxon were also tabulated as a percentage of the total numbers of species listed.

Some general trends can be derived for the subtidal hyperbenthic communities along the European coast. Amphipods are generally the most diverse taxon while mysids and cumaceans are of secondary importance. This pattern is generally quite similar for surf zone hyperbenthos, but the latter biotope often harbours a higher variety of isopods (San Vicente & Sorbe 1999; Beyst *et al.* in press a; Beyst & Mees submitted). Moreover, isopods and cumaceans are very diverse in continental slope communities (Elizalde *et al.* 1993; Cartes & Sorbe 1996, 1997; Cunha *et al.* 1997; Dauvin *et al.* 1995; Chapter 3).

Mysids and amphipods also invariably reach highest densities, their importance varying regionally and with depth (Table 6). Highest numbers of mysids were encountered during this study, comparable densities were reached in the Bay of Biscay (Sorbe 1989) and off Portugal (Cunha *et al.* 1997). High densities for mysids might be induced by increased food availability as supposed by several authors (Clutter 1967; Fosså 1985; Hargreaves 1985; Cunha *et al.* 1997; Chapters 1 and 2) and will be discussed later for the Belgian coastal area. Euphausiids are of considerable importance in the hyperbenthal of coastal areas adjacent to the deep ocean (e.g. western English Channel, Bay of Biscay and Portugal), which is not the case for this study. A marked difference with the Channel hyperbenthos in terms of densities is the large contribution of amphipods in the latter area and a subdominance of mysids. Holoplanktonic amphipods, like the genus *Apherusa*, were very abundant in the Channel and rarely caught during this study. This difference may be correlated with differences in food web structure, being more planktonic in the Channel since its strong current regime prevents the settlement of organic matter (Dauvin *et al.* 2000).

Gradients on the Belgian continental shelf

The brackish reaches of the Westerschelde estuary are characterized by a species-poor community attaining high densities, which has been well examined previously (Mees *et al.* 1993b; Mees 1994). After omitting this community, the multivariate analyses revealed two structuring gradients in the study area: a major onshore-offshore gradient and a less pronounced east-west gradient. Six communities could be identified and some principal characteristics for the holo- and merohyperbenthos are summarized in the simplified scheme in Fig 11.

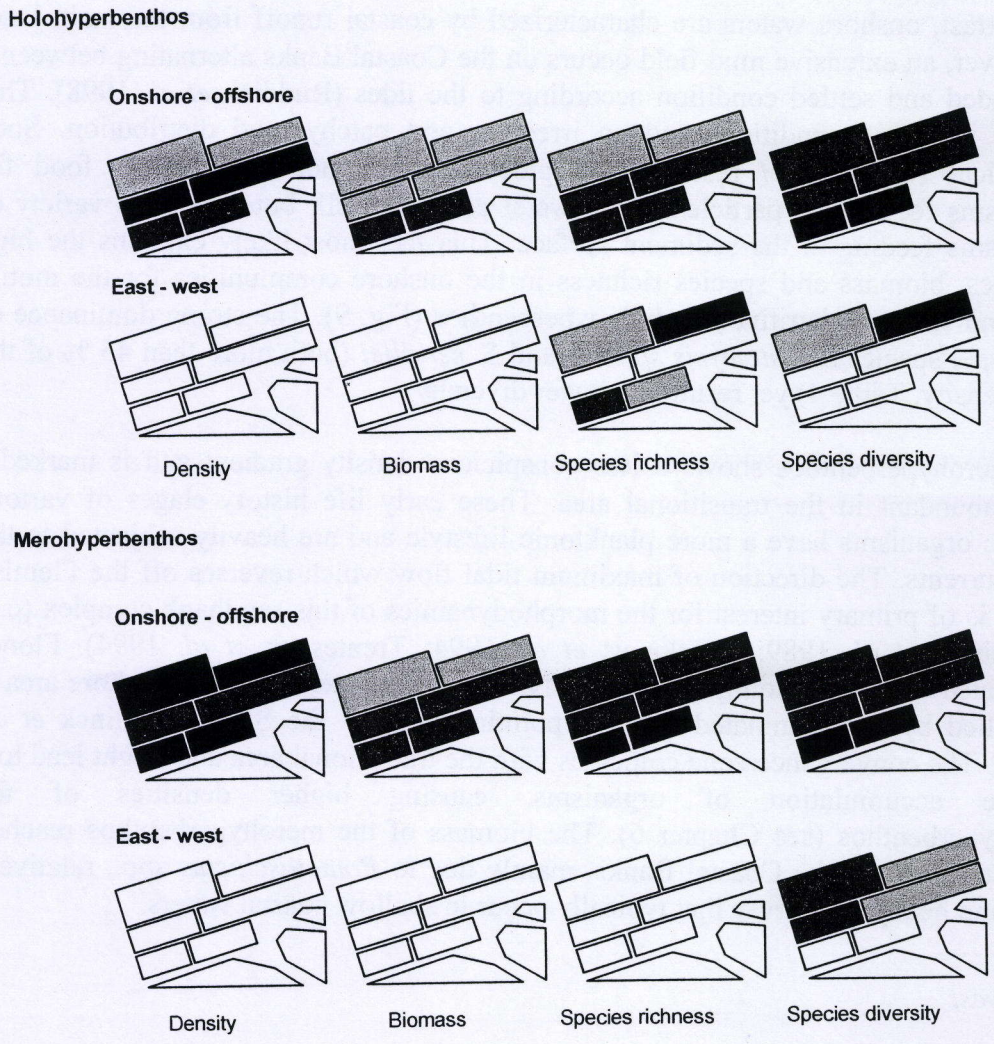

Fig. 11. Summarising scheme of onshore-offshore and east-west gradients for the holo- and merohyperbenthos in the study area, based on the Kruskal-Wallis and ANOVA results (Table 3). The boxes represent the 6 communities on the continental shelf; highest grey-shade corresponds with highest value.

Onshore-offshore

The gradient perpendicular to the coastline is most pronounced for density and biomass (Fig. 10): both decline with increasing distance from the coast. Ordination analyses revealed a relation with sediment structure and water column characteristics such as salinity and turbidity. These result from the hydrodynamical forces acting in the area. The Hinder Banks are subjected to the southern intrusion of Atlantic water of high salinity and experience little coastal influence (Hecq *et al.* 1992; Djenidi *et al.* 1996; Baeyens *et al.* 1998). Sediments are coarser due to the strong currents in the area. This further implies that suspended matter, generally poorer offshore (Ruddick *et al.* 1998), gets little chance to settle. Only planktonic taxa, being less dependent on deposited food sources, are thriving well. This counts for a high variety of early larval stages belonging to the merohyperbenthos and a smaller fraction of holohyperbenthic taxa like hydromedusae and chaetognaths. The overall low biomass and the very low abundance of the holohyperbenthos in the offshore area may thus be attributed to these mechanisms.

In contrast, onshore waters are characterized by coastal runoff from the main land. Moreover, an extensive mud field occurs on the Coastal Banks alternating between a suspended and settled condition according to the tides (Ruddick *et al.* 1998). This results in turbid conditions and an irregular and patchy mud distribution. Such episodical suspension / resuspension processes may not only deliver food for organisms feeding on particles in the water column itself, but also for a variety of organisms feeding at the sediment surface. This fact most likely explains the high densities, biomass and species richness in the onshore communities for the motile and omnivorous / detritivorous holohyperbenthos (Fig. 9). The strong dominance of the mysid species *Schistomysis spiritus* and *S. kervillei* (both more than 45 % of the total density, Table 4) yet result in a lower diversity.

The merohyperbenthos shows a less conspicious density gradient and is markedly more abundant in the transitional area. These early life history stages of various benthic organisms have a more planktonic lifestyle and are heavily subjected to the tidal currents. The direction of maximum tidal flow which reverses off the Flemish Banks is of primary interest for the morphodynamics of this sandbank complex (e.g. Vlaeminck *et al.* 1989; Lanckneus *et al.* 1994; Trentesaux *et al.* 1994). Flood-dominated currents heading towards the NE occur onshore, while the offshore area is controlled by ebb-dominated currents pointing towards the SW (Vlaeminck *et al.* 1989). The convergence zone coincides with the transitional area and might lead to a passive accumulation of organisms, causing higher densities of the merohyperbenthos (see Chapter 6). The biomass of the merohyperbenthos reached highest values on the Coastal Banks, mainly due to *Pomatoschistus* spp., relatively large and heavy fish larvae that typically occur in shallow coastal waters.

East-west

The east-west gradient along the Belgian coastline is mainly reflected in species richness and diversity. Run-off from the Westerschelde estuary and the influence of the nearby Dutch delta area (i.e. Rhine and Meuse) cause the intrusion of low salinity and nutrient-rich water. On top, the Westerschelde is heavily subjected to pollution (Heip 1988). The Westerschelde plume has an influence as far as Oostende and can be identified by its physico-chemical characteristics (Hecq *et al.* 1992). As shown in Fig. 8, patterns in chlorophyll *a* and salinity were quite distinctive along an east-west direction. Further, the general NE directed residual current turns slightly to the NW from Oostende onwards, due to the estuarine outflow (Baeyens *et al.* 1998). Only species that are resistant to this estuarine influence may thrive well under such fluctuating environmental conditions. This might explain the low species richness for holohyperbenthos at the 'E Coast' compared to the 'W Coast'. Most species of the 'E Coast' community do also occur in the polyhaline zone of the Westerschelde estuary (Mees *et al.* 1993b).

A reverse pattern is found for the offshore communities, i.e. the holohyperbenthos at the offshore part of the Zeeland Banks is more diverse than at the Hinder Banks. This 'off Zeeland' community is situated at a closer distance to the shore and still under coastal influence. Salinity and turbidity were lower compared to the Hinder Banks (Fig. 8). This might increase the food availability as discussed for the onshore-offshore gradient.

Merohyperbenthos species diversity was higher at the Flemish and Hinder Banks as compared to the Zeeland Banks. This may be explained in several ways. First of all, the NE directed residual current suggests a larval supply from the Channel, which generally harbours a richer fauna (Rees *et al.* 1999). Secondly, the sandbanks are more extensive on the Belgian continental shelf, creating a wealth in habitats and supporting a higher capacity of various species. Additionally, the presence of a considerable coarse sediment fraction (Fig. 8) and the patchy occurrence of pebbles and boulders in the offshore swales may increase the habitat heterogeneity. For example, anomuran larvae were mainly found on the Flemish and Hinder Banks (Table 4). Dauvin *et al.* (2000) also reported highest diversity for the Channel hyperbenthos at a substratum with pebbles. And finally, the water mass in front of Zeeland is still subjected to the Westerschelde outflow and, to a lesser extent, by the Rhine and Meuse discharges (Nienhuis 1992). As suggested by Nihoul *et al.* (1984), this flow may determine the spatial distribution of planktonic animals drifting with the current. As a remark, the most abundant species on the Zeeland Banks were *Liocarcinus* spp. and *Carcinus maenas* larvae, both being very abundant in the extended shallow waters of the Delta area (Adema 1991; Hamerlynck *et al.* 1992).

Final remarks

A similar onshore-offshore gradient on the Belgian continental shelf has also been reported for other benthic assemblages, such as the meio-, macro- and epibenthos (Cattrijsse & Vincx 2001) and for pelagic communities such as the phyto- and zooplankton (M'harzi *et al.* 1998). The decrease of coastal influence with increasing distance from the shore is a common structuring factor. The E Coast has often been reported to be impoverished for several biotic components (Cattrijsse & Vincx 2001). Both the natural estuarine outflow and anthropogenic mediation may play a role, though their specific influence on the hyperbenthic communities requires further research.

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Community	H/M	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Phylum Cnidaria								
Subphylum Medusozoa								
Classis Hydroidomedusae								
Bougainvillia spp. HM	H	*	*	*	*			
Mitrocomella spp. HM	H	*	**	*	**	***	**	**
Phylum Ctenophora								
Pleurobrachia pileus	H	**	***	**	***	***	*	**
Beroe cucumis	H				*			
Beroe gracile	H				*			
Beroe spp.	H		*	*	*	*		
Phylum Annelida								
Classis Polychaeta								
Harmothoe spp. LA	M				*	*		
Lanice conchilega LA	M		*	*	**	**	**	**
Phylum Chaetognatha								
Sagitta elegans	H	*	*	***	***	**	**	**
Phylum Mollusca								
Classis Gastropoda								
Subclassis Opisthobranchia								
Ordo Nudibranchia								
Nudibranchia spp.	H					*		
Classis Cephalopoda								
Sepiola atlantica	H			*	*	*		*
Phylum Arthropoda								
Subphylum Crustacea								
Classis Copepoda								
Ordo Calanoida								
Centropages typicus	H		*	*	*	*	*	*
Temora longicornis	H					*	*	
Calanus helgolandicus	H	*	*	*	**	**	*	**
Classis Malacostraca								
Subclassis Eumalacostraca								
Superordo Eucarida								
Ordo Euphausiacea								
Nyctiphanes couchi	H						*	
Ordo Decapoda								
Subordo Pleocyemata								
Infraordo Caridea								
Palaemon elegans PO	M				*			
Palaemonidae spp. ZO	M	*					*	*
Alpheus glaber ZO	M							*
Hippolyte varians PO	M	*	*	*	*	**	*	*
Hippolyte varians ZO	M		*	*	*	*	*	*
Thoralus cranchii PO	M				*			
Processa canaliculata PO	M				*	*		
Processa modica PO	M						*	*
Processa modica ZO	M						*	*
Pandalina brevirostris PO	M				*	*	*	*
Pandalina brevirostris ZO	M							*
Crangon crangon PO	M	*	***	***	**	**	*	*
Philocheras trispinosus PO	M		*	*	**	**	**	**
Crangonidae spp. ZO	M	*	**	**	***	***	**	**
Infraordo Thalassinidea								
Callianassa spp. ZO	M				*	*	*	*
Upogebia spp. PO	M					*	*	
Upogebia spp. ZO	M				*	*	*	
Infraordo Anomura								
Galathea intermedia PO	M				*	*	*	**
Galathea intermedia ZO	M					*		*
Pisidia longicornis PO	M			*	*	**	*	**
Pisidia longicornis ZO	M			*	*	**	*	*
Anapagurus laevis ZO	M						*	*
Pagurus bernhardus ZO	M						*	
Pagurus prideauxi ZO	M							*
Paguridae spp. PO	M	*	*	*	*	*	*	*
Infraordo Brachyura								
Inachus spp. ME	M					*		
Macropodia spp. ME	M			*	*	**	*	*
Macropodia spp. ZO	M			*	*	*	*	
Thia scutellata ME	M			*		*	*	*
Corystes cassivelaunus ME	M				*			
Liocarcinus spp. ME	M	*	*	**	***	***	**	***
Liocarcinus spp. ZO	M			*	*	**	***	***
Carcinus maenas ME	M	*	**	**	**	**	*	*
Carcinus maenas ZO	M	*	**	*	**	**	*	*
Portumnus latipes ME	M			*	*	*	*	
Pilumnus hirtellus ME	M			*	**	**	**	*
Ebalia spp. ME	M			*	*	*	*	*
Brachyura spp. ZO	M			**	*	**	*	*
Superordo Peracarida								
Ordo Mysidacea								
Subordo Mysida								
Siriella armata	H				*			
Gastrosaccus spinifer	H	**	***	***	***	**	**	**
Mysidopsis gibbosa	H			*	*	**	*	*
Acanthomysis longicornis	H			*	*	**	*	*
Mesopodopsis slabberi	H	***	***	**	**	*		
Neomysis integer	H	***						
Paramysis arenosa	H					*	*	*
Praunus flexuosus	H	*						
Schistomysis kervillei	H		*	***	***	**	*	
Schistomysis spiritus	H		*	***	***	**	*	*

	H/M	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Ordo Cumacea								
Bodotria pulchella	H			*				
Bodotria scorpioides	H			*	*	*		*
Iphinoe trispinosa	H					*	*	
Pseudocuma longicornis	H			*				
Pseudocuma similis	H			*	*	*	*	*
Diastylis bradyi	H		**	**	*	*	*	*
Diastylis rathkei	H		*	*	*	*		
Ordo Amphipoda								
Subordo Caprellidea								
Pariambus typicus	H		*	***	*	*		*
Phtisica marina	H			*	*	*	*	*
Subordo Gammaridea								
Ampelisca brevicornis	H				*			
Amphilochus neapolitanus	H			*				
Aora gracilis	H			*	*	*		*
Atylus falcatus	H		*	*	*	*	*	*
Atylus swammerdami	H	*	**	**	**	**	**	**
Apherusa bispinosa	H						*	
Apherusa ovalipes	H							
Apherusa spp.	H					*	*	
Corophium acherusicum	H	*						
Corophium sextonae	H			*				
Corophium volutator	H		*					
Corophium spp.	H						*	
Gammarus crinicornis	H	*	**	**	*			
Gammarus salinus	H	*						
Iphimedia minuta	H			*				
Microprotopus maculatus	H			***	*			
Jassa falcata	H		*	*				
Leucothoe incisa	H				*			
Orchomenella nana	H		*	*	*		*	
Megaluropus agilis	H				*	*		*
Melita obtusata	H			*	*	*	*	*
Melphidippella macra	H						*	
Perioculodes longimanus	H				*	*		*
Pontocrates altamarinus	H		*	*	*	*	*	*
Pontocrates arenarius	H					*	*	
Pleusymtes glaber	H	*						
Bathyporeia spp.	H			*	*	*	*	
Stenothoe marina	H			**	*	*	*	
Urothoe brevicornis	H					*	*	
Subordo Hyperiidea								
Hyperia galba	H		*	*	*			
Ordo Isopoda								
Subordo Flabellifera								
Eurydice pulchra	H	*						
Subordo Valvifera								
Idotea linearis	H		*	**	*	*		
Idotea pelagica	H			*				
Subphylum Chelicerata								
Classis Pycnogonida								
Nymphon rubrum	H	*		*				
Achelia longipes	H			*				
Phoxichilidium femoratum	H			*				
Endeis laevis	H			*				
Phylum Chordata								
Subphylum Vertebrata								
Classis Actinopterygii								
Clupeidae spp. PO	M		*	*	*	*	*	
Trisopterus luscus PO	M						*	
Chelon labrosus PO	M				*	*	*	
Syngnathinae spp. PO	M	*	*	*	*	*	*	*
Agonus cataphractus PO	M			*				
Trachurus trachurus PO	M				*	*	*	*
Ammodytes tobianus PO	M						*	*
Hyperoplus lanceolatus PO	M					*		*
Ammodytidae spp. PO	M			*	*		*	
Echiichthys vipera PO	M						*	*
Callionymus lyra PO	M						*	
Callionymus reticulatus PO	M					*	*	*
Callionymus spp. *PO*	M					*	*	*
Pomatoschistus microps PO	M			*				
Pomatoschistus spp. *PO*	M	*	**	**	**	*	*	*
Arnoglossus laterna PO	M		*			*	*	
Solea solea PO	M				*	*	*	

(1) WS meso
(2) E Coast
(3) W Coast
(4) Flemish
(5) Zeeland trans
(6) Hinder
(7) Zeeland off

* 0.01 - 10 ind. 100 m^{-3}
** 10.1 - 100 ind. 100 m^{-3}
*** >100 ind. 100 m^{-3}

Addendum. Species list with gross density classes per community for all hyperbenthos caught, with indication of holo- (H) and merohyperbenthos (M); hydromedusa (HM), larva (LA), zoea (ZO), postlarva (PO), megalopa (ME).

Chapter 5. Habitat utilization and temporal variability of the hyperbenthos of Belgian coastal waters (North Sea)

Ann Dewicke, Bregje Beyst, Jan Mees & Magda Vincx

Summary

The Belgian continental shelf is characterised by an extensive sandbank complex merging into gently sloping sandy beaches, and extending eastwards into the mouth of the Westerschelde estuary. The coincidence of these features is rare along the NW European coast, providing high habitat heterogeneity and hence shelter and feeding opportunities for various species. In order to evaluate its importance for the hyperbenthic fauna, monthly surveys (from September 1994 until December 1995) were carried out at the Coastal and Flemish Banks (13 sites in total).

A total of 93 holohyperbenthic species were recorded. Spatial structure, corresponding to a major cross-shore and secondary alongshore gradient, persisted throughout the year. The Flemish Banks harboured the most diverse community, characterised by planktonic species (chaetognaths, copepods, hydromedusae and ctenophores) accountable for half of the total density in this area. Scarce food supply and strong flow in this offshore area are less favourable for bottom-dependent animals compared to onshore waters. Mysid dominance typified the Coastal Banks, and community structure changed along the east-west direction. Densities were highest for the East Coast but diversity was low. This is believed to be due to the nearby mouth of the Westerschelde estuary leading to variable fluctuations in the environment.

Temporal variability in community structure was most pronounced during spring, with increased amphipod densities and a conspicuous ctenophore bloom. The amphipod *Atylus swammerdami* showed a distinct density increase at the Flemish Banks in May, coinciding with the decaying phase of a *Phaeocystis* bloom. In addition, various epifaunal amphipods (e.g. *Microprotopus maculatus*, *Pariambus typicus*, *Phtisica marina*) were encountered in association with hydrozoan colonies at the Coastal Banks. *Gammarus crinicornis*, being confined to and strongly dominant on the E Coast, similarly co-occurred with hydrozoans. Its persistence during subsequent months probably indicates detrivory after collapse of the hydrozoan populations.

Mysids were most abundant during summer. However, density fluctuations were species-specific and fairly irregular. The dominant mysid *Schistomysis kervillei* (annual mean density of 293 ind. m^{-3} at the E Coast) occurred year-round at the Coastal Banks and appears to seek out turbid environments, which are favourable for feeding. *Schistomysis spiritus* is believed to be more sensitive to extremes conditions, like strong wave action, and probably migrates to more sheltered areas. The most extreme temporal fluctuation in density was found in *Mesopodopsis slabberi*, possibly caused by migrations between the adjacent biotopes of the coastal area. Several mysid species only occurred during a limited period; total species numbers tended to be maximal during winter.

The merohyperbenthos community was predominantly temporally structured, due to differential recruitment peaks of various postlarval fish (at least 21 species) and decapod larvae (at least 29 species). Both species richness and total abundance of fish larvae were highest during April - May. Species successions were conspicuous, recruitment often being restricted to a single month. Sole *Solea solea* (confined to May) was the most abundant fish species throughout the study area with densities at times exceeding 100 ind. 100 m^{-3}. Other common species were *Pomatoschistus* spp. (all year with peaks in May and July), flounder *Pleuronectes flesus* (confined to April), clupeids (peak in February and May) and dab *Limanda limanda* (confined to May). Recruitment for decapod larvae was most pronounced from late spring to late summer, with respect to both species richness and densities. Common shrimp *Crangon crangon* (annual mean density of 137 ind. m^{-3} at the E Coast), swimming crab *Liocarcinus holsatus*, shore crab *Carcinus maenas*, and porcelain crab *Pisidia longicornis* were most abundant.

Masked by this strong temporal pattern, an underlying onshore-offshore gradient for the merohyperbenthos community existed as well. The Flemish Banks were most diverse; several species, like most anomurans and certain fish species, preferentially occurred in this area. Moreover, decapods showed ontogenetic differences in spatial distribution. Zoea stages of nearly all species were typically found at the Flemish Banks, whereas postlarval carideans were more abundant at the Coastal Banks. Diversity was distinctly lower at the East Coast. *Crangon crangon* and *Lanice conchilega* larvae strongly dominated in the latter area (together more than 80 % of the total density), whereas Brachyura were poorly represented. Merohyperbenthos community structure appears to be largely regulated by the hydrodynamical setting and morphodynamical characteristics of the area.

In conclusion, the estuarine outflow on the one hand and the hydrodynamic setting and protective function of the sandbanks on the other hand create diverse environs along the Belgian coastal zone, sustaining rich communities of holohyperbenthic species and early life history stages when compared to the adjacent areas.

Introduction

Coastal areas are characterised by a great range in habitats as compared to the open ocean and are more vulnerable to human interference (Gray 1997). Shallow sandbanks close to the shore reduce the energy from offshore waves giving rise to sheltered areas (Dyer & Huntley 1999). The interaction of the sandbanks' morphodynamics and the hydrodynamic characteristics of the area in which they occur, create a high diversity in habitats. Coastal sandbank systems are ecologically unique and they have often been mentioned as being of value for early life history stages of fish and macrocrustaceans (Dyer & Huntley 1999). There exists therefore a need to protect this habitat and its underwater landscape diversity (Gray 1997).

An extensive sandbank complex extending in gently sloping sandy beaches is present on the Belgian continental shelf. The area is impacted by the southern intrusion of Channel water and by coastal runoff, mainly from the adjacent Westerschelde estuary (Nihoul & Hecq 1984; Hecq *et al.* 1992; Baeyens *et al.* 1998) (see Fig. 1). Data on the species composition and spatial community structure of the hyperbenthos, i.e. the fauna living at the interface of the bottom and water column (Mees & Jones 1997) has only recently become available (Chapter 4). This particular ecosystem compartment harbours planktonic, endobenthic and strictly hyperbenthic (e.g. mysids) species (Mees & Jones 1997). Strong gradients in density, biomass and diversity on the Belgian continental shelf were found and these are related to the distance from the shore and to the proximity of the mouth of the Westerschelde estuary (Chapter 4).

Literature on the hyperbenthos of the North Atlantic and the North Sea has only been accumulating since the last decade (Mees & Jones 1997; Dauvin *et al.* 2000). Most studies deal with data describing species composition, spatial community structure and diurnal and tidal variation. Research on the annual variation of the hyperbenthos communities is very limited. Temporal data from subtidal waters in the NE Atlantic exists for the Bay of Biscay (Sorbe 1989), the English Channel (Vallet & Dauvin 1999; Dauvin *et al.* 2000; Mouny *et al.* 2000) and the Dutch Voordelta (Hamerlynck & Mees 1991). These studies were often restricted to few sampling sites (Sorbe 1989; Vallet & Dauvin 1999), very shallow depths (Hamerlynck & Mees 1991; Mouny *et al.* 2000) or rather large time intervals (Dauvin *et al.* 2000). Data on spatio-temporal variability in estuarine environments or brackish lagoons has been reported by Mees (1994), Azeiteiro & Marques (1999), Cunha *et al.* (1999), Mouny *et al.* (2000), while data on sandy beaches is dealt with by San Vicente & Sorbe (1999), San Vicente & Sorbe (in press) and Beyst *et al.* (in press a).

The high diversity of taxa thriving in the hyperbenthal zone and consequently the wide range of ecological and behavioural traits make it complex to gain insight into the wax and wane of this fauna. Several species are also known to perform migrations between habitats such as different depth-strata of subtidal waters, estuarine and intertidal areas and beach environments (Mauchline 1980). Habitat preferences for most species remain largely unknown. In contrast, their significance as prey items in shallow coastal and estuarine food webs is better documented (Mauchline 1980; Mees & Jones 1997). A high variety of demersal fish feed on hyperbenthic prey during its juvenile or adult life stage, as there are several gobies *Pomatoschistus* species, bib *Trisopterus luscus*, whiting *Merlangius merlangus*, sole *Solea solea*, plaice *Pleuronectes platessa*, dab *Limanda limanda*, brill *Scophthalmus*

rhombus and turbot *S. maximus* (Hamerlynck & Hostens 1993; Beyst *et al.* 1999a; Hostens & Mees 1999; Pedersen 1999). The diet of adult shrimp has been shown to be dominated by hyperbenthic prey too, as described for common shrimp *Crangon crangon* (Oh *et al.* 2001; Hostens unpubl. data).

This paper deals with the temporal patterns of the hyperbenthic communities of the Belgian coastal area. Besides a structural description of the fauna, emphasis is laid on its occurrence in different biotopes of the study area. The presented data is unique in the sense that both an onshore-offshore gradient (corresponding to 7 to 29 m depth) and an alongshore gradient (related to estuarine outflow) were included in the sampling design. The discussion focuses on this specific issue as well as on some remarkable differences with the hyperbenthos of adjacent biotopes like the surf zone, the Westerschelde estuary and tidal marshes.

Material and methods

Sampling strategy

Monthly sampling was carried out at 13 sites in the Belgian coastal area (Fig. 1), from September 1994 until December 1995. Eight sites were located on the Coastal Banks, covering both the West Coast, i.e. from De Panne to Oostende (6 sites) and the East Coast, i.e. from Oostende to the Westerschelde mouth (2 sites). The more offshore Flemish Banks were sampled at 4 sites and the Zeeland Banks at 1 site. These fixed sampling stations were generally situated as close as possible to the crest of the sandbank (site name ending with 'c'). Five sites were situated in the swales of the sandbank system (site name ending with 's'), always adjacent to a crest site (except for site C5c). No samples were collected in January and September 1995 and a limited sampling program was conducted during July and August 1995. In total, 164 samples were collected. The geographical position of the sampling sites is shown in Fig.1; Table 1 gives an overview of the collected samples. A detailed description of the sandbanks can be found in Bastin (1974) (see also Chapter 4).

All sampling was carried out from the *RV* Belgica with a modified hyperbenthic sledge after Sorbe (1983). Two superimposed nets (1 mm mesh size, 3 m long, 71 cm wide) were fixed on the sledge, sampling the water layer from 0 to 50 cm (lower net) and from 50 to 100 cm (upper net) above the sea floor. The sledge was equipped with an opening-closing mechanism and an odometer (for details see Sorbe 1983). A flow meter (*Hydrobios 438-110*) was fixed in the upper net. All sampling was performed during daytime; towing lasted five minutes at an average ship speed of 1.5 knot relative to the bottom and against the current. On average, towing distance was 170 ± 5.7 m and a water volume of 116 ± 2.9 m^3 was filtered. The catches from the upper and lower nets were rinsed separately over a 1 mm mesh size sieve and preserved in a buffered formaldehyde solution (7 % final concentration). Before each tow, sediment and water sampling was carried out and a number of environmental variables were registered.

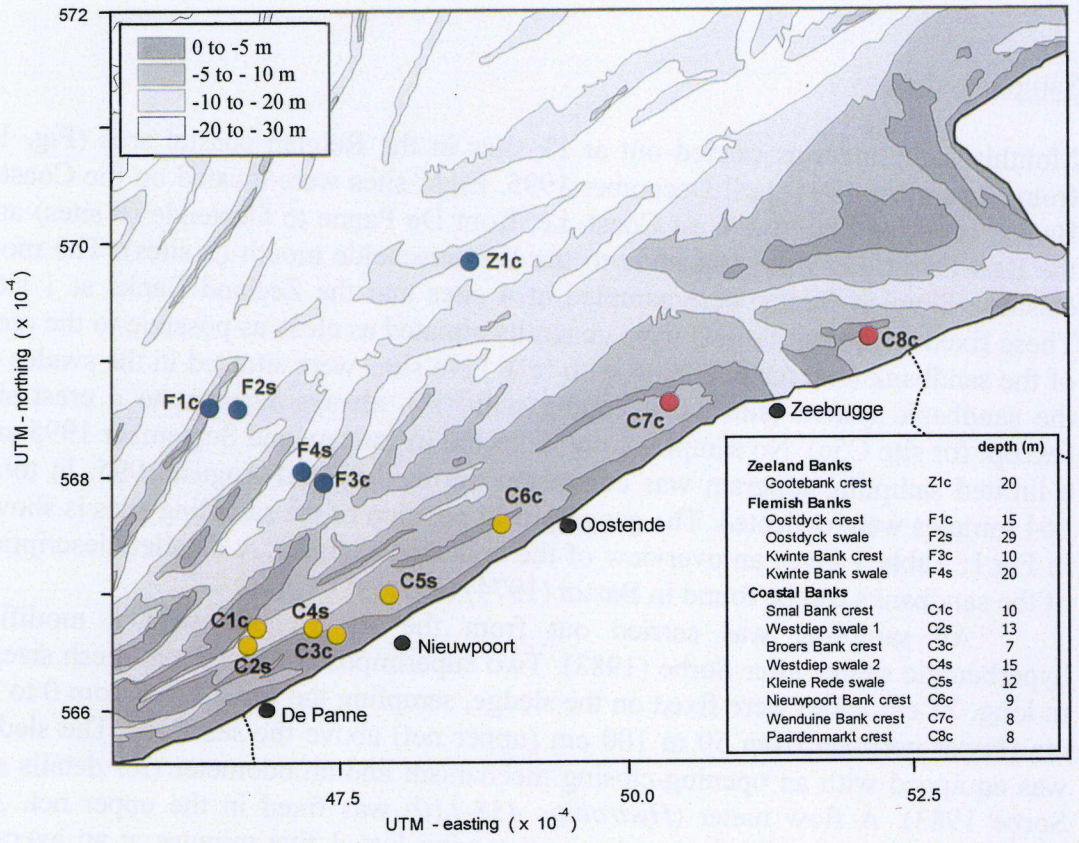

Fig. 1. Map of the study area showing the location of the sampling sites. Symbols refer to the identified communities (see Chapter 6). The sandbanks dealt with are listed for each sandbank complex in the table above.

				1994				1995										
Site	**Longitude**	**Latitude**	**Depth (m)**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Z1c	2° 48.15' E	51° 26.09' N	20	-	7	4	21	-	10	24	27	23	21	-	17	-	10	8	20
F1c	2° 29.42' E	51° 19.17' N	15	6	7	4	20	-	9	24	26	22	21	-	-	-	10	7	19
F2s	2° 28.20' E	51° 19.54' N	29	6	7	4	20	-	9	23	26	22	21	-	-	-	10	7	19
F3c	2° 36.93' E	51° 16.83' N	10	6	7	3	20	-	8	22	26	22	21	-	-	-	10	7	19
F4s	2° 36.90' E	51° 16.73' N	20	6	7	3	20	-	8	22	26	22	21	-	-	-	10	7	19
C1c	2° 32.72' E	51° 9.27' N	10	6	10	2	20	-	9	23	26	23	20	-	-	-	10	8	18
C2s	2° 32.12' E	51° 8.46' N	13	6	10	2	20	-	9	23	26	23	20	-	-	-	10	8	18
C3c	2° 36.95' E	51° 8.94' N	7	6	10	3	20	-	2	23	26	23	20	10	-	-	9	8	18
C4s	2° 36.32' E	51° 9.38' N	15	6	10	3	20	-	2	23	26	23	20	10	-	-	9	8	18
C5s	2° 42.10' E	51° 10.99' N	12	6	6	3	20	-	7	23	24	23	20	10	-	-	9	8	18
C6c	2° 50.26' E	51° 14.68' N	9	5	6	3	19	-	2	22	24	23	20	10	7*	-	9	6	18
C7c	3° 3.05' E	51° 16.60' N	8	5	6	3	19	-	2	22	24	22	19	10	-	-	9	7	18
C8c	3° 18.66' E	51° 22.63' N	8	7	6	2	19	-	6	22	25	22	20	11	-	-	9	7	20

Table 1. Overview of the collected samples with exact sampling date; (-) no sampling performed, (*) two samples were taken at this site.

Environmental variables

Water depth was recorded during sampling and was standardised to local Mean Lowest Low Water Spring (MLLWS) level. Temperature and salinity (thermosalinograph, *Sea-bird SBE21*) were registered for surface waters (3 m depth). Turbidity was measured at a depth of 3 m above the sea floor with an Optical Backscatter Sensor (*D&A Instrument's OBS^{TM} sensor, Sea-Bird SBE*) and is reported in nephelometric turbidity units (ntu). Turbidity was not measured on a regular basis covering only 60% of all samples.

Sediment samples were collected, using a box corer (*Reineck*). The upper 2 cm of the sediment were sampled for grain fraction analysis by means of a particle size analyser (*Coulter LS100*); the organic fraction was not burnt prior to analysis. Sediment fractions were defined using the Wentworth scale (Buchanan 1984).

A Niskin-bottle was lowered to collect water samples at 3 m above the sea floor. An amount of 20 ml was frozen on board for further nutrient analysis in the lab. $NO_3^- - N$ (including $NO_2^- - N$) (nitrate) , $NH_4^+ - N$ (ammonia) and SiO_2 (silica) were quantified with an auto-analyser *(type AII flow system, SKALAR*). An additional volume of 1000 ml was passed through Whatman glass-fibre filters (GF/C) and immediately deep-frozen for pigment analyses (chlorophyll *a* and fucoxanthin). An extraction with aceton (90 %) was performed prior to chromatography, with a HPLC-chain (High-Performance Liquid Chromatography, *Gilson*), according to the method of Mantoura & Llewellyn (1983).

Data acquisition

After sorting all organisms, they were identified - if possible - to species level. For certain taxa, further classification was done based on the life history stage, such as the distinction between zoea and megalopa or postlarva stages for decapods. All animals were counted on species and stage level. In case of uncertain identification, specimens were reported on a higher taxon level (indicated as 'spp.' and further also called species). Certain samples contained stolons of hydrozoan colonies, which have been weighed after oven-drying in order to obtain a rough quantification of their occurrence.

After finishing identification, non-hyperbenthic representatives were removed from the 'catch-dataset' (i.e. all animals that were caught by the Sorbe-sledge and retained on a 1 mm sieve). Rejected animals comprise all juvenile and adult decapods, polychaetes (except the planktonic Tomopteridae), echinoderms, scyphozoans, fish eggs, and sedentary and parasitic organisms (see Introduction). Further, holo- and merohyperbenthos were dealt with separately. Holohyperbenthos is defined as animals that spend variable periods of their adult life in the hyperbenthal zone (Mees & Jones 1997). It comprises a group of taxa with a rather small adult habitus (generally < 20 mm), like several peracarid orders (mysids, amhipods, isopods, cumaceans), copepods, chaetognaths and hydromedusae. The merohyperbenthos consists of early life history stages, generally originating from larger animals and is mainly represented by decapod larvae (< 10 mm), fish larvae (generally < 20 mm) and larval polychaetes (modified after Mees & Jones 1997). Density was expressed as numbers of individuals per 100 m^{-3}. Since the catch efficiency of sledges is largely unknown (Mees & Jones 1997), densities were reported as such and should be considered as minimum values.

Numerical analysis

Spatio-temporal patterns were examined with multivariate statistical analyses, which are dealt with in Chapter 6. To further reduce complexity, three 'areas' that may be considered to be characterised by distinct 'communities' are dealt with: the E Coast, the W Coast and the Flemish Banks. The latter also covered the single station of the Zeeland Banks. The temporal variance was more complex and will therefore mainly be dealt within this chapter (see Chapter 6 for more details on the multivariate analyses).

Species richness was estimated as Hill's diversity number N_0, which is equal to the number of species in a sample (Hill 1973). The expected number of species for a sample of 100 individuals $E(S_{100})$ (Hurlbert 1971) and Hill's numbers N_1 and N_2 were calculated to estimate species diversity. N_1 is the inverse natural logarithm of the Shannon-Wiener diversity index and N_2 is the reciprocal of Simpson's dominance index (Hill 1973). Species reported on a higher taxonomic level were considered as a single species if no other representative of the same taxonomic level was present or if they were distinctly different. Thus, diversity is considered as a minimum estimate.

In order to compare characteristics between communities, one-way ANOVA and subsequent *post-hoc* tests (Scheffé-test) were performed for variables meeting the assumptions (after transformation) for parametric statistics (Sokal & Rohlf 1995). If the assumptions for ANOVA were not met, non-parametric statistics were used (Mann-Whitney U-test, Kruskal-Wallis test with subsequent *post-hoc* multiple comparisons according to Conover (1971)) (Sokal & Rohlf 1995). The relation between some variables was assessed by calculating Spearman's correlation coefficient, r_s (Sokal & Rohlf 1995).

Feeding guild structure

Species were classified into feeding guilds based on three criteria: (1) their food source (carnivores versus omnivores), (2) their behaviour (being predominantly benthic or pelagic), and (3) their feeding mechanism (suspension versus deposit feeders). As feeding ecology is poorly known for the hyperbenthos, only those species generally considered as being strictly carnivorous were separately grouped. All others were considered as omnivores. The majority of them might also consume detritus, thus the term omnivore is applied as including detritivorous species. Classification related to feeding mechanism was only applied for omnivores with a benthic behaviour. Omnivorous suspension feeders are here considered as animals that may feed in the water column itself but may also bring bottom material in suspension (e.g. by making use of antennal scales as for mysids and postlarval decapods). Deposit feeders generally consume directly on sedimented matter and are mainly detritivores. Omnivorous pelagic feeders, mostly small larvae and copepods, are morphologically less adapted to feed on bottom material. This way, five feeding guilds were defined (Table 2). The classification is based on literature (see Table 2), general morphology and on the results of the presented data, such as the Bottom Association index giving an indication of species' vertical distribution in the hyperbenthal zone (see Chapter 1). The contribution of each taxon to a certain guild is also presented in Table 2. This makes it possible to estimate bias caused by generalising feeding habits being unavoidable due to due to the scarce knowledge on hyperbenthic food preferences.

Biomass estimates for mysids, amphipods and cumaceans are derived from mean values per species as calculated for September 1993 (Chapter 4); assigned values were used for the other species. For the methodology we refer to Chapter 4. It should therefore be stressed that the used biomass estimates are rather rough, but are preferred to densities since they yield a more realistic picture concerning food chain structure.

Feeding guild	Taxon	Abs biom	% biom	Reference
	Carnivores (predators)			
	Pelagic feeders (presumably feeding in the entire water column)			
Carnivorous pelagic feeders	Hydromedusae	0.07	0.02	Purcell (1991, 1997)
	Ctenophora	0.01	0.00	Purcell (1991, 1997)
	Chaetognatha	0.96	0.22	Pierrot-Bults & Chidgey (1988)
	Cephalopoda	0.46	0.10	Ruppert & Barnes (1994)
	postlarvae of pelagic fish (Clupeidae)	12.32	2.81	Russell (1976)
	Tomopteridae	0.00	0.00	Pleijel & Dales (1991)
	Hyperiidae	0.00	0.00	Todd *et al.* (1992)
	Benthic feeders (presumably feeding in the hyperbenthic zone or on the seabed)			
Carnivor. benthic feeders	Postlarvae of demersal fish	37.57	8.56	Russell (1976)
	Pycnogonida	0.01	0.00	King (1974)
	Nudibranchia	0.09	0.02	Ruppert & Barnes (1994)
	Omnivores (including detritivores)			
	Pelagic feeders (mainly planktivores feeding on bacteria, detritus, phyto- or zooplankton in the entire water column)			
Omnivorous pelagic feeders	Polychaete larvae	2.44	0.56	Boidron-Métairon (1995)
	Decapod larvae (except postlarval shrimp)	25.89	5.90	Boidron-Métairon (1995)
	Copepoda	1.05	0.24	Mauchline (1998)
	Suspension feeders (have the ability to bring bottom matter in suspension)			
Omnivor. suspensio n feeders	Mysidacea	221.22	50.42	Mauchline (1980)
	Euphausiacea	0.12	0.03	Mauchline (1980)
	Postlarval carideans	19.06	4.34	Pihl & Rosenberg (1984), Boddeke *et al.* (1986)
	Deposit feeders (mainly detritus feeders, feeding on of near the bottom)			
Omnivorous feeders deposit	Cumacea	3.72	0.85	Jones (1976)
	Amphipoda	112.24	25.58	Caine (1977), Conradi & Cervera (1995), Ruppert & Barnes (1994)
	Isopoda	1.48	0.34	Naylor (1972)
	Nebaliacea	0.00	0.00	Mauchline (1984)

Table 2. Overview of the feeding guild classification. The average absolute biomass (Abs biom) is expressed as mg ADW 100 m^{-3}. The relative contribution to the total biomass (% biom) is calculated over all samples.

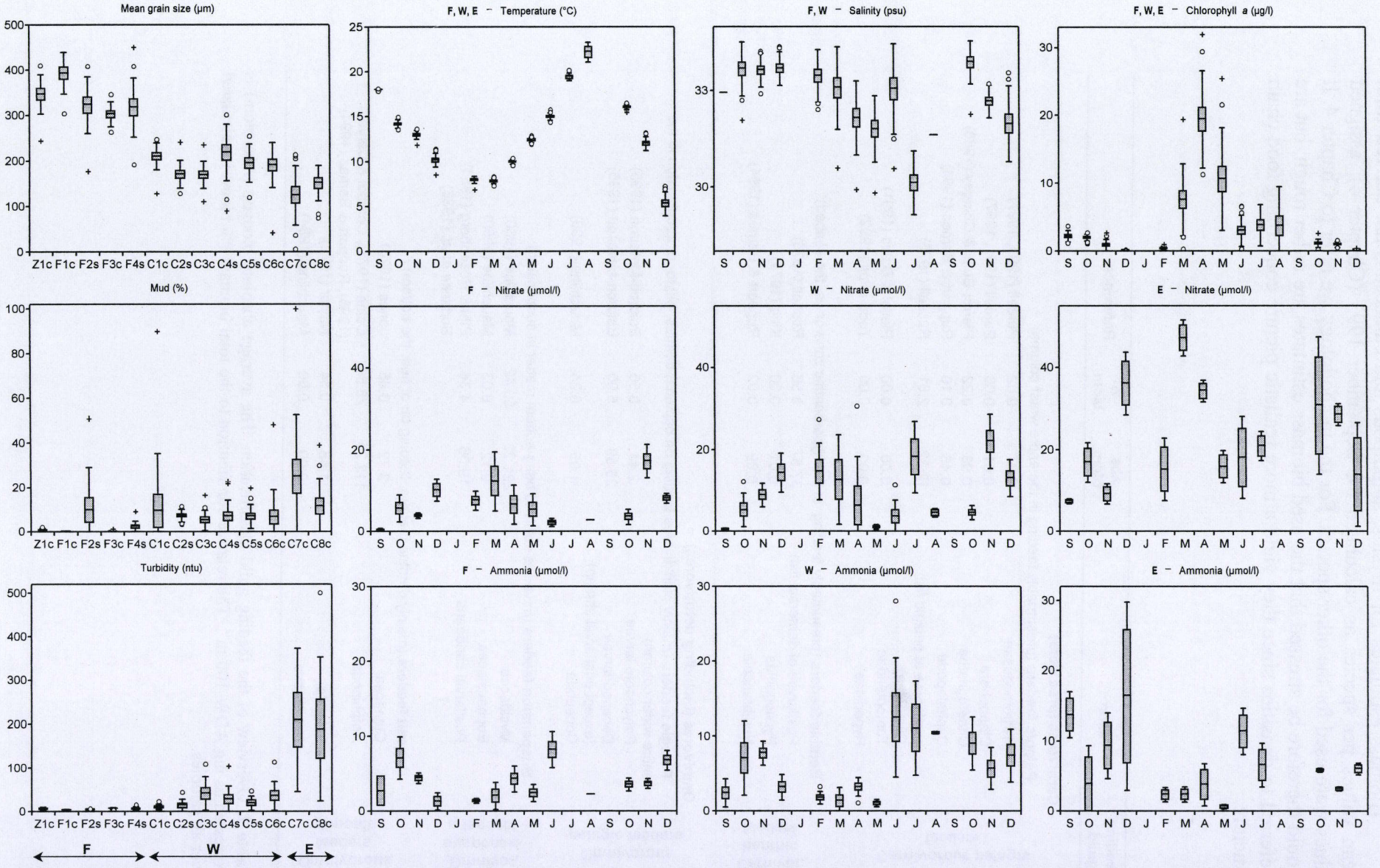

Fig. 2. Spatio-temporal variability for some environmental characteristics. Boxes represent mean values with standard error and whiskers indicating the standard deviation; outliers (o) and extremes (*) are also shown. Mean grain size, turbidity and mud fraction are figured per site and represent data over all months. Temperature, salinity, chlorophyll *a*, nitrate and ammonia are figured from September 1994 until December 1995. Data were pooled over all sites for temperature and chlorophyll *a*. Salinity represents only the values for the Flemish Banks and the W-Coast. Nitrate and ammonia are separately shown for the Flemish Banks (F), W Coast (W) and E Coast (E).

Results

Summary of results of numerical analysis

For the holohyperbenthos, spatial and temporal species variance were of similar importance and amounted to 22.8 % and 24.1 % of the total variance in the datamatrix, respectively. The merohyperbenthos was more temporally structured (39.6 % temporal and 13.3 % spatial variance, respectively). Spatial structure was largely confined to a principal onshore-offshore (Coastal Banks versus Flemish and Zeeland Banks) and a minor east-west gradient on the Coastal Banks (E Coast versus W Coast). This east-west gradient was less clear for the merohyperbenthos. (See Chapter 6 for more details on these analyses.)

Habitat characterisation and its variability

The depth of the sampling sites ranged from 7 to 29 m (Table 1). Mean grain size (ANOVA, $p < 0.001$) and mud fraction (Kruskal-Wallis, $p < 0.001$) of the sediment differed significantly between the three areas (Fig. 2, Table 3). The Coastal Banks were characterised by fine sands (136 ± 11.3 µm for the E Coast and 194 ± 5.2 µm for the W Coast) and the Flemish Banks by medium sand (336 ± 7.7 µm). The percentage mud was fairly high and very variable at the E Coast (18.2 ± 4.26 %) and much lower at the W Coast and Flemish Banks (5.8 ± 0.82 % and 2.5 ± 1.16 %, respectively). A significant difference for the percentage of mud was found between the crests and the swales of the Flemish Banks (Mann-Whitney U-test, $p < 0.001$). The sediment at the crests consisted always of pure sand. The swales however were characterised by small amounts of mud, particularly after stormy weather.

Turbidity was clearly highest and very variable at the E Coast with lowest values for the Flemish Banks (Fig. 2). Significant differences were found between the three areas (Kruskal-Wallis, $p < 0.001$, Table 3).

Monthly averages (all sites) of temperature reached a maximum in August (22.2 ± 0.64°C) and minima in February (7.8 ± 0.09°C) and December 1995 (5.3 ± 0.37 °C) (Fig. 2). Salinity differed significantly between the three areas (Kruskal-Wallis, $p < 0.001$, Table 3). At the E Coast, salinity (30.3 ± 0.33 psu) was strongly dependent on the tides at the moment of sampling, due to the Westerschelde outflow. The salinity at the W Coast (32.6 ± 0.15 psu) and at the Flemish Banks (33.2 ± 0.13 psu) was lowest in July (Fig. 2).

The spring phytoplankton bloom was mainly observed from March till May, with a chlorophyll *a* peak in April (19.4 ± 1.79 µg l^{-1}). Apart from these spring months, a mean value of 1.4 ± 0.13 µg l^{-1} was noted. Fucoxanthin (not presented) showed a similar pattern and was positively correlated ($r_s = 0.88$, $p < 0.001$) with chlorophyll *a*.

Nitrate concentrations were significantly different among the sandbanks (Kruskal-Wallis, $p < 0.001$, Table 3), with increasing values from west to east along the coast (not shown). Highest values were recorded at the E Coast (22.6 ± 2.21 µmol l^{-1}) with a very irregular temporal fluctuation (Fig. 2.). At the Flemish Banks and at the W Coast, nitrate concentrations gradually increased towards the late-autumn and winter months (maxima in February and November 1995) with mean values of 6.7 ± 0.71 µmol l^{-1} and 9.2 ± 0.97 µmol l^{-1}, respectively. It also showed a peak for the W Coast area in July. Nitrate was positively correlated with silicate

	Method	Main effect	F - W	F - E	W - E
Mean grain size	(1)	***	***	***	***
% mud	(2)	***	***	***	**
Turbidity	(2)	***	***	***	***
Temperature	(1)	ns			
Salinity	(2)	***	**	***	***
Chlorophyll *a*	(2)	ns			
Fucoxanthin	(2)	ns			
Nitrate	(2)	***	ns	***	***
Ammonia	(2)	ns			
Silicate	(2)	***	*	***	**

Table 3. Significance levels of the (1) one-way ANOVA or (2) Kruskal-Wallis test for some environmental variables among the Flemish Banks (F), W Coast (W) and E Coast (E) (main effect); and subsequent multiple comparisons between the three areas; $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), not significant (ns).

	Flemish			W Coast			E Coast			All
	Mean		F	Mean		F	Mean		F	F
	Abs	%	(10)	Abs	%	(11)	Abs	%	(10)	%
Holohyperbenthos										
Schistomysis kervillei				116	26	10	293	28	10	89
Pleurobrachia pileus	94	23	4	92	21	5	51	5	5	54
Pariambus typicus				62	14	5				82
Atylus swammerdami	140	34	6	28	6	7	34	3	4	98
Beroe spp.	6	1	1	26	6	3				13
Schistomysis spiritus				24	5	6				67
Gastrosaccus spinifer	24	6	8	17	4	6	64	6	4	91
Microprotopus maculatus				13	3	3				29
Bougainvillea britannica HM				9	2	2				8
Melita obtusata				8	2	2				44
Gammarus crinicornis				7	2	1	518	49	6	34
Mesopodopsis slabberi				6	1	1				65
Mitrcomella polydiademata HM	32	8	4							33
Pseudocuma similis	23	5	3							29
Calanus helgolandicus	18	4	5							84
Sagitta setosa	17	4	4							54
Acanthomysis longicornis	14	3	3							38
Sagitta elegans	6	1	3							37
Merohyperbenthos										
Lanice conchilega	138	38	7	73	26	5	125	39	2	63
Crangon crangon	23	6	7	72	26	9	137	43	7	94
Liocarcinus spp.	70	19	8	34	12	5				84
Carcinus maenas	33	9	6	31	11	5	13	4	4	80
Solea solea	11	3	1	12	4	2	10	3	1	31
Pomatoschistus spp.				10	4	1	11	4	3	73
Pleuronectes flesus				10	4	1				16
Pisidia longicornis	26	7	4	8	3	2				58
Clupeidae spp.	9	3	2	4	1	2				59
Pagurus bernhardus	19	5	4							73

Table 4. Summary of some ecological characteristics of the most common holo- and merohyperbenthic taxa observed during this study. All species of each community having an annual mean density > 5 ind. 100 m^{-3} are listed. Annual mean density (Mean) is absolutely reported as ind. 100 m^{-3} (Abs) and relatively (%) as the fraction of the total density of each community. The number of months in which a species was recorded is noted as frequency (F); the number of months in which samples have been taken is given below. Percentage occurrence (F) over all samples (125) during a one-year period is reported in the last column (All). Note that this table presents annual data, thus comprising the samples taken from September 1994 until August 1995.

(r_s = 0.69, $p < 0.001$). Ammonia levels were highest in autumn 1994 (October-November)and from June till December 1995 (Fig. 2) and did not differ significantly among the three areas (Table 3).

Spatial and temporal variability of the hyperbenthos

In total, 147 species were observed. The holohyperbenthos consisted of 93 species, predominantly belonging to the Amphipoda (38 species) and Mysidacea (16 species). Fewer species (54) were encountered in the merohyperbenthos. More than half of these belonged to the Decapoda (29 species); 21 fish species were identified. Mean density (average over all samples) was higher for the holohyperbenthos (537 ± 62.9 ind. 100 m^{-3}) than for the merohyperbenthos (262 ± 28.7 ind. 100 m^{-3}). Holo- and merohyperbenthos are treated separately when further describing the results. Some data on density and occurrence of the most common species of each community is listed in Table 4. Annual mean values always refer to data gathered from September 1994 until August 1995.

Holohyperbenthos

Annual mean density and diversity

Annual mean density for the holohyperbenthos was highest at the E Coast (1064 ± 334.6 ind. 100 m^{-3}), the other two regions only comprising less than half of that value (458 ± 79.2 ind. 100 m^{-3} at the W Coast, 412 ± 104.8 ind. 100 m^{-3} at the Flemish Banks) (Fig. 3). Fig. 3 also shows that the swales of the Flemish Banks harboured slightly density-richer assemblages than their crests.

Species richness (N_0) was quite similar for the whole study area (17.5 ± 0.47). Only stations C3c and C4s (W Coast) (19.6 ± 0.78) and the swales of the Flemish Banks were richer (21.2 ± 1.5) (Fig. 3). Significant differences among the three areas were found for species diversity, calculated as N_1, N_2 and $E(S_{100})$ (Table 5). Both N_1 and $E(S_{100})$ (7.9 ± 0.56) were lowest at the E Coast. N_1 gradually increased from west (C2s) to east (C8c) at the W Coast, while $E(S_{100})$ was comparable at these sites (9.8 ± 0.41) while higher for the E Coast. Species diversity was highest at the Flemish Banks ($E(S_{100})$ = 11.2 ± 0.48) and showed a similar pattern as was described for species richness, i.e. estimates were higher at the swales (Mann-Whitney U-test, $p < 0.05$ for N_0 and $E(S_{100})$ between the crest and swale samples).

	Method	Main effect	F - W	F - E	W - E
Holohyperbenthos					
Density	(1)	*	ns	*	ns
N_0	(2)	ns			
N_1	(2)	**	*	***	ns
N_2	(2)	*	*	**	ns
$E(S_{100})$	(2)	**	*	***	*
Merohyperbenthos					
density	(1)	ns			
N_0	(2)	*	*	***	**
N_1	(2)	***	*	***	***
N_2	(2)	***	*	***	***
$E(S_{100})$	(2)	***	*	***	***

Table 5. Significance levels of the (1) one-way ANOVA or (2) Kruskal-Wallis test for the total holo- and mero-hyperbenthos density and the diversity estimates among the Flemish Banks (F), W Coast (W) and E Coast (E) (main effect); and subsequent multiple comparisons between the three areas; $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), not significant (ns).

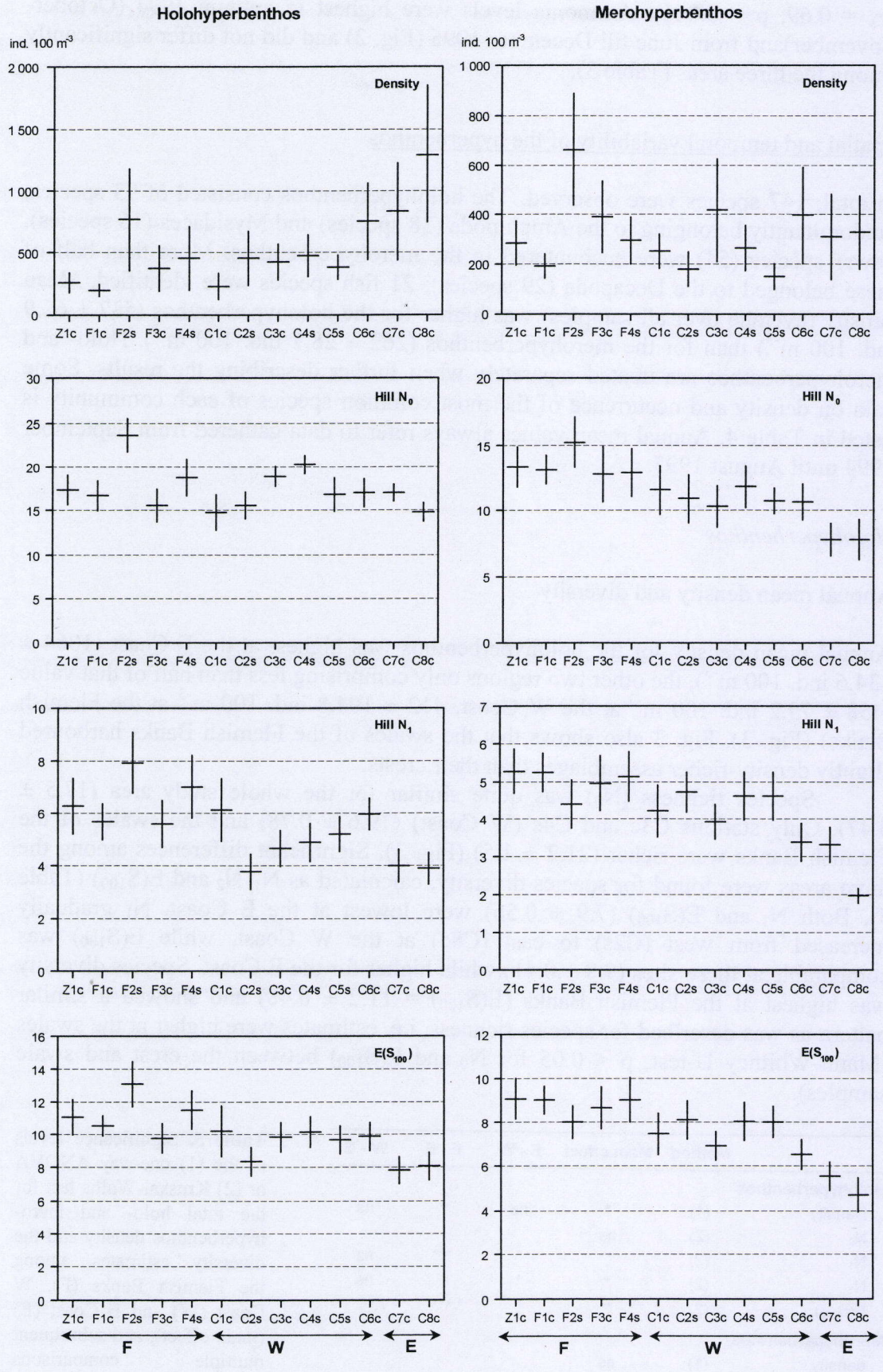

Fig. 3. Annual mean values with standard error for the total density, the Hill diversity numbers N_0 and N_1 and Hurlbert's $E(S_{100})$. N_2 is not presented but revealed a similar pattern as N_1. Data are presented per site for holo- **(left)** and merohyperbenthos **(right)**. Annual means were calculated from September 1994 until August 1995; Flemish Banks (F), W Coast (W), E Coast (E).

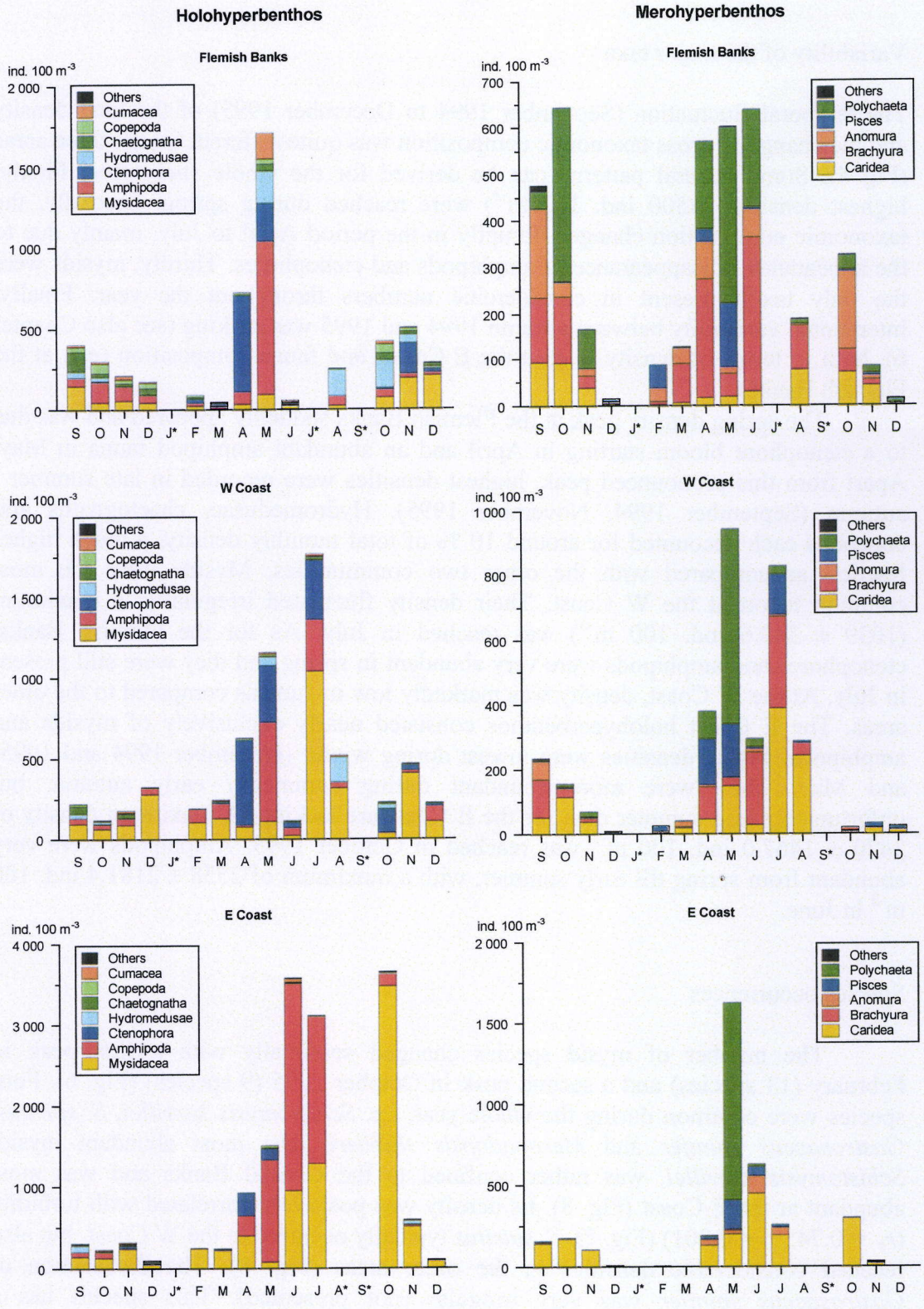

Fig. 4. Taxonomic composition and density fluctuation for the total holo- **(left)** and merohyperbenthos **(right)**, from September 1994 until December 1995. Data are separately presented for the Flemish Banks, W Coast and E Coast, (*) no sampling was carried out at these months.

Variability of the major taxa

The temporal fluctuation (September 1994 to December 1995) of the total density and the change in gross taxonomic composition was quite different for the three areas (Fig 4). Some general patterns can be derived for the whole study area. Firstly, highest densities (1500 ind. 100 m^{-3}) were reached during spring. Secondly, the taxonomic composition changed abruptly in the period April to July, mainly due to the appearance / disappearance of amphipods and ctenophores. Thirdly, mysids were the only taxon present in considerable numbers throughout the year. Finally, interannual variability between autumn 1994 and 1995 was striking (see also Chapter 6), both in terms of density (e.g. at the E Coast) and fauna composition (e.g. at the Flemish Banks).

The spring density peak at the Flemish Banks suddenly appeared and was due to a ctenophore bloom starting in April and an abundant amphipod fauna in May. Apart from this pronounced peak, highest densities were recorded in late summer / autumn (September 1994, November 1995). Hydromedusae, chaetognaths and copepods each accounted for around 10 % of total monthly density, a much higher fraction as compared with the other two communities. Mysids were the most common taxon at the W Coast. Their density fluctuated irregularly; a maximum (1039 ± 340.6 ind. 100 m^{-3}) was reached in July. As for the Flemish Banks, ctenophores and amphipods were very abundant in spring and they were still present in July. At the W Coast, density was markedly low in June as compared to the other areas. The E Coast holohyperbenthos consisted nearly exclusively of mysids and amphipods. Mysid densities were lowest during winter (December 1994 and 1995) and May. They were more abundant during summer / early autumn, but unfortunately mid summer data for the E Coast are lacking. A maximum density of 3470 ± 1467.0 ind. 100 m^{-3} was reached in October 1995. Amphipods were very abundant from spring till early summer, with a maximum of 2558 ± 2181.4 ind. 100 m^{-3} in June.

Species occurrences

The number of mysid species changed seasonally with a first peak in February (13 species) and a second peak in October 1995 (9 species) (Fig. 6). Four species were common during the whole year, i.e. *Schistomysis kervillei*, *S. spiritus*, *Gastrosaccus spinifer* and *Mesopodopsis slabberi*. The most abundant mysid, *Schistomysis kervillei*, was rather confined to the Coastal Banks and was most abundant at the E Coast (Fig. 8). Its density was positively correlated with turbidity ($r_s = 0.74$, $p < 0.001$) (Fig. 7). *S. spiritus* typically occurred at the W Coast, but also reached considerable densities in the other areas (Fig. 8). The distribution of *Gastrosaccus spinifer* was very irregular (not presented). This species has a burrowing behaviour therefore masking its distribution. *Mesopodopsis slabberi* was markedly more abundant in the autumn of 1995 (Fig. 8). *Acanthomysis longicornis* and *Mysidopsis gibbosa* were mainly caught during autumn, though always in low numbers. All other species were recorded occasionally and always in low numbers. Some of these may have been washed out from intertidal or estuarine areas (see Table 6).

The total number of amphipod species encountered at the W Coast and at the Flemish Banks was quite comparable (33 and 30 species, resp.) and was slightly

lower at the E Coast (24 species). The extreme abundances in May (Fig. 5) were due to an increase of several species. *Atylus swammerdami* strongly dominated at the Flemish Banks (98 % of the amphipod fauna of this area). Species dominance was less pronounced at the W Coast where *Pariambus typicus*, *Atylus swammerdami*, *Microprotopus maculatus* and *Melita obtusata* were the most common species. These species also occurred in appreciable numbers at the E Coast, with the exception of *Melita obtusata*. *Gammarus crinicornis* was mainly restricted to the E Coast and reached very high densities in this area (2460 ± 2156.5 ind. 100 m^{-3} in June).

The two ctenophores encountered in the area were *Pleurobrachia pileus* and *Beroe* spp. A pronounced bloom of the former occurred in April - May (606 ± 104.0 ind. 100 m^{-3} in April, Flemish Banks) and a much smaller bloom was recorded during the autumn of 1995 (mainly in November). *Beroe* spp. was present from May till July, but was less abundant (maximum of 358 ± 288.9 ind. 100 m^{-3} in July, W Coast).

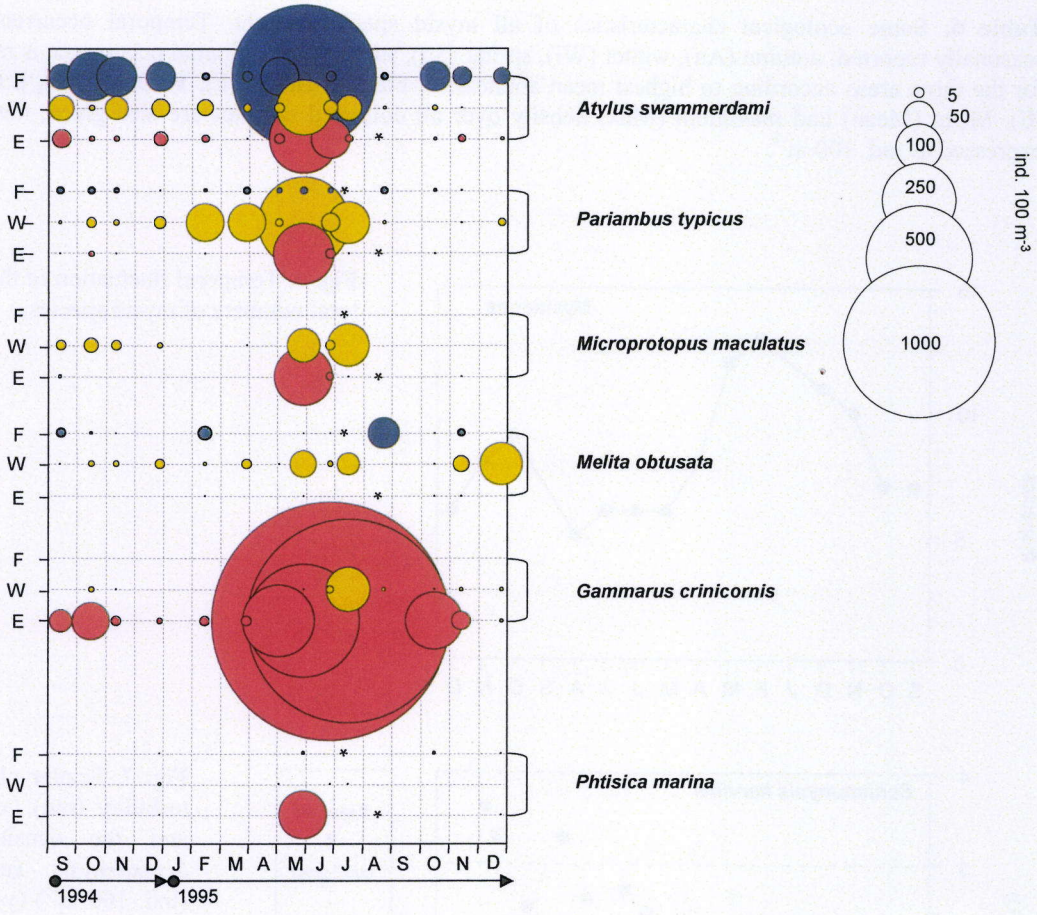

Fig. 5. Spatio-temporal variability for some common amphipods. The bubble chart represents mean densities. The x-axis is scaled in Julian days, months are also indicated. Note that no sampling was carried out in January and September 1995, certain samples which were lacking for the other months are indicated as '*' (see Table 1). Species abundances are figured separately for the Flemish Banks (F), W Coast (W) and E Coast (E) along the y-axis.

Mysidacea	Temporal	Spatial	Mean	Max
Very abundant				
Schistomysis kervillei	all year	E > W > F	163.9	4277.4
Schistomysis spiritus	all year	W > E > F	25.4	450.7
Gastrosaccus spinifer	all year	E > F > W	25.4	772.3
Mesopodopsis slabberi	all year	E > W = F	22.8	653.1
Less abundant				
Acanthomysis longicornis	Au, (Wi), (Sp), (Su)	F > W > E	5.7	303.7
Mysidopsis gibbosa	Au, (Wi), (Sp), (Su)	F > W > E	1.3	22.0
Occasionally				
Anchialina agilis	(Au), Wi, (Sp)	F > W > E	0.2	7.5
Paramysis bacescoi	Wi	W > F	0.2	21.8
Paramysis arenosa	Au, (Wi), (Sp)	F > W	0.1	2.3
Neomysis integer	estuarine outflow?	E > W	0.0	5.2
Siriella armata	(Au), Wi	W > F	0.0	1.1
Siriella clausii	Wi	F > W	0.0	1.2
Leptomysis lingvura	Wi	W	0.0	1.6
Siriella jaltensis	Wi	F	0.0	1.0
Praunus flexuosus	from the intertidal?	E	0.0	0.9
Schistomysis ornata	rarely	W	0.0	0.3

Table 6. Some ecological characteristics of all mysid species caught. Temporal occurrence is seasonally reported; autumn (Au), winter (Wi), spring (Sp), summer (Su). Spatial occurrence is ranked for the three areas according to highest mean abundance; Flemish Banks (F), W Coast (W), E Coast (E). Mean (Mean) and maximum (Max) density over all collected samples are also given, they are expressed as ind. 100 m^{-3}.

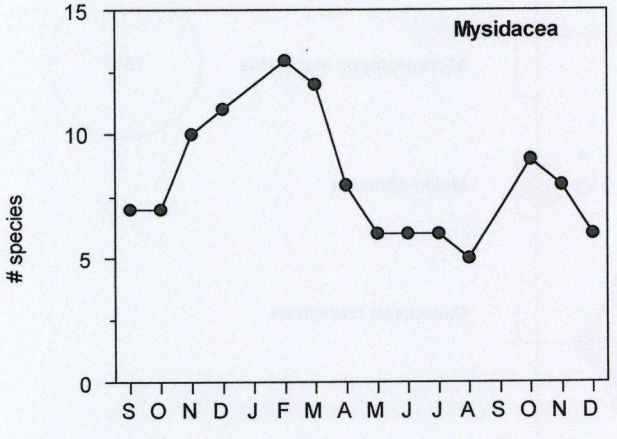

Fig. 6. Temporal fluctuation of the total numbers of mysid species.

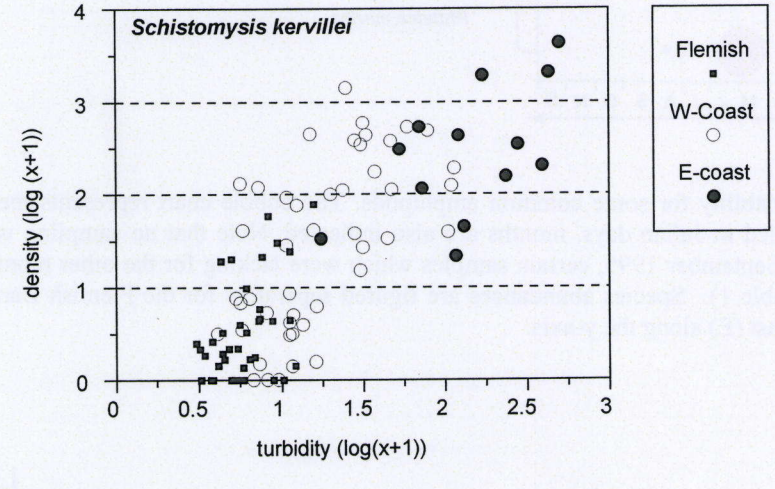

Fig. 7. Scatter plot for turbidity (ntu) (x-axis) and the density of *Schistomysis kervillei* (ind. 100 m^{-3}) (y-axis). Both variables are log(x+1) transformed.

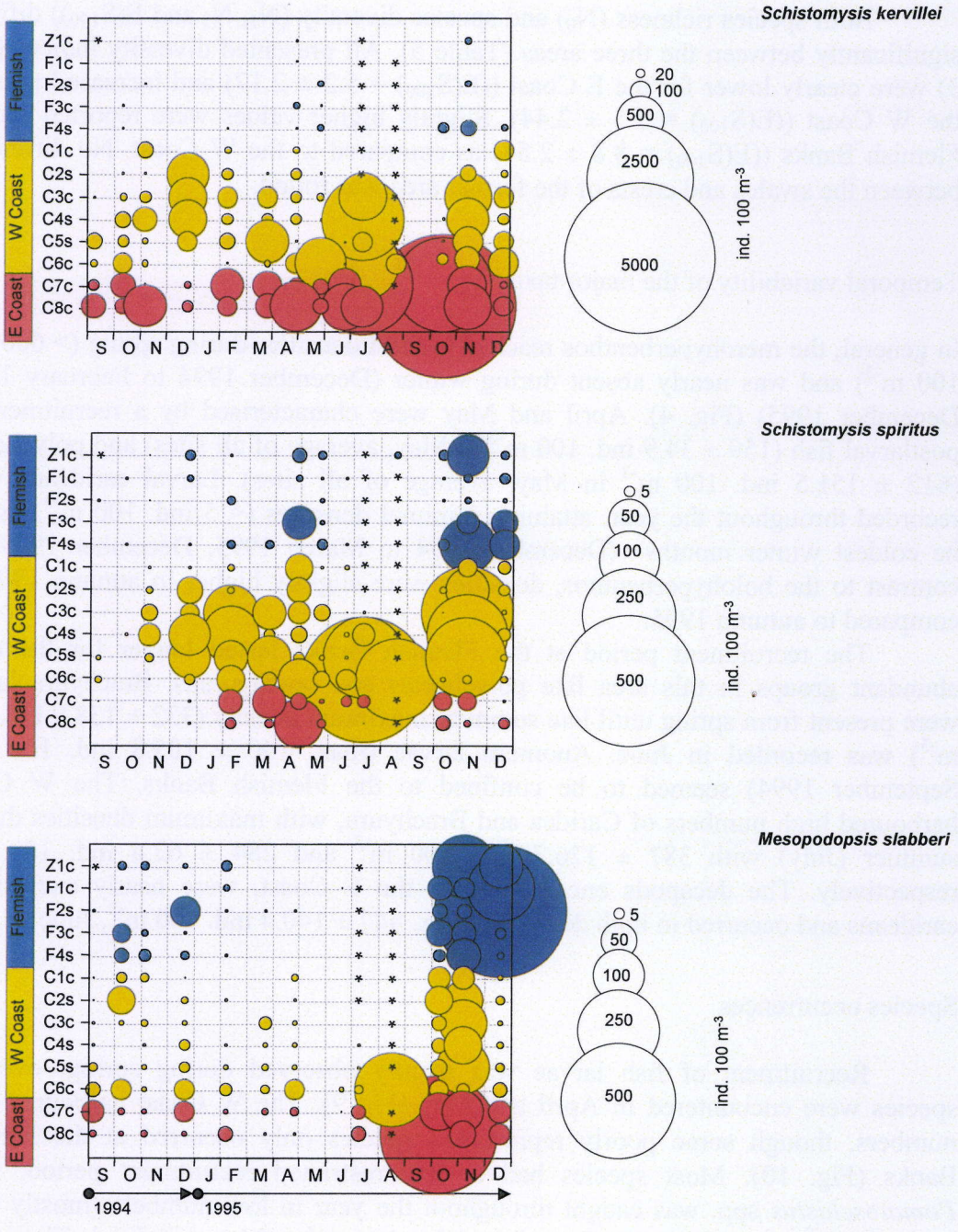

Fig. 8. Spatio-temporal variability for *Schistomysis kervillei*, *S. spiritus* and *Mesopodopsis slabberi*. The bubble charts represent densities per sample, with the months on the x-axis, scaled in Julian days, and the sites on the y-axis. Note that no sampling was carried out in January and September 1995, certain samples which were lacking for the other months are indicated as '*' (see Table 1).

Merohyperbenthos

Annual density and diversity

Highest mean densities for merohyperbenthos were recorded at station F2s (663 ± 224.9 ind. 100 m^{-3}) and lowest values at station C5s (150 ± 51.1 ind. 100 m^{-3}) (Fig. 3).

Both species richness (N_0) and species diversity (N_1, N_2 and $E(S_{100})$) differed significantly between the three areas (Table 5). All presented diversity indices (Fig. 3) were clearly lower for the E Coast (($E(S_{100})$ = 5.2 ± 2.17) and increased towards the W Coast (($E(S_{100})$ = 7.5 ± 2.44). Slightly higher values were reported for the Flemish Banks (($E(S_{100})$ = 8.8 ± 2.54) as compared to the W Coast. No difference between the swales and crests of the former area was found.

Temporal variability of the major taxa

In general, the merohyperbenthos reached highest densities during spring (> 600 ind. 100 m^{-3}) and was nearly absent during winter (December 1994 to February 1995, December 1995) (Fig. 4). April and May were characterised by a recruitment of postlarval fish (159 ± 34.9 ind. 100 m^{-3} in May, average of all sites) and polychaetes (612 ± 151.5 ind. 100 m^{-3} in May, average of all sites). Larval carideans were recorded throughout the year, attaining minimal densities (< 5 ind. 100 m^{-3}) during he coldest winter months (December 1994 to March 1995, December 1995). In contrast to the holohyperbenthos, densities were slightly higher in autumn 1994 as compared to autumn 1995.

The recruitment period at the Flemish Banks lasted longer for the most abundant groups in this area like polychaetes and brachyurans. Brachyura larvae were present from spring until late summer; maximum density (332 ± 138.9 ind. 100 m^{-3}) was recorded in June. Anomura larvae (max. 190 ± 105.8 ind. 100 m^{-3}, September 1994) seemed to be confined to the Flemish Banks. The W Coast harboured high numbers of Caridea and Brachyura, with maximum densities during summer (July) with 387 ± 126.7 ind. 100 m^{-3} and 284 ± 62.4 ind. 100 m^{-3}, respectively. The decapods encountered at the E Coast, were nearly exclusively carideans and occurred in high densities (max. 447 ± 140.4 ind. 100 m^{-3}, June).

Species occurrences

Recruitment of fish larvae was mainly observed during spring: over 15 species were encountered in April and May (Fig 9). The W Coast harboured high numbers, though some poorly represented species only occurred at the Flemish Banks (Fig. 10). Most species had a very restricted recruitment period. Only *Pomatoschistus* spp. was caught throughout the year in low numbers (mostly < 10 ind. 100 m^{-3}), but they still showed two density peaks (May and July). They were rather restricted to the Coastal Banks. A clear species succession was observed from February until July. Clupeids were the first recruits (February) mainly restricted to the Flemish Banks. They reached a second peak in April in the whole area. Flounder *Pleuronectes flesus* was the most abundant species in April and was mainly found at the W Coast; whiting *Merlangius merlangus* also appeared in April. May recruits

were sole *Solea solea*, dab *Limanda limanda* and bib *Trisopterus luscus*. Sole was the most abundant species occurring in the whole area with densities several times exceeding 100 ind. 100 m^{-3}.

Decapod larvae recruited mainly from March till November with a maximum during summer. More than 20 species were recorded (Fig. 11). In general, the recruitment period for carideans lasted a little longer than for brachyurans (Fig. 12). The recruitment period for Anomura and Thalassinidea was slightly different as compared to the other decapods: they were often recorded during winter (e.g. *Pagurus bernhardus*, March) or in late summer (e.g. *Pisidia longicornis*, September 1994, October 1995). Zoea stages were nearly exclusively caught at the Flemish Banks, while certain postlarval carideans and megalopae of brachyurans attained highest densities at the Coastal Banks. This was the case for the common species Crangonidae spp. (mainly *Crangon crangon*) and *Carcinus maenas*, but not for *Liocarcinus* spp. (mainly *Liocarcinus holsatus*). For the latter species, both zoea and megalopa stages occurred in higher densities at the Flemish Banks.

The polychaete larvae encountered were nearly exclusively aulophora stages of *Lanice conchilega*. They attained highest densities in May, at the E Coast (1221 ± 161.9 ind. 100 m^{-3}.

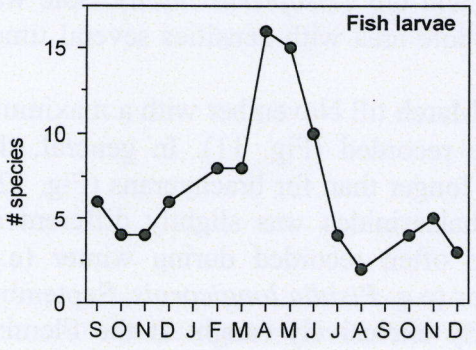

Fig. 9. Temporal fluctuation of the total species numbers of fish larvae.

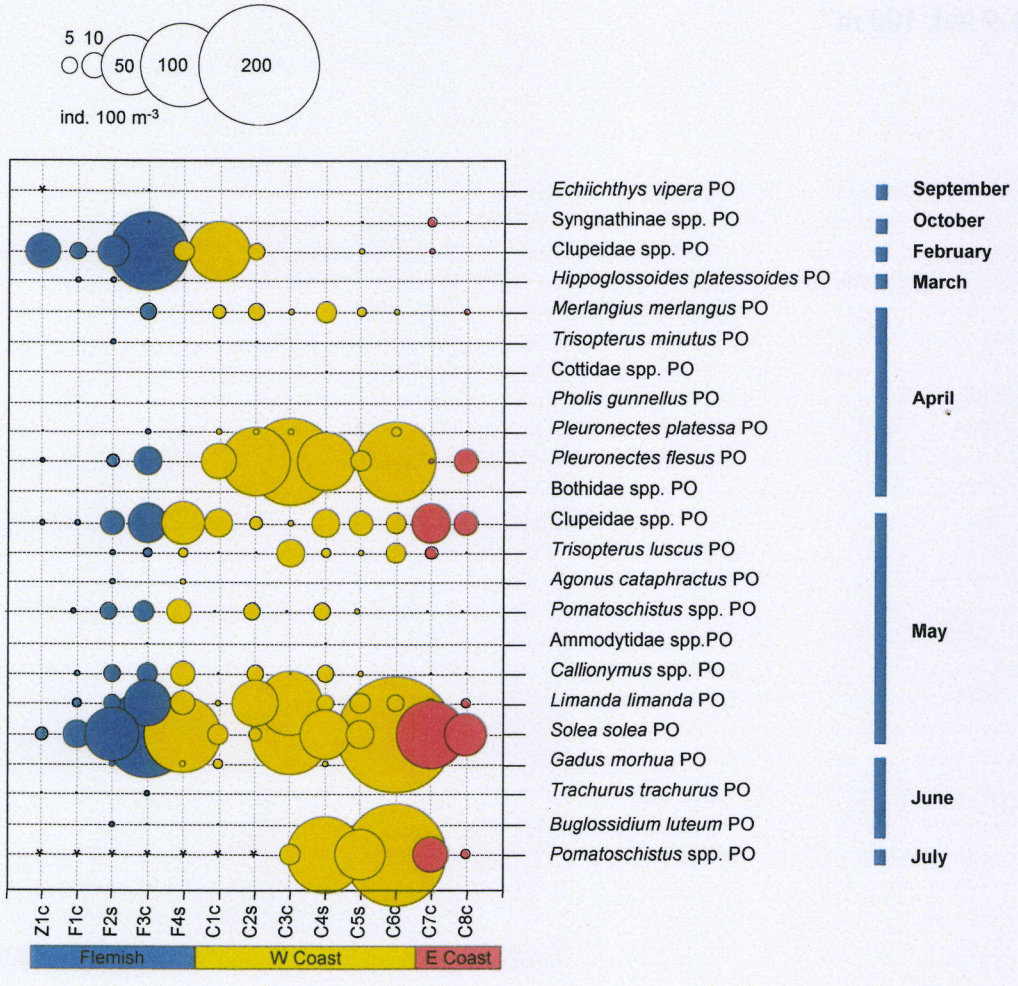

Fig. 10. Spatio-temporal variability for all fish larvae caught. The bubble chart represents densities per site for the month in which the species attained a maximum average abundance. Postlarva of clupeids and *Pomatoschistus* spp. are represented twice since they showed a bimodal annual fluctuation. Sites are shown along the x-axis and the species, grouped per month, on the y-axis.

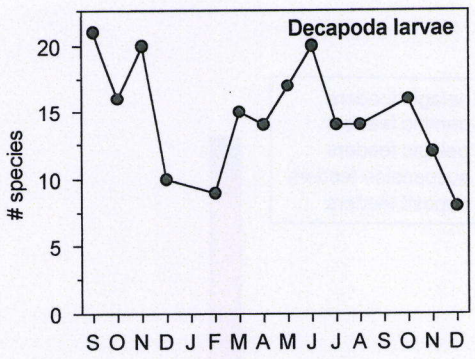

Fig. 11. Temporal fluctuation of the total species numbers of decapod larvae.

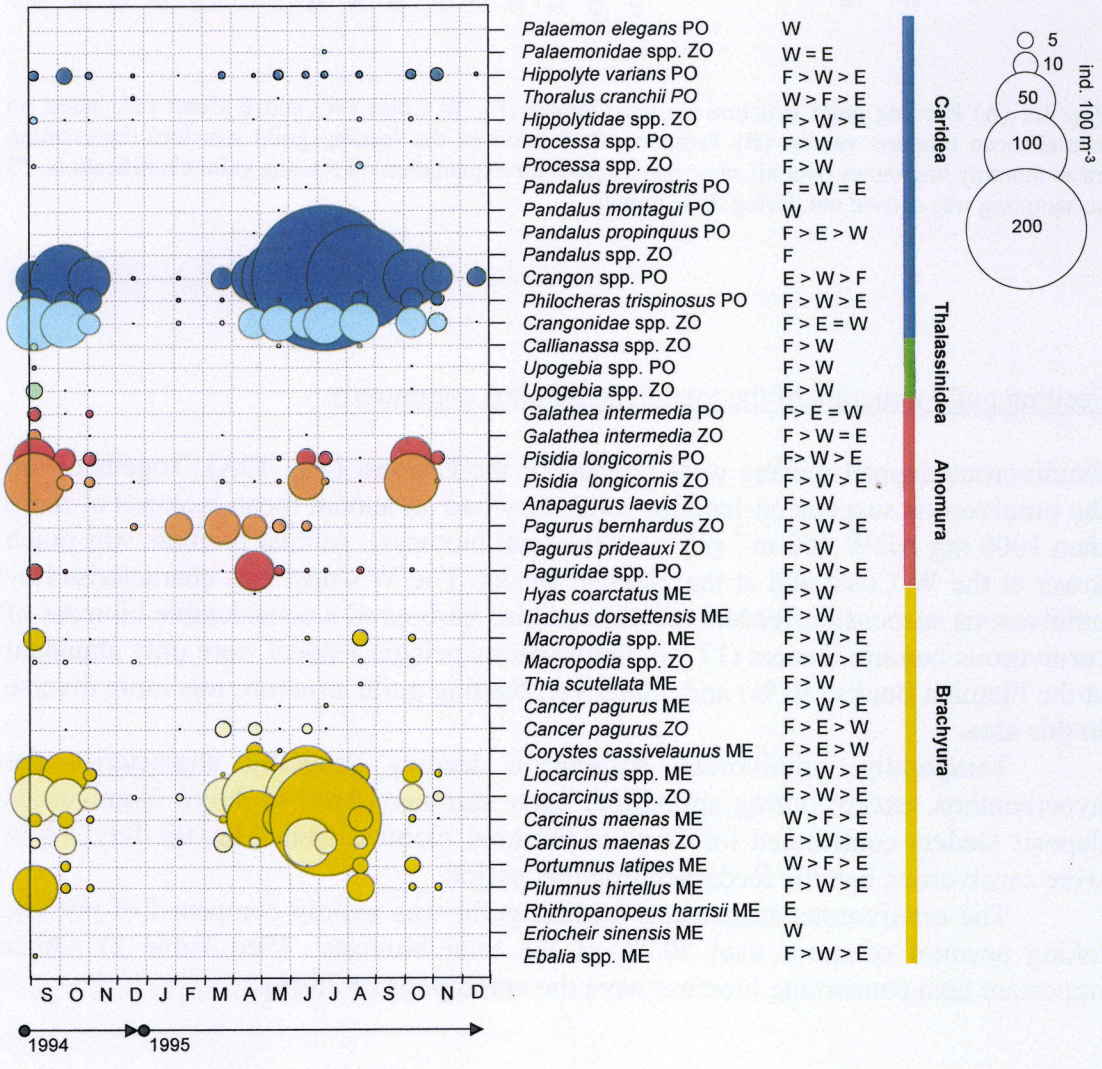

Fig. 12. Spatio-temporal variability for all decapod larvae caught. The bubble charts represent mean densities per month over all sites. Zoea (ZO) and postlarva (PO) or megalopa (ME) are separately presented. Months are shown along the x-axis, scaled in Julian days. Note that no sampling was carried out in January and September 1995. Taxa and life stages are grouped per infra-order and presented along the y-axis. Spatial occurrence is ranked for the three areas according to highest mean abundance; Flemish (F), W Coast (W), E Coast (E).

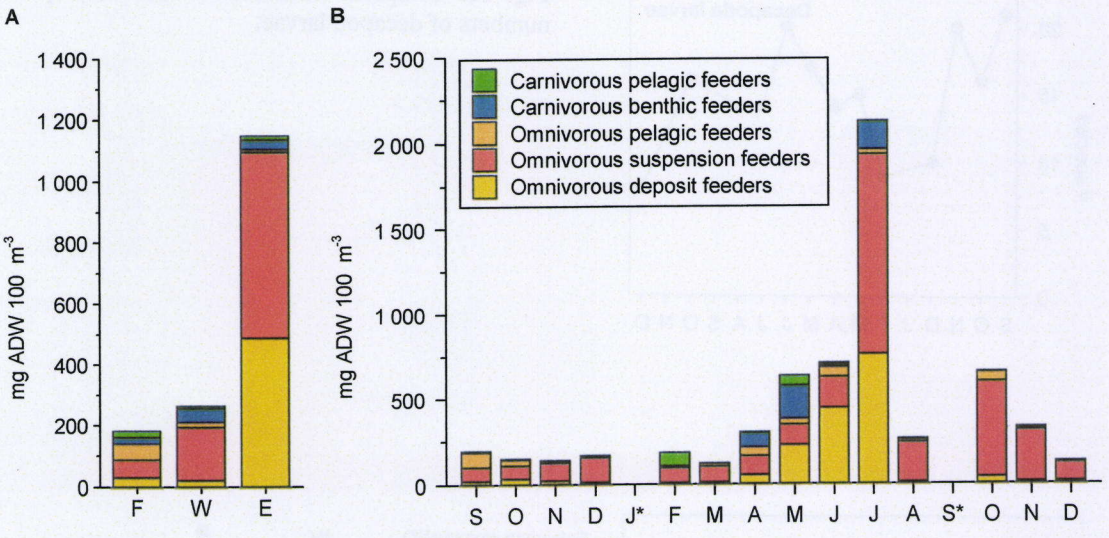

Fig. 13. (A) Feeding guild structure for the Flemish (F), W Coast (W) and E Coast (E), based on annual mean biomass values. **(B)** Temporal fluctuation of the feeding guild structure representing mean monthly biomasses over all sites. See Table 2 for explanation on feeding guild classification; (*) no sampling was carried out during these months.

Feeding guild structure of the total hyperbenthos community

Omnivorous deposit feeders were typical for the E Coast (Fig. 13A). Together with the omnivorous suspension-feeding guild, they had an annual mean biomass of more than 1000 mg ADW 100 m^{-3} (95 % of the total biomass). Annual biomass was much lower at the W Coast and at the Flemish Banks. The W Coast was characterised by omnivorous suspension feeders (65 %) and also harboured a considerable biomass of carnivorous benthic feeders (17 %). Omnivorous pelagic feeders were only abundant at the Flemish Banks (30 %) and, moreover, feeding guild structure was more diverse in this area.

Temporally, omnivorous suspension feeders generally characterise the hyperbenthos, except during spring and early summer (April to July). Omnivorous deposit feeders contributed for 44 % to the total biomass from May till July; 14 % were carnivorous benthic feeders during this period.

The omnivorous suspension feeding guild was mainly composed of mysids, taking account of more than 50 % of the total biomass (See Table 2). Other important taxa concerning biomass were the amphipods (> 25 %).

Discussion

Habitat variability

The Belgian coastal area is characterised by a high diversity of habitats. This is related to the morphodynamics of the sandbank complexes and to the outflow of a large estuary. Low salinity and high and irregular nutrient concentrations along the East Coast are due to the outflow of the Westerschelde being heavily, organically and chemically polluted (Heip 1988). The Flemish Banks are mainly under influence of offshore water masses, coming from the Channel (Hecq *et al.* 1992; Baeyens *et al.* 1998) and are characterised by a classical annual cycle with high nutrient levels in winter (Fig. 2). The whole area is characterised by a pronounced spring phytoplankton bloom dominated by *Phaeocystis*, which contributes for 70 % to the net primary production and causes a disruption of the linear phytoplankton-to-mesozooplankton food chain (Rousseau *et al.* 2000).

The variability of mud and turbidity on the Coastal Banks is attributed to the presence of a mud field extending from the mouth of the Westerschelde up to Oostende (Van Lancker & Jacobs 1996; Ruddick *et al.* 1998). Resuspension processes due to the strong tidal currents result in a region of high turbidity along the coast (Nihoul & Hecq 1984; Ruddick *et al.* 1998). Maximal suspended matter values are reached twice during a tidal cycle and decrease to very low values at slack tide leading to a settlement of most of the particulate matter (Fransaer 1994; Van Lancker 1999). This muddy fraction seems to be dynamically trapped in the Coastal Banks area as a combined result of the residual currents and orbital wave motion (Van Lancker & Jacobs 1996). An upper, loosely packed bottom layer of about 5 mm is continuously moving horizontally and vertically, while interacting with a suspension load (Bastin 1974; Van Lancker 1999). Mean concentrations (long-term data) of suspended matter at 3 m below the sea surface fluctuate between 0.02 and 0.20 g l^{-1} at the Coastal Banks and are highest eastwards from Nieuwpoort up to the Westerschelde mouth (Nihoul & Hecq 1984; Eurosense 1994; Ruddick *et al.* 1998). At 20 km off the shore (e.g. along the Flemish Banks) suspended matter concentrations reduce and range between 0.02 and 0.04 g l^{-1} (Nihoul & Hecq 1984; Eurosense 1994; Ruddick *et al.* 1998). These events largely explain the observed differences in mud fraction and turbidity between the Flemish and Coastal Banks, though extremely high values were recorded at the E Coast. During sampling, turbidity profiles indicate the presence of drifting clouds of suspended matter, which were often visible at the water surface. In this view, it is worthwhile remarking that the two E Coast stations (C7c and C8c) are located close to dumping sites for - usually heavily polluted - dredged material (Maes *et al.* 2000). Intensive dredging activities and dumping continue throughout the year to maintain the accessibility of the ports of Antwerpen and Zeebrugge (Maes *et al.* 2000).

Habitat preferences and seasonal variability in habitat utilisation

The holohyperbenthos of the area is dominated by mysids throughout the year, except during spring and in offshore waters. The number of mysid species fluctuated in time and ranged from 6 (May-August, December 1995) to 13 in February 1995. Nearly half of the 16 mysid species have never been recorded before for the study area (discussed in Chapter 4). Four species (*Schistomysis kervillei*, *S. spiritus*, *Gastrosaccus spinifer* and *Mesopodopsis slabberi*) occurred in more than 60 % of the samples, their average density exceeding 20 ind. 100 m^{-3}. They typically inhabit shallow coastal waters (discussed in Chapter 4).

A positive correlation between numbers of mysid species with the residual current was found. Highest numbers mainly occurred after a long period of a NE directed flow (Chapter 6). It is not surprising thus that several of these 'temporal visitors' also occur in the eastern English Channel (Zouhiri *et al.* 1998; Dauvin *et al.* 2000). *Praunus flexuosus* is a characteristic species for the adjacent sandy beaches (Beyst *et al.* in press a) and *Neomysis integer* for the brackish reaches of the Westerschelde estuary (Mees *et al.* 1993b; Mees 1994).

Spatio-temporal density patterns of *Schistomysis kervillei*, *S. spiritus* and *Mesopodopsis slabberi* are highly variable (Fig. 8) and hard to explain. Small-scale variability may be related to current strength (Mauchline 1980), as experimentally evidenced for the brackish water endemic *Neomysis integer* (Roast *et al.* 1998; Lawrie *et al.* 1999). *Schistomysis kervillei* and *S. spiritus* showed tide-dependent density fluctuations both at the E Coast and at the W Coast, examined by 24 hour sampling (A. Dewicke unpubl. data). Immigration from the nearby intertidal has also been reported as an escape behaviour from harsh conditions on the shore, such as strong wave action (Colman & Segrove 1955; Munilla *et al.* 1998; San Vicente & Sorbe 1999; Beyst & Mees submitted). According to Mauchline (1971a), density fluctuations on a large scale are due to seasonal migrations and recruitment peaks. For this study, the autumn interannual variability for the total holohyperbenthos community was found to be related to the residual current as assessed by multivariate techniques (Chapter 6). It is suggested that the observed patterns are due to a combination of species-specific ecological preferences, migration behaviour and an interaction with the current regime.

In order to reduce bias caused by small-scale variability, information gathered from nearby biotopes was included to discuss their habitat preference. Data are presented for the shallow subtidal (5-10 m depth) of the Voordelta (Mees *et al.* 1993a), the surf zone of adjacent beaches (Beyst *et al.* in press a) and the poly- and mesohaline zones of the Westerschelde estuary and its salt marshes (Mees *et al.* 1993a; Mees 1994; Cattrijsse *et al.* 1994) (Table 7).

Habitat preferences: Schistomysis kervillei and S. spiritus

The co-occurrence of *Schistomysis kervillei* and *S. spiritus* has also been reported from other regions (Mauchline 1971b; Sorbe 1989; Wang & Dauvin 1994; San Vicente & Sorbe 1995, see Chapter 4). Compared to the adjacent biotopes, highest densities were reached in the shallow subtidal of the Belgian coast (this study) and the adjacent surf zone, although *S. spiritus* was more abundant in the latter biotope. *S. spiritus* is morphologically better adapted for swimming (Mauchline 1980; San Vicente & Sorbe 1995) and less confined to the bottom as compared to *S. kervillei*

(San Vicente & Sorbe 1995). These latter authors suggested that such vertical segregation behaviour could exclude direct competition between both species. *S. spiritus* has also been reported to be less opportunistic than *S. kervillei*, judging from its lower fecundity, abundance variability and P/B ratio (San Vicente & Sorbe 1995). This was not concluded from the presented data, but some remarks can be made related to their habitat preference:

(1) *S. spiritus* might be less tolerant to an unstable or polluted environment. It was much more abundant on the W Coast than on the estuarine influenced E Coast, while *S. kervillei* showed a reverse pattern (Fig. 8, Table 6) and even seemed to favour very turbid conditions (Fig. 7). Still, the latter species was dominant in both areas. A similar east-west distribution for these congeneric species was found in September 1993 (Chapter 4) and October 1996 (A. Dewicke unpubl. data). The Westerschelde estuary harboured low numbers of *S. spiritus* as well, though this species is often quite abundant in other European estuaries (Collins & Williams 1982; Mees *et al.* 1995; Azeiteiro *et al.* 1999).

(2) *S. spiritus* might have a preference for sheltered and / or sandy habitats (Mauchline 1971a), such as the subtidal of the W Coast where current velocities are lower than at the E Coast (Chapter 6). In addition, it was more dominant than *S. kervillei* on the sandy beaches of the W Coast, in the sheltered Voordelta inlet, and it temporally occurred in the polyhaline tidal marsh of Waarde.

(3) *S. spiritus* seemed to occur further offshore during certain times of the year, (in May and autumn 1995, Fig. 6), while *S. kervillei* remained continuously closer to the shore and might therefore be more tolerant for environmental changes.

Seasonality in habitat utilisation: Mesopodopsis slabberi

Mesopodopsis slabberi was never very abundant in the subtidal of the Belgian coast, except during autumn 1995. This strongly euryhaline species is extremely abundant in the mesohaline zone of the Westerschelde estuary, in the tidal marshes of Saefthinghe and - to a lesser extent - in the surf zone of sandy beaches (Table 7). Its high abundance in estuaries, coastal lagoons and on sandy beaches is well documented in literature (discussed in Chapter 4). Several authors reported on a winter disappearance from brackish environments (Delgado *et al.* 1997; Azeiteiro *et al.* 1999; Mouny *et al.* 2000), which was also described for the Westerschelde and its marshes (Mees *et al.* 1993b) and for the surf zone (Beyst *et al.* in press a). The winter maxima in the deep subtidal (Fig. 6) may therefore be the result of migration behaviour towards deeper areas. The reason for performing such migrations has been suggested escaping low temperatures (Mauchline 1980; Beyst *et al.* in press a). From this point of view, the strong interannual difference in density between autumn 1994 and 1995 (Fig. 6) is probably related to the sudden drop in temperature during autumn and the cold winter of 1995 (Fig 2). Even higher densities (642 ind. 100 m^{-3}) as compared to this study were recorded further offshore (40 km off the coastline, 25 m depth) during autumn 1997 (A. Cattrijsse unpubl. data). Such migration behaviour might also hold true for *Schistomysis kervillei* and *S. spiritus*. It was much more complex to explain the occurrence of these species since no clear patterns could be detected.

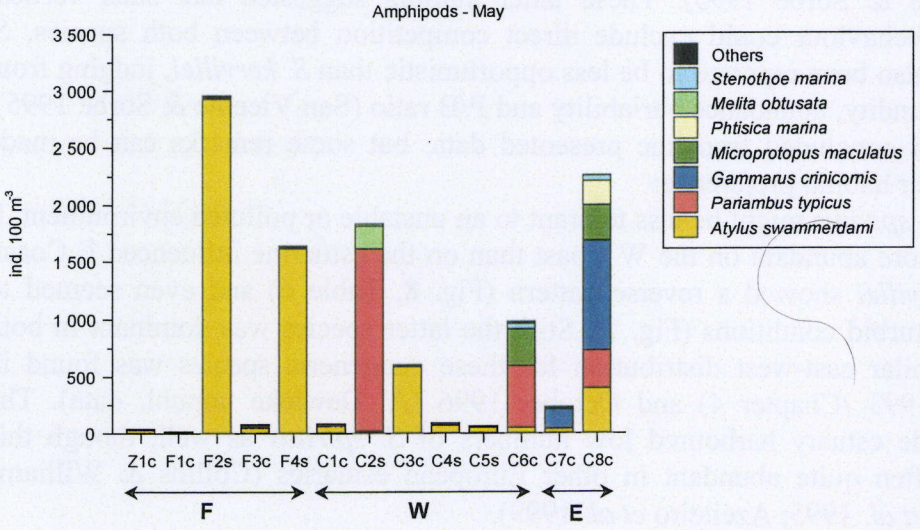

Fig. 14. Total density and species composition of the amphipod fauna encountered in May, presented per site; Flemish (F), W Coast (W), E Coast (E).

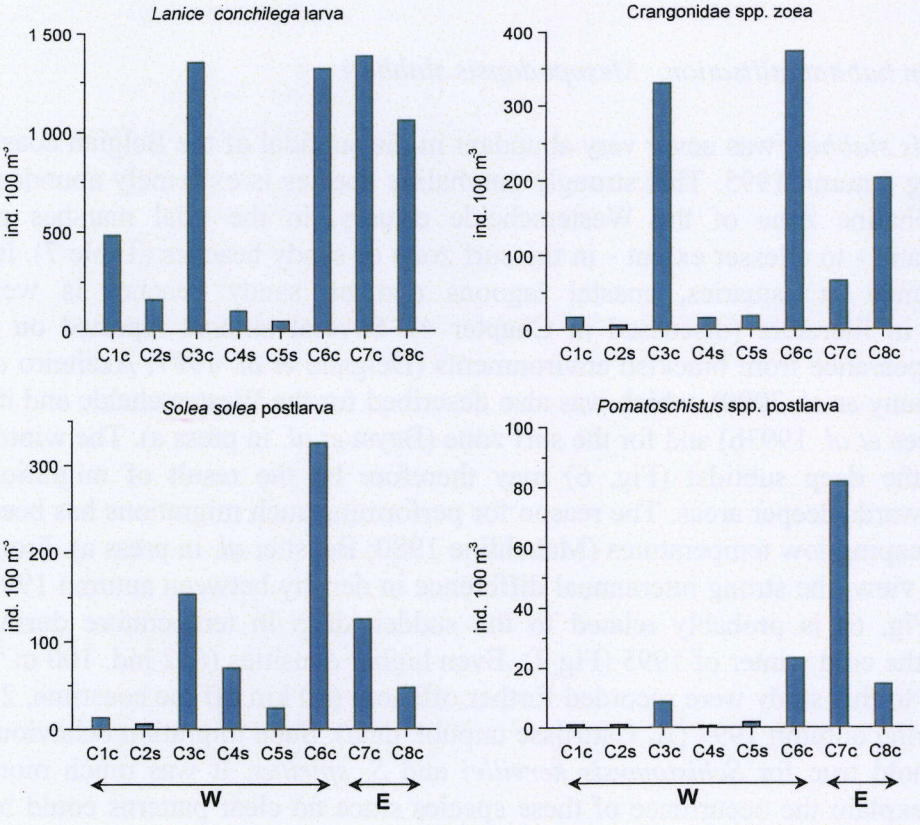

Fig. 15. May densities at the Coastal Banks (shown per site) for the aulophora larvae of *Lanice conchilega, Crangon crangon* postlarva, *Solea solea* postlarva and *Pomatoschistus* spp. postlarva; W Coast (W), E Coast (E).

Microhabitats favouring hyperbenthic biodiversity

The amphipod peak observed in spring is from dual origin. Firstly, amphipod densities in May suddenly increased with a factor of >10 at the swales in-between the Flemish Banks (Fig 4) (see below). Secondly, a variety of epifaunal representatives were recorded at the Coastal Banks, such as the caprellids *Pariambus typicus* and *Phtisica marina* and the small gammaridean *Microprotopus maculatus* and *Stenothoe marina* (illustrated in Fig. 14 for May). They are all feeding upon fowling species such as colonial hydrozoans observed at particular sites (mainly at C3c, C6c, C7c and C8c), providing microhabitats for a variety of species. *Gammarus crinicornis* also belonged to this assemblage associated with hydrozoans, but it only occurred at the E Coast. This species is often reported from the mouth region and the polyhaline zone of estuaries in association with detritus (Sorbe 1978; Cattrijsse *et al.* 1993; Mees *et al.* 1995). Rather than using the hydrozoans as a substrate, it thus probably takes advantage of the associated organic matter.

The hydrozoan colonies grew from May until July and were also observed during previous and following years (A. Dewicke pers. observ., S. Degraer pers. comm.). The substrate on which they develop is most probably produced by the tube-building polychaete *Lanice conchilega*, forming reef-like structures (Berné *et al.* 1988; Degraer *et al.* in press) suitable for settlement (S. Degraer, pers. comm.). Such reef structures are a few meters wide and seem to be predominantly located at the lee side of the Coastal Banks, at a depth of 4 m (S. Degraer pers. comm.). They may act as local islands of enhanced density and presumably also biodiversity. This is due to their functional variety for several organisms, e.g. as a substrate for smaller epifauna, as a shelter for fish larvae or as a feeding area for larger predators. As an illustration, the distribution pattern of *Lanice conchilega* aulophora larvae (pre-settlement stages) in May coincided with the sites where hydrozoans and associated fauna were encountered and also with the presence of some dominant merohyperbenthic species, e.g. *Solea solea*, *Pomatoschistus* spp. and *Crangon crangon* postlarvae (Fig. 15). Furthermore, *Pariambus typicus*, *Microprotopus maculatus* and the radioli of *Lanice conchilega* are an important prey during summer in the diet of *Pomatoschistus minutus* and *P. lozanoi,* occurring at the Coastal Banks (Hamerlynck *et al.* 1990; Hamerlynck & Cattrijsse 1994).

Key role of the Flemish Banks for dispersal mechanisms

The Belgian subtidal waters harbour a great variety of early life history stages of macrocrustaceans, whose densities are often higher than in the adjacent biotopes (Table 7). The earliest life stages of decapods, i.e. zoea larvae, were much more abundant on the Flemish Banks (Fig. 12). The further offshore Hinder Banks harboured fewer larvae (Chapter 4). Tidal flow is strongly flood-dominated (higher current velocities towards the N than to the S) at the Coastal Banks. Flood-dominance decreases with distance off the shore and becomes ebb-dominated off the Flemish Banks (higher current velocities towards the S than to the N) (see Chapter 6). The ebb dominated tidal flow off the Flemish Banks area probably prevents that larvae, hatched in coastal waters, are swept further offshore. In addition, larval supply from further offshore (e.g. from the Hinder Banks) might be supported by this ebb-dominated current (discussed in Chapter 6). Later larval stages (megalopae or postlarvae) of certain species reached highest densities on the Coastal Banks. These stages generally have a better retention behaviour and may gradually reach their juvenile / adult habitat by selective tidal stream transport (Shanks 1995).

Selective tidal stream transport is well described for the larvae of *Carcinus maenas* (Zeng & Naylor 1996; Queiroga 1998), an abundant species in the adjacent intertidal and estuarine biotopes of the study area (Hostens 2000; Beyst *et al.* in press b). The annual mean abundances for its zoea life stage were highest on the Flemish Banks (Fig. 12), though a maximum was recorded at the Coastal Banks in June (Table 7). The megalopa stage is very common on the W Coast, the adjacent beaches and in the estuarine tidal marshes (Table 7). This was not the case for *Liocarcinus* spp. (mainly *Liocarcinus holsatus*) of which both larval stages largely remained in subtidal waters (Fig.12, Table 6). Adult *Liocarcinus holsatus* is common both in the subtidal and intertidal waters of the Belgian coastal area (Beyst *et al.* in press b, A. Cattrijsse unpubl. data).

Annual mean densities for *Crangon crangon* zoeae were highest at the Flemish Banks, though they reached a maximum monthly density at the E Coast (Fig.12, Table 7). It is the only decapod species whose zoea stage occurs in high numbers in the E Coast area. They may be the offspring of adults thriving in the Westerschelde. Zoea stages are only occasionally encountered in the estuary itself (Table 7). It has been shown that early postlarval stages enter the estuary and use the nearby tidal marshes as a nursery (Cattrijsse *et al.* 1997). On the other hand, adult *Crangon crangon* are also very abundant in the surf zone of Belgian sandy beaches (Beyst *et al.* in press b). It is not clear if this is the same population as the one in the Westerschelde estuary. Judging from the high densities of zoeae at the Flemish Banks and the occurrence of postlarvae on the Coastal Banks and in the surf zone, it cannot be excluded that *Crangon crangon* completes its entire larval development in this biotope.

Nursery potential for fish larvae

Seasonal occurrence

Recruitment of fish larvae was mainly restricted to April and May, except for clupeids (two distinct peaks in February and May) and *Pomatoschistus* species (peaks in May and July). The temporal species succession is in agreement with the current knowledge of North Sea populations (Russell 1976; Beyst *et al.* 1999b; Grioche *et al.* 1999; Beyst *et al.* in press a). The first recruitment period for clupeids already started in December and is most probably derived from autumn spawning herring *Clupea harengus* (Daan *et al.* 1990; Knijn *et al.* 1993). These larvae were still very small and remained offshore, probably on their drift towards more northern nursery areas. Also, clupeid larvae have not been reported from the nearby shallow waters at that time of the year (Table 7). It is most likely that the May recruits are sprat *Sprattus sprattus*, since they are the only clupeids reported from the plankton of the area, sampled two weeks earlier (Grioche *et al.* 1999). Judging from the residual circulation, the most probable spawning sites both for herring and sprat, are located in the English Channel, near Gravelines and more to the south in Picarde Bay (Daan *et al.* 1990; Knijn *et al.* 1993; Woehrling & Le Fèvre-Lehoërff 1998; Grioche *et al.* 1999).

The *Pomatoschistus* larvae were most probably a mixture of the sand goby *Pomatoschistus minutus* and Lozano's goby *Pomatoschistus lozanoi*, which are both common in the shallow waters at the Belgian coast (Hamerlynck *et al.* 1986). Larvae occurred throughout the year in small numbers, yet the two peaks correspond to the spawning periods of the respective species. *Pomatoschistus minutus* spawns from March to June (peak in May, mainly at the E Coast) and *P. lozanoi* from June to August (peak in July, mainly at the W Coast) (Hamerlynck *et al.* 1986).

The most abundant species in spring were the flatfish sole *Solea solea* (peak in May) and flounder *Pleuronectes flesus* (peak in April). The density of sole was very high and often exceeded 100 ind. 100 m^{-3}. It was the most dominant fish larva in the study area on an annual basis (Table 7). Spawning of sole takes place in April-May, in coastal areas within the 30 m depth contour (Knijn *et al.* 1993). The Belgian coast is known as a major spawning site for sole (Knijn *et al.* 1993; Woehrling 1985). It is likely that sole larvae remain in coastal waters throughout their entire development (Knijn *et al.* 1993; Grioche *et al.* 1999). This has been attributed to selective tidal current transport since even the youngest stages are able to perform tidal and vertical migrations (Grioche *et al.* 2000). In contrast with such retention behaviour for sole, flounder has two different phases during its ontogenical migration. They drift with the residual current until reaching the stage of notochord flexion (Grioche *et al.* 2000). From then on, they occur in the hyperbenthal zone and start to perform vertical migrations, leading to an efficient and fast transport towards coastal nursery grounds (Grioche *et al.* 2000). The spawning grounds (at 25-40 m depth, Knijn *et al.* 1993) are thus presumably the ones located in the eastern part of the English Channel (Grioche *et al.* 1999). Knijn *et al.* (1993) however mention the Belgian and Dutch coasts as important spawning areas for flounder as well.

			Subtidal				Surf zone		Estuary		Saltmarsh	
			Deep	Shallow					Poly	Meso	Meso	
			F	W	E	VD	SU-W	SU-E	WS-P	WS-M	WA	SA
Mysidacea												
Schistomysis spiritus		mean	2	43	8	20	597	4	0		12	0
		max	32	194	41	82	4308	24	1		153	0
Schistomysis kervillei		mean	3	139	293	2	204	16	4		0	0
		max	26	798	3102	12	1445	90	27		1	0
Mesopodopsis slabberi		mean	2	21	5	4	422	525	12	1184	72	3133
		max	180	205	281	22	1856	1710	34	6106	632	23498
Decapoda larvae												
Crangonidae spp.	PO	mean	30	354	439	4	120	64	30	612	2074	2763
		month	Oct	Jul	Jun	May	Jul	Jun	May	Apr	Apr	Jun
Crangonidae spp.	ZO	mean	57	40	62	19	20	1	6	0	0	
		month	Sep	Sep	May	May	May	May	May	Sep	Apr	
Pisidia longicornis	PO	mean	62	19	6	3	3		0			
		month	Okt	Sep	Nov	Aug	Aug		Jun			
Pisidia longicornis	ZO	mean	116	30	3	1	1		3			
		month	Sep	Sep	Sep	May	Aug		June			
Liocarcinus spp.	ME	mean	97	19	17	57	1		3			0
		month	Jun	Apr	Jun	Jun	Jun		May			Aug
Liocarcinus spp.	ZO	mean	97	123	25	60	1		38			0
		month	Apr	Jun	Jun	Jun	May		Apr			Aug
Carcinus maenas	ME	mean	106	243	48	138	358	253	30		186	535
		month	Jun	Jul	Jun	Jun	Jun	Jun	Jun		Jun	Jun
Carcinus maenas	ZO	mean	32	46	11	33		15	32	0	0	1
		month	Jun	Jun	Jun	Jun		Jun	May	Jul	May	Sep
Fish larvae												
Clupeidae spp.	PO	mean	50	18	2	10						
		month	Feb	Feb	Dec	Mar						
		mean	22	14	29	26	135	8	13	11	7	67
		month	May	May	May	Jun	May	May	Apr	May	June	June
Merlangius merlangus	PO	mean	2	6	1	0						
		month	Apr	Apr	Apr	Apr						
Trisopterus luscus	PO	mean	4	8	4	0	0					
		month	Apr	May	May	Jun	Feb					
Callionymus spp.	PO	mean	9	4	1	2			1			
		month	May	May	May	Jun			May			
Pomatoschistus spp.	PO	mean	2	6	48	4	205	44	5	5	28	9
		month	May	May	May	Jun	Jul	Aug	Jul	May	Oct	Jun
		mean	5	123	18	5			4	28		
		month	Nov	Jul	Jul	Aug			Aug	Aug		
Limanda limanda	PO	mean	17	33	4	0						
		month	May	May	May	Jun						
Pleuronectes flesus	PO	mean	6	99	9		16	25	2	44	21	444
		month	Apr	Apr	Apr		May	May	Apr	Apr	May	April
Solea solea	PO	mean	87	99	87	7	5	0	1			
		month	May	May	May	Jun	May	May	May			

Table 7. Comparison of the temporal occurrence of the most common mysids, decapods and fish larvae observed during this study (Flemish (F), W coast (W) and E Coast (E)) with the adjacent shallow subtidal area (5-10 m depth) of the Voordelta (VD) (Hamerlynck & Mees 1991; Mees *et al.* 1993a; Beyst *et al.* 1999b), the adjacent surf zone from the E Coast (SU-E) and the W Coast (SU-W) (Beyst *et al.* in press a), the poly- (WS-P) and mesohaline (WS-M) zone of the Westerschelde estuary (Mees *et al.* 1993b; Mees 1994) and the Waarde (WA) and Saefthinghe (SA) saltmarsh (Mees *et al.* 1993a; Cattrijsse *et al.* 1994). Annual mean densities (Mean) and maximum density (Max) reported at a certain site are tabulated for mysids. Densities for decapods and fish larvae are mean values for the month in which the species attained a maximum average abundance; Zoea stages (ZO) and postlarva (PO) or megalopa (ME) of decapods are separately presented. Densities from this study are expressed as ind. 100 m^{-3} and for the other studies as ind. 100 m^{-2}. All studies deal with temporal data obtained by regular sampling, at least during 10 subsequent months within a whole year. For the geographical location of these areas, see Fig. 16.

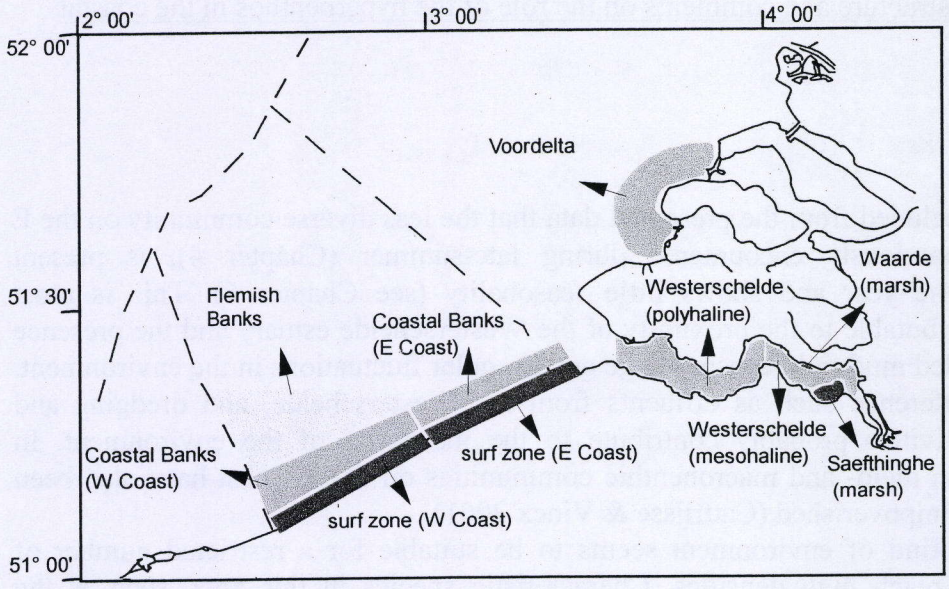

Fig. 16. The study area and the location of the adjacent biotopes discussed . (See Table 7).

Adjacent biotopes

The densities of the dominant species encountered during this study were compared with those reported from the adjacent biotopes (Fig. 16, Table 7).

Three species were found to occur in higher numbers in the adjacent biotopes: clupeids (Belgian beaches and Saefthinghe marsh), larval gobies (Belgian beaches) and *Pleuronectes flesus* (Saefthinghe marsh). In contrast, sole postlarvae are rare in the former biotopes. Also dab *Limanda limanda*, the Callionymidae and the Gadidae *Merlangius merlangus* and *Trisopterus luscus* seemed to be confined to the subtidal. These species are also common in the plankton from subtidal waters of the eastern English Channel (Grioche *et al.* 1999).

As discussed for macrocrustaceans, the Flemish Banks may also play a crucial role in the dispersion phase for fish larvae due to its particular current regime (Chapter 6). High numbers of fish eggs (around 2000 per 100 m^{-3} on average) were caught in April at the Flemish Banks. Most species encountered in the entire study area do occur as juveniles in the nearby nurseries, as there are the surf zone (Beyst *et al.* in press b) or the Westerschelde (Hostens 2000). A nursery should meet three conditions, i.e. provide larval supply and transport, food, and refuge (Boesch & Turner 1984). This automatically reveals the issue of the potential of the studied Coastal Banks as a nursery area. As illustrated by the high numbers and variety of fish larvae in this study and the hydrodynamic characteristics of the area (discussed in Chapter 6) it is concluded that the first condition is met. The other conditions still have to be assessed. The authors however strongly presume that the area is a particularly valuable feeding ground for sole. The stomachs of the sole larvae were filled with copepods (A. Dewicke pers. observ.) and juvenile sole is abundant in the shallow subtidal (B. Beyst pers. comm.) and surf zone (Table 6).

Community structure and comments on the role of the hyperbenthos in the coastal ecosystem

Spatial patterns

It can be concluded from the presented data that the less diverse community on the E Coast, as previously encountered during late-summer (Chapter 4), is present throughout the year and shows little seasonality (see Chapter 6). This is most probably attributable to the proximity of the Westerschelde estuary and the presence of the extended mud field causing large and irregular fluctuations in the environment. Human interference such as effluents from the Westerschelde, and dredging and dumping activities probably contribute to the instability of the environment. In addition, both meio- and macrobenthic communities on the E Coast have also been shown to be impoverished (Cattrijsse & Vincx 2001).

This kind of environment seems to be suitable for a restricted number of species that reach high densities. Characteristic species in this area, such as the amphipod *Gammarus crinicornis*, the isopod *Idotea linearis* and the mysid *Schistomysis kervillei*, are often reported from habitats characterised by extensive salinity ranges and do also occur in the polyhaline zone of estuaries and surf environs (Sorbe 1978; Cattrijsse *et al.* 1993; Mees *et al.* 1993a, 1993b; Beyst *et al.* in press a). The high biomass and dominance of the omnivorous deposit and suspension feeders (Fig. 13) may be attributed to feeding benefits resulting from the periodical resuspension processes releasing organic matter from the muddy bottom layer. Attraction of mysids to areas of increased food availability and increased densities on muddy substrata have been reported by several authors (e.g. Clutter 1967; Fosså 1985; Hargreaves 1985). Species occurring in the coastal area however must be able to resist from being swept offshore, since the dominant tidal flow strongly heads northwards in this area (Chapter 6). This is less problematic for taxa such as mysids and amphipods (i.e. the dominant taxa in the area) that live very closely to the bottom as compared to strictly planktonic species (Chapter 6).

Both the Flemish Banks and W Coast are quite diverse, though community and feeding guild structure differ. Similar as for the E Coast, omnivorous suspension feeders are dominant at the W Coast but attain much lower densities. This might be linked to the geographical position of the mud field that is more extensive along the E Coast (Van Lancker & Jacobs 1996; Fig. 2). The amount of organic matter that gets resuspended at the W Coast might therefore be less.

The W Coast is characterised by lowest current velocities (Chapter 6) and local current conditions may provide sheltered habitats close to the bottom, suitable for the settlement of a variety of organisms. The most illustrative example is the reef structures formed by polychaete settlement and presumably associated hydrozoan growth at the W Coast. Such microhabitats can be colonised by a variety of hyperbenthic crustaceans and provide protection for postlarval fish.

The tidal currents on the Flemish Banks are slightly ebb-dominated (directed towards the S), enhancing the potential for animals dispersed in offshore waters to reach the coastal area. Species largely subjected to tidal streams may therefore be trapped in the area since the current gets flood-dominated (directed towards the N) towards the shore (Chapter 6). The current strength prevents also sedimentation of suspended matter (which is generally lower at the Flemish Banks, Fig. 2), particular for the

sandbanks crests. The coincidence of these mechanisms might explain the notable presence of pelagic feeders. Fauna drifting with the offshore water mass coming from the Channel, might contribute to both the species and trophic diversity on the Flemish Banks as well.

The coastal food web in spring

The success of the deposit feeders and, to a lesser extent, the carnivorous feeding guild in spring indicates a notable change in food web structure. *Atylus swammerdami* was strongly dominant at the Flemish Banks and occurred in very high numbers in the swales (Fig. 14). At the same time, cumaceans reached maximal abundance in this area (Fig. 4). This conspicuous peak predominantly consisting of detritus feeders coincided with the end of the *Phaeocystis* bloom (late May) that is a typical spring event in the coastal waters of the Southern Bight of the North Sea (Lancelot 1995). Sticky *Phaeocystis*-derived aggregates ('fluff-layer') (see Lancelot 1995) were observed above the sea floor while sampling, particularly in the swales in-between the Flemish Banks (A. Dewicke pers. observ.). This fluff-layer caused partly clogging of the nets resulting in a lower amount of water filtered in May (95 ± 5.6 m^3) than for the other months (121 ± 8 m^3). Densities expressed per 100 m^2 (using the distance trawled) were still much higher (approximately 40 times) for amphipods and cumaceans compared to April and June. The observed differences are thus certainly not due to sampling bias. We therefore rather believe that the reported densities for May are strongly underestimated due to low sampling efficiency and escape behaviour of fast swimming animals.

Rousseau *et al.* (2000) suggested that the 1998 spring *Phaeocystis* (*P. globosa*) bloom in Belgian coastal waters was mainly remineralised in the water column. They suggested however that this possible remineralization is not always the dominant fate, as accumulation onto the bottom at the final phase of the bloom is reported by other authors and might differ between years (e.g. Peperzak *et al.* 1998; Riebesell 1993) (Rousseau *et al.* 2000). Further, Rousseau *et al.* (2000) emphasized that their model did not include the benthic communities, which should therefore definitely be investigated. The *Phaeocystis* bloom may vary in ecological role in relation to the different bloom phases and the varying proportions of the single cells and colonies (Weisse *et al.* 1994). If accumulating on the sea floor, the senescent phase and its derived aggregates colonized by various auto- and heterotrophic micro-organisms (Lancelot 1995), may indeed affect the fauna living in the hyperbenthal layer.

As reviewed by Weisse *et al.* (1994), evidence of the trophic significance of *Phaeocystis* blooms is often contradictory in literature: both positive as well as harmful effects have been reported. For the Belgian coastal zone, it has been shown that *Phaeocystis globosa* is not an adequate food source for the spring copepods *Acartia clausii*, *Centropages hamatus* and *Temora longicornis* (Gasparini *et al.* 2000). In the German Bight however, laboratory and field experimental work has indicated *Centropages hamatus*, *Temora longicornis* and *Calanus helgolandicus* (the most abundant copepod species encountered in May during this study) to preferentially ingest the colony form of *Phaeocystis globosa*. This author reported highest feeding rates for *Calanus helgolandicus* and *Temora longicornis*, but also emphasized opposite results (negligible feeding rates) for *T. longicornis* obtained by field experiments carried out in the Dutch Wadden Sea (Hansen 1995). According to Estep *et al.* (1990), copepods avoid healthy colonies of *Phaeocystis* while preferring

senescent colonies of the late bloom stage to graze upon. Larvae of the decapod species *Liocarcinus holsatus* and *Galathea intermedia*, encountered during this study, have further been reported to feed on *Phaeocystis globosa* (Hansen 1995). A variety of other taxa potentially occurring in the hyperbenthal zone do consume *Phaeocystis*, such as euphausiids and fish (e.g. flounder, cod) (Pedersen 1989; Weisse *et al.* 1994; Hamm *et al.* 2001). Almost no information exists on the feeding potential of amphipods and cumaceans on *Phaeocystis*. Only an Antartic amphipod species has been reported to consume these algae (Weisse *et al.* 1994). The coincidence of high amphipod and cumacean densities on the Flemish Banks and the late stage of the *Phaeocystis* bloom, nevertheless suggests a direct or indirect relation.

Hamm *et al.* (1999) recently found that the *Phaeocystis globosa* colony is enclosed by a thin but very tough skin and concluded that it effectively protects the colony cells from a wide range of planktonic grazers. Only large zooplankton therefore may have the potential to feed on *Phaeocystis* colonies if they possess the means to rupture this skin (Hamm *et al.* 1999). Euphausiids (*Thysanoëssa raschi*) have been found to graze efficiently on *Phaeocystis* colonies in a northern Norway fjord, causing sedimentation of *Phaeocystis*-derived organic matter via faecal strings (Hamm *et al.* 2001). No information on *Phaeocystis* consumption by mysids exists, though they were reported to consume highly refractory detritus matter (Kost & Knight 1975; Jansen 1985) and are presumably able to rupture the *Phaeocystis* skin with their well-developed mandibles (Mauchline 1980). Their densities reported in May were low and might be biased due to escape behaviour, as clogging of the nets did occur. *Schistomysis spiritus* was quite abundant at the Flemish Banks' sites though, where *Phaeocystis* fluff was encountered (Fig. 8). As mysids are very abundant in the coastal area, one might try revealing their possible role into the fate of *Phaeocystis* blooms and the consequent energy transfer to higher trophic levels.

Negative effects of *Phaeocystis* on the hyperbenthic fauna may also occur. *Phaeocystis pouchetii* releases toxins in the surrounding waters holding anaesthetic properties (Stabell *et al.* 1999). This release appears to increase during the final stage of the bloom (Stabell *et al.* 1999). The presence of toxins does not affect copepod feeding behaviour (Stabell *et al.* 1999), while reduced appetite at elevated toxin levels are believed to arise for fish larvae (Eilertsen & Raa 1995). Stabell *et al.* (1999) suggested these properties to be harmful for fish larvae following ingestion. Rogers & Lockwood (1990) found that juvenile flatfish (sole, dab, plaice) moved away from *Phaeocystis*-affected nursery grounds in the Irish Sea. Herring schools have also been reported to avoid *Phaeocystis* blooms (Weisse *et al.* 1994). Less motile species might suffer from anoxic conditions however (Rogers & Lockwood 1990). Other harmful effects such as clogging of the filter mechanisms in suspension feeders have been reported (Weisse *et al.* 1994). The co-occurrence in April / May of the recruitment period of many fish species and the *Phaeocystis* bloom may have harmful consequences for these vulnerable life stages (Aanesen *et al.* 1998; Stabell *et al.* 1999).

In June, holohyperbenthos densities suddenly dropped in the hyperbenthal layer at the Flemish Banks and at the W Coast leading to the overall lowest densities figures (Fig. 4). The water column in June was strikingly transparent (A. Dewicke pers. observ.), a yearly recurring phenomenon due to the sudden complete disappearance of senescent colonies and their derived aggregates (Lancelot 1995, C. Lancelot pers. comm.). The mechanism of this sudden 'clearance of particles' remains poorly known (C. Lancelot pers. comm.) but might also affect the fauna of

the hyperbenthal zone. In conclusion, the drastic changes in the food web structure in the hyperbenthal zone are far from understood and are worth considering for future research.

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Chapter 6. The role of tidal and residual currents in regulating hyperbenthic communities

Ann Dewicke, Dries Van den Eynde, Jan Mees & Magda Vincx

Summary

The particular hydrodynamical regime of the Southern Bight of the North Sea has given rise to extensive offshore sandbank complexes, especially on the Belgian continental shelf. Many biota are known to be structured along an onshore-offshore gradient, with respect to coastal influence. However, structuring factors have seldom been examined from a hydrodynamical point of view. This study focuses on the structuring influence of hydrodynamic processes on the hyperbenthic fauna of the Belgian coastal area. Monthly sampling was carried out (from September 1994 until December 1995) at 13 sites, covering the Coastal Banks and the Flemish Banks.

In addition to the cross-shore gradient in sedimentological and physico-chemical variables, tidal flow is hypothesized to play an important role in the spatial structuring of the hyperbenthic communities. Onshore, tides are asymmetric and flood dominated (i.e. towards the north). The relative strength of flood versus ebb current gradually decreases with offshore distance, and the ebb current (i.e. towards the south) gets dominant off the Flemish Banks. Differential swimming abilities and potential of maintaining position in flow may lead to an onshore - offshore segregation among taxa.

The Coastal Banks are characterised by high suspended matter load. Low current velocities may permit settlement enabling growth of a variety of organisms that live or feed in the near-bottom water layer. Animals having the ability to maintain their position and avoiding offshore transport by the flood dominated flow, such as mysids, amphipods and postlarval shrimp, were most abundant. Suspended matter concentration is much lower at the Flemish Banks, and deposition on its crests is prevented by a persisting strong flow. Planktonic organisms like cnidarians, hydromedusae and decapod zoeae tend to accumulate in this area. They may be swept in from the shore by the flood-dominated current, and from further offshore where flow is ebb dominated. Although of minor importance, organic matter sedimentation at the Flemish Banks may occur in the swales, which are characterised by slower currents at the turning of the tides, and thus permitting development of populations of bottom-dependent animals.

Differential recruitment peaks of various postlarval fish and decapod larvae lead to strong temperature-related temporal patterns in community structure. Yet, temporal variability was also to a certain extent related to fluctuations in residual flow. A conspicuous correlation was found between the monthly numbers of mysid species and this residual flow. Interannual variability between autumn 1994 and 1995 can possibly be attributed to this phenomenon, which is probably driven by variations in wind conditions. It is not unlikely that hydrodynamic conditions *per se* play a major role in structuring coastal hyperbenthic communities, especially with respect to larval recruitment events.

Introduction

The hyperbenthal zone is the water stratum adjacent to the sea floor. It harbours a particular fauna (i.e. the hyperbenthos) with planktonic, benthic and strictly hyperbenthic (e.g. mysids) representatives (Mees & Jones 1997). Their trophic role in food webs of coastal and estuarine ecosystems is well recognised as they are important prey for juvenile fish and adult shrimp (Mauchline 1980; Hamerlynck & Hostens 1993; Mees & Jones 1997; Beyst *et al.* 1999a; Hostens & Mees 1999; Pedersen 1999; Oh *et al.* 2001). Despite the growing knowledge of the hyperbenthos, spatio-temporal variability of its taxa remains poorly understood.

Holohyperbenthos (generally smaller than 20 mm) is defined as the animals that spend a variable period of their adult life in the hyperbenthal zone. Mysids often dominate this fauna in shallow coastal waters (Mees & Jones 1997; Chapters 4 and 5). Several species occur in a broad range of habitats and they exhibit a diversity of behavioural patterns with respect to physical, chemical and biological stimuli (Mauchline 1980). They may show inter- or intraspecific zonation in near-shore waters (Clutter 1967, 1969; Mauchline 1971; Wooldridge 1981, 1989; Takahashi & Kawaguchi 1995). Zonation of surf-zone mysids has been related to food availability (Clutter 1967; Wooldridge 1989; Webb & Wooldridge 1990), predation avoidance (Wooldridge 1981; Takahashi & Kawaguchi 1998) or to wave action and flow regimes near the bottom (Wooldridge 1981; Takahashi & Kawaguchi 1995). Their spatial distribution in estuaries has often been related to physical and chemical variables such as salinity, temperature and turbidity (Mauchline 1971c; Williams & Collins 1984; Mees *et al.* 1993b, 1995). In subtidal waters, several mysid species seem to be attracted to food-enriched areas (Clutter 1967; Fosså 1985; Hargreaves 1985; Cunha *et al.* 1997; Chapters 1 and 2). Annual variability in mysid densities has mostly been attributed to recruitment or seasonal migrations (Buhl-Jensen & Fosså 1991; Mauchline 1980; Mees *et al.* 1993a; Mouny *et al.* 1998; Vallet & Dauvin 1999; Mouny *et al.* 2000). However, mysid populations may locally completely disappear on very short time scales, in particular in strongly dynamic environments like the intertidal and subtidal (Mauchline 1980).

Recently, Roast *et al.* (1998) experimentally examined the relationship between swimming behaviour and current strength for the brackish water mysid *Neomysis integer*. Current velocity was hypothesized to be an important controlling factor for mysid position maintenance, and could be linked with distribution patterns in the field (Roast *et al.* 1998). Spatio-temporal variability in flow characteristics is complex and is difficult to quantify, although it is generally assumed to be of importance to mysid distribution (e.g. Mauchline 1980; Clutter 1969; Kaartvedt 1993; Takahashi & Kawaguchi 1995; Kimmerer *et al.* 1998; Lawrie *et al.* 1999).

The merohyperbenthos consists of early life history stages (Mees & Jones 1997). They are transitional between a fully planktonic and fully benthic behaviour. Larvae of benthic organisms (e.g. decapods, demersal fish and polychaetes) are numerous in the hyperbenthal zone of coastal areas (Mees & Jones 1997; Chapters 4 and 5). Flow velocity and direction are of crucial importance for recruitment success (Scheltema 1986). Local circulation patterns may either aid or obstruct larval stages to reach their preferred habitat. Moreover, settlement and post-settlement is influenced by bottom-boundary flows and resuspension events (Thiébaut *et al.* 1998).

This chapter aims to examine the spatio-temporal community structure of the hyperbenthos in relation to environmental characteristics of the Belgian coastal area. Emphasis is put on the possible role of the tidal and residual flows, although sedimentological, physico-chemical and biological variables are considered as well.

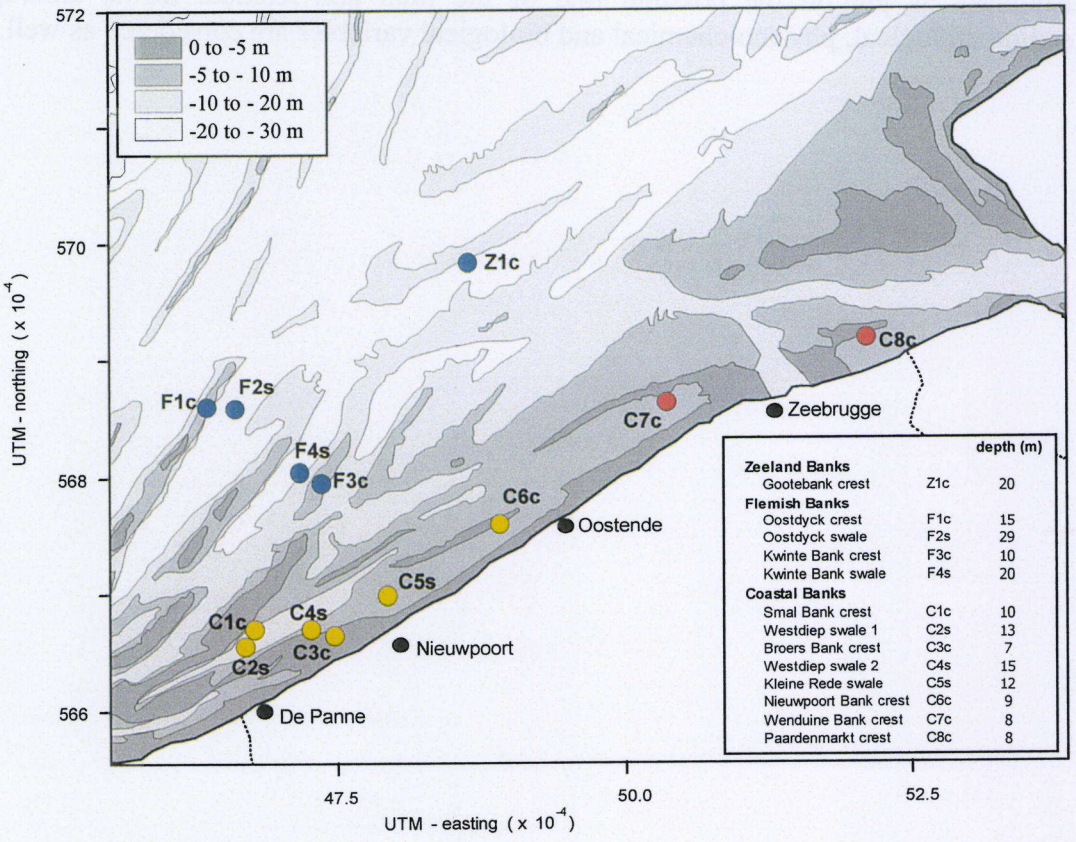

Fig. 1. Map of the study area showing the location of the sampling sites. Symbols refer to the biotic communities (see Results). The sandbanks dealt with are listed for each sandbank complex in the table above.

				1994				1995										
Site	**Longitude**	**Latitude**	**Depth (m)**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**
Z1c	2° 48.15' E	51° 26.09' N	20	-	7	4	21	-	10	24	27	23	21	-	17	-	10	8	20
F1c	2° 29.42' E	51° 19.17' N	15	6	7	4	20	-	9	24	26	22	21	-	-	-	10	7	19
F2s	2° 28.20' E	51° 19.54' N	29	6	7	4	20	-	9	23	26	22	21	-	-	-	10	7	19
F3c	2° 36.93' E	51° 16.83' N	10	6	7	3	20	-	8	22	26	22	21	-	-	-	10	7	19
F4s	2° 36.90' E	51° 16.73' N	20	6	7	3	20	-	8	22	26	22	21	-	-	-	10	7	19
C1c	2° 32.72' E	51° 09.27' N	10	6	10	2	20	-	9	23	26	23	20	-	-	-	10	8	18
C2s	2° 32.12' E	51° 08.46' N	13	6	10	2	20	-	9	23	26	23	20	-	-	-	10	8	18
C3c	2° 36.95' E	51° 08.94' N	7	6	10	3	20	-	2	23	26	23	20	10	-	-	9	8	18
C4s	2° 36.32' E	51° 09.38' N	15	6	10	3	20	-	2	23	26	23	20	10	-	-	9	8	18
C5s	2° 42.10' E	51° 10.99' N	12	6	6	3	20	-	7	23	24	23	20	10	-	-	9	8	18
C6c	2° 50.26' E	51° 14.68' N	9	5	6	3	19	-	2	22	24	23	20	10	7*	-	9	6	18
C7c	3° 03.05' E	51° 16.60' N	8	5	6	3	19	-	2	22	24	22	19	10	-	-	9	7	18
C8c	3° 18.66' E	51° 22.63' N	8	7	6	2	19	-	6	22	25	22	20	11	-	-	9	7	20

Table 1. Overview of the collected samples. Exact sampling dates are given for each month; (-) no sampling performed, (*) two samples were taken at this site.

Material and methods

Study area

The Belgian continental shelf is influenced by a saline (33.5 - 34.5 psu) Channel water mass flowing in a NE direction, and by the SW oriented Westerschelde outflow (Nihoul & Hecq 1984; Baeyens *et al.* 1998). The semi-diurnal tidal regime is macro tidal with mean tidal amplitude at Zeebrugge of 4.3 m at spring tide and 2.8 m at neap tide (Administratie Waterwegen en Zeewezen 1999). The water column at the Belgian coast is well mixed during the entire year (de Ruiter *et al.* 1987) and is not stratified by salinity or temperature gradients. The depth-average current velocity exceeds 1 m s^{-1} during spring tide (Beheerseenheid Mathematisch Model Noordzee 1996). Near-bottom currents (1.3 m above the seabed) may be 30 % lower compared to near-surface flow (5.0 m below the sea surface), judging from measurements performed at the Flemish Banks (Stolk 1993; Lanckneus *et al.* 1994). The general orientation of the tidal flow coincides with the NE-SW axis. Flood currents are headed towards the NE while the SW is the dominant direction of the ebb tidal flow. The tides are slightly asymmetric onshore. This area is characterised by flood dominance, i.e. peak flood currents are stronger than peak ebb currents, with a flood / ebb ratio of 0.5 (Lanckneus *et al.* 1994). Flood dominance however decreases in the cross-shore direction and the tides become symmetrical (peak ebb currents are approximately equal to peak flood currents) or ebb dominated offshore (Lanckneus *et al.* 1994). The residual current (movements of water masses over a period longer than a tidal cycle) amounts to 2.7 cm s^{-1} (Baeyens *et al.* 1998). Residence time of the water masses flowing through the coastal zone (70 km length) was estimated to be one month (Baeyens *et al.* 1998).

A number of isolated sandbank sets occur in the area: the Coastal Banks, the Flemish Banks, the Zeeland Banks, and the Hinder Banks (Bastin 1974, see also Chapter 4). This study was performed in the area covering the Coastal Banks, the Flemish Banks and part of the Zeeland Banks (Fig. 1). The Coastal Banks (max. 20 km long and 1 km wide) stretch parallel along the coastline within a distance of 10 km from the shore; the crests are situated 2-3 m below MLLWS (Mean Lowest Low Water Spring Level). The Flemish Banks are situated to the west of Oostende and at 10-30 km from the shore (max. 15-25 km long and 3-6 km wide). They are NE directed with crests at some 4 m below MLLWS. To the east of Oostende, the Zeeland Banks occur. Like the Flemish Banks, they are situated at a distance of 15-30 km from the shore, but they are oriented in a parallel way. They have crests below 10 m MLLWS.

Sampling

Monthly sampling was performed at 13 sites in the Belgian coastal area, from September 1994 until December 1995. Eight sites were situated at the Coastal Banks, spread along the coastline, i.e. from the West Coast (De Panne to Oostende) towards the East Coast (around Zeebrugge). Four sites were selected at the Flemish Banks and one site at the Zeeland Banks. In total, eight sites were located as close as possible to the crest of the sandbanks (site name ending with 'c'). Five sites were situated in the inter-bank swales (site name ending with 's'), always close to a corresponding crest site (except for site C5s). Depth of the sampling sites ranged

	Holohyperbenthos		Merohyperbenthos	
	% expl	p-level	% expl	p-level
SPCB variables				
Sedimentological variables				
Mean grain size (µm)	4.6	***	3.6	***
% mud	2.1	***	2.4	***
% very fine sand	5.4	***	3.2	***
% fine sand	5.4	***	3.2	***
% medium sand	5.4	***	3.6	***
% coarse sand	5.4	***	2.4	***
Physico-chemical variables				
Depth (m)	7.1	***	3.2	***
Temperature (°C)	3.8	***	7.5	***
Salinity (psu)	7.1	***	5.9	***
Nitrate (µmol l^{-1})	5.4	***	4.0	***
Ammonia (µmol l^{-1})	2.1	***	3.6	***
Silicate (µmol l^{-1})	4.6	***	4.4	***
Biological variables				
Chlorophyll *a* (µg l^{-1})	3.8	***	7.9	***
Fucoxanthin (µg l^{-1})	3.3	***	7.1	***
Current velocity variables				
maxT (m s^{-1})	3.3	***	7.1	***
maxN (m s^{-1})	4.6	***	3.6	***
maxS (m s^{-1})	7.1	***	4.8	***
maxE (m s^{-1})	2.5	***	5.5	***
maxW (m s^{-1})	2.9	***	2.0	***
domN (m s^{-1})	5.4	***	3.6	***
domE (m s^{-1})	1.7	***	4.8	***
resN3 (m s^{-1})	2.1	***	2.0	***
resE3 (m s^{-1})	1.3	**	1.6	**
resN7 (m s^{-1})	1.7	***	1.6	**
resE7 (m s^{-1})	1.3	**	1.2	*
resN21 (m s^{-1})	2.5	***	2.4	***
resE21 (m s^{-1})	2.1	***	3.2	***

Table 2. Overview of all environmental variables used for the multivariate analyses. The independent fraction explained (% expl) for each single variable to the total holo- and merohyperbenthos species variance is listed, together with its significance level; $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*).

from 7 to 29 m (see Fig. 1). No samples were collected in January and September 1995 and not all sites were sampled in July and August 1995. In total, 164 samples were taken (see Table 1).

All sampling was done from the *RV* Belgica. The hyperbenthos was sampled with a modified hyperbenthic sledge after Sorbe (1983). Two superimposed nets (1 mm mesh size, 3 m long, 71 cm wide) were fixed on the sledge and sampled the water layer from 0 to 50 cm (lower net) and from 50 to 100 cm (upper net) above the sea floor. The sledge was equipped with an opening-closing mechanism and an odometer (for details see Sorbe 1983). A flow meter (*Hydrobios 438-110*) was fixed in the upper net. All sampling was carried out during daytime; towing lasted five minutes at an average ship speed of 1.5 knot relative to the sea floor and against the current. On average, towing distance was 170 ± 5.7 m and a water volume of 116 ± 2.9 m^3 was filtered. Before each tow, sediment and water sampling was carried out and a number of environmental variables were registered (see Chapter 5).

Data acquisition

Hyperbenthos density data

After sorting the organisms, they were identified to species level. A distinction was made between zoea and postlarva or megalopa stages for decapods. These were treated as separate taxa. All animals were counted on species and stage level and their density, expressed as numbers of individuals per 100 m^{-3}, was calculated. The total density data matrix was split into two, according to the holo- and merohyperbenthos species. The holohyperbenthos comprises a group of taxa with a rather small adult habitus (generally < 20 mm), such as several peracarid orders (mysids, amhipods, isopods, cumaceans), hydromedusae, copepods, chaetognaths and pycnogonids. The merohyperbenthos consists of early life history stages, generally derived from larger animals, and was mainly represented by decapod larvae (< 10 mm), fish larvae (generally < 20 mm) and larval polychaetes (modified after Mees & Jones 1997). All field and laboratory methods are fully described in Chapter 5.

Environmental variables sampled in the field

The methodology for the analysis of the environmental samples is fully given in Chapter 5. For the description of their spatio-temporal fluctuations, it is also referred to this chapter. For this study, six sedimentological variables (mean grain size, % mud, % very fine sand, % fine sand, % medium sand and % coarse sand) (Wentworth scale, Buchanan 1984) were used, and a number of variables measured in the water column: five physico-chemical (temperature, salinity, nitrate, ammonia, and silicate) and two biological (chlorophyll *a* and fucoxanthin). Water depth is a fixed variable per site since it is standardised to local Mean Lowest Low Water Spring level (MLLWS).

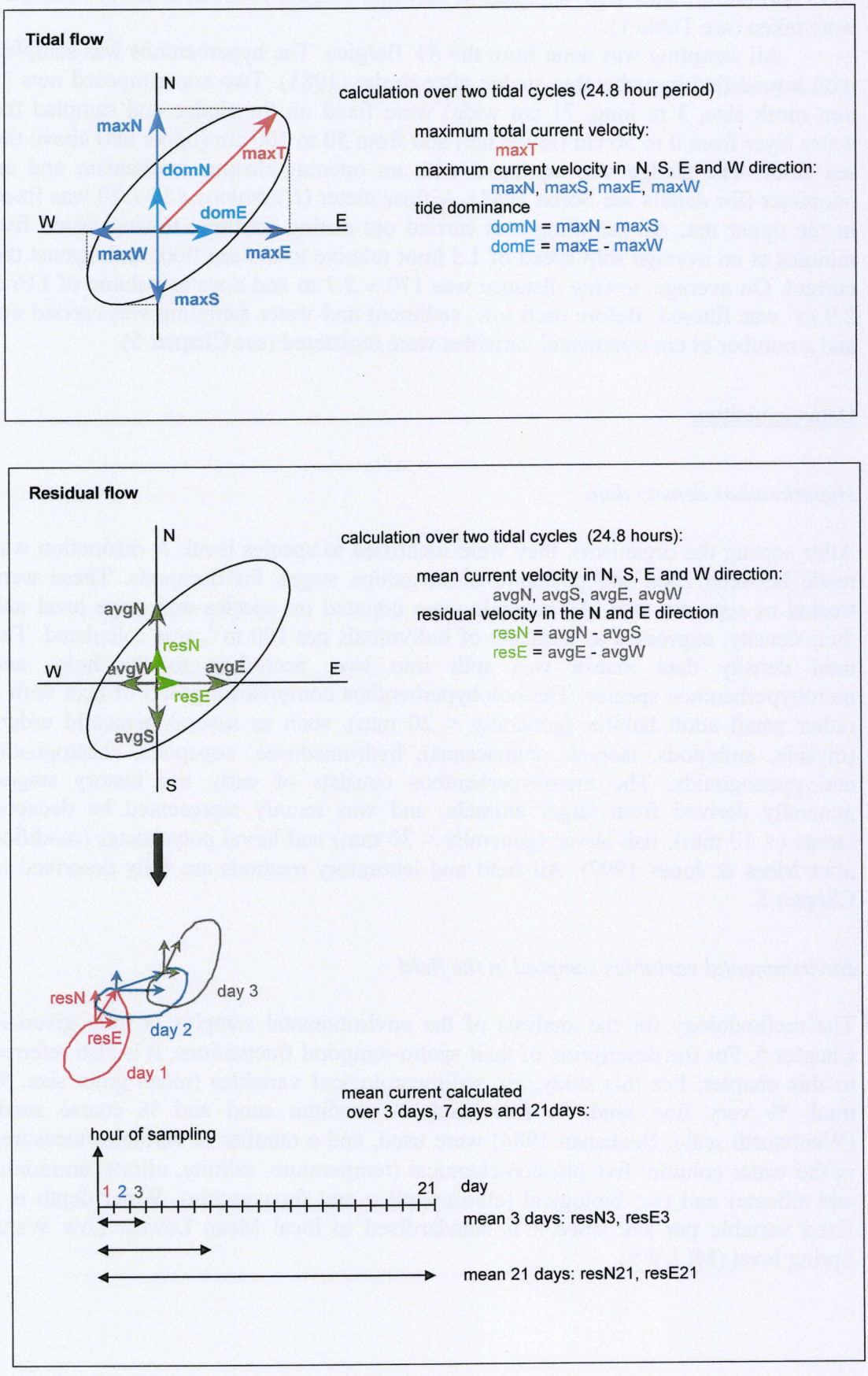

Fig. 2. Schematic representation of the construction of tidal and residual current variables.

Current velocity variables derived from the MU-BCZ model

All current velocity variables were generated by the hydrodynamical model MU-BCZ (Adam 1979; Van den Eynde 1994). The two-dimensional hydrodynamic model calculates the depth-integrated current velocity and the mean water level over the model grid being under influence of tides and meteorological effects. The model solves the classical shallow-water wave equations and an equation for the conservation of mass in a system of Cartesian coordinates. The model was implemented on a geographical grid, covering the Belgian coastal area and the Flemish Banks. The model grid has a resolution of 25" in longitude to 40" in latitude (approximately 750 m x 750 m). The model was run over the whole sampling period (September 1994 to December 1995).

For each sampling station the current velocity and direction was extracted from the model results, at 60 minutes intervals. The data were used to construct the mean tidal stream ellipses for each station (Fig. 3). These represent the direction and current velocity during a tidal cycle, averaged over the full sampling period.

Based on the characteristics of the tidal ellipses, a number of variables was carefully selected from the model, on the basis of its possible value to hyperbenthic structuring (see Fig. 2). Tidal current strength was considered during 24.8 hours (2 tidal cycles) prior to time of sampling. The maximum tidal flow velocity (maxT) was considered and the maximum directional velocities pointing towards the N, S, E and W were separately examined (maxN, maxS, maxE and maxW, respectively) (see Fig. 2). Flow towards the N and the E indicates flood tide, while flow towards the S and W points to ebb tide. Tide dominance was calculated by subtracting the maximum velocities towards the N from those towards the S (variable domN) and similarly for the E and W current (variable domE). As such, positive values for the domN and domE variables indicate flood dominance pointing at strongest maximum current velocity in northerly and easterly direction respectively. Negative values on the other hand correspond with ebb dominance with strongest maximum current velocities in both southerly and westerly direction.

Temporal fluctuation of the residual current was assessed by considering the (vector) mean current over a three-weeks period. Again, the mean current strength in the N, S, E and W directions during 24.8 hours (2 tidal cycles) prior to time of sampling, was calculated. The residual flow in the N and E direction was calculated by subtracting the mean velocities towards the N from those towards the S (variable resN) and likewise for the E and W current (variable resE). This procedure was repeated for a period of 21 days prior to sampling. The obtained values per 24.8 hours were averaged over 3, 7 and 21 days prior to sampling (indicated with extension 3, 7 and 21). Positive values for the resN and resE variables indicate a residual flow towards the N and the E, respectively. Negative values correspond with a residual flow towards the S and the W. Thus, a total of 7 tidal and 6 residual current variables were used. A schematic overview of their construction is shown in Fig. 2.

Numerical analysis

Ordination analyses were performed by using the program package CANOCO 4 (ter Braak & Smilauer 1998). Two datasets of response variables were analysed: the species density data of the holohyperbenthos and of the merohyperbenthos. All analyses were separately performed on holo- and merohyperbenthic species data.

Transformation and species reduction

Raw density data were log(x+1) transformed (Legendre & Legendre 1998). A suitable transformation was performed on the environmental variables to obtain normal distribution of the data (Legendre & Legendre 1998). Sediment fractions were arcsine transformed, current variables were used as such, and a log(x+10) transformation was used for all remaining variables. Some species were excluded using selection criteria based on species tolerance, t_k as a measure of niche width (excluded when $t_k < 2$), and percentage fit (excluded if $N_2 < 3$). These were assessed by running preliminary ordinations (CA, see further). For the exact calculation of t_k, and N_2, it is referred to ter Braak & Smilauer (1998). No samples were rejected in the first place.

Selection of the ordination method

Five multivariate techniques were applied: DCA (Detrended Correspondence Analysis), PCA (Principal Components Analysis), CA (Correspondence Analysis), RDA (Redundancy Analysis), and CCA (Canonical Correspondence Analysis). Exploratory DCAs (with detrending by segments) were always performed for each dataset in order to estimate the gradient length (g.l.) of species variance (ter Braak & Prentice 1988). If the gradient length, expressed in standard deviation (s.d.) units, is less than 1.5, monotonic species response curves could be expected and a linear method (PCA or RDA) was subsequently applied. Gradient lengths exceeding 3 s.d. units indicate a predominance of unimodal responses, asking for ordination methods based on weighted averaging (CA or CCA) (ter Braak & Prentice 1988; Van Wijngaarden *et al.* 1995). CA and CCA were applied on both the full holo- and merohyperbenthos dataset. Certain analyses were performed after reducing the number of samples. In these cases, PCA and RDA were the most appropriate techniques.

Indirect techniques aim to generate hypotheses about species-environment relationships (Økland 1996). Unconstrained analyses (CA and PCA) were therefore applied to detect and to visualise the major gradients in community structure rendering the most accurate ordination diagrams. This made it possible to give the explanatory variables a merely passive role in the presented ordination diagrams keeping them from forcing any patterns. Constrained analyses (RDA and CCA) were then used as a parallel application to assess the fraction of species variance explained by the explanatory variables (Økland 1996).

In certain cases, spatial or temporal variance was strong. This variance was further eliminated by performing partial analyses using dummy covariables (ter Braak & Verdonschot 1995; Økland 1996, Legendre & Legendre 1998). Two additional data matrices were therefore constructed containing dummy variables for each station (dataset S) and each month (dataset T) respectively (Legendre &

Legendre 1998). Dataset S was meant to eliminate the spatial species variance while dataset T should be dealing with the temporal species variance.

Selection of the explanatory variables

All environmental variables were divided into two explanatory datasets. Sedimentological, physico-chemical and biological variables were grouped and are further indicated as 'SPCB' variables; the current velocity dataset comprises all current strength variables. Preliminary constrained analyses were performed in order to assess the independent contribution of each single environmental variable in explaining variance in the species data (Borcard *et al.* 1992; Økland & Eilertsen 1994; ter Braak & Verdonschot 1995). The significance of each single variable was tested by means of a Monte Carlo permutation test (Manly 1997) (999 unrestricted permutations), using the forward selection option in CANOCO 4 (see Table 2). Non-significant variables ($p<0.01$) were excluded from any further analysis (Økland & Eilertsen 1994). This procedure was repeated for the partial analyses (with covariables) as well as for the dataset with a reduced number of samples.

Relation with the environment

Community structure was always examined by considering the species variance along the first two ordination axes of the unconstrained analysis. Only those variables that had a significant contribution in explaining the total species variance, as assessed by the constrained form of the presented analysis, were passively entered. As the tidal current variables seemed to be only meaningful on a spatial scale, they were only then taken into account if spatial structure prevailed. The residual flow variables were then again used, if temporal patterns were more prominent.

The variance partitioning method as described by Borcard *et al.* (1992), (see also Økland & Eilertsen 1994; Pinel-Alloul *et al.* 1995, 1999; Aude & Lawesson 1998; Avois *et al.* 2000; Muylaert *et al.* 2000), was performed to determine the amount of spatially and temporally structured variation. This was done by running constrained analyses (CCA) with the datasets S (for estimation of the spatial structured variance) and T (for estimation of the temporal structured variance) as explanatory variables, and by using the Monte Carlo approach.

The SPCB and current strength variables that were most explanatory to the species variance were furthermore selected in order to determine their contribution in explaining the spatially or temporally structured species variance. This was achieved by running a CCA in order to estimate the total fraction of the species variance explained by the single explanatory variable. Partial CCAs were used to separate the fraction variance explained which is spatially ($E \cap S$) and temporally ($E \cap T$) structured, by entering dataset S and T as covariable datamatrix, respectively. This procedure was repeated for each variable.

The overlap in the fraction explained by the most meaningful SPCB variables and the most important tidal stream variable, was similarly dealt with. Partial CCAs were performed with a single SPCB variable as explanatory variable and the current strength variable as single covariable. This allowed the overlap to be assessed. An overview the analyses performed for the variation partitioning is presented in Table 3. For each analysis, a Monte Carlo test was performed. Only significant contributions ($p < 0.01$) in explaining the total variation were further considered.

One-way ANOVAs and subsequent *post-hoc* tests (Scheffé-test) were performed for variables meeting the assumptions (after transformation) for parametric statistics (Sokal & Rohlf 1995). If the assumptions for ANOVA were not met, non-parametric statistics were used (Mann-Whitney U-test, Kruskal-Wallis test with subsequent *post-hoc* multiple comparisons according to Conover (1971)) (Sokal & Rohlf 1995). The relation between some variables was assessed by calculating Pearson's correlation coefficient, r_p (Sokal & Rohlf 1995).

Results

Assessment of the tidal ellipses and residual flow

The tidal ellipses illustrate the general NE-SW orientation of the tidal flow. The sites located at the Coastal Banks are characterised by more elongated ellipses as compared to the offshore sites (Flemish Banks). This indicates a stronger confinement to the NE-SW axis and sudden changes in amplitude of current strength leading to periods with high velocities alternating with short periods of low current velocities. Tidal stream velocities are slightly higher at the Flemish Banks. The current orientation in the swales roughly corresponds with that of the adjacent sandbanks but differs from that on the crests. Also, current strength remains quite high during the entire tidal at the crests' environment.

Tidal flow is flood dominated (towards the NE) at the Coastal Banks and slightly ebb dominated (towards the SW) at the Flemish Banks, as illustrated for the N-component in Fig. 4A. The temporal fluctuation of the residual flow towards the N (calculated over 21 days) is illustrated in Fig 4B.

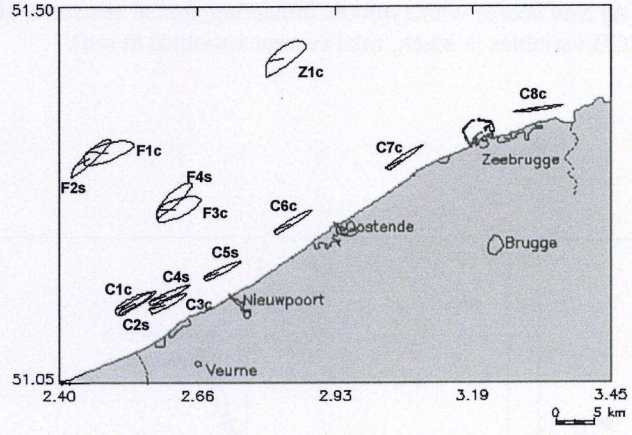

Fig. 3. Tidal stream ellipses presented for each site.

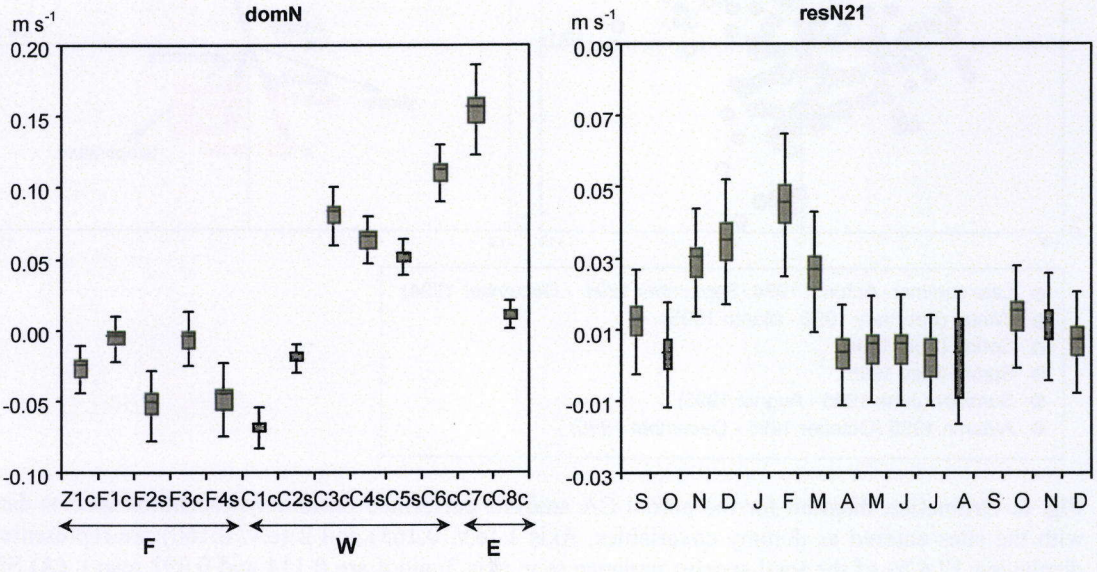

Fig. 4. Variability of **(A)** domN, per site presented and **(B)** resN, per month presented. Boxes are representing mean values with standard error and whiskers indicate the standard deviation.

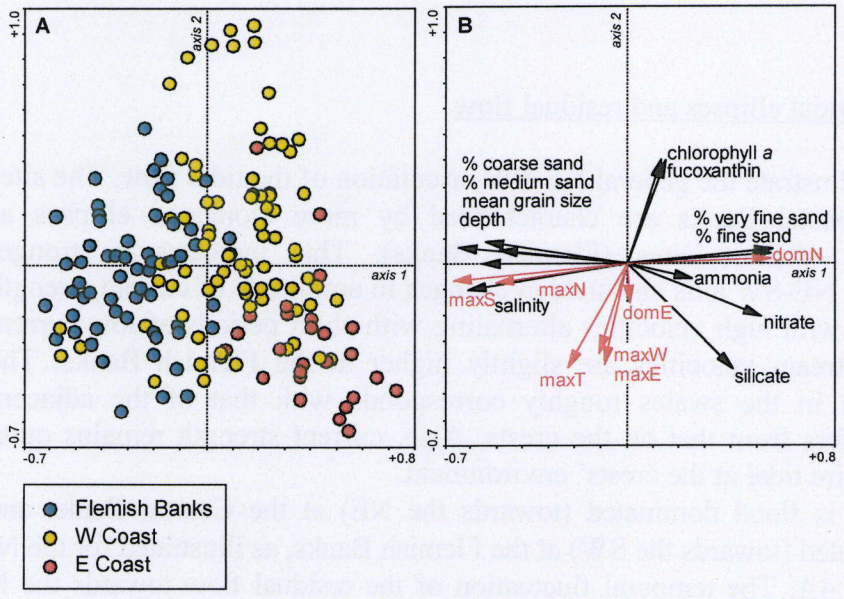

Fig. 5. Ordination diagram for the CA analysis performed on holohyperbenthos species densities. Axis 1 (e.v. 0.301) and 2 (e.v. 0.179) are represented, displaying 20.1 % of the total species variance (e.v. axis 3 and 4 are 0.162 and 0.153 resp.). **(A)** Site scores with symbols indicating spatial structure, **(B)** scores for the environmental variables (SPCB variables in black, tidal current variables in red).

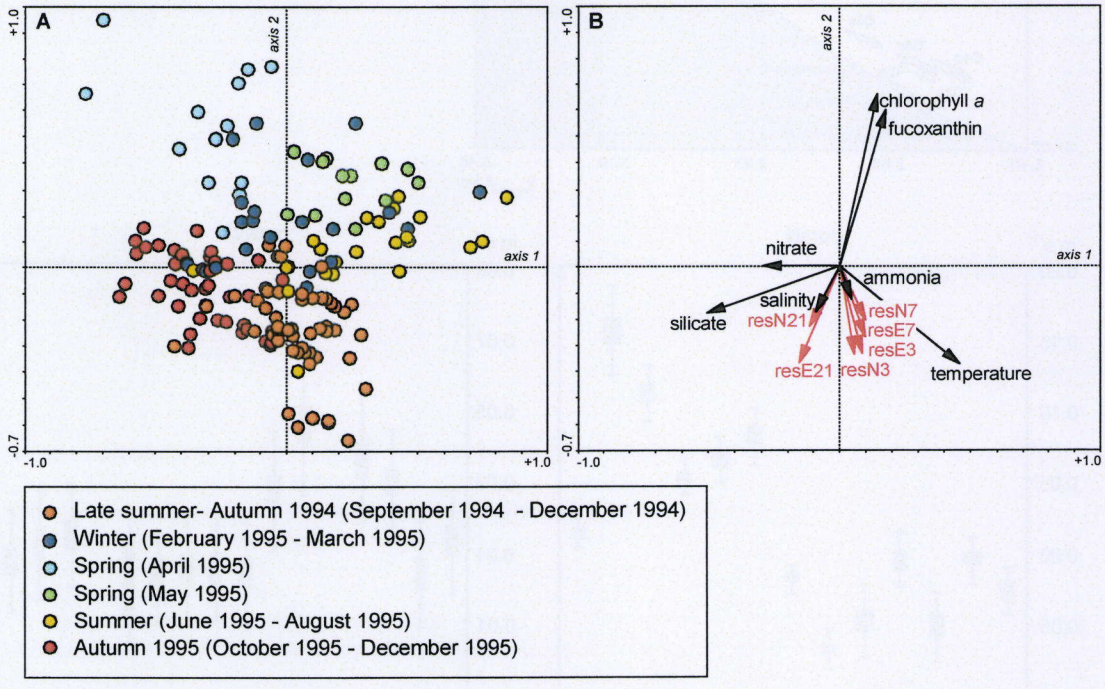

Fig. 6. Ordination diagram for the partial CA analysis performed on holohyperbenthos species data, with the sites entered as dummy covariables. Axis 1 (e.v. 0.165) and 2 (e.v. 0.160) are represented, displaying 17.6 % of the total species variance (e.v. axis 3 and 4 are 0.114 and 0.092 resp.). **(A)** Site scores indicating temporal structure, **(B)** scores for the environmental variables (SPCB variables in black, residual current variables in red).

Major structuring gradients

A total of 93 holohyperbenthic species was recorded and total density ranged from 6 to 5622 ind. 100 m^{-3}. Mysids, amphipods, hydromedusae, copepods and chaetognaths were the main representatives. The merohyperbenthos was mainly represented by decapod larvae, postlarval fish, and polychaete larvae. The merohyperbenthos species matrix consisted of 54 species with total abundance varying between 2 and 2188 ind. 100 m^{-3}. For detailed description of the hyperbenthic fauna, see Chapter 5. The behaviour of the single sampling site on the Zeeland Banks (Z1c) was always quite similar to the Flemish Banks sites as described below and is therefore merged with the latter area.

Holohyperbenthos

Spatio-temporal patterns

After elimination of 21 species from the holohyperbenthos dataset, a CA (g.l. exploratory DCA 2.567 s.d.) was done. The first (eigenvalue (e.v.) 0.301) and second axis (e.v. 0.179), together represent 20.1 % of the total variance in species composition. Sample scores along the first axis (displaying 12.6 %) reveal a spatial structure, which is conform to the sandbank complexes (Fig. 5A). Samples plotted on the left hand side of the diagram belong to the Flemish Banks and are most distinct from the E Coast samples. The W Coast samples are to be intermediately found. The deeper Flemish Banks are characterised by highest salinity and stronger tidal velocities in the north-south direction (maxN and maxS). Moreover, sediments are coarser. The tide dominance variable domN points in the opposite direction and indicates a gradient with more conspicuous flood dominance (domN) on the Coastal Banks. The second axis reveals an east-west gradient along the Coastal Banks, yet this axis mainly represents temporal variance in the species data (not shown in Fig. 5), which will be dealt with further through a partial analysis. As the E Coast samples were all located in the lower right quadrant of the diagram (except for the two single samples plotted in the upper part of Figure 5A, which are from May), they did not show a strong seasonal pattern.

In general, the holohyperbenthos was dominated by mysids and amphipods (Table 4A). Mean densities for mysids, chaetognaths and copepods differed significantly among the three areas. Mysids reached highest densities on the E Coast. The Flemish Banks harboured a small but significant fraction of copepods and chaetognaths (see Chapter 5).

In order to assess temporal structure, a partial CA was performed on the holohyperbenthos species data with the stations as dummy covariables. Here, 77.2 % of the total variance remained. The first two axes are of equal importance (0.165 and 0.160 resp.) and represent 17.6 % of the remaining variance (Fig. 6A). A certain temporal pattern can be distinguished though not obviously linked with a seasonal succession. The first axis reveals an interannual difference between the autumn samples of 1994 (right) and 1995 (left). Samples from April and May are well separated along this axis too, illustrating a high species variance on a small temporal scale. The spread of samples along the second axis shows a difference between

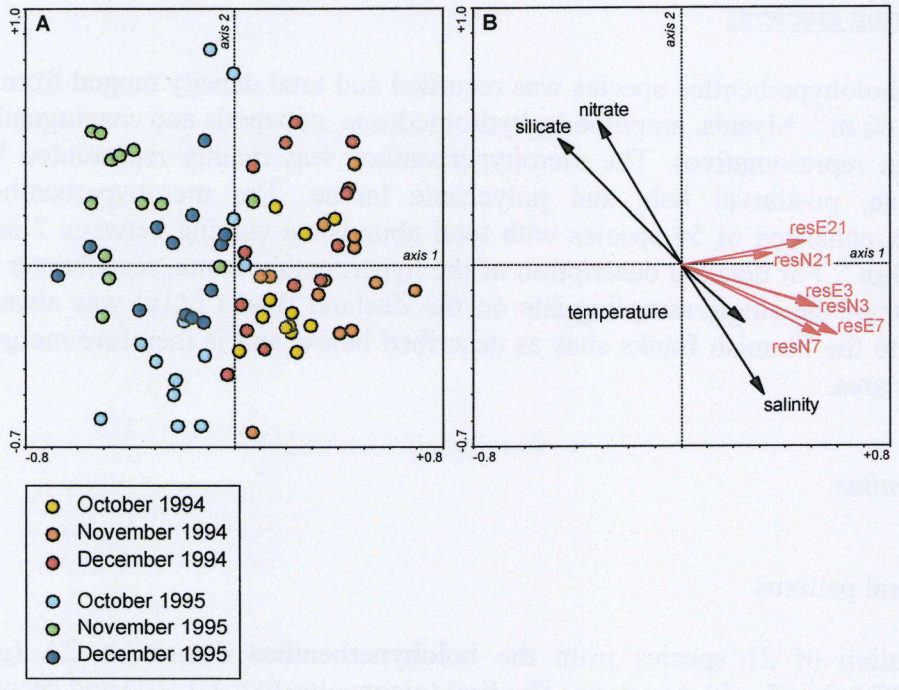

Fig. 7. Ordination diagrams for the partial PCA analysis performed on the holohyperbenthos data of the autumn samples from 1994 and 1995, with the sites entered as dummy covariables. Axis 1 (e.v. 0.161) and 2 (e.v. 0.101) are represented, displaying 40.7 % of the total species variance (e.v. axis 3 and 4 are 0.082 and 0.047 resp.). **(A)** samples scores with sites marked per month, **(B)** scores for the environmental variables (SPCB variables in black, residual current variables in red).

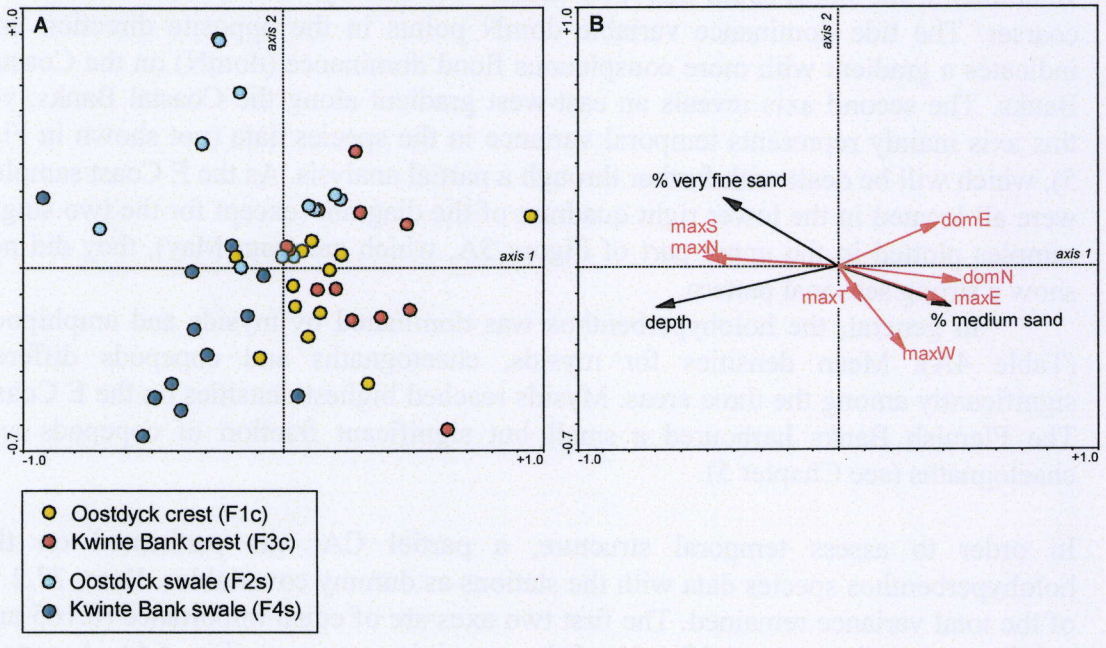

Fig. 8. Ordination diagrams for the partial PCA analysis performed on the holohyperbenthos data of the Flemish Banks (Kwinte Bank and Oostdyck), with the months entered as dummy covariables. Axis 1 (e.v. 0.116) and 2 (e.v. 0.066) are represented, displaying 41.9 % of the total species variance (e.v. axis 3 and 4 are 0.047 and 0.034 resp.). **(A)** samples scores with sites marked according to the sandbanks and their crest or swale environment, **(B)** scores for the environmental variables (SPCB variables in black, tidal current variables in red).

spring and autumn. Silicate and nitrate are negatively correlated with the first axis, indicating highest levels for autumn 1995 and early spring. Chlorophyll *a* and fucoxanthin distinguish spring from autumn along the second axis, pointing towards the spring samples. Moreover, all variables expressing residual current strength, are negatively correlated with the second axis.

The gradient along the second axis corresponded with the most obvious change in community composition, being the dominance of amphipods and ctenophores in spring (see Chapter 5).

Autumn 1994 and 1995

The autumn samples from 1994 and 1995 were separately analysed in order to assess the interannual difference by running a partial PCA (g.l. DCA 0.654 s.d.) with the stations as dummy covariables (Fig. 7A). The samples of the two successive years are separated along the first axis (e.v. 0.161). The variation in species composition coincides with a gradient in residual current with a stronger component towards the N and the E during autumn 1994. Salinity, nitrate and silicate were rather correlated with the second axis (e.v. 0.101), pointing to differences between the successive autumn months within a year.

Several taxa attained significantly higher densities in autumn 1995 compared to the same period in 1994 (Table 4B) and gross taxonomic composition differed moreover (Chapter 5).

Flemish Banks

The Flemish Banks (the Oostdyck and Kwinte Bank) were dealt with separately for examining any differences in species variance between the two sandbanks or among the crests and adjacent swales. A partial PCA analysis (l.g. exploratory DCA 1.770 s.d.) was performed with the months as dummy covariables. Highest variability in species composition was found between the crests and swales, as shown along the first axis (e.v. 0.116) of the ordination diagram (Fig. 8A). A much weaker gradient appears between the two sandbanks in the direction of the second axis (e.v. 0.066). The fauna of the swales corresponds with higher current velocities in the north-south direction (maxN, maxS); flood dominance is stronger at the sandbanks' crests (domN, domE) (Fig. 8B).

Holohyperbenthic taxa were nearly twice as abundant in the swales, except for hydromedusae and ctenophores (Table 4C).

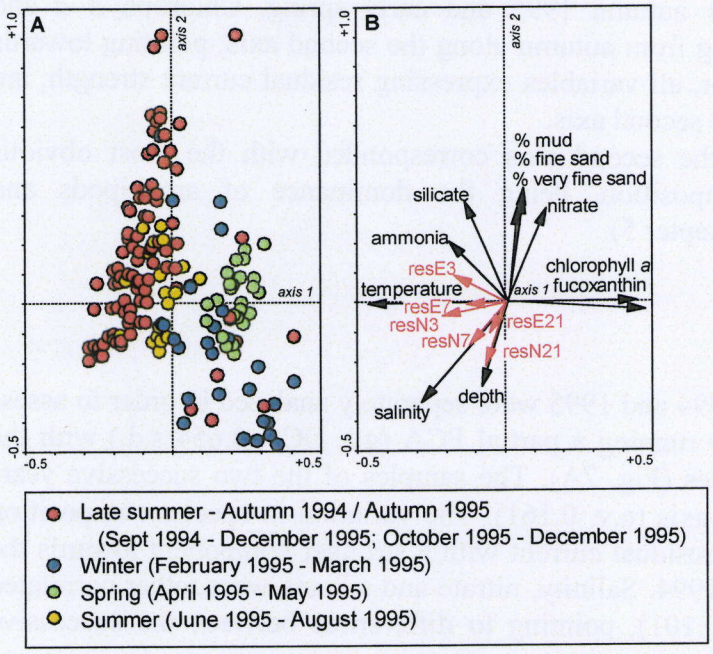

Fig. 9. Ordination diagrams for the CA analysis performed on merohyperbenthos species data. Axis 1 (e.v. 0.362) and 2 (e.v. 0.259) are represented, displaying 24.6 % of the total species variance (e.v. axis 3 and 4 are 0.213 and 0.191 resp.). **(A)** samples scores with symbols referring to temporal structure, **(B)** scores for the environmental variables (SPCB variables in black, residual current variables in red).

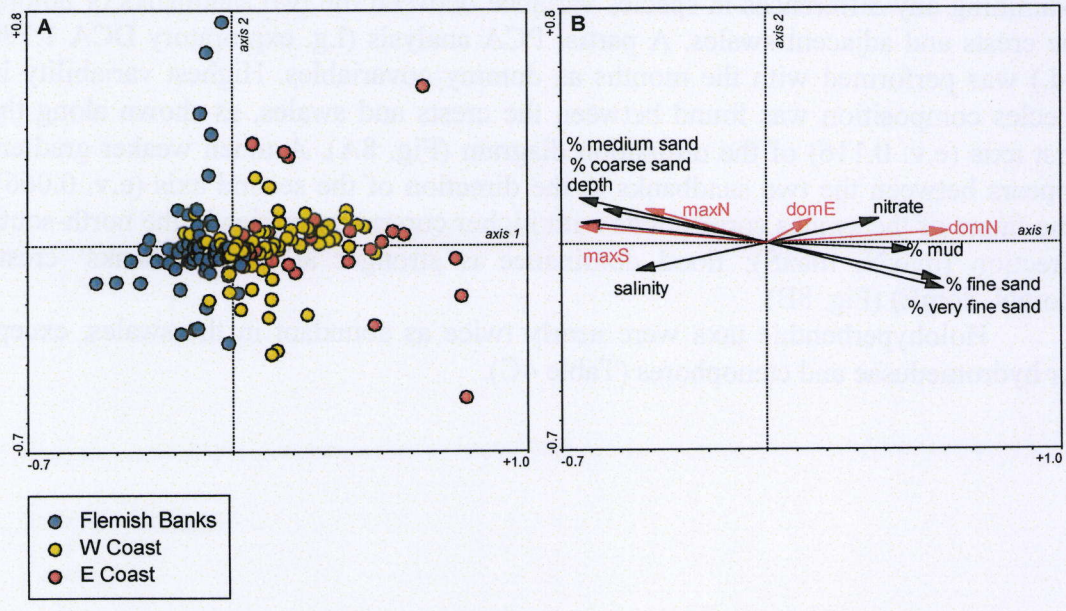

Fig. 10. Ordination diagrams for the partial CA analysis performed on merohyperbenthos data, with the months entered as dummy covariables. Axis 1 (e.v. 0.178) and 2 (e.v. 0.086) are represented, displaying 20.6 % of the total species variance (e.v. axis 3 and 4 are 0.072 and 0.066 resp.). **(A)** samples scores indicating spatial structure **(B)** scores for the environmental variables (SPCB variables in black, tidal current variables in red).

Merohyperbenthos

A CA was performed on the merohyperbenthos dataset (g.l. explanatory DCA 2.606 s.d.), after exclusion of 6 species. Axis 1 (e.v. 0.362) and 2 (e.v. 0.259) together represent 24.6 % of the species variance (Fig 9A). The merohyperbenthos is mainly temporally structured as concluded from the spread of sample scores along the first axis. This axis alone already displays 14.3 % of the species variance. The samples from winter and spring (to the right) are quite distinct from those of summer and autumn (to the left). Few samples from December 1994 (belonging to the late summer-autumn group) are found among the winter samples. The arrow for chlorophyll *a* and fucoxanthin heads towards the winter and spring samples and is highly correlated with the first axis (Fig. 9B). It is negatively correlated with temperature moreover. The second axis represents an additional 10.3 % of the species variance and reveals a spatial gradient between the Flemish (lower part) and the E Coast (upper part) (not shown in Fig. 9A).

The spring samples were quite distinctive from the others, due to the recruitment of several flatfish species and by the presence of polychaete larvae. Decapod larvae were the most dominant group from summer to autumn, several species being present during a long period (see Chapter 5). Densities were generally low in winter, yet larval clupeids and some early recruits of decapods were already present, explaining the close position of winter and spring samples in the diagram.

Only 60.5 % of the total species variance remained after removing the temporal fraction by performing a partial CA with the months as dummy covariables. The ordination diagram shaped by the first (e.v. 0.178) and second axis (e.v. 0.086) displays 20.6 % of this remaining variance (Fig. 10A). The spatial structure is mainly determined by an onshore-offshore gradient (Flemish Banks versus Coastal Banks). Several E Coast samples reach very high scores along the first axis. A clear east-west gradient along the Coastal Banks, such as existing for the holohyperbenthos, is not present. Depth, salinity, maxN, maxS and domN are strongly correlated with the presented structure, as was also indicated for the holohyperbenthos (Fig. 10B). No obvious spatial structure can be found along the second axis.

The onshore-offshore structure was reflected in taxonomic composition and revealed ontogenetic differences for decapods. Decapod zoeae, brachyuran megalopa and polychaete larvae reached significantly higher densities at the Flemish Banks. Postlarval carideans were more abundant on the Coastal Banks (Table 4D).

Variation accounted for in the species data	Abbreviation	Analysis	Expl. var.	Covar.	Calculation
Spatially and temporally structured variation					
All variation		CA	none	none	(1)
Spatially structured variation	S	CCA	dataset S	none	(2)
Temporally structured variation	T	CCA	dataset T	none	(3)
Spatially and temporally structured variation explained by single environmental variables					
Variation explained by the single env. var.	E	CCA	single env. var.	none	(4)
Non-spatially structured variation explained by the single env. var.	$E \mid S$	partial CCA	single env. var.	dataset S	(5)
Non-temporally structured variation explained by the single env. var.	$E \mid T$	partial CCA	single env. var.	dataset T	(6)
Spatially structured variation explained by the single env. var.	$E \cap S$				(7) = (4) - (5)
Temporally structured variation explained by the single env. var.	$E \cap T$				(8) = (4) - (6)
Non-spatially or non-temporally structured variation explained by the single env. var.	$E \mid (S \cup T)$				(9) = (4) - (7) - (8)
Shared fraction explained by the most explanatory tidal flow and SPCB variables, and their independent contribution					
Variation explained by the single flow var.	F	CCA	single flow var.	none	(10)
Variation explained by the single SPCB var.	E	CCA	single SPCB var.	none	(11)
Variation explained by the flow var., not shared with the single SPCB var.	$F \mid E$	partial CCA	single flow var.	single SPCB var.	(12)
Shared fraction of variation explained	$F \cap E$				(13) = (10) - (12)
Variation explained by the single SPCB var., not shared with the flow var.	$E \mid F$				(14) = (11) - (13)

Table 3. Overview of the different analyses and calculations performed for the variation partitioning on the holo- and merohyperbenthos species matrices. For each analysis, the variance accounted for with abbreviation as used in Fig. 12 is given; the applied ordination technique (Analysis), the dataset entered as explanatory variables (Expl. var.) and as covariables (Covar.) are also indicated. Most explanatory tidal flow variables (F) were maxS and maxT for holo- and merohyperbenthos, resp.

Variance partitioning

An overview of all analyses and calculations performed for variance partitioning is given in Table 3, together with the abbreviations used. The fraction of the total species variance explained for each single variable in listed in Table 2. The spatially and temporally structured variance for the holohyperbenthos was quite similar and amounted to 22.8 % and 24.1 % of the total species variance in the dataset respectively. A large part of the merohyperbenthos variance was temporally structured (39.6 %), while the spatial component amounted only up to 13.3 %.

The fraction of the total holohyperbenthos species variance explained by depth, mean grain size, salinity and nitrate was predominantly spatially structured (Fig. 12A); chlorophyll *a* was most explanatory for the temporal component of the species variance. Also note that temperature only explained a small fraction of the temporally structured species variance. Chlorophyll *a* (correlated with fucoxanthin) and temperature were the most explanatory variables for the merohyperbenthos (more than 7 %) and were uniquely explaining temporal variance (Fig. 12B).

The fraction variance explained by previous SPCB variables that is shared with the most explanatory tidal flow variables, is also presented in Fig. 12. MaxS was most explanatory for the holohyperbenthos (Table 2) and showed a considerable overlap for its percentage variance explained with depth, mean grain size, salinity and nitrate (Fig. 12C). For merohyperbenthos, maxT contributed most conspicuously in explaining the species variance (Table 2) and shared the highest fraction explained with temperature and chlorophyll *a* (Fig. 12D).

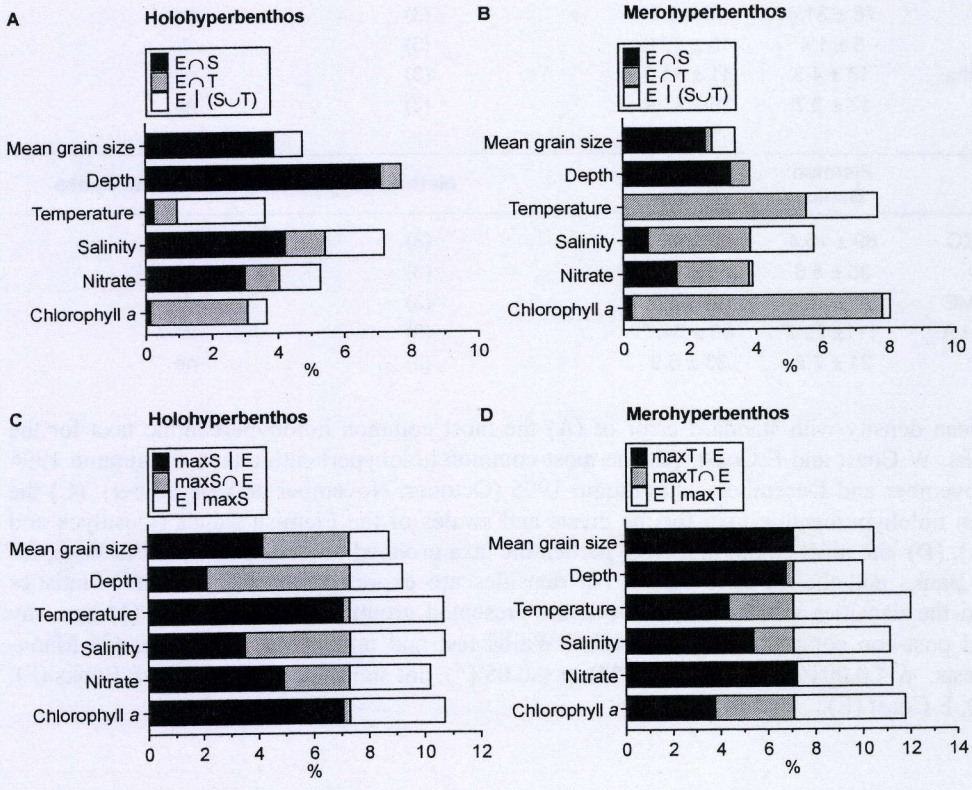

Fig. 12. Overview of the results of the variation partitioning. Spatially and temporally structured variation explained by selected single environmental variables for **(A)** holoyperbenthos and **(B)** merohyperbenthos. Shared fraction explained by the most explanatory tidal flow and SPCB variables, and their independent contribution for **(C)** holohyperbenthos and **(D)** merohyperbenthos. For explanation, see text and Table 3.

A	Flemish Banks	W Coast	E Coast	Method	All	F vs W	F vs E	W vs E
Mysidacea	74 ± 15.1	177 ± 33.8	597 ± 204.5	(1)	***	ns	***	***
Amphipoda	123 ± 55.4	104 ± 28.5	479 ± 210.6	(2)	ns			
Ctenophora	95 ± 26.5	107 ± 25.9	41 ± 19.8	(2)	ns			
Cnidaria	44 ± 14.0	15 ± 5.6	11 ± 7.1	(2)	ns			
Cumacea	22 ± 9.3	5 ± 0.9	9 ± 2.8	(2)	ns			
Chaetognatha	27 ± 5.0	9 ± 2.5	6 ± 1.2	(1)	***	***	**	ns
Copepoda	25 ± 4.9	5 ± 1.1	6 ± 2.1	(1)	***	***	***	ns

B	1994	1995	Method	1994 vs 1995
Holohyperbenthos	219 ± 26.7	524 ± 138.2	(3)	**
Mysidacea	105 ± 21.9	351 ± 133.9	(3)	*
Amphipoda	56 ± 8.8	40 ± 12.0	(3)	**
Ctenophora	5 ± 1.8	62 ± 21.2	(3)	***
Cnidaria	7 ± 2.4	37 ± 12.6	(3)	*
Cumacea	8 ± 1.7	9 ± 2.4	(3)	ns
Chaetognatha	17 ± 3.4	14 ± 3.5	(3)	ns
Copepoda	17 ± 6.2	12 ± 4.3	(3)	ns

C	Crest	Swale	Method	Crest vs Swale
Mysidacea	42 ± 8.4	101± 29.2	(3)	*
Amphipoda	33 ± 7.9	243 ± 136.1	(3)	ns
Ctenophora	98 ± 45.7	69 ± 32.3	(3)	ns
Cnidaria	76 ± 31.4	18 ± 9.5	(3)	ns
Cumacea	5 ± 1.4	45 ± 22.6	(3)	*
Chaetognatha	16 ± 4.3	41 ± 11.0	(3)	ns
Copepoda	17 ± 3.7	36 ± 11.0	(3)	ns

D	Flemish Banks	Coastal Banks	Method	Flemish vs Coastal Banks
Decapoda ZO	89 ± 15.4	37 ± 7.6	(3)	***
Caridea PO	35 ± 5.6	71 ± 12.4	(3)	ns
Brachyura ME	53 ± 12.7	26 ± 5.9	(3)	*
Polychaeta LA	111± 29.7	68 ± 24.7	(3)	***
Pisces PO	21 ± 7.2	33 ± 6.9	(3)	ns

Table 4. Mean density with standard error of **(A)** the most common holohyperbenthic taxa for the Flemish Banks, W Coast and E Coast. **(B)** the most common holohyperbenthic taxa for autumn 1994 (October, November and December) and autumn 1995 (October, November and December). **(C)** the most common holohyperbenthic taxa for the crests and swales of the Flemish Banks (Oostdyck and Kwinte Bank). **(D)** the most common merohyperbenthic taxa grouped according to their life stage, for the Flemish Banks and the Coastal Banks. All densities are expressed as ind. 100 m^{-3}. Statistics performed on the densities among and between the presented groups are summarized; (1) one-way ANOVA and post-hoc comparisons, (2) Kruskal-Wallis test and multiple comparisons; (3) Mann-Whitney U-tests; $p < 0.001$ (***), $p < 0.01$ (**), $p < 0.05$ (*), not significant (ns); Flemish Banks (F), W Coast (W), E Coast (E).

Discussion

Restrictions

This chapter was to find out if any correlation exists between current strength and hyperbenthic community structure, using field-based density data. This is the first time ever to address this issue in such a manner. A plethora of variables was therefore examined, expressing characteristics of both tidal and residual flow. It is important to note that these variables were not measured in the field, but are derived from a hydrodynamical model which was implemented on the Belgian continental shelf on a grid with a resolution of 25" x 40". The model is two-dimensional and only calculates the vertical-integrated current. The vertical structure of the currents is not calculated in the model itself. Due to the nature and the resolution of the model, small-scale eddies and current variations are parametrised and cannot be reproduced. This study however deals with large-scale patterns in space as well as time and therefore only aims to detect major patterns. The results are now considered in terms of the prevailing hydrodynamical knowledge of the area and the possible variations in the near-bottom layer.

SPCB versus current strength

Despite the overlap (< 50 %) of the fraction explained by the most explanatory SPCB and current strength variables, they do explain a significant independent fraction of the holo- and merohyperbenthos species variance (Fig. 12C and 12D). Their influence should therefore be evaluated based on the knowledge of species ecology thus possibly revealing distinct structuring aspects concerning the SPCB versus the current velocity variables.

Granulometric characteristics of the biotope in which species are found, are generally reported in hyperbenthos literature (e.g. Cunha *et al.* 1997; Dauvin *et al.* 2000). Still, evidence for species-specific relations remains poorly documented. Muddy bottoms are often thought to have potential food availability. The grain size distribution is here believed to reflect the exposure and dynamics of the area. The majority of the hyperbenthic fauna is non-burrowing and may rather be dependent on the hydrodynamical mechanisms causing deposition and resuspension, than on the sediment structure itself. Yet, several exceptions certainly exist, as there are the burrowing mysid genus *Gastrosaccus* (Nel *et al.* 1999) and several amphipod and cumacean species (Jones 1976; Lincoln 1979). Presettlement stages of benthic organisms also have a certain potential to select a suitable habitat possibly guided by sedimentological characteristics (Butman 1987).

The relation of species occurrences and certain physico-chemical and biological variables is better documented. Salinity and nitrate explained a high fraction of the spatially structured variance of the holohyperbenthos in this study (Fig. 5 and 12A). High nutrient levels and low-salinity water masses, typical for the E Coast, are due to the outflow of the Westerschelde estuary. The species reported for this area often resist strong salinity changes and the majority also occurs in the polyhaline zone of the Westerschelde estuary (see Chapter 5). Yet, some of these like the most abundant mysid species do also occur in fully marine habitats (see Chapters 4 and 5). According to Webb *et al.* (1997), salinity is not of major importance regarding spatial distribution of mysids in coastal waters, judging from their

osmoregulation (Webb *et al.* 1997). Moreover, Roast *et al.* (1998) experimentally showed a stronger response to flow velocity than to salinity for the brackish water mysid *Neomysis integer*.

Temperature and chlorophyll *a* explained only little (less than 4 %) of the holohyperbenthos species variance (Fig. 12A). As the majority of these animals are omnivores or detritivores (see Chapter 5), they probably do not rely on primary production. This was also presumed by Vallet & Dauvin (1998). High temperatures often induce higher secondary reproduction for mysids or amphipods (e.g. Mauchline 1980; Mees *et al.* 1994; Drake & Arias 1995). Nevertheless, apart from density fluctuations caused by the production of young, mysid abundance is locally also affected by aggregation or migration behaviour and may thus be apparent (Mauchline 1971a). Such behaviour remains very difficult to unravel and possibly masks a recruitment-related correlation with temperature.

Temperature and chlorophyll *a* were of major importance for explaining the temporal variance in the merohyperbenthic community (Fig. 9 and 12B). The causal relationship with temperature is obvious. Hatching and recruitment of decapod larvae and fish larvae is often triggered by water temperature (Russell 1976; Lindley 1998). The fraction explained by temperature and chlorophyll *a* showed an overlap of 28 %. Still, chlorophyll *a* may indicate the presence of food sources for herbivores. Peaks of abundance of planktivorous larvae are indeed often linked to phytoplankton blooms (Starr *et al.* 1990).

The sedimentological, physico-chemical and biological variables are therefore to a certain extent related to both holo- as well as merohyperbenthic community structure. The lack of knowledge on species ecology however hampers further insight into possible direct relations. The relation of the SPCB variables with the main spatial patterns, i.e. a pronounced onshore-offshore and less conspicuous east-west gradient roughly correspond as discussed in Chapter 4. The temporal patterns were examined in detail in Chapter 5. Further discussion is focused on the possible influence of the tidal and residual flow on the spatio-temporal species variance of the hyperbenthos.

Tidal flow: structuring factor for holohyperbenthos?

Onshore versus offshore

Spatial structure of holohyperbenthos was mainly correlated with the maximum velocity in the NS direction and the dominant tide. The Coastal Banks are characterised by lowest flow velocities and a flood-dominated current regime (see Fig. 4A). Mysids were by far the most dominant taxa on the Coastal Banks, suggesting that the occurring species are able to resist being swept offshore by the flood-dominated flow. These animals are generally good swimmers and exhibit strong rheotaxic (i.e. response to the stimulus of a current) behaviour (Mauchline 1980). Swimming speed for marine mysid species are however poorly documented, but differs among species and age groups (Clutter 1969). The few data reported in literature range between 2.5 cm s^{-1} (for juveniles) and 40 cm s^{-1} (maximum speed during short period) (Clutter 1969; Mauchline 1980). Yet, normal cruising speed for several species with a body length of 5-9 mm, i.e. being representative for many species, may be around 5-7 cm s^{-1} (Clutter 1969; Mauchline 1980). As they occur very close to the seabed (see Chapter 1), they are expected to benefit from the slower near-bottom flow. This has been shown for *Mesopodopsis slabberi* in an estuarine

environment. It remains close to the substratum in order to maintain position during ebb tide, avoiding seawards displacement (Wooldridge & Erasmus 1980).

The advantage of staying close to the shore for these omnivores might originate from feeding requirements, since suspension and resuspension processes are highest onshore (see Chapters 4 and 5).

The Flemish Banks

Community structure for holohyperbenthos differed between the crests and the adjacent swales of the Flemish Banks. The ordination analysis revealed a correlation with the dominant tide, which is ebb-linked for the swales (Fig 4A and 8B). Except for hydromedusae and ctenophores, the holohyperbenthic taxa were nearly twice as abundant in the swales (Table 4C). Several explanations are possible.

Firstly, current strength on the crests is quite high throughout the tidal cycle (Fig. 3) and the steep slope of the 10-20 m high sandbanks suggests the generation of a strong bottom friction at shallow depths. This implies that suspended matter probably has little chance to settle. Small amounts of mud were encountered in the adjacent swales, mainly after heavy weather (Chapter 5). Despite the strong NS current, velocities in the gullies diminish during a tidal cycle therefore making way for sedimentation of particular matter. The swales therefore may be more attractive than the crests in terms of feeding for bottom-dependent animals in particular. Other benthic taxa like meiobenthos indeed also attain higher densities in the swales (Vanaverbeke *et al.* 2000). This is probably also the case for macrobenthos suggested by intense bioturbation in the swale environs, as revealed by seismic profiling (Trentesaux *et al.* 1994).

Secondly, individuals occurring onshore may loose their retention mechanism with an increasing flood-dominated flow (e.g. during storm events) consequently being transported towards the Flemish Banks. The mysids occurring in the gullies were indeed often juveniles of the most abundant onshore species, apart from species that were rather confined to more offshore waters. A behavioural response to increased flow is documented for the brackish species *Neomysis integer*. When currents are getting stronger, it has been shown to sit on, attach to, or even burry into the bottom (Roast *et al.* 1998), but it looses retention at flows exceeding 6 to 12 cm s^{-1} (Roast *et al.* 1998; Lawrie *et al.* 1999).

Alternatively, mysids are reported to actively migrate to deeper areas in order to escape strong wave action on the shore (Colman & Segrove 1955; Mauchline 1980; San Vicente & Sorbe 1995; Beyst *et al.* in press a). At shallow depths, wave action might persist throughout the entire water column during heavy weather, while the gullies of the Flemish Banks (30 m depth) may still provide considerable shelter.

Residual current

Seasonality in community structure was most distinctive between spring and autumn (Fig. 6). The ordination analysis applied on the full holohyperbenthos species data revealed however an interannual variability between autumn 1994 and the same period in 1995, along the main structuring axis (Fig.6). Thus, differences in community structure between years might be more pronounced than seasonal variability. This autumn interannual variability was related to the residual current

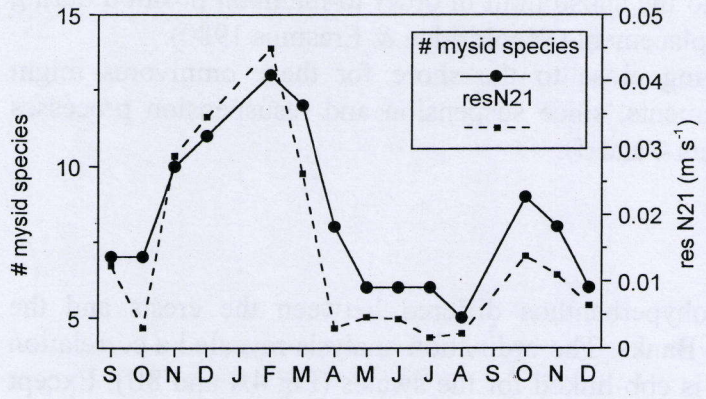

Fig. 13. Temporal fluctuation of the total numbers of mysid species in relation to residual flow.

calculated over a 21-day period (Fig. 7). The residual current during autumn 1994 was indeed stronger pointing towards the NE compared to autumn 1995, as illustrated in Fig. 4B for its N-component. Total holohyperbenthos density was higher during autumn 1995 and significant differences in density for several taxa could been indicated between the two years (Table 4B).

The residual flow is strongly affected by wind conditions (and atmospheric pressure), predominantly blowing from a SSW to SW direction in the studied area (Ministerie van de Vlaamse Gemeenschap 1993; Van Lancker 1999). Although variation in the wind climate might show seasonality, wind direction during stormy periods may largely differ (Van Lancker 1999). The strongest winds generally blow from a WSW to NW direction or are generated from the NE (Ministerie van de Vlaamse Gemeenschap 1993). Thus, the interannual variability might be induced by a different wind climate. Fluctuations in planktonic taxa, like the cnidarians and hydromedusae encountered during this study, have often been related to wind-induced transport (Belgrano *et al.* 1995). This remains questionable for mysid populations, as certain species may actively look for shelter when weather conditions are harsh (Colman & Segrove 1955; Munilla *et al.* 1998; San Vicente & Sorbe 1999; Beyst & Mees submitted), while on the other hand, they might loose retention leading to a passive transport.

However, the temporal fluctuation of the total numbers of mysid species attained two peaks, one in February and a smaller one in October 1995 (Fig. 13). Total species numbers were strongly correlated with the residual current, both with the N-component (Pearson $r = 0.92$, $p < 0.001$, Fig. 13) and the E-component (Pearson $r = 0.92$, $p < 0.001$, not presented). Highest numbers coincided with strongest NE directed residual flow. The water mass sampled then is more influenced by the adjacent beaches and / or by the English Channel. The majority of the species caught during this period is indeed reported for the English Channel (Zouhiri *et al.* 1998; Dauvin *et al.* 2000; Chapter 5) and most of them occur occasionally in the adjacent surf zone (Beyst *et al.* in press a; Beyst & Mees submitted). Unusual findings of a species (*Paramysis bacescoi*), only reported for estuaries and beaches (Labat 1953; Cunha *et al.* 1999; San Vicente & Sorbe in press) and unknown for the Belgian fauna until now, were recorded in considerable numbers during the first peak of NE directed residual flow (see Chapter 5). Thus, irrespective of mysid behaviour, these findings clearly illustrate the importance of hydrodynamics (and probably also the wind climate) in understanding temporal variability of mysid occurrence.

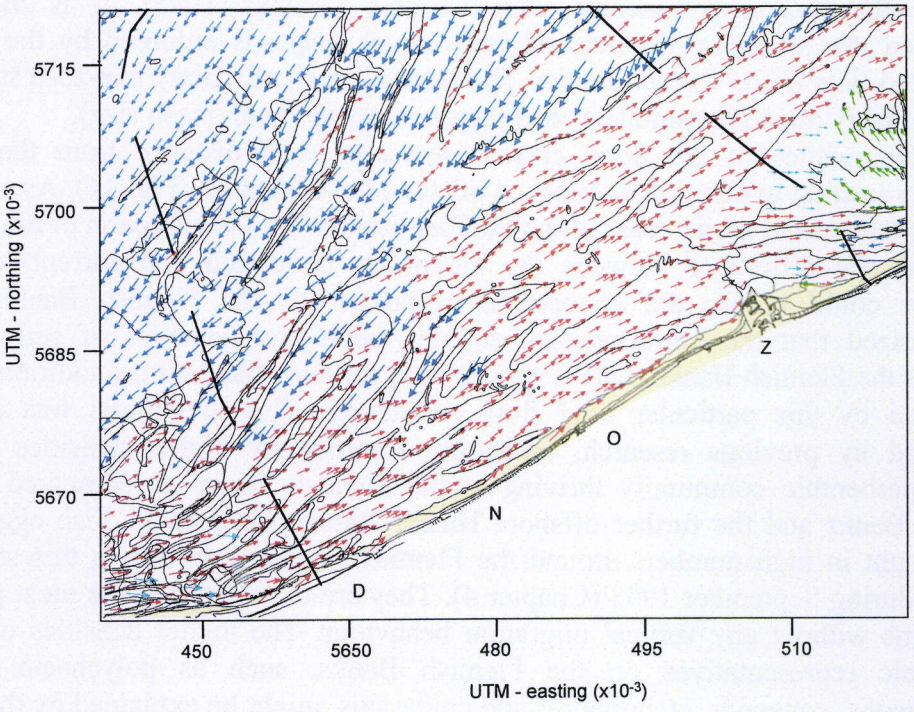

Fig. 14. Maximum current velocity and its direction in the study area, for a spring tide tidal cycle. Data were generated by the MU-BCZ hydrodynamical model (Adam 1979; Van den Eynde 1994). Colors refer to the directional quarter sectors in which a maximum velocity is reached (after Lackneus *et al.* 2001).

Dispersal hypothesis

The Flemish Banks harboured the highest numbers of decapod zoeae, though postlarval shrimp were more abundant onshore. The most common decapod species encountered, i.e. *Crangon crangon*, *Carcinus maenas* and *Liocarcinus holsatus*, (see Chapter 5) occur as adults in the shallow subtidal and intertidal reaches of the Belgian coast (Beyst *et al.* in press b; Cattrijsse & Vincx 2001). The latter also inhabits the deeper subtidal (Adema 1991; Jennings *et al.* 1999; A. Cattrijsse unpubl. data).

Larval release by adults living close to the shore is often focused on offshore transport in order to maximize dispersion and to avoid predation and beaching (Morgan 1995; Zeng & Naylor 1996; Amend & Shanks 1999). Early brachyuran stages are generally positively phototactic, promoting an upward transport (Sulkin 1984). However, there is a recent strong believe that many swimming larvae have the ability to regulate their horizontal dispersal by vertically migrating in order to enjoy selective tidal stream transport (Shanks 1995; Metaxas 2001). But, to avoid offshore transport, larvae must migrate either to the bottom or at least into the near-bottom waters. This region shows the ebb tide current being slowed by bottom friction (Shanks 1995). The morphology of early larval stages nevertheless suggests that they are not adapted to sit on the sea floor. At this developmental stage therefore, they are most probably not able to fully resist tidal flow (Shanks 1995). It is moreover highly

swimming. Their swimming capacity (several mm to cm s^{-1}, Sulkin 1984) seldom exceeds the typical continental shelf currents (Shanks 1995). It is therefore postulated that offshore dispersal of early larval stages is enforced by the flood-dominated flow at the Coastal Banks. The skewed catch of mainly late-zoea stages is most probably due to the smallest zoea stages escaping (1mm mesh size).

Dominance of the flood current decreases with distance from the shore gradually leading to ebb tide dominance off the Flemish Banks (Fig. 14). As a result, offshore larval drift might cease along the Flemish Banks. The direction of maximum flow and the difference between the maximum flood and ebb current velocity therefore could induce the entrapment of larvae off the Flemish Banks. It is hypothesized that these mechanisms explain the higher densities of early larval stages at the Flemish Banks. Larval supply from further offshore may additionally be supported by this particular tidal flow circulation. This hypothesis was already supported by previous research, indicating significantly higher densities of the merohyperbenthic community thriving at the Flemish Banks as compared to the Coastal Banks and the further offshore Hinder Banks (Chapter 4). Fish eggs were also caught in high numbers around the Flemish Banks, both during this study as well as during September 1993 (Chapter 4). They are considered as the most passive organisms without any vertical migration behaviour. The higher densities of other planktonic representatives on the Flemish Banks, such as polychaete larvae, chaetognaths, copepods, ctenophores and cnidarians, might be explained by the same mechanism.

During ontogenetic development, planktonic larvae of benthic organisms become negatively buoyant, positively geotactic and negatively phototactic, which increases their probability to descent to the benthos (Metaxas 2001). Besides behavioural changes, their swimming ability increases (Shanks 1995). Later stages gain the ability to settle and must therefore migrate to their preferred habitat. Many postlarval crustaceans are strong swimmers (5 to 10's of cm s^{-1}) (Shanks 1995). Their morphology (e.g. crab megalopae, postlarval shrimp) suggests a capability of sitting on the bottom (Shanks 1995) thereby avoiding the ebb tide current. As postlarval shrimp were more abundant onshore, it is suggested that they are progressively reaching their adult habitat in the more shallow subtidal and intertidal reaches. Selective tidal stream transport is also well documented for fish larvae (e.g. Rijnsdorp *et al.* 1985; Bos 1999; Jager 1999; Jager & Mulder 1999). During spring, high numbers of metamorphosing flatfish were caught. After a planktonic drift stage, the ability to regulate transport towards suitable nursery grounds increases at the following metamorphosing stage (Grioche *et al.* 1997; Grioche *et al.* 2000).

Finally, the distinct tidal stream characteristics between the sandbanks' crests and swales, as illustrated by the tidal ellipses, might have a role in the transport of fauna on a broader spatial scale. The tidal flow component in the east-west direction at the crests, largely disappears in the swales. As discussed above, animals might benefit from the ebb-dominated flow in order to reach preferred habitats in the coastal area. The residual current close to the bottom, not being dealt with for this study, is additionally directed towards the shore for this part of the southern North Sea (Djenidi *et al.* 1996). It is therefore postulated that these particular tidal characteristics occurring at the Flemish Banks, could possibly be a way for animals from adjacent areas to reach the shallow coastal waters and its adjacent nurseries.

Conclusions

Due to the interaction between the hydrodynamic system and the morphodynamics of the sandbanks in the Belgian coastal zone, tidal currents are very complex, as compared to areas without such formations. The particular current regime off the Flemish Banks might be of significance for: (1) preventing larvae from being swept off the coastal area; (2) an additional further larval supply from offshore waters; and (3) a further overall support to the biodiversity of the sandbanks possibly extending to the Coastal Banks. Sampling designs with a fine spatial scale combined with the assessment of detailed flow variability might be a key to successfully track species dispersal patterns. This should be further underpinned by experimental studies on the behaviour of larval organisms in the hyperbenthal zone.

Changes in residual flow and wind climate might prevent or trigger larvae to reach the shallow, sheltered areas on the Coastal Banks. It is therefore not unlikely to consider such events as possible explanation for interannual recruitment success of various species.

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Summary

The North Sea is one of the environmentally most diverse regions in the NE Atlantic (Glémarec 1973; Lee 1980) and one of the most productive oceanic regions in the world (Backhaus 1980). It has a long history of multiple uses by many people, exerting strong pressure on the health of the North Sea ecosystem. Despite the fact that scientific research has been intense in the North Sea region, there is still a need in knowledge of its biodiversity for proper management of the area (Cripps & Christiansen 2001; Ducrotoy *et al.* 2000). Baseline data for the hyperbenthos, i.e. the small animals living in the water layer close to the seabed (Mees & Jones 1997), is virtually lacking for most parts of the North Sea. The holohyperbenthos (organisms spending variable periods of their adult life in the hyperbenthal zone) plays an important role in trophic food webs, being consumed by various juvenile demersal fish and adult shrimp (Mauchline 1980; Mees & Jones 1997; Cartes 1998). Further, larval stages of many benthic organisms (belonging to the merohyperbenthos) occur in the near-bottom water layer, prior to their settlement.

The primary aim of this study was to provide baseline data of the spatio-temporal distribution of the hyperbenthos communities of the North Sea and to focus on regulating factors shaping these communities. This was approached by examining species composition, density, biomass and diversity of the hyperbenthos within well-chosen areas of the North Sea. The main working area was the Belgian continental shelf (Chapters 4, 5 and 6). This area is characterised by an extensive sandbank system merging into gently sloping sandy beaches, and extending eastwards into the mouth of the Westerschelde estuary. Two working areas were selected to the north of the Belgian continental shelf, i.e. the Dogger Bank (Chapter 1) and the Frisian front (Chapter 2). The Dogger Bank is an offshore shallow sandbank in the central North Sea, while the Frisian front area (off the N Netherlands) area is special regarding its organically enriched seabed. Both are located at the transition zone between mixed and stratified water masses in the North Sea. Towards the south, emphasis was put on the fauna of the shelf break and the upper continental slope, delineating the European continental shelf from the N Atlantic deep sea (Chapter 3). In each area, a modified hyperbenthic sledge after Sorbe (1983) was used for sampling, collecting the fauna of the 100 cm water layer above the seafloor. All organisms caught within a size range of 1 mm up to approximately 20 mm were examined.

Dogger Bank, Frisian front and the shelf break / continental slope

Dogger Bank

The hyperbenthos of the Dogger Bank was sampled in August 1994, along a south-to-north transect, covering water masses on the most shallow part of the sandbank and from its deeper surroundings (9 sites). A total of 158 species were recorded, belonging to at least 28 orders. Amphipods and mysids were the most abundant taxa.

The total density of the holohyperbenthos ranged from 47 to 3681 ind. 100 m^{-2} and peaked at the deepest sites. Highly motile species such as the mysids *Schistomysis ornata* and *Erythrops elegans* attained highest densities on a muddy

seabed, supposedly providing feeding opportunities for these animals. These species dominated the community both to the north as well as to the south of the Dogger Bank, together with a number of detritivorous amphipods and cumaceans. The fauna north of the Dogger Bank was much more diverse with a drastically different species composition compared to more southern sites, due to the appearance of boreal species.

Merohyperbenthic species (mainly larval decapods and postlarval fish) attained prominent density peaks (maximum of 1350 ind. 100 m^{-2}) at the northern shallow part of the Dogger Bank itself, except for postlarval Caridea. Brachyura larvae were the most abundant. This increase in density coincided with a drop in surface temperature and salinity, presumably due to the intrusion of a water mass from coastal origin.

It was hypothesized that the observed pattern in community structure may be related to the occurrence of the summer tidal mixing front in the area.

Frisian front

The Frisian front and its surrounding waters was investigated along two cross-frontal transects in August 1994 and April 1996 (22 samples in total). A total of 111 species was recorded, mainly peracarid crustaceans and decapods. On average, *Calanus* spp. (Copepoda), *Schistomysis ornata* (Mysidacea) and *Scopelocheirus hopei* (Amphipoda) represented more than 40 % of the total density, while *S. ornata* dominated the biomass for 30 %. Community structure differed strongly between both months, as shown by the species composition and the fact that densities and biomasses were much lower in April.

In August, the density of the holohyperbenthos fraction reached quite pronounced peaks in the area coinciding with the Frisian front (> 3000 ind. 100 m^{-2}): densities for chaetognaths, copepods, amphipods and mysids were one order of magnitude higher compared to the surrounding waters. Diversity was also highest at the Frisian front. The high abundances may be explained by active migration and/or by passive transport to the food-enriched area. Merohyperbenthic species showed a less distinct increase in density in the front zone, but a clear south-to-north change in community structure was observed. These species are more heavily subjected to the prevailing current regime. The Frisian front fauna seems to be transitional between two merohyperbenthic communities established in late summer, belonging to the environmentally different sandy Southern Bight to the south and the silty Oyster Ground to the north.

In spring, no such hyperbenthic enrichment over the Frisian front was observed. This is most probably due to the strong seasonality of the hyperbenthic fauna and the low water temperature suggesting that production and subsequent recruitment does not have started yet. Alternatively, winter storms could have resuspended particulate organic matter, followed by a rapid reaction of the motile hyperbenthos to more northern depositional areas and thus leading to a temporal density decline. It was concluded that the Frisian front is an enriched area for the hyperbenthos at the end of summer, as was already reported for the benthic system below.

Shelf break and upper continental slope

The hyperbenthos in the benthic boundary layer of the shelf break and the upper continental slope of the northern margin of the Bay of Biscay (Eperon Berthois) was investigated. Six sites within a depth range from 200 to 700 m depth were sampled in September 1995. A total of 214 species were caught and a pronounced shift in community structure between the shelf break (250 - 300 m depth) and the upper slope (600 - 700 m depth) was present.

The shelf break hyperbenthos (862 ind. 100 m^{-2}) mainly consisted of mysids (33 %), amphipods (28 %) and euphausiids (19 %). Densities at the upper slope were slightly higher (959 ind. 100 m^{-2}) and amphipods represented 45 % of the total community; subdominant taxa were cumaceans (26 %) and isopods (13 %). Estimates of species richness and species diversity indicated a more diverse fauna at the upper slope. This was attributed to high species numbers of isopods and cumaceans (as for the asellote isopod families and Cumacea of the family Nannastacidae) and an increase in the number of copepod species. The amphipod assemblage was only slightly more diverse at the upper slope than at the shelf break, but a clear transition in family composition was observed. Similarly, a change in the mysid assemblage was observed at the genus level. The Mysidacea was the only peracarid taxon for which species richness was observed to decrease with depth. The bathymetric distribution of mysids, euphausiids and decapods was believed to be rather related to properties of the water column (light transmission, particulate organic matter, ...), than to sediment characteristics. Bottom-dependent taxa such as amphipods, cumaceans and isopods, may be more dependent on sediment composition, linked to variations in organic particle transport in the benthic boundary layer.

Belgian continental shelf

Spatial patterns in community structure at the Belgian continental shelf and adjacent areas

A baseline spatial study (62 sites) of the hyperbenthos of the Belgian continental shelf, the continental shelf off Zeeland and the Westerschelde estuary was carried out in the summer of 1993.

A total of 109 taxa were recorded, half of which were amphipods and decapods. Mysids were the most important taxon in terms of density and biomass. In all, seven hyperbenthic communities were identified. Their geographical occurrence was correlated with the presence of isolated sandbank systems in the area. The community in the mesohaline reaches of the Westerschelde estuary was very different from the shelf hyperbenthos and was characterized by the highest density and biomass and lowest diversity. Two gradients in community structure were detected on the continental shelf: the principal onshore-offshore gradient perpendicular to the coastline and a less pronounced east-west gradient parallel to the coastline. The first gradient mainly indicated differences in density and biomass, while the second reflected species richness and diversity.

The holohyperbenthos attained highest densities at the Coastal Banks and consisted nearly exclusively of mysids; *Schistomysis spiritus* and *S. kervillei* were the most common species. Community composition altered with distance from the shore

and planktonic species gained in abundance. The most diverse communities were found at the Flemish and Zeeland Banks.

The merohyperbenthos was most abundant at the Flemish and Zeeland Banks and was mainly composed of a variety of larval decapods. Biomass peaked at the Coastal Banks with a dominance of postlarval gobies. A strong diversity gradient was found for the merohyperbenthos with a richer fauna off the Belgian coast as compared to the Zeeland offshore waters.

Spatio-temporal patterns at the Coastal and Flemish Banks

In order to evaluate temporal patterns in community structure of the hyperbenthos thriving in Belgian coastal waters, monthly surveys (from September 1994 until December 1995) were carried out at the Coastal and Flemish Banks (13 sites in total).

For holohyperbenthos, spatial structure, corresponding to the major cross-shore and secondary alongshore gradient, persisted throughout the year. The Flemish Banks harboured year-round the most diverse community, characterised by planktonic species (chaetognaths, copepods, hydromedusae and ctenophores) accounting for half of the total density in this area. Highest densities were encountered at the E Coast. Mysid dominance typified this area and diversity was in general low. A total of 93 holohyperbenthic species were recorded during this temporal survey. The onshore-offshore gradient for the merohyperbenthos community existed as well, although masked by a much stronger temporal pattern. As for the holohyperbenthos, the Flemish Banks were most diverse; several species, like most anomurans and certain fish species, preferentially occurred in this area. Moreover, decapods showed ontogenetic differences in spatial distribution. Zoea stages of nearly all species were typically found at the Flemish Banks, whereas postlarval carideans were more abundant at the Coastal Banks. Diversity for the merohyperbenthos was also distinctly lower at the E Coast. *Crangon crangon* and *Lanice conchilega* larvae strongly dominated in the latter area (together more than 80 % of the total density), whereas Brachyura larvae were poorly represented.

Temporal variability in community structure for holohyperbenthos was most pronounced during spring, attributed to increased amphipod densities and a conspicuous ctenophore bloom. The amphipod *Atylus swammerdami* showed a distinct density increase at the Flemish Banks in May, coinciding with the decaying phase of a *Phaeocystis* bloom. In addition, various epifaunal amphipods (e.g. *Microprotopus maculatus*, *Pariambus typicus*, *Phtisica marina*) were encountered in association with hydrozoan colonies at the Coastal Banks. *Gammarus crinicornis*, being confined to and strongly dominant on the E Coast, similarly co-occurred with hydrozoans. Its persistence during subsequent months probably indicates detritivory after collapse of the hydrozoan populations. Mysids were most abundant during summer. However, density fluctuations were species-specific and fairly irregular. The dominant mysid *Schistomysis kervillei* (annual mean density of 293 ind. m^{-3} at the E Coast) occurred year-round at the Coastal Banks and appears to seek out turbid environments, which are favourable for feeding. *Schistomysis spiritus* is believed to be more sensitive to extremes conditions, like strong wave action, and probably migrates towards more sheltered areas. The most extreme temporal fluctuation in density was found in *Mesopodopsis slabberi*, possibly linked to migrations between the adjacent biotopes of the coastal area. Several less abundant mysid species only

occurred during a limited period; total species numbers tended to be maximal during winter.

The merohyperbenthos community was strongly temporally structured, due to differential recruitment peaks of various postlarval fish (at least 21 species) and decapod larvae (at least 29 species). Both species richness and total abundance of fish larvae were highest during April - May. Species successions were conspicuous, recruitment often being restricted to a single month. Sole *Solea solea* (confined to May) was the most abundant fish species throughout the study area with densities at times exceeding 100 ind. 100 m^{-3}. Other common species were *Pomatoschistus* spp. (all year with peaks in May and July), flounder *Pleuronectes flesus* (confined to April), clupeids (peak in February and May) and dab *Limanda limanda* (confined to May). Recruitment for decapod larvae was most pronounced from late spring to late summer, with respect to both species richness and densities. Common shrimp *Crangon crangon* (annual mean density of 137 ind. 100 m^{-3} at the E Coast), swimming crab *Liocarcinus holsatus*, shore crab *Carcinus maenas*, and porcelain crab *Pisidia longicornis* were most abundant.

Structuring factors

Habitat heterogeneity and water mass flow characteristics were believed to be of major importance in regulating the hyperbenthos in the Belgian and Zeeland coastal area.

The cross-shore gradient in community structure was related to sedimentological and physico-chemical variables, with finer sediments and the influence of coastal run-off onshore. High levels of suspended matter and the presence of a mud field at the Belgian Coastal Banks favour bottom-dependent animals in terms of food. Outflow from the Westerschelde estuary, nutrient-enriched and less saline water, most probably explains the diversity decline at the E Coast. Resistant species were however thriving in high numbers at the mouth of the estuary, despite the unpredictable fluctuations in its environs. The influence of Channel water at the offshore Flemish and Hinder Banks on the one hand and the heterogeneity in seabed structure on the other hand, might play a role in sustaining more diverse communities in these areas as compared to the area off Zeeland.

In addition, tidal flow was hypothesized to play an important role in the spatial structuring of the hyperbenthic communities in the Belgian coastal zone. Onshore, tides are asymmetric and flood-dominated (i.e. towards the north). The relative strength of flood versus ebb current gradually decreases with offshore distance, and the ebb current (i.e. towards the south) gets dominant off the Flemish Banks. Differential swimming abilities and potential of maintaining position in flow were believed to lead to an onshore - offshore segregation among taxa.

Low current velocities at the Coastal Banks may permit settlement of the suspended matter load, enabling growth of a variety of organisms that live or feed in the near-bottom water layer. Mysids, amphipods and postlarval shrimp favour this area and have the ability to maintain their position and avoiding offshore transport by the flood-dominated flow. Suspended matter concentration is *in se* lower at the Flemish Banks, and deposition on its crests is moreover prevented by a persisting strong flow. Although of minor importance, organic matter sedimentation at the Flemish Banks may occur in the swales, which are characterised by slower currents at the turning of the tides, and thus permitting development of populations of bottom-

dependent animals. High densities of planktonic organisms in this area, like cnidarians, hydromedusae and decapod zoeae, can be due to accumulation processes, induced by the particular current regime. Flood-dominance on the shore might lead to dispersal in a seawards direction, while ebb-dominated flow north of the Flemish Banks could deliver an additional supply of organisms from farther offshore waters.

The temporal pattern in holohyperbenthos community structure did not show a clear meaningful correlation with any measured environmental variable. Some phenomena, like the conspicuous *Phaeocystis* bloom during spring and the growth of hydrozoan colonies during summer were believed to be of structural importance. Moreover, migration behaviour of many species might mask seasonality. It is well known that recruitment of merohyperbenthic species, like larval fish and decapod larvae, shows a relation to temperature and probably also to phytoplankton blooms, which was also revealed by this study. Temporal variability was moreover to a certain extent related to fluctuations in residual flow. A conspicuous correlation was found between the monthly numbers of mysid species and this residual flow. Interannual variability, observed between autumn 1994 and 1995 could been linked to differential directions in residual flow, which is probably driven by variations in wind conditions. It is not unlikely that hydrodynamic conditions *per se* play a major role in structuring coastal hyperbenthic communities, especially with respect to larval recruitment events.

In conclusion, the estuarine outflow on the one hand and the hydrodynamic setting and protective function of the sandbanks on the other hand create diverse environs along the Belgian coastal zone, sustaining rich communities of holohyperbenthic species and early life history stages when compared to the adjacent areas.

Samenvatting

De Noorzee is één van de meest productieve zeeën ter wereld (Glémarec 1973; Lee 1980) en wordt gekarakteriseerd door een brede waaier aan variabiliteit in z'n milieu (Backhaus 1980). De gezondheid van het Noordzee ecosysteem is sinds jaren in het gedrang door frequente antropogene activiteiten van allerlei aard. Niettegenstaande er diverse wetenschappelijke studies zijn gebeurd in het Noordzee gebied, is er toch een nijpend gebrek aan kennis over zijn biodiversiteit, wat noodzakelijk is voor een adequaat beheer (Cripps & Christiansen 2001; Ducrotoy *et al.* 2000).. Het hyperbenthos, de kleinere organismen die in nabijheid van de zeebodem vertoeven (Mees & Jones 1997), werd in de Noordzee nog maar zelden bestudeerd. Nochtans is het belang van deze organismen in estuariene- en kustecosystemen als voedselbron voor juveniele vissen en adulte garnalen erkend (Mauchline 1980; Mees & Jones 1997; Cartes 1998). Bovendien vertoeven larvale levensstadia van vele bodemdieren een welbepaalde periode in de hyperbenthale zone vooraleer ze recruteren in hun finale habitat.

Het doel van deze studie is een analyse van de ruimtelijke en temporele dynamiek van de hyperbenthische gemeenschappen in de Noordzee en de relatie tussen de waargenomen patronen en enkele belangrijke milieuvariabelen te onderzoeken. Daartoe werd de soortensamenstelling, densiteit, biomassa en diversiteit van het hyperbenthos bestudeerd in een aantal geselecteerde gebieden. De klemtoon van deze studie werd gelegd op het Belgisch continentaal plat. Dit gebied wordt gekarakteriseerd door een uitgestrekt zandbanken systeem dat overgaat in een zandige strandkust. Bovendien mondt het Westerschelde estuarium uit in het oostelijk deel van het gebied. Twee gebieden werden bestudeerd ten noorden van het Belgisch continentaal plat, nl. de Dogger Bank en het Friese Front. De Dogger Bank is een ondiepe zandbank gelegen in de centrale Noordzee. Het Friese front is gesitueerd ten noorden van Nederland en wordt gekarakteriseerd door een verrijking aan organisch materiaal in de bodem. Beide studie gebieden zijn gelocaliseerd in de overgangszone tussen gemengde en gestratifieerde watermassa's van de Noordzee. In een zuidelijke richting werd een dieptegradiënt bestudeerd, in de overgangszone tussen het Europees continentaal plat en de N Atlantische diepzee. Alle stalen voor deze studie werden genomen met een hyperbenthische slede, die geconstrueerd werd naar het model ontworpen door Sorbe (1983). Deze slede bemonstert het hyperbenthaal tussen 0 en 100 cm boven de zeebodem. Alle organismen die gevangen werden in de grootte-orde tussen 1 en 20 mm werden onderzocht.

De Dogger Bank, het Friese front en de 'shelf break' / continentale helling

<u>De Dogger Bank</u>

Het hyperbenthos van de Dogger Bank werd in augustus 1994 bemonsterd volgens een transect van zuid naar noord (negen stations). Het transect besloeg zowel de watermassa's ten zuiden en ten noorden van de bank als ter hoogte van de bank zelf. Over het volledige transect werden 158 soorten aangetroffen, behorende tot minstens 28 ordes. Amphipoda en Mysidacea waren de meest talrijke taxa.

De totale densiteit van het holohyperbenthos varieerde tussen 47 en 3681 ind. 100 m^{-2}, hoogste waarden werden bereikt in de diepere zones. Sterk mobiele soorten zoals de Mysidacea *Schistomysis ornata* en *Erythrops elegans* vertoonden de hoogste abundantie op een modderige zeebodem, welke vermoedelijk een goede voedselaanvoer levert voor deze organismen. Beide soorten domineerden de gemeenschap zowel ten noorden als ten zuiden van de Dogger Bank, samen met een aantal detritus-voedende Amphipoda en Cumacea. De meest diverse fauna werd aangetroffen ten noorden van de Dogger Bank en de soortensamenstelling was er duidelijk verschillend in vergelijking met de meer zuidelijke stations langsheen het transect. Dit was voornamelijk te wijten aan het voorkomen van boreale soorten.

Merohyperbenthische soorten (voornamelijk larvale Decapoda en postlarvale vissen) vertoonden duidelijke densiteitspieken (maximum 1350 ind. 100 m^{-2}) op het noordelijke, ondiepe deel van de Dogger Bank zelf, met uitzondering van de postlarvale Caridea. Larvale Brachyura waren het meest talrijk. Deze sterke stijging in densiteit was gerelateerd met een opvallende daling in temperatuur en saliniteit, vermoedelijk te wijten aan de intrusie van een kustgebonden watermassa.

Het Friese front

Het hyperbenthos van het Friese front werd bemonsterd langsheen twee parallelle transecten die zowel de watermassa's ten zuiden als ten noorden van het front beslaan. Het traject werd tweemaal afgevaren: in september 1994 (10 stations) en in april 1996 (12 stations). In het totaal werden 111 soorten aangetroffen, voornamelijk behorende tot de peracaride Crustacea en Decapoda. *Calanus* spp. (Copepoda), *Schistomysis ornata* (Mysidacea) and *Scopelocheirus hopei* (Amphipoda) maakten meer dan 40 % uit van de totale densiteit. *S. ornata* leverde een bijdrage van 30 % voor de totale biomassa. Het hyperbenthos vertoonde een sterk seizoenaal patroon in gemeenschapstructuur, zowel in de taxonomische samenstelling van de fauna als in de densiteit en biomassa, die veel lager waren in april 1996.

In augustus 1994 vertoonde het holohyperbenthos een uitgesproken hoge abundantie ter hoogte van het Friese front. De waargenomen densiteiten voor Chaetognatha, Copepoda, Amphipoda en Mysidacea waren een grootte-orde hoger in vergelijking met de naburige watermassa's. Ook de diversiteit was er hoger. Deze respons van de hyperbenthische fauna kan verklaard worden door een actief migratiegedrag en / of passieve transportprocessen naar de voedselrijke zone. Merohyperbenthische soorten vertoonden een minder uitgesproken stijging in densiteit ter hoogte van het Friese front, maar er werd wel een duidelijke noord-zuid gradiënt in gemeenschapsstructuur waargenomen. Het Friese front herbergt tijdens het einde van de zomer een overgangsfauna, tussen de merohyperbenthische gemeenschappen van de Zuidelijke Bocht in het zuiden, en die van de slibrijke Oestergronden in het noorden.

Dergelijke respons in verhoogde densiteit en biomassa ter hoogte van het front werd niet waargenomen in de lente. Enerzijds kan dit te wijten zijn aan de temperatuur, die vermoedelijk nog te laag was om productie en recrutering te induceren. Anderzijds is het ook mogelijk dat het organisch materiaal van de verrijkte zone in suspensie was gebracht door winterstormen en naar meer noordelijke depositiegebieden getransporteerd werd.

Samengevat is het duidelijk dat het Friese front op het einde van de zomer een verrijking van het hyperbenthos vertoont, net zoals is aangetoond voor de benthische infauna van het systeem.

De 'Shelf break' en de continentale helling

De gemeenschapsstructuur, densiteit, biomassa en diversiteit van het hyperbenthos werd bestudeerd in de overgangszone tussen het Europees continentaal plat en de continentale helling ter hoogte van Eperon Berthois, gelegen in het noordelijk grensgebied van de Golf van Biscay. Zes stations werden bemonsterd in de bathymetrische zone tussen 200 en 700 m diepte.

In het totaal werden 214 soorten waargenomen. Een sterk verschillende gemeenschap werd aangetroffen op de rand van het continentaal plat (250 - 300 m diepte, 'shelf break') in vergelijking met het stratum van de continentale helling op een diepte van 600 tot 700 m ('upper slope').

Het hyperbenthos van de 'shelf break' (862 ind. 100 m^{-2}) bestond voornamelijk uit Mysidacea (33 %), Amphipoda (28 %) en Euphausiacea (19 %). De totale densiteit was iets hoger in het 600-700 m stratum (959 ind. 100 m^{-2}) en de Amphipoda waren er dominant (45 %); subdominante taxa waren de Cumacea (26 %) en de Isopoda (13 %). De diversiteit ter hoogte van de 'upper slope' was beduidend hoger, te wijten aan het groot aantal soorten Isopoda (voornamelijk asellote families), Cumacea (voornamelijk Nannastacidae) en Copepoda. De diversiteit tussen beide dieptestrata voor de Amphipoda was eerder vergelijkbaar, maar deze orde vertoonde een wijziging in samenstelling op familieniveau. Een gelijkaardige verandering van de Mysidacea gemeenschap werd waargenomen op het genusniveau. De Mysidacea vertoonden als enig peracarid taxon een dalende tendens in soortenrijkdom met de diepte. De distributie van Mysidacea, Euphausiacea en Decapoda is vermoedelijk meer gerelateerd aan karakteristieken van de waterkolom (lichttransmissie, gesuspendeerd materiaal, voedselbeschikbaarheid,...), dan aan typische bodem kenmerken. Bodemafhankelijke taxa zoals Amphipoda, Cumacea en Isopoda zijn daarentegen eerder beïnvloed door sedimentsamenstelling en door de aanvoer van particulair organisch materiaal in de benthische grenslaag.

Het Belgisch continentaal plat

Ruimtelijke patronen in het hyperbenthos van het Belgisch continentaal plat en aangrenzende gebieden

In september 1993 werd de hyperbenthische fauna van het Belgisch continentaal plat, het Westerschelde estuarium en de Nederlandse Voordelta uitvoerig bemonsterd (62 stations). In het totaal werden 109 soorten waargenomen, waarvan de helft tot de Amphipoda en de Decapoda behoorden. De Mysidacea leverden de grootste bijdrage zowel tot de densiteit als tot de biomassa. Zeven hyperbenthische gemeenschappen werden geïdentificeerd, hun geografisch voorkomen was sterk gebonden aan de geografische locatie van de zandbanken in het studiegebied. De meest aberrante fauna werd aangetroffen in de mesohaliene zone van de Westerschelde en was gekarakteriseerd door een hoge densiteit en biomassa, maar vertoonde een lage diversiteit. Twee gradiënten in gemeenschapsstructuur konden aangetoond worden op het continentaal plat: een sterke 'onshore-offshore' gradiënt loodrecht op de kustlijn en een minder uitgesproken oost-west gradiënt evenwijdig met de kustlijn. De eerste gradiënt was voornamelijk gereflecteerd in densiteit en biomassa, terwijl de oost-west gradiënt meer gerelateerd was aan soortenrijkdom en diversiteit.

Het holohyperbenthos bereikte de hoogste densiteiten ter hoogte van de Kustbanken en bestond bijna uitsluitend uit Mysidacea; *Schistomysis spiritus* en *S. kervillei* waren de meest algemene soorten. De gemeenschapsstructuur wijzigde in samenstelling in een zeewaartse richting, met een toenemend belang aan planktonische soorten. De meest diverse gemeenschappen werden aangetroffen ter hoogte van de Vlaamse Banken en de Zeelandbanken.

Het merohyperbenthos was talrijker ter hoogte van de Vlaamse Banken en de Zeelandbanken en bestond uit een grote variatie aan Decapoda larven. Biomassa was echter het hoogst voor de Kustbanken, dit was vooral te wijten aan de aanwezigheid van postlarvale grondels. De merohyperbenthische fauna vertoonde een sterk oost-west patroon in diversiteit, de fauna ter hoogte van de Belgische kust was namelijk veel diverser in vergelijking met de Zeelandse kustwateren.

Ruimtelijke en temporele patronen in het hyperbenthos van de Kustbanken en de Vlaamse Banken

Het hyperbenthos van de Kustbanken en de Vlaamse Banken werd maandelijks bemonsterd in 13 stations gedurende de periode vanaf september 1994 tot en met december 1995.

De hoger beschreven 'onshore-offshore' en oost-west gradiënt waren permanent aanwezig voor het holohyperbenthos. Op jaarbasis waren de Vlaamse Banken het meest divers. Planktonische soorten (Chaetognatha, Copepoda, hydromedusen en Ctenophora) karakteriseerden dit gebied en waren samen verantwoordelijk voor de helft van de totale densiteit. Mysidacea daarentegen waren eerder typisch voor het Kustbanken gebied. De hoogste densiteit werd aangetroffen aan de Oostkust, maar de fauna in dit gebied was weinig divers. Gedurende deze temporele staalnames werd een totaal van 93 holohyperbenthische soorten aangetroffen.

De 'onshore-offshore' gradient kon ook gedetecteerd worden voor het merohyperbenthos, alhoewel de gemeenschapsstructuur van deze fauna veel sterker gedomineerd werd door een temporeel patroon. Net zoals voor het holohyperbenthos, waren de Vlaamse banken het meest divers. Een aantal vislarven en bijna alle larvale Anomura kwamen in hogere mate voor in dit gebied. Decapoda larven vertoonden een ontogenetisch gerelateerd distributiepatroon. Bijna alle zoëlarven kwamen preferentieel voor in het Vlaamse Banken gebied, terwijl postlarvale Caridea een hogere densiteit bereikten ter hoogte van de Kustbanken. De Oostkust vertoonde eveneens een lagere diversiteit voor de merohyperbenthische fauna. *Crangon Crangon* en *Lanice conchilega* larven waren sterk dominant in dit gebied (meer dan 80 % van de totale densiteit), terwijl de Brachyura opvallend lage densiteiten bereikten.

Temporele variabiliteit in gemeenschapsstructuur was het meest uitgesproken tijdens de lente, vooral te wijten aan een opvallende densiteitspiek voor Amphipoda en een zeedruiven bloei. De amphipode *Atylus swammerdami* bereikte enorm hoge densiteiten in mei ter hoogte van de Vlaamse Banken. Opvallend is dat deze piek samenviel met de eindfase van een *Phaeocystis* bloei. Anderzijds werd er in het Kustbanken gebied een groot aantal epifauna amphipoden (*Microprotopus maculatus*, *Pariambus typicus*, *Phtisica marina*) aangetroffen in associatie met kolonievormende Hydrozoa. Mysidacea bereikten de hoogste densiteiten in de zomer. Deze organismen vertoonden echter soortspecifieke en vrij onregelmatige

fluctuaties in hun densiteitspatroon. *Schistomysis kervillei* (jaargemiddelde densiteit: 293 ind. 100 m^{-3}) was de meest dominante soort en werd het hele jaar door aangetroffen in het Kustbanken gebied. Deze soort zoekt vermoedelijk troebel - bovendien vaak voedselrijk - water op. *S. spiritus* lijkt meer gevoelig voor extreme milieu omstandigheden (bijvoorbeeld de inwerking van sterke golfslag) en migreert dan waarschijnlijk naar meer beschutte plaatsen. Het temporeel distributiepatroon van *Mesopodopsis slabberi* vertoonde sterke schommelingen, misschien het gevolg van een migratiegedrag tussen de nabije biotopen van het studiegebied. Een aantal minder abundante Mysidacea soorten kwam enkel gedurende een beperkte periode voor; het totale aantal soorten was het hoogst tijdens de winter.

Het sterke temporele patroon in gemeenschapsstructuur van het merohyperbenthos was te wijten aan de opeenvolgende recrutering van verscheidene larvale vissen (minstens 21 soorten) en Decapoda (minstens 29 soorten). Soortenrijkdom en densiteit waren het hoogst gedurende de maanden april en mei. Het voorkomen van de meeste vislarven was vaak beperkt tot één bepaalde maand. Tong *Solea solea* (beperkt tot mei) was de meest abundante soort in het studiegebied; densiteiten hoger dan 100 ind. 100 m^{-3} werden meermaals genoteerd. Andere abundante soorten waren *Pomatoschistus* spp. (gans het jaar met densiteitspieken in mei en juli), bot *Pleuronectes flesus* (beperkt tot april), haringachtigen (densiteitspiek in februari en mei) en schar *Limanda limanda* (beperkt tot mei). Recrutering van decapoden had vooral plaats vanaf de vroege lente tot het einde van de zomer. Grijze garnaal *Crangon crangon* (jaargemiddelde densiteit: 137 ind. 100 m^{-3}), zwemkrab (*Liocarcinus holsatus*), strandkrab (*Carcinus maenas*), en het porcelein krabbetje (*Pisidia longicornis*) waren het meest algemeen.

Regulerende factoren

De heterogeniteit aan habitats en het voorkomen van meerdere watermassa's zijn vermoedelijk sterk bepalend voor de structuur van de hyperbenthische gemeenschappen in het kustgebied van België en Zeeland.

De onshore-offshore gradiënt in gemeenschapsstructuur vertoonde een korrelatie met sedimentologische, fysische en chemische variabelen; fijne sedimenten en de invloed van terrigene afvoeiing waren typerend voor de Kustbanken. De hoge concentratie aan gesuspendeerd materiaal en de aanwezigheid van een uitgestrekt slibveld ter hoogte van de Kustbanken dragen vermoedelijk bij tot een aantrekkelijke voedingsgrond voor bodemafhankelijke dieren. De aanwezigheid van Westerschelde water - nutriëntenrijk en met een lagere saliniteit - kan een verklaring zijn voor de lagere diversiteit van de hyperbenthische fauna aan de Oostkust. Resistente soorten kwamen in grote aantallen voor aan de monding van het estuarium, ondanks de vrij sterke en bovendien onregelmatige fluctuaties in dit milieu. De Hinder Banken en de Vlaamse Banken daarentegen worden vooral beinvloed door een watermassa aangevoerd vanuit het Kanaal, waarschijnlijk de belangrijkste verklaring voor de hogere diversiteit in deze gebieden. Bovendien kan de morfologische heterogeniteit van deze uitgebreide zandbank complexen, zoals bijvoorbeeld het karakter van de diepe geulen enerzijds en de sterk geëxposeerde toppen anderzijds, de habitat diversiteit - en dus ook de diversiteit van de fauna - verhogen.

Bovendien werd aangetoond dat het karakteristieke systeem van getijdenstromingen in het gebied een belangrijke rol speelt in de ruimtelijke structuur van het hyperbenthos. De Kustbanken worden gekarakteriseerd door een asymmetrisch getij met een sterke vloedstroom (naar het noorden gericht). De sterkte van de vloedstroom neemt af in de zeewaartse richting en de ebstroom wordt de dominante getijdenstroom ter hoogte van de Vlaamse Banken. De brede waaier aan zwemcapaciteiten en retentievermogen van de hyperbenthische taxa, kunnen aanleiding geven tot een onshore-offshore segregatie.

Lage stroomsnelheden, karakteristiek voor de Kustbanken, laten sedimentatie toe van gesuspendeerd materiaal. Organismen die zich in het hyperbenthaal voeden, zoals Mysidacea, Amphipoda en postlarvale garnaal worden vermoedelijk aangetrokken door dergelijke voedselrijke gebieden en kunnen bovendien weerstand bieden aan de sterke vloedstroom. De watermassa ter hoogte van de Vlaamse Banken is op zich al voedselarm en bovendien wordt sedimentatie verhinderd door de sterke stroming, vooral op de toppen van de banken. Alhoewel van minder belang, kan er depositie van organisch materiaal optreden in de geulen, vooral tijdens kentering wanneer de stroomsnelheden beduidend lager zijn. Dit verklaart waarom bodem-afhankelijke organismen in het algemeen hogere densiteiten bereikten in de geulen in vergelijking met de toppen van de banken.

De opvallend hoge densiteiten van planktonisch organismen op de Vlaamse Banken, zoald Cnidaria, hydromedusen en Decapoda larven kan te wijten zijn aan accumulatieprocessen geïnduceerd door het getijderegime. De vloedstroom nabij de kust kan tot een zeewaartse dispersie leiden, terwijl de ebstroom ter hoogte van de Vlaamse Banken organismen kan aanvoeren van meer zeewaarts voorkomende watermassa's.

Het temporeel patroon in gemeenschapsstructuur van het holohyperbenthos vertoonde geen duidelijke correlatie met de gemeten omgevingsvariabelen. Biotische factoren, zoals de uitgesproken *Phaeocystis* bloei die geobserveerd werd gedurende de maand mei en de groei van de kolonievormende Hydrozoa zouden van structureel belang kunnen zijn voor het hyperbenthos. Bovendien vertonen vele organismen een migratiegedrag, zodanig dat het moeilijk blijft om de temporele variabiliteit te ontrafelen.

De recrutering van merohyperbenthische soorten is sterk temperatuursafhankelijk en vermoedelijk ook gelinkt met fytoplankton productie. Dit was ook het geval in deze studie. Temporele variatie was echter ook gerelateerd met een fluctuatie in residuele stroming. Er werd een sterke correlatie aangetoond tussen het aantal aangetroffen soorten Mysidacea per maand en de temporele variatie in residuele stroming. Bovendien kon de variabiliteit in gemeenschapsstructuur tussen de herfst van 1994 en 1995 gekoppeld worden aan variaties in de richting van de residuele stroming. Het is daarom best mogelijk dat de hydrodynamica op zich een belangrijke regulerende functie uitoefent in de structuur van de hyperbenthische gemeenschappen. Dit kan vooral van belang zijn voor het begrijpen van larvale recruteringsprocesssen.

Tot slot, de invloed van de Westerschelde en het hydrodynamisch karakter van het zandbanken systeem creeëren een hogere variabiliteit aan habitats in het Belgische kustgebied. Rijkere holo- and merohyperbenthische gemeenschappen in vergelijking met naburige gebieden, kunnen zich daardoor handhaven

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Appendix 1. Definitions of ecological terms

Marine organisms and biotic communities

pelagic organism Inhabit the open sea and ocean, excluding the sea bottom.

nekton Actively swimming pelagic organisms able to move independently of water currents; typically within the size range 20 mm to 20 m (Lincoln & Boxshall 1987 in Hiscock *et al.* 1999).

plankton Organisms which drift in the water column and have limited powers of locomotion in comparison with the horizontal water movements. Many benthic animals have planktonic larvae which act as a dispersive phase. (Hawkins & Jones 1992 in Hiscock *et al.* 1999).

zooplankton The animal component of the plankton (Lincoln *et al.* 1998).

holoplankton Plankton with a completely pelagic life style (Baretta-Bekker *et al.* 1998).

meroplankton Temporary plankton consisting of pelagic stages which also have benthic stages. Mainly the larvae of sedentary organisms (Baretta-Bekker *et al.* 1992).

benthos Those organisms attached to, or living on, in or near, the seabed (Lincoln & Boxshall 1987 in Hiscock *et al.* 1999).

Division on position relative to the sediment / water interface:

epibenthos All organisms living on the surface of the seabed (Hiscock *et al.* 1999)

endobenthos Benthic organisms that live in the sediment (Baretta-Bekker *et al.* 1998).

hyperbenthos Small animals which spend part or all of all their lives in the water layer close to the sea bed (Mees & Jones 1997).

(terminology used for deep sea: **benthopelagic organisms** (Mees & Jones 1997)) (see Fig. 1).

holohyperbenthos Small animals that spend variable periods of their adult life in the water layer close to the sea bed (Hamerlynck & Mees 1991).

merohyperbenthos Small animals that spend only part of their early life history in the water layer close to the sea bed and recruit to the nekton, epibenthos or endobenthos (Mees & Jones 1997)

Division on size:

macrobenthos The larger organisms of the benthos, exceeding 500-1000 µm in length (Lincoln & Boxshall 1987 in Hiscock *et al.* 1999).

Note: the hyperbenthos considered in this study can be classified as 'macro-hyperbenthos'.

meiobenthos Small benthic organisms of a size roughly between 50 µm and 1 mm (Baretta-Bekker *et al.* 1998).

Bathymetric zonation and habitat classification

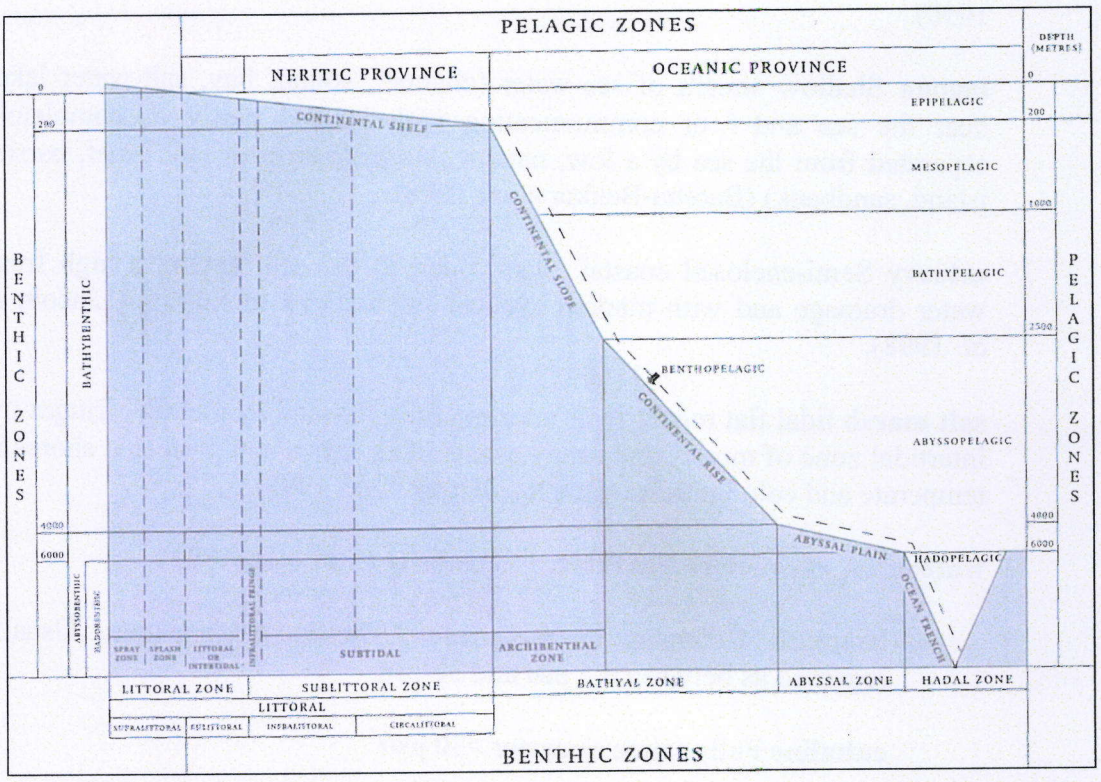

Fig. 1. Marine depth zones (source: Lincoln et al. 1998)

Continental shelf

coastal zone The space in which terrestrial environments influence marine environments and *vice versa*. The coastal zone is of variable width and may also change in time. Delimitation of zonal boundaries is not normally possible; more often such limits are marked by an environmental gradient or transition. At any one locality the coastal zone may be characterised according to physical, biological or cultural criteria, which need not, and rarely do, coincide (Carter 1988 in Hiscock *et al.* 1999).

surf zone The near-shore zone where both sea and swell waves peak up and break into surf, and change from waves of oscillation to waves of translation (Baretta-Bekker *et al.* 1998).

intertidal zone (littoral) (see Fig. 1) The zone between tide marks, i.e. between high-tide and low-tide level (Baretta-Bekker *et al.* 1998).

subtidal zone (sublittoral) (see Fig. 1) The zone below low water and usually down to the shelf edge (ca. 200 m) (Baretta-Bekker *et al.* 1998).

fjord Long narrow inlet or sea-arm, steep-walled and with a U-shape profile due to previous glacier erosion often several hundred meters deep. A fjord is typically situated in a mountainous coast at higher latitudes. It has a shallow

sill or treshold near its mouth and becomes deeper inland. Due to this morphology the deep water layers may be anoxic (Baretta-Bekker *et al.* 1998).

lagoon Shallow stretch of sea-water (channel, sound, bay, salt-water lake) near the sea and / or communicating with it, and partly or completely separated from the sea by a low, narrow, elongate strip of land (reef, barrier island, sandbank) (Baretta-Bekker *et al.* 1998).

estuary Semi-enclosed coastal water, open to the sea, having a high fresh water drainage and with marked cyclical fluctuations in salinity (Lincoln *et al.* 1998).

salt marsh tidal flat regularly or intermittently flooded by the tide, fringes the intertidal zone of muddy and sandy coasts of estuaries and protected shores in temperate and cold latitudes (Baretta-Bekker *et al.* 1998).

watermass characteristics related to salinity (McLusky 1993).

brackish Referring to mixtures of fresh and seawater. Usually regarded as between 0.5 psu and 30 psu

euhaline Fully saline seawater >30 psu.

polyhaline Pertaining to brackish water having a salinity between 18 psu and 30 psu .

mesohaline Pertaining to brackish water between 5 psu and 18 psu.

oligohaline Pertaining to brackish water between 0.5 psu and 5 psu.

Deep Sea (see Fig. 1)

shelf break The outer margin of the continental shelf marked by a pronounced increase in the slope of the sea bed (Lincoln *et al.* 1998).

continental slope The steeply sloping sea bed leading from the outer edge of the continental shelf to the continental rise (Lincoln *et al.* 1998).

bathyal Pertaining to zones below the sublittoral roughly from the outer shelf down to ca. 2000 m (Lincoln *et al.* 1998).

abyssal Pertaining to zones of great depths in the oceans roughly between 2000 and 6000 m (Lincoln *et al.* 1998).

Others terms

benthic boundary layer Refers to the (water) layer just above and in the surface of the seabed. The biological, chemical and physical properties are controlled by the presence of, and activity at, the boundary between the seabed and the overlying water (Baretta-Bekker *et al.* 1998).

biodiversity "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and ecosystems." (UN Convention on Biological Diversity 1992 in Hiscock *et al.* 1999).

biotope The physical 'habitat' with its biological 'community'; a term which refers to the combination of physical environment (habitat) and its distinctive assemblage of conspicuous species (Hiscock *et al.* 1999).

boreal Pertaining to cool or cold temperate regions of the northern hemisphere (Lincoln *et al.* 1998).

community A group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and identifiable by means of ecological survey from other groups (Mills 1969 in Hiscock *et al.* 1999).

demersal Living at or near the bottom of the sea, but having the capacity for active swimming (Lincoln *et al.* 1998).

ecosystem A community of organisms and their physical environment interacting as an ecological unit (Lincoln *et al.* 1998). Those parts of the biosphere, whose internal interactions are much stronger than the interactions with the outer world, might be considered as an ecosystem. Usage can thus include reference to large units such as the North Sea down to much smaller units such as a sea area with strong currents (Baretta-Bekker *et al.* 1998; Lincoln *et al.* 1998).

environment The complex of biotic climatic, edaphic and other conditions which comprise the immediate habitat of an organism; the physical, chemical and biological surroundings of an organism at any given time (Lincoln *et al.* 1998).

habitat The characteristic space occupied by an individual, a population or a species. It is defined for the marine environment according to geographical location, physiographic features and the physical and chemical environment (including salinity, wave exposure, strength of tidal streams, geology, biological zone, substratum, 'features' (e.g. crevices, overhangs, rockpools) and 'modifiers' (e.g. sand-scour, wave-surge, substratum mobility) (Baretta-Bekker *et al.* 1998).

lusitanian Referring to a biogeographical region centred to the south of the British Isles and influencing the extreme south-west of the British Isles (Hiscock *et al.* 1999). Having affinities with the Iberian peninsula (Lincoln *et al.* 1998).

microhabitat A small part of the habitat which has distinct physical conditions (Hiscock *et al.* 1999).

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Appendix 2. Digital database

All environmental and biological data are digitally delivered (CD in annex) ***(This data may not be used without prior reference to the authors)***. The respective files can be found in Table 1; an overview of the data provided per area is listed in Table 2.

	Frisian front	Dogger Bank	shelf break / upper slope	BCS - spatial	BCS - temporal
Abiotic	ffenv.wk4	doenv.wk4	slenv.wk4	sbcsenv.wk4	tbcsenv.wk4
Hyperbenthos density	ffdens.wk4	dodens.wk4	sldens.wk4	sbcsdens.wk4	tbcsdens.wk4
Hyperbenthos biomass	ffbiom.wk4	dobiom.wk4	slbiom.wk4	sbcsbiom.wk4	tbcsbiom.wk4

Table 1. Digital data

Species lists are ordered according to taxonomical hierarchy, using following sources:

Hierarchy of Phyla according to BIOSIS

Division of Phyla and further hierarchy according to Ruppert & Barnes (1994); detailed taxonomic hierarchy according to following sources:

Phylum Cnidaria: Bouillon (1999), Russell (1953)
Phylum Ctenophora: Mianzan (1999)
Classis Polychaeta: Fauchald (1977)
Phylum Chaetognatha: Casanova (1999)
Ordo Nudibranchia: Thompson & Brown (1976)
Classis Cephalopoda: Nesis (1999)
Ordo Calanoida: Mauchline (1998)
Ordo Euphausiacea: Mauchline (1984)
Subordo Dendrobranchiata: Holthuis (1980)
Infraordo Caridea: Smaldon (1979)
Infraordo Astacidea, Thalassinidea, Anomura and Brachuyra : Ingle (1992)
Ordo Mysidacea: Tattersall & Tattersall (1951)
Ordo Cumacea: Jones (1976), Fage (1951)
Ordo Amphipoda: Lincoln (1979), Ruffo (1982; 1989; 1993; 1998), Dauvin (1999), ERMS
Ordo Isopoda: Naylor (1972), Svavarsson *et al.* (1993), ERMS
Classis Pycnogonida: Hayward & Ryland (1996)
Subphylum Vertebrata: Nelson (1994)

Major identification keys:

- Fage (1951), Naylor (1972), King (1974), Jones (1976), Lincoln (1979), Ingle (1992), Holdich & Jones (1983), Mauchline (1984; 1998), Ruffo (1982; 1989; 1993; 1998), Russell (1953; 1976), Smaldon (1993), Hayward & Ryland (1996), Todd et al. (1996).
- An appeal was done on the personal library of Jean Claude Sorbe (Laboratoire d'Océanographie Biologique, UMR 5805 (CNRS/UB1), 2 rue

Jolyet, 33120 Arcachon, France) for the identification of the shelf break / continental slope fauna.

	Frisian front	Dogger Bank	shelf break upper slope	BCS spatial	BCS temporal
	August 1994 and April 1996	August 1994	September 1995	September 1993	Monthly from September 1994 until December 1995
# stations	12	9	6	62	13
# samples	22	9	6	62	164
Biotic data (hyperbenthos)					
Density	*	*	*	*	*
Biomass	*	*	*	*	
Abiotic data					
Geographical position					
Longitude (DGPS)	*	*	*	*	*
Latutide (DPGS)	*	*	*	*	*
UTM (easting)	*	*	*	*	*
UTM (northing)	*	*	*	*	*
Distance along the transect (km)	*	*	*		
Sampling data					
Date	*	*	*	*	*
Trawling duration (')	*	*	*	*	*
Distance trawled (m)	*	*	*	*	*
Volume filtered (m^3)	*	*	*	*	*
Environmental variables measured					
In situ depth (m)	*	*	*		*
Depth below MLLWS (m)				*	*
Surface temperature (°C)	*	*		*	*
Near-bottom temperature (°C)			*		
Surface salinity (psu)	*	*		*	*
Near-bottom salinity (psu)			*		
Near-bottom dissolved oxygen (µmol/kg)			*		
Secchi depth (m)				*	
Surface turbidity (ntu)					*
Near-bottom turbidity (ntu)					*
Near-bottom nitrate-N (µmol/l)					*
Near-bottom ammonia-N (µmol/l)					*
Near-bottom silicate (µmol/l)					*
Near-bottom chlorophyll a (µg/l)				*	*
Near-bottom fucoxanthin (µg/l)				*	*
Mean grain size (µm)	*	*	*	*	*
Median grain size (µm)	*	*	*	*	*
% mud (< 63 µm)	*	*	*	*	*
% very fine sand (63 - 125 µm)	*	*	*	*	*
% fine sand (125 - 250 µm)	*	*	*	*	*
% medium sand (250 - 500 µm)	*	*	*	*	*
% coarse sand (500 - 850 µm)	*	*	*	*	*
Flow velocity (MU-BCZ model)					
maxT1 (m/s)					*
maxE1 (m/s)					*
maxW1 (m/s)					*
maxN1 (m/s)					*
maxS1 (m/s)					*
domE (m/s)					*
domN (m/s)					*
resE3 (m/s)					*
resN3 (m/s)					*
resE7 (m/s)					*
resN7 (m/s)					*
resE21 (m/s)					*
resN21(m/s)					*

Table 2. Overview of digital data per working area.

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Appendix 3. Species list

Species list and **(A)** density per working area for all taxa recorded during the late summer surveys. Since the density showed a strong variability, both the mean density (Mean) over all samples and the maximum density (Max) for a certain sample are listed. Dogger Bank (do), Frisian front (ff), shelf break and upper slope (sl), Belgian continental shelf (bcs). **(B).** Annual mean density (from September 1994 until August 1995) (A Mean) for the Belgian continental shelf and the maximum density (A Max) recorded at a certain site during the temporal survey. Density for the Dogger Bank, the Frisian front and the shelf break / upper continental slope is reported as ind. 100 m^{-2}; densities for the Belgian continental shelf is expressed as ind. 100 m^{-3}. Holohyperbenthos (H), merohyperbenthos (M); hydromedusa (HM), juvenile (JU), larva (LA), megalopa (ME), postlarva (PO), zoea (ZO).

			A								B	
			do	do	ff	ff	sl	sl	bcs	bcs	bcs	bcs
Taxonomy	Species	Stage	H/M	mean	max	mean	max	mean	max	mean	max	A mean	A max
Phylum Cnidaria													
Subphylum Medusozoa													
Superclassis Hydrozoa													
Classis Hydroidomedusae													
Subclassis Anthomedusae													
Ordo Filifera													
Subordo Margelina													
Familia Bougainvilliidae													
Subfamilia Bougainvilliinae													
	Bougainvillia spp.	HM	H	0.1	0.5					0.2	7.7	4.8	288.5
Subordo Tiarida													
Familia Pandeidae													
Subfamilia Pandeinae													
	Leuckartiara spp.	HM	H	0.4	3.2								
Ordo Capitata													
Subordo Tubulariida													
Familia Corynidae													
	Sarsia tubulosa	HM	H									0.1	3.4
Subclassis Leptomedusae													
Familia Eirenidae													
	Eutima gracilis	HM	H									0.0	0.8
	Eutonina indicans	HM	H	0.2	1.6							0.5	25.1
Familia Mitrocomidae													
	Mitrocomella spp.	HM	H	0.5	2.1	404.9	1616.8			34.9	804.0	15.7	666.5
Subclassis Trachymedusae													
Familia Rhopalonematidae													
	Aglantha digitale	HM	H	17.6	63.2								
	Hydroidomedusae species 1 (dc	HM	H	0.0	0.4								
	Hydroidomedusae species 1 (ff)	HM	H			0.1	0.5						
	Hydroidomedusae species 2 (ff)	HM	H			0.1	0.7						
	Hydroidomedusae species 1 (sl)	HM	H					1.5	8.6				
	Hydroidomedusae species 2 (sl)	HM	H					0.4	1.9				
Phylum Ctenophora													
Classis Tentaculata													
Ordo Cydippida													
Familia Pleurobrachiidae													
	Pleurobrachia pileus		H	11.0	74.5	7.9	47.7			54.8	2538.3	86.0	921.2
Ordo Beroida													
Familia Beroidae													
	Beroe cucumis		H							0.0	3.6		
	Beroe gracile		H							0.0	2.3		
	Beroe spp.		H							0.6	52.4	15.4	1219.9
Phylum Annelida													
Classis Polychaeta													
Ordo Phyllodocida													
Subordo Aphroditiformia													
Superfamilia Aphroditacea													
Familia Polynoidae													
Subfamilia Harmothoinae													
	Harmothoe spp.	LA	M							0.0	2.2	2.2	159.6

Taxonomy Species	Stage	H/M	A do mean	do max	ff mean	ff max	sl mean	sl max	bcs mean	bcs max	B bcs A mean	bcs A max
Phylum Cnidaria												
(not identified subordo)												
Familia Tomopteridae												
Tomopteridae spp.		H	2.6	9.3	1.0	7.9					0.0	0.4
Ordo Terebellida												
Familia Terebellidae												
Subfamilia Amphitritinae												
Lanice conchilega	LA	M							9.0	164.5	105.2	1383.4
Polychaeta spp.	LA	M	0.0	0.4							0.3	13.1
Phylum Chaetognatha												
Classis Sagittoidea												
Subclassis Chorismogonata												
Ordo Monophragmophora												
Familia Spadellidae												
Spadella cephaloptera		H	0.8	7.0								
Familia Eukrohniidae												
Eukrohnia fowleri		H					2.4	6.5				
Eukrohnia spp.		H					0.2	1.1				
Ordo Aphragmophora												
Familia Sagittidae												
Sagitta elegans		H	47.9	174.9	49.6	392.8			36.5	935.9	4.3	112.3
Sagitta setosa		H			45.6	195.6					9.5	189.5
Sagitta aff. *tasmanica*		H					0.2	0.9				
Sagitta spp.		H			55.9	458.9	0.4	2.6			1.5	68.4
Chaetognatha spp.		H					1.2	6.8				
Phylum Mollusca												
Classis Gastropoda												
Subclassis Opisthobranchia												
Ordo Gymnosomata												
Gymnosomata species 1 (sl)		H					0.8	1.9				
Ordo Nudibranchia												
Subordo Aeolidacea												
Familia Coryphellidae												
Coryphella borealis		H	25.0	212.3								
Nudibranchia spp.		H							0.0	2.2	0.0	1.5
Classis Cephalopoda												
Subclassis Coleoidea												
Ordo Sepiida												
Subordo Sepiina												
Familia Sepiolidae												
Subfamilia Sepiolinae												
Sepiola atlantica		H	0.7	2.2					1.3	26.9	0.2	2.6
Ordo Teuthida												
Subordo Myopsida												
Familia Loliginidae												
Loligo forbesii	JU	M	1.0	5.1	0.1	0.5						
Loligo vulgaris	JU	M									0.0	1.4
Loligo species 1 (sl)	JU	M					0.0	0.2				
Phylum Arthropoda												
Subphylum Crustacea												
Classis Copepoda												
Ordo Calanoida												
Superfamilia Aritelloidea												
Familia Heterorhabdidae												
Heterorhabdus papilliger		H					1.9	5.1				
Familia Metridinidae												
*Metridia s*pecies 1 (sl)		H					0.1	0.3				
Pleuromamma robusta		H					1.2	7.1				
Pleuromamma spp.		H					1.8	4.1				
Familia Phyllopodidae												
Phyllopus bidentatus		H					0.2	1.3				
Superfamilia Centropagoidea												
Familia Candacidae												
Candacia armata		H					0.3	1.6			0.1	11.7
Familia Centropagidae												
Centropages hamatus		H					0.2	1.1			0.4	14.5
Centropages typicus		H	1.0	6.2	0.4	3.0	0.3	1.0	0.4	13.8	0.8	57.7
Familia Parapontellidae												
Parapontella brevicornis		H									0.1	4.6
Familia Pontellidae												
Anomalocera patersoni		H	0.7	2.4	0.0	0.4						
Labidocera wollastoni		H	0.2	0.7	5.8	44.4					0.2	6.7
Familia Temoridae												
Temora longicornis		H	0.0	0.4	0.2	2.2	0.1	0.5	0.0	0.8	1.8	35.3

Taxonomy	Species	Stage	H/M	A do mean	A do max	A ff mean	A ff max	A sl mean	A sl max	A bcs mean	A bcs max	B bcs A mean	B bcs A max
	Superfamilia Megacalanoidea												
	Familia Calanidae												
	Calanus helgolandicus		H			110.1	726.8			6.0	197.9	9.5	227.3
	Calanus spp.		H	12.1	74.8								
	Calanidae spp.		H					0.9	2.2				
	Familia Megacalanidae												
	Megacalanus longicornis		H					0.1	0.6				
	Superfamilia Eucalanoidea												
	Familia Eucalanidae												
	Eucalanus crassus		H					0.6	1.9				
	Rhincalanus nasutus		H					0.6	2.8				
	Superfamilia Clausocalanoidea												
	Familia Aetideidae												
	Aetideus armatus		H					22.5	91.2				
	Chiridius armatus		H					1.8	7.7				
	Gaetanus kruppi		H					0.3	1.9				
	Gaetanus latifrons		H					0.1	0.3				
	Gaetanus pileatus		H					0.1	0.6				
	Familia Euchaetidae												
	Euchaeta spp.		H					6.0	15.4				
	Familia Phaennidae												
	Brachycalanus atlanticus		H					0.1	0.5				
	Oothrix bidentata		H					0.1	0.3				
	Familia Scolecitrichidae												
	Lophothrix frontalis		H					0.6	1.5				
	Familia Tharybidae												
	Undinella simplex		H					4.9	21.5				
	Calanoida species 1 (do)		H	0.0	0.4								
	Calanoida species 1 (sl)		H					0.1	0.6				
	Calanoida species 2 (sl)		H					1.0	4.4				
	Calanoida species 3 (sl)		H					0.0	0.2				
	Calanoida species 4 (sl)		H					0.1	0.3				
	Calanoida species 5 (sl)		H					1.5	4.1				
	Calanoida species 6 (sl)		H					0.0	0.2				
Classis Malacostraca													
Subclassis Phyllocarida													
Ordo Nebaliacea													
	Nebalia bipes		H	0.3	2.1	0.3	1.4					0.0	0.8
	Nebaliacea spp.		H					0.2	1.0				
Subclassis Eumalacostraca													
Superordo Eucarida													
Ordo Euphausiacea													
	Familia Euphausiidae												
	Euphausia krohni		H					0.8	1.6				
	Meganyctiphanes norvegica		H					0.0	0.2				
	Nyctiphanes couchi		H	3.5	26.1	13.6	86.5	58.1	165.7	0.0	0.7	0.2	11.0
	Thysanoëssa inermis		H					0.3	1.2				
	Thysanoëssa raschi		H	2.2	12.0								
Ordo Decapoda													
Subordo Dendrobranchiata													
Infraordo Penaeidea													
Superfamilia Penaeoidea													
Familia Penaeidae													
	Penaeidae spp.	PO	M					0.4	1.2				
	Penaeidae spp.	ZO	M					0.1	0.3				
Superfamilia Sergestoidea													
Familia Sergestidae													
	Sergestidae spp.	PO	M					0.2	1.3				
Subordo Pleocyemata													
Infraordo Caridea													
Familia Palaemonidae													
Subfamilia Palaemoninae													
	Palaemon elegans	PO	M							0.0	0.8	0.0	0.5
	Palaemonidae spp.	ZO	M							0.4	15.6	0.0	1.4
Familia Alpheidae													
	Alpheus glaber	ZO	M							0.0	0.7		
Familia Hippolytidae													
	Caridion gordoni	PO	M					0.0	0.3				
	Hippolyte holthuisi	PO	M					5.2	27.9				
	Hippolyte varians	PO	M	1.6	6.5	1.6	3.7			7.7	208.2	1.7	12.6
	Hippolyte varians	ZO	M	0.1	0.4					2.5	26.6		
	Thoralus cranchii	PO	M	0.2	2.1					0.0	0.9	0.1	3.7
	Hippolytidae spp.	PO	M					0.1	0.6				
	Hippolytidae spp.	ZO	M									0.3	7.0

Taxonomy	Species	Stage	H/M	A do mean	A do max	A ff mean	A ff max	A sl mean	A sl max	A bcs mean	A bcs max	B bcs A mean	B bcs A max
Phylum Cnidaria													
	Familia Processidae												
	Processa canaliculata	PO	M							0.0	1.7		
	Processa edulis subsp. *crassipe*	PO	M										
	Processa modica	PO	M			3.1	12.8			0.3	18.8		
	Processa modica	ZO	M							0.8	15.0		
	Processa nouveli subsp. *holthui*	PO	M			21.8	80.4	2.0	6.2				
	Processa spp.	PO	M	11.5	95.8	28.1	84.7					0.0	1.7
	Processa spp.	ZO	M	0.5	1.7	2.4	9.5					0.1	3.9
	Familia Pandalidae												
	Pandalina brevirostris	PO	M	8.0	42.5	1.0	3.0			0.1	2.1	0.0	1.3
	Pandalina brevirostris	ZO	M	0.1	0.7					0.0	0.7		
	Pandalina profunda	PO	M					7.3	25.8				
	Pandalus montagui	PO	M									0.0	4.6
	Pandalus propinquus	PO	M									0.1	3.8
	Pandalidae spp.	PO	M					14.1	56.6				
	Pandalidae spp.	ZO	M									0.0	0.7
	Familia Crangonidae												
	Crangon allmanni	PO	M	43.8	313.5	3.3	19.5						
	Crangon crangon	PO	M			1.5	8.3			45.0	580.3		
	Crangon spp.	PO	M			16.9	58.8					50.0	648.3
	Philocheras bispinosus	PO	M	106.2	391.1	9.0	21.0	2.0	11.9				
	Philocheras echinulatus	PO	M					0.5	3.0				
	Philocheras trispinosus	PO	M	0.7	2.5	0.5	2.5			13.4	121.9	3.1	47.5
	Pontophilus spinosus	PO	M	1.2	6.6								
	Crangonidae spp.	ZO	M	0.5	1.7	4.0	29.0	0.2	1.0	40.7	401.3	15.8	135.0
	Caridea spp.	PO	M					0.3	0.9				
	Infraordo Astacidea												
	Superfamilia Nephropoidea												
	Familia Nephropidae												
	Nephrops norvegicus	PO	M	0.0	0.3								
	Nephrops norvegicus	ZO	M	0.1	0.7								
	Infraordo Thalassinidea												
	Superfamilia Thalassinoidea												
	Familia Callianassidae												
	Callianassa spp.	PO	M	4.3	30.9							0.3	16.9
	Callianassa spp.	ZO	M	14.0	40.5	1.7	11.1			0.2	3.2	0.2	12.5
	Familia Upogebiidae												
	Upogebia deltaura	PO	M			0.7	4.6						
	Upogebia spp.	PO	M	7.6	17.3					0.2	4.3	0.1	4.6
	Upogebia spp.	ZO	M	24.3	124.1	2.0	15.3			0.5	12.0	0.5	24.9
	Infraordo Anomura												
	Superfamilia Galatheoidea												
	Familia Galatheidae												
	Galathea dispersa	PO	M	0.2	1.7								
	Galathea intermedia	PO	M	3.3	12.4	0.1	0.5			2.5	44.9	0.5	16.6
	Galathea intermedia	ZO	M							0.2	4.5	0.5	30.7
	Galathea spp.	ZO	M	0.6	3.6	0.1	0.9						
	Familia Porcellanidae												
	Pisidia longicornis	PO	M	13.0	69.9	4.3	10.6			12.5	108.1	4.6	127.4
	Pisidia longicornis	ZO	M	4.2	13.8					2.9	58.0	8.2	333.2
	Superfamilia Paguroidea												
	Familia Paguridae												
	Anapagurus laevis	ZO	M	0.4	1.7			0.0	0.3	0.1	7.5	0.1	3.3
	Pagurus bernhardus	PO	M			0.2	1.2						
	Pagurus bernhardus	ZO	M	8.8	13.1	0.0	0.5			0.2	5.8	5.3	108.5
	Pagurus cuanensis	PO	M			0.1	0.9						
	Pagurus prideauxi	ZO	M	1.1	4.3	0.0	0.5			0.1	3.6	0.0	4.2
	Paguridae spp.	PO	M	7.3	35.9	0.1	1.5			1.6	17.8	3.4	154.9
	Paguridae spp.	ZO	M					0.0	0.2				
	Anomura spp.	ZO	M					0.1	0.3				
	Infraordo Brachyura												
	Section Oxyrhyncha												
	Superfamilia Majoidea												
	Familia Majidae												
	Subfamilia Oregoniinae												
	Hyas coarctatus	ME	M									0.0	1.4
	Hyas spp.	ZO	M	0.3	1.6								
	Subfamilia Inachinae												
	Inachus dorsettensis	ME	M									0.0	1.2
	Inachus spp.	ME	M	0.9	6.4					0.0	1.2		
	Inachus spp.	ZO	M	0.2	1.1								
	Macropodia rostrata	ME	M										
	Macropodia spp.	ME	M	18.4	78.1					2.5	42.3	0.9	32.7
	Macropodia spp.	ZO	M	20.1	92.7					1.1	28.2	0.3	5.3

Taxonomy	Species	Stage	H/M	A do mean	A do max	A ff mean	A ff max	A sl mean	A sl max	A bcs mean	A bcs max	B bcs A mean	B bcs A max
	Section Cancridea												
	Familia Thiidae												
	Thia scutellata	ME	M	0.1	0.7	0.6	3.0			0.7	10.3	0.0	2.6
	Familia Cancridae												
	Cancer pagurus	ME	M	8.7	32.2	0.9	2.7					0.1	3.2
	Cancer pagurus	ZO	M									1.1	57.5
	Familia Corystidae												
	Corystes cassivelaunus	ME	M	0.0	0.3					0.0	0.3	0.6	37.9
	Section Brachyrhyncha												
	Superfamilia Portunoidea												
	Familia Portunidae												
	Subfamilia Polybiinae												
	Liocarcinus holsatus	ME	M	152.3	923.6	25.4	92.1					15.3	294.3
	Liocarcinus spp.	ME	M							83.1	1652.0		
	Liocarcinus spp.	ZO	M							38.1	535.7	26.8	377.0
	Subfamilia Carcininae												
	Carcinus maenas	ME	M	0.0	0.4	0.5	2.2			10.8	232.2	23.4	461.8
	Carcinus maenas	ZO	M							6.8	117.5	6.1	128.2
	Portumnus latipes	ME	M							1.2	39.2	0.6	12.7
	Superfamilia Xanthoidea												
	Familia Pilumnidae												
	Pilumnus hirtellus	ME	M	0.0	0.4					12.8	184.9	3.7	73.2
	Familia Panopeidae												
	Rhithropanopeus harrisii	ME	M									0.0	0.4
	Rhithropanopeus harrisii	ZO	M			0.0	0.5						
	Superfamilia Pinnotheroidea												
	Familia Pinnotheridae												
	Subfamilia Pinnotherinae												
	Pinnotheres pisum	ME	M										
	Superfamilia Grapsidoidea												
	Familia Grapsidae												
	Subfamilia Varuninae												
	Eriocheir sinensis	ME	M									0.0	0.5
	Section Oxystomata												
	Superfamilia Leucosoidea												
	Familia Leucosiidae												
	Subfamilia Ebaliinae												
	Ebalia spp.	ME	M	2.1	8.6	0.3	1.9			1.2	30.2	0.5	5.9
	Brachyura aff. *Liocarcinus*	ZO	M					0.4	1.2				
	Brachyura species 1 (do)	ME	M	0.0	0.4								
	Brachyura species 2 (do)	ZO	M	0.0	0.4								
	Brachyura spp.	ME	M					0.2	0.6				
	Brachyura spp.	ZO	M	26.8	83.7	3.5	15.3			4.5	51.7		
	Decapoda species 1 (sl)	PO	M					0.1	0.4				
	Decapoda species 2 (sl)	PO	M					0.1	0.3				
	Superordo Peracarida												
	Ordo Mysidacea												
	Subordo Lophogastrida												
	Familia Lophogastridae												
	Lophogaster typicus		H					0.2	1.3				
	Subordo Mysida												
	Familia Mysidae												
	Subfamilia Boreomysinae												
	Boreomysis arctica		H					0.8	4.2				
	Boreomysis megalops		H					7.6	37.3				
	Boreomysis tridens		H					0.0	0.2				
	Boreomysis spp.		H					0.0	0.2				
	Subfamilia Siriellinae												
	Siriella armata		H							0.3	22.1	0.0	1.1
	Siriella clausii		H					0.2	1.0			0.0	1.2
	Siriella jaltensis		H									0.0	1.0
	Subfamilia Gastrosaccinae												
	Anchialina agilis		H	0.0	0.3	0.1	0.5	1.2	5.4			0.2	7.5
	Gastrosaccus spinifer		H	0.2	0.7	1.5	11.5			119.9	1203.9	27.1	772.3
	Haplostylus normani		H					1.8	10.4				
	Subfamilia Mysinae												
	Tribus Erythropini												
	Amblyops abbreviata		H					0.5	1.9				
	Amblyops tenuicauda		H					0.0	0.2				
	Dactylerythrops dimorpha		H					0.2	1.2				
	Erythrops elegans		H	110.1	704.2								
	Erythrops neapolitana		H					28.9	101.2				
	Erythrops serrata		H	10.1	90.5			1.3	7.8				
	Erythrops spp.		H					0.2	0.8				
	Hypererythrops serriventer		H					27.1	126.9				
	Paramblyops rostrata		H					14.0	62.3				
	Parapseudomma calloplura		H					1.7	9.9				

Taxonomy	Species	Stage	H/M	A do mean	A do max	ff mean	ff max	sl mean	sl max	bcs mean	bcs max	B bcs A mean	B bcs A max
	Parerythrops obesa		H					3.4	10.0				
	Pseudomma affine		H					51.6	190.3				
	Pseudomma nanum		H					0.5	2.4				
	Pseudomma spp.		H					4.0	23.9				
	Tribus Leptomysini												
	Leptomysis gracilis		H	0.4	2.9								
	Leptomysis lingvura		H	0.0	0.3			0.1	0.3			0.0	1.6
	Mysideis insignis		H					0.2	0.3				
	Mysidopsis angusta		H	12.7	46.7	0.1	1.2						
	Mysidopsis didelphys		H	5.7	27.7			1.3	7.5				
	Mysidopsis gibbosa		H	4.2	6.8			0.5	3.1	3.9	61.9	1.6	22.0
	Tribus Mysini												
	Acanthomysis longicornis		H	0.5	1.4	14.1	58.2			4.7	49.0	7.3	303.7
	Mesopodopsis slabberi		H	0.1	0.8	0.7	5.1			774.4	51977	4.7	653.1
	Neomysis integer		H							147.8	13206	0.0	5.2
	Paramysis arenosa		H							0.2	10.3	0.1	2.2
	Paramysis bacescoi		H									0.2	21.8
	Praunus flexuosus		H							0.0	4.4	0.0	0.9
	Schistomysis kervillei		H	2.5	13.2					398.0	6017.4	105.2	4277.4
	Schistomysis ornata		H	91.1	527.9	114.7	272.0	0.0	0.2			0.0	0.3
	Schistomysis spiritus		H			0.1	0.5			457.3	8339.4	14.3	450.7
	Tribus Heteromysini												
	Heteromysis microps		H			0.1	0.7						
	Heteromysis norvegica		H	0.1	0.7								
Ordo Cumacea													
	Familia Bodotriidae												
	Subfamilia Vaunthompsoniinae												
	Cumopsis spp.		H									0.0	0.4
	Subfamilia Bodotriinae												
	Bodotria arenosa		H					0.0	0.3				
	Bodotria pulchella		H							0.0	0.3		
	Bodotria spp.		H									0.0	13.3
	Bodotria scorpioides		H			0.3	1.4			0.7	14.7	0.5	12.9
	Cyclaspis longicaudata		H					10.5	30.2				
	Iphinoe trispinosa		H	0.2	0.5	0.3	1.5			0.0	1.4	0.0	0.4
	Familia Leuconidae												
	Eudorella truncatulla		H	6.3	54.5	3.0	15.7						
	Leucon nasica		H	7.8	70.2								
	Familia Nannastacidae												
	Campylaspis costata		H	1.1	9.9								
	Campylaspis glabra		H					10.6	28.7				
	Campylaspis horridoides		H					0.1	0.3				
	Campylaspis legendrei		H									0.0	0.6
	Campylaspis macrophthalma		H					0.4	1.3				
	Campylaspis rostrata		H					0.2	1.3				
	Campylaspis rubicanda		H	4.2	38.0								
	Campylaspis squamifera		H					0.0	0.2				
	Campylaspis verrucosa		H					7.5	22.5				
	Procampylaspis armata		H					1.7	10.1				
	Familia Pseudocumatidae												
	Petalosarsia declivis		H	3.5	31.4								
	Pseudocuma longicornis		H	1.7	10.0	0.2	0.9			0.0	0.3	0.4	20.0
	Pseudocuma similis		H	3.6	19.0	0.1	1.5	0.0	0.3	0.4	4.2	8.2	452.9
	Familia Lampropidae												
	Hemilamprops normani		H					6.9	26.6				
	Hemilamprops rosea		H	47.8	430.4							0.0	0.4
	Hemilamprops uniplicata		H					25.4	99.2				
	Paralamprops species 1 (sl)		H					14.3	58.7				
	Platysympus typicus		H					22.9	78.4				
	Familia Diastylidae												
	Diastylis bradyi		H							4.2	72.8	3.3	32.1
	Diastylis laevis		H	13.3	92.1								
	Diastylis lucifera		H	1.2	9.3								
	Diastylis rathkei		H							0.8	53.6	1.6	69.5
	Diastylis rugosa		H	0.9	5.2								
	Diastylis spp.		H			21.7	64.3						
	Diastyloides bacescoi		H					6.4	16.2				
	Diastyloides biplicata		H	9.9	88.8								
	Leptostylis villosa		H	5.2	46.7								
	Makrokylindrus josephinae		H					21.1	98.1				
Ordo Amphipoda													
Subordo Caprellidea													
	Familia Caprellidae												
	Caprella linearis		H	2.4	21.5							0.0	0.6
	Familia Pariambidae												
	Pariambus typicus		H	6.3	30.4	2.1	20.7			8.8	910.8	32.7	1598.2
	Pseudoprotella phasma		H	0.3	2.0								

Taxonomy	Species	Stage	H/M	A do mean	A do max	A ff mean	A ff max	A sl mean	A sl max	A bcs mean	A bcs max	B bcs A mean	B bcs A max
	Familia Phtisicidae												
	Phtisica marina		H	42.8	305.6	0.2	0.7	1.6	8.5	0.2	7.4	1.9	209.5
	Subordo Gammaridea												
	Familia Ampeliscidae												
	Ampelisca aequicornis		H					1.7	4.6				
	Ampelisca brevicornis		H	0.5	3.1					0.1	7.3	0.0	0.6
	Ampelisca diadema		H			0.6	2.8						
	Ampelisca gibba		H			0.4	2.2	21.4	45.2				
	Ampelisca spinipes		H					0.3	0.9				
	Ampelisca tenuicornis		H	2.1	11.6	0.3	1.9						
	Ampelisca spp.		H					1.1	4.8				
	Byblis guernei		H					5.3	15.1				
	Haploops setosa		H					0.7	2.6				
	Familia Amphilochidae												
	Amphilochoides boecki		H					1.8	8.3				
	Amphilochus neapolitanus		H	0.6	4.8					0.0	0.3	0.0	2.7
	Paramphilochoides intermedius		H	1.4	7.2								
	Paramphilochoides odontonyx		H					0.0	0.2				
	Familia Aoridae												
	Aora gracilis		H	7.9	32.1					0.4	22.8	0.1	3.4
	Autonoe spp.		H					0.0	0.2				
	Lembos longipes		H	7.8	70.2								
	Lembos spp.		H					1.6	8.5				
	Microdeutopus gryllotalpa		H									0.0	1.4
	Unciola crenatipalma		H	0.0	0.4								
	Unciola species 1 (sl)		H					0.0	0.3				
	Unciolella lunata		H					2.2	6.5				
	Aoridae spp.		H									0.0	1.5
	Familia Argissidae												
	Argissa hamatipes		H	13.8	118.1	0.4	4.2	0.8	5.0				
	Familia Astyridae												
	Astyra aff. *abyssi*		H					0.5	1.5				
	Familia Atylidae												
	Atylus falcatus		H	0.1	0.7					0.4	7.8	1.4	57.7
	Atylus swammerdami		H	15.0	86.3	3.1	8.7			32.6	689.5	69.2	2928.3
	Atylus vedlomensis		H	0.6	4.1			0.2	0.8				
	Familia Calliopiidae												
	Apherusa bispinosa		H	2.1	15.3			1.7	4.9	0.0	0.7	0.0	1.8
	Apherusa clevei		H					0.2	0.8				
	Apherusa ovalipes		H	0.1	0.7	5.2	22.8	0.9	5.2	0.0	0.0	0.7	21.0
	Apherusa spp.		H					0.0	0.3	0.0	1.4	0.0	0.6
	Familia Corophiidae												
	Corophium acherusicum		H							0.0	0.4	0.0	1.0
	Corophium arenarium		H									0.0	1.4
	Corophium multisetosum		H			0.0	0.5						
	Corophium sextonae		H							0.0	0.3	0.0	0.6
	Corophium volutator		H							0.0	0.6	0.0	3.4
	Corophium spp.		H							0.0	0.4		
	Siphonoecetes kroyeranus		H			0.1	1.0						
	Siphonoecetes striatus		H	1.7	5.9			2.7	12.2				
	Familia Cressidae												
	Cressa aff. *abyssicola*		H					1.9	11.4				
	Familia Epimeriidae												
	Epimeria cornigera		H					7.8	18.0				
	Epimeria spp.		H					0.0	0.0				
	Familia Eusiridae												
	Cleonardopsis carinata		H					0.1	0.3				
	Eusirus longipes		H					6.7	15.9				
	Rhachotropis helleri		H					2.7	16.0				
	Rhachotropis integricauda		H					31.6	185.0				
	Rhachotropis rostrata		H					0.0	0.2				
	Rhachotropis aff. *rostrata*		H					26.6	100.9				
	Familia Gammaridae												
	Gammarus crinicornis		H							13.4	641.6	86.2	4617.1
	Gammarus locusta		H									0.0	0.4
	Gammarus salinus		H							0.3	21.2		
	Familia Iphimediidae												
	Iphimedia minuta		H	0.1	0.4					0.0	0.3		
	Iphimedia obesa		H	3.7	25.6			0.1	0.3				
	Familia Isaeidae												
	Gammaropsis maculata		H					0.9	4.7				
	Gammaropsis nitida		H	0.7	5.0							0.0	0.7
	Gammaropsis palmata		H	1.0	8.7								
	Gammaropsis species 1		H					0.7	2.5				
	Megamphopus cornutus		H	1.6	10.3			0.1	0.8				
	Microprotopus maculatus		H	8.3	67.0	0.1	0.5			16.2	1939.7	9.5	319.0
	Photis longicaudata		H	1.5	11.6								
	Isaeidae spp.		H									0.0	0.8

Taxonomy	Species	Stage	H/M	A do mean	A do max	A ff mean	A ff max	A sl mean	A sl max	A bcs mean	A bcs max	B bcs A mean	B bcs A max
	Familia Ischyroceridae												
	Ericthonius fasciatus		H					5.3	31.5				
	Ericthonius aff. *fasciatus*		H					0.3	1.9				
	Ericthonius spp.		H					2.8	16.6				
	Jassa falcata		H							0.0	1.7	0.1	3.2
	Jassa marmorata		H									0.0	0.3
	Jassa pusilla		H	0.9	6.6								
	Microjassa cumbrensis		H	0.2	1.7								
	Familia Lepechinellidae												
	Lepechinella manco		H					8.8	30.0				
	Familia Leucothoidae												
	Leucothoe incisa		H	0.2	0.8	0.1	1.5			0.0	1.6	0.1	6.6
	Leucothoe lilljeborgi		H					0.5	3.0				
	Leucothoe procera		H			0.0	0.4						
	Familia Liljeborgiidae												
	Liljeborgia fissicornis		H					2.9	13.8				
	Familia Lysianassidae												
	Acidostoma nodiferum		H	0.8	7.4								
	Acidostoma obesum		H	1.1	6.6								
	Hippomedon denticulatus		H	0.6	4.1			7.3	29.5				
	Hippomedon spp.		H					0.1	0.2				
	Lepidepecreum longicorne		H	0.0	0.4								
	Lepidepecreum subclypeatum		H					0.0	0.3				
	Lysianassa plumosa		H					1.6	4.3				
	Normanion chevreuxi		H					0.0	0.2				
	Orchomene oxystoma		H					0.7	2.4				
	Orchomenella nana		H	22.4	159.7	47.8	283.6	0.4	2.0	0.3	8.0	0.8	18.4
	Perrierella audouiniana		H					0.2	0.6				
	Podoprion bolivari		H					0.2	0.7				
	Scopelocheirus hopei		H	5.7	35.0	95.4	507.5	0.6	1.6				
	Scopelocheirus spp.		H					0.0	0.2				
	Socarnes erytrophthalmus		H					0.2	0.5				
	Socarnes filicornis		H					1.5	9.0				
	Tmetonyx cicada		H	0.1	0.8								
	Tmetonyx similis		H					0.2	0.8				
	Trischizostoma raschi		H					0.0	0.2				
	Tryphosella horingi		H					0.1	0.3				
	Tryphosella laevis		H					0.2	1.0				
	Tryphosella nanoides		H					0.1	0.8				
	Tryphosella sarsi		H					0.0	0.2				
	Tryphosites alleni		H					2.4	9.0				
	Tryphosites longipes		H	5.6	47.5								
	Lysianassidae spp.		H					0.1	0.3				
	Familia Megaluropidae												
	Megaluropus agilis		H	2.3	5.8	0.0	0.5			0.1	1.8	0.2	5.2
	Familia Melitidae												
	Abludomelita aculeata		H					0.1	0.8				
	Cheirocratus intermedius		H			0.4	1.8	1.1	6.3				
	Cheirocratus sundevallii		H	0.5	2.5								
	Cheirocratus spp.		H			0.8	5.1						
	Maera othonis		H	0.1	0.7			0.1	0.3				
	Melita gladiosa		H					2.4	11.2				
	Melita obtusata		H	17.2	62.8	0.3	3.0			1.4	27.9	4.7	347.7
	Melita palmata		H									0.0	0.4
	Familia Melphidippidae												
	Melphidippa goesi		H					11.6	41.6				
	Melphidippa macrura		H					1.0	3.4				
	Melphidippella macra		H	1.1	7.0			9.0	33.0	0.0	0.7	0.0	0.7
	Melphidippidae spp.		H					32.5	134.2				
	Familia Oedicerotidae												
	Bathymedon longirostris		H					2.3	10.2				
	Monoculodes carinatus		H	0.6	5.8								
	Monoculodes gibbosus		H					0.1	0.8				
	Monoculodes packardi		H					4.2	17.2				
	Oediceropsis brevicornis		H					0.8	3.9				
	Perioculodes longimanus		H	19.5	146.3	5.3	21.3			0.1	5.6	0.2	10.7
	Pontocrates altamarinus		H	0.2	1.7			0.0	0.3	1.5	25.3	0.8	15.4
	Pontocrates arenarius		H	0.1	0.7					0.0	0.7	0.0	0.9
	Synchelidium haplocheles		H	1.7	15.3			0.1	0.3				
	Synchelidium maculatum		H					1.6	5.7				
	Westwoodilla caecula		H	40.3	310.6			5.6	18.3				
	Oedicerotidae spp.		H					0.2	0.8				
	Familia Pardaliscidae												
	Halicoides anomala		H					0.2	0.8				
	Nicippe tumida		H					8.8	25.8				
	Pardaliscidae spp.		H					0.0	0.0				

Taxonomy	Species	Stage	H/M	A do mean	A do max	A ff mean	A ff max	A sl mean	A sl max	A bcs mean	A bcs max	B bcs A mean	B bcs A max
Phylum Cnidaria													
	Familia Phoxocephalidae												
	Harpinia antennaria		H	2.1	13.4	1.3	4.6						
	Harpinia crenulata		H	0.3	2.5	0.1	0.6						
	Harpinia pectinata		H			1.4	6.5	0.5	2.2				
	Familia Pleustidae												
	Parapleustes assimilis		H	3.6	32.6								
	Parapleustes bicuspis		H	3.0	27.3								
	Pleusymtes glaber		H							0.0	1.2		
	Stenopleustes aff. *malmgreni*		H					0.0	0.2				
	Familia Podoceridae												
	Dyopedos monacantha		H	10.5	93.8							0.0	0.4
	Dyopedos porrectus		H	0.4	3.3								
	Laetmatophilus tuberculatus		H					3.1	12.0				
	Paradulichia spp.		H	25.9	233.4								
	Xenodice frauendeldti		H					0.2	0.9				
	Familia Pontoporeidae												
	Bathyporeia spp.		H	0.4	1.7			0.0	0.3	0.2	5.7	0.1	2.0
	Familia Stegocephalidae		H										
	Stegocephaloides christianiensis		H					11.1	24.2				
	Familia Stenothoidae												
	Metopa alderi		H	0.2	2.1								
	Metopa bruzelii		H										
	Metopella nasuta		H	2.5	22.7								
	Stenothoe marina		H	1.3	6.2	0.0	0.5	0.9	5.5	1.1	84.6	2.0	49.2
	Stenula rubrovittata		H	1.7	14.9	0.0	0.0						
	Familia Synopiidae												
	Bruzelia typica		H					4.7	14.9				
	Syrrhoe affinis		H					24.3	57.0				
	Syrrhoites walkeri		H					7.8	21.5				
	Familia Talitridae												
	Talitridae spp.		H									0.0	0.6
	Familia Urothoidae												
	Urothoe brevicornis		H							0.1	8.0	0.0	1.4
	Urothoe elegans		H					1.6	4.4			0.1	5.6
	Urothoe poseidonis		H									0.0	1.5
	Gammaridea species 1 (do)		H	0.0	0.3								
	Gammaridea spp.		H					0.0	0.3				
	Subordo Hyperiidea												
	Familia Hyperiidae												
	Hyperia galba		H	1.5	12.0	0.9	5.6	0.8	2.2	0.0	1.6	0.0	0.5
	Parathemisto gaudichaudi		H					10.0	39.3				
	Ordo Isopoda												
	Subordo Gnathiidae												
	Familia Gnathiidae												
	Gnathia oxyuraea		H					0.7	1.9				
	Gnathia species 1 (sl)		H					0.0	0.3				
	Gnathia spp.		H					0.5	2.2				
	Subordo Flabellifera												
	Familia Aegidae												
	Aega species 1 (sl)		H					0.1	0.7				
	Familia Anthuridae												
	Anthuridae species 1 (sl)		H					0.1	0.7				
	Familia Cirolanidae												
	Eurydice pulchra		H			0.0	0.5			0.0	0.4	0.0	1.7
	Eurydice species 1 (sl)		H					1.9	9.6				
	Metacirolana hanseni		H					0.1	0.9				
	Natatolana borealis		H					1.8	5.3				
	Natatolana caeca		H					0.2	1.1				
	Familia Paranthuridae												
	Leptanthura tenuis		H					0.0	0.2				
	Familia Sphaeromatidae												
	Bathycopea typhlops		H					31.1	80.8				
	Subordo Valvifera												
	Familia Idoteidae												
	Idotea linearis		H			0.1	0.5			3.8	312.0	1.1	40.9
	Idotea pelagica		H							0.0	0.6	0.0	2.1
	Familia Arcturidae												
	Arcturella dilatata		H	2.7	24.4			3.2	16.4				
	Astacilla longicornis		H	0.1	1.2								
	Astacilla species 1 (sl)		H					0.2	0.7				
	Astacilla species 2 (sl)		H					5.2	27.0				
	Astacilla spp.		H					0.3	1.5				
	Subordo Asellota												
	Familia Eurycopidae												
	Disconectes latirostris		H					9.0	29.9				
	Munnopsurus species 1 (sl)		H					0.2	0.7				
	Tytthocope megalura		H					6.5	27.2				

Taxonomy	Species	Stage	H/M	A do mean	do max	ff mean	ff max	sl mean	sl max	bcs mean	bcs max	B bcs A mean	bcs A max
	Familia Ilyarachnidae												
	Aspidarachna clypeata		H					0.1	0.7				
	Ilyarachna longicornis		H					2.4	8.3				
	Familia Ischnomesidae												
	Ischnomesus species 1 (sl)		H					0.2	1.1				
	Familia Janiridae												
	Janiridae species 1 (sl)		H					0.2	1.3				
	Familia Munnidae												
	Munna limicola		H					0.4	0.9				
	Familia Munnopsidae												
	Munnopsis beddardi		H					0.9	3.4				
	Ordo Tanaidacea												
	Subordo Apseudomorpha												
	Familia Apseudidae												
	Apseudes grossimanus		H					0.0	0.2				
	Apseudes spinosus		H					0.1	0.9				
	Subordo Tanaidomorpha												
	Familia Leptognathiidae												
	Typhlotanais aequiremis		H					1.0	3.1				
Subphylum Chelicerata													
Classis Pycnogonida													
	Familia Nymphonidae												
	Nymphon gracile		H					0.1	0.3				
	Nymphon rubrum		H							0.0	1.2	0.0	4.1
	Nymphonidae species 1 (sl)		H					0.3	1.4				
	Familia Acheliidae												
	Achelia echinata		H									0.0	1.3
	Achelia longipes		H							0.0	0.3		
	Familia Ammotheidae												
	Phoxichilidium femoratum		H							0.0	0.3		
	Ammotheidae species 1 (sl)		H					0.1	0.3				
	Ammotheidae species 2 (sl)		H					3.6	19.5				
	Ammotheidae species 3 (sl)		H					0.0	0.2				
	Familia Endeidae												
	Endeis laevis		H							0.0	4.3		
	Familia Pycnogonidae												
	Pycnogonum littorale		H									0.0	0.6
	Familia Callipallenidae												
	Callipallene brevirostris		H									0.0	0.5
	Callipallene phantoma		H					0.3	1.5				
	Familia Anoplodactylidae												
	Anoplodactylus petiolatus		H	0.6	5.0							0.0	0.7
	Pycnogonida species 1 (sl)		H					3.4	19.7				
	Pycnogonida spp.		H									0.0	0.8
Phylum Hemichordata													
Classis Enteropneusta													
	Enteropneusta spp.	LA	M	0.2	1.2								
Phylum Chordata													
Subphylum Vertebrata													
Superclassis Gnathostomata													
Classis Actinopterygii													
Subclassis Neopterygii													
Division Teleostei													
Subdivision Clupeomorpha													
Ordo Clupeiformes													
Subordo Clupeoidei													
Familia Clupeidae													
Subfamilia Clupeinae													
	Clupeidae spp.	PO	M	4.8	34.7	0.1	0.9			2.4	64.2	6.1	159.5
Subdivision Euteleostei													
Superordo Protacanthopterygii													
Ordo Osmeriformes													
Subordo Argentinoidei													
Superfamilia Argentinoidea													
Familia Argentinidae													
	Argentinidae species 1 (sl)	PO	M					0.0	0.3				
Superordo Paracanthopterygii													
Ordo Gadiformes													
Familia Gadidae													
Subfamilia Gadinae													
	Gadus morhua	PO	M									0.1	4.5
	Merlangius merlangus	PO	M	0.0	0.4							0.5	12.9
	Trisopterus luscus	PO	M							0.0	1.6	0.8	24.0
	Trisopterus minutus	PO	M									0.1	2.1

Taxonomy	Species	Stage	H/M	A do mean	A do max	A ff mean	A ff max	A sl mean	A sl max	A bcs mean	A bcs max	B bcs A mean	B bcs A max
Superordo Acanthopterygii													
Series Mugilomorpha													
Ordo Mugiliformes													
Familia Mugilidae													
	Chelon labrosus	PO	M							0.1	3.8		
Series Percomorpha													
Ordo Gasterosteiformes													
Subordo Syngnathoidei													
Infraordo Syngnata													
Superfamilia Syngnathoidea													
Familia Syngnathidae													
Subfamilia Syngnathinae													
	Syngnathus acus	PO	M									0.1	3.5
	Syngnathinae spp.	PO	M	0.1	0.7					2.7	96.0	0.2	4.6
Ordo Scorpaeniformes													
Subordo Cottoidei													
Superfamilia Cottoidea													
Familia Cottidae													
	Cottidae spp.	PO	M									0.0	0.5
Familia Agonidae													
Subfamilia Agoninae													
	Agonus cataphractus	PO	M	0.0	0.4					0.0	1.2	0.1	2.6
Ordo Perciformes													
Subordo Percoidei													
Familia Carangidae													
Subfamilia Caranginae													
	Trachurus trachurus	PO	M	0.2	1.7	0.2	0.7			0.4	7.8	0.0	1.7
Subordo Zoarcoidae													
Familia Pholidae													
Subfamilia Pholinae													
	Pholis gunnellus	PO	M									0.0	1.0
Subordo Trachinoidei													
Familia Ammodytidae													
	Ammodytes tobianus	PO	M							0.6	72.1		
	Hyperoplus lanceolatus	PO	M							3.4	304.1		
	Ammodytidae spp.	PO	M	1.3	3.8	0.1	0.9			0.2	6.6	0.0	0.7
Familia Trachinidae													
	Echiichthys vipera	PO	M	2.5	7.3					0.1	4.1	0.0	0.4
Subordo Gobiesocoidae													
Familia Gobiesocidae													
	Diplecogaster bimaculata		H	1.2	7.2							0.0	0.4
Subordo Callionymoidei													
Familia Callionymidae													
	Callionymus lyra	PO	M			0.2	0.9			0.2	15.2	0.4	8.5
	Callionymus reticulatus	PO	M	1.9	4.8			0.0	0.3	0.0	1.6		
	Callionymus spp.	PO	M							0.1	2.0		
Subordo Gobioidei													
Familia Gobiidae													
Subfamilia Gobiinae													
	Pomatoschistus lozanoi	PO	M			0.6	5.5						
	Pomatoschistus microps	PO	M			0.5	5.1			0.0	2.2		
	Pomatoschistus spp.	PO	M							61.2	1455.5	7.3	260.6
	Gobiidae species 1 (sl)	PO	M					0.0	0.3				
	Gobiidae spp.	PO	M	28.9	118.0	16.3	51.3						
Ordo Pleuronectiformes													
Subordo Pleuronectoidei													
Familia Bothidae													
	Arnoglossus laterna	PO	M	3.1	8.3	0.3	1.9			0.3	10.0		
	Bothidae spp.	PO	M									0.0	0.7
Familia Pleuronectidae													
Subfamilia Pleuronectinae													
Tribus Hippoglossini													
	Hippoglossoides platessoides	PO	M									0.1	2.4
Tribus Pleuronectini													
	Limanda limanda	PO	M	2.8	24.4	0.1	0.7					2.4	111.8
	Microstomus kitt	PO	M	0.0	0.3								
	Pleuronectes platessa	PO	M									0.2	5.9
	Pleuronectes flesus	PO	M									5.3	186.5
Familia Soleidae													
	Buglossidium luteum	PO	M	0.1	0.4							0.0	2.3
	Pegusa lascaris	PO	M										
	Solea solea	PO	M							0.1	2.5	11.4	325.2
	Pisces species 1 (sl)	PO	M					0.0	0.2				
	Pisces species 2 (sl)	PO	M					0.0	0.2				
	Pisces species 3 (sl)	PO	M					0.0	0.2				
	Pisces species 4 (sl)	PO	M					0.0	0.2				
	Pisces species 5 (sl)	PO	M					0.1	0.3				