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Epi- and hyperbenthic communities of Belgian sandy beaches

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Epi- en hyperbenthische gemeenschappen van Belgische zandstranden

Bregje Beyst

Promotor: Prof. Dr. M. Vincx
Copromotor: Dr. J. Mees

Verhandeling voorgelegd tot
het behalen van de graad van
Doctor in de Wetenschappen,
Groep Biologie

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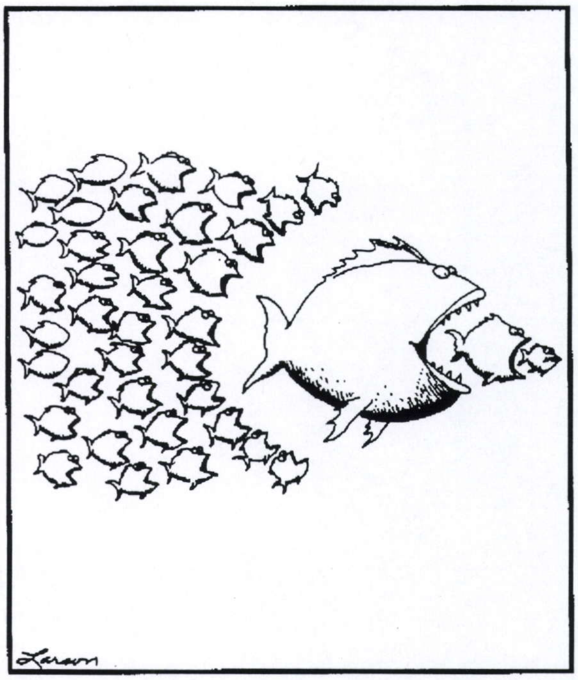
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SUMMARY - SAMENVATTING

ABSTRACT

This is the first study on the epi- and hyperbenthic fauna of the surf zone of sandy beaches of the Belgian coast. Therefore, as a first objective of this thesis, a lot of attention has been paid to the inventarisation (species composition), and to the investigation of the temporal and spatial distribution patterns of both communities. A temporal and a spatial campaign were performed during which the hyper- and epibenthos was sampled. During the temporal campaign monthly samples were taken at 4 selected stations and the spatial campaign involved sampling of 12 stations along the Belgian coast. All in all, the surf zone of the Belgian coast is a habitat for a considerable number of species. The surf zone harbours a rich hyperbenthic fauna and also the epibenthic assemblage is diverse. Total hyper- and epibenthic densities were comparable or even higher than those of the adjacent, subtidal regions. It seems that the Belgian surf zone can be seen as an extension of the rich shallow sand bank system in front of the coast. Differences in total hyperbenthic densities with other European sandy beaches might be linked to the degree of exposure.

An attempt was made to elucidate the major environmental variables structuring the communities. Therefore several environmental variables were measured at the moments of sampling. Different uni- and multivariate statistical techniques were used for the analyses of the data. Although clear temperature-related seasonal distribution patterns were observed, the hyper- and epibenthic communities of the surf zone can also be influenced severely by hydrodynamic factors and this both by short-term events (e.g. storm) and long-term effects (influence on morphodynamics of the beach). Spatial differences were found both in species richness and in density. In general, highest hyper- and epibenthic densities were found on flat, wide beaches, but also intermediate sites and sites with a high turbidity were characterised with high densities and a high number of species. Although clear distribution patterns could be observed, the much lower densities of the epibenthos compared to the hyperbenthos, might require a higher sampling effort with replicate sampling in future research. Furthermore, this study indicates that both intertidal and subtidal characteristics should be considered if the (mobile) surf zone fauna is investigated.

Stomach/gut content analyses were performed on five common flatfish fish species from epibenthic samples taken during the temporal campaign in order to unravel part of the surf zone food web. Additional fish were obtained from commercial fishermen. Prey items of all species included hyperbenthic (e.g. mysids), endobenthic (e.g. polychaetes) and epibenthic (e.g. shrimps) species. Little dietary overlap was observed. If diet overlap did occur, it mainly involved prey species that are dominant in the surf zone of the studied beaches, such as shrimps and mysids. These results confirm the opportunistic utilisation by flatfish of the available food resources in surf zone ecosystems. Such opportunistic utilisation of food resources can be important for teleosts frequenting physically stressed environments such as surf-exposed beaches. The diets of turbot *Scophthalmus maximus* and brill *Scophthalmus rhombus* reveal part of the main interactions between the hyper- and epibenthos, whereas those of plaice *Pleuronectes platessa*, dab *Limanda limanda* and sole *Solea solea* reveal important links between the epibenthos and the macro-endobenthos within the local surf zone food web.

Three 24-hours sampling cycles were performed to study short term migration patterns. Again the hyper- and epibenthos was sampled alternatingly each hour. Stomach content analyses were performed on juvenile plaice *Pleuronectes platessa* of the first 24h-cycle (spring tide). Possible interactions between the epi- and hyperbenthic organisms are discussed. Despite the turbulent conditions of the studied sites, clear tidal (e.g. I-group plaice *Pleuronectes platessa*, the brown shrimp *Crangon crangon*) and diurnal (e.g. juvenile sole *Solea solea*) periodicities were observed in many macrocrustacean and demersal fish species. An opportunistic

utilisation of available food resources is again suggested as I-group plaice clearly migrate high up the beach during flood to disperse in order to profit from the rich macrobenthic area (mainly the polychaete *Scolelepis squamata* and ends of *Arenicola* species), while the 0-group feeds mainly on the most abundant hyper- and macrobenthic organisms from somewhat deeper water (mainly palps of the polychaete *Magelona papillicornis* and cyprid larvae).
Finally, it can be concluded that the Belgian surf zone functions as a nursery and/or transient area for hyper- as well as epibenthic stages of several species.

SUMMARY

Each chapter is briefly discussed and some general conclusions are formulated. The main results will be illustrated by the results on the flatfish species plaice *Pleuronectes platessa*. This species is one of the dominant components of both the hyperbenthic (as postlarvae) and epibenthic (as 0- and I-group juveniles) communities. The species has already been recognised as a common resident in the surf zone of sandy beaches by other authors (see Wennhage & Pihl (1994) and references herein, Gibson et al. 1993, 1996) and it feeds to a large extent on hyperbenthic species (see below).

Chapter I deals with the inventory and description of distribution patterns of the hyperbenthos of the surf zone of Belgian sandy beaches and is divided into two parts.

A first part gives a detailed inventory of the surf-zone hyperbenthos and discusses the seasonal patterns of the hyperbenthic species (**Chapter I**, **Part A**). Monthly samples were taken in the surf zone of 4 sandy beaches along the Belgian coast from May 1996 until July 1997. A distinction was made between temporary hyperbenthic organisms (merohyperbenthos, e.g. early life stages of fish and macrocrustaceans), and permanent members of the hyperbenthos (holohyperbenthos, e.g. mysids and amphipods). In total, 172 functional species were recorded. More than 75% of the average total sample composition consisted of mysids, mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei*. Within the merohyperbenthos, postlarval decapods and fish were the dominant organisms (e.g. plaice). Average densities per month exceeded 1500 individuals per 100m². Yearly biomass averages ranged from 300 to over 3000 mg ashfree dry weight per 100m². The number of species occurring in the surf zone was comparable to that of the adjacent, subtidal areas and recorded total hyperbenthic densities were slightly higher. If species were classified according to their occurrence, 15 residents and 10 migrants could be distinguished. Other species did occur irregularly or only sporadically. Most of the residents have a true hyperbenthic life style (e.g. most mysids, the amphipod *Atylus swammerdami*), some are known to inhabit the underlying sand and make vertical excursions into the water column (e.g. the isopod *Eurydice pulchra*, the amphipod species of the genus *Bathyporeia*) and some are known to be associated with drifting detritus (e.g. the amphipod *Gammarus crinicornis*). Almost all 'migrants' have a planktonic (e.g. jellyfish, copepods) or endobenthic (e.g. burrowing amphipods, polychaetes) life style. Planktonic organisms are most likely passively transported towards the coast and their presence is mainly related to their seasonal patterns of occurrence. During the year, three recruitment peaks (mainly of postlarval fish and decapods) were observed: in winter, spring and summer. Winter was characterised by very low total density and diversity, and by the presence of fish eggs. In spring, total merohyperbenthic densities were highest and postlarvae of the shore crab *Carcinus maenas* dominated, while in summer the merohyperbenthos was dominated by postlarvae of gobies *Pomatoschistus* species. Postlarval plaice was caught from February to May. Next to water temperature as a major structuring force, the occurrence of most of the organisms was influenced by hydrodynamic factors such as wave height and turbidity.

The factors influencing the spatial occurrence of surf zone hyperbenthos is discussed in the second part of Chapter I (**Chapter I**, **Part B**). The hyperbenthos of the surf zone of 12 sandy beaches along the Belgian coast was sampled in spring of 1996. In order to assess the major influencing factors on the spatial occurrence of hyperbenthic assemblages of the surf zones, a wide variety of environmental variables were measured simultaneously. Multivariate statistical techniques were used to analyse the hyperbenthic distribution patterns and to evaluate the environmental variables measured. Small morphodynamical differences between the beaches still seem to be large enough to have an influence on hyperbenthic community structure. Next to 'external' (temporal) variables such as water temperature and extreme hydrodynamic forces, local morphological beach characteristics, and especially their intertidal and subtidal slope, are suggested to be important structuring variables. Holohyperbenthic as well as merohyperbenthic organisms both seem to respond, although in different ways, to these variables. The effect of the intertidal slope (and correlated variables) on hyperbenthic density is mainly reflected in the holohyperbenthos, and especially the mysids. These actively migrating organisms were found along the whole coast, but highest densities were reported from with flat and wide beaches. Less mobile and more sediment-associated animals such as cumaceans and several amphipod species were rather restricted to certain types of beaches. Merohyperbenthic organisms were mainly found on beaches characterised by intermediate subtidal slopes and high turbidity, and this both in terms of density and number of species. It is suggested that protection from visual predatorsmay be important in providing refuges in the turbulent and relatively homogeneous surf zone of these sandy beaches.

The second chapter (**Chapter II**) deals with the utilisation of the surf zone by demersal fish and macrocrustaceans (epibenthos): temporal and spatial distribution patterns are described and discussed.

A first part on the temporal patterns of the epibenthos, starts with a detailed inventory (**Chapter II**, **Part A**). A time series of monthly samples, taken at the same 4 stations from May 1996 until July 1997, was analysed. In total, 34 species were recorded: 3 caridean shrimps, 5 anomuran and brachyuran crabs, 2 cephalopods and 24 teleost fish. The brown shrimp *Crangon crangon* dominated almost all samples (>80% of total density). on several occasions, total densities exceeded 400 individuals per $100m^2$ (10 individuals per $100m^2$ if *C. crangon* is excluded). Several fish species such as plaice *Pleuronectes platessa*, were exclusively caught as juveniles. Although juvenile plaice are less abundant on the Belgian coast as compared to the shallow bays of the UK and continental NW Europe (Rogers et al. 1998), catch densities are still higher in the surf zone of the sandy beaches as compared to the adjacent shallow subtidal habitats of the Belgian coast (see also Table 2 in **Chapter V**, Cattrijsse unpublished data). The surf zone of the Belgian sandy beaches may act as a nursery for longer (e.g. plaice *Pleuronectes platessa*) or shorter (e.g. brill *Scophthalmus rhombus*) periods of time. The zone also seems to function as a transient area to other nurseries like estuaries (e.g. bass *Dicentrarchus labrax*) or between an estuarine nursery area and the fully marine environment (e.g. dab *Limanda limanda*). Seasonal patterns in the epibenthos were discussed after classifying each species according to their resident status. Seven resident (e.g. juvenile plaice) and 10 migrant species were identified. Temporal variation in community structure was greatly masked by spatial differences between sites. Although variables such as salinity and hydrodynamic characteristics may have influenced the data, clear temperature-related, seasonal patterns were detected. Most probably, low temperature conditions and subsequent migration of organisms to deeper waters caused a decline in both density and diversity in winter. The observed growth of 0-group plaice in the surf zone was compared to the optimal growth model of Fonds (1979). For this exercise, fish were obtained both from the by-catch of artisanal fishermen fishing with horses in the surf zone and from the own epibenthos samples described above (monthly samples from May 1996 to June 1997). Standard length was measuredand stomach fullness indices (FIs), which can reveal temporal changes in feeding rhythm, were calculated per month. The observed growth rate was much lower than the growth expected under optimal circumstances. Although average FIs per month were rather low, food is unlikely to be limiting, since the surf zone of Belgian sandy beaches has been shown to be a very rich area with respect to macro-endobenthic (Degraer et al. 1999) and hyperbenthic (this study) organisms, the major prey items of 0-group plaice. Probably, young plaice spend much time and energy coping with the highly dynamic circumstances in the Belgian surf zone. Currents, general turbulence and wave action all have the potential to reduce growth rate by decreasing food intake below that possible in calm waters (Gibson 1994).

The second part of Chapter II (**Chapter II**, **Part B**) deals with the spatial variation in the epibenthos of the surf zone: what factors influence the fish and macrocrustacean communities? During the spatial campaign, epibenthic samples were taken at 12 stations along the coast. In total, 26 species were recorded: 4 caridean shrimps, 5 brachyuran crabs, 1 cephalopod and 16 teleost fish. Again, the brown shrimp *Crangon crangon* dominated almost all samples (>80% of total density). Total densities exceeded 250 individuals per 100m² on several occasions (10 per 100m² if *C. crangon* is excluded). A difference between the east and west coast of Belgium, as reported for other benthic components in deeper waters, was not found in this study. Spatial variation was mainly correlated with local conditions like turbidity of the water and the morphodynamic characteristics of the beach and the adjacent subtidal area. Few other studies to date have dealt with the effects of exposure on the surf zone fauna, and in general only the intertidal slope is considered when characterising the sampled beaches. High epibenthic densities and low diversities were observed on sites with long, flat slopes (when both the inter- and the shallow subtidal are considered). Highest diversity and densities were found at sites with intermediate profiles. The sites with highest turbidities were characterised by the highest number of species and high densities. Although turbulence and turbidity may have affected sampling efficiency, the mobile and relatively homogenous nature of the substratum on sandy beaches means that few refuges are availableand that protection due to higher turbidity might be important. Also, the protection that is gained by occurring on flat, shallow beaches (less predation, less wave exposure) is probably outbalanced by increased fluctuations in environmental variables such as salinity and higher risks of retention on the beach at ebb-tide, resulting in a higher diversity at intermediate sites. Juvenile plaice could not directly be linked to these patterns, the species occurred in comparable densities at all sites investigated along the coast.

Chapter III focusses on the interactions between the epi- and hyperbenthos. The feeding ecology of juvenile flatfish species in the surf zone was investigated. The diet of five 0- and I-group flatfish species of the surf zone was studied both numerically and gravimetrically by means of stomach and/or gut content analyses. Monthly samples were obtained from the by-catch of artisanal fishermen from May until December 1996. To assess the niche width of, and the niche segregation between, the different species, multivariate analyses were performed on the numerical data. the five flatfish species were plaice *Pleuronectes platessa*, sole *Solea solea*, brill *Scophthalmus rhombus*, turbot *Scophthalmus maximus* and dab *Limanda limanda*. Prey items of all flatfish species included hyperbenthic (e.g. mysids), endobenthic (e.g.

polychaetes) and epibenthic (e.g. shrimps) species. Little dietary overlap was observed. If diet overlap did occur, it mainly involved prey species that are dominant in the surf zone of Belgian beaches such as shrimps and mysids. These results suggest an opportunistic utilisation of the available food resources in surf zone ecosystems.

Also, two strategically different feeding habits could be distinguished. Turbot and brill mainly fed on large, highly mobile prey (e.g. fish, mysids) and had a rather narrow prey-spectrum, whereas plaice, dab and sole ate more benthic prey (e.g. polychaetes) and had a broader prey-spectrum.

In **Chapter IV**, short term migration patterns of the epi- and hyperbenthic organisms are discussed. Three consecutive 24h-sampling-cycles were performed in spring of 1996, during which hyper- and epibenthic samples were taken on alternate hours. Multivariate statistical techniques and three-way ANOVAs were used to evaluate the effects of the environmental variables measured. Inspite of the strong turbulent conditions of the studied site, clear tidal (e.g. the brown shrimp *Crangon crangon* and juvenile plaice *Pleuronectes platessa*) and diurnal (e.g. sole *Solea solea* and clupeids, respectively caught mainly during the night and during the day) periodicities of many macrocrustacean and demersal fish species were observed. Nevertheless, the extremely turbulent conditions of the surf zone possibly had their effect on the behaviour of many species (e.g. juvenile brown shrimp are not able to bury themselves as the water retreats). Within this chapter, special attention was given to juvenile plaice and the question is asked whether the high dynamics of the surf zone suppress the ability of young plaice to actively search for food. In order to answer this question, additional stomach content analyses were performed. Also, the interactions with potential prey species was investigated: the hyperbenthic fauna was sampled simultaneously and data on macrobenthos of an adjacent beach were obtained from literature. Clearly, the Belgian sandy beaches are used as a feeding ground by I-group plaice. An opportunistic utilisation of available food resources is suggested. I-group plaice clearly migrate high up the beach during flood tide, where they disperse to profit from the rich macrobenthic fauna. In contrast, the 0-group mainly feeds on the most abundant hyper- and macrobenthic organisms from somewhat deeper water.

Finally, in **Chapter V**, general conclusions, some remarks and recommendations for future research are given. One of the major conclusions is that the surf zone of the Belgian coast, despite its turbulence, is by no means a marine desert, but is used intensively by a number of hyper- as well as epibenthic species. Even more, it is used as a nursery and/or transient area for several early life stages of fish and macrocrustaceans. Although the strong hydrodynamic conditions of the Belgian surf zone are important in structuring hyper- as well as epibenthic communities, it is remarkable that several species seem to cope so well with this turbulence. Future research should include a thorough study of the feeding ecology and behaviour of the brown shrimp *Crangon crangon* as it is the dominant epibenthic species of the study area. Since the food web of surf zones of exposed sandy beaches is dominated by the phytoplankton-zooplankton-fish pathway, additional information on the phytoplankton component is of major importance to understand the interactions. Also estimations of primary and secondary production is necessary to assess the relative importance of the faunistic groups studied here.

ABSTRACT

Dit is de eerste studie over de hyper- en epibenthische fauna van de surfzone van Belgische zandstranden. Daarom, als een eerste doelstelling voor deze thesis, werd er in eerste instantie veel aandacht besteed aan de inventarisatie (soortensamenstelling) en de beschrijving van de temporele en ruimtelijke distributiepatronen van de twee gemeenschappen. Een temporele en een ruimtelijke campagne werden uitgevoerd, waarbij telkens het hyper- en epibenthos werd bemonsterd. Tijdens de temporele campagne werden maandelijks stalen genomen in 4 geselecteerde stations, terwijl de ruimtelijke campagne een staalname inhield in 12 stations langsheen de Belgische kust. Uiteindelijk blijkt de surfzone van de Belgische kust een habitat te zijn voor een groot aantal soorten. Een rijke hyperbenthische gemeenschap is aanwezig en ook het epibenthos is divers. Totale hyper- en epibenthische densiteiten waren vergelijkbaar of zelfs hoger dan die van de aangrenzende, subtidale gebieden. De Belgische surfzone kan hierdoor bekeken worden als een belangrijke uitbreiding van het rijke zandbankengebied voor de kust. Verschillen in totale hyperbenthische densiteiten met andere Europese surfzones zijn waarschijnlijk gelinkt aan de graad van blootstelling van de stranden.

Tijdens deze studie werd een poging gedaan om de belangrijkste structurerende variabelen voor de hyper- en epibenthische gemeenschap te identificeren. Hiervoor werd een brede waaier aan omgevingsvariabelen gemeten tijdens het moment van staalname. Verschillende uni- en multivariate statistische technieken werden gebruikt voor de analyse van de datasets. Ondanks de duidelijke temperatuur-gerelateerde seizoenale distributiepatronen, worden de hyper- en epibenthische gemeenschappen van de surfzone ook duidelijk beïnvloed door hydrodynamische factoren. Deze invloed laat zich voelen tijdens korte termijn gebeurtenissen (b.v. storm) of door langere termijn effecten (invloed op de morfodynamiek van het strand). Ruimtelijke verschillen werden gevonden in soortenrijkdom en densiteit. In het algemeen werden de hoogste hyper- en epibenthische densiteiten gevonden op vlakke, brede stranden, maar ook op intermediaire stranden en bij hoge turbiditeit werden hoge densiteiten en een groot aantal soorten gevonden. Ondanks de duidelijke distributiepatronen, vereisen de veel lagere densiteiten van het epibenthos in vergelijking met het hyperbenthos waarschijnlijk een hogere staalname-inspanning en gerepliceerde staalname in toekomstige studies. Deze studie toont ook aan dat zowel de intertidale als de ondiep subtidale karakteristieken moeten in rekening gebracht worden indien de (mobiele) fauna van de surfzone wordt onderzocht.

Maag-/darminhoud analyses werden uitgevoerd op vijf algemene platvissoorten om een deel van het surfzone voedselweb te ontrafelen. De vissen waren afkomstig van de stalen genomen tijdens de temporele campagne en additionele individuen werden bekomen uit de bijvangst van commerciële strandvissers. Prooien van de vijf soorten behoorden tot het hyperbenthos (b.v. aasgarnalen), endobenthos (b.v. polychaeten) en epibenthos (b.v. garnalen). Slechts zeer weinig overlap van hun diëten kon worden aangetoond. Indien dit wel het geval was, ging het voornamelijk over soorten die veel voorkomen in de Belgische surfzones, zoals aasgarnalen en garnalen. Deze resultaten bevestigen het opportunistische gebruik van de beschikbare voedselbronnen in het surfzone ecosysteem door de onderzochte platvissen. Zo'n opportunistisch gebruik van voedselbronnen kan belangrijk zijn voor vissen die dikwijls in de surf zone foerageren, aangezien de meeste stranden, blootgesteld aan een aanzienlijke golfactie, fysisch gestresseerde omgevingen kunnen zijn. Het dieet van tarbot *Scophthalmus maximus* en griet *Scophthalmus rhombus* illustreert een deel van de interacties die optreden tussen het hyper- en epibenthos in het lokale voedselweb van de surfzone, terwijl dat van schol *Pleuronectes platessa*, schar *Limanda limanda* en tong *Solea solea* belangrijke delen van de links tussen het epi- en macro-endobenthos blootlegt.

Drie 24-uur staalnamecycli werden uitgevoerd om de korte-termijn migraties te onderzoeken. Opnieuw werden hiervoor elk uur het hyper- en epibenthos alternerend bemonsterd. Maaganalyses werden uitgevoerd van juveniele schol uit de eerste cyclus (springtij). Mogelijke interacties tussen het hyper- en epibenthos worden bediscussieerd. Ondanks de turbulente condities van de bestudeerde stranden, werden toch duidelijke tidale (b.v. I-groep schol *Pleuronectes platessa*, de grijze garnaal *Crangon crangon*) en diurnale (b.v. juveniele tong *Solea solea*) patronen waargenomen voor verschillende demersale vissoorten en macrocrustaceeën. Opnieuw werd een opportunistisch gebruik van de aanwezige voedselbronnen gesuggereerd: I-groep schollen migreren hoog op het strand tijdens vloed, waar ze zich verpreiden om te profiteren van de rijke macrobenthische gemeenschap in deze zone (vooral de polychaet *Scolelepis squamata* en achtereindes van *Arenicola* species). De 0-groep schollen daarentegen voeden zich voornamelijk met de meest abundante organismen van wat diepere zones (voornamelijk palpen van de polychaet *Magelona papillicornis* en cypride larven werden geconsumeerd).
Tenslotte kan geconcludeerd worden dat de Belgische surfzone zowel als een kinderkamer als een overgangsgebied functioneert voor hyper- én epibenthische stadia van verschillende soorten.

SAMENVATTING

In deze samenvatting zal elk hoofdstuk kort aangehaald worden en zullen algemene besluiten geformuleerd worden. Om de onderliggende structuur van dit proefschrif te verduidelijken, worden de resultaten over schol *Pleuronectes platessa* als rode draad doorheen deze samenvatting geweven. Deze soort is namelijk een van de belangrijkste componenten van zowel het hyper- (als postlarve) als het epibenthos (als 0- en I-groep juveniel). Vele auteurs (b.v. Wennhage & Pihl (1994) en referenties daarin, Gibson et al. 1993, 1996) erkenden schol reeds als een veel voorkomende permanente bewoner (resident) van surfzones van zandstranden. De juvenielen voeden zich voor een groot deel met hyperbenthische soorten (zie verder).

Het eerste hoofstuk van dit proefschrift (**Chapter I**) bestaat uit twee delen en behandelt zowel de inventarisatie van het hyperbenthos van Belgische surfzones als de beschrijving van de distributiepatronen van deze fauna.

Het eerste deel van dit hoofdstuk (**Chapter I, Part A**) geeft een gedetailleerde beschrijving van het hyperbenthos van de Belgische zandstranden en bediscussieert seizoenale patronen van hyperbenthische soorten. De surfzones van vier geselecteerde stations werden maandelijks bemonsterd van mei 1996 tot en met juli 1997. Er werd een onderscheid gemaakt tussen tijdelijk hyperbenthos (merohyperbenthos, b.v. vroege levensstadia van vissen en grotere schaaldieren) en permanent hyperbenthos (holohyperbenthos, b.v. aasgarnalen en vlokreeftjes). In totaal werden 172 functionele soorten gevonden. De gemiddelde totale samenstelling van de stalen bestond voor meer dan 75% uit aasgarnalen, voornamelijk *Mesopodopsis slabberi*, *Schistomysis spiritus* en *Schistomysis kervilleii* (allemaal behorende tot het holohyperbenthos). Het merohyperbenthos daarentegen werd gedomineerd door postlarvale decapoden en vissen (b.v. postlarvale schol). Maandelijkse gemiddelde densiteiten waren hoger dan 1500 ind./100m^2. Jaarlijkse gemiddelde biomassawaarden lagen tussen 300 en >3000 mg ADW/100m^2. De soortenrijkdom (aantal aanwezige soorten) in de surfzones is vergelijkbaar met die van aanpalende gebieden, totale hyperbenthische densiteiten zijn echter iets hoger. Een classificatie van soorten volgens hun voorkomen in het studiegebied leverde 15 'permanente bewoners' en 10 'migranten' op. Andere soorten werden onregelmatig of slechts sporadisch aangetroffen. De meeste residentiële soorten vertonen een echte hyperbenthische levenswijze (b.v. de meeste aasgarnalen, de amphipode *Atylis swammerdami*), terwijl een aantal andere soorten bewoners zijn van het sediment die regelmatige verticale excursies in de waterkolom maken (b.v. de isopode *Euridyce pulchra*, en de amphipoden-soorten die tot het genus *Batyporeia* behoren). Andere soorten zijn dan weer geassocieerd met drijvend detritus (b.v. de amphipode *Gammarus crinicornis*). Bijna alle 'migranten' hebben een echte planktonische (b.v. kleine kwalletjes, copepoden) of endobenthische levenswijze (b.v. de meeste amphipoden, polychaeten). Planktonische organismen worden hoogstwaarschijnlijk passief naar de kust getransporteerd. Hun aanwezigheid in de surfzones is daarom hoofdzakelijk gerelateerd aan seizoenale trends. Tijdens het jaar werden drie recruteringsperiodes (voornamelijk van postlarvale vissen en decapoden) opgemerkt: in de winter, de lente en de zomer. Tijdens de winter waren de diversiteit en densiteit heel laag en werden voornamelijk visse-eieren aangetroffen. Totale densiteiten van het merohyperbentos waren het hoogst in de lente en postlarvale strandkrabbetjes waren de dominante organismen. De zomergemeenschap werd gedomineerd door postlarvale grondels. Postlarvale schol werd gevangen van februari tot mei. Het voorkomen van de meeste organismen bleek voornamelijk gelinkt met de watertemperatuur, maar hydrodynamische variabelen zoals golfhoogte en turbiditeit bleken ook van belang te zijn.

De factoren die de ruimtelijke verspreiding van het hyperbenthos in de surfzone beïnvloeden worden in het tweede deel van het eerste hoofdstuk bestudeerd (**Chapter I, part B**). Het hyperbenthos van de surfzones van 12 zandstranden langsheen de kust werd bemonsterd tijdens het voorjaar van 1996. Om de belangrijkste factoren te identificeren die de ruimtelijke verspreiding beïnvloeden, werd een brede waaier aan omgevingsvariabelen simultaan gemeten. Multivariate statistische technieken werden toegepast om de ruimtelijke distributiepatronen te ontrafelen én om het belang van de gemeten omgevingsvariabelen te analyseren. Alhoewel er weinig verschillen in morfodynamische kenmerken tussen de stranden merkbaar waren, bleken deze verschillen toch groot genoeg om de samenstelling van de hyperbenthische gemeenschap te beïnvloeden. Naast 'externe' (temporele) variabelen zoals watertemperatuur en extreme hydrodynamische krachten, werden lokale strandkarakteristieken, meer bepaald de intertidale en subtidale hellingen, aangeduid als belangrijke structurerende variabelen. Zowel het holo- als het merohyperbenthos vertonen een duidelijke respons op deze variabelen, zij het elk op zijn eigen manier. Het effect van de intertidale helling (en daarmee gecorreleerde variabelen) op de densiteiten van het hyperbenthos wordt voornamelijk teruggevonden in het holohyperbenthos, meer bepaald in de aasgarnalen. Deze actief migrerende organismen werden langs de volledige kustlijn teruggevonden, maar de hoogste densiteiten waren voornamelijk gecorreleerd met vlakke, brede stranden. Minder mobiele organismen, of organismen die meer geassocieerd met het sediment leven (b.v. Cumacea en verschillende Amphipoda), waren meer (soortspecifiek) beperkt tot bepaalde strandtypes. Merohyperbenthische gemeenschappen vertoonden hogere aantallen en hogere soortenrijkdom op stranden met intermediaire subtidale hellingen en bij hoge turbiditeit. Bescherming voor visuele predatoren door hogere turbiditeit kan belangrijk zijn in de turbulente en relatief homogene surfzone van zandstranden.

In het tweede hoofdstuk (**Chapter II**) wordt het gebruik van de surfzone door demersale vissen en epibenthische macrocrustaceeën bestudeerd aan de hand van hun temporele en ruimtelijke verspreidingspatronen.

Het eerste deel van dit hoofdstuk (**Chapter II, part A**) behandelt de temporele patronen van het epibenthos en geeft een gedetailleerde inventarisatie van het epibenthos van de Belgische zandstranden. Maandelijkse stalen, genomen tijdens temporele campagne (mei 1996 tot en met juli 1997) op vier gelecteerde zandstranden werden daarvoor uitgewerkt. In totaal werden 34 soorten aangetroffen: 3 garnalen, 5 anomure en brachyure krabben, 2 soorten cephalopoden en 24 vissesoorten. De grijze garnaal *Crangon crangon* was dominant in alle stalen (> 80%). De totale densiteiten overschreden meerder malen 400 ind./100m². Als *C. crangon* niet werd meegerekend, lagen de aantallen meermaals boven 10 ind./100m². Verschillende vissesoorten zoals schol werden enkel als juveniel gevangen. Alhoewel juveniele schol minder abundant voorkomt aan de Belgische kust in vergelijking met ondiepe baaien in de naburige gebieden van het Verenigd Koninkrijk en continentaal Noord-West Europa (Rogers et al. 1998), zijn de dichtheden in de Belgische surfzone hoger dan in het aangrenzende subtidaal van de Belgische kust (Cattrijsse, ongepubliceerde data). De surfzone van de Belgische zandstranden fungeert als kinderkamer voor langere (b.v. schol, *Pleuronectes platessa*) of korte (b.v. griet *Scophthalmus rombhus*) periodes. De surfzone blijkt daarnaast ook te functioneren als tussenstap naar andere kinderkamers zoals estuaria (zeebaars *Dicentrarchus labrax*) of als halte tussen een kinderkamer en het echte mariene milieu (b.v. schar *Limanda limanda*). Na het rangschikken van de verschillende soorten volgens hun voorkomen, werden seizoenale patronen binnen het epibenthos besproken. Zeven 'permanente bewoners' (b.v. juveniele schol) en 10 'migranten' werden geïdentificeerd. Temporele variatie in gemeenschapsstructuur werd grotendeels gemaskeerd door ruimtelijke verschillen tussen de staalnameplaatsen. Alhoewel bepaalde variabelen zoals saliniteit en hydrodynamiek de dataset zullen beïnvoed hebben, bleken duidelijke, aan temperatuur gerelateerde, seizoenale patronen op te duiken. Hoogst waarschijnlijk veroorzaakten de extreme omstandigheden in de winter een migratie van organismen naar diepere wateren, waardoor lagere waarden voor densiteit en diversiteit opgetekend werden.
De waargenomen groei van 0-groep schol in de surfzone werd vergeleken met het optimale groeimodel van Fonds (1979). De bestudeerde vissen waren afkomstig van eigen epibenthosstalen of werden maandelijks bekomen uit de bijvangst van commerciële vissers tijdens de periode mei 1996 tot en met juli 1997. Standaardlengtes werden per maand gemeten en maagvullingsindexen (VI's) werden maandelijks berekend om temporele veranderingen in voedingsritmes te achterhalen. Alhoewel de vullingsindexen elke maand tamelijk laag waren, wordt geen voedsellimitatie vooropgesteld. De surfzone van Belgische zandstranden blijkt een rijk gebied te zijn voor wat betreft macrobenthos (Degraer et al. 1999) en hyperbenthische organismen (deze studie). Deze groepen vormen de voornaamste prooien van 0-groep schol. Waarschijnlijk moeten jonge scholletjes te veel tijd en energie spenderen om aan de sterke hydrodynamische krachten in de surfzone te kunnen weerstaan. Stromingen, algemene turbulentie en golfbewegingen hebben allemaal de potentie om de groeisnelheid te reduceren door de voedselopname te belemmeren in vergelijking met kalmer water (Gibson 1994).

Het tweede deel van Hoofdstuk II (**Chapter II, Part B**) behandelt de ruimtelijke variatie in de epibenthische gemeenschappen van Belgische surfzones, m.a.w. er werd onderzocht welke factoren de vis- en macrocrustaceagemeenschappen beïnvloeden. Tijdens de ruimtelijke campagne werden epibenthosstalen verzameld op 12 stations langsheen de kust. In totaal werden 26 soorten teruggevonden, onderverdeeld in garnalen (4 soorten), brachyure krabben (5 soorten), cephalopoden (1 soort) en vis (16 soorten). De grijze garnaal *Crangon crangon* was opnieuw dominant in alle stalen. Totale dichtheden waren meerdere malen hoger dan 250 ind./100m². Als *C crangon* buiten beschouwing werd gelaten, was dit 10 ind./100m². Een oost-west tegenstelling, zoals reeds gevonden in andere benthosstudies in diepere wateren van de Belgische kustzone, werd hier niet aangetroffen. Ruimtelijke variatie was vooral gecorreleerd met lokale karakteristieken zoals turbiditeit en de morfodynamische kenmerken van zowel het strand als het aangrenzende subtidaal. Weinig andere studies behandelen het effect van geëxposeerde stranden op de fauna van surfzones en normaal wordt alleen maar de helling van het intertidaal in rekening gebracht bij de karakterisering van het strand. Hoge epibenthische dichtheden en een lage diversiteit werden teruggevonden bij gemeenschappen afkomstig van stranden met lange, vlakke hellingen (als zowel het intertidale als het ondiepe subtidaal in rekening wordt gebracht). Hoge diversiteit én hoge densiteiten werden aangetroffen op stranden met intermediaire profielen. De stations met de hoogste turbiditeit werden gekenmerkt door gemeenschappen met de hoogste dichtheden en een hoog soortenaantal. Alhoewel turbulentie en turbiditeit de staalname-efficiëntie kunnen beïnvloed hebben, zorgt de mobiliteit en relatieve homogene structuur van het substraat voor weinig beschutting, zodat bescherming door hoge turbiditeit belangrijk kan zijn. Daarnaast wordt het voordeel van de bescherming die geboden wordt door het verblijf op een vlak, ondiep strand (verminderde predatiedruk en lagere blootstelling aan golfslag) waarschijnlijk overschaduwd door verhoogde schommelingen in omgevingsvariabelen (zoals saliniteit) én het risico op achterblijven op het strand bij eb, zodat een hogere diversiteit wordt aangetroffen op intermediaire stranden. Het voorkomen van jonge schol kon echter niet onmiddellijk in verband gebracht worden met deze patronen, jonge schol bleek overal aan de kust aanwezig te zijn in vergelijkbare densiteiten.

In Hoofdstuk III worden de interacties tussen het epi- en hyperbenthos nader bestudeerd. De voedingsecologie van juveniele platvissen in de surfzone werd onderzocht. Het dieet van 0- en I- groep platvissen uit de surfzone werd zowel numeriek als gravimetrisch onderzocht aan de hand van maag- en/of darminhouden. Maandelijkse stalen werden bekomen van de bijvangst van commerciële vissers voor de periode mei tot december 1996. Om de nichebreedte en nichesegregatie van de verschillende soorten te bestuderen werden multivariate analyses toegepast op de numerieke data. Er werden vijf platvissoorten aangetroffen: schol *Pleuronectes platessa*, tong *Solea solea*, schar *Limanda limanda*, tarbot *Scophthalmus maximus* en griet *Scophthalmus rhombus*. Prooien van alle platvissen omvatten hyperbenthische (b.v. aasgarnalen), endobenthische (b.v. polychaeten) en epibenthische (b.v. garnalen) soorten. Hun diëten overlapten slechts zeer weinig. Als prooien gemeenschappelijk waren ging het over organismen die dominant waren in de surfzone van Belgische stranden zoals garnalen en aasgarnalen. Deze resultaten wijzen op een opportunistisch gebruik van het beschikbare voedselaanbod in surfzones door platvissen.
Hiernaast konden ook twee verschillende voedingsstrategieën worden onderscheiden tussen de 5 platvissoorten. Tarbot en griet voedden zich voornamelijk met grote, erg mobiele prooien (b.v. vissen en aasgarnalen) en hadden en nauw prooispectrum, terwijl schol, schar en tong meer benthische prooien (b.v. polychaeten) consumeerden. Deze laatste soorten hadden ook een breder prooispectrum.

In Hoofdstuk IV (**Chapter IV**) worden de korte-termijnsmigraties van zowel epibenthische als hyperbenthische organismen besproken. Drie opeenvolgende 24-uurstaalnames werden uitgevoerd in het voorjaar van 1996. Tijdens deze staalnames werden elk uur alternerend stalen genomen voor het epi- en het hyperbenthos. Multivariate statistische technieken en drieweg-ANOVA's werden toegepast om de invloed van de omgevingsvariabelen op de gemeenschappen na te gaan. Ondanks de sterk turbulente stromingen in het staalnamepunt, konden duidelijke tidale (b.v. de grijze garnaal *Crangon crangon* en juveniele schol *Pleuronectes platessa*) en diurnale (b.v. juveniele tong *Solea solea* en haringachtigen, voornamelijk gevangen respectievelijk tijdens de nacht en tijdens de dag) patronen in het voorkomen van vele macrocrustaceeën en demersale vissen worden aangetoond. De extreem turbulente omgeving van de surfzone blijkt echter toch een invloed te hebben op het gedrag van verschillende soorten (b.v. juveniele garnaal graven zich niet in als het water zich terug trekt). In dit hoofdstuk werd speciale aandacht geschonken aan juveniele schol. Er werd nagegaan of de sterke dynamiek in de surfzone het actief zoeken naar voedsel door jonge scholletjes verstoort. Daarom werden bijkomende maaganalyses uitgevoerd. De interacties met mogelijke prooisoorten werd nagegaan: de hyperbenthische fauna werd simultaan bemonsterd en data betreffende het macrobenthos van een nabijgelegen strand waren beschikbaar uit de literatuur. De zandstranden van de Belgische kust worden duidelijk gebruikt als voedselgronden voor I-groep schol. Er wordt een opportunistisch gebruik van dit voedselaanbod gesuggereerd. I-groep schol migreert duidelijk hoger op het strand tijdens vloed om zich daar te verspreiden om te profiteren van de rijke macrobenthische gemeenschappen die daar aanwezig zijn. De 0-groep daarentegen voedt zich voornamelijk met de meest abundante hyper- en macrobenthische gemeenschappen afkomstig uit de diepere wateren.

In het laatste hoofdstuk **(Chapter V)** worden algemene conclusies vooropgesteld en worden aanbevelingen voor toekomstig onderzoek naar voor gebracht. Een van de belangrijkste conclusies is zeker dat de surfzones van de Belgische kust, ondanks hun turbulentie, in geen geval als een mariene woestijn kunnen worden beschouwd. Deze zone wordt daarentegen intensief gebruikt door een groot aantal hyper- en epibenthische soorten. Het is daarenboven een kinderkamer en/of doorgangsgebied voor verschillende vroege levensstadia van vissen en macrocrustaceeën. Alhoewel de sterke hydrodynamische omgeving van de Belgische surfzone een belangrijke rol speelt in het structureren van zowel de hyper- als de epibenthische gemeenschap, is het opmerkelijk dat verschillende soorten heel goed aangepast blijken te zijn aan dit milieu.

Toekomstig onderzoek zou zich voornamelijk moeten toeleggen op de voedingsecologie en het gedrag van de grijze garnaal, aangezien dit toch de dominante epibenthische soort is van het studiegebied. Vermits het voedselweb binnen de surf zone van geëxposeerde stranden voornamelijk gedomineerd wordt door de fytoplankton-zooplankton-vis-route, is bijkomende informatie over de fytoplankton component van groot belang om de verschillende interacties te begrijpen. Ook schattingen van primaire en secundaire productie zijn noodzakelijk om het relatieve belang van de bestudeerde groepen te kunnen inschatten.

INTRODUCTION

Motivation

As an easily accessible transition site between two well-studied ecosystems (the Westerschelde estuary in the east and an extensive sand bank system in the west), it is remarkable how often the surf zone of sandy beaches has been neglected in ecological research (McLachlan 1983). In some cases, the surf zone may be very turbulent, causing sampling to be a difficult and sometimes dangerous task. This turbulence is also suggested to be pernicious for the survival of many (fragile) organisms. Moreover, the surf zone and the underlying intertidal area of most sandy beaches of the southern bight of the North Sea, are characterised by strong gradients: temperature and salinity can change severely during one tidal cycle. Nevertheless, strong evidence exists that surf zones can harbour rich fauna's (McLachlan 1983). Intertidal and shallow subtidal areas can function as nurseries for larval, postlarval and 0+ demersal fish and epibenthic macrocrustaceans (e.g. shrimp). The early life stages of these animals are, after a short planktonic phase, members of the temporary hyperbenthos. Other hyperbenthic taxa (e.g. shrimp, amphipods) are important prey for larger, demersal size-classes of these organisms (Mauchline 1980). In these early life stages, a number of important biological and physiological processes take place, that determine recruitment towards the (exploitable) adult stock (Blaxter et al. 1989). It is more and more accepted that the year-class strength of demersal fish is mainly determined during the first year (Beverton et al. 1984, Van der Veer & Bergman 1987). Therefore, it is recommended to gather more information about the ecology of young hyperbenthic and demersal stages. These findings, together with the intensive use of the surf zone by man as a recreational area and the effects of other anthropogenic pressures (e.g. fisheries, coastal defence works, harbour construction, shipping), emphasise the importance of good beach management. As two major components of surf zone fauna, the hyperbenthos (a missing link within surf zone research), and epibenthic macrucrustaceans and demersal fish as their main predators (known to actively use surf zones), were chosen to study for the purpose of this thesis.

Terminology

Some terminology used throughout the text will first be clarified. A **surf zone** is defined here as the moving water envelope between the extent from the water up-rush on the shore to the most seaward breaker[1]. The **hyperbenthos** is defined as the association of small animals (in this study > 1mm) living in the water layer close to the sea bed (Mees & Jones 1997). In this study, it is used as a work definition: all animals caught with the hyperbenthic sledge (with exclusion of larger, epibenthic animals) were retained for further analyses. The most abundant hyperbenthic taxa are mysids, early life stages of caridean shrimps, brachyuran crabs and fish, isopods and amphipods. The term **merohyperbenthos** is applied to all species that spend only part of their early life history in the hyperbenthos and subsequently recruit to the nekton, epibenthos or endobenthos communities, and **holohyperbenthos** for animals that spend variable periods of their adult life in the hyperbenthos (Hamerlynck & Mees 1991). The **epibenthos** comprises all benthic organisms living on or in close proximity of the sediment of the sea and that are retained in a net with a mesh-size of 5 mm (Baretta-Bekker et al. 1992). Common epibenthic organisms are for example demersal fish, shrimp, crabs and echinoderms. Both faunistic terms (hyper- and epibenthos) are used here as work definitions: all animals caugth with the sampling device were identified. However, some animals were excluded from further analyses (see also Appendix 2). For the hyperbenthos, strictly endobenthic, larger epibenthic, sessile and parasitic organisms were excluded, while for the

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[1] source: http://www.tpub.com/weather1/6h.htm

epibenthos, small animals, which were more efficiently caught with the hyperbenthic sledge, were retained. A **nursery** is used here as a restricted area in which juvenile (early life stage) individuals of a species spend a defined period of their lifetime, separated from older conspecifics (Bergman et al. 1988).

Hyperbenthos

Figure 1. The mysid *Mesopodopsis slabberi*.

With the exception of a pilot-study of Lock et al. (1999) (**Appendix 11**), no information is available about hyperbenthic communities of the surf zone of Belgian sandy beaches. World-wide, only a few studies exist about hyperbenthos inhabiting surf zones. While several taxonomic papers describe species collected on sandy beaches, few of them sampled the surf zone or include ecological notes (for a review see McLachlan 1983). Moreover, ecological studies rarely describe whole assemblages: they are mostly restricted to the ecology of one species (e.g. San Vicente & Sorbe 1993a, Hanamura 1999) or one taxonomic group (e.g. mysids: Wooldridge 1983, 1989; fish larvae: Kinoshita 1993, Harris & Cyrus 1996). Research areas are scattered; except for the Mediterranean (e.g. Moran 1972, Macquart-Moulin 1977, San Vicente & Sorbe 1999), the only surf zone studies in European waters are those in the United Kingdom (Colman & Segrove 1955, Fincham 1970) and the Bay of Biscay (San Vicente & Sorbe 1993a).

Nevertheless, the hyperbenthos of the surf zone seems to be characterised by high biomass (McLachlan 1983). Since most fish species occurring in the surf zone of sandy beaches show a high degree of opportunism in feeding, all feeding types may predate heavily on zooplankton and larger schooling crustaceans when they are locally abundant (McLachlan 1983). This has already been demonstrated for gobies (*Pomatoschistus* spp.), Nilsson's pipefish *Syngnathus rostellatus* and several juvenile flatfish species (Cattrijsse et al. 1993, Hamerlynck et al. 1990, 1993, Hamerlynck & Hostens 1993, Beyst et al. 1999a). Hyperbenthic animals are therefore an important (and often neglected) link to the higher trophic levels within the local food webs (McLachlan 1983). Also the link to the lower levels has largely been neglected, but this falls out of the scope of this study. Knowledge about the distribution patterns, densities and biomass of the hyperbenthos is therefore of major importance to understand the functioning and natural variability of surf zone ecosystems.

Epibenthos

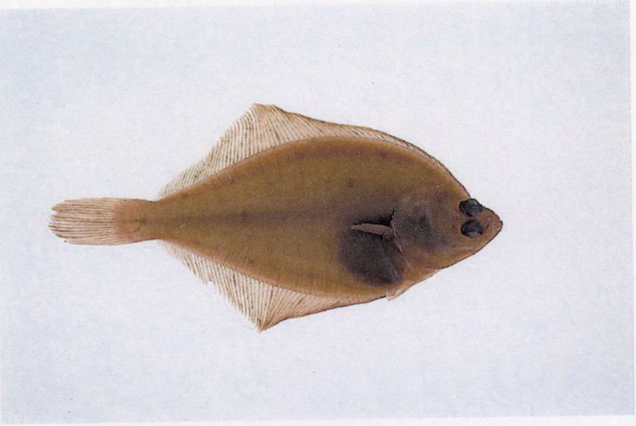

Figure 2. Juvenile plaice *Pleuronectes platessa*.

Temporal variation of epibenthic surf zone (fish) fauna is well documented. Although the shallow area of the Wadden Sea has been studied intensively (e.g. Kuipers 1973, van der Veer & Bergman 1986), no information is available about the epibenthic macrocrustacean and fish surf zone communities of the exposed beaches of the eastern side of the Southern Bight of the North Sea. Furthermore, few studies of the surf zone fauna of sandy beaches have considered both fish and marocrustacean assemblages (Pihl 1986, Ross et al. 1987, Gibson et al. 1993). Most comparable research has been done in South Africa (e.g. Lasiak 1981, 1984, Lamberth et al. 1995, Clark et al. 1996a,b), Mexico (e.g. Modde & Ross 1981, Ross et al. 1987), USA (Texas, Maine) (e.g. McFarland 1963, Hook 1991, Lazzari et al. 1999) and Scotland (e.g. Nash & Gibson 1982, Gibson et al. 1993, 1996).

Trophic ecology of fishes in the surf zone of sandy beaches is also poorly documented and most research has been done in the southern hemisphere (e.g. Lasiak, 1984, 1986; Lasiak & McLachlan, 1987). Other areas investigated include the Irish Sea (Macer, 1967), Mexico (Modde & Ross, 1983), southern Wales (Wyche & Shackley, 1986) and Scotland (Ansell & Gibson, 1990). Trophic relationships within the surf zone of Belgian beaches have never been investigated. Furthermore, much confusion exists over the factors influencing or controlling temporal and spatial variations in epibenthic communities, covering a wide variety of both biological and physical variables (Clark et al. 1996b).

Nursery function

The importance of surf zones of sandy beaches as nurseries or as orientation sites leading to nearby nursery grounds for early life history stages of fish and other marine organisms has been emphasised several times (e.g. Lasiak 1981, Kinoshita 1993, Harris & Cyrus 1996). A nursery can be characterised by its location (supply and transport of early life stages), its food availability (foraging function) and the availability of refuges (Boesch & Turner 1984). The location of the sandy beaches of the Belgian coast suggests a high supply of early life stages to the surf zone, since the area is characterised by the presence of an extensive shallow sand bank system at the western side on the one hand and the nearby presence of the large Westerschelde estuary in the East on the other hand (Figure 1). The Westerschelde is an important nursery for several fish and crustacean species (Creutzberg & Fonds 1971, Zijlstra 1972, Hostens 2000) and also the shallow offshore sand bank system is characterised by high densities of early life stages of fish and macrocrustaceans (Cattrijsse & Dewicke in press). At least some Belgian sandy beaches harbour rich intertidal macro-endobenthic faunas (Degraer et al. 1999), which may serve as potential food for the epibenthic species. Although not many refuges are available at the open beaches (e.g. attached macrophytes are absent), larger predators are likely to avoid the shallow and turbulent surf zone. The potential nursery function for early life history stages (postlarvae in the hyperbenthos and juveniles in the epibenthos) of the Belgian surf zone is therefore worthwhile to investigate.

Objectives

In function of a good management of beaches strongly affected by several potentially harmful influences, it is important to understand the structure, the functioning and the natural variability of those ecosystems (Elliott & Taylor 1989). To understand the biological interactions within this biotope, it is not only necessary to know which species occur (species composition, diversity), where (horizontal and vertical distribution patterns), and when (recruitment periods, tidal and diurnal migration patterns, seasonality) they use this biotope, but also what place they take within the ecosystem. To assess the importance of the hyperbenthos as food for the higher trophic levels, it is necessary to know how much the secondary production is, and what and how much is eaten by which species. Investigation of migration patterns can allow to gain insight into the availability of this food item and into the feeding rhythms of the predators. The main objective of this study is to better understand the structure, the functioning and the natural variability of the Belgian surf zone and to determine in what this surf zone differs from other locations, such as the adjacent shallow subtidal.

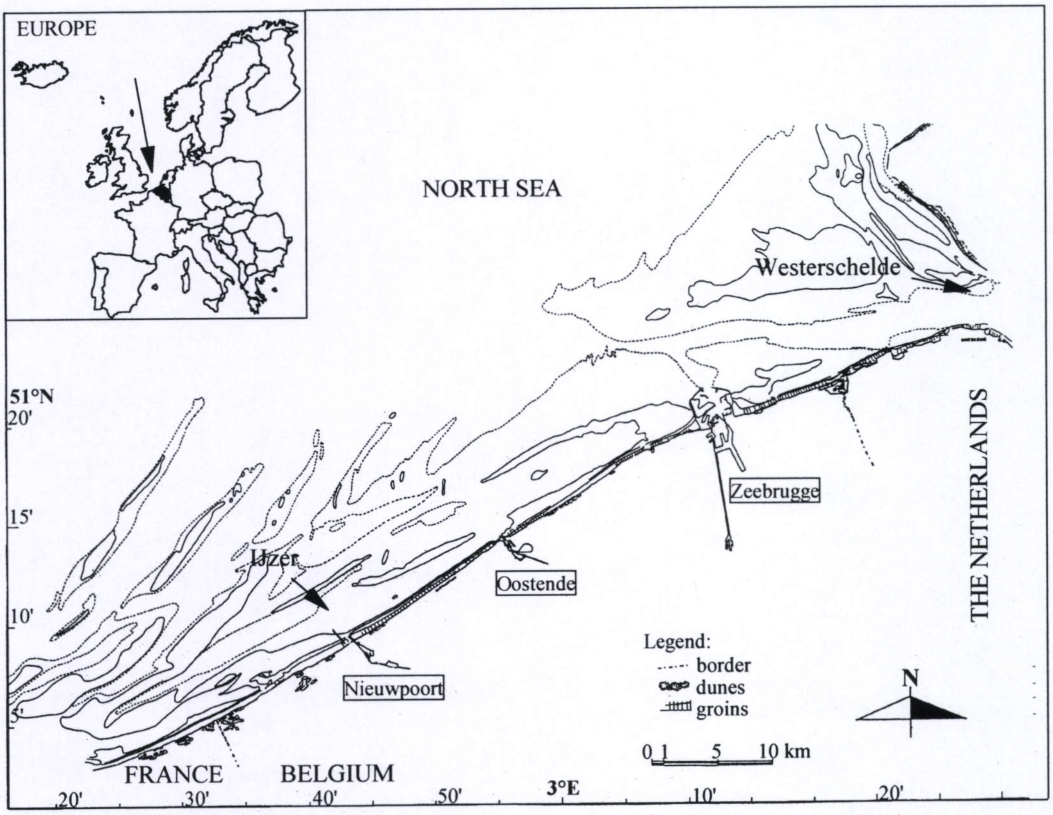

Figure 3. Study area: Belgian coast.

Since up to now no information is available about hyper- and epibenthic communities of Belgian sandy beaches, a thorough inventory is of primary importance. This inventory is followed by a description of the temporal and spatial distribution patterns of the organisms, in terms of species composition, diversity, density and biomass, and the identification of the main structuring variables of the communities. Therefore, hyper- and epibenthic samples were taken almost simultaneously during a temporal and spatial sampling campaign. For the temporal campaign, monthly samples were taken in 4 stations during more than one year (from May 1996 to July 1997). The spatial campaign involved sampling in spring of 1996, when samples were taken at 12 stations along the coast. A great variety of environmental variables were measured simultaneously. These large datasets were analysed by means of multivariate statistical techniques. Due to the large amount of data, this thesis will mainly focuson the presentation of these results (**Chapters I** and **II**).

Secondly, some functional aspects were considered and possible interactions between the epi- and hyperbenthic communities were highlighted. Investigation of the diet of a number of species in **Chapter III**, may reveal part of the local surf zone food web. Stomach and/or gut content analyses were performed on different flatfish species. The analysed fish were obtained from the by-catch of commercial fishermen on the beach of Oostduinkerke (monthly) and additional individuals were taken from own samples (see Chapter 1). In **Chapter IV**, tidal and diurnal periodicity of the epibenthos was studied in relation to food availability, to reveal some interactions between the two studied groups. Therefore, during three subsequent 24-hour-sampling campaigns, hyper- and epibenthic samples were taken alternating each hour and environmental variables were measured. Stomach content of juvenile plaice was analysed.

Finally, general conclusions, some remarks and recommendations for future research are made (**Chapter V**). The recurrent theme throughout the synthesis is plaice *Pleuronectes platessa*, one of the major species inhabiting the surf zone. As postlarva, this species is an important member of the hyperbenthos and other hyperbenthic animals may serve as prey for larger, demersal stages of the species. These juveniles are in their turn important members of the epibenthos.

Outline

Several parts of this thesis have already been published in international literature and most of the remaining data are submitted for publication. Due to the limitation of space in the journals, not all figures and tables of the output of the analyses, are depicted. I have tried to compensate this by including some additional figures, and appendices with all the raw data discussed in the individual chapters.

Of the two subdivisions of **Chapter I**, the part dealing with the temporal variation of the hyperbenthos (**Part A**) is to be published in Estuarine, Coastal and Shelf Science. One summarising table has been added. The second part on the spatial variation (**Part B**) is submitted.

> *Beyst, B., D. Buysse, A. Dewicke & J. Mees (in press). Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns. Estuarine, Coastal and Shelf Science.*
>
> *Beyst, B. & J. Mees (submitted). Factors influencing the spatial occurrence of surf zone hyperbenthos of Belgian sandy beaches.*

Also **Chapter II** is divided in two subdivisions: the first part on temporal patterns of the epibenthos (**Part A**) is to be published in Journal of Sea Research, but has been extended with preliminary growth data of juvenile plaice. The second part on spatial variation (**Part B**) is submitted.

Beyst, B., K. Hostens & J. Mees (in press). Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. Journal of Sea Research.

Beyst, B., K. Hostens & J. Mees (submitted). Factors influencing spatial variation in fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium.

Chapter III about the feeding ecology of the juvenile flatfish inhabiting the surf zone, has been published as such in Journal of Fish Biology.

Beyst, B., A. Cattrijsse, J. Mees (1999). Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. Journal of Fish Biology 55: 1171-1186.

Chapter IV is to be published in Marine Ecology Progress Series. One table on hyperbenthic data has been added.

Beyst, B., J. Vanaverbeke, M. Vincx & J. Mees (in press). Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice (Pleuronectes platessa L.). Marine Ecology Progress Series.

Finally, two Appendices (**Appendix 10** and **Appendix 11**) were published in Journal of the Marine Biological Association of the United Kingdom and Belgian Journal of Zoology, respectively.

Beyst, B., J. Mees & A. Cattrijsse (1999). Early postlarval fish in the hyperbenthos of the Dutch Delta (south-west Netherlands). Journal of the Marine Biological Association of the United Kingdom 79: 709-724.

Lock, K., B. Beyst & J. Mees (1999). Circadiel patterns in the tidal plankton of a sandy beach in Zeebrugge (Belgium). Belgian Journal of Zoology 129(2): 339-352.

CHAPTER I

THE HYPERBENTHOS OF THE SURF ZONE OF SANDY BEACHES: TEMPORAL AND SPATIAL PATTERNS

Part A. Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns

Part B. Factors influencing the spatial occurrence of surf zone hyperbenthos of Belgian sandy beaches

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Chapter I
Part A

Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns

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Results presented in:

Bregje Beyst, David Buysse, Ann Dewicke & Jan Mees (in press). Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns. Estuarine Coastal and Shelf Science.

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Surf zone and intertidal area at a west-coast site

ABSTRACT

Since surf zone hyperbenthos, although highly important in local food webs, has often been neglected and very little information is available, a survey of the Belgian sandy beaches was carried out from May 1996 until July 1997. Monthly samples were taken to give a complete inventarisation of hyperbenthic organisms occurring in the surf zone of Belgian sandy beaches and to evaluate the intensitivity by which this surf zone is used. In total 172 species were recorded. The number of species occurring in the surf zone is comparable to that of the adjacent areas. Next to true hyperbenthic species, endobenthic as well as planktonic organisms were sampled. More than 75% of the average total sample composition consisted of mysids, mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei* (holohyperbenthos). Next to several resident species, active and passive seasonal migration towards the surf zone by a number of species is suggested. A large number of sporadics adds to the typical composition of surf zone hyperbenthos. Within the merohyperbenthos, postlarval decapods and fish were the dominant organisms. During the year, three recruitment peaks were observed. Average densities per month exceeded 1500 ind./100m². Yearly biomass averages ranged from 300 to over 3000 mg ADW/100m². Densities of the common species are slightly higher in the surf zone than in other habitats, emphasising the importance of the area. Besides a possible nursery function, the surf zone may also be used as a transient area between different habitats.

Finally, the influence of several abiotic factors on the hyperbenthic assemblages was evaluated. The main structuring variables determining the occurrence of most of the organisms are water temperature and hydrodynamic factors such as wave height and turbidity. The influence of wave height seems to be two-fold: several good swimmers such as mysids

and some fish species are suggested to be able to actively avoid severe wave conditions, whereas other, more planktonic organisms, are passively transported towards the area if wave heigth increases.

INTRODUCTION

A **surf zone** is defined here as the moving water envelope between the extent from the water up-rush on the shore to the most seaward breaker. The **hyperbenthos** is the association of small animals living in the water layer close to the sea bed (Mees & Jones 1997). Studies on these small organisms within the surf zones are very scarce. While several taxonomic papers describe species collected on sandy beaches, few of them sampled the surf zone or include ecological notes (reviewed by McLachlan 1983). Moreover, ecological studies rarely describe whole assemblages, they are mostly restricted to the ecology of one species (e.g. San Vicente & Sorbe 1993a, Hanamura 1999) or one taxonomic group (e.g. mysids: Wooldridge 1983, 1989; fish larvae: Kinoshita 1993, Harris & Cyrus 1996). Research areas are very scattered; except for the Mediterranean (e.g. Moran 1972, Macquart-Moulin 1977, San Vicente & Sorbe 1999), the only surf zone studies in European waters are those in the United Kingdom (Colman & Segrove 1955, Fincham 1970), the Bay of Biscay (San Vicente & Sorbe 1993a) and the Belgian coast (Lock et al 1999, see also Appendix 11). With the exception of San Vicente & Sorbe (1993a), none of these report temporal data.

Nevertheless, the hyperbenthos of the surf zone seems to be characterised by high biomass (McLachlan 1983). For example, *Schistomysis parkeri* in the Bay of Biscay, was found to have an estimated annual production of 52.6 mg/m², with a corresponding production/biomass ratio (P/B) of 9.7 (San Vicente & Sorbe 1993a). Since most fish species occurring within the surf zone of sandy beaches show a high degree of opportunism in feeding, all feeding types may predate heavily on zooplankton and larger schooling crustaceans when they are locally abundant (McLachlan 1983), as already proven for several gobies (*Pomatoschistus* spp.), Nilsson's pipefish *Syngnathus rostellatus* and several juvenile flatfish species (Cattrijsse et al. 1993, Hamerlynck et al. 1990, 1993, Hamerlynck & Hostens 1993, Beyst et al. 1999a). Hyperbenthic animals are therefore an important (and often neglected) link within the local food webs (McLachlan 1983). Knowledge about the distribution patterns, densities and biomass of the hyperbenthos is of major importance to understand the functioning and natural variability of surf zone ecosystems.

In order to enhance the current knowledge of the European surf zone ecosystems, the purpose of this study is primarily (1) to give a complete inventarisation of hyperbenthic organisms occurring in the surf zone of Belgian sandy beaches, (2) to evaluate the intensitivity by which this surf zone is used, by studying the temporal patterns within the assemblages and finally (3) to identify what abiotic factors are responsible for structuring these hyperbenthic assemblages.

MATERIALS AND METHODS

Study area

The study area comprises the surf zone of 4 sandy beaches of the Belgian coast (Figure 1) in the most southern part of the Southern Bight of the North Sea. The Belgian coastline is 67 km long and is characterised by built-on dykes which are interrupted by dune areas, and groins on most of the beaches. In some parts these groins are less than 300m apart, while elsewhere they are absent for several kilometres. Three major harbours (Zeebrugge, Oostende and Nieuwpoort) are situated in the eastern, middle and western part of the coast. A smaller harbour is present in Blankenberge. The mouth of the IJzer estuary is situated in the western part, while just over the Belgian-Dutch border the large Westerschelde estuary opens. A strong semi-diurnal tidal regime and a net tidal current running north-east parallel to the coastline are characteristic for the area. According to the morphodynamic classification scheme of Masselink & Short (1993) all beaches studied were low-tide bar/rip beaches (LTBR). These beaches are characterised by a relatively steep upper intertidal zone, but fronted by a low gradient mid-intertidal zone, possibly with swash bars, and then bar and rip morphology around low tide level. The main characteristics of each site are given by Table 1. In general, only the slope of the intertidal area is measured. Since the morphodynamic features may however change severely beneath the low water line and these changes are more likely to characterise the shallow surf zone habitat, slopes of the **shallow subtidal** (first 300m after MLLWS, < 8 m depth) are also reported.

Table 1. Study site characteristics (D: low tide beach sediment size averaged over whole study period (µm), MSR: mean spring tide range (m), SE: standard error, IT: intertidal, ST: first 300m of shallow subtidal).

	D±SE (µm)	MSR (m)	beach width (m)	slope IT	slope ST	groins	bar/rip IT	bar/rip ST
Oostduinkerke (Oo)	186±1	4.92	390	1:128	1:210		+	+
Lombardsijde (Lo)	187±1	4.78	180	1:55	1:108	+	+	+
Wenduine (We)	263±5	4.45	195	1:49	1:62	+	+	+
Knokke (Kn)	344±11	4.28	174	1:57	1:41	+	+	

Sampling

Monthly samples were taken from May 1996 until July 1997. In July and November ‘96, persistent bad weather conditions prevented sampling in all stations. This was also the case in January ’97 for Lombardsijde (Lo), in February ‘97 for Wenduine (We) and Knokke (Kn) and in April ‘97 for We. In Lo, 1 additional sample was taken in April and 1 in May ’97. All samples were taken with a hyperbenthic sledge at day-time neap tide and ebb. The sledge was especially designed for this study. The metal frame measured 100 x 40cm and it was equipped with two nets, one above the other. Both nets were 3m long, and (at the mouth) 20cm high, with a mesh size of 1x1mm. The sledge was pulled by 2 persons in the surf zone parallel to the coastline at a depth of approximately 1m. One haul lasted approximately 20 (We and Kn) or 30 (Oostduinkerke (Oo) and Lo) minutes and covered a distance of 450-500m. When groins were present, the sledge was lifted over the obstacle. Since the sledge remained in motion during this proces, sampling efficiency was not affected. The catch was preserved in a 8% formalin solution.

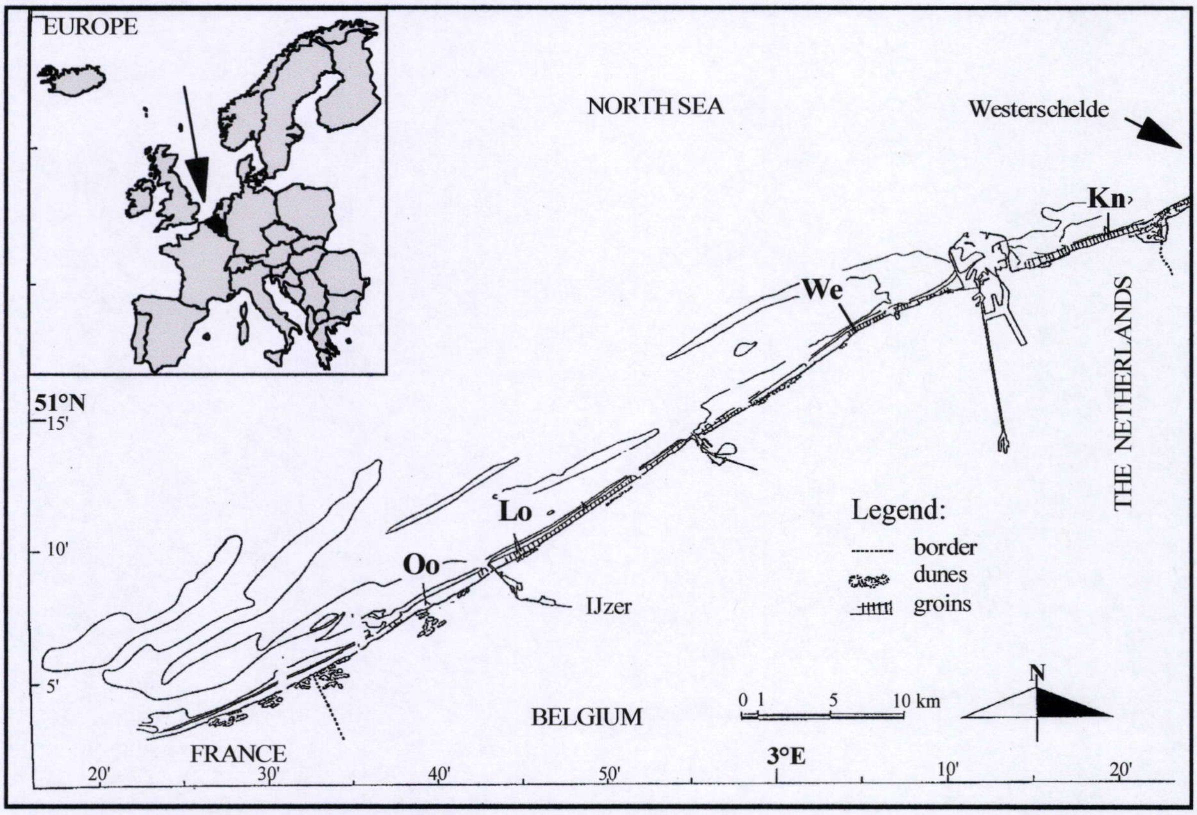

Figure 1. Study area with indication of sampling sites.

Environmental variables

Portable conductivity and oximeters (WTW) were used for measurements of water temperature and salinity and oxygen content, respectively. Turbidity was measured with a portable microprocessor turbidity meter (HANNA). For the analyses of pigments (chlorophyll-*a* and *c* and fucoxanthine) and particulate organic carbon (POC), water samples were passed through Whatman GF/F filters. For the pigments, an immediate extraction with aceton (90%) was performed prior to a chromatography, with a Gilson high-performance liquid chromatography chain using the method of Mantoura & Llewellyn (1983). For POC an automatic CN-analyzer (Carlo Erba) was used. The concentrations of nitrate plus nitrite, phosphate, ammonia and silicium were measured through an automatic chain (SAN^{plus} segmented flow analyser, SKALAR). Median grain size was determined with a Coulter Counter LS particle size analyser. For the measurement of organic matter within the sediment (OM), samples were dried at 110°C for 2 hours and subsequently burned at 540°C for 2 hours. Hydrodynamic variables (wave height, wind speed and direction) at the moment of sampling were obtained from the Coastal Waterways' Division of the Department of Environment and Infrastructure (Ministry of the Flemish Community). Wave height is expressed as H33: the average of the 33% highest waves occurring during a period of 15 minutes. Wind speed is given as the average speed and wind direction as the scalar average of the measured directions, over a period of 10 minutes.

Data treatment

In the laboratory, all hyperbenthic animals were identified and counted. Identification was not always possible to the lowest level. Several organisms were damaged, and the available identification keys were not always sufficient (e.g. in case of metamorphosing individuals such as some clupeids, or if confusing species descriptions were given such as for *Bathyporeia* species). In some cases the preservation method caused contraction of structures, prohibiting a concise identification (e.g. *Bougainvillia* species). Different developmental stages of decapods (zoeae, megalopae, postlarvae and juveniles) were treated as separate 'species' since they have a different ecology, and a distinction was made between holo- and merohyperbenthos. **Holohyperbenthos** is defined as animals spending variable periods of their adult life in the hyperbenthos, whereas **merohyperbenthos** is applied to those that spend only part of their early life history in the hyperbenthos and recruit to the nekton, epibenthos or endobenthos (Hamerlynck & Mees 1991). Total biomass was calculated for the samples of one station at the west (Oo) and one at the east coast (Kn). Assigned ashfree dry weight (ADW) values, independent of the animals' length, were used to estimate biomasses of cnidarians, ctenophores and small crustaceans. Of all other animals, total or standard lengths were measured and their ADW was estimated from length-ADW regressions. Assigned ADW values and length-ADW regressions were derived from Mees et al. (1994), Beyst et al. (1999a) and Dewicke and Mees (unpublished data). For this paper the contents of both nets were combined and treated as one sample. Densities and biomasses are expressed as number of individuals and mg ADW per 100m² respectively. Averages are reported ± their standard error (SE). Since net efficiency is unknown, all density and biomass values are considered as minimum estimates (Mees & Hamerlynck 1992). Diversity was calculated and expressed as Hill numbers of the order of 0, 1, 2 and $+\infty$ (Hill 1973). The indices differ in their tendency to include or ignore the relatively rarer species: the impact of dominance increases and the influence of species richness decreases with an increasing order of the diversity number.

Spatio-temporal patterns were examined with the following multivariate statistical techniques: Correspondence Analysis (CA), (Ter Braak 1986, 1988), Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979) and cluster analysis using group average sorting and the Bray-Curtis dissimilarity index (Bray & Curtis 1957). Empty samples were excluded from the analyses. A fourth root transformation (Field et al. 1982) was performed on the abundance data prior to the analyses. Differences between the obtained groups of samples were assessed using the non-parametric Kruskal-Wallis Test. The influence of environmental factors on temporal variations in total density was examined using multiple stepwise regression analyses using an adjusted multiple coefficient of determination (R^2_{adj}) as an index of fit (Sokal & Rohlf 1981). If variables were significantly correlated (Spearman Rank correlations, $p < 0.05$), only one of them was retained for further analyses. This selection was done after performing preliminary Canonical Correspondence Analyses (CCA) with forward selection, to determine which environmental variables in each group explained the greatest amount of variance in the hyperbenthic data (Hall & Smol 1992). Since wind direction is a circular variable, it was transformed to a linear scale by using the cosine of the angle that the wind made on a set of axes aligned perpendicularly onshore (Clark et al. 1996b). Offshore winds at each site were allocated the greatest values (+1), onshore winds the lowest (-1), while winds with a cross-shore component from either direction received scores between +0.9 and -0.9. Wave height was expressed as the height reached by 33% of the waves. For wind speed and wave height values are expressed into arbitrary classes ranging from 0 to 4, with class 4 indicating values of 20 knots and 100cm, repectively.

RESULTS

Environmental variables

The selected and excluded environmental variables after evaluation of their correlation coefficients and forward selection, are given by Table 2 (see also Appendix 1A). Median grain size differed substantially between the four stations (Table 1): while the two west coast stations (Oo and Lo) were characterised by fine sediments (median grain size between 125 and 250 µm), the two east coast stations (We and Kn) consisted of medium sands (median grain size between 250 and 500 µm). The monthly variation of the other selected variables is shown in Figure 2. The winter of 1996-1997 was extremely cold. In January '97 surf zone temperatures were below zero and ice covered the whole beach area. Of several variables maximum values were reported during winter (average of 4 stations): wind speed (15-20 knots), turbidity (770±440 ftu), and ammonia (29±19 µmol/l). The latter peak again during early summer of 1997 (34±11 µmol/l), together with wave height (±75 cm), surf zone water temperature (21,3±0.4 °C) and chlorophyll-*a* (54±31 µg/l).

Community composition

In total 172 functional species were found (Table 3, see also Appendix 3A): 104 were holo- and 68 were merohyperbenthic species, all belonging to 17 higher taxonomical levels. More than 75% of the average total sample composition were mysids, mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei* (holohyperbenthos). Other common groups were early life stages of caridean shrimps, brachyuran crabs and fish, smal cnidarians, isopods and amphipods (>1%). Of the merohyperbenthos, postlarval decapods such as the shore crab *Carcinus maenas* and the brown shrimp *Crangon crangon*, and postlarval fish such as gobies *Pomatoschistus* species (a mixture of sand goby *P. minutus* and Lozano's goby *P.*

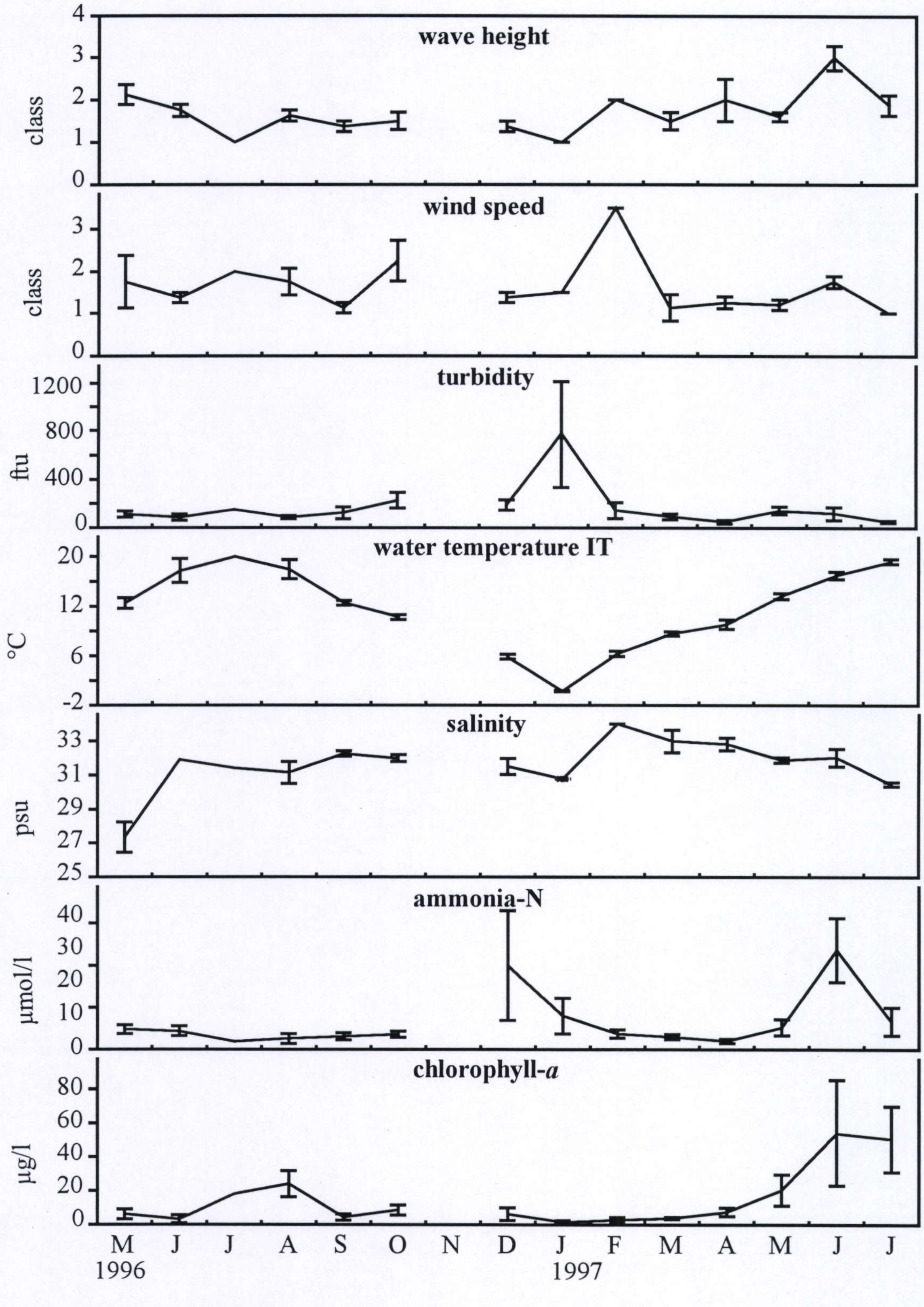

Figure 2. Average ± SE of selected environmental variables per month (IT: intertidal).

lozanoi) and clupeids (herring *Clupea harengus* and sprat *Sprattus sprattus*), were the dominant organisms.

Table 2. Selected and excluded environmental variables together with an indication (*) of their correlation (Spearman Rank correlation coefficient, only shown if $p<0.05$ and $R>0.5$) (IT: intertidal, ST: shallow subtidal).

Selected variables	**Excluded variables**											
	water temperature ST	oxygen content	salinity	wind direction	current speed	POC	organic matter	oxidized nitrogen-N	phosphate-P	silicium	chlorophyll-*c*	fucoxanthine
water temperature IT		*		*		*		*		*		
chlorophyll-*a*	*										*	*
median grain size			*		*							
turbidity												
wave height		*										
wind speed												
ammonia-N							*	*	*	*		

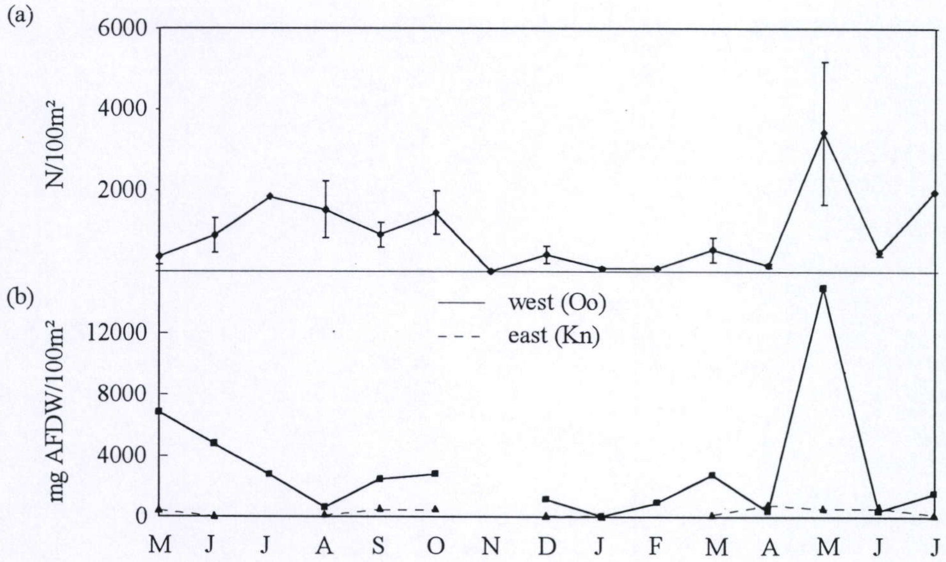

Figure 3. Average total hyperbenthic density (±SE) (a) and total biomass (b) per month.

Average total densities of the 4 stations per month exceeded 1500 ind./100m². Maxima were found in May 1997 (3430±1760 ind./100m²) (Figure 3a). In January, several samples yielded no specimens. The average total density over all months (yearly average) of the holohyperbenthos was higher than that of the merohyperbenthos; 920±220 ind./100m² compared to 110±40 ind./100m². Only in Kn yearly average total densities were lower than

Table 3. Species list with indication of stage and type (H: holohyperbenthic, M: merohyperbenthic, la: larva, pl: postlarva, juv: juvenile).

Taxon	Stage	Type	Taxon	Stage	Type	Taxon	Stage	Type	Taxon	Stage	Type	Taxon	Stage	Type
Cnidaria			Caridea			*Ebalia tuberosa*	pl	M	Amphipoda			*Hyperia galba*		H
Cnidaria species		H	*Crangon crangon*	pl	M	*Necora puber*	pl	M	*Pariambus typicus*		H	Mollusca		
Sarsia tubulosa		H	Crangonidae species	zoeae	M	Mysidacea			*Caprella linearis*		H	Opistobranchia species	juv	M
Phialidium hemisphaericum		H	*Hippolyte varians*	zoeae	M	*Anchialina agilis*		H	*Phtisica marina*		H	*Sepiola atlantica*	juv	M
Phialella quadrata		H	*Hippolyte varians*	pl	M	*Gastrosaccus spinifer*		H	Amphipoda species		H	Bivalvia species	spat	M
Margelopsis haeckeli		H	*Philocheras trispinosus*	pl	M	*Mesopodopsis slabberi*		H	*Atylus falcatus*		H	Echinodermata		
Eutonina indicans		H	*Palaemon* cf. *longirostris*	pl	M	*Neomysis integer*		H	*Atylus guttatus*		H	*Ophiura* species	juv	M
Eucheilota maculata		H	*Palaemon* species1	pl	M	*Praunus flexuosus*		H	*Atylus swammerdami*		H	*Asterias rubens*	juv	M
Bougainvillia species		H	*Palaemon* species2	pl	M	*Schistomysis kervillei*		H	*Bathyporeia sarsi*		H	Chaetognatha		
Aequorea forskalea		H	*Palaemon* species	pl	M	*Schistomysis spiritus*		H	*Bathyporeia pilosa*		H	*Sagitta elegans*		H
Ctenophora			Processidae species	juv	H	*Mysidopsis gibbosa*		H	*Bathyporeia* species		H	*Sagitta setosa*		H
Beroe gracilis		H	Anomura			*Siriella clausii*		H	*Calliopius laevisculus*		H	Pisces		
Pleurobrachia pileus		H	*Pagurus bernhardus*	pl	M	*Siriella jaltensis*		H	*Corophium acherusicum*		H	*Ammodytes tobianus*	juv	M
Polychaeta			*Pagurus bernhardus*	zoeae	M	*Siriella armata*		H	*Corophium insidiosum*		H	*Ammodytes tobianus*	pl	M
Polychaeta species		H	*Diogenes pugilator*	juv	M	Mysidacea species		H	*Corophium* species		H	*Anguilla anguilla*	juv	M
Spionidae species		H	*Diogenes pugilator*	pl	M	Cumacea			Gammaridae species		H	*Clupea harengus*	juv	M
Phyllodocidae species		H	Paguridae species	pl	M	*Cumopsis goodsiri*		H	*Gammarus crinicornis*		H	Clupeidae species	pl	M
Polynoidae species		H	*Achaeus cranchii*	pl	M	*Diastylis bradyi*		H	*Gammaris insensibilis*		H	Clupeidae species	juv	M
Eulalia pusillus		H	*Achaeus cranchii*	juv	M	*Diastylis rathkei*		H	*Gammarus locusta*		H	*Myoxocephalus scorpius*	pl	M
Spio species		H	Majidae species	juv	M	*Diastylis laevis*		H	*Gammarus zaddachi*		H	*Pleuronectes flesus*	pl	M
Spiophanes bombyx		H	*Porcellana platycheles*	pl	M	Isopoda			*Haustorius arenarius*		H	*Pleuronectes platessa*	juv	M
Scolelepis squamata		H	*Porcellana species*	pl	M	*Eurydice affinis*		H	Ischyroceridae species		H	*Pleuronectes platessa*	pl	M
Typosyllis species		H	*Pisidia longicornis*	pl	M	*Eurydice pulchra*		H	*Jassa falcata*		H	*Pomatoschistus* species	pl	M
Lanice species	la	M	*Pisidia* species1	pl	M	*Idotea granulosa*		H	*Jassa* cf. *marmorata*		H	*Solea solea*	pl	M
Lanice conchilega		H	Brachyura			*Idotea linearis*		H	*Jassa* species		H	*Solea solea*	juv	M
Nephthys cirrosa		H	Brachuyra species	juv	M	*Idotea pelagica*		H	*Pontocrates altamarinus*		H	*Buglossidium luteum*	pl	M
Nereis species		H	Brachyura species	pl	M	*Idotea baltica*		H	*Pontocrates arenarius*		H	*Sprattus sprattus*	juv	M
Polydora species		H	Brachyura species	zoeae	M	*Idotea metallica*		H	*Stenothoe marina*		H	*Syngnathus rostellatus*	pl	M
Eteone species		H	*Carcinus maenas*	juv	M	*Idotea emarginata*		H	*Urothoe poseidonis*		H	*Syngnathus rostellatus*	juv	M
Ophelia rathkei		H	*Carcinus maenas*	pl	M	*Idotea* species		H	*Urothoe marina*		H	*Trisopterus minutus*	pl	M
Anaitides species		H	*Carcinus maenas*	zoeae	M	*Jaera nordmanni*		H	*Hyale nilssoni*		H	*Dicentrarchus labrax*	pl	M
Copepoda			*Corystes cassivelaunus*	pl	M	Pycnogonida			*Melita* species1		H	*Dicentrarchus labrax*	juv	M
Calanus helgolandicus		H	*Liocarcinus holsatus*	juv	M	*Nymphon rubrum*		H	*Melita palmata*		H	*Belone belone*	pl	M
Centropages hamatus		H	*Liocarcinus holsatus*	pl	M	*Nymphon brevirostris*		H	*Melita dentata*		H	*Agonus cataphractus*	juv	M
Anomalocera patersoni		H	*Liocarcinus holsatus*	zoeae	M	*Nymphon* species		H	*Melita hergensis*		H	*Ciliata mustela*	juv	M
Temora longicornis		H	*Portumnus latipes*	juv	M	*Callipallene brevirostris*		H	*Melita obtusata*		H	Mugilidae species	pl	M
Euphausiacea			*Portumnus latipes*	pl	M	*Phoxichilidium tubulariae*		H	*Melita* species		H	Pisces species	pl-juv	M
Nyctiphanes couchi		H	*Pilumnus hirtellus*	pl	M				*Orchomene nana*		H	Pisces species	eggs	M

1000 ind./100m² (280±120 ind./100m²). Yearly averages of the total biomass were much higher at the west coast (Oo: 3020±1040 mg ADW/100m²) than at the east coast (Kn: 340±80 mg ADW/100m²) (Figure 3b, Appendix 4A). In both stations maxima were recorded in spring (up to ±15000 mg ADW/100m² at Oo and ±820 mg ADW/100m² at Kn) and a second, but lower peak, was reported in September. High biomass in spring was mainly due to mysids (Oo) and isopods (Kn), whereas the second peak could be attributed to fish. Finally, multivariate statistical techniques (TWINSPAN and CA), indicated that seasonal patterns dominated spatial patterns (not figured). The latter will therefore not be discussed further in this paper.

Seasonal occurrence: holohyperbenthos

To investigate the seasonal occurrence of the different species, a distinction was made between holo- and merohyperbenthic organisms. Table 4 gives the average monthly density for the holohyperbenthic species together with an indication of their resident status within the surf zone. Species were classified as 'residents' if they were present in the catches more or less throughout the year (Clark et al. 1996b). 'Migrants' are species which only occurred during certain periods in the surf zone or during the same month in the subsequent years. Other species were classified as 'sporadics'. Fifteen resident species were reported (Cnidaria species not taken into account since they were not identified to a lower taxonomical level); many of them were absent during January and February. Only 10 species could be classified as migrants. Most of them were present in the surf zone from May until June (July), only a few species occurred later in the year (e.g. *Eucheilota maculata* from June to January) or appeared earlier (e.g. *Calanus helgolandicus* from October to May). For 13 other (possibly migratory) species the patterns where less obvious (indicated as S/M in Table 4) and densities were low (monthly densities ≤ 5 ind./100m²). The remaining majority showed no clear occurrency patterns and therefore were classified as sporadics.

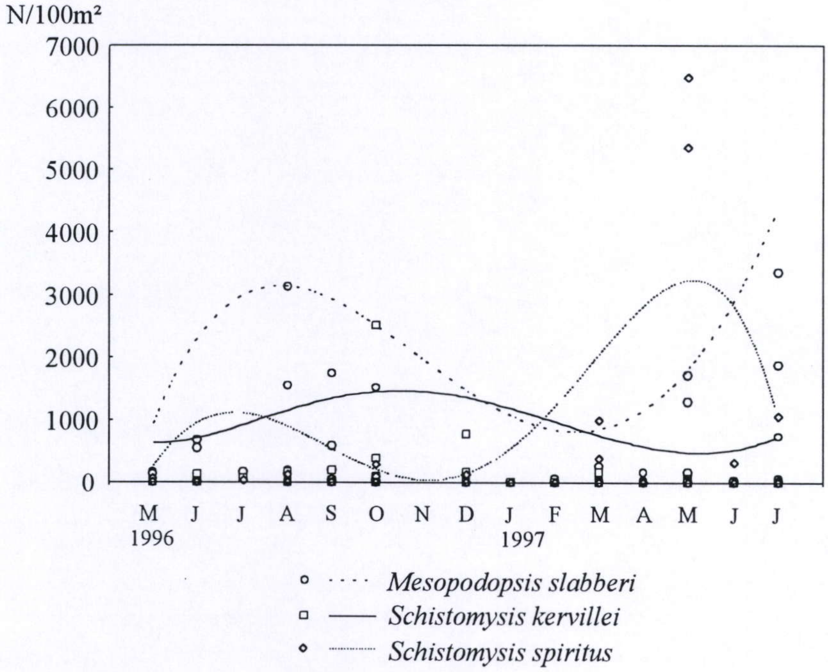

Figure 4. Seasonal occurrence of the three dominant species with indication of a trend line (scale is only for points, trend line is relative).

Table 4. Average holohyperbenthic density of the 4 stations per month (ind./100m²), with indication of their resident status within the surf zone (sporadics not included) (-: no data, *: <= 5 ind./100m², **: 5.1-20 ind./100m², ***: 20.1-100 ind./100m², ****: 100.1-500 ind./100m², *****: > 500 ind./100m², R: resident, M: migrant, S: sporadic).

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97	**Type**
Cnidaria species	*	*	***	*	**	*	-		***		*	*	*		*	R
Gastrosaccus spinifer	*	*	**	*	*	*	-	*		*	**	*	*	*	*	R
Mesopodopsis slabberi	***	****	****	*****	*****	*****	-	*		***	***	***	*****	**	*****	R
Neomysis integer		*	*		*	***	-	***	*	*	*	*		*	*	R
Praunus flexuosus	*	*	*	*	*		-	*		***	*	*	*		*	R
Schistomysis kervillei	*	***	***	***	***	*****	-	****	*	**	***	*	**	*	**	R
Schistomysis spiritus	**	*	***	***	***	***	-	***	*	*	****	*	*****	***	****	R
Eurydice pulchra	**	*	*		*	*	-			*	*	*	*	*		R
Idotea linearis		**	****	*	**	**	-	*			*	*	*	**	**	R
Atylus swammerdami	**	**	*	*	*	*	-	*			*	*	*	**	*	R
Bathyporeia sarsi	*	*	*		*		-	*	*	*	*	*	*	*	*	R
Bathyporeia species	*	*				*	-	*	*	*	*	*	*	*	*	R
Gammarus crinicornis	*	****	*	*	****	**	-	***	*	*	*	*	**	***	***	R
Jassa cf. *marmorata*	*	*		*	*	*	-	*			*	*	*	*	*	R
Pontocrates altamarinus	**	*	*	*	*	**	-	*			*	*	*	**	**	R
Diastylis rathkei				*	*	*	-	*		*	*	*	*	*	*	R?
Eteone species		*					-				*		*	*	*	M?
Anchialina agilis							-				*	*				M?
Sarsia tubulosa	*						-				*	*				M
Margelopsis haeckeli	*	**					-						****	*		M
Eutonina indicans	**						-				*		*			M
Eucheilota maculata			****	***	**	*	-	*	**					**	*	M
Bougainvillia species		*	*****	*	*	*	-				*		*	*	*	M
Polydora species	***	*					-					*	*	*	*	M
Corophium insidiosum	*	*					-				*		*	*		M
Sagitta elegans	*						-						*			M
Spio species	*						-					*				S/M
Scolelepis squamata						*	-	*	*		*	*	*			S/M
Calanus helgolandicus	*					*	-			*	*	*	*			S/M
Centropages hamatus							-				*		*			S/M
Cumopsis goodsiri	*	*					-	*			*	*	*	*		S/M
Jaera nordmanni		*					-					*		*		S/M
Atylus falcatus		*				*	-						*	*	*	S/M
Haustorius arenarius							-				*	*				S/M
Jassa species		*					-							*	*	S/M
Stenothoe marina	*	*					-				*	*				S/M
Hyale nilssoni		*					-				*			*		S/M
Melita palmata						*	-	*								S/M
Melita species	*						-				*					S/M

Figure 4 shows the seasonal appearance of the 3 most common species in more detail. For the clarity of the figures, the indication of a trend line was preferred above monthly averages. There was a clear seasonal pattern of abundance. *Schistomysis spiritus* reached its maximum abundance in May, *Mesopodopsis slabberi* in July-September, and finally *Schistomysis kervillei* in October-December. The first two species were virtually absent in the surf zone during the winter months, whereas the lowest densities of the latter were observed during spring and summer.

Seasonal occurrence: merohyperbenthos

Table 5 gives the seasonal occurrence of the merohyperbenthic species. Postlarvae and zoeae of the common shrimp and gobies occurred during most months, whereas a clear seasonal pattern could be observed for the other species. Multivariate analyses (only TWINSPAN depicted, Figure 5) revealed the presence of three major recruitment periods into the surf zone. First, the summer-autumn samples were separated (TWIN1) and secondly a distinction was made between spring (TWIN2) and winter (TWIN3). Misclassified and borderline samples were excluded from further analyses (6 in total).

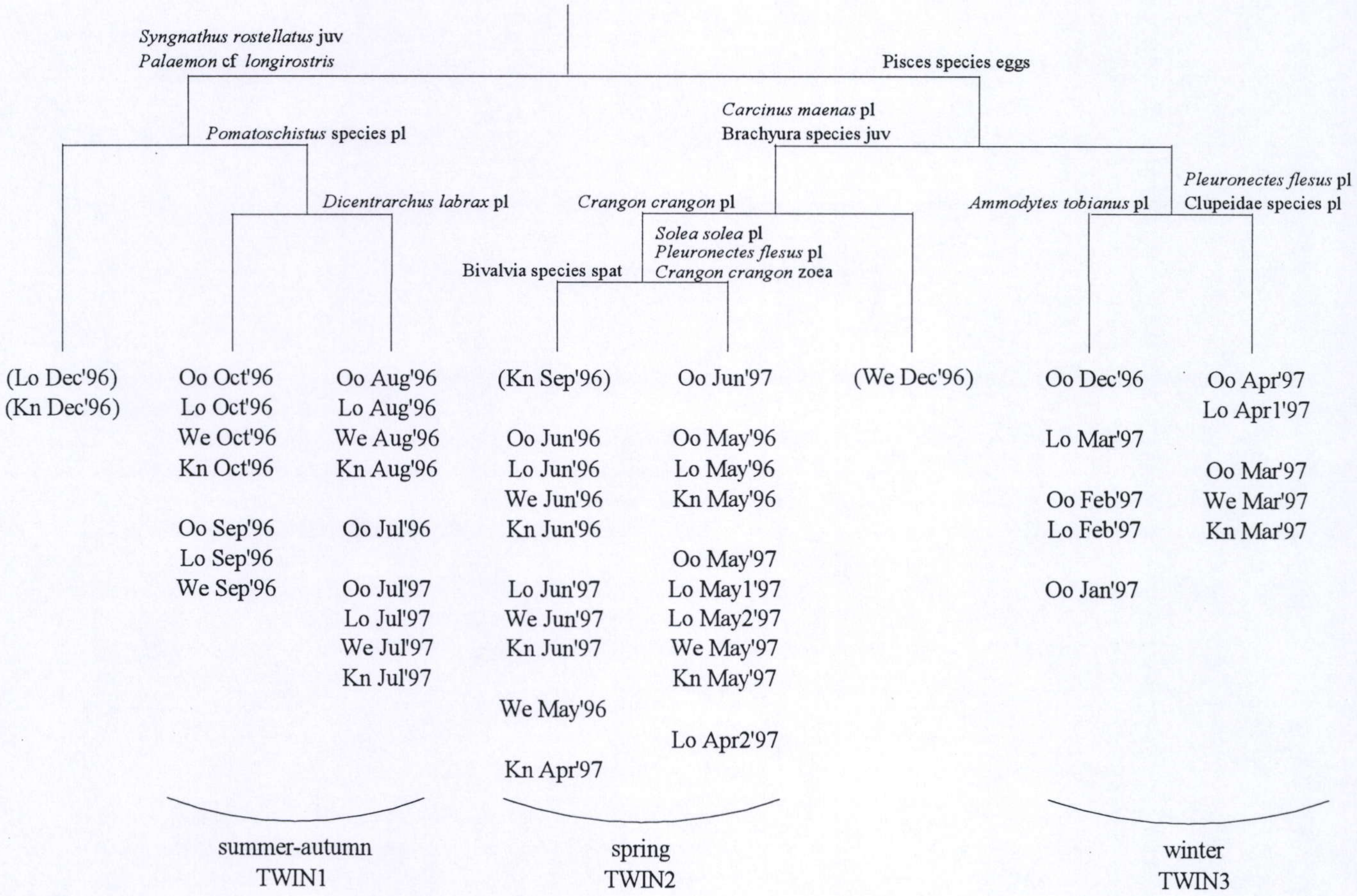

Figure 5. TWINSPAN dendrogram based on the presence/absence of the merohyperbenthic data (misclassified and borderline samples between brackets).

Table 5. Average merohyperbenthic density of the 4 stations per month (ind./100m^2), species sorted by seasonal occurrence (-: no data, *: <=5 ind.100m^2, **: 5.1-20 ind./100m^2, ***: 20.1-100 ind./100m^2, ****: 100.1-500 ind./100m^2, *****: > 500 ind./100m^2).

Taxon	**Stage**	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Crangon crangon	pl	***	***	****	***	***	**	-	*	*	*	*	**	***	**	*
Crangonidae species	zoa	**	*	*	*	*	*	-			*	*		*	*	*
Pomatoschistus species	pl	***	*	****	***	*	*	-	*		*	*		*	*	***
Ammodytes tobianus	pl	*	*					-	*		*	*		*	*	*
Ammodytes tobianus	juv	*	*		*	*	*	-			*	*		*	*	*
Anguilla anguilla	juv							-			*	*				
Pleuronectes platessa	pl	*						-			*	*	*	*		
Trisopterus minutus	pl							-			*					
Pisces species	eggs	**	*					-			*	**	**	*		
Hippolyte varians	zoa							-				*				
Brachuyra species	juv	*	**	**	*	*	*	-					*	**	**	*
Carcinus maenas	juv	*	**	*	*	*	*	-					*	*	*	*
Liocarcinus holsatus	zoa	*	*					-				*		*		*
Opistobranchia species	juv							-				*		*	*	
Bivalvia species	spat		*					-				*	*	*	*	*
Ophiura species	juv							-				*				
Asterias rubens	juv		*					-				*		*	*	*
Clupea harengus	juv	*	*			*	*	-	*			*	*			
Clupeidae species	pl	***	**	**	*	*	*	-				**	*	**	*	*
Pleuronectes flesus	pl	**						-				*	**	**		
Solea solea	pl	*						-				*		*		
Solea solea	juv		*	*				-					*			
Syngnathus rostellatus	juv	*		*	**	*	**	-				*				*
Lanice species	la	*	*				*	-							*	*
Palaemon species2	pl			*	*			-							*	*
Palaemon species	pl			*	*			-								*
Pagurus bernhardus	pl	*		*	*			-						*		
Pagurus bernhardus	zoa	*	*					-						*		
Paguridae species	pl	*						-								
Brachyura species	zoa	*	*					-								
Carcinus maenas	pl	**	****	***	***	*	*	-						***	****	***
Carcinus maenas	zoa		**					-								

Taxon	**Stage**	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Corystes cassivelaunus	pl	*						-								
Liocarcinus holsatus	juv	*		*	*		*	-						*	*	*
Liocarcinus holsatus	pl	*	*		*			-						*	*	*
Necora puber	pl	*			*			-								*
Sepiola atlantica	juv							-						*		
Clupeidae species	juv	*	*					-								
Myoxocephalus scorpius	pl	*						-								
Pleuronectes platessa	juv	*	*	*		*	*	-	*						*	
Buglossidium luteum	pl							-						*		
Sprattus sprattus	juv	*	*					-								*
Syngnathus rostellatus	pl	*		*	*			-								*
Dicentrarchus labrax	pl		*	**	*			-							*	*
Belone belone	pl		*					-							*	
Agonus cataphractus	juv		*			*		-								
Hippolyte varians	pl			*		*	*	-	*			*				
Philocheras trispinosus	pl			*	*	*		-								
Palaemon cf. *longirostris*	pl			**	*		*	-								*
Palaemon species1	pl			*	**	*		-								*
Diogenes pugilator	juv				*			-								
Diogenes pugilator	pl			*				-								*
Achaeus cranchii	pl				*			-								
Achaeus cranchii	juv				*			-								
Majidae species	juv			*				-								
Porcellana platycheles	pl			*				-								*
Porcellana species	pl			*		*		-								
Pisidia longicornis	pl				*		*	-								
Pisidia species1	pl				*			-								*
Brachyura species	pl							-								*
Portumnus latipes	juv			*	*	*		-								*
Portumnus latipes	pl			*	*	*		-								
Pilumnus hirtellus	pl				*	*		-								
Dicentrarchus labrax	juv				*			-								
Ciliata mustela	juv				*			-								
Mugilidae species	pl					*		-								
Ebalia tuberosa	pl						*	-								
Pisces species	pl-juv				*	*		-				*	*			

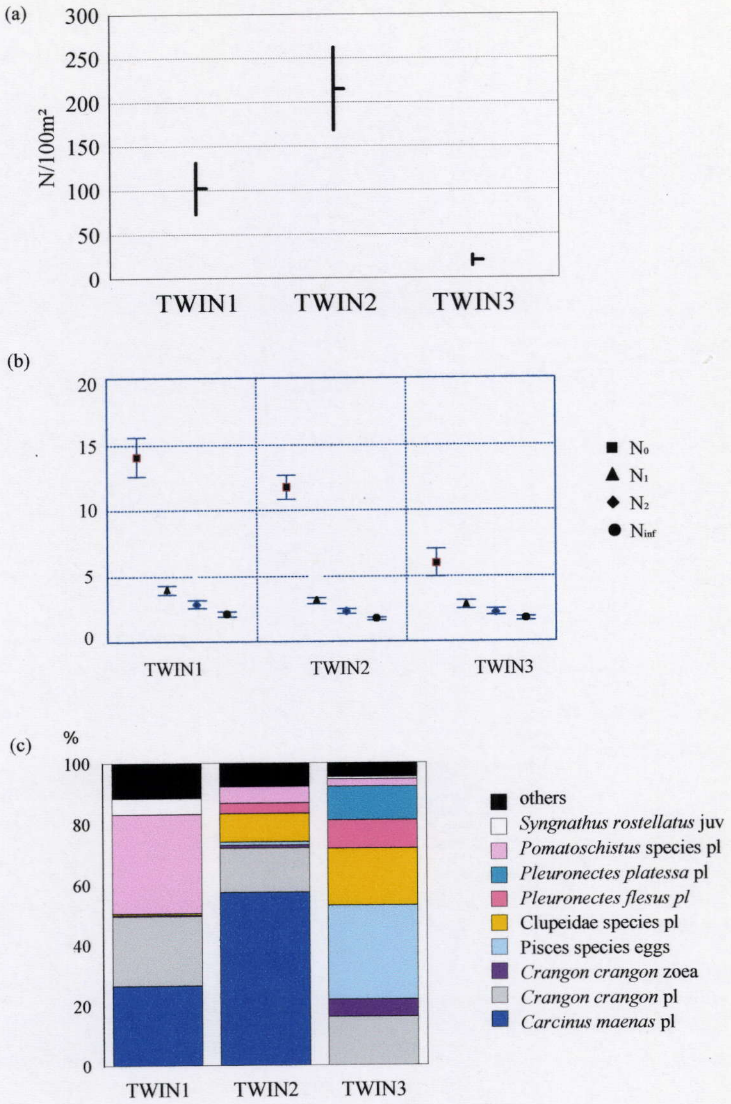

Figure 6. Average total density (±SE) (a), average Hill numbers (± SE) (b) and relative species composition (c) per TWIN group (merohyperbenthos).

Average total densities and number of species (N_0) were significantly different between the TWIN groups (Kruskal-Wallis Test, $p<0.05$) (Figures 6a & b). Total density was highest in spring (220±50 ind./100m²) and lowest during winter (20±6 ind/100m²). On average, more than 12 species per sample were found between spring and autumn (the total number of species caught during this period exceeded 40) compared to 6±1 species in the winter sample (total number 23). Also the relative species composition of the three TWINgroups differed substantially (Figure 6c, depicted species that represent at least 5% of one of the groups), the eveness being lowest during spring. Densities of all these species (except zoeae of the common shrimp andpostlarvae of clupeids) differed significantly between the three TWIN groups (Kruskal-Wallis Test, $p<0.05$).

Figures 7a,b (fish) & 7c (decapods) show the seasonal appearance of the most common species in more detail. Postlarvae of plaice *Pleuronectes platessa* appeared first in February-March (mean standard length (SL) of ±12 mm), followed by postlarval flounder *Pleuronectes flesus* in April-May (mean SL ±7 mm) and clupeid larvae in May-June (mean SL ±30 mm) (Figure 7a). Maximal densities of these three species were 7, 40 and 240 ind/100m² respectively. Postlarval gobies became more abundant between June and August. Nilsson's pipefish *Syngnathus rostellatus* mainly occurred from August until October (Figure 7b). The latter two species were found at maximal densities of 210 and 40 ind./100m² and mean lengths of 13 and 79 mm SL respectively. Fish eggs were found commonly during March and

April (maximum of 40 ind./100m²). Zoeae of the common shrimp first appeared in March and were still very abundant in May, while postlarvae of the same species were abundant from May-July (maxima of 40 and 120 ind/100m² respectively) (Figure 7c). Megalopae of the shore crab reached their maximum densities in June (620 ind./100m²).

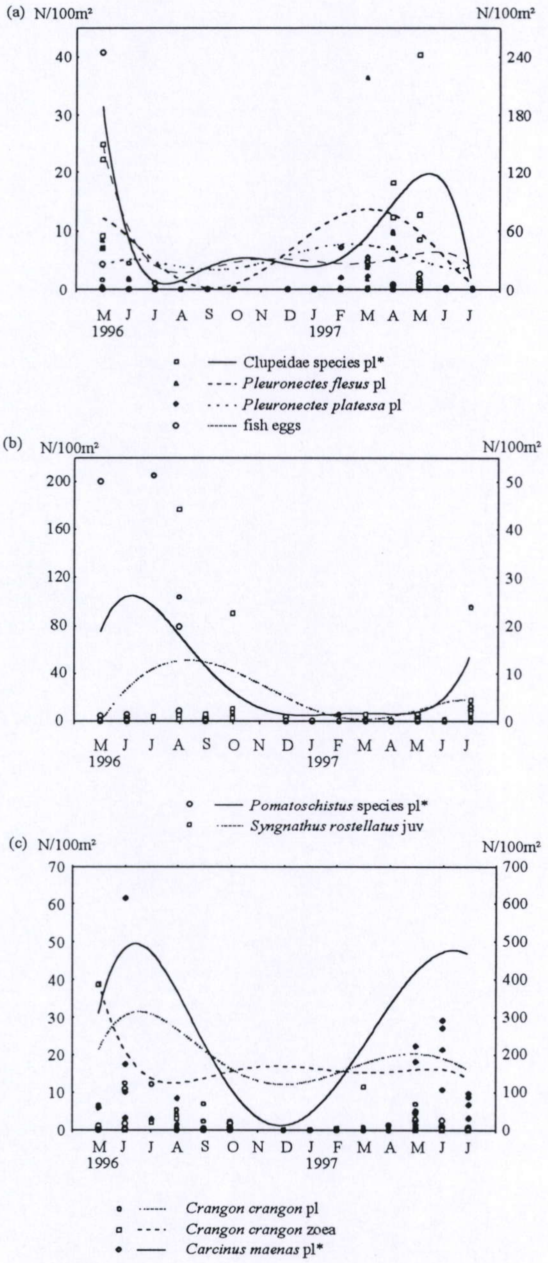

Figure 7. Seasonal occurrence of merohyperbenthos: (a) winter and spring recruitment of fish eggs and postlarvae; (b) summer recruitment of postlarval fish and (c) zoeae and postlarval crustaceans (*: right axis) (scale on Y-axis is only for points, trend line is relative).

Influencing factors

The influence of the environmental variables on the total density, the total density per taxonomic group and the individual densities of the three main species was examined using stepwise multiple regression analyses. In total 7 variables were retained after exclusion of correlated variables (Table 2). Only significant variables ($p<0.05$) were retained in the model. Again, holo- and merohyperbenthic data were treated seperately.

Holohyperbenthos. Water temperature and wave height predicted 24% of the temporal variability in the total holohyperbenthic density (Table 6). Although water temperature of the surf zone was not selected as such for the taxonomic groups seperately, chlorophyll-*a* was the single selected variable for mysids, cumaceans and amphipods ($R^2_{adj} < 0.15$). Hydrodynamic variables (turbidity, wave height and wind speed) were selected for cnidarians, polychaetes and chaetognaths, suggesting that respectively 27, 17 and 7% of the variability associated with monthly fluctuations in their densities could be predicted by these variables. Finally, median grain size was selected for ctenophores ($R^2_{adj} = 0.20$). For the remaining taxonomic groups, selected variables were not significant. While inshore water temperatures predicted 13% of the temporal variability of *Mesopodopsis slabberi*, chlorophyll-*a* concentrations were correlated with the occurrence of *Schistomysis spiritus* ($R^2_{adj} = 0.48$). Median grain size only predicted 7% of the variability of *Schistomysis kervillei*. In contrast to cnidarians, polychaetes and chaetognaths, total densities were negatively correlated with hydrodynamical variables.

Table 6. Results of the stepwise multiple regression analyses of the influence of 7 selected variables on the holohyperbenthic total density, density per higher taxonomical group and individual density of the 3 dominant species. The adjusted R² (R^2_{adj}) is included for each combination of variables selected by the model.

	water temperature IT	chlorophyll *a*	median grain size	turbidity	wave height	wind speed	ammonia-N	R²adj
Total density	x				x			0.24
Cnidaria				x				0.27
Ctenophora			x					0.2
Polychaeta				x	x			0.17
Copepoda								-
Euphausiacea								-
Caridea								-
Mysidacea		x						0.11
Cumacea		x						0.11
Isopoda								-
Pycnogonida								-
Amphipoda		x						0.14
Chaetognatha						x		0.07
Mesopodopsis slabberi	x							0.13
Schistomysis spiritus		x						0.48
Schistomysis kervillei			x					0.07

Merohyperbenthos. As expected, water temperature seemed to be the main variable associated with the monthly variations of total merohyperbenthic density as well as with the densities of most taxonomic groups and species (Table 7). Wave height was positively correlated with polychaete larvae and early life stages of crabs, but a negative correlation was found with postlarval gobies. Other selected variables were chlorophyll-*a* (Brachyura), median grain size (postlarval brown shrimp) and wind speed (postlarval gobies). Although in most cases the adjusted R² was lower than 0.15, more than 30% of the temporal variability in the total density of the merohyperbenthos, as well as in that of the early life stages of crabs, postlarval brown shrimps and postlarval gobies, could be predicted by the selected variables.

Table 7. Results of the stepwise multiple regression analyses of the influence of 7 selected variables on the merohyperbenthic total density, density per higher taxonomical group and individual density of the 9 dominant merohyperbenthic species. The adjusted R^2 (R^2_{adj}) is included for each combination of variables selected by the model.

	water temperature	chlorophyll *a*	median grain size	turbidity	wave height	wind speed	ammonia-N	R^2adj
Total density	x							0.52
Polychaeta					x			0.11
Caridea	x							0.13
Anomura	x							0.07
Brachyura		x			x			0.32
Mollusca	x							0.09
Echinodermata								-
Pisces	x							0.07
Pleuronectes flesus pl								-
Pleuronectes platessa pl								-
Pomatoschistus species pl	x				x	x		0.34
Syngnathus rostellatus juv								-
Clupeidae species pl	x							0.08
Pisces eggs								-
Crangon crangon pl	x		x					0.3
Crangon crangon zoa	x							0.07
Carcinus maenas pl	x				x			0.36

DISCUSSION

Sampling efficiency

Very little is known about net efficiency of hyperbenthic sledges (discussed in Mees & Jones 1997). Most sledges are at best semi-quantitative. The efficiency, judged by its ability to capture all the animals within its sweep, is usually low. For epifauna dredges, and when total fauna is considered, a value of 10% is thought to be realistic (Eleftheriou & Holme 1984). Mysids have been observed to avoid capture by swimming in front of trawls (Lasenby & Sherman 1991). According to Mees & Jones (1997), towing speed should always be as low as possible. Since no adjustment for net efficiency could be made for the present study, all density and biomass values should be considered as minimum estimates.

Surf zone hyperbenthos

Number of species. Several authors described difficulties for organisms inhabiting the surf zone (e.g. Clutter 1967, Brown & McLachlan 1990, Romer 1990, Clark et al. 1996b). Nevertheless, it seems to be used intensively by several taxonomic groups. In total 172 species were recorded in the surf zone hyperbenthos. To standardize between the different studies, the total number of species will only be discussed further as the total number of decapods and pericarids. The number of surf zone species (80) was then comparable to those found in temporal studies of the deeper regions (68-141), although survey duration and number of sites have previously been recognised as confounding factors in such comparisons (Ross 1983), as has the influence of depth (Gibson 1973, Riley et al. 1981). The average number of species (decapods and pericarids) found per month during this study was 31±2. This number was somewhat higher than in most other studies of surf zones (mostly between 22 and 25) (San Vicente & Sorbe 1993b, Munilla & Corrales 1995, Lock et al. 1999). Colman & Segrove (1955) reported much higher numbers during night catches, however these were more diverse than the day catches.

Density & biomass. In the North Sea, hyperbenthic studies have been restricted to the deeper subtidal area. Of these studies, yearly averages of both total density and biomass of the hyperbenthic community were only given by Hamerlynck & Mees (1991) (Dutch Delta). Yearly averages of total density were also reported by Vallet & Dauvin (1999) for the western English Channel and Dewicke (unpublished data) for the shallow subtidal of the Belgian coast. Total densities were highest in the surf zone (present study), and only comparable to those of Dewicke (unpublished, >900 ind./100m²). Also, total surf zone biomass was slightly higher than in the Dutch Delta (between 300-3000 and 200-1000 mg ADW/100m² respectively) (Hamerlynck & Mees 1991). These results emphasise the importance of the shallow surf zone habitat at the Belgian coast for hyperbenthic animals.

Since a community approach has rarely been applied to hyperbenthic surf zone assemblages, there are very few other studies to compare with (Table 8). Total hyperbenthic densities are of the same order of magnitude as those found in most Mediterannean studies (San Vicente & Sorbe 1993b, Munilla et al. 1998, San Vicente & Sorbe 1999). Much lower densities were found at a sandy beach of England (Colman & Segrove 1955), the Atlantic (San Vicente & Sorbe 1993b) and the Belgian coast (Lock et al. 1999). The latter, however, was carried out during late autumn when densities were also low in the present study (420±210 ind./100m² in December). Next to sampling device, the differences in total densities between the different study areas might be linked to the degree of exposure: the Meditteranean beaches are the least exposed, the North Sea is semi-enclosed (Ducrotoy et al. 2000) and can be considered as intermediate exposure. Moreover, the Belgian coast is characterised by an extensive sand bank system in front of the shore that might buffer wave action. Total hyperbenthic biomass is reported by Wooldridge (in McLachlan 1983), but only per m³.

Table 8. List of studies of hyperbenthic communities of surf zones of sandy beaches (HS: hyperbenthic sledge, N: total density, B: total biomass in AFDW, ya: yearly average, ma: monthly average, da: diurnal average, *: only decapods and pericarids).

author(s)	**study area**	**sampling depth**	**sampling gear**		**# species**	**N**		**B**		**dominant species**
Elmhirst (1932)					30?					
Colman & Segrove (1955)	UK	1m	HS (71cmx34cm)		82 (58*)	60±30	da, N/100m^2 Jun	-		*Carcinus maenas* pl, *Atylus swammerdami,* *Schistomysis spiritus,* *Leptomysis lingvura*
Cockcroft (1979)	East Cape (South Africa)	1-10m	'large nets'					6-980	mg/m^3	*Macropetasma africana,* *Mesopodopsis slabberi*
Wooldridge (1983, in McLachlan 198	East Cape (South Africa)	3-20m (behind breakers)	plankton net (1,5m)					250	mg/m^3	*M. slabberi*
San Vicente & Sorbe	Mediterranean	< 1m	HS		35 (29*)	1080±840	N/100m^2	-		*Schistomysis assimilis*
(1993b)	Atlantic	1m	(50cmx20cm)		25 (24*)	490	Mar	-		*Schistomysis parkeri*
Munilla & Corrales (1995)	Mediterranean	1m	HS (50cmx20cm)		33 (22*)	570	N/100m^2 Jul	-		*Leptomysis lingvura,* *Atylus swammerdami,* *Pseudaphia ferreri*
Munilla et al. (1998)	Mediterranean	1m	HS (50m^2)		-	3400±1160	N/100m^2 13 beaches	-		mysids
Lock et al. (1999)	Belgian coast	1m	HS (50cmx20cm)		41 (25*)	430±200	da/100m^2 Nov	-		*M. slabberi,* *Mitrocomella polydiademata,* *Cumopsis goodsiri,* *Eurydice pulchra*
San Vicente & Sorbe (1999)	Mediterranean	0.5-3.5m (< 1m)	HS (50cmx20cm)		97 (77*)	1890±430 (820±220)	ya, N/100m^2	-		*Schistomysis assimilis,* *Mesopodopsis slabberi*
this study	Belgian coast	1m	HS (100cmx40cm)	total:	138 (80*)	1060 ± 230	ya, N/100m^2			*Mesopodopsis slabberi,*
				east:	39	680 ± 210	ya, N/100m^2	340± 80	ya, mg/100m^2	*Schistomysis spiritus,*
				west:	35	1380 ± 370	ya, N/100m^2	3020 ± 1040	ya, mg/100m^2	*Schistomysis kervillei*

Community composition: holohyperbenthos

Resident status. For the 15 resident species found in the surf zone, three different life styles can be observed. Most of them have a true hyperbenthic life style (e.g. most mysids, *Atylus swammerdami*), some are known to inhabit the underlying sand and make vertical excursions to the water culumn (e.g. *Eurydice pulchra*, *Bathyporeia* species) (Watkin 1939, 1941, Colman & Segrove 1955) and some are associated with drifting detritus (e.g. *Gammarus crinicornis*) (Jones & Naylor 1967, Lincoln 1979, Mauchline 1980). Although indicated as residents, most of them were absent in January when temperatures dropped below 1°C. Also during July and August when average temperatures were higher than 20°C, several species were absent from the samples. Field and laboratory observations suggest that some mysids perform seasonal migrations to avoid unfavourable temperatures (Tattersall & Tattersall 1951, Hesthagen 1973). Also endobenthic species show a decrease in density on the Belgian sandy beaches in winter (Degraer et al. 1999). This decline is probably a result of population dynamics and/or shifts in the distribution up and down the beach (e.g. Jaramillo et al. 1996).

Almost all species indicated as 'migrants' have a real planktonic (e.g. jellyfish, copepods), or endobenthic (e.g. most amphipods, polychaets) lifestyle. Planktonic organisms are likely passively transported toward the coast seasonally. Most of them occur in spring: e.g. the jellyfish *Margelopsis haeckeli* (June), which has not been recorded from the British coast but was found at the Belgian coast in June by Kramp (1930). Also *Eutonina indicans* and *Sarsia tubulosa*, were only caught in the surf zone between March and May. Other species are present at different times of the year: for example, *Eucheilota maculata* (June-January) and *Bougainvillia brittanica* (June-October). These results of seasonal occurrence are in general agreement with the current knowledge (Sanderson 1930, Watson 1930, Russel 1953). Active migration may be plausible for species like the chaetognath *Sagitta elegans*. Of the endobenthic 'migrants', some species are mainly found during their breeding season. The polychaet *Eteone longa*, for example, leaves the sediment during this period (March-May) and is known to swim close to the water surface and eggs are deposited superficially on the sediment (Hartmann & Schröder 1971). *Polydora ciliata* reproduces from April until September and is mainly found in the present study as a juvenile. In contrast, *Scolelepis squamata* was caught only outside its reproduction period (late spring, early summer). This species is known to swim during longer or shorter periods (Hartmann & Schröder 1971).

Species that occurred sporadically may be common in deeper waters and accidentally caught in the surf zone or moved into the surf zone periodically (e.g. *Melita dentata*, Lincoln 1979). Some of the sporadics are typical intertidal endobenthic organisms which only occur in low densities in the water column (e.g. *Cumopsis goodsiri*, *Eurydice affinis*, Jones & Naylor 1967, Jones 1976), some are true planktonic (e.g. *Anomalocera patersoni*, Mauchline 1998) or associated with hydroids and/or algae (e.g. sea spiders, King 1974, *Idotea metallica*, Naylor 1957) and thus not likely to be caught with a hyperbenthic sledge in deeper waters. Organisms may be washed out of the nearby estuaries (e.g. *Gammarus zaddachi* is an estuarine species that prefers areas of very low salinity, Lincoln 1979) or of the higher reaches of the beach (e.g. *Jaera nordmanni* is mainly found under stones in freshwater streams flowing down the shore, Naylor 1972). Still, some species are restricted to the water column of shallow water or intertidal areas: *Idotea granulosa* (Naylor 1955), *Corophium insidiosum*, *Corophium acherusicum* and *Hyale nilssoni* (Lincoln 1979). Most of all species found however, have a wide distribution area and can occur in the shallow surf zone as well as in the deeper subtidal region.

Common species. Of the most common species, *Mesopodopsis slabberi* is a very widely distributed mysid that is also dominant in the surf zone of sandy beaches in South Africa (Wooldridge 1983). Of the other two mysids, only *Schistomysis spiritus* was reported in surf zone assemblages (Colman & Segrove 1955). Although indicated as a brackish water species by Tattersall & Tattersall (1951), *Mesopodopsis slabberi* was much more abundant in the surf zone of the Belgian coast than in the adjacent estuarine areas (yearly averages of 420±110 ind./100m² in the surf and 10±3ind./100m² in the Westerschelde estuary, Mees et al. 1993). Furthermore, in the adjacent shallow subtidal (5-10m depth) it occurred mainly in winter but also in much lower densities (yearly average of 20±8 ind./100m², Dewicke unpublished data). These data and the absence of the species in the surf zone during the cold months, suggest migration towards deeper waters to avoid cold temperatures during winter. This migration pattern was also found by Zatkutskiy (1970) and Van der Baan & Holthuis (1971) and is further confirmed by the selection of water temperature by multiple regression analysis as an important variable explaining variation in the monthly densities of this species. An offshore migration towards deeper water and/or migration into the estuary during winter is also suggested for both *Schistomysis* species, although other factors might be important (see further).

Community composition: merohyperbenthos

Recruitment peaks & seasonal occurrence. In general three recruitment peaks were observed in Belgian surf zones: winter, spring and summer. The winter is characterised by very low total densities and diversity, and by the presence of fish eggs. In spring total merohyperbenthic densities are highest and postlarvae of the shore crab dominate, while in summer the merohyperbenthos is dominated by postlarvae of gobies.

The surf zones of the Belgian coast seem to be used intensively by a number of (post)larval organisms. Postlarvae and zoeae of the common shrimp and postlarval gobies are found nearly all year. Furthermore, a clear succession can be observed as several fish species appear for longer or shorter periods within the surf zone during the year. Postlarval plaice appears in February, followed by flounder (March-April), clupeids (April-May), gobies (May-August) and finally pipefish in October. These results are in general agreement with current knowledge about the North Sea populations of the dominant species (Russel 1976, Beyst et al. 1999b). However, maximal average densities per month were mostly higher in the surf zone than in the Dutch Delta or Westerschelde (Table 9, Beyst et al. 1999b). Although interannual variability might be responsible for these differences, surf zones of sandy beaches are generally considered to be nurseries for several fish species such as juvenile plaice (Edwards & Steele 1968, Gibson 1973). The importance of these areas as a nursery and as an orientation area leading to next nursery grounds for pelagic larvae was emphasised by Kinoshita (1993) and Harris & Cyrus (1996). The former author demonstrates that surf zones provide a good food environment for larval (and juvenile) fishes and that it seems to be significant for survival of transforming individuals. In the present study, both clupeids and flounder were caught at the onset of metamorphosis. It is also suggested that postlarval plaice concentrate in the surf zone at the onset of their demersal life style, since most organisms were caught just after their metamorphosis was completed (±12 mm). Settlement of larval flatfish within surf zones of sandy beaches have been reported by Amarullah et al. (1991) and Subiyanto et al. (1993) for Japanese flounder *Paralichthys olivaceus*.

Table 9. Comparison of maximal average densities (ind./100m²) of the dominant fish larvae within different regions (pl: postlarvae, juv: juveniles).

	this study 1996-1997	Dutch Delta 1988-1989 (Beyst et al. 1999)	Westerschelde estuary 1990-1991 (Beyst et al. 1999)
Clupeidae species pl	70±58	50±19	10±5
	May	May	May
Pleuronectes flesus pl	16±5	<1	10±8
	May	May	Apr
Pleuronectes platessa pl	5±3	1±0,5	2±0,5
	Feb	May	Mar
Pomatoschistus species pl	205	6±3	7±5
	Jul	Sep	Aug
Syngnathus rostllatus juv	12±11	2±0,3	4±1
	Aug	Sep	Aug

Influencing factors

Holohyperbenthos. Temporal variations in surf zone assemblages and the factors that control these variations may be visualized as a hierarchy (Ross et al. 1987), ranging from climatic events that influence annual variations in year class strength, through reproductive and feeding movements that result in seasonal patterns of occurrence and abundance, to short-term fluctuations in physico-chemical factors such as wave height, salinity, temperature and wind speed that influence point abundance. In this study, water temperature appears to be (directly or indirectly) the primary driving mechanism in structuring the hyperbenthic assemblages. As a typical surf zone species, *Mesopodopsis slabberi*, is likely to respond to changes in surf zone water temperature; only during extreme low temperatures, it migrates to deeper water (see above). *Schistomysis spiritus* on the other hand was mainly related to chlorophyll-*a* concentrations, an indicator of phytoplankton biomass and thus primary production (Kramer et al. 1994). This species also feeds on diatoms and dinoflagellates and is capable of actively search for food (Mauchline 1980). Densities of this species, although slightly higher in the surf zone, were of the same order of magnitude in the adjacent subtidal (Dewicke unpublished data). It probably actively migrates towards areas with high food concentrations, regardless changes between sub- or intertidal habitat. The correlation between *Schistomysis kervillei* and median grain size, although rather weak, reflects a spatial pattern. Densities were highest at the west coast (yearly average of 290±180 ind./100m² in Oo) and gradually decreased towards the east (yearly average < 2 ind./100m² in Kn) ($p < 0.01$, Kruskall-Wallis Test). Furthermore, hydrodynamic factors are largely responsible for the passive transport of true planktonic organisms such as cnidarians, ctenophores and chaetognaths towards the surf zone, although the latter may also actively follow their prey. Both turbidity and wave height were positively correlated with the polychaete densities: under highly turbulent conditions sediment can be suspended hereby bringing endobenthic organisms into the water column. Total holohyperbenthic density was however negatively correlated with wave height. Colman & Segrove (1955) suggested that with severe weather conditions, good swimmers (e.g. mysids) are capable of leaving the surf zone and avoiding the turbulence, resulting in a decline of the total density. However, sampling in severe conditions may also be responsible for the absence of mysids in the samples. Although no direct link was made, strong wave action was thought to be of major importance in studies of hyperbenthic communities in the Meditteranean (Munilla et al. 1998, San Vicente & Sorbe 1999).

Merohyperbenthos. Since recruitment patterns are primarily driven by temperature related processes, it is not supprisingly that water temperature (and correlated variables) was selected as most important structuring factor for almost all taxonomic groups and species. Increasing wave height might result in higher densities of larval polychaetes and postlarvae of the shore crab probably by passive transport towards the shore. A negative correlation existed however with postlarval gobies: most likely their swimming capacities enable them to escape these less than optimal conditions and move to deeper waters. Temperature and turbidity were found to be the most important environmental variables related to larval fish densities at another site (Harris & Cyrus 1996).

Chapter I
Part B

Factors influencing the spatial occurrence of surf zone hyperbenthos of Belgian sandy beaches

Results presented in:

Bregje Beyst & Jan Mees (submitted). Factors influencing the spatial occurrence of surf zone hyperbenthos of Belgian sandy beaches.

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Hyperbenthic sledge

ABSTRACT

The surf zone of Belgian sandy beaches is a very rich area that harbours high densities of hyperbenthic animals. Because the hyperbenthos is important in coastal food webs and it serves as a source of recruits to the other benthic and pelagic ecosystem components, the present study is both timely and important to understand the surf zone habitat. The hyperbenthos of the surf zone of 12 sandy beaches along the Belgian coast was sampled in spring of 1996. In order to assess the major influencing factors on the spatial occurrence of hyperbenthic assemblages of surf zones, a wide variety of environmental variables were measured simultaneously. Multivariate statistical techniques were used to analyse the hyperbenthic distribution patterns and to evaluate the environmental variables measured.

Next to mysids (mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei*), the surf zone of the Belgian coast is used intensively by several early life stages of fish and macrocrustaceans. Although the morphodynamic differences between the beaches were relatively small, they seem to be large enough to reveal their influence on the hyperbenthos sampled. Next to 'external' variables such as water temperature and extreme hydrodynamic forces, local beach characteristics, and especially their intertidal and subtidal slope are indicated as important structuring variables. Holohyperbenthic as well as merohyperbenthic organisms both seem to respond, although in different ways, on these variables. The effect of intertidal slope (and correlated variables) on hyperbenthic density is mainly reflected in the holohyperbenthos and especially by the mysids. These actively migrating organisms were found along the whole coast, but high densities were mainly correlated with flat, wide beaches. Less mobile and more sediment-associated animals such as cumaceans and several amphipods were more restricted to certain types of beaches, which was reflected in the number of species. Merohyperbenthic organisms were mainly found on beaches with intermediate subtidal slopes characterised by a high turbidity and this both in density and in number of species. Protection due to higher turbidity might be important in providing refuges in the turbulent and relatively homogenous surf zone of sandy shores.

INTRODUCTION

Surf zones of sandy beaches can function as nurseries or as orientation sites leading to nearby nursery grounds for early life stages of fish and other marine organisms (e.g. Lasiak 1981, Kinoshita 1993, Harris & Cyrus 1996). A nursery can be characterised by its location (supply and transport early life stages), its food availability (fouraging function) and the availability of refuges (Boesch & Turner 1984). The location of the sandy beaches of the Belgian coast suggests a high supply of early life stages to the surf zone since it is mainly characterised by the presence of an extensive shallow sand bank system at the western side on the one hand and the nearby presence of the large Westerschelde estuary in the East on the other hand. The Westerschelde is an important nursery for several fish and crustacean species (Creutzberg & Fonds 1971, Zijlstra 1972, Hostens 2000) and also the shallow sand bank system is characterised by high densities of early life stages of fish and macrocrustaceans (Cattrijsse & Dewicke in press). Notwithstanding the mobile substrate of most sandy beaches and the lack of attached macrophytes, they are hardly 'marine deserts' and their surf zones can be very rich (McLachlan 1983). In general, very few refuges are available on sandy beaches, but a higher turbidity and the shallow nature might protect early life stages from their predators.

Hyperbenthic organisms represent a very important part of the surf zone fauna (McLachlan 1983). The hyperbenthos is the association of small animals living in the water layer close to the sea bed (Mees & Jones 1997). A distinction can be made between holohyperbenthos, defined as animals spending variable periods of their adult life in the hyperbenthos, and merohyperbenthos which is applied to those that spend only part of their early life history in the hyperbenthos and recruit to the nekton, epibenthos or endobenthos (Hamerlynck & Mees 1991). Since hyperbenthic animals occur in very high densities and biomasses and their turnover rate can be very high (McLachlan 1983), they can be of great importance in local food webs. Indeed, it has been proven several times that hyperbenthic organisms constitute a major part of the diet of several juvenile surf zone fish species (e.g. Wyche & Shackley 1986, Lasiak & McLachlan 1987, Beyst et al. 1999a). However, very few studies deal with the hyperbenthic fauna as a whole, most studies are restricted to the ecology of only 1 species or group of species (e.g. San Vicente & Sorbe 1993a, Hanamura 1999).

To evaluate the importance of the surf zones of the Belgian sandy beaches as a nursery, a thorough examination of the hyperbenthos, clearly one of the major ecosystem components, is necessary. The hyperbenthos as a whole is an important food resource for juvenile fish and epibenthic crustaceans on one hand, and on the other hand several components of the hyperbenthos may actually use the surf zone as a nursery themselves. During the year, the hyperbenthic surf zone community is mainly structured by water temperature and hydrodynamic variables such as wave height (Beyst et al. in press a) and several studies report the importance of local beach characteristics on the hyperbenthic surf zone community (e.g. Munilla et al. 1998, San Vicente & Sorbe 1999). None of these however, make a direct link between both. Spatial differences are thought to be related to the severe and fluctuating conditions of most surf zones or are controlled by site-specific characteristics. For the present study, a wide variety of environmental variables was measured at 12 locations along the Belgian coast in order to characterise the spatial variation. Does an east-west gradient exists or are local characteristics more significant? Subsequently, are these differences large and/or important enough to reveal a spatial response of the hyperbenthos, or are differences in community structure merely due to temporal events (e.g. seasonal trends, storm)?

The aim of this paper is to assess the hyperbenthic assemblages of several types of beaches distributed along the Belgian coast. The hypotheses that (1) the clear east-west distinction existing in the shallow subtidal hyperbenthic communities of the Belgian coast (Cattrijsse in press), also exists in the surf zone assemblages and (2) that holo- and merohyperbenthic animals respond in the same way to the important structuring factors, will be evaluated.

MATERIAL AND METHODS

Study area

The study area is situated in the most southern part of the Southern Bight of the North Sea and comprises the surf zone of 11 sandy beaches of the Belgian coast extended with 1 site in the North of France (Figure 1). The Belgian coastline is 67 km long and is characterised by built-on dykes that are interrupted by dune areas, and a discontinuous appearance of groins on the beaches. In some parts these groins are less than 300m apart, while elsewhere they are absent for several kilometres. Three major harbours (Zeebrugge, Oostende and Nieuwpoort) are situated on the eastern, middle and western part of the coast respectively. A smaller harbour is present in Blankenberge. The mouth of the IJzer estuary is situated in the western part, while just over the Belgian-Dutch border the large Westerschelde estuary opens. A strong semi-diurnal tidal regime and a net tidal current running northeast parallel to the coastline are characteristic. According to the morphodynamic classification scheme of Masselink & Short (1993) all beaches studied were low-tide bar/rip (LTBR) or ultra-dissipative (UD) beaches. Table 1 gives the main characteristics of each site. In general, only the slope of the intertidal area is considered. Since the morphodynamic features may however change severely beneath the low water line and these changes are more likely to characterise the shallow subtidal habitat, slopes of the shallow subtidal (first 300m, depth < 8m) are also reported. Slopes are derived from plumb line soundings of the Department of Environment and Infrastructure, Ministry of the Flemish Community.

Table 1. Main characteristics of the sandy beaches studied (D: mean low tide beach sediment size, MSR: mean spring tide range, IT: intertidal, ST: first 300m of shallow subtidal, UD: ultra-dissipative, LTBR: low tide bar/rip).

Site	D (µm)	MSR (m)	beach type	beach width (m)	slope IT	slope ST	groins
BD	214	5.03	UD	348	1:79	1:71	
DP	246	4.97	UD	317	1:118	1:45	
Oo	269	4.92	LTBR	390	1:128	1:210	
Ni	203	4.86	UD	275	1:70	1:117	
Lo	321	4.78	LTBR	180	1:55	1:108	+
Mi	268	4.74	LTBR	226	1:44	1:73	+
Ma	285	4.68	LTBR	214	1:35	1:49	+
Br	243	4.57	UD	220	1:49	1:75	+
DH	333	4.51	LTBR	232	1:61	1:155	
Bl	236	4.38	UD	195	1:54	1:86	+
Ze	242	4.34	UD	225	1:79	1:216	
Kn	391	4.28	LTBR	174	1:57	1:41	+

Sampling

Samples were taken during an intensive campaign of three weeks in April-May 1996 in an *ad random* sequence. All samples were taken with a hyperbenthic sledge during daytime and around ebb tide. The sledge was especially designed for this study. Its metal frame was situated 5cm above the bottom and measured 100 x 40cm. It was equipped with two nets one above the other, each of 3m long and with a mesh size of 1x1mm. The sledge was pulled by 2 persons in the surf zone parallel to the coastline at a depth of approximately 1m. One haul lasted approximately 20 to 30 minutes and covered a distance of 450-500m. When groins were present, the sledge was lifted over the obstacle. The catch was preserved in an 8% formalin solution.

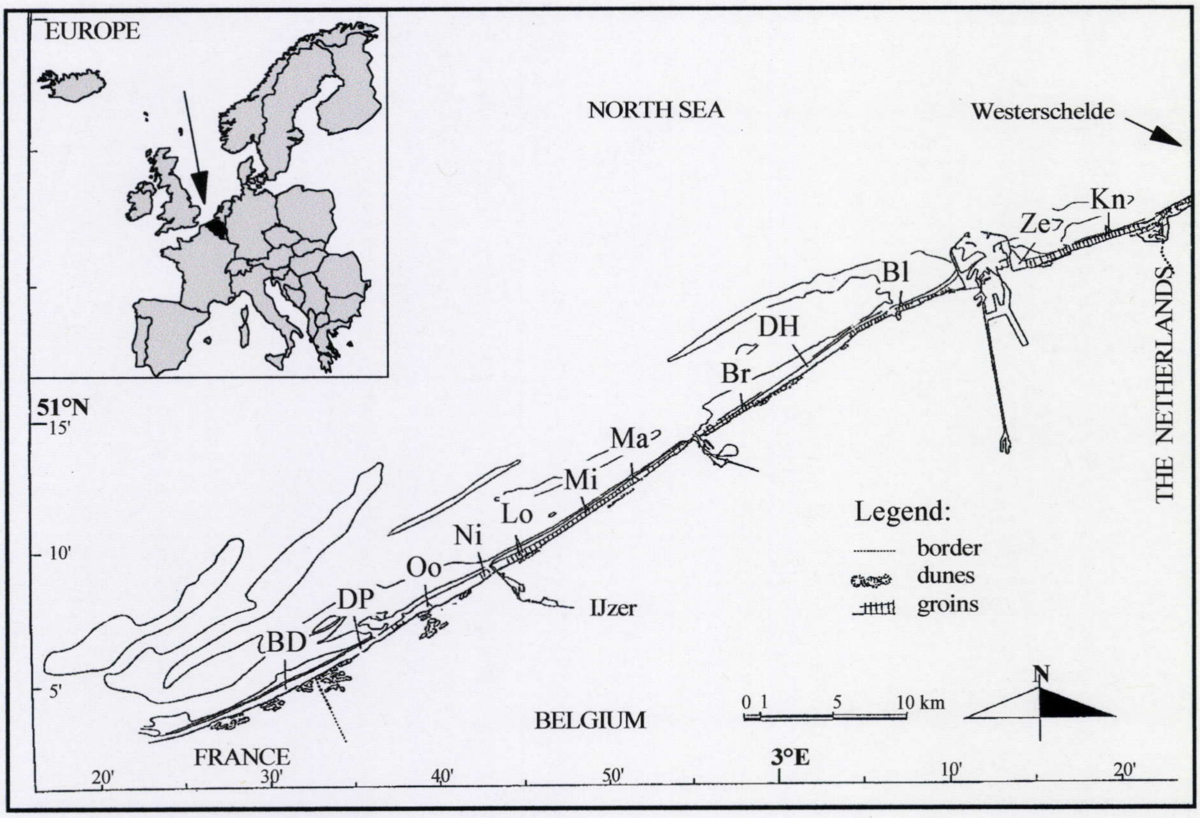

Figure 1. Study area with indication of sampling sites.

Environmental variables

At each sampling occasion, environmental variables were measured. Portable conductivity and oximeters (WTW) were used for *in situ* measurements of water temperature and salinity and oxygen content respectively. Turbidity was measured by means of a portable microprocessor turbidity meter (HANNA). Sediment and water samples were taken. For the analyses of pigments (chlorophyll-*a* and *c* and fucoxanthine) and particulate organic carbon (POC), the water samples were passed through Whatman GF/F filters. For the pigments, an immediate extraction with acetone (90%) was performed prior to a chromatography, with a Gilson high-performance liquid chromatography chain, using a slightly modified method of Mantoura & Llewellyn (1983). For POC analysis an automatic CN-analyser (Carlo Erba) was used. The concentrations of nitrate plus nitrite, phosphate, ammonia and silicium were measured through an automatic chain (SAN^{plus} segmented flow analyser, SKALAR). Median grain size was determined with a Coulter Counter LS particle size analyser and for the measurement of organic matter within the sediment (OM), samples were dried at 110°C for 2 hours and subsequently burned at 540°C for another 2 hours. Water temperature and salinity of the adjacent subtidal and hydrodynamic variables (wave height, wind speed and direction) at the moment of sampling were obtained from the Coastal Waterways' Division of the

Department of Environment and Infrastructure (Ministry of the Flemish Community). Wave height is expressed as the significant wave height H33: the average crest-to-trough height of the 33% highest waves in a wave record (15 minutes) (Anonymous 1996). Wind speed is given as the average speed and wind direction as the scalar average of the measured directions, over a period of 10 minutes (Gilhousen 1987).

Data treatment

In the laboratory, all animals were identified to species level (if possible) and counted. For the analyses, different developmental stages of single decapod species (zoeae, megalopae, postlarvae and juveniles) were treated as separate 'species' (functional species) since they have a different ecology, and a distinction was made between holo- and merohyperbenthos. The term hyperbenthos is used here as a work definition: all animals caught with a hyperbenthic sledge were retained for further analyses, with exception of large fish and Scyphozoa, adult shrimps and crabs and epibenthic molluscs, which were excluded. Densities are expressed as number of individuals per 100m². Since net efficiency was considered to be 100%, all density values are considered as minimum estimates (Mees & Hamerlynck 1992).

The multivariate statistical techniques Correspondence Analysis (CA, Ter Braak 1986, 1988) and a Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979) were used to analyse the species data. A fourth root transformation (Field et al. 1982) was performed on the density data prior to the analyses. Non parametric Multi-Response Permutation Procedures (MRPP) were used for testing multivariate differences among pre-defined groups (Mielke et al. 1976, Whaley 1983, Zimmerman et al. 1985). To evaluate the community structure relative to the measured environmental variables, a Canonical Correspondence Analysis (CCA, Ter Braak 1986, 1988) was performed with a small number of selected variables. Selection of variables was based on their mutual correlation coefficients (Spearman Rank correlations) and the forward selection option together with the Monte Carlo permutation Test in the Canoco package. If variables were significantly correlated ($p < 0.05$), only the one explaining the highest percentage of variation within the species dataset was retained for further analyses. Differences between communities were assessed using the non-parametric Mann-Whitney-U or Kruskal-Wallis Test (Sokal & Rohlf 1981). Regression analyses were performed. After fitting a regression equation, assumptions for residuals were tested.

Since wind direction is a circular variable, it was transformed to a linear variable by using the cosine of the angle that the wind made on a set of axes aligned perpendicularly onshore at each site (Clark et al. 1996b). Offshore winds at each site were allocated the greatest values (+1), onshore winds the lowest (-1), while winds with a cross-shore component from either direction received scores between +0,9 and -0,9. For wind speed and wave height values are expressed into classes ranging from 0 to 5, with class 5 indicating values of 25 knots and 125 cm receptively.

RESULTS

Environmental variables

In all occasions except one (Ze), sampling was done during calm weather conditions (Table 2). Wind speed never exceeded 10 knots (15-20 knots at Ze), and 33% of the waves did not exceed 50 cm (100-125 cm at Ze). Offshore and longshore winds (W-SW) prevailed in most occasions (northern wind at Ze). Water temperature in the shallow subtidal increased from 7.5

to 10.0°C, but in the intertidal range it varied between 8.5 and 14.0 °C. In the shallow subtidal, a clear distinction could be observed in salinity: at the east coast values varied between 29.5 and 32.0 psu, while at the west coast salinity values were somewhat lower: 28.5 - 29.0 psu. This distinction was not present at the intertidal (26.5 - 35.5 psu). Also no spatial gradient could be observed for the other variables: they varied distinctively between the sites. With two exceptions (DH and Ze), the intertidal slope of the beaches west of the IJzer were less steep (< 1:60) than at the eastern side (Table 1). The selected and excluded environmental variables are given by Table 3.

Table 2. Environmental variables per site (dw: dry weight, IT: intertidal, ST: subtidal).

	BD	**DP**	**Oo**	**Ni**	**Lo**	**Mi**	**Ma**	**Br**	**DH**	**Bl**	**Ze**	**Kn**
33% wave height (cm)	25-50	25-50	25-50	25-50	25	25-50	0-25	0-25	25-50	25-50	100-12	25
wind speed (kn)	5-10	5	10	5-10	5-10	5-10	15	5	5-10	10	15-20	5-10
wind direction (°)	80	290	255	30	270	340	235	235	250	255	25	325
organic material of sediment (g/100g dw)	0.843	2.449	0.799	0.803	0.837	1.128	0.586	0.473	0.880	0.614	0.805	0.661
salinity IT (psu)	32.1	26.4	35.4	34.6	29.6	28.4	28.7	31.8	30.6	30.2	31.0	27.9
salinity ST (psu)	28.5	28.5	29.0	28.5	29.0	29.0	31.8	31.8	29.4	29.5	30.0	29.8
turbidity (ftu)	310	15	76	320	112	49	31	274	80	292	140	27
water temperature IT (°C)	9.5	12.5	14.0	18.0	12.0	12.0	12.5	12.0	11.5	10.0	10.0	14.0
water temperature ST (°C)	9.8	10.0	8.0	10.0	8.0	10.0	7.8	7.8	7.9	7.9	10.0	9.8
POC water column (%C)	0.4	2.3	2.7	3.6	5.2	2.2	4.0	3.9	3.0	5.6	4.6	1.9
oxidized nitrogen (µmol/l)	0.591	0.000	0.616	1.009	0.141	0.000	0.527	12.665	10.575	14.446	15.318	3.829
ammonia (µmol/l)	2.821	0.190	8.214	2.537	1.980	0.705	46.000	3.852	14.579	2.509	4.591	1.464
phosphate (µmol/l)	0.794	0.462	0.569	0.496	0.746	0.429	0.256	0.223	1.298	0.306	0.339	0.543
silicium (µmol/l)	0.978	0.715	1.614	1.338	0.978	0.000	0.000	2.351	1.023	0.000	0.414	0.677
chlorophyll-*a* (µg/l)	48.65	8.38	20.09	23.32	12.88	13.48	72.51	50.07	49.97	25.76	21.58	5.43
chlorophyll-*c* (µg/l)	4.50	1.48	2.70	3.70	1.53	2.06	5.84	3.91	6.11	5.39	1.95	0.80
fucoxanthine (µg/l)	28.23	4.40	11.03	12.81	7.20	6.45	41.72	34.38	25.69	14.70	12.83	2.43
median grain size (low tide) (µm)	179	181	181	180	181	301	304	244	288	246	232	294

Community composition

In total 86 functional species were found (77 taxonomical species): 52 were holo- and 34 were merohyperbenthic species, all belonging to 14 higher taxonomical levels (Table 4, Appendix 3B). More than 50% of the average total sample composition were mysids, mainly *Mesopodopsis slabberi* (39%), *Schistomysis kervillei* (9%) and *Schistomysis spiritus* (3%) (holohyperbenthos). Other important groups were early life stages of fish (23% postlarvae and 15% eggs), caridean shrimps (5%), copepods and ctenophores (both 2%). Within the merohyperbenthos, postlarval fish, such as flounder *Pleuronectes flesus* and clupeids (a mixture of herring *Clupea harengus* and sprat *Sprattus sprattus*) and postlarval brown shrimp *Crangon crangon* were the dominant organisms. They represented 11%, 3% and 5% of the average total sample composition respectively.

Table 3. Selected and excluded environmental variables together with an indication (*) of their correlation (Spearman Rank correlation coefficient, only shown if p<0,05 and R>0,5) (IT: intertidal, ST: shallow subtidal).

Excluded variables	**Selected variables**				
	slope IT	salinity IT	water temperature ST	ammonia-N	phosphate-P
beach width	*				
33% wave height	*		*		
wind speed					
wind direction			*	*	
slope ST		*			
median grain size	*				
organic matter sediment			*		
salinity ST	*		*		*
water temperature IT					
turbidity		*			
POC water column					
oxidized nitrogen-N					
silicium		*			
chlorophyll-*a*			*	*	
chlorophyll-*c*			*	*	
fucoxanthine			*	*	

The number of functional species per sample varied between 24 and 52. Average total densities per sample exceeded several times 3000 ind./100m² and generally ranged between 300 and 4000 ind./100m². The average density of the holohyperbenthos (940±260 ind./100m²) was slightly higher than that of the merohyperbenthos (710±200 ind./100m²) (total hyperbenthic density: 1650±370 ind./100m²).

Community analyses

After the first analyses (not figured), 1 outlier was excluded (Ze). A successive TWINSPAN resulted in the distinction of two groups of stations (TWIN1 and TWIN2, indicated in Figure 2). The corresponding CA (Figure 2) gave similar results: both groups of sites could be distinguished along the first ordination axis (eigenvalues of the first 3 axes: 0.163, 0.122 and 0.098 respectively). TWIN1 appeared to be a relatively homogeneous group and consisted of all stations west of the IJzer estuary together with 1 station at the east coast (DH), whereas the variation within TWIN2 (remaining sites east of the IJzer estuary) seemed to be rather high (variation mainly along the second axis). Although the CA site plot could be interpreted as a gradient rather than two groups of sites, MRPP was significant ($p < 0.05$), indicating that the 2 groups were significantly different.

Mean total hyperbenthic density was slightly higher in TWIN1 (2140±620 ind.100m²) compared to TWIN2 (1470±510 ind./100m²). These differences however, were not significant (Mann-Whitney U Test, $p > 0.05$). Also the number of species was comparable: on average 34±4 species were found per sample in TWIN1 and 37±5 in TWIN2. Total density and sample composition varied substantially within both groups (Figure 3). Total and individual

Table 4. Species list together with their stage, type and frequency of occurrence (%F) on steep (S, < 1:55), intermediate (I, 1:55-1:75) and flat (F, > 1:75) beaches respectively (e: ephyra, m: medusa, z: zoea, l: larva, pl: postlarva, juv: juvenile, a: adult, H: holohyperbenthos, M: merohyperbenthos).

Taxon		**Stage**	**Type**	**F%**		
				S	**I**	**F**
Cnidaria	*Sarsia tubulosa*		H	100	100	100
	Hybocodon prolifer		H	25		
	Eutonina indicans		H		50	75
	Cnidaria species	e	M	50	25	75
		m	H	50	25	50
Ctenophora	*Pleurobrachia pileus*		H	75	75	100
	Beroë gracilis		H	75	25	75
Polychaeta	*Lanice* species	l	M	100	50	25
	Polydora species		H	50	50	25
	Polychaeta species	juv+a	H		25	
Copepoda	*Calanus helgolandicus*		H	100	75	75
	Centropages hamatus		H	75	25	75
	Temora longicornis		H	50	25	25
	Copepoda species		H	25		25
Euphausiacea	*Nyctiphanes couchi*		H	75		75
Caridea	*Crangon crangon*	pl	M	100	100	100
	Philocheras trispinosus	pl	M	25		
	Hippolyte varians	z	M			25
		pl	M	25		50
	Crangonidae species	z	M	75	25	100
	Caridea species	pl	M			25
Anomura	*Pagurus bernhardus*	z	M	25		50
		pl	M	25	50	50
	Porcellana platycheles	pl	M	25		
Brachyura	*Pinnotheres pisum*		H			25
	Carcinus maenas	pl	M	50	25	100
		juv	M	25	25	50
	Liocarcinus holsatus	z	M	25		25
		pl	M	75		75
		juv	M	25		
	Brachyura species	z	M	75		
		pl	M	75		
		juv	M	75	25	50
Mysidacea	*Gastrosaccus spinifer*		H	100	100	100
	Mesopodopsis slabberi		H	100	100	100
	Schistomysis kervillei		H	100	100	75
	Schistomysis spiritus		H	100	100	75
	Neomysis integer		H	100	75	100
	Praunus flexuosus		H	75	100	75
	Anchialina agilis		H	50		
Cumacea	*Cumopsis goodsiri*		H	25		75
	Bodotria scorpioides		H	25		25
	Diastylis rathkei		H	75		25
	Diastylis bradyi		H	50		
	Diastylis lucifera		H	25		
Isopoda	*Eurydice pulchra*		H	100	75	100
	Eurydice affinis		H		25	25
	Idotea linearis		H	25	25	25
	Idotea granulosa		H		25	
	Idotea pelagica		H	75		
	Jaera 'albifrons' group		H		25	
Amphipoda	*Atylus swammerdami*		H	100	75	75
	Atylus falcatus		H	25		50
	Atylus guttatus		H			25
	Pontocrates altamarinus		H	50	50	75
	Pontocrates arenarius		H	25	25	25
	Gammarus crinicornis		H	75		75
	Apherusa ovalipes		H	25		25
	Synchelidium maculatum		H		25	
	Bathyporeia species		H	50	75	75
	Corophium insidiosum		H	50		
	Corophium archerusicum		H	100	25	25
	Corophium arenarium		H			25
	Corophium volutator		H	25	25	
	Jassa falcata		H			25
	Jassa cf *marmorata*		H	75	25	
	Haustorius arenarius		H		25	
	Stenothoë marina		H	25		
	Gammarus locusta		H			25
	Melita palmata		H			25
	Ischyroceridae species		H	25		
	Gammaridae species		H	50		50
	Pariambus typicus		H	75	25	25
	Pseudoprotella phasma		H	25		
Chaetognatha	*Sagitta setosa*	a	H	25	50	75
Pisces	*Syngnathus rostellatus*	juv	M			75
	Clupea harengus	juv	M	25		75
	Sprattus sprattus	juv	M	50		
	Clupeidae species	pl	M	100	100	75
	Pomatoschistus species	pl	M	50		
	Merlangius merlangus	juv	M	25		
		pl	M	100	50	50
	Solea solea	pl	M		25	75
	Pleuronectes platessa	juv	M	25		
		pl	M	100	100	100
	Pleuronectes flesus	pl	M	100	100	100
	Ammodytes tobianus	juv	M	75	25	75
	Taurulus bubalis	pl	M			25
	Anguilla anguilla	juv	M	50		
	Myoxocephalus scorpius	pl	M	100	25	25
	Trisopterus minutus	pl	M	25		
	Pisces species	pl/juv	M	50	50	25
		eggs	M	100	100	100

densities which differed significantly between both groups (Mann-Whitney U Test, $p < 0.05$) are indicated in Table 5. Mysid density (total density as well as the density of *Mesopodopsis slabberi* and *Schistomysis spiritus*), density of the cnidarian *Eutonina indicans*, the isopod *Eurydice pulchra* and postlarvae of sole *Solea solea* were significantly higher in TWIN1, whereas the larval polychaet *Lanice* species, the mysid *Neomysis integer* and postlarval bull-rout *Myoxocephalus scorpius* were mainly abundant or only present in TWIN2.

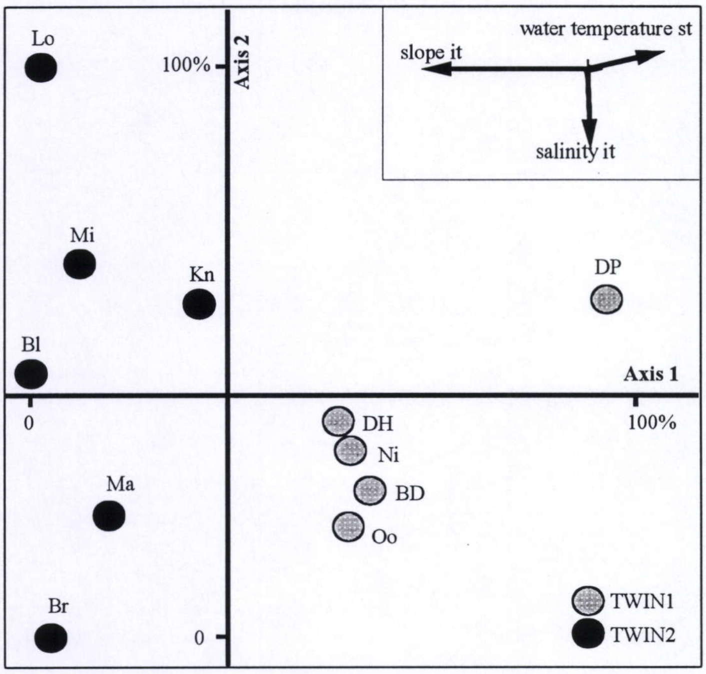

Figure 2. CA site plot of the complete dataset with indication of TWIN groups. Each axis is scaled in proportion to the longest axis and environmental variables are plotted passively.

Structuring variables

Multivariate community analyses. In a first CCA, the outlier Ze was clearly correlated with wave height (not figured). After exclusion of this sample, both TWIN groups could be observed along the first ordination axis (eigenvalues of the first 3 axes: 0.157, 0.094 and 0.067 respectively). The main variables correlated with the first axis were the intertidal slope and the water temperature of the adjacent subtidal area (and correlated variables). 23% of the variation within the dataset could be explained by the first axis. The second and third axes did not reveal important additional information.

Only the morphodynamic variables (beach width, intertidal slope and median grain size) and salinity of the adjacent subtidal differed significantly (Mann-Whitney U tests $p < 0.05$) between both TWIN groups (Table 5). TWIN1 contained sites characterised by a rather flat (± 1:83) and wide (310±30 m) intertidal area with fine sands (median grain size 200±20 µm), compared to TWIN2 from which the sites are mainly characterised by steeper (±1:48) and shorter (200±10 m) intertidal areas (Figure 4). Sediments of the latter consisted of medium sand (median grain size: 260±20 µm).

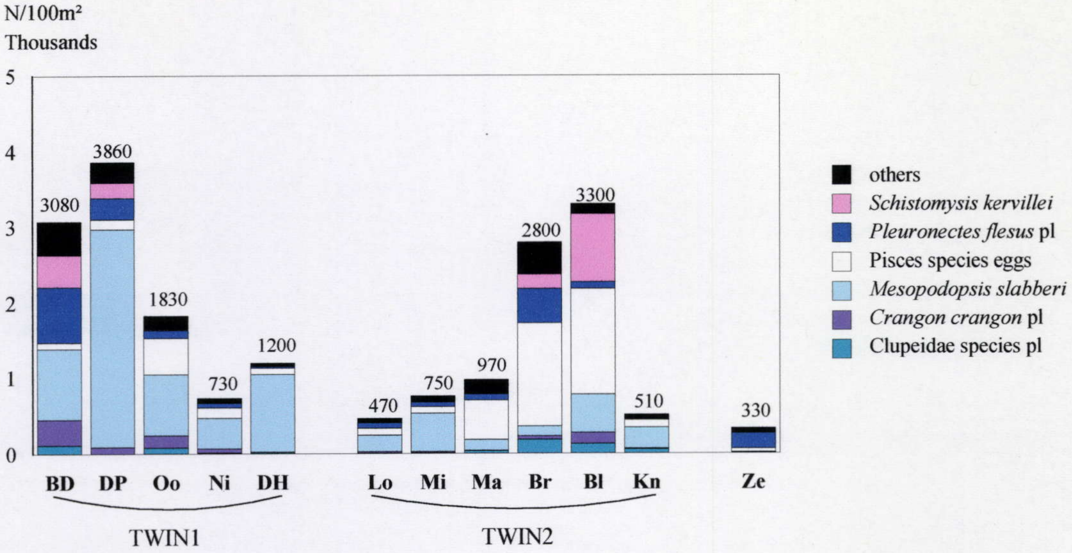

Figure 3. Relative species composition and total hyperbenthic density per site and per TWIN group.

Table 5. Mean values (± SE) per TWIN group of variables which differ significantly between both groups (Mann-Withney U test, p < 0.05) (it: intertidal, st: subtidal, l: larva, pl: postlarva).

	TWIN1	TWIN2
beach width (m)	310±30	200±10
it slope		
median grain size (µm)	200±20	260±20
salinity st (psu)	28.8±0.2	30.2±0.5
density (ind./100m²)		
Mysidacea	1440±490	500±200
Eutonina indicans	17±9	0
Lanice species l	0	8±8
Mesopodopsis slabberi	1210±430	290±70
Schistomysis spiritus	100±30	5±4
Neomysis integer	0.6±0.2	5.5±4
Eurydice pulchra	1.9±1.0	0.3±0.1
Solea solea pl	3±2	0
Myoxocephalus scorpius pl	0.04±0.05	0.85±0.45

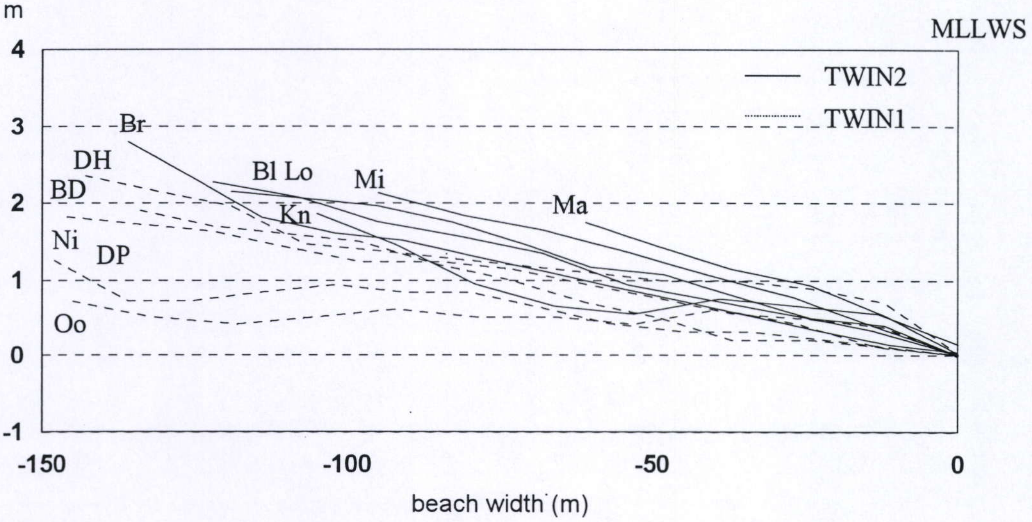

Figure 4. Intertidal beach profiles per TWIN group.

Beach slope vs. community parameters

A detailed investigation of the relationship between the beach slope and some community parameters (total and individual densities of dominant species and number of species) revealed following trends. First of all, the number of functional species was lowest on beaches with an intermediate intertidal slope (1:55 – 1:75) (Figure 5a). Table 4 gives an overview of the species with their frequency of occurrence on the steep, intermediate and flat beaches respectively. For the holohyperbenthos, no differences can be observed between the three types of slopes for the more planktonic species (cnidarians, ctenophores, copepods, larval polychaetes, mysids, isopods and chaetognaths), whereas cumaceans were absent on intermediate beaches. Other differences mainly concerned amphipods. For the merohyperbenthos, the main differences were found for juvenile fishes: most of them were absent at the intermediate beaches.

Total hyperbenthic densities could not be related directly to hydromorphologic variables. However when the holo- and merohyperbenthic data were treated separately and the storm sample was excluded, several trends became clear. Total holohyperbenthic density seemed to increase with a decreasing intertidal slope ($p < 0.05$, Figure 6a). Of the three dominant holohyperbenthic species, significant regressions ($p < 0.05$) were found which describe the densities of *Schistomysis spiritus* and *Mesopodopsis slabberi* as a log function of intertidal slope respectively (Figure 6b,c).

No relationship could be detected with the third dominant species *Schistomysis kervillei*, or with total merohyperbenthic density. However, if the adjacent subtidal slope is considered, highest merohyperbenthic densities and total number of species were found on intermediate slopes (1:60 – 1:100) (Figures 5b,c). Moreover, turbidity was the only variable which differed significantly between the sites with steep, intermediate and flat subtidal slopes respectively (Kruskal-Wallis Test, $p < 0.05$): highest values were found at intermediate sites (231±62 ftu, compared to 146±45 ftu and 24±5 ftu at flat and steep subtidal slopes respectively). If multivariate analyses were repeated on merohyperbenthic data alone, turbidity and salinity (the latter significantly correlated with subtidal slope) were highly correlated with the second ordination axis (Figure 7). However, intertidal slope and subtidal water temperature remained the most important structuring variables.

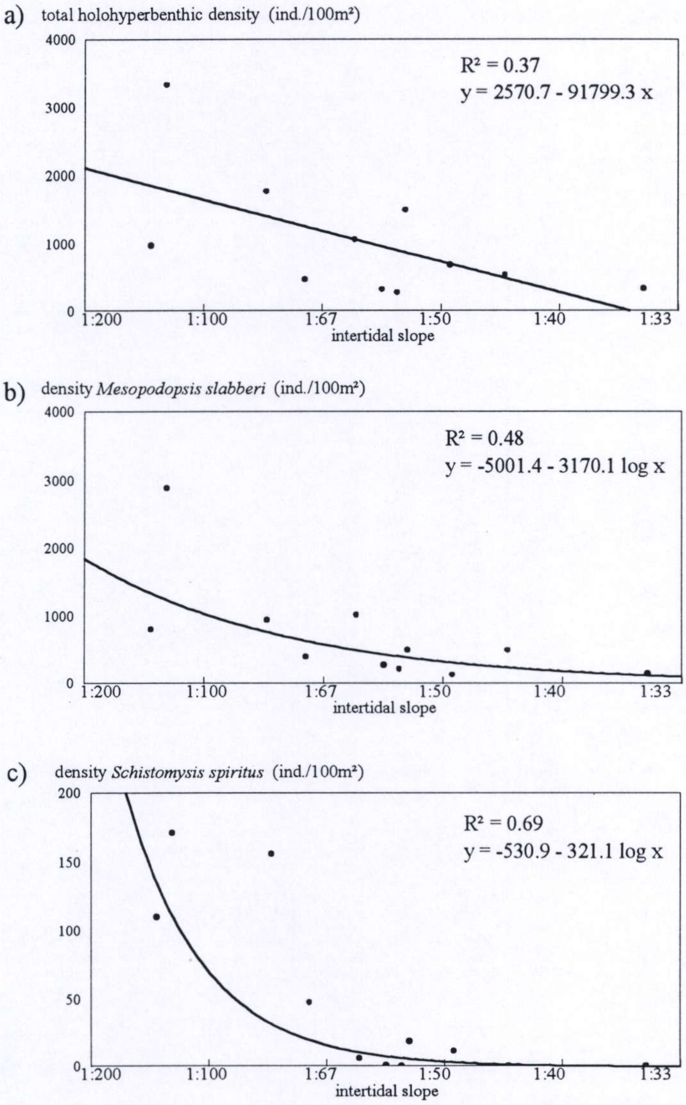

Figure 5. Relationship between the number of functional species and intertidal (a) and subtidal (b) slope respectively and between the total merohyperbenthic density and subtidal slope (c). A curve is fitted to the XY coordinate data according to the distance-weighted least squares smoothing procedure.

DISCUSSION

Community composition

The surf zone of the Belgian coast is used intensively by several early life stages of fish and macrocrustaceans. The mean total density per beach (1650±370 ind./100m²) was much higher than densities found on another North Sea, an Atlantic and a Mediterranean beach respectively (< 600 ind./100m²) (Colman & Segrove 1955, San Vicente & Sorbe 1993b, Munilla & Corrales 1995). All their samples were also taken during spring or summer. Lock et al. (1999) found much lower densities on a beach at the Belgian coast (430±200 ind./100m²), but their samples were taken in November. Comparable total densities were only found by San Vicente & Sorbe (1993b) and Munilla et al. (1998), both on Mediterranean beaches (1080±840 ind./100m² and 3400±1160 ind./100m² respectively). Although locally determined, most Atlantic beaches are much more exposed than the Belgian beaches, the opposite is true for the Mediterranean. The North Sea is semi-enclosed (Ducrotoy et al. 2000) and can be considered as an intermediate situation between the open Atlantic and almost closed Mediterranean. Moreover, the western Belgian coast is characterised by the presence of a rich shallow sandbank system just in front of the coastline (Cattrijsse & Vincx in press), which might explain the high densities found here.

Community analysis & structuring variables

Multivariate community analyses. Two hyperbenthic communities could be distinguished. The stations west of the IJzer, together with two east coast sites (DH and Ze), were separated from the remaining stations. Although the eigenvalues of the CA axes were rather low and the variation within the second TWIN group was quite large, the two multivariate statistical techniques revealed the same pattern and MRPP indicated that the two groups were significant. The large variation in the dataset resulting in rather weak patterns, can possibly largely be explained by the dynamic and turbulent nature of the Belgian coast. These conditions might not only have affected species distribution but also sampling efficiency. However, up to now nothing is known about catch efficiency of hyperbenthic sledges (Mees & Jones 1997).

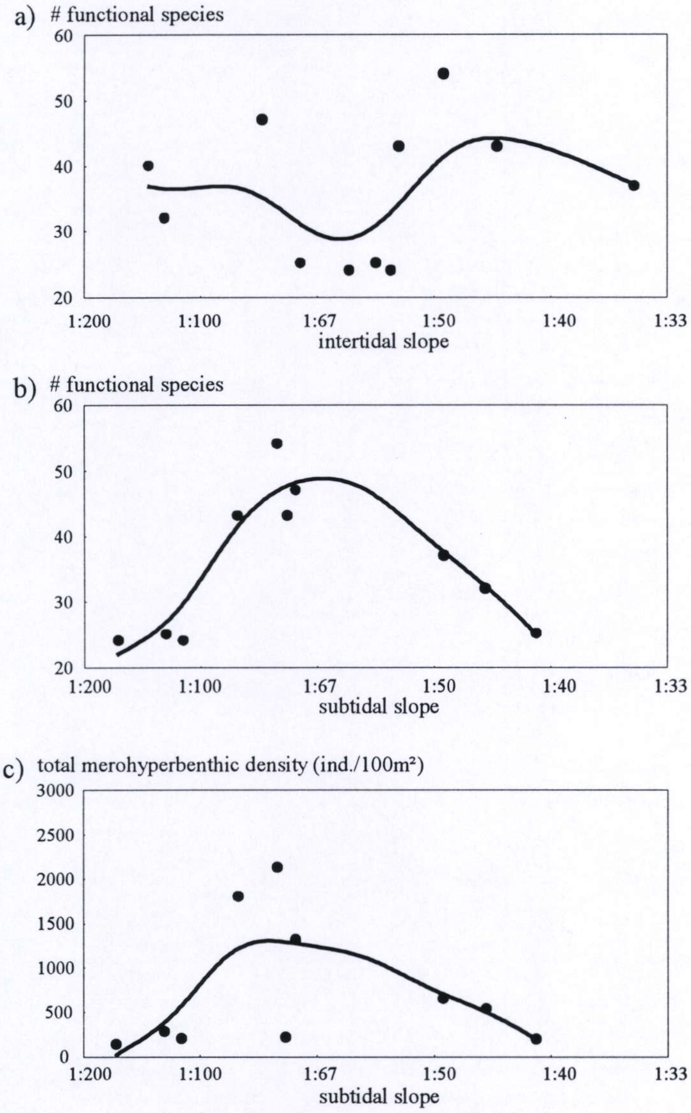

Figure 6. Relationship between intertidal slope and (a) total hyperbenthic density, (b) density of *Mesopodopsis slabberi* and (c) density of *Schistomysis spiritus* respectively.

CCA indicated water temperature (subtidal) and intertidal slope (and correlated variables) as important structuring factors. Since the sampling was done in spring and lasted for approximately 3 weeks, the appearance of new recruits during this period can possibly explain the strong correlation of the first axis with subtidal water temperature, which varied between 8 and 10°C. However, water temperature was not significantly different between both groups, in contrast to the intertidal slope. Eighteen percent of the variation explained by the first ordination axis could be explained with intertidal slope alone, which was significantly correlated with median grain size of the sediment, wave height and subtidal salinity. Salinity measured in the shallow subtidal was slightly lower at the west coast (28.5-29.0 psu) than at the east coast (29.5-32.0 psu), reflecting a spatial pattern. This spatial pattern could only partly be found in the variation in intertidal slopes. The presence of groins can also influence the community structure both indirectly by influencing the hydrodynamic features of the beach, and directly by providing a hard substrate and additional microhabitats. However, if organisms known to prefer hard substrates occurred (e.g. *Polydora* species), no direct relationship was found with the presence of groins on the beach.

Holo- vs. merohyperbenthos. Hydromorphologic features of a beach can be expressed in several variables, which are consequently linked to each other. The high hydrodynamic forces on the upper beach of low-tide bar/rip (LTBR) beaches are for example directly responsible for a larger median grain size. To express all these features together, beaches can be classified into a certain type (e.g. Masselink & Short 1993). The morphodynamic classification into UD and LTBR beaches however, could not explain the two different communities found in this study, indicating that some variables might be more important than others or that valuable information gets lost by using only one index value. In this study, intertidal slope (and/or correlated variables) seems to be the best variable to explain structural differences between the communities. This is especially true for the holohyperbenthos, which is reflected in their total density as well as in the occurrence of several dominant species. Although most of these dominant organisms can be found on different beach types (each reflecting specific hydrodynamic conditions), their densities are higher in surf zones of beaches with wide and flat slopes and fine sand. Organisms which are more closely associated with the sediment such as cumaceans and several amphipods, are consequently more influenced by hydromorphologic features.

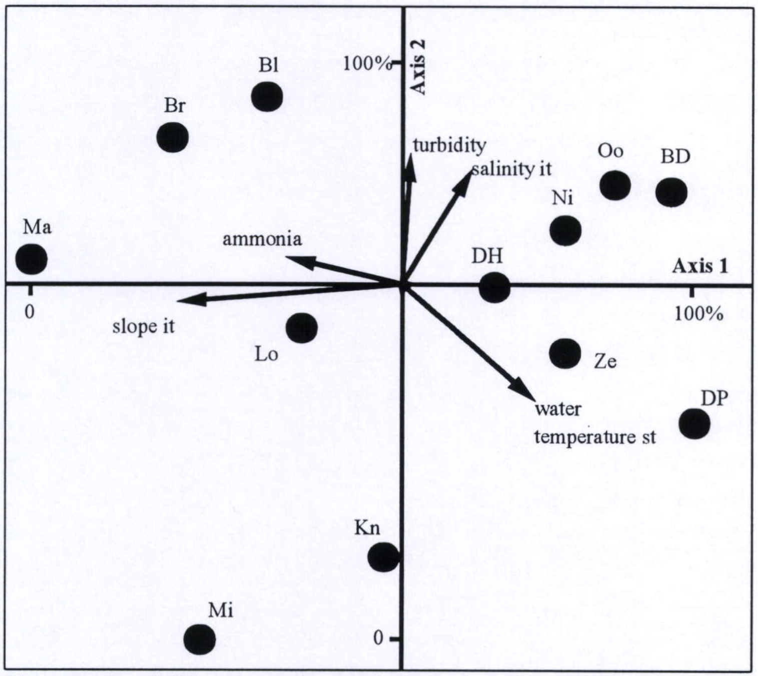

Figure 7. CCA site plot of the merohyperbenthic data. Each axis is scaled in proportion to the longest axis and environmental variables are plotted passively.

For the merohyperbenthos, the situation is more complex and trends are not so obvious. Although intertidal slope (and correlated variables) was indicated by CCA as most important structuring variable, no direct relationship was found with total merohyperbenthic densities. Furthermore, the morphodynamics of the adjacent shallow subtidal and turbidity were identified as important structuring environmental variables. Since early life stages of most organisms are more susceptible to water movements and thus to the circumstances further offshore, the importance of subtidal hydromorphologic features as a structuring variable for merohyperbenthic assemblages can be explained. Since the mobile and relatively homogenous nature of the sediment on sandy shores provides few refuges, protection due to higher turbidity might be important. The fact that several juvenile fish species were totally absent on intermediate beaches can largely be explained by coincidental capture of most of these species.

Weather conditions. Spatial patterns in hyperbenthic surf zone assemblages might be affected by (short-term) temporal events. Stormy weather conditions for example, seem to influence the hyperbenthic community severely. Colman & Segrove (1955) already suggested the migration from the surf zone towards deeper waters by mysids during stormy weather conditions. Mysids are known to be able to respond to fluctuations in hydrostatic pressure and turbulence near the bottom (Rice 1961, Clutter 1967). The latter also suggested a possible relationship between wave action and the occurrence of *Metamysidopsis* species. Beyst et al. (in press a) found a relationship between temporary hyperbenthic animals and hydrodynamic variables. A correlation with mysids was not found, but sampling was never done in stormy conditions. Although severe weather conditions only occurred in Ze at the moment of sampling, its influence was rather clear. Hardly any mysids were present in this sample, whereas copepods, fish eggs and postlarvae (mainly flounder) were quite abundant. Although a larger escape response of mysids is possible with increasing wave height, it is suggested that mysids can possibly withstand severe wave action until a critical value. When stronger wave action is prevailing, they leave the surf zone towards calmer waters. If wave stress has a clear effect on species distribution, also the preceding time history of this environmental variable might be important, which might be reflected in temporal variability. Furthermore, wave energy dissipation can strongly affect beach morphology.

CHAPTER II

THE EPIBENTHOS OF THE SURF ZONE OF SANDY BEACHES: TEMPORAL AND SPATIAL PATTERNS

Part A. Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. Journal of Sea Research.

Part B. Factors influencing spatial variation in fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium

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Chapter II
Part A

Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation

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Results presented in:

Bregje Beyst, Kris Hostens & Jan Mees (in press). Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. Journal of Sea Research.

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Surf zone

ABSTRACT

Monthly samples were taken in the surf zone of sandy beaches along the Belgian coast from May 1996 until July 1997 at 4 selected stations. After recording the macrocrustacean and fish species residing the surf zone, temporal patterns were investigated as well as the abiotic variables structuring the community. In total 34 species were recorded belonging to caridean shrimps (3), anomuran and brachyuran crabs (5), cephalopods (2) and fish (24). The brown shrimp *Crangon crangon* dominated almost all samples (>80%). Several times total densities exceeded 400 ind./100m², if *C. crangon* was excluded 10 ind./100m². Notwithstanding the harsh hydrodynamic conditions, the surf zone of Belgian sandy beaches is used intensively by a number of epibenthic macro-crustaceans and demersal fish species. Seven resident and 10 migrant species were identified. As mainly juvenile fishes were present, the surf zone of the Belgian sandy beaches may act as a nursery for longer (e.g. plaice *Pleuronectes platessa*) or shorter (e.g. brill *Scophthalmus rhombus*) periods. However, its nursery function should be studied in more detail, since the highly dynamic circumstances and more specifically wave height and wind speed might be important structuring factors for the epibenthic communities. The surf zone of Belgian sandy beaches also seems to function as a transient area to other nurseries (e.g. bass *Dicentrarchus labrax*) or between a nursery and the true marine environment (e.g. dab *Limanda limanda*).

Temporal variation in community structure was partly masked by spatial differences between sites. Although variables such as salinity and hydrodynamic factors may have influenced the data, clear temperature-related, seasonal patterns occur. Most likely extreme winter conditions and subsequent migration of organisms to deeper waters caused a decline in winter in both density and diversity.

INTRODUCTION

Temporal variation of epibenthic surf-zone (fish) fauna is well documented. Although the shallow area of the Wadden Sea has been studied intensively (e.g. Kuipers 1973, van der Veer & Bergman 1986), no information is available about the epibenthic macrocrustacean and fish surf zone communities of the exposed beaches of the eastern side of the Southern Bight of the North Sea. Furthermore, few studies of surf zone fauna of sandy beaches have considered both fish and marocrustacean assemblages (Pihl 1986, Ross et al. 1987, Gibson et al. 1993). Most research has been done in South Africa (e.g. Lasiak 1981, 1984b, Lamberth et al. 1995, Clark et al. 1996a,b), Mexico (e.g. Modde & Ross 1981, Ross et al. 1987), USA (Texas, Maine) (e.g. McFarland 1963, Hook 1991, Lazzari et al. 1999) and Scotland (e.g. Gibson et al. 1993, 1996). Still, much confusion exists over the factors influencing or controlling temporal variations, covering a wide variety of both biological and physical variables (Clark et al. 1996b).

The importance of surf zones of sandy beaches as nurseries has been stressed several times (e.g. Lasiak 1981). The Belgian coast is part of an extensive coastal plain extending from northern France to Denmark, which is bordered on the seaward side by a sandy coastal barrier adjacent to sandy beaches (Eisma & Fey 1982) (Figure 1). Because of the presence of an extensive shallow sandbank system in front of the western part of the Belgian coast and the Westerschelde estuary in the East, the surf zone of the intermittent sandy beaches may also play an important role as a transient area between these environments. Recent evidence emphasises the importance of the sand bank system for early life history stages of many species (Dewicke unpublished data). Besides the Wadden Sea and some other estuaries, the Westerschelde estuary functions as a nursery for the North Sea populations of flatfish, clupeids and gadoids (Creutzberg & Fonds 1971, Zijlstra 1972).

In this paper, the temporal changes in the epibenthic community composition are analysed to evaluate the hypotheses that the surf zone of the open Belgian sandy beaches is too dynamic to support important species assemblages and that hydrodynamic factors therefore have a major influence on the community structure. The aims of this study are: (1) to list macrocrustacean and fish species prevalent in the surf zone of Belgian sandy beaches, and (2) to evaluate the influence of some abiotic environmental variables on the temporal variation within the assemblages.

MATERIAL AND METHODS

Study area

The study area comprises the surf zone of sandy beaches of the Belgian coast (Figure 1), which is situated in the Southern Bight of the North Sea. The Belgian coastline is 67 km long and is characterized by built-on dykes that are interrupted by dune areas, and sporadic groins on the beaches. In some areas these groins are less than 300 m apart, while elsewhere they are absent for several kilometers. The mouth of the IJzer estuary is situated in the western part, while the large Westerschelde estuary opens just over the Belgian-Dutch border. A strong semi-diurnal tidal regime and a net tidal current running northeast parallel to the coastline are characteristic. All beaches were low-tide bar/rip (LTBR) beaches according to the morphodynamic classification scheme of Masselink & Short (1993). The main characteristics of each site are given in Table 1.

Table 1. Main characteristics of the sandy beaches studied (D: mean high tide beach sediment grain size, MSR: mean spring tide range, IT: intertidal, ST: first 300m of shallow subtidal).

Site	D (µm)	MSR (m)	beach width (m)	slope IT	slope ST	groins	bar/rip IT	bar/rip ST
Oostduinkerke (Oo)	270	4.92	390	1:128	1:210	-	+	+
Lombardsijde (Lo)	320	4.78	180	1:55	1:108	+	+	+
Wenduine (We	270	4.45	195	1:49	1:62	+	+	+
Knokke (Kn)	390	4.28	175	1:57	1:41	+	+	-

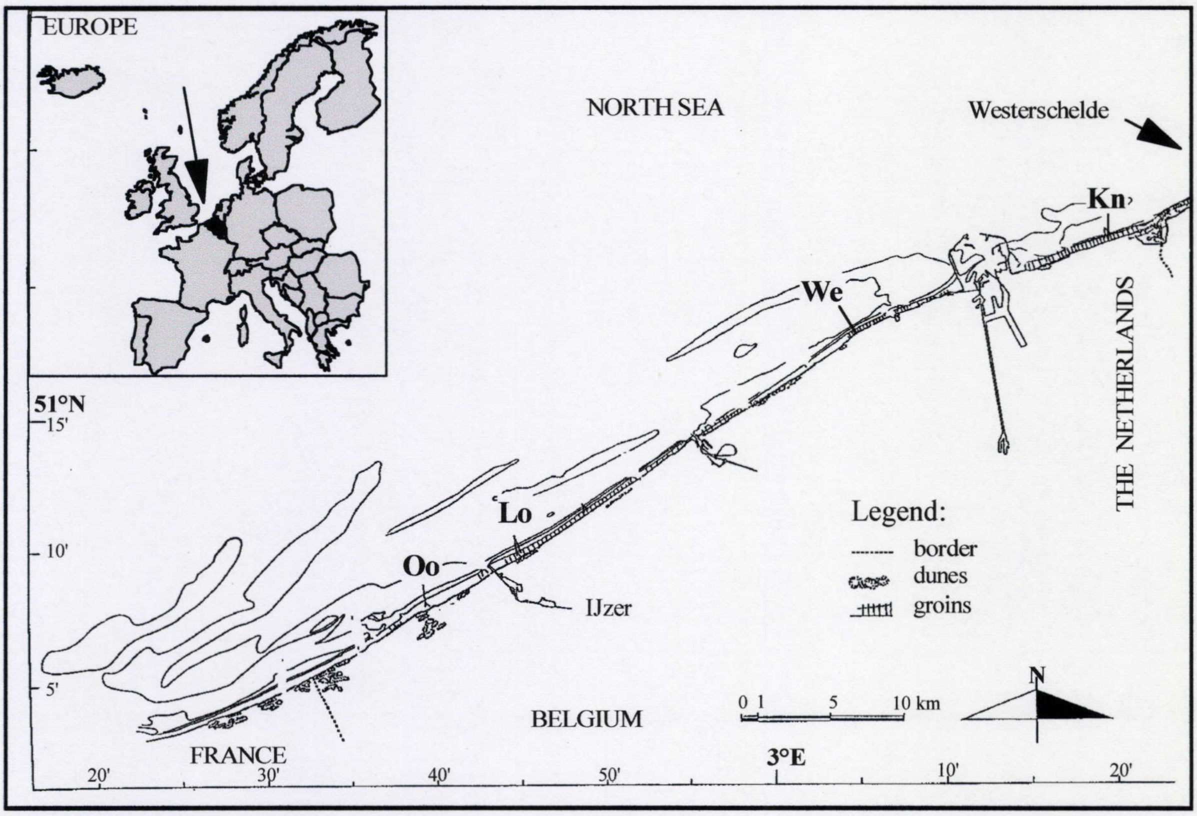

Figure 1. Study site with indication of sampling sites.

Sampling

Monthly samples were taken from May 1996 until July 1997 at 4 beaches: 2 at the western side of the coast (Oo and Lo) and 2 at the eastern side (We and Kn). In contrast to the other 3 stations, Oo has no groins and a flat and wide intertidal area. Persistent bad weather conditions prevented sampling at several occassions. All samples were taken with a 2m-beam trawl at neap tide during daytime and around ebb. The fishing net was 3 m long, had a mesh size of 5x5 mm and was equipped with a tickler-chain in the ground rope. It was pulled by 2 persons in the surf zone parallel to the coastline at a depth of approximately 1m. One haul lasted 15 min and covered a distance of 450-500m. Due to practical reasons, only one haul was taken at each occasion. When groins were present, the net was lifted over the obstacle. The catch was anaesthetised in a dilute solution of benzocaine (ethylamino-4-benzoate) and then preserved in an 8% formalin solution. In the laboratory, all animals were identified to species level, measured and counted.

Environmental variables

After each haul, portable conductivity and oximeters (WTW) were used for *in situ* measurements of water temperature, salinity and oxygen content. Turbidity was measured with a portable microprocessor turbidity meter (HANNA). Water samples were further processed in the laboratory, where they were filtered through Whatman GF/F filters prior to analyses. For the pigments (chlorophyll-*a* and *c* and fucoxanthine), an immediate extraction with acetone (90%) was performed prior to a chromatography, with a Gilson high-performance liquid chromatography chain, following a slightly modified method of Mantoura & Llewellyn (1983). For particulate organic carbon (POC) an automatic CN-analyser (Carlo Erba) was used. The concentrations of nitrate plus nitrite, phosphate, ammonia and silicium were measured with an automatic chain ($\mathrm{SAN}^{\mathrm{plus}}$ segmented flow analyser, SKALAR). From the sediment sample, median grain size was determined in the laboratory with a Coulter Counter LS particle size analyser. For the measurement of organic matter within the sediment (OM) samples were dried at 110°C for 2 hours and subsequently burned at 540°C for another 2 h. Beach width was measured from the water line at ebb tide to the high-water mark. Hydrodynamic variables (wave height, wind speed and direction) at the moment of sampling and slope of the beaches (beach profiles) were obtained from the Coastal Waterways' Division of the Department of Environment and Infrastructure (Ministry of the Flemish Community). Wave height is expressed as the significant wave height H33: the average crest-to-trough height of the 33% highest waves in a wave record (15 minutes) (Anonymous 1996). Wind speed is given as the average speed and wind direction as the scalar average of the measured directions, over a period of 10 minutes (Gilhousen 1987).

Data treatment

Catch densities are expressed as number of individuals per $100\mathrm{m}^2$. Small sized crustaceans (e.g. isopods, mysids), early postlarval fish (e.g. clupeids), jellyfish and sedentary animals (e.g. the starfish *Asterias rubens*) were excluded from further analyses. Diversity was calculated and expressed as Hill numbers of the order 0, 1, 2 and $+\infty$ (Hill 1973). Temporal patterns were examined with the following multivariate statistical techniques: Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) (Ter Braak 1986, 1988), Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979) and cluster analysis using group average sorting and the Bray-Curtis dissimilarity index (Bray & Curtis 1957). A fourth root transformation (Field et al. 1982) was performed on the abundance data prior to the analyses.

In order to assess the importance of the measured variables in structuring the communities, the forward selection option together with the Monte Carlo permutation Test in the Canoco package were used prior to CCA's. The influence of environmental factors on temporal variations in total density was examined using multiple stepwise regression analyses with an adjusted multiple coefficient of determination (R^2) as an index of predictive value (Sokal & Rohlf 1981). If variables were significantly correlated (Spearman Rank correlation's, p<

Table 2. Average monthly catch data (4 stations), total number caught and indication of the life history stage and resident status following Clark et al. (1996b) (R: resident, M: migrant, S: sporadic, j: juvenile, a: adult, *: < 1 ind./100m²).

Taxon	**Stage**	**May'96**	**Jun'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**	**Status**	**#caught**
Crangon crangon	j+a	25	114	394	380	261	63	*	72	77	59	146	152	649	R	95730
Pleuronectes platessa	j	3	2	2	2	1	3	*	*	1	*	1	1	1	R	760
Carcinus maenas	j+a	1	1	3	1	1	*	*		*	1	1	1	3	R	570
Clupeidae species	j	13				*									S	540
Sprattus sprattus	j		1	1	*	1	1		*	*		*		7	R	430
Liocarcinus holsatus	j+a	*	1	2	*	1				*		*	*	5	M	430
Clupea harengus	j	2	2	3	1	*	1	*	*	*		*	*	1	R	410
Pomatoschistus minutus	j+a		*	1	*	3	2		1	1	*		*	*	R	250
Pomatoschistus lozanoi	j+a		*	*	*	1	*	*	*	1	*			*	R	120
Philocheras trispinosus	a	*	2	*										1	M	100
Portumnes latipes	j+a	1	*		*		*	*			*	*	*	1	S	86
Solea solea	j		2	*		*	*			*				*	S	84
Syngnathus rostellatus	j+a	*	1		*					*				1	S	62
Pomatoschistus microps	a		*	*			*							1	M	61
Scophthalmus rhombus	j		*	*	*		*						*	*	M	35
Zoarces viviparus	j	*	*									*	*		M	33
Echiichthys vipera	j+a	*	*	*		*					*				M	26
Loligo vulgaris	j					1									S	22
Ciliata mustela	j+a			*		*	*								S	20
Dicentrarchus labrax	j			*			*		*						M	20
Limanda limanda	j				*	*	*								M	20
Scophthalmus maximus	j				*										M	15
Liza ramada	j									*					S	11
Sepiola atlantica	j+a		*												S	10
Osmerus eperlanus	j+a	*													S	10
Pleuronectes flesus	j								*						S	10
Gasterosteus aculeatus	a								*						S	10
Cancer pagurus	j+a	*	*												M	5
Atherina presbyter	j										*				S	4
Ammodytes tobianus	j	*													S	2
Myoxocephalus scorpius	j+a						*								S	2
Agonus cataphractus	j		*												S	2
Palaemon species	a						*								S	1
Reptantia species	j+a									*					S	1
Taurulus bubalis	j+a					*									S	1

0.05), only one of them was retained for further analyses. Since wind direction is a circular variable, it was transformed to a linear variable by using the cosine of the angle that the wind made on a set of axes aligned perpendicularly onshore at each site (Clark et al. 1996b). Offshore winds at each site were allocated the greatest values (+1), onshore winds the lowest (-1), while winds with a cross-shore component from either direction received scores between +0,9 and -0,9. For wind speed and wave height values are expressed into classes ranging from 0 to 4, with class 4 indicating values of 20 knots and 100cm respectively.

RESULTS

Species composition

In total, 34 species were recorded: 3 caridean shrimps, 5 anomuran and brachyuran crabs, 2 cephalopods and 24 teleost fish (Table 2). The brown shrimp *Crangon crangon* was dominant in almost all samples (>80%). This species and the shore crab *Carcinus maenas* were 'resident' species (according to the terminology of Clark et al. 1996b), since they were present in the surf zone more or less throughout the year. Also, 5 resident fish species were recorded (juvenile plaice *Pleuronectes platessa*, herring *Clupea harengus* and sprat *Sprattus sprattus*, and the gobies *Pomatoschistus minutus* and *P. lozanoi*). Almost all of these species reached yearly catch averages of more than 1 ind./100m² in at least one site. Ten species were classified as 'migrants' (most abundant during a certain period of the year and in several stations), half of them being juveniles. All other species were recorded 'sporadically'. Sixteen species were caught as juveniles only, while the shrimp *Philocheras trispinosus*, the three-spined stickleback *Gasterosteus aculeatus* and the common goby *Pomatoschistus microps* were exclusively caught as adults.

Table 3. Yearly average density (N/100m², total number of species and average Hill numbers per station (*: < 0.05 ind./100m²).

Taxon		Oo	Lo	We	Kn
Caridea	*Crangon crangon*	249	189	177	145
	Palaemon species			*	
	Philocheras trispinosus	0.8			
Anomura	Reptantia species			*	
Brachyura	*Cancer pagurus*			*	
	Carcinus maenas	0.1	1.7	0.4	2.2
	Liocarcinus holsatus	1.7	0.6	0.5	0.5
	Portumnes latipes	0.3	0.2	0.1	
Mollusca	*Sepiola atlantica*		0.1		
	Loligo vulgaris	*	0.2		
Pisces	*Clupea harengus*	*	1.1	1.9	0.3
	Clupeidae species	4.1			*
	Sprattus sprattus	1.2		0.6	1.7
	Osmerus eperlanus		0.1		
	Ciliata mustela		0.1	0.1	
	Atherina presbyter		*		
	Gasterosteus aculeatus		0.1		
	Syngnathus rostellatus	0.4	*	*	

	Myoxocephalus scorpius				*
	Taurulus bubalis	*			
	Agonus cataphractus	*			
	Dicentrarchus labrax		0.1	0.1	*
	Liza ramada	0.1			
	Zoarces viviparus	0.1	0.2		
	Echiichthys vipera	*	0.2	*	*
	Ammodytes tobianus				*
	Pomatoschistus lozanoi	0.5	0.3	0.1	*
	Pomatoschistus microps	0.2	0.1		0.1
	Pomatoschistus minutus	0.7	0.8	0.5	0.2
	Limanda limanda	*	0.1	*	*
	Pleuronectes flesus		0.1		
	Pleuronectes platessa	1.5	1.6	1.7	1.3
	Scophthalmus maximus	*	0.1	*	
	Scophthalmus rhombus		0.2	*	0.1
	Solea solea	0.5	0.1	*	0.1
Total density		262	197	184	151
Total density without *C. crangon*		13	8	6	7
Total # species		22	24	20	17
Hill numbers	N_0 (SE < 1)	8	8	7	6
	N_1 (SE < 0,4)	1.5	2.1	1.5	1.5
	N_2 (SE < 0,3)	1.2	1.6	1.3	1.4
	N_∞ (SE < 0,3)	1.1	1.2	1.1	1.3

Seasonal patterns

Environmental variables. In January 1997 seawater temperatures dropped below zero and ice covered the whole beach area, which is exceptional for the Southern Bight. Maximum values of several variables were reported during winter (Figure 2, Appendix IA): wind speed (15-20 knots), turbidity (774±438 ftu), salinity (34±0 psu) and ammonia (399±262 µg/l). The latter peaking again during early summer of 1997 (473±152 µg/l), together with wave height (±75 cm), water temperature (21,3±0.4 °C) and chlorophyll-*a* (54±31 µg/l).

Diversity. Eleven species were recorded in all 4 stations, but several species were found at 1 station only (Table 3). Both the total and average number of species per station (Table 3) was slightly higher at the west coast (Oo and Lo) compared to the eastern sites (We and –especially- Kn). Other Hill numbers indicated a low evenness in Oo. In all stations diversity seemed to be higher in 1996 than in 1997 (Figure 3). N_0 was generally higher during the summer-autumn period (> 8). *Crangon crangon* dominated all stations with yearly averages of more than 95% of the total catch (Table 4). If this species is excluded, *Pleuronectes platessa* represented ±20% or more of the average community per station (12% in Oo), as did *Carcinus maenas* in Lo and Kn (> 5% in the other stations). Clupeids were also important in all 4 stations (> 30% in Oo and Kn and > 10% in Lo and We).

Multivariate analyses. Catch densities of all species are presented in Appendix 5A. CA, TWINSPAN and cluster analyses revealed clear seasonal patterns within each site when the stations were treated separately (extremely deviating samples were excluded from the

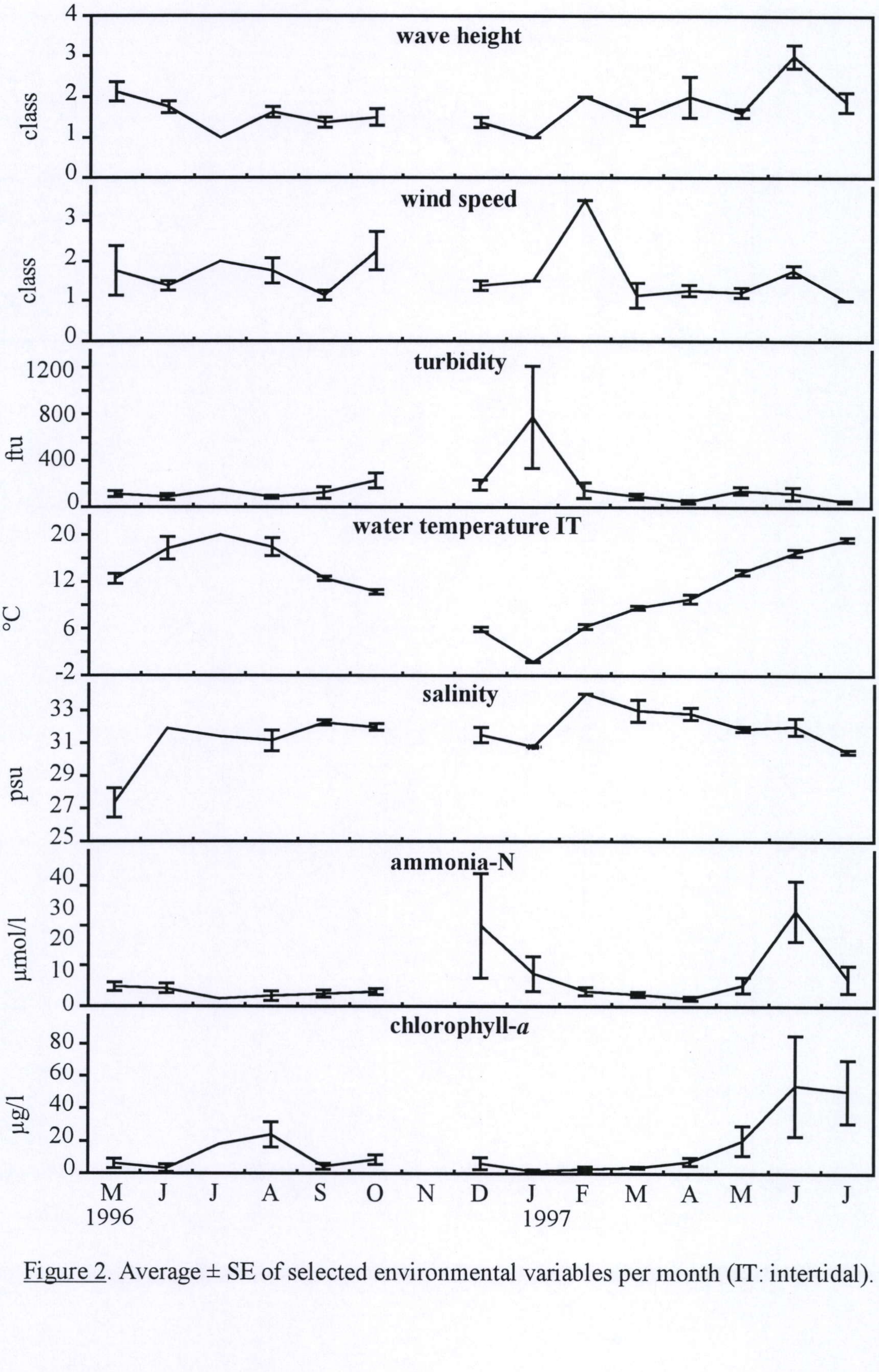

Figure 2. Average ± SE of selected environmental variables per month (IT: intertidal).

analyses). However, variation within these gradients suggests the influence of other factors on community structure. Stable clusters formed by these analyses are indicated as TWIN groups in Figure 4.

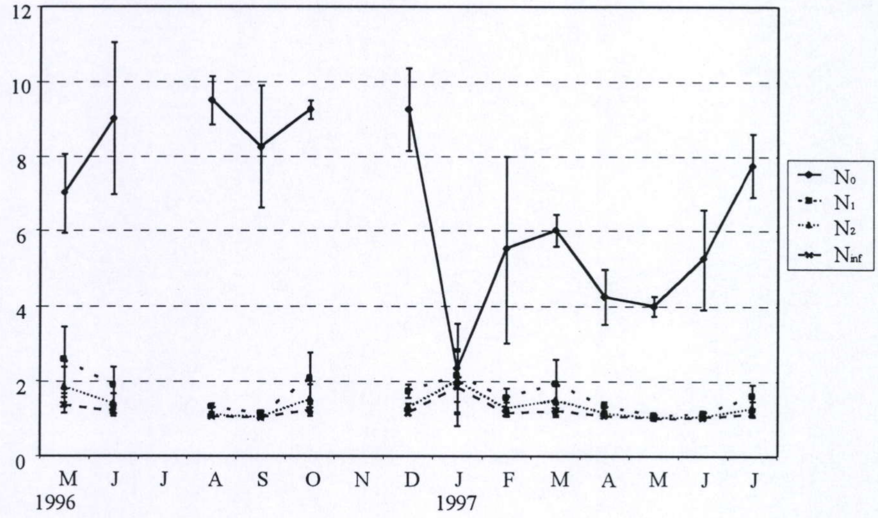

Figure 3. Average Hill numbers (± SE) per month.

Table 4. Relative species composition per station.

	Oo		Lo		We		Kn
Crangon crangon	95.2		95.9		96.7		95.5
Without *C. crangon*:							
Clupeidae species	32.4	*Carcinus maenas*	21.4	*C. harengus*	30.7	*C. maenas*	33.2
Liocarcinus holsatus	13.6	*P. platessa*	20.2	*P. platessa*	27.8	*S. sprattus*	25.6
Pleuronectes platessa	11.5	*Clupea harengus*	13.7	*S. sprattus*	9.5	*P. platessa*	19.4
Sprattus sprattus	9.6	*P. minutus*	9.6	*L. holsatus*	7.8	*L. holsatus*	8.1
Philocheras trispinos	6.1	*L. holsatus*	7.3	*P. minutus*	7.6	*C. harengus*	4.8
Pomatoschistus minut	5.7	Brachyura species	3.6	*C. maenas*	6.2	*P. minutus*	2.5
Pomatoschistus lozan	4.0	*P. lozanoi*	3.3	Brachyura species	1.9	*P. microps*	1.4
Solea solea	3.8	*P. latipes*	2.8	*P. lozanoi*	1.9	*S. solea*	1.3
Syngnathus rostellatu	3.5	*Zoarces viviparus*	2.3	*Ciliata mustela*	1.6	*S. rhombus*	1.2
Portumnus latipes	2.7	*Scophthalmus rhomb*	2.0	*Dicentrarchus labrax*	1.2	Clupeidae species	0.4
Pomatoschistus micr	2.0	*Echiichthys vipera*	1.9	*P. latipes*	1.1	Brachyura species	0.4
others	5.0	others	11.9	others	2.8	others	1.6

In total 7 out of 19 environmental variables were retained after exclusion of correlated variables (Table 5). Temperature and wind speed (and correlated variables) were indicated as important factors for all sites (wind speed not in We). Salinity and median grain size were selected in 2 stations and chlorophyll-*a*, turbidity and wave height were important each in 1 station. In the subsequent CCA's, the same gradients as found by the CA could be found for 2 of the 4 sites (Oo and We), in Lo it was less clear and in Kn a totally different pattern was found (Figure 5). Eigenvalues (first axes never exceeded 0.3) and percentage variation explained by the variables (first two axes between 20 and 40%) were rather low. Temperature and primary production might have masked the effect of other (e.g. hydrodynamic) variables.

Their influence was removed by treating them as covariables, which resulted more or less in the same patterns as in the former CA's. This indicates that the remaining variables, especially wind speed, did have an additional structuring effect on the data.

Table 5. Selected and excluded environmental variables (Spearman Rank correlations only shown if p<0,05 and R>0,5) and influence of these selected variables on density values (multiple regression analyses, the adjusted R² (R²adj) is included for each combination of variables selected by the model) (IT: intertidal, ST: shallow subtidal).

Excluded variables	**Selected variables**							
	water temperature IT	chlorophyll-*a*	salinity	turbidity	wave height	wind speed	ammonia-N	
water temperature ST		*						
oxygen content	*				*			
median grain size			*					
wind direction	*							
current speed			*					
POC	*							
organic matter							*	
oxidized nitrogen-N	*						*	
phosphate-P							*	
silicium	*						*	
chlorophyll-*c*		*						
fucoxanthine		*						
								R²adj
Total density	*							0.15
Total density without *C. crangon*	*		*		*	*		0.40

As maximum 14 observations were available per site, stepwise multiple regression analyses could only be performed on the total dataset, and not for each site separately (Table 5). Only significant ($p<0.05$) variables were retained in the model. Salinity, temperature, wind speed and wave height were able to predict 40% of the temporal variability of the total catch density if *C. crangon* was excluded. However, when *C. crangon* was included, only water temperature was selected, suggesting that 15% of the variability associated with monthly fluctuations in the total catch density in the surf zone could be predicted by this variable.

Species associations. Separation of the species per station by TWINSPAN also showed a clear seasonal pattern (Figure 6). Species could be grouped according to their appearance or presence in the surf zone during spring, summer-autumn or winter. Furthermore, a distinction was made between the resident species and the remaining migrant and sporadic species.

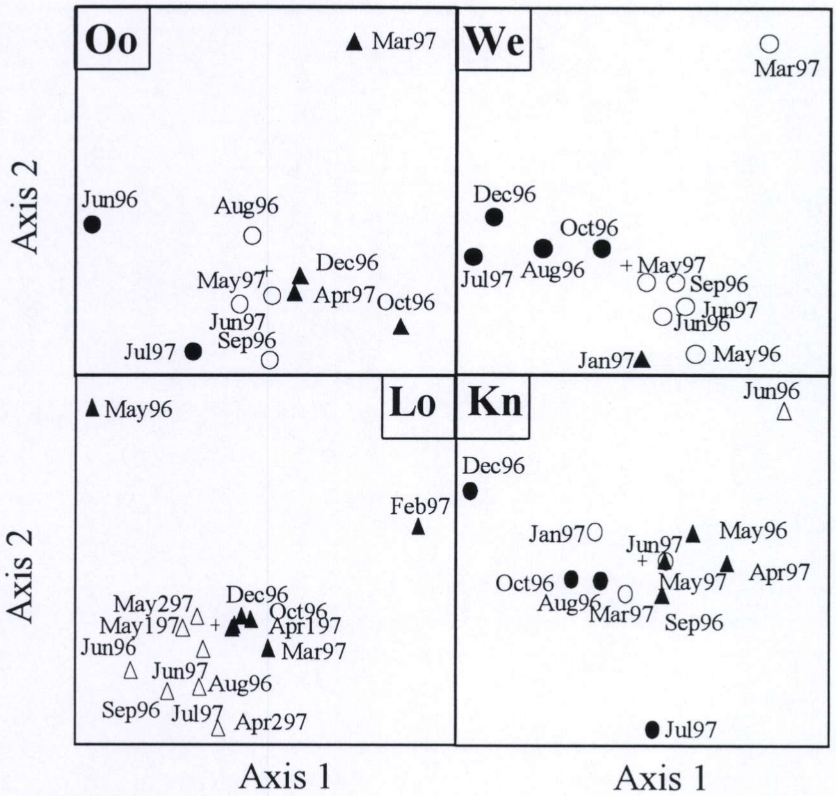

Figure 4. Sample plots of the final CA's per station (see text) with indication of TWIN groups. Each axis is scaled in proportion to the longest axes.

DISCUSSION

Catch efficiency

Since only one haul was made at each sampling occasion, no indication can be given of the variation likely to be encountered between trawls on the same beach. Furthermore, the ability of the catch data to accurately describe the inshore fish and macrocrustacean assemblages is based upon the assumption that the 2m-beam trawl is efficient at sampling the small, demersal species. The catch density and the species richness will be a function of their distribution with depth and substratum type, their ability to avoid the gear, the mesh-size selectivity, and many other local conditions such as water temperature and turbidity (Kuipers et al. 1992). Since the efficiency almost certainly varies with both size and species and because of the harsh sampling environment, the reported densities and species richness are certainly underestimated. In total 35 species were encountered, but the number of species found per site varied around 20. Although there are few comparable studies, survey duration has been recognised as a confounding factor in such comparisons (Ross 1983) as has the influence of depth on species abundance and distribution (Gibson 1973, Riley et al. 1981). Still, Poxton (1992) also estimated the number of species caught by trawl on Scottish beaches to be around 20. In the North Se, fish communities with 15-20 species are common (Rogers et al. 1998). They noted the lowest diversity in shallow and gently shelving areas with a uniform sandy substrate. Since in the present study, all samples in the present study were taken during the day and at the same tidal event (ebb/neap tide), diel and/or tidal variations in species abundance and richness are not considered.

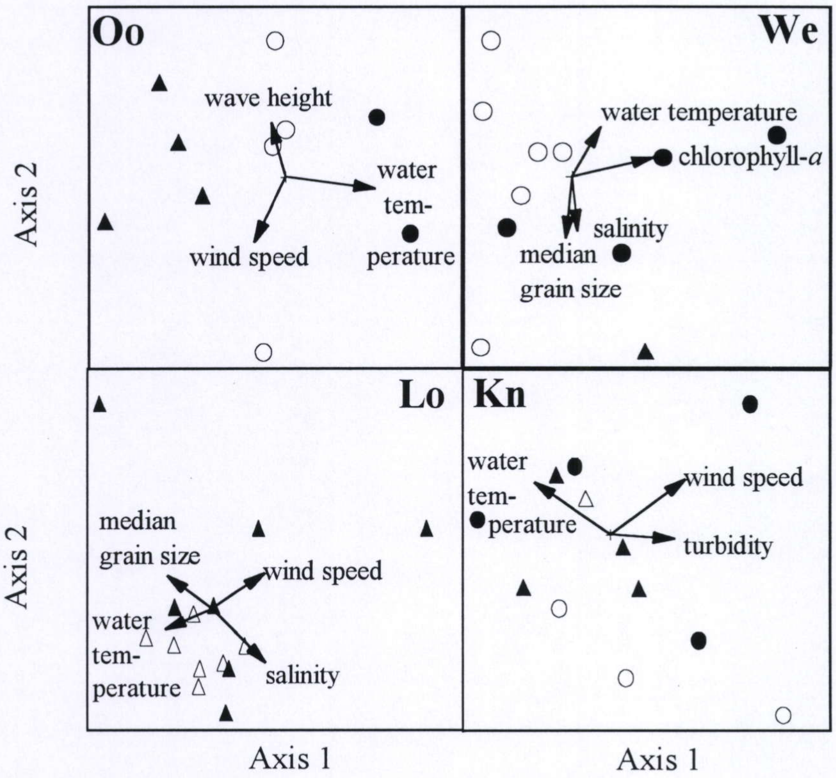

Figure 5. Sample plots of the final CCA's per station (see text) with indication of TWIN groups. Each axis is scaled in proportion to the longest axes.

'Residential' status of species abundance

Resident status. As in most shallow water communities, a few species are dominant both in terms of numbers and biomass (Allen & Horn 1975). In the Belgian surf zones, the brown shrimp *Crangon crangon* dominated most samples (> 80%). This crustacean species, together with the shore crab *Carcinus maenas*, are both ubiquitous members of the larger motile epifauna on northern European beaches (see Gibson et al. 1993). All 5 resident fish species in our study (juvenile plaice *Pleuronectes platessa*, the gobies *Pomatoschistus minutus* and *P. lozanoi* and the clupeids herring *Clupea harengus* and sprat *Sprattus sprattus*) have already been recognised as common residents in surf zones of sandy beaches by many authors (Miller 1986, Gibson et al. 1993, 1996, Wennhage & Pihl 1994 and references therein, Hayward & Ryland 1996, Rogers & Millner 1996). In the present study, plaice, herring and sprat were exclusively caught as juveniles. The other fish and crustacean residents probably spend large parts of their life cycle in the surf zone, since juveniles as well as adults were found. Indeed, hyperbenthic studies in the same area (Beyst et al. in press a), recorded larval as well as postlarval and juvenile *C. crangon*, *C. maenas* and gobies.

Among the 'migrant' species of the Belgian beaches, some apparently move to deeper waters as water temperature drops below a critical value (e.g. the crabs *Liocarcinus holsatus* and *Cancer pagurus* and the weever *Echiichthys vipera*). Similarly, the estuarine three-spined stickleback *Gasterosteus aculeatus* migrates to the sea (Nijssen & De Groot 1987), as it was found only in Lo, near the mouth of the IJzer estuary in February. Many juvenile marine fishes use the Westerschelde estuary as a nursery ground (e.g. De Veen et al. 1979, Cattrijsse et al. 1994, Hostens 2000). In the present study, some of these species were found during well-defined periods in the surf zone: dab *Limanda limanda* between September and December, turbot *Scophthalmus maximus* only in September and bass *Dicentrarchus labrax* mainly in December. They may use the surf zone as a transient area when they migrate from the estuary to the open sea (or vice versa). Other species were found more sporadically during the year (e.g. sole *Solea solea*) or during longer periods (brill *Scophthalmus rhombus*). Some species may possibly enter the surf zone to breed, since only (gravid) adult individuals were found and they only occurred during their breeding season. The shrimp *Philocheras trispinosus*, for example, was found between May and August and is known to breed mainly from March until September (Smaldon 1979).

Seasonal patterns. Catch densities and numbers of fish species varied considerably between samples and fluctuations in abundance at the different sites were not in phase with one another. Few temporal studies deal with more than one site, but comparable patterns were found by Clark et al. (1996b). However in the present study, when the stations were treated as separate communities, clear seasonal patterns could be observed. Although the highest number of species (and catch density) was found during summer-autumn, a clear dominance of *Crangon crangon* resulted in a low evenness. The variation in the crustacean community largely reflects the variability in numbers of the single dominant species *C. crangon*, whose seasonal migrations are well documented, especially for estuarine situations (e.g. Lloyd & Younge 1947, Boddeke 1976, Henderson et al. 1990). Several species absent in winter appeared again in spring. The abundance of intertidal fish species is generally highest in late spring and summer due to the influx of juveniles of both resident and transient species following their breeding seasons (Gibson & Yoshiyama 1999). In most temperate regions, an offshore migration of fish species in late summer and autumn is observed, which results in a decline of both density and diversity in the community (Gibson 1999). Also *Carcinus maenas* shows seasonal differences in behaviour that affects the numbers found intertidally, but there is no complete offshore migration (Naylor 1962, Klein Breteler 1976).

Interannual variation. Diversity was lower during 1997 when compared with the corresponding months in 1996. The pattern in total density and diversity seems to be approximately 1 month later in 1997. Most likely, the extreme winter conditions in January 1997 are responsible for this shift. The seasonal movement of many species allows them to avoid adverse conditions in winter (Gibson 1999). Because food webs of surf zone systems tend to be based on phytoplankton and suspended organic detritus (McLachlan et al. 1981, Lewin & Schaefer 1983), food might be a limiting factor as plankton productivity declines during the colder months (Ross et al. 1987).

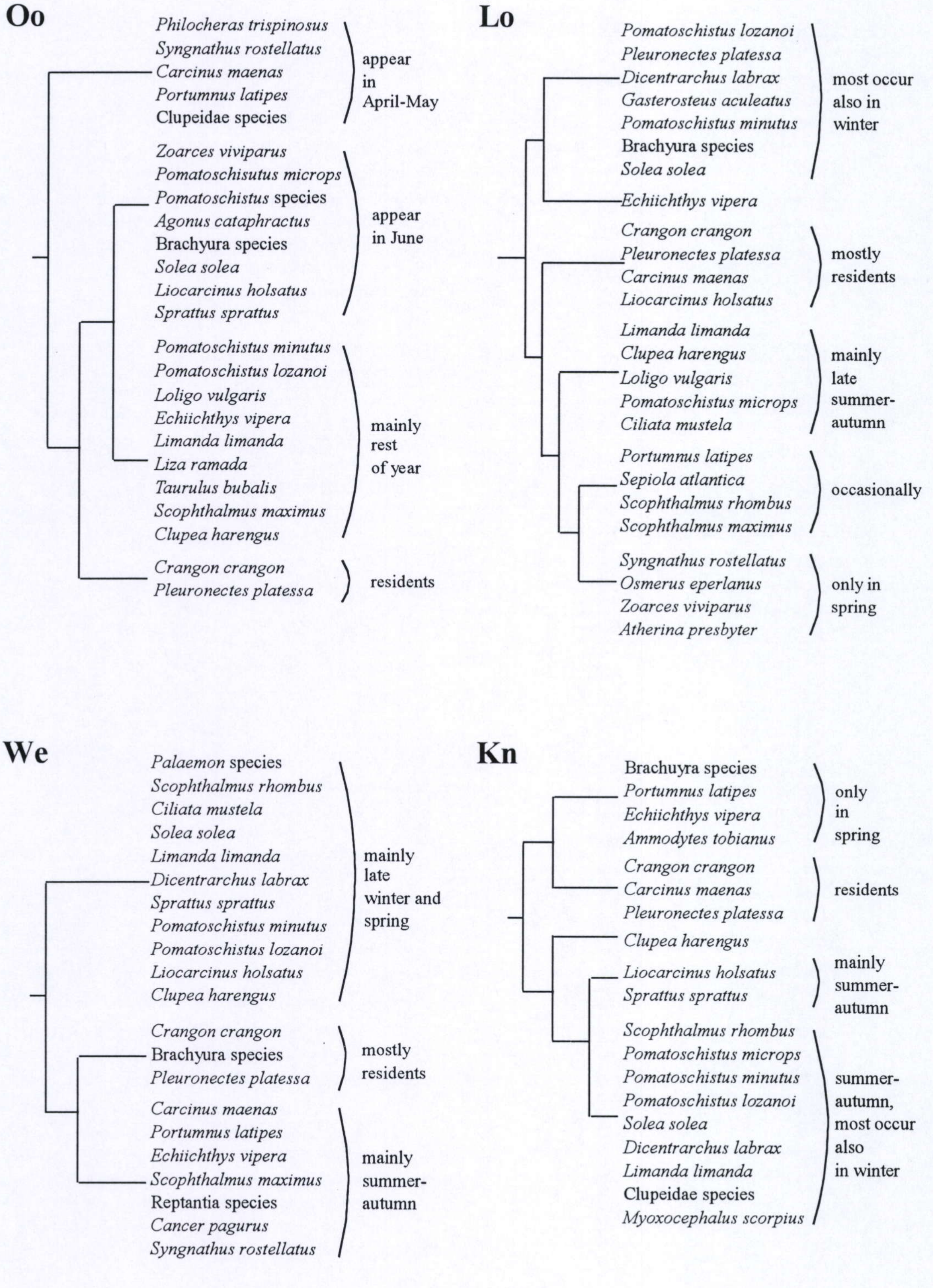

Figure 6. Grouping of species per station by TWINSPAN.

The shift in total density and diversity was not reflected by the species composition (except in Oo). Jaccard's similarity coefficients (based on presence/absence data) between the corresponding months of both years were higher or equal to that of the subsequent months (Table 6). The reappearance of organisms at Oo might be slower due to the sand bank system in front of the beach. The exact species composition of the community is unpredictable and gives raise to relatively low species similarities among years (Gibson et al. 1993). Seasonal and annual fluctuations in species richness and composition seem to be typical for many fish communities of sandy beaches (e.g. Modde & Ross 1981, Reina-Hervas & Serrano 1987, Ross et al. 1987, Brown & McLachlan 1991, Hook 1991).

Table 6. Jaccard's similarity coefficient between the overlapping months of 1996 and 1997 per station.

		May'97	June'97	July'97
Oo	May'96	0.4	0.5	-
	June'96	-	0.3	0.6
Lo	May'96	0.5	0.4	-
	June'96	-	0.4	0.4
We	May'96	0.5	0.3	-
	June'96	-	0.4	0.4
Kn	May'96	0.8	0.8	-
	June'96	-	0.5	0.4

Influencing factors

Temporal variations and their controlling factors in surf zone assemblages are hierarchical, ranging from climatic events that influence inter-annual variations in year class strength, through reproductive and feeding movements that result in seasonal patterns in occurrence and abundance, to short-term fluctuations in physico-chemical factors such as wave height, salinity, temperature and wind speed that influence point abundance (Ross et al. 1987). In the present study the relationship between temporal variations in the epibenthic data and environmental variables was rather weak, so the influence of other, not measured or hidden correlated variables cannot be ignored as they can control or at least strongly modify the measured variables (Clark et al. 1996a). Furthermore, correlations found between community parameters and environmental variables do not necessarily reflect causal relationships. Factors like shoaling behaviour (Lasiak 1982, Ross et al. 1987, Gibson et al. 1993) and variations in netting efficiency (Hunter & Wisby 1964, Lyons 1986, Pierce et al. 1990) can increase the difficulty of interpreting the data.

Still, the multivariate analsyes confirm that, water temperature and salinity are both important regulating factors in surf zone communities (e.g. Anderson et al. 1977, Whitfield et al. 1981, Lazzari et al. 1999). However, although no sampling was performed during extreme weather conditions, hydrodynamic variables such as wind speed and wave height might have influenced community structure in the present study. All environmental variables were measured at the time of sampling. The influences of these factors prior to sampling or the duration over which these variables were active were not included in the analyses. This possibly explains the low correlation between wind speed and wave height. A positive correlation with wind speed was found for total densities (excluding *Crangon crangon*). According to Lasiak (1982, 1984b), at some sites wind might be a primary structuring abiotic variable in correlation with fish abundance, as it has the ability to influence wave action, turbidity and localised water temperature. Gibson et al. (1993) however, found no relationship between fish abundance and wind strength and direction on a Scottish sandy beach. In the

Horn Island surf zone, the number of fishes increased through the interaction of wind direction (i.e. inshore winds) with temperature (Modde & Ross 1981).

A negative correlation was found between total epibenthic catch density (excluding *Crangon crangon*) and wave height. However, increasing wave height might also affect sampling efficiency, which may thus not be neglected. The degree of exposure to wave action is also generally considered to be one of the main structuring factors of invertebrate and fish communities frequenting sandy beach environments (Clark 1997 and ref. therein). Clark (1997) found an increased overall teleost abundance (mean density) as wave exposure decreased. Highest species richness and diversity and lowest dominance were recorded at intermediate levels of exposure. These trends were attributed primarily to the availability and abundance of suitable food resources, and to physical disturbance introduced by breaking waves.

Strong hydrodynamic circumstances not only influence variations in community structure, but can be energetically expensive. For example, juvenile plaice is less abundant at the Belgian coast than in the surrounding areas of NW Europe (Rogers et al. 1998), but densities are still higher in the surf zone (present study), compared to the adjacent shallow subtidal area of the Belgian coast (< 0.2 ind./100m² in autumn) (Cattrijsse, unpublished data). However, growth of the 0-group seems to be limited compared to the optimal growth model of Fonds (1979) (Figure 7). The observed growth presented here must be interpreted with care as larger fish move offshore throughout the season and fishing has only been done at a depth of 1m. The increase in the mean size of the population might therefore be underestimated. Still, stomach fullness indices (FI, Berg 1979) were rather low during the summer of 1996 (FI < 0.5, Figure 8). Food limitation seems unlikely, since their favorite prey organisms are highly abundant compared to other sandy beach ecosystems (Beyst et al. 1999a, Beyst et al.in press c, Degraer et al. 1999). Probably, young plaice spend too much time and energy in the highly dynamic Belgian surf zone. Currents, general turbulence and wave action all have the potential to reduce growth rate by decreasing food intake below that possible in calm waters (Gibson 1994). Plaice indeed prefers sheltered areas (Riley et al. 1981) in contrast with other species like brill *Scophthalmus rhombus* and turbot *Scophthalmus maximus*, which were found to feed intensively in the Belgian surf zone (Beyst et al. 1999a).

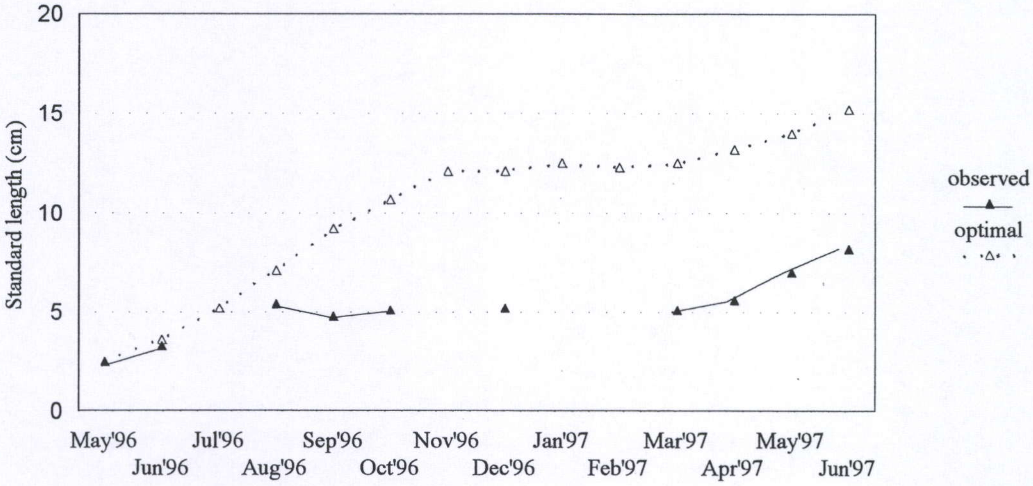

Figure 7.Observed and optimal growth (model of Fonds 1979) of juvenile plaice in the Belgian surf zone.

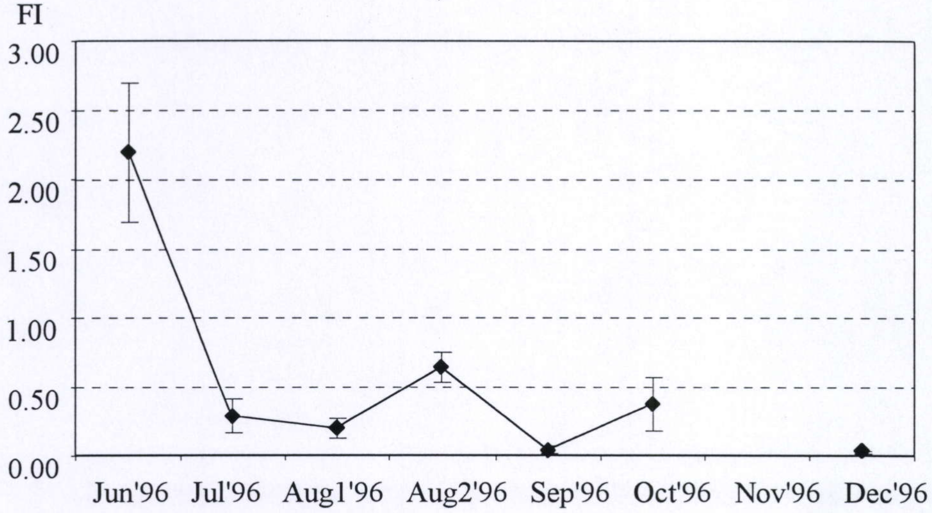

Figure 8. Fullness Index (FI) (±SE) per month of juvenile plaice.

CONCLUSIONS

Notwithstanding the harsh hydrodynamic conditions, the surf zone of Belgian sandy beaches seems to be used intensively by a number of epibenthic macro-crustaceans and demersal fish species. As mainly juvenile fishes are present, the surf zone of the Belgian sandy beaches can act as a nursery for longer (e.g. plaice *Pleuronectes platessa*) or shorter (e.g. brill *Scophthalmus rhombus*) periods. This is in common with sandy beaches in many parts of the world (Brown & McLachlan 1991, Hook 1991, Gibson et al. 1993). However, its nursery function should be studied in more detail, since the highly dynamic circumstances and more specifically wave height and wind speed might be important structuring factors for the epibenthic communities. They might cause severe stress for at least some species. The surf zone of Belgian sandy beaches also functions as a transient area to other nurseries (e.g. bass *Dicentrarchus labrax*) or between a nursery and the true marine environment (e.g. dab *Limanda limanda*).

Chapter II
Part B

Factors influencing the spatial variation in fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium

Results presented in:

Bregje Beyst, Kris Hostens & Jan Mees (submitted). Factors influencing the spatial variation in fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium.

Acknowledgements

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Surf zone and intertidal area at an east-coast site

ABSTRACT

This study comprises a first inventarisation of fish and epibenthic macrocrustaceans of the surf zones of sandy beaches along the Belgian coast. The surf zones were sampled intensively with a 2m-beam trawl in April-May 1996 (12 stations). In total 26 species were recorded belonging to caridean shrimps (4), brachyuran crabs (5), cephalopods (1) and fish (16). The brown shrimp *Crangon crangon* dominated almost all samples (>80%). Total densities exceeded several times 250 ind./100m², and 10 ind./100m² if *C. crangon* was excluded. An east-west distinction as found in other (epi)benthic studies in deeper waters of the Belgian coast, was not found in the surf zone during this study. Spatial variation was mainly correlated with local characteristics such as turbidity of the water and the morphodynamic features of both the beach and the adjacent subtidal area. Although these factors may have influenced sampling efficiency, further investigation is needed. The mobile and relatively homogenous nature of the substratum on sandy shores means that few refuges from predators are available thus protection due to higher turbidity might be important. Also, the protection that organisms gain by occurring on flat, shallow beaches (less predation, less wave exposure) is probably outweighed by increased fluctuations in environmental variables such as salinity and higher risks of retention on the beach by ebb-tide, resulting in a higher diversity at intermediate sites.

INTRODUCTION

Although several aspects of the ecology of surf zone fish (e.g. Macer 1967, Creutzberg & Fonds 1971, Reina-Hervas & Serrano 1987, Gibson et al. 1996) and macrocrustaceans (e.g. Salvat 1962, Beukema 1976, Dexter 1990, Gibson et al. 1993) have received considerable attention, comparatively few studies have dealt with spatial variability in the composition and abundance of epibenthic surf zone assemblages of sandy beaches (Clark et al. 1996a). Despite the structurally homogeneous environment, several authors suggest that fluctuations in physical variables (e.g. wave exposure, sediment particle size and turbidity) have a strong influence on the relative abundance of certain species and may alter the composition and species richness (Hillman et al. 1977, Blaber & Blaber 1980, Pihl 1986, Tallmark & Evans 1986, Romer 1990, Pihl & van der Veer 1992, Clark et al. 1996a). Adjacent subtidal habitat heterogeneity and the presence of rocky substrates and estuarine habitats may also contribute significantly to spatial variability (Robertson & Lenanton 1984, Romer & McLachlan 1986, Peters & Nelson 1987, Wright 1989, Romer 1990).

Up to now, no information is available of epibenthic communities of the Belgian surf zones. This is in contrast to the shallow subtidal epibenthic communities of the Belgian coast. Within these communities clear east-west differences exist (Cattrijsse in press). Highest diversity and total density is found at the west coast compared to the east side. The negative influence of the polluted water of the Westerschelde estuary causes the eastern coast to be 'poorer' both in terms of diversity and abundance as compared to the western end of the Belgian coast (Cattrijsse & Vincx in press). In this paper, after a first spatial inventarisation, the hypotheses that these east-west differences also exist in the surf zone assemblages, will be evaluated. The aim of this study is therefore to investigate if spatial heterogeneity along the coastline results in the presence of different epibenthic communities and to determine which factors influence the occurrence of these communities.

MATERIAL AND METHODS

Study area

The study area comprises the surf zone of sandy beaches of the Belgian coast (Figure 1), which is situated in the Southern Bight of the North Sea. One additional sample was taken at the coast of northern France. The Belgian coastline is 67 km long and is characterized by built-on dykes that are interrupted by dune areas and sporadic groins on the beaches. In some parts these groins are less than 300 m apart, while elsewhere they are absent for several kilometers. Three major harbours, Zeebrugge, Oostende and Nieuwpoort are situated in the eastern, middle and western part of the coast respectively. A smaller harbour is present in Blankenberge. The mouth of the IJzer estuary is situated in the western part, while the large Westerschelde estuary opens just over the Belgian-Dutch border. A strong semi-diurnal tidal regime and a net tidal current running northeast parallel to the coastline are characteristic. All beaches could be classified into 2 types according to the morphodynamic classification scheme of Masselink & Short (1993): 7 low-tide bar/rip (LTBR) and 6 ultra-dissipative (UD) beaches were studied. The main characteristics of each site are given in Table 1.

Sampling

A sampling campaign in April-May 1996 covered 11 stations along the Belgian coast and 1 additional station in France (Bray-Dunes). All samples were taken with a 2m-beam trawl during daytime and around ebb. The fishing net was 3 m long, had a mesh size of 5x5 mm and was equipped with a tickler-chain in the ground rope. It was pulled by 2 persons in the surf zone parallel to the coastline at a depth of approximately 1m. One haul lasted 15 minutes and covered a distance of 450-500m. Due to practical reasons, only one haul was taken at each occasion. When groins were present, the net was lifted over the obstacle. The catch was anaesthetised in a dilute solution of benzocaine (ethylamino-4-benzoate) and then preserved in an 8% formalin solution. In the laboratory, all animals were identified to species level, measured and counted.

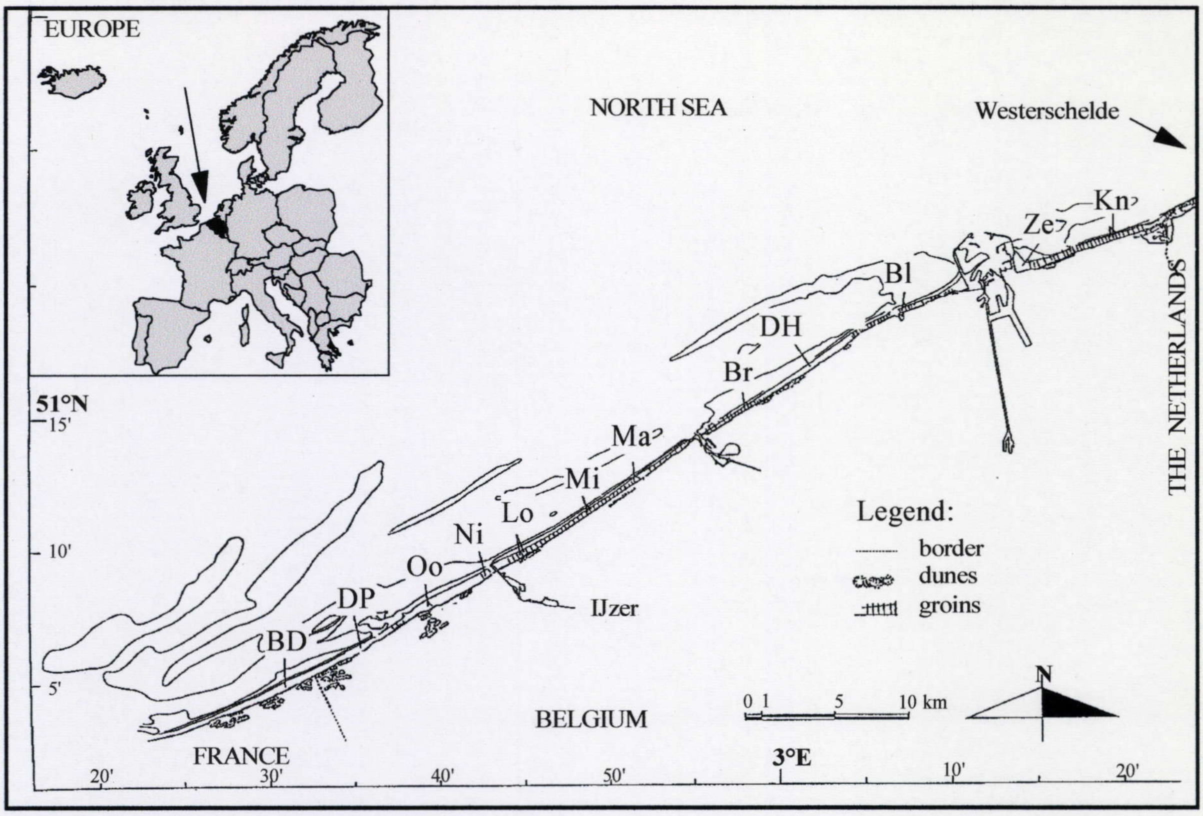


Figure 1. Study area with indication of sampling sites.

Table 1. Main characteristics of the sandy beaches studied (D: mean high tide beach sediment grain size; MSR: mean spring tide range, IT: intertidal, ST: first 300m of shallow subtidal, UD: ultra-dissipative, LTBR: low tide bar/rip).

Site	**D (µm)**	**MSR (m)**	**beach type**	**beach width (m)**	**slope IT**	**slope ST**	**groins**	**bar/rip IT**	**bar/rip ST**
BD	214	5.03	UD	348	1:79	1:71		+	+
DP	246	4.97	UD	317	1:118	1:45		+	
Oo	269	4.92	LTBR	390	1:128	1:210		+	+
Ni	203	4.86	UD	275	1:70	1:117			
Lo	321	4.78	LTBR	180	1:55	1:108	+	+	+
Mi	268	4.74	LTBR	226	1:44	1:73	+		+
Ma	285	4.68	LTBR	214	1:35	1:49	+		+
Br	243	4.57	UD	220	1:49	1:75	+	+	+
DH	333	4.51	LTBR	232	1:61	1:155		+	+
Bl	236	4.38	UD	195	1:54	1:86	+		+
Ze	242	4.34	UD	225	1:79	1:216			
Kn	391	4.28	LTBR	174	1:57	1:41	+	+	

Environmental variables

After each haul, portable conductivity and oximeters (WTW) were used for *in situ* measurements of water temperature, salinity and oxygen content. Turbidity was measured with a portable microprocessor turbidity meter (HANNA). Water samples were further processed in the laboratory, where they were filtered through Whatman GF/F filters prior to analyses. For the pigments (chlorophyll-*a* and *c* and fucoxanthine), an immediate extraction with acetone (90%) was performed prior to a chromatography, with a Gilson high-performance liquid chromatography chain, following a slightly modified method of Mantoura & Llewellyn (1983). For particulate organic carbon (POC) an automatic CN-analyser (Carlo Erba) was used. The concentrations of nitrate plus nitrite, phosphate, ammonia and silicium were measured with an automatic chain (SAN^{plus} segmented flow analyser, SKALAR). From the sediment sample, median grain size was determined in the laboratory with a Coulter Counter LS particle size analyser. For the measurement of organic matter within the sediment (OM) samples were dried at 110°C for 2 hours and subsequently burned at 540°C for another 2 hours. Beach width was measured from the water line at ebb tide to the high-water mark. Hydrodynamic variables (wave height, wind speed and direction) at the moment of sampling and slope of the beaches (beach profiles) were obtained from the Coastal Waterways' Division of the Department of Environment and Infrastructure (Ministry of the Flemish Community). Wave height is expressed as the significant wave height H33: the average crest-to-trough height of the 33% highest waves in a wave record (15 minutes) (Anonymous 1996). Wind speed is given as the average speed and wind direction as the scalar average of the measured directions, over a period of 10 minutes (Gilhousen 1987).

Data treatment

Catch densities are expressed as number of individuals per 100m². Small sized crustaceans (e.g. isopods, mysids), early postlarval fish (e.g. clupeids), jellyfish and sedentary animals (e.g. the starfish *Asterias rubens*) were excluded from further analyses. Spatial patterns were examined with the following multivariate statistical techniques: Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) (Ter Braak 1986, 1988), Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979) and cluster analysis using group average sorting and the Bray-Curtis dissimilarity index (Bray & Curtis 1957). Non-parametric Multi-Response Permutation Procedures (MRPP) were used for testing multivariate differences among pre-defined groups (Mielke et al. 1976, Whaley 1983, Zimmerman et al. 1995). A fourth root transformation (Field et al. 1982) was performed on the abundance data prior to the analyses. Differences between the obtained communities were assessed using the non-parametric Kruskall-Wallis Test (Sokal & Rohlf 1981).

In order to assess the importance of the measured variables in structuring the communities, the forward selection option together with the Monte Carlo permutation Test in the Canoco package were used prior to CCA's. If variables were significantly correlated (Spearman Rank correlation's, $p< 0.05$), only one of them was retained for further analyses. Since wind direction is a circular variable, it was transformed to a linear variable by using the cosine of the angle that the wind made on a set of axes aligned perpendicularly onshore at each site (Clark et al. 1996b). Offshore winds at each site were allocated the greatest values (+1), onshore winds the lowest (-1), while winds with a cross-shore component from either direction received scores between +0,9 and -0,9. For wind speed and wave height values are expressed into arbitrary classes ranging from 0 to 4, with class 4 indicating values of 20 knots and 100cm respectively.

RESULTS

Environmental variables

With exception of oxidized nitrogen concentrations, which were higher at the eastern stations, no clear geographical gradients in environmental variables were found along the coast (Table 2). However, variations in intertidal temperature and salinity were higher at the western side. The average water temperature and salinity of the surf zone were higher than in the adjacent subtidal habitat: 12±1 °C and 31±1 psu compared to 9±0,3 °C and 30±0,3 psu respectively. At all sampling occasions 33% of the waves was always lower than 50 cm and wind speed almost never exceeded 10 knots. Only at Ze 33% of the waves varied between 100 and 125 cm and wind speed varied between 15 and 20 knots.

Table 2. Environmental variables per site (dw: dry weight, IT: intertidal, ST: subtidal).

	BD	**DP**	**Oo**	**Ni**	**Lo**	**Mi**	**Ma**	**Br**	**DH**	**Bl**	**Ze**	**Kn**
33% wave height (cm)	25-50	25-50	25-50	25-50	25	25-50	0-25	0-25	25-50	25-50	00-12	25
wind speed (kn)	5-10	5	10	5-10	5-10	5-10	15	5	5-10	10	15-20	5-10
wind direction (°)	80	290	255	30	270	340	235	235	250	255	25	325
organic material of sediment (g/100g dw)	0.843	2.449	0.799	0.803	0.837	1.128	0.586	0.473	0.880	0.614	0.805	0.661
salinity IT (psu)	32.1	26.4	35.4	34.6	29.6	28.4	28.7	31.8	30.6	30.2	31.0	27.9
salinity ST (psu)	28.5	28.5	29.0	28.5	29.0	29.0	31.8	31.8	29.4	29.5	30.0	29.8
turbidity (ftu)	310	15	76	320	112	49	31	274	80	292	140	27
water temperature IT (°C)	9.5	12.5	14.0	18.0	12.0	12.0	12.5	12.0	11.5	10.0	10.0	14.0
water temperature ST (°C)	9.8	10.0	8.0	10.0	8.0	10.0	7.8	7.8	7.9	7.9	10.0	9.8
POC water column (%C)	0.4	2.3	2.7	3.6	5.2	2.2	4.0	3.9	3.0	5.6	4.6	1.9
oxidized nitrogen-N (µmol	0.591	0.000	0.616	1.009	0.141	0.000	0.527	12.665	10.575	14.446	15.318	3.829
ammonia-N (µmol/l)	2.821	0.190	8.214	2.537	1.980	0.705	46.000	3.852	14.579	2.509	4.591	1.464
phosphate-P (µmol/l)	0.794	0.462	0.569	0.496	0.746	0.429	0.256	0.223	1.298	0.306	0.339	0.543
silicium (µmol/l)	0.978	0.715	1.614	1.338	0.978	0.000	0.000	2.351	1.023	0.000	0.414	0.677
chlorophyll-*a* (µg/l)	48.65	8.38	20.09	23.32	12.88	13.48	72.51	50.07	49.97	25.76	21.58	5.43
chlorophyll-*c* (µg/l)	4.50	1.48	2.70	3.70	1.53	2.06	5.84	3.91	6.11	5.39	1.95	0.80
fucoxanthine (µg/l)	28.23	4.40	11.03	12.81	7.20	6.45	41.72	34.38	25.69	14.70	12.83	2.43
median grain size (low tide) (µm)	179	181	181	180	181	301	304	244	288	246	232	294

Species composition

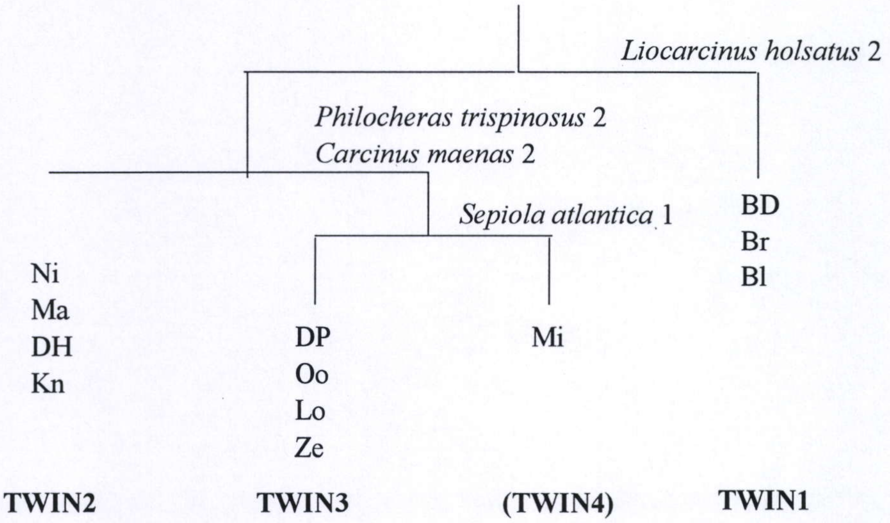
In total 26 species were recorded, belonging to caridean shrimps (4), brachyuran crabs (5), cephalopods (1) and fish (16) (Table 3, Appendix 5B). The number of species per sample varied between 4 and 12. The brown shrimp *Crangon crangon* dominated almost all samples (>80%). Total densities exceeded several times 250 ind. 100m^{-2}, and 10 ind. 100m^{-2} if *C. crangon* was excluded. Only the brown shrimp and plaice *Pleuronectes platessa* were found along the whole coast and 4 other species were present in more than half of the stations: the shrimp *Philocheras trispinosus*, the crabs *Carcinus maenas* and *Portumnus latipes* and the common goby *Pomatoschistus microps*. Several species were only caught in one station. Many juveniles were present and some species, such as plaice, were exclusively caught at this stage.

Table 3. Species list together with their stage, catch densities per station (ind./100m²) and total numbers caught (N) (* = < 1 ind./100m²).

Taxon		**Stage**	**Catch density per station**												**N**
			BD	DP	Oo	Ni	Lo	Mi	Ma	Br	DH	Bl	Ze	Kn	
Caridea	*Palaemon longirostris*	a										*			3
	Palaemon serratus	a							*			*			2
	Crangon crangon	a	130	153	248	67	262	482	82	95	63	508	69	29	19443
	Philocheras trispinosus	a		2	2		2	4		*		*	*	*	98
Brachyura	*Cancer pagurus*	a					*								1
	Liocarcinus holsatus	a	3		*			*		*		*			35
	Carcinus maenas	a	*	*			3	*		*		*	2	*	65
	Portumnus latipes	a		*	*		*	*		*	*	*	*		17
	Eriocheir sinensis	a					*								1
Cephalopoda	*Sepiola atlantica*	j						*							3
Pisces	*Clupea harengus*	j						*			*				4
	Sprattus sprattus	j+a				*		*	*	*	*	*			21
	Syngnathus rostellatus	j+a	*									*			6
	Agonus cataphractus	j								*		*			2
	Zoarces viviparus	a						*							1
	Echiichthys vipera	j+a	*												3
	Ammodytes tobianus	j+a				*	*				*			*	10
	Pomatoschistus lozanoi	j+a	9		*				*	11		*			182
	Pomatoschistus microps	j+a			*	*	*		*	*		1		*	19
	Pomatoschistus minutus	j+a	14	*	*					*					131
	Pomatoschistus species	j						*		*					3
	Scophthalmus rhombus	j							*		*			*	3
	Scophthalmus maximus	j	*												3
	Limanda limanda	j	*												1
	Pleuronectes flesus	j						*							1
	Pleuronectes platessa	j	6	*	2	3		*	15	*	*	*	4	*	287
	Solea solea	a	*												1
	Total catch density		160	160	250	70	270	490	100	110	60	510	80	30	

Multivariate analyses

Multivariate analyses divided the stations into 4 groups with TWIN4 being a single station group (only TWINSPAN depicted: Figure 2). If the single station group was excluded, MRPP was highly significant ($p < 0.001$), indicating that the 3 groups were significantly different. Total catch density, diversity and relative species composition differed substantially between the four communities (Table 4). The number of species and the densities of the brown shrimp *Crangon crangon*, the swimming crab *Liocarcinus holstatus*, Lozano's goby *Pomatoschistus lozanoi* and brill *Scophthalmus rhombus* differed significantly ($p < 0{,}05$) between the first three TWIN groups according to Kruskall-Wallis Tests: most being much higher in TWIN1 (and TWIN3 for *C. crangon*) and only *S. rhombus* being more abundant in TWIN2. TWIN4 was mainly characterised by a high number of species (12) and a high total catch density (489 ind./100m²). This division of stations did not reflect an east-west (or other) gradient along the coastline, nor could the absence or presence of groins or harbours directly explain the distinction.



Figuur 2. TWINSPAN dendrogram with indication of 'indicator species' and cutlevel (cutlevels used: 0, 0.6, 1.0, 2.0, 5.0).

Table 4. Main characteristics of TWIN groups (SE: standard error).

	TWIN1		TWIN2		TWIN3		TWIN4
Mean N0 (SE<1)	12		7		7		12
Mean total density ± SE	260±130		70±10		190±50		489
Mean total density without *Crangon crangon* ± SE	17±9		6±3		5±1		16
Relative community composition (%)							
C. crangon	93.4		90.8		97.4		98.6
Excluding *C. crangon* (%)							
Pomatoschistus lozanoi	39.1	*P. platessa*	76.2	*P. trispinosus*	33.9	*P. trispinosus*	52.5
Pomatoschistus minutus	27.0	*Sprattus sprattus*	7.6	*P. platessa*	30.5	*C. maenas*	11.5
Pleuronectes platessa	13.5	*Ammodytes tobianus*	4.2	*C. maenas*	24.9	*P. platessa*	9.8
Liocarcinus holsatus	7.4	Clupeidae species	3.5	*P. minutus*	3.4	*Sepiola atlantica*	4.9
Pomatoschistus microps	2.9	*Portumnus latipes*	3.0	*P. latipes*	2.8	Clupeidae species	4.9
Carcinus maenas	2.9	*P. microps*	1.8	*P. microps*	1.1	*Clupea harengus*	4.9
Syngnathus rostellatus	1.3	*Scophthalmus rhombus*	1.4	*Cancer pagurus*	0.6	*P. latipes*	3.3
Philocheras trispinosus	1.1	*P. trispinosus*	0.5	*L. holsatus*	0.6	*L. holsatus*	1.6
others	4.9	others	1.8	others	2.3	others	0.0

The forward selection option together with the Monte Carlo permutation Test in the Canoco package identified turbidity and to a lesser extent POC (and/or correlated variables) as only significant variables correlated with the variation in epibenthic community structure. Together, they could explain 31% of the variation present in this data set. Turbidity was correlated with intertidal salinity and POC with no other variables measured. Turbidity was higher in TWIN1 as compared to most other stations (Figure 3). Although separate variables such as slope and beach width could not explain the observed pattern, a combination of these factors might have been of some influence. Figure 4 shows the profiles of the sampled sites for the TWIN groups. TWIN1 contained only UD beaches with intermediate slopes (shallow subtidal slopes between 1:71 and 1:86), with bars and rips in the shallow subtidal (first 500m). TWIN2 on the other hand contained mainly LTBR beaches with a rather steep intertidal area (1:35 to 1:70). Both UD and LTBR beaches were present in TWIN3, but at most sites the intertidal area was wider than 225 m and the slopes remained rather flat (less than 3 m depth 400 m after the MLLWS level). In TWIN4 Mi had a rather steep intertidal (1:44) and a shallow subtidal area (1:73) with bars en rips. However, all these patterns were rather weak and must be interpreted with care.

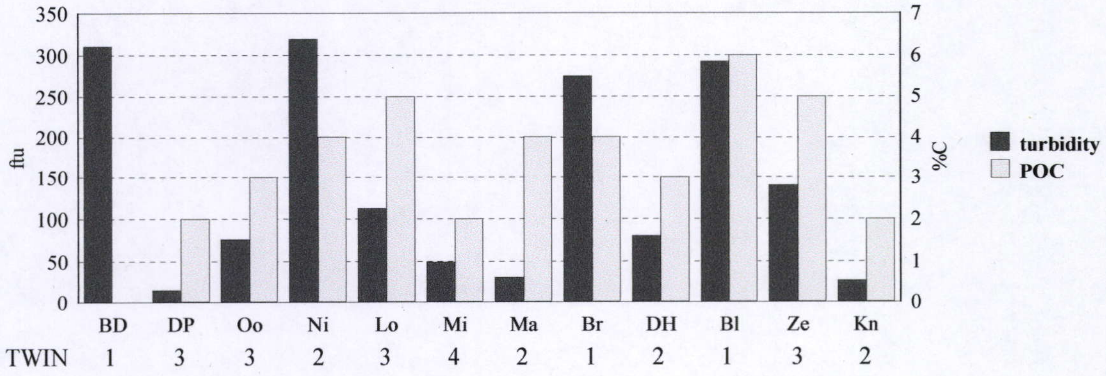


Figure 3. Turbidity (ftu) and POC (%C) per station with indication of TWIN groups.

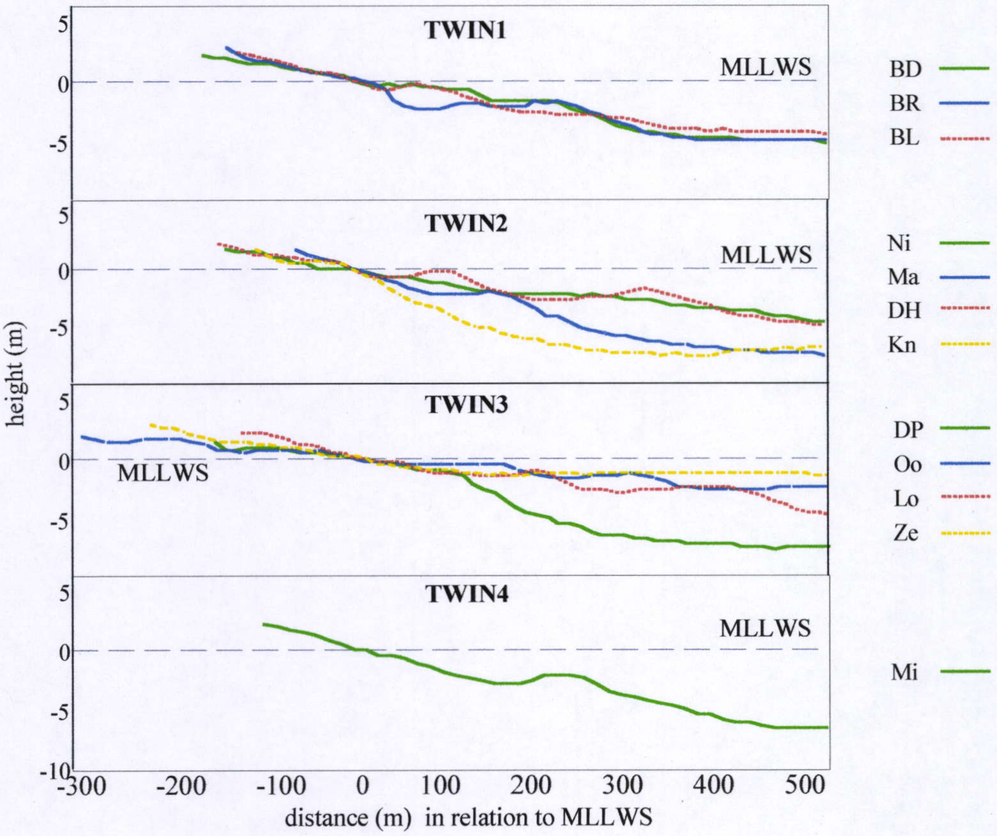


Figure 4. Site profiles per TWIN group (MLLWS: mean low water spring).

DISCUSSION

Three different communities could be distinguished. These appear discontinuously along the coastline. No east-west gradient along the coast was found. This is in contrast to earlier studies of the shallow subtidal areas (5-10 m depth): here a clear distinction could be made between the epibenthic communities of the east and west coasts respectively (Cattrijsse & Vincx in press). The negative influence of the polluted water of the Westerschelde estuary causes the eastern coast to be 'poorer' both in terms of diversity and abundance as compared to the western end of the Belgian coast. Due to several factors such as run-off from the beach, presence of groins *etc.*, the intertidal area is less homogenous than deeper water masses. This was also reflected in the environmental variables measured: no geographical gradients could be detected. Each beach site is probably highly influenced by local characteristics, which might be reflected in the variation in epibenthic community structure. Replicate sampling in future research might be necessary to support these results.

Few studies deal with the effects of exposure on surf zone fauna, and in general only the intertidal slope is considered (e.g. Clark 1997). Local characteristics of the beaches might however be of major importance. In the present study, highest diversity and high densities were found at sites with intermediate profiles (if both the intertidal and shallow subtidal are considered). High densities were also observed on sites with long flat slopes, but diversity was much lower there. Sites with steep intertidal areas were characterised by low densities and low diversity. While steep slopes increase wave exposure (long-term effect), flat slopes can increase the local fluctuations of several environmental variables, such as water temperature and salinity. A decrease in wave height might result in higher catch efficiency, but with one exception (Ze), weather and wave conditions at the moments of sampling (short-term effect) were comparable and thus not likely to be responsible for these results.

Turbidity (and correlated variables) was identified as an important structuring environmental variable. Together with POC it could explain 31% of the total variation within the catch density data. The stations with the highest turbidity were characterised by the highest number of species and high total densities. However sampling efficiency might be higher (lower escape response) in turbid water, several studies in both estuarine and marine habitats indicate that fish abundance is usually higher in turbid waters (e.g. Swenson 1978, Blaber & Blaber 1980, Clark et al. 1996a, Clark 1997), while low catches are attributed to the presence of clear waters (e.g. Lasiak 1982, Blaber et al. 1985, Ross et al. 1987). The presence of turbid waters in estuaries is generally considered to be advantageous for juvenile fish, as they provide cover from predators and frequently harbour higher densities of invertebrate prey than clear waters (Blaber & Blaber 1980, Blaber 1981, Cyrus 1983, Cyrus & Blaber 1987a,b). Since the mobile and relatively homogenous nature of the substratum on sandy shores provides few refuges, protection due to higher turbidity might be important.

CONCLUSIONS

In conclusion, within the epibenthic macrocrustacean and fish assemblages of the Belgian coast, a lot of variation exists. This variation might be linked with sampling efficiency (and intensity), but the correlation with turbidity of the water and the morphodynamic features of both the beach and the adjacent shallow subtidal area, should be investigated further. Many juveniles were present and some species were exclusively caught at this stage. The mobile and relatively homogenous nature of the substratum on sandy shores means that few refuges are available thus protection due to higher turbidity might be important. Also the protection that organisms gain by occurring on flat, shallow beaches (less predation, less wave exposure) is probably outweighed by increased fluctuations in environmental variables such as salinity and higher risks of retention on the beach by ebb-tide, resulting in a higher diversity at intermediate sites.

CHAPTER III

SURF ZONE FLATFISH: FEEDING ECOLOGY

Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach

Chapter III

Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach

Results presented in:

Bregje Beyst, André Cattrijsse & Jan Mees (1999). Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. Journal of Fish Biology 55, 1171-1186.

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Commercial shrimp fisherman

ABSTRACT

The fish fauna of the surf zone of a Belgian sandy beach was sampled monthly from May until December 1996. Samples were taken at ebb tide with a beam trawl and sampling depth varied between 1 and 1.5 m. Five flatfish species were recorded: plaice *Pleuronectes platessa* Linnaeus, 1758, sole *Solea solea* (Linnaeus 1758), brill *Scophthalmus rhombus* (Linnaeus 1758), turbot *Scophthalmus maximus* (Linnaeus 1758) and dab *Limanda limanda* (Linnaeus 1758). All individuals caught were 0- and I-group fishes.

The feeding ecology of the different species was investigated by means of stomach/gut content analyses and the diet of each species is described. This involved numerical and gravimetrical diet analyses and the calculation of the frequency of occurrence of the different prey items. Stomach contents were further analysed with ordination techniques in order to visualise dietary overlap between the species.

Prey items of all flatfish species included hyperbenthic (e.g. mysids), endobenthic (e.g. polychaetes) and epibenthic (e.g. shrimps) species. Little dietary overlap was observed. If diet overlap did occur, it mainly involved prey species that are dominant in the surf zone of Belgian beaches such as shrimps and mysids. These results suggest an opportunistic utilisation by flatfish of the available food resources in surf zone ecosystems.

Also, two strategically different feeding habits could be distinguished between the 5 flatfish species. Turbot and brill mainly fed on large, highly mobile prey (e.g. fish, mysids) and had a rather narrow prey-spectrum, whereas plaice, dab and sole ate more benthic prey (e.g. polychaetes) and had a broader prey-spectrum.

INTRODUCTION

The surf zone of most western European sandy beaches is generally distinguished from most other shallow water marine ecosystems by the very strong regulating phenomenon of the tides and is characterised by distinct gradients of different environmental variables like salinity, emersion, light and temperature. The function of the surf zone as a nursery for different species has been emphasised by several authors (e.g. Lasiak 1981). Most studies on fish assemblages associated with surf-exposed beaches have concentrated on community structure (e.g. McFarland 1963, Gibson et al. 1993, Clark 1997) or are confined to the behaviour of only one species (e.g. Gibson 1973, Thijssen et al. 1974). Trophic relationships between fishes in the surf zone of sandy beaches are less well documented and most research has been done in the southern hemisphere (e.g. Lasiak 1984a, 1986, Lasiak & McLachlan 1987). Other areas investigated include the Irish Sea (Macer 1967), Mexico (Modde & Ross 1983), southern Wales (Wyche & Shackley 1986) and Scotland (Ansell & Gibson 1990). Trophic relationships within the surf zone of Belgian beaches have never been investigated. The aim of this study is therefore to investigate these trophic interactions within a sandy beach surf zone of the Belgian coast. More specifically, this paper will focus on the feeding ecology of the flatfishes.

MATERIALS AND METHODS

Study area

The investigated sandy beach is situated near the village of Oostduinkerke (51°7,5N; 3°40'E) along the western part of the Belgian coast (Figure 1). It has several shallow troughs and bars parallel to the water edge in which the water is retained at low tide. The beach has an intertidal zone of approximately 500m with a tidal range of 5m. Because of the combination of fine sand (median < 250µm) and a shallow slope, the beach rates as dissipative according to Wright *et al.* (1979). Another characteristic of dissipative beaches, is the heavy wave action dissipated in a wide surf zone (McLachlan 1990). This situation however, only takes place during heavy winter storms. The beach can thus be characterised as a low-energy, dissipative beach (Short 1996). Maximum seawater temperature is about 20°C in summer, while in winter minimum temperatures are around 0 °C.

Sampling

Qualitative samples were taken from the by-catch of commercial shrimp fishermen. These fishermen use a 3-m beam trawl (mesh size 10x10mm) which is pulled by a horse for approximately 30 minutes at a depth of 1-1.5m. Their beam trawl was equipped with a tickler chain. All samples were taken during daytime and around ebb tide. Sampling was performed monthly from May 1996 until December 1996. Immediately after capture, all fishes were put into a benzocaine solution (ethylamino-4-benzoate) in order to avoid unnecessary suffering and regurgitation of their stomach content. They were then preserved in a formaldehyde solution (8% final concentration). Shrinkage in formalin stabilises after a few hours and is less than 3% for 0-group plaice (Lockwood 1973).

Treatment of samples and data analysis

In the laboratory, a few months after capture, all flatfishes were sorted out, identified, counted and their standard length (SL) was measured to the nearest mm. The fish were then divided into 4 or 5mm length classes. For the purpose of stomach and/or gut content analyses, a maximum of 20 individuals was selected at random from the most abundant size classes. All items present in the stomachs/guts were identified (if possible) to species level. For nematodes, polychaete palps, siphons of bivalves, copepods and other small crustaceans, assigned ashfree dry weight (ADW) values, independent of the animals length, were used (Appendix 7). All other animals were measured and their ADW prior to digestion was estimated from length-ADW regressions (Appendix 7). The original size of incomplete prey was estimated from regressions relating unbroken parts, e.g. a telson or an antennal scale, to standard length. Food composition is expressed as mean gravimetric percentage (%G) and as mean numerical percentage (%N). Another way of assessing the importance of a prey is the calculation of the frequency of occurrence (%F, the percentage of stomachs in which a certain prey item occurs). Finally, multivariate analyses (Detrended Correspondence Analyses, DCA) were performed on the numerical data to assess the niche width of and the niche segregation between the different species. Multivariate analyses were preferred over the classical diversity and similarity indices because of the unequal and generally small number of fishes examined. We focused on two months within the study period: May and August. The May samples consisted of the I-group individuals of the flatfishes and those taken in August comprised mainly the 0-group.

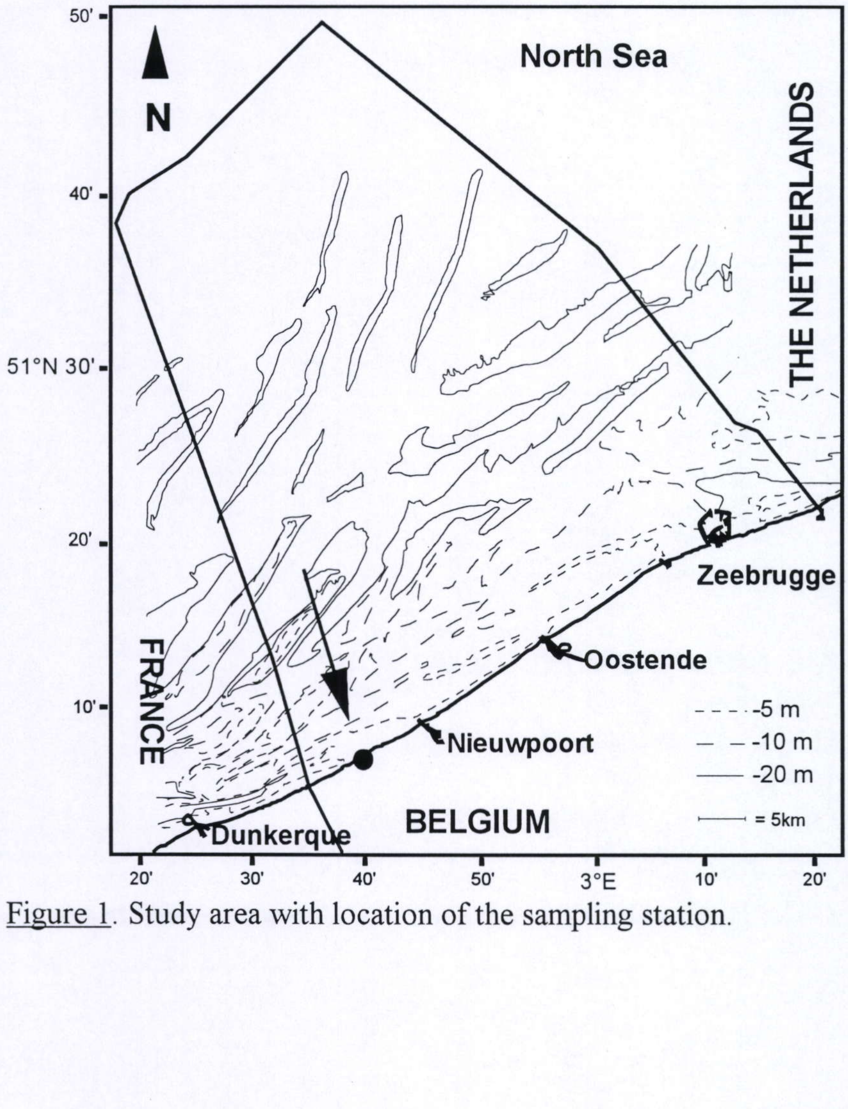


Figure 1. Study area with location of the sampling station.

RESULTS

Species composition and occurrence

Five species of flatfish were recorded from the samples: plaice *Pleuronectes platessa* Linnaeus,1758, dab *Limanda limanda* (Linnaeus 1758) (Pleuronectidae), turbot *Scophthalmus maximus* (Linnaeus 1758), brill *Scophthalmus rhombus* (Linnaeus 1758) (Bothidae) and sole *Solea solea* (Linnaeus 1758) (Soleidae). Turbot, plaice and sole occurred during the whole study period, brill was absent in May and dab mainly occurred from September until December and only in low numbers (see Table 2). Plaice was by far the most abundant species. Data on the exact densities and the accompanying fauna will be reported elsewhere.

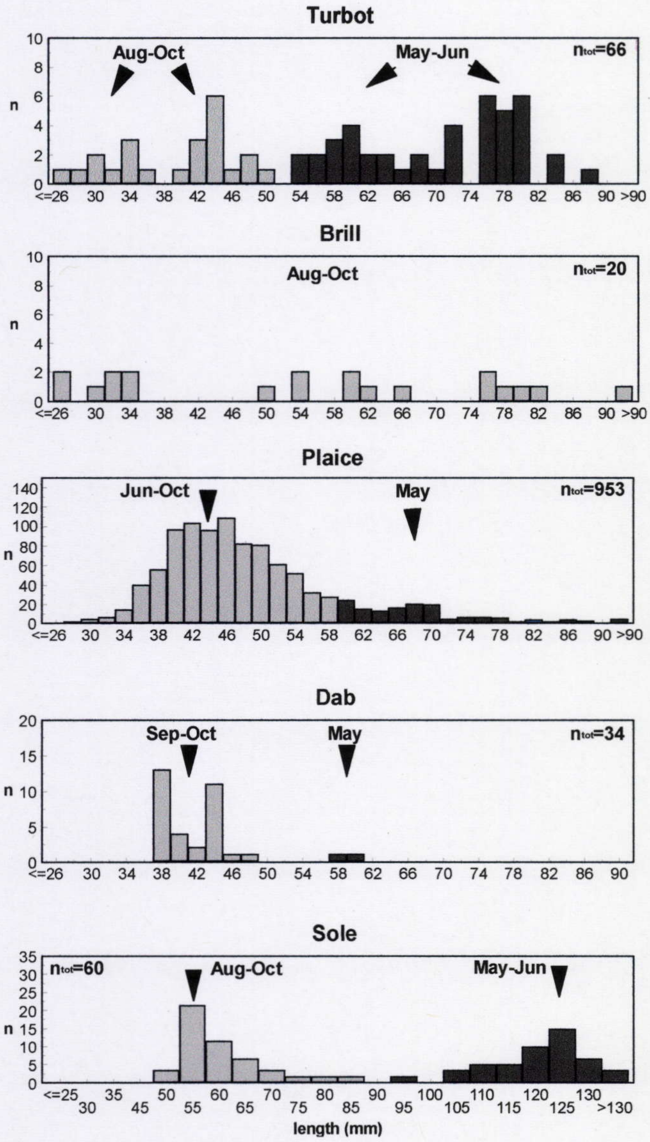


Figure 2. Length-frequency distributions of the five flatfish species.

Length-frequency distribution

Nearly all individuals caught were juveniles, ranging in size from 25 to 90mm SL (Figure 2). Only larger soles were present. The median length of all species was generally larger in May than in the rest of the study period, suggesting that two year classes were sampled. In May, most turbot measured 60 or 76-80 mm SL while from August till October most individuals belonged to size classes 34 and 44. For brill, no length-frequency distribution pattern was found. In contrast, a clear bimodal pattern was observed for plaice (median lengths: 46 and 68 mm SL respectively) and sole (median lengths: 55 and 125 mm SL respectively). The median length of dab was smaller than 50mm SL, and almost no larger individuals were recorded (a few specimens in May).

Description of the diet

For turbot, brill and plaice, only the content of the stomach was analysed, whereas for dab and sole both the stomachs and guts were examined (Appendices 8A and 9A). Turbot and brill have a large, well-defined stomach and prey items present in their guts were always fully digested. Plaice, dab and sole on the other hand, have a rather small stomach and a long alimentary tract; food is rapidly removed from their stomachs and it is therefore advisable to analyse both stomach and gut content. However, since most stomachs of plaice were full, and since preliminary analyses of the guts did not yield additional information about the food spectrum, but only delayed the research severely, further investigations concerned only the stomach contents. Empty stomachs/guts were not included in the diet analysis (see Table 2).

Table 1. Mean numerical and gravimetrical diet composition for each flatfish species. Others: prey items recorded only once or very rare.

	turbot		brill		plaice		dab		sole	
	%N	%G	%N	%G	%N	%G	%N	%G	%N	%G
Hydrozoa	-	-	-	-	<0,1	<0,1	17.4	5.6	<0,1	<0,1
Foraminifera	-	-	-	-	0.1	<0,1	-	-	0.1	<0,1
Nematoda	1.7	<0,1	-	-	0.7	<0,1	-	-	1.3	<0,1
Polychaeta	5.8	0.1	-	-	52.9	14.8	2.2	0.1	21.0	52.7
Ostracoda	-	-	-	-	-	-	-	-	0.1	<0,1
Cirripedia	-	-	1.1	<0,1	0.3	0.1	41.3	2.9	4.0	0.1
Copepoda	-	-	-	-	5.5	0.1	4.3	2.3	12.4	1.1
Caridea	15.0	12.3	12.6	3.3	16.6	76.2	4.3	57.9	42.2	28.2
Anomura	-	-	-	-	0.1	0.5	8.7	4.3	0.2	<0,1
Brachyura	2.9	0.1	1.1	<0,1	0.1	0.1	-	-	2.7	1.7
Mysidacea	26.6	4.4	67.4	9.7	0.2	0.7	-	-	0.2	0.6
Cumacea	-	-	-	-	1.4	0.7	15.2	1.4	1.7	0.1
Isopoda	2.9	0.1	-	-	0.1	<0,1	-	-	0.2	<0,1
Amphipoda	7.5	0.3	3.2	0.3	1.0	1.4	2.2	18.0	5.8	1.6
Bivalvia	-	-	-	-	15.9	2.1	2.2	5.5	1.8	0.1
Pisces	30.6	82.7	14.7	86.6	1.0	3.3	-	-	3.6	13.5
others	6.9	<0,1	-	-	4.2	<0,1	2.2	2.0	2.7	0.1

The mean diet composition of each species is presented both in numerical (%N) and gravimetrical (%G) terms in Table 1. The dominant prey items in turbot and brill were mysids (mainly *Schistomysis kervillei*), (sub)adult shrimp (almost exclusively *Crangon crangon*) and fish (turbot: mostly postlarvae of the clupeids herring *Clupea harengus* and sprat *Sprattus sprattus*; brill: juvenile or adult *Pomatoschistus* species). Together these prey items accounted for more than 70%N (turbot) or more than 90%N (brill) of the diet. Their diet was mainly supplemented with amphipods (mainly *Bathyporeia* species) (turbot: 7.5%N; brill: 3.2%N). Since most fish eaten were large postlarval stages and even some adult gobies, fish were gravimetrically by far the most important prey item (~ 85%G) in both species. However, the relative abundance of the other prey differed substantially for both species. Caridea represented 12.3%G of the diet of turbot while this was only 3.3%G for brill. The opposite was true for mysids: 4.4%G for turbot and 9.8%G for brill.

A completely different prey spectrum was observed for the other three species. Juvenile plaice mainly fed on polychaetes (mainly *Scolelepis squamata*) or polychaete palps (52.9%N, 13.5%G), postlarval *Crangon crangon* (16.6%N, 76.2%G) and siphons of bivalves (15.9%N, 2.1%G). Polychaetes (mainly *Nephtys cirrosa*) and postlarval shrimps were also important prey items for sole (20.9%N and 42.2%N respectively), together with copepods (mainly *Temora longicornis* and *Centropages hamatus*, 12.4%N). Amphipoda (mainly *Pontocrates altamarinus*) and cyprid larvae of Cirripedia contributed for respectively 5.8%N and 3.7%N. In gravimetric terms, polychaetes dominated the diet of sole with 52.7%G, followed by postlarval shrimps (28.2%G) and postlarval fish (e.g. postlarval plaice) (13.5%G). Numerically, the mean diet of dab mainly consisted of cyprid larvae (41.3%N), hydrozoans (17.4%N) and cumaceans (15.2%N), while gravimetrically, postlarval Caridea (57.9%G) and Amphipoda (mainly *Pontocrates altamarinus*) (17.9%G) were the dominant groups.

Table 2. Frequency of occurrence (%F) of prey items (higher taxonomic levels) in the five flatfish species. Between brackets: (number of fish analysed; number of empty alimentary tracts).

	turbot (66; 24)	**brill** (20; 2)	**plaice** (162; 47)	**dab** (34; 6)	**sole** (60; 6)
Foraminifera	-	-	2.2	-	1.9
Hydrozoa	-	-	2.2	51.9	-
Nematoda	4.4	-	11.7	-	7.4
Polychaeta palp	-	-	43.8	29.6	7.4
Polychaeta	8.9	-	70.1	-	59.3
Bivalvia	-	-	13.1	29.6	9.3
Bivalvia siphon	-	-	38.0	-	7.4
Ostracoda	-	-	-	-	1.9
Calanoida	-	-	17.5	29.6	44.4
Harpacticoida	-	-	15.3	74.1	16.7
Cirripedia	-	5.6	12.4	74.1	18.5
Caridea	40.0	50.0	40.9	40.7	81.5
Anomura	-	-	2.2	33.3	3.7
Brachyura	8.9	5.6	2.9	-	14.8
Mysidacea	40.0	61.1	4.4	-	3.7
Cumacea	-	-	10.2	33.3	20.4
Isopoda	4.4	-	3.6	-	3.7
Amphipoda	15.6	16.7	12.4	59.3	48.1
Pisces	71.1	50.0	5.1	-	24.1
others	6.7	-	19.7	51.9	27.8
Nr. taxa	9	6	19	11	19

The percentage of stomachs/guts in which the different prey items (higher taxonomic levels only) occurred, is presented in Table 2. The number of taxa in turbot and brill (9 and 6 respectively) was much lower than in the other species (19 in plaice and sole; 11 in dab). Several prey items (e.g. Caridea, Pisces) were found to be important in the diet of more than one -or even all 5- species, suggesting an important dietary overlap. At a lower taxonomic level however, this apparent overlap largely disappeared. Table 3 presents all the prey items that occurred in more than 20% of the stomachs of any fish species. In some cases the diet segregation between two species was very distinct: e.g. polychaetes were the main food item in the diet of plaice and sole, but plaice mainly fed on *Scolelepis squamata* and other Spionidae, while sole only ate *Nephtys cirrosa*. Also turbot and brill consumed different fish species: turbot mainly fed on postlarvae of Clupeidae, while brill only fed upon juvenile or adult *Pomatoschistus* species. Nevertheless, for some prey items (e.g. postlarval shrimp, mysids) a dietary overlap could be observed between the flatfish species.

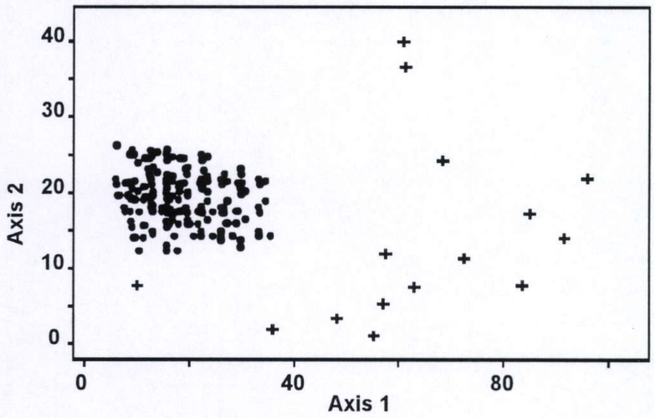
Table 3. Frequency of occurrence of the most important prey items (%F>20) in the five flatfish species (juv: juvenile; pl: postlarva; a: adult).

	turbot	**brill**	**plaice**	**dab**	**sole**
Hydrozoa species					
Hydrozoa species				***	
Polychaeta					
Spionidae species					
(*Scolelepis squamata*)			***		
Nephtys cirrosa					***
Arenicola marina end					***
Magelona papillicornis palp			***		
Bivalvia					
Bivalvia siphons			***		
Copepoda					
Temora longicornis					***
Centropages hamatus					***
Harpacticoida species				***	
Cirrepedia					
Cirripedia cyprid larva				***	
Caridea					
Crangon crangon juv,a	***	***			
Crangon crangon pl			***		***
Mysidacea					
Schistomysis kervillei	***	***			
Pontocrates altamarinus				***	***
Pisces					
Clupeidae species larva	***				
Pomatoschistus species juv,a		***			

Multivariate analyses

The output of the Detrended Correspondence Analyses is presented in Figures 3-4. In May, brill was absent and only two dabs were taken into account. Still, a very clear pattern could be observed (Figure 3a): after a first analysis turbot was separated from the other species along the first axis which had an eigenvalue of 0.750. Characterising prey items were fish (mainly clupeid postlarvae) and mysids (*Schistomysis kervillei*). When turbot was excluded from the analyses, a clear segregation was observed between the three remaining species (Figure 3b). The eigenvalues of the first and second axes were now 0.563 and 0.280, respectively. Some characterising prey items were bivalves and polychaete palps for plaice, the polychaete *Nephtys cirrosa* and cumaceans for sole and hydrozoans and harpacticoids for dab. In August, only three turbot were caught, but a first analysis (which is not shown) revealed the same pattern as in the previous plot. Dab was absent in August. More or less the same segregation could be observed for sole and plaice (Figure 4) after exclusion of turbot from the analysis. Moreover, brill was also very clearly segregated from these two species, with postlarval plaice and (sub)adult shrimp as characterising prey items. Again the separation of the three groups occurred along the first axis, which had an eigenvalue of 0.672.

a) **fish plot**



b) **fish plot**

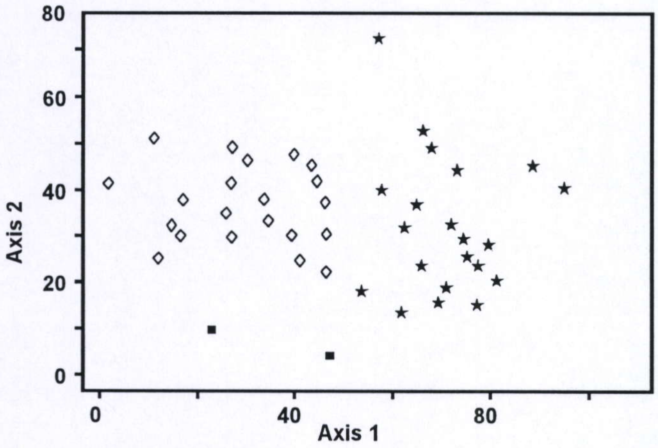


Figure 3. Detrended Correspondence Analysis of numerical data of May: (a) all data included (●: others, +: turbot); (b) turbot excluded (◇: sole, ■: dab, ★: plaice).

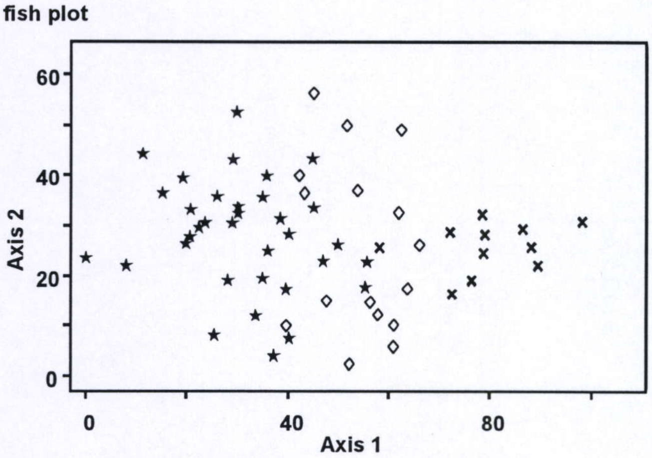


Figure 4. Detrended Correspondence Analysis of numerical data of August (turbot excluded) (★: plaice; ◇: sole; ✕: brill).

DISCUSSION

No marked differences in digestion were found between the prey items of the five flatfishes. Even most of the soft-bodied organisms like polychaetes could be identified down to species level. Thus the results do not seem to be strongly biased by differential digestion. This was also the case for sole, despite the fact that food was only found in their guts. However, in some cases most individuals were broken into several pieces or only parts of organisms were found. This probably resulted in an underestimation of the gravimetrical percentage of the polychaetes in the diet composition of plaice, since length-ADW-regressions were used on parts of individuals instead of whole animals. For the other species it was easier to avoid this bias since most polychaetes were found intact.

Although the diet of each of the five flatfish species included planktonic (e.g. copepods), hyperbenthic (e.g. mysids), endobenthic (e.g. polychaetes) and epibenthic (e.g. shrimps) species, clear niche segregation could be observed between the different flatfishes. If their diet showed some kind of overlap, the relative importance of the different prey items in the diet differed substantially between the species and/or it concerned prey species which are highly abundant in the surf zone: *Crangon crangon* is the dominant epibenthic species, mysids are the dominant hyperbenthic organisms (Beyst et al. in press a and b) and polychaetes dominate the macrobenthos (Degraer et al. 1999). This clear diet segregation also holds true when seasonal and ontogenetic factors are taken into account as revealed by the multivariate analyses of the numerical data. In May, a clear distinction between the diets of the I-group turbot, sole, plaice and dab was observed, while in August the same pattern was found for 0-group brill, turbot, sole and plaice. Also, it can be noticed that despite the fact that in some cases low numbers of fish were examined, these segregation patterns are very distinct.

Two strategically different feeding habits could be distinguished: turbot and brill mainly fed on large, highly mobile prey like fish and mysids and had a rather narrow prey-spectrum; whereas plaice, dab and sole mainly fed on small benthic and demersal prey like polychaetes and bivalves and had a much more diverse diet. These differences in feeding behaviour between families is also confirmed by Holmes & Gibson (1983). Bothids are basically daylight predators. Their prey are generally fast moving with elaborate escape tactics. Bothids often leave the bottom to perform feeding activities in pursuit of prey in the water column. Plaice are also visual feeders which take mainly slow-moving bottom-living food but also feed on active crustaceans. Soles on the other hand, feed on sessile or barely mobile organisms. They are night feeders with a poorly-developed sense of vision. Both the mouth gape and the morphology of the alimentary tract restrict the size of prey predators can ingest (De Groot 1971, Ringler 1979). Turbot and brill have a big mouth gape and a large oesophagus and stomach which enables them to ingest large prey such as fish, whereas the other species have a smaller mouth size, oesophagus and stomach and a complicated intestinal loop appropriate for frequent consumption of small-sized prey (De Groot 1971).

In turbot the change to the adult diet begins at a size of 10-15cm when they start to eat fish and shrimps (Braber & De Groot 1973, Jones 1973). However, e.g. Aarnio et al. (1996) found that in the Baltic Sea, this change occurred already at a length of 30mm when the young turbots started to feed on mysids, amphipods and juvenile gobies. Gobies usually are the first fish in their diet (Braber & De Groot 1973). In our study, fish and shrimps (next to mysids and -to a lesser extent-polychaetes) already represented a substantial part (55 and 24% respectively) of the diet of the smallest cohort (25-60mm) (86 and 11% respectively in the diet of the larger cohort of 60-90mm). However, for both cohorts it mainly concerned postlarval clupeids and almost no juvenile gobies. In contrast, gobies were the main food item in brill larger than 50mm. Brill smaller than 50mm fed almost exclusively on mysids (85%). These results are in full agreement with the results of Wyche & Shackley (1986) and Braber & De Groot (1973) who also found that 0-group brill mainly fed on mysids. Subsequently, the latter authors found that at a length of 60mm, brill started to feed on fish. In May, brill was absent from the samples and therefore competition for food between I-group individuals of brill and turbot can be excluded. The fact that almost no gobies were found in the diet of I-group turbot can possibly be explained by the very low numbers of *Pomatoschistus* species during this period in the surf zone (Beyst et al. in press b).

According to Wyche & Shackley (1986) and Lockwood (1984), plaice preferably consumes commonly occurring species, whereas dab utilises any available food source. This wider range of food organisms of dab in comparison with plaice is also confirmed by other authors such as Jones (1952) and Braber & De Groot (1973) and is probably due to differences in feeding posture (Wyche & Shackley 1986). In our study, only very few prey items were found in the alimentary tract of dab and only a small number of animals could be examined (34, 6 empty). The variation of their gut and stomach contents however, was rather small. For the other species, even if the number of individuals examined was low, their stomachs or guts were usually full and the content was very stable. Dab mainly fed on larvae of Cirripedia, small crustaceans and hydroids (dab of less than 40mm mainly ate harpacticoid copepods: 60%). Wyche & Shackley (1986) found that larger individuals (I-group and older) had fed on amphipods living on hydroids, rather than on the hydroids themselves. In their study, the preference of younger dabs for amphipods was clear in October when the frequency of occurrence of hydroids decreased with increasing age of fish. Furthermore, although the juvenile plaice and dab populations overlap, the zones where each is most abundant are separate (Edwards & Steele 1968). The plaice population usually lies inside the 4m-depth line and about half the population may enter the littoral zone with the rising tide. The dabs, on the other hand, do not appear to enter the littoral zone and the maximum population density is found at 4m (Edwards & Steele 1968, Pihl 1989). The diet composition of sole presumably reflects environmental changes in prey availability; the most frequent and abundant prey in the stomachs should be among the most abundant species in the environment (Molinero & Flos 1992). In this case it seems that plaice forages more in the high intertidal, since *Scolelepis squamata* is confined to this area where it is the most abundant polychaete (~40 ind./m2 on a similar neighbouring beach, Elliott et al. 1996), while sole feeds in the lower intertidal or shallow subtidal, where *Nephtys cirrosa* is dominant (~140 ind./m2, Elliott et al. 1996). However, according to these authors, *Nephtys cirrosa* occurs (in lower densities) in the whole intertidal zone. Finally, not only a spatial segregation in feeding habitat was observed: while sole seems to have a nocturnal feeding activity (food was only found in their guts), plaice mainly feeds during daytime (e.g. Thijssen et al. 1974). For sole, this nocturnal foraging activity was found by several authors in subtidal areas where food is continuously available (e.g. Kruuk 1963, De Groot 1971, Legardère 1987). However, in intertidal areas young sole were found to adopt a bimodal feeding rhythm with one peak at night and one during the day (Le 1983). Again, these results support the suggestion that potential interspecific competition is avoided by spatially as well as temporally feeding activities.

CONCLUSIONS

Since the dietary overlap observed between the five flatfish species only concerned prey items which are probably very abundant in the surf zone of the investigated beach, an opportunistic utilisation of these available food resources seems probable. This phenomenon has already been described by several authors (e.g. in the surf zone of a sandy beach in southern Africa by Lasiak & McLachlan 1987). Such opportunistic utilisation of food resources can be important for teleosts frequenting physically stressed environments such as surf-exposed beaches (Lasiak & McLachlan 1987). The surf zone itself is not only a physically dynamic habitat; many of the associated faunal assemblages are themselves highly dynamic. Short-term variations in wind strength and direction and their subsequent effects on surf conditions probably play a major part in the control and interaction of these assemblages (McLachlan 1983, Lasiak 1984). Furthermore, the suggestion of partitioning of food resources by prey kind and size and the spatial as well as temporal separation of foraging habitats shown by these species (also found by Modde & Ross (1983) in a surf zone habitat in the northern Gulf of Mexico) is surprising in view of the apparent physical harshness, low spatial heterogeneity and the temporary use of the habitat.

CHAPTER IV

TIDAL AND DIURNAL RHYTHMS OF THE EPIBENTHOS

Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice (*Pleuronectes platessa* L.)

Chapter IV

Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice (*Pleuronectes platessa* L.)

Results presented in:

Bregje Beyst, Jan Vanaverbeke, Magda Vincx & Jan Mees (in press). Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice (*Pleuronectes platessa* L.). Marine Ecology Progress Series.

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An impression of the sampling atmosphere at 5:00 am during the 24h-sampling cycles

ABSTRACT

Macrocrustaceans and juvenile demersal fish were sampled in spring of 1997 in the surf zone of an exposed sandy beach at the Belgian coast. Three subsequent 24h-cycles were sampled in order to investigate tidal, diurnal and/or semi-lunar distribution patterns within the epibenthic community. Multivariate statistical techniques and three-way ANOVAs were used to evaluate the effects of the environmental variables measured. Mainly the state of the tide (ebb/flood), but also light intensity (day/night) were indicated by the analyses as most important variables correlated with the variation in epibenthic catch density. Also the individual catch density of several species differed significantly over the three 24h-cycles. In spite of the strong turbulent conditions of the site studied, clear tidal (e.g. the brown shrimp *Crangon crangon*, juvenile plaice *Pleuronectes platessa*) and diurnal (e.g. juvenile sole *Solea solea* and clupeids respectively caught mainly during the night and during the day) periodicities of many macrocrustacean and demersal fish species were observed. Nevertheless, the extremely turbulent conditions of the surf zone possibly affect the behaviour of many species (e.g. juvenile brown shrimp are not able to bury themselves as the water retreats).

To investigate if the high dynamics of the surf zone suppress the ability of juvenile plaice to actively search for food, stomach content analyses were performed. Also, the interaction with potential prey was investigated: the hyperbenthic fauna was sampled simultaneously and macrobenthic data were available from literature. Clearly, the Belgian sandy beaches are used as a feeding ground by I-group plaice. An opportunistic utilisation of available food resources is suggested. I-group plaice clearly migrate high up the beach during the flood tide in order to profit from the rich macrobenthic intertidal area, while the 0-group feeds mainly on the most abundant hyper- and macrobenthic organisms from somewhat deeper water. The presence of the 0-group in the intertidal area is possibly linked to refuge for predators or influenced by the strong surf zone currents.

INTRODUCTION

Tidal and diurnal periodicity in epibenthic macrocrustaceans and demersal fish of surf zones of sandy beaches, although rarely studied together, are well documented (e.g. Edwards 1958, Janssen & Kuipers 1980, Burrows et al. 1994, Gibson et al. 1996). Most studies, however, only include sheltered or semi-exposed beaches. Data on exposed coasts are rare and mainly restricted to the southern hemisphere. Despite the fact that these exposed beaches are highly dynamic, they can harbour many species and often in high densities and biomasses (e.g. Clark et al. 1996b). Their importance is probably highly underestimated. The hyper- and epibenthic communities of the surf zones of the exposed Belgian sandy beaches have been studied intensively by the present authors; spatial and temporal distribution patterns will be published elsewhere (e.g. Beyst et al. in press a and b).

It is likely that the distribution patterns of intertidal organisms are a mixture of responses to the physical environment modified by direct interactions with other organisms such as predators, competitors or prey (Burrows 1994, Gibson et al. 1998). Data on all of these factors together are rarely available. During this study, an attempt was made to integrate data on the epibenthic surf zone community and their potential prey (hyper- and macrobenthos). Hyperbenthic samples were taken simultaneously and macrobenthic data are available from other studies performed on an adjacent beach (Elliott et al. 1996, Degraer et al. 1999). Stomach content analyses were used to gain more insight in the feeding ecology of the dominant fish species.

This paper reports the results of an integrated study of the tidal and/or diurnal rhythms of macrocrustaceans and juvenile demersal fish on an open macrotidal sandy beach on the Belgian coast. The following hypotheses will be evaluated: (1) the surf zone of the Belgian coast is too turbulent to detect tidal or diurnal distribution patterns within the epibenthic community and (2) its turbulence inhibits the active foraging behaviour in the surf zone of the dominant fish species.

MATERIAL AND METHODS

Study area

The study area comprises the surf zone of a sandy beach near Nieuwpoort at the exposed Belgian coast in the Southern Bight of the North Sea (51°10'N; 2°45'E, Figure 1). The mouth of the IJzer estuary opens at approximately 2 km to the west of the site. A strong semi-diurnal tidal regime and a net tidal current running north-east parallel to the coastline are characteristic for the Belgian coast. According to the morphodynamic classification scheme of Masselink & Short (1993), the beach is classified as a low-tide bar/rip beach. The beach consists of fine sand (median grain size of 200µm) and is mainly characterised by the presence of groins approximately 300m apart from each other. Several shallow troughs and bars in which the water is retained at low tide, run parallel to the water edge. The site has an intertidal zone of approximately 200m, with a tidal range of 4.8m. The difference in water height between spring and neap tide is approximately 1m.

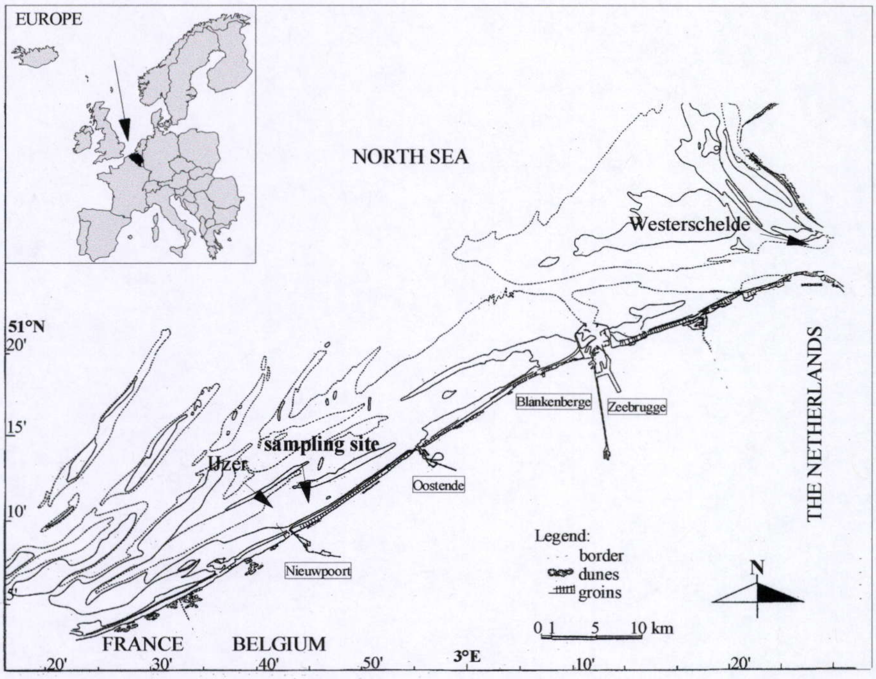

Figure 1. Study area with indication of sampling site.

Sampling

Three campaigns of 24 hour sampling were performed in spring of 1996: at the time of spring (24-25 April) and neap tide (30 April - 1 May) and one in between (27-28 April). Epi- and hyperbenthic samples were taken alternating every 2 hours, starting at 15:00h Central European Time (CET) with the hyperbenthos and ending the next day also at 15:00h CET. During the intermediate cycle only, the last sample was taken at 14:00h CET (epibenthos). This resulted in a total of 36 epi- and 38 hyperbenthos samples. Time constraints and the rapidly changing tidal conditions did not allow replicate hauls to be taken. The hyperbenthos was sampled as it includes many prey items of epibenthic organisms. All epibenthic samples were taken with a 2m-beam trawl. The net was 3 m long, had a mesh size of 5x5 mm and was equipped with a tickler-chain in the ground rope. The hyperbenthos was sampled by means of a hyperbenthic sledge especially designed for this study. Its metal frame measured 100 x 40cm and it was equipped with two nets one above the other, each 3m long and with a mesh size of 1x1mm. Both sampling gears were pulled by 2 persons in the surf zone parallel to the coastline at a depth of approximately 1m, following the tide. Each haul lasted 15 and 20 minutes respectively for the epi- and hyperbenthos and covered a distance of 225 m back and 225 m forth, so that the total distance covered by the trawl in each sample was 450 m. The catch was anaesthetised in a dilute solution of benzocaine (ethylamino-4-benzoate) and then preserved in an 8% formalin solution.

Analysis of samples

In the laboratory, all animals were identified to species, measured and counted, and their standard (or total) length was measured to the nearest mm. For the hyperbenthos total Ash free Dry Weight (ADW) was estimated based on assigned values (cnidarians, ctenophores and small crustaceans) or length-ADW regressions (Mees 1994, Beyst et al. 1999a, Dewicke unpublished data). From the epibenthos, a maximum of 20 juvenile plaice per sample was selected at random from the most abundant size classes caught during spring tide, for the purpose of stomach content analyses. A detailed description of the analyses is given in Beyst et al. (1999a). Diet composition was expressed as mean gravimetric percentage (%G) and as mean numerical percentage (%N) of prey items. The Fullness Index (FI), a measure of the degree of fullness of the digestive tract (in this case stomach), was used to detect changes in feeding rhythm (Berg 1979).

Environmental variables

Every 2 hours, water and sediment samples were taken. Next to some general variables (e.g. salinity, water temperature, sediment analyses), nutrient and pigment concentrations of the water column were measured (see also Appendix 1C). These latter factors might give some indications of (potential) primary production. As many prey items of the epibenthic species follow these patterns, they might reveal some important underlying mechanisms. Portable conductivity and oximeters (WTW) were used for *in situ* measurements of water temperature, salinity and oxygen content. Turbidity was measured with a portable microprocessor turbidity meter (HANNA). Water samples were filtered through Whatman GF/F filters, which were frozen immediately. In the laboratory, for pigment analyses (chlorophyll-*a* and *c* and fucoxanthine), an immediate extraction with acetone (90%) was performed prior to a chromatography. A Gilson high-performance liquid chromatography chain was used, following a slightly modified method of Mantoura & Llewellyn (1983). The concentrations of nitrate plus nitrite, phosphate, ammonia and silicium were measured with an automatic chain (SAN^{plus} segmented flow analyser, SKALAR). From the sediment sample, median grain size was determined in the laboratory with a Coulter Counter LS particle size analyser. Light intensity was measured by means of a portable PAR radiation sensor and measuring unit (Skye). The Coastal Waterways' Division of the Department of Environment and Infrastructure (Ministry of the Flemish Community) provided measurements of hydrodynamic variables at the moment of sampling such as wave height, wind speed and direction.

Data treatment

The exact water height at the moment of sampling was derived from the tide curve from the nearest harbour (Nieuwpoort), obtained from the Coastal Waterways' Division of the Department of Environment and Infrastructure (Ministry of the Flemish Community). Catch densities are expressed as number of individuals per 100m². 'Epi'- and 'hyperbenthos' are used here as working definitions, indicating all animals caught with the beamtrawl and sledge respectively. Exceptions are: small sized crustaceans (e.g. isopods, mysids), early postlarval fish (e.g. clupeids) and sedentary animals (e.g. the starfish *Asterias rubens*) which were excluded from further analyses of the epibenthos, and large fish, Scyphozoa, adult shrimps and crabs and molluscs, which were excluded from the hyperbenthos.

Multivariate statistical techniques were used in order to detect distribution patterns within the epibenthic data: Correspondence Analysis (CA), (Ter Braak 1986, 1988) and Two-Way INdicator SPecies ANalysis (TWINSPAN, Hill 1979). A fourth root transformation (Field et al. 1982) was performed on the abundance data prior to the analyses. In order to assess the importance of the measured variables in structuring the community, the forward selection option together with the Monte Carlo permutation Test in the Canoco package were used prior to Canonical Correspondence Analyses (CCA). If variables were significantly correlated (Spearman Rank correlations, $p< 0.05$), only one of them was retained for further analysis. Since wind direction is a circular variable, it was transformed to a linear variable by using the cosine of the angle that the wind made on a set of axes aligned perpendicularly onshore at each site (Clark et al. 1996b, Zar 1996). Offshore winds at each site were allocated the greatest values (+1), onshore winds the lowest (-1), while winds with a cross-shore component from either direction received scores between +0,9 and -0,9. Wave height was expressed as the height, which was reached by 33% of the waves. The state of tide at the moment of sampling was represented by the time relative to the closest high water, from low water 6h before high water to 6h after high water. Cosines and sines of the angular equivalent of the state of the cycle [2π x (time relative to time of high water)/12.5h] were included in the analyses (Zar 1996). The cosines reflect changes from low water to high water while sines reflect differences between incoming (flood) and outgoing (ebb) water. In order to evaluate the effects of the selected variables and the effects of their mutual interaction on the epibenthos, ANOVAs were performed on log(x+1) transformed density data and number of species. As the sampling scheme is inherently unbalanced (unequal number of combinations) the complete multiple regression was computed. To test the hypothesis that the effects are zero, Type III of the sum of squares was used, appropriate for any unbalanced ANOVA design with no missing cells (Milliken & Johnson 1984). If the assumptions for ANOVA were not met, non-parametric statistics were used (Kruskal-Wallis and Mann-Whitney U tests).

RESULTS

Hydrodynamic conditions

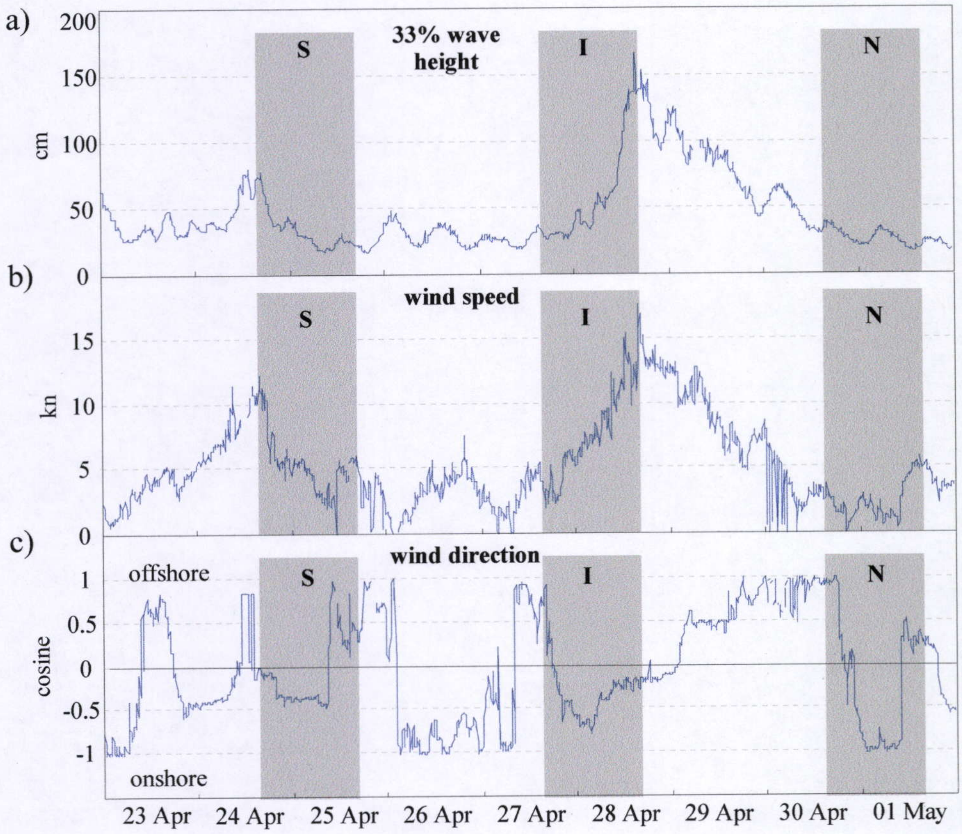

Figure 2. Daily variation (Central European Time) of hydrodynamical variables around the period of sampling, 24h-sampling campaigns are indicated as the shaded areas S, I and N respectively (S: spring tide, I: intermediate tide, N: neap tide).

Around the moment of sampling (from 23/04/1996 until the end of 01/05/1996), 33% of the waves measured on average (±SE) 45±1 cm and wind speed was on average 5±0.01 kn. At least one period of heavy wave action could be detected (Figure 2a,b): it reached its peak at the end of the intermediate 24h-cycle with 33% of the waves > 150 cm and with a wind speed of > 15 kn. Although a second peak could be distinguished at the beginning of the first 24h cycle, 33% of the waves did not exceed 100 cm. The prevailing winds were offshore or longshore during the sampling campaign (Figure 2c), except during the last 24h cycle when onshore winds prevailed. During the last 24h-cycle, a dense mist depressed the light intensity until 7.30h in the morning.

Rhythmic changes in the catch of the dominant epibenthic species and the hyperbenthos

Table 1. Species list and summary of significant differences of Mann-Whitney U and Kruskal-Wallis tests: (***: $p < 0.001$; **: $0.001 < p < 0.01$; $0.01 < p < 0.05$; ns: not significant, -: see Table 3).

	Tide Mann-Whitney U test	**Day/Night** Mann-Whitney U test	**Cycle** Kruskal-Wallis test
total density	***	*	ns
Scyphozoa species	ns	ns	*
Cyanea lamarckii	ns	ns	**
Aurelia aurita	ns	ns	ns
Palaemon serratus	ns	ns	ns
Crangon crangon	***	*	ns
Liocarcinus holsatus	ns	ns	ns
Carcinus maenas	***	ns	ns
Opistobranchia species	ns	ns	ns
Sepiola atlantica	*	ns	ns
Clupea harengus	ns	ns	**
Sprattus sprattus	ns	ns	ns
Ciliata mustela	ns	ns	ns
Atherina presbyter	ns	ns	ns
Syngnathus rostellatus	*	ns	ns
Zoarces viviparus	ns	ns	ns
Echiichthys vipera	ns	ns	ns
Ammodytes tobianus	ns	ns	ns
Pomatoschistus lozanoi	ns	ns	ns
Pomatoschistus microps	ns	ns	ns
Pomatoschistus minutus	ns	ns	*
Pomatoschistus species	ns	ns	ns
Scophthalmus maximus	ns	ns	ns
Pleuronectes flesus	*	ns	ns
Pleuronectes platessa	-	-	-
Solea solea	*	*	ns

A total of 24 epibenthic species were caught: 16 fish, 2 caridean shrimp, 2 brachyuran crabs, 2 molluscs and 2 scyphozoans (Table 1, Appendix 5C). On average 20±1 species were recorded per 24-hour cycle. The brown shrimp *Crangon crangon* represented on average > 90% of the total epibenthic community during all three cycles. Without this species, juvenile plaice *Pleuronectes platessa* accounted for more than 20% during all cycles. Other important species are given in Table 2. Maximum total catch density was found around ebb tide (Figure 3) and reached over 250 ind./100m².

Table 2. Relative species composition of the epibenthos (%) and total density ± SE (ind./100m²) per 24h-cycle (averages of all samples per cycle).

spring tide		**intermediate tide**		**neap tide**	
Crangon crangon	96.3	*Crangon crangon*	91.7	*Crangon crangon*	93.5
Without *C. crangon*					
Pleuronectes platessa	34.2	*Clupea harengus*	52.4	*Cyanea lamarckii*	49.1
Sprattus sprattus	26.5	*Pleuronectes platessa*	29.0	*Pleuronectes platessa*	22.1
Carcinus maenas	15.8	*Pomatoschistus lozanoi*	6.0	*Carcinus maenas*	11.1
Pomatoschistus minutus	5.9	*Carcinus maenas*	3.8	*Clupea harengus*	5.9
Pomatoschistus lozanoi	3.5	*Solea solea*	1.7	*Solea solea*	3.8
others	14.2	others	7.1	others	8.1
Total density ± SE	94±28		85±24		53±20

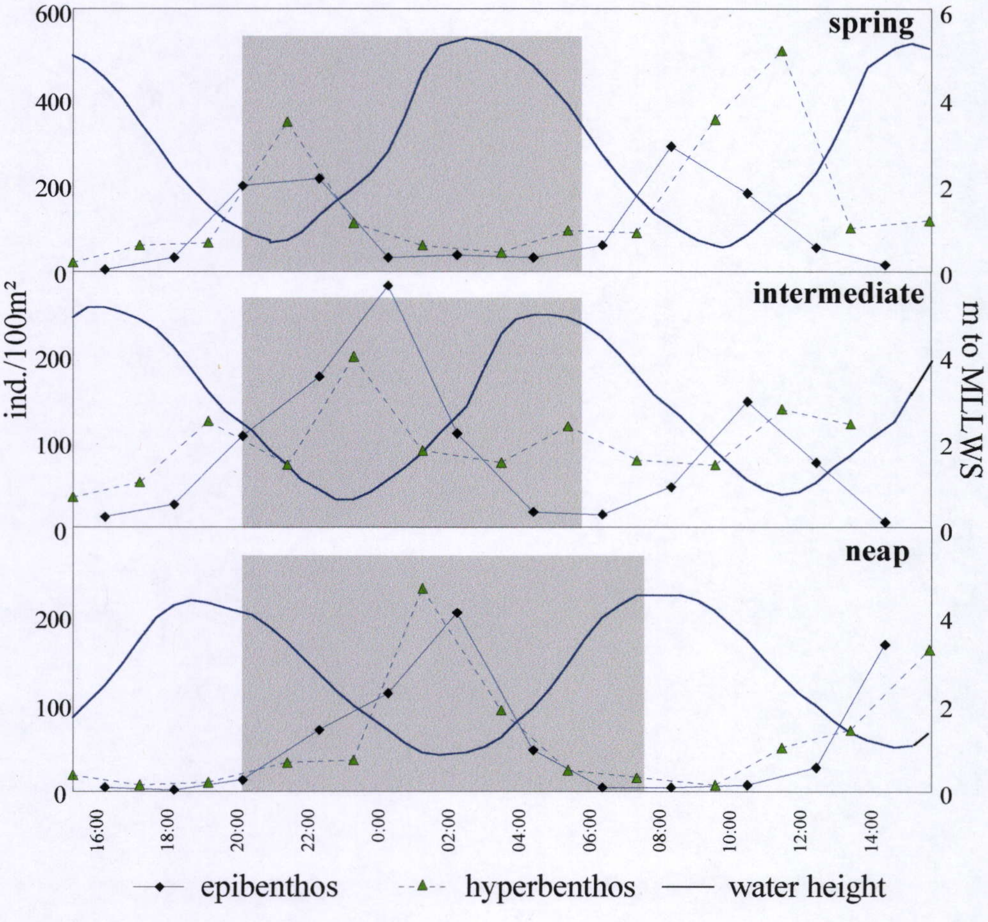

Figure 3. Hourly variation (Central European Time) in total density of the epi- and hyperbenthos (ind./100m²) and water height (m to MLLWS) (MLLWS: Mean Low Low Water Spring) during the three 24h-cycles at spring and neap tide and during the intermediate situation. The darker area indicates the dark hours.

After exclusion of three outliers, both TWINSPAN and CA (eigenvalues of the first three axes: 0.258; 0.213 and 0.191 respectively) resulted in the same pattern: two groups of samples could be distinguished (TWIN groups are indicated in Figure 4). After forward selection and Monte Carlo permutation tests, only water temperature and cosine (tide) were retained. 15% of the variation within the dataset was explained by these two variables in a subsequent CCA (eigenvalues of the first two axes: 0.165 and 0.095, Figure 4). Cosine (tide) was significantly correlated with median grain size, fucoxanthine and chlorophyll-*c*, and water temperature with light intensity, salinity and phosphate content of the water column ($p < 0.05$, Spearman Rank correlations).

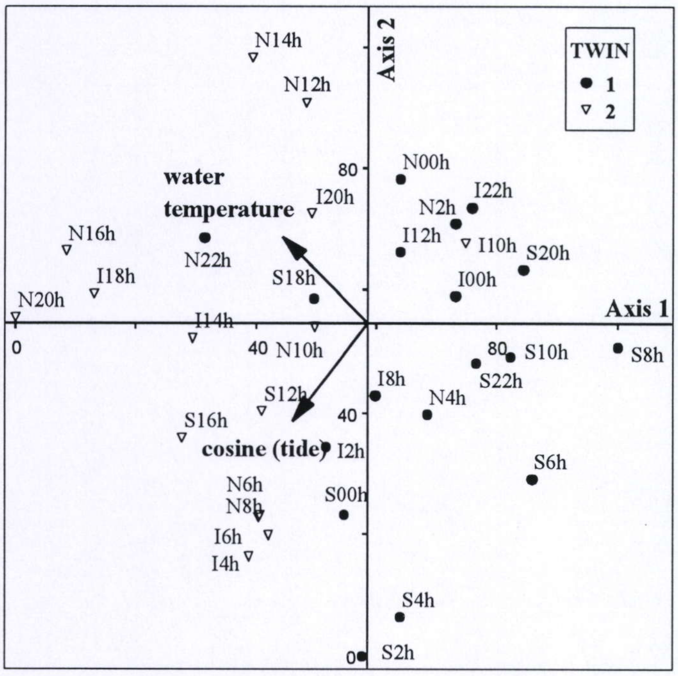

Figure 4. Sample plots of the final CCA with indication of TWIN groups (codes of samples consist of the 24h-cycle (S, I, N) together with the hour of sampling (S: spring tide, I: intermediate tide, N: neap tide). Each axis is scaled in proportion to the longest axes.

Since water temperature not only changed during the day (cf. light intensity) but also increased from sampling date to sampling date (from a maximum of 11.6°C at spring tide, to 13.3°C and 14.4°C for the subsequent 24h-cycles), the effect of time (reflected in the three different 24h-cycles) could not be neglected. The single and combined effects of tide, day/night as well as 24h-cycle on total and individual species catch density and number of species was tested using three-way ANOVAs. However, only the number of species and the catch density of juvenile plaice met the assumptions of ANOVA (Table 3). The number of species was significantly ($p < 0.05$) higher around low water (7±1) and during daytime (7±1) than at high water (4±0.3) and during the night (5±0.4). Also the combined effect tide by day/night on the number of species was significant. The effect of time represented by the three 24h-cycles was however not significant. Tide, day/night and cycle, all had significant effects on the distribution patterns of juvenile plaice: highest catch densities were found at low water (1.8±0.3 ind./100m^2), during the day (1.9±0.3 ind./100m^2) and during the intermediate 24h-cycle (2.5±0.5 ind/100m²), as compared to high water (0.9±0.2 ind/100m²), night (1.1±0.3 ind/100m²) and the other two 24h-cycles (< 1.5 ind/100m²). Combined effects were not significant.

Table 3. Three-way ANOVA: summary of significant differences (***: p < 0.001, **: 0.001 < p < 0.01, 0.01 < p < 0.05, ns: not significant).

Effect	df Effect	# species		*Pleuronectes platessa*	
		F	p	F	p
Tide	1	16.99	***	5.36	*
Day/Night	1	4.59	*	4.92	*
Cycle	2	0.38	ns	4.94	*
Tide by Day/Night	1	7.76	*	1.03	ns
Tide by Cycle	2	0.11	ns	0.59	ns
Day/Night by Cycle	2	2.09	ns	0.20	ns
Tide by Day/Night by Cycle	2	1.19	ns	0.76	ns

The assumptions for ANOVA for the total catch density and the individual catch density of the other species were not met, therefore only the single effect of the three variables could be evaluated by means of Mann-Whitney U (tide, day/night) or Kruskal-Wallis (cycle) tests (Table 1). Total catch density was also found to be significantly ($p < 0.05$) higher around low water (130±20 ind./100m²) compared with high water (30±7 ind/100m²), but lower catch densities occurred during the night (60±20 ind./100m² and 100±20 ind./100m² respectively). These latter results mainly reflected the distribution patterns found for the brown shrimp as this species strongly dominated the samples. The only other species for which significant differences were found between tide as well as time of day, was juvenile sole *Solea solea*. This species was also more abundant at low water and during the night (0.18±0.07 ind./100m² and 0.22±0.07 ind./100m² respectively). At high water and during the day it was virtually absent (< 0.05 ind./100m²). For the remaining species, only one of the three possible effects was significant: e.g. tide was important for the shore crab *Carcinus maenas* and the catch densities of juvenile herring *Clupea harengus* and sand goby *Pomatoschistus minutus* differed between the three 24h cycles.

The hyperbenthos mainly consisted of mysids (80% during spring tide and > 25% during the other two 24h cycles) and early life stages of fish (14% during spring tide and > 30% during the other two cycles) (Table 4, Appendices 3C and 4C). During the intermediate and neap tide cycles, larval polychaetes (±18%) and cnidarians were also important (5% and 14% respectively). Maximum total density and biomass of the hyperbenthos were also found around ebb tide (Figure 3). Densities generally ranged from 200 ind./100m² to peaks of more than 4000 ind./100m², while biomass values reached up to 8000 mg ADW/100m².

Abundance and length distribution of the brown shrimp and juvenile plaice

For both of the most important species, the brown shrimp and juvenile plaice, two cohorts could be distinguished at the moment of sampling. For the brown shrimp, median standard length (SL) was 22 and 32 mm respectively; for plaice 30 and 70 mm SL (probably representing 0-group and I-group plaice). Both cohorts of the brown shrimp showed the same distribution pattern during the three 24 hour cycles (not figured). For juvenile plaice however, two different patterns could be observed (Figure 5): the 0-group showed no clear abundance pattern, whereas the I-group plaice clearly performed a tidal migration pattern with highest catch densities during ebb tide.

Table 4. Relative species composition of the hyperbenthos (%) and total density ± SE (ind./100m²) per 24h-cycle (averages of all samples per cycle, *: < 0.05%, u.i.: unidentified).

	spring tide	**intermediate tide**	**neap tide**
Cnidaria	*	5.0	14.0
Ctenophora	5.1	6.6	0.1
Polychaeta	0.1	17.9	18.4
Copepoda	*	0.9	0.3
Caridea	7.5	14.1	7.7
Anomura	-	*	*
Brachyura	*	0.7	0.1
Cumacea	0.1	0.2	0.4
Mysidacea	79.5	26.4	31.1
Isopoda	0.7	1.0	0.7
Amphipoda	0.9	1.4	1.7
Euphausiacea	*	*	*
Mollusca	-	*	*
Echinodermata	-	-	*
Chaetognatha	*	*	*
Pisces	4.9	8.7	12.6
Pisces eggs	1.2	15.1	12.7
u.i.	-	-	0.2
Total density ± SE	1500±420	970±130	580±190

Stomach content and feeding rhythm of juvenile plaice

The stomach contents of 122 plaice were analysed: 29 (13 empty) of the 0-group and 93 (18 empty) of the I-group. The diet of the 0 and I-group plaice differed substantially (Table 5): a clear shift in diet could be observed. For the 0-group the most abundant prey items were palps of the polychaete *Magelona papillicornis* (30%), followed by cirripedes (cyprid larvae, 14%) and the polychaetes *Pygospio elegans* and *Spio* species (each 12%). Gravimetrically, the amphipod *Bathyporeia* species was most important (37%), followed by the hyperbenthic calanoid copepods *Centropages hamatus* (16%) and *Temora longicornis* (10%). The diet of I-group plaice included also other prey items (endobenthic): free-living nematodes (18%, e.g. *Pseudonchus deconincki*, *Mesacanthion* species and *Daptonema tenuispiculum*) and the polychaete *Scolelepis squamata* (9%) were numerically abundant. Gravimetrically only *S. squamata* (70%) and the hind parts of *Arenicola* species (16%) were important.

Maximal average fullness indices (FI) of the I-group were recorded a few hours after high water, with highest values during the first period of the 24-hour cycle (Figure 6). FIs of the 0-group were very erratic but they are not figured since only 16 individuals were taken into account.

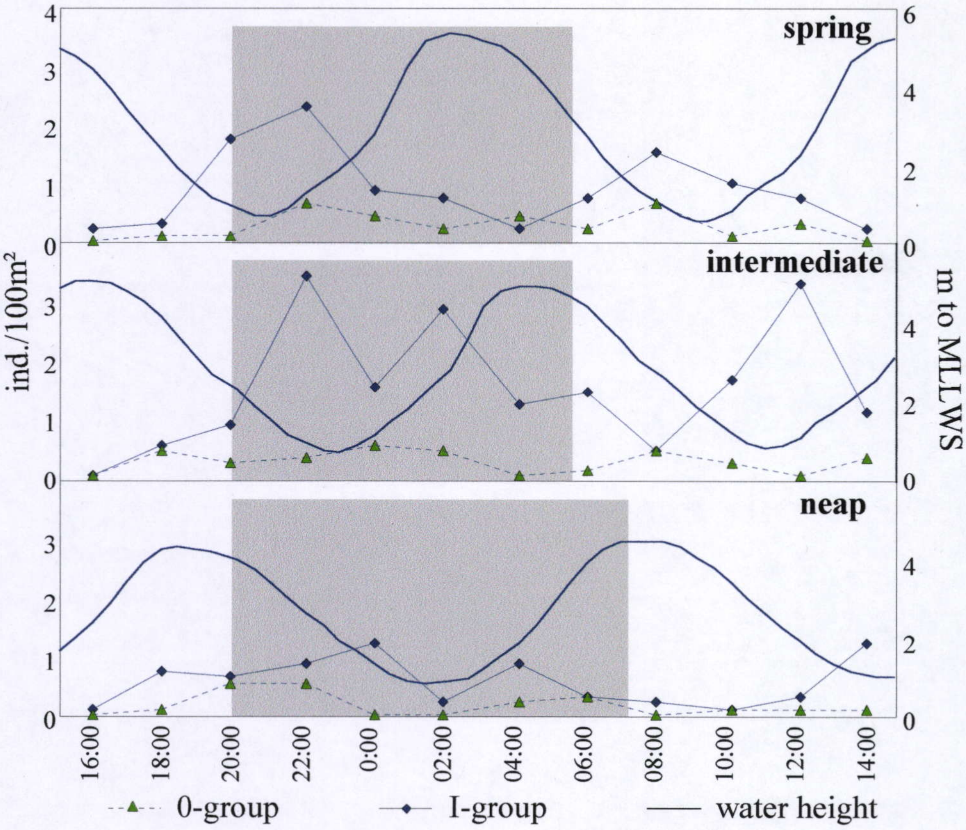

Figure 5. Hourly variation (Central European Time) in catch density of the 0- and I-group plaice (ind./100m²) and water height (m to MLLWS) (MLLWS: Mean Low Low Water Spring) during the three 24h-cycles at spring and neap tide and during the intermediate situation. The darker area indicates the dark hours.

DISCUSSION

Rhythmic changes

The dominant epibenthic species found during this study are numerically dominant in most studies of epibenthic macrocrustaceans and demersal fish in shallow waters in the Northeast Atlantic region (Macer 1967, Pihl & Rosenberg 1982, Evans 1983, Gibson et al. 1993). Catch densities reported probably do not represent true abundances because the efficiency of the 2-m beam trawl is unknown for most species. The catch density of the species recorded as well as the species richness, will be a function of their distribution with depth and substratum type, their ability to avoid the gear, the size selectivity of the meshes, and many other local conditions such as water temperature and turbidity (Kuipers et al. 1992). Highest catch densities of most species were found around ebb tide. In areas with large tidal ranges, the sandy beach fauna often follows the tide, thereby utilising the upshore areas for feeding and as a refuge from predation during high tide (Gibson 1973, Van der Veer & Bergman 1986, Ansell & Gibson 1990). A burying behaviour by shrimp (especially concerning juvenile individuals) in the intertidal area as the water retreats has been described by many authors (e.g. Beukema 1976, Janssen & Kuipers 1980). Since both cohorts of the brown shrimp showed the same distribution pattern during the three 24 hour cycles, it seems unlikely that they bury themselves as the water retreats. The former studies deal with more sheltered areas such as the Wadden Sea. The surf zone of the Belgian sandy beaches is probably too dynamical to allow this kind of behaviour.

Table 5. Numerical (%N) and gravimetrical (%G) diet composition of the 0- and I-group plaice, with indication of the number of fish analysed (p: palps, cl: cyprid larvae, s: siphons).

	%N		%G	
	0-group	**I-group**	**0-group**	**I-group**
# fish analysed	29	93	29	93
# stomachs empty	13	18	13	18
Pygospio elegans	11.7	10.4	5.7	0.9
Scolelepis squamata	0.7	9.1	6.7	70.0
Polydora species	2.1	0.9		
Spio species	11.7	4.9	6.8	0.5
Polychaeta species	1.4	3.4		
Magelona papillicornis p	30.3	14.1	6.9	0.5
Arenicola species end			0.0	15.5
Polychaeta species p	6.9	4.6		
Nematoda species		18.1		
Harpacticoida species	2.1	0.1		
Centropages hamatus	5.5	0.1	15.8	0.0
Temora longicornis	3.4	0.1	9.9	0.0
Cirripedia species cl	14.5	8.6	6.5	0.6
Bathyporeia species	3.4	6.0	37.0	6.5
Bivalvia species spat		3.5		
Bivalvia species s	1.4	3.5		
others	8.3	13.8	4.7	7.9

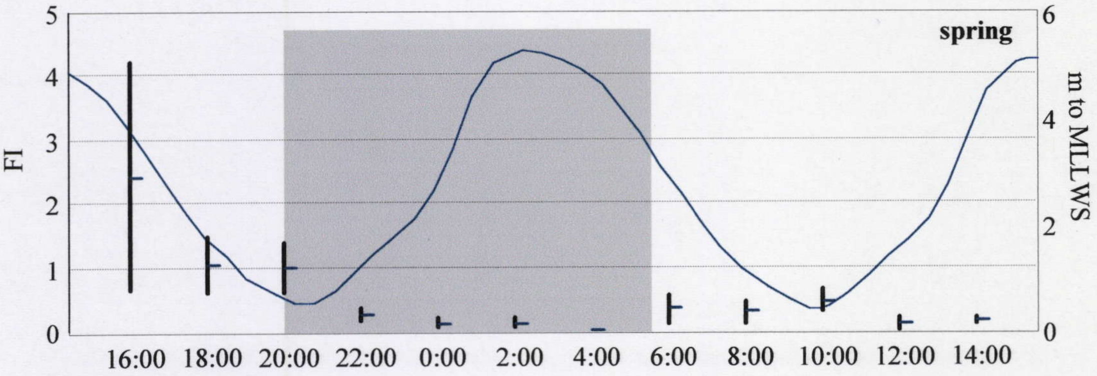

Figure 6. Hourly variation (Central European Time) of the Fullness Index (FI) (mean ± SE) calculated for the I-group plaice during the 24h-cycle at spring tide. The darker area indicates the dark hours.

Some species were found to be more abundant at night (e.g. Lozano's goby and juvenile sole), suggesting an onshore migration at dusk and a subsequent offshore migration by dawn or reflecting nocturnal behaviour (e.g. sole, Kruuk 1963). This diurnal movement pattern has already been described for e.g. gadoid species by several authors (e.g. Pihl 1982, Keats & Steele 1992, Gibson et al. 1998) although the patterns of movement and the possible explanations differ between areas. Net avoidance might also have been greater during the day as reported by Gibson et al. (1996) for gadoids. However, in contrast to the findings of Gibson et al. (1996), the total number of species caught in the present study was highest during the day. The circadian pattern as described for clupeids (e.g. Stickney 1972), is also suggested during our study as they were exclusively caught by daylight independently of the tidal cycle. Finally, differences between the three 24h-cycles might be explained by several factors: the increase over time of the water temperature (appearance of new recruits), the existence of semi-lunar distribution patterns for some species or the prevailing hydrodynamic conditions. The last can be responsible for wind induced transport of organisms towards the shore in case of prevailing offshore winds (possibly for e.g. the cnidarian *Cyanea lamarckii* which was most abundant during the neap tide 24h-cycle).

Water temperature and tide (and correlated variables) were indeed indicated by the multivariate analyses as most important structuring variables; water temperature reflecting both the effect of day and night and differences between 24h-cycles. Univariate statistical techniques confirmed that in general tide, but also the diurnal cycle and the differences between the cycles most likely influenced species richness and total and individual catch densities of several species. The first hypothesis can be rejected since clear tidal and diurnal distribution patterns were found in spite of the turbulence, characteristic for the surf zone. However, integration of the results of similar situations in future research, i.e. in such a way that more than one spring, intermediate and neap tide cycle are sampled, should improve the reliability of these results. Overall it is likely that the behaviour patterns are a mixture of responses to the physical environment modified by direct interactions with other organisms such as predators, competitors or prey (Burrows 1994, Gibson et al. 1998). Data on predators are not available from the studied area, but they are probably largely negligible. The interaction with hyper- and macrobenthic prey will be further discussed on the basis of juvenile plaice. Other flatfish species as potential competitors of plaice in the surf zone of the Belgian coast, are discussed in Beyst et al. (1999a).

Pleuronectes platessa

According to Gibson (1973) the basic rhythm of juvenile plaice is circadian, but under tidal conditions it can be entrained to keep phase with the tides. The two cohorts of juvenile plaice present at the moment of sampling clearly perform different strategies. Although densities were very low, the small 0-group individuals seem to follow the water mass (actively or passively) as it enters and retreats from the beach. The larger I-group juveniles clearly perform tidal rhythmic behaviour as they were caught in significantly higher densities at low tide.

Young plaice mainly feed on macro- and hyperbenthic organisms (e.g. Beyst et al. 1999a) both of which are more abundant in the proximity of the intertidal area compared with the deeper (5-10m) adjacent subtidal (Degraer 1999, Beyst et al. in press a, Cattrijsse & Dewicke in press). The 0-group plaice examined during this study, fed more on hyperbenthic animals (e.g. calanoid copepods) than the larger individuals. These results are in accordance with those of Kuipers (1973): 0-group plaice mainly fed on mysids and small shrimps, whereas the diet of the I-group mainly consisted of the posterior parts of *Arenicola* species. They are however in contrast to the findings of Lockwood (1984), who found that plaice of 20-40 mm basically had a grazing diet (e.g. harpacticoid copepods), whereas the I-group mainly fed on mobile prey (e.g. amphipods, polychaetes, cumaceans). However, he suggested that young plaice preferably consume commonly occurring species, which was also supported by Wyche & Shackley (1986). The hyperbenthos also reached its maximum density and biomass around ebb tide. Either hyperbenthic organisms disperse actively on the beach at high water and concentrate along the water edge as the water retreats, or they are more abundant in somewhat deeper waters (1 -<5 m). Macrobenthic density and biomass on a nearby beach were found to be highest at the mean high water neap tide level (5500 ind./m² and 2000 mg ADW/m² respectively) and lowest between the mean tidal and mean low water neap tide level (Degraer et al. 1999). I-group plaice mainly fed on prey typically from the intertidal (e.g. the polychaete *Scolelepis squamata*, Elliott et al. 1996). They clearly profit from the rich area higher on the beach when the water covers the beach and concentrate along the water edge at ebb tide in anticipation of high water. Berghahn (1987) also found that in the Wadden Sea, larger juvenile plaice migrate further from the channels onto the tidal flats. Next to more hyperbenthic prey, one of their major prey items of the smaller 0-group plaice were palps of the polychaete *Magelona papillicornis*. This species (and other prey items) is mostly found in somewhat deeper waters (Elliott et al. 1996, Degraer et al. 1999), suggesting that these small juveniles do not feed on the beach but at deeper sites. These results suggest an opportunistic utilisation of the available food resources by juvenile plaice. The occurrence of this phenomenon has already been described before (e.g. Lasiak & McLachlan 1987, Beyst et al. 1999a). It can be an important strategy for animals frequenting physically stressed environments such as surf-exposed beaches. Young plaice generally prefer more sheltered areas (Riley et al. 1981), but still they are found in higher densities in the surf zone of the studied area than in the adjacent shallow subtidal (Beyst et al. in press b, Cattrijsse unpublished data). Moreover, since 0-group plaice were found in equal catch densities during the whole tidal cycle, their presence in the intertidal area might be explained by avoidance of predators or passive transport by the surf zone currents. However, these results should be interpreted with care, as only very low densities were caught.

Finally, it is interesting to note that the FIs of the I-group were higher when wave height was greater. These results suggest that there may be longer term patterns in feeding succes of these animals. Moreover, the second hypothesis that the strong turbulence within the surf zone inhibits the active foraging behaviour in the intertidal area, is hereby rejected for the I-group plaice, at least for the conditions met during this study. The turbulence within the surf zone is primarily generated through breaking waves and to a lesser extent by shear at the bottom boundary layer. It is widely acknowledged that wave breaking at the surface provides the dominant source of water column turbulence[1].

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[1] source: http://www.agu.org/revgeophys/holman01/node10.html

CHAPTER V

GENERAL DISCUSSION

INTRODUCTION

Studying the surf zone of the sandy beaches along the Belgian coast, three important aspects should be taken into account: (1) the influence of hydrodynamical and physical-chemical environmental variables (e.g. weather conditions, temperature, nutrients), (2) biotic interactions (e.g. predator-prey relationships, aggregation and schooling behaviour) and (3) anthropogenic influence (e.g. coastal defence works, fisheries, pollution, tourism). In the present study, both the structuring environmental factors and some biotic interactions were assessed after a first inventory and description of the temporal and spatial distribution patterns of the hyper- and epibenthic assemblages.

In this final chapter, several important aspects of surf zone research are highlighted and some recommendations for future research are given. Where appropriate or necessary, additional data and figures are included in order to give a complete overview of the data gathered during this investigation. Finally, some general conclusions are given.

DISCUSSION

The Belgian surf zone: a rich area

Species richness. All in all, the surf zone of the Belgian coast is a habitat for a considerable number of species. It is certainly no marine desert as could be suggested (discussed in McLachlan 1983), since no attached macrophytes are present and hydrodynamic conditions and fluctuations in several environmental variables can be severe. The surf zone harbours a rich hyperbenthic fauna and also the epibenthic assemblage is diverse (Chapters I and II). The number of surf zone species (both hyper- and epibenthic) is comparable to those found in long-term studies of the adjacent subtidal region (**hyperbenthos**: see Chapter 1, Part A, **epibenthos**: between 30 and 35 species both in the present study and in the adjacent subtidal, Cattrijsse unpublished data). Although the number of species recorded from an area depends on factors such as sampling device and duration (e.g. Ross 1983), the number of fish species collected (24) is within the range (26 to 71) reported in previous surf-zone ichthyofaunal studies (Brown & McLachlan 1990). Several common (subtidal) species are replaced by typical surf zone species (see below).

Total density and biomass. As compared to other studies performed in the Southern North Sea (Dutch Delta: Hamerlynck & Mees 1991, western English Channel: Vallet & Dauvin 1999, subtidal of Belgian coast: Dewicke unpublished), total yearly average density and biomass of the **hyperbenthos** were highest in the present study (> 1000 individuals per 100m² and 300-3000 mg AFDW/100m² per station), and only comparable to those of Dewicke (unpublished) in the shallow subtidal of the Belgian coast (Chapter IA). It seems that the Belgian surf zone can be seen as an extension of the rich shallow sand bank system in front of the coast. Total hyperbenthic densities are of the same order of magnitude as those found at sandy beaches of most Mediterranean studies (San Vicente & Sorbe 1993b, Munilla et al. 1998, San Vicente & Sorbe 1999) and much higher than those reported of other, more exposed study areas such as a sandy beach of England (Colman & Segrove 1955) or a beach along the Atlantic coast (San Vicente & Sorbe 1993b). Those differences in total hyperbenthic densities of sandy beaches might be linked to the degree of exposure: the North Sea is semi-enclosed and can be considered as intermediately exposed (Ducrotoy et al. 2000). Moreover, an extensive coastal sand bank system might buffer wave action (especially at the Belgian west coast, see Introduction). On a 20-points exposure scale developed for studies on the intertidal fauna (McLachlan 1980), the studied beaches scored between 9 (sheltered) and 15 (exposed) (Table 1), indicating that the western sites were indeed more sheltered than most eastern sites. This index is, however, rather subjective, since many criteria are quite arbitrary. Moreover, conditions may be variable along the intertidal area of a specific beach: groins for example, might be responsible for strong local differences in exposure (e.g. at study site Lo). Also, the beach profile may be responsible for exposure differences along the beach.

Table 1. Beach types and descriptions according to the exposure rate index of McLachlan (1980).

Score	Beach type	Description	Sites
1 to 5	very sheltered	virtually no wave action, shallow reduced layers, abundant macrofaunal burrows	none
6 to 10	sheltered	little wave action, reduced layers present, usually some macrofaunal burrows	BD, DP, Oo, Ni, Br, Ze
11 to 15	exposed	moderate to heavy wave action, reduced layers deep, usually no macrofaunal burrows	Lo, Mi, Ma, Bl, DH, Kn
16 to 20	very exposed	heavy wave action, no reduced layers, macrofauna of highly mobile forms only	none

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[1] source: Aerographer's/Meteorologist's basic training series. http://www.tpub.com/weather1/index.htm.

Another way of visualising the exposure of the studied area is the comparison between the fetch and the dominant wind direction (Figure 1). **Fetch** is an area of the sea surface over which a wind with a constant direction and speed is blowing, and generating sea waves[2]. Data on wind directions and waves were obtained from the Coastal Waterways' Division of the Department of Environment and Infrastructure (Ministry of the Flemish Community, Anonymous 1995). The North Sea opens broadly to the Atlantic in the North. The fetch is therefore largest in the northern direction (Figure 1b). Few winds however come from the north; the main wind direction was south-west during the years 1996 and 1997 (Figure 1a), which might result in a lower exposure rate for the Belgian coast. However, surge is an important feature in this semi-enclosed marine ecosystem (Bijl 1997). The characteristic shape of the basin can produce strong storm surges, which can increase in their effects southwards. In 1996, 85% of the waves were smaller than 100 cm, but in 1997 this was the case for only 58%. Moreover, tidal currents are very strong: tides mainly enter around the northern British coast but are then constrained by narrowing and shallowing of the sea, resulting in tidal ranges at the Belgian coast between 4 and 5 m. All in all, the North Sea can be considered as intermediately exposed. Although the west side of the Belgian coast might be more sheltered due to the extensive sand bank system, tidal currents are still very strong and the open nature of the surf zone makes it very vulnerable to events further offshore.

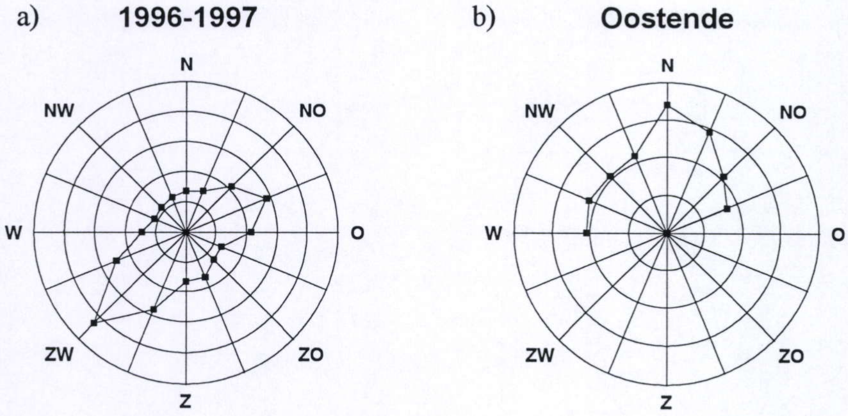

Figure 1. (a) The prevailing wind direction during the years 1996–1997 and (b) the fetch given for Oostende (the latter data are log(x+1) transformed and plotted on a scale from 0 to 4).

Total **epibenthic** catch density exceeded 400 individuals per 100m² on several occasions, while data of shallow subtidal stations along the Belgian coast (< 10 m depth) reported all total catch densities to be lower than 40 individuals per 100m² in autumn of 1997 and 1998 (Cattrijsse unpublished data, Table 2). Although sampling device and strategy differed, these results might give indications of minimum estimates of the expected densities. During the year total catch biomass in the surf zone exceeded several times 20 g AFDW/100m² and maxima of > 45 g AFDW/100m² were reported (see also Appendix 6). Although many juveniles are present in the surf zone, these data are comparable with those of the adjacent subtidal, where total catch biomass exceeded in several subtidal stations 40 g AFDW/100m² (Cattrijsse unpublished data). Thus, also for the epibenthos, the Belgian surf zone can be indicated as an important area.

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[2] source: Aerographer's/Meteorologist's basic training series. http://www.tpub.com/weather1/index.htm.

Table 2. Epibenthic catch censity of autumn 1997 and 1998 of 4 stations in the shallow subtidal of the Belgian coast (unpublished data from Cattrijsse).

	1997				1998			
station	**115**	**120**	**140**	**702**	**115**	**120**	**140**	**702**
Pleuronectes platessa	0.04	0	0.04	0.04	-	0.19	0	0.22
TOTAL	12.33	5.15	34.26	29.74	-	29.41	1.12	17.19

Community composition. Although both assemblages were clearly dominated by one or more species (> 75% of the **hyperbenthos** were the mysids, mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei*, > 80% of the **epibenthos** was represented by the brown shrimp *Crangon crangon*), many other species were also recorded (180 biological and 207 functional hyperbenthic species, 32 biological and 36 functional epibenthic species in total) (Chapters I and II, Appendix 2). Surf zone habitats are typically dominated by relatively few species (Lasiak 1984b, Ross et al. 1987, Brown & McLachlan 1990, Romer 1990). Generally, exposed and dissipative sandy beaches are characterised by a certain faunistic originality, few resident species (mainly good swimmers), high dominance of a few species (e.g. mysids), high densities and biomasses and patchy distributions (Brown & McLachlan 1990), which is supported by the present study.

All these results indicate the importance of the surf zone of the Belgian sandy beaches for hyper- and epibenthic organisms. An important number of species can be found in the surf zone and high total density and biomass are recorded.

Residential status hyper- and epibenthic species in the Belgian surf zone

'Residents'. Several species were found to reside within the surf zone habitat during most of the year (15 hyperbenthic and 7 epibenthic species, see Tables 4 and 2 of Chapters IA and IIA respectively), although migration towards deeper waters to avoid cold temperatures during winter is probable for at least some of these species (e.g. the mysid *Mesopodopsis slabberi*). Most of the residential **hyperbenthic** species have a true hyperbenthic life style (e.g. most mysids and the amphipod *Atylus swammerdami*). Some are known to inhabit the underlying sand and make more or less frequent vertical excursions into the water column (e.g. the isopod *Eurydice pulchra*, and amphipods of the genus *Bathyporeia*) (Watkin 1939, 1941, Colman & Segrove 1955). Still others are associated with drifting detritus (e.g. the amphipod *Gammarus crinicornis*) (Jones & Naylor 1967, Lincoln 1979, Mauchline 1980). All residential **epibenthic** species, have previously been reported as common residents in the surf zone of sandy beaches by several authors (e.g. Miller 1986, Gibson et al. 1993, 1996, Wennhage & Pihl 1994 and references therein, Hayward & Ryland 1996, Rogers & Millner 1996). The two crustaceans, the brown shrimp *Crangon crangon* and the shore crab *Carcinus maenas*, are ubiquitous members of the larger motile epifauna on northern European beaches (see Gibson et al. 1993 and references therein). Of the residential fish species, plaice *Pleuronectes platessa*, herring *Clupea harengus* and sprat *Sprattus sprattus* were exclusively caught as juveniles, as was the case for most other fish species caught. The resident gobies *Pomatoschistus minutus* and *Pomatoschistus lozanoi* spend large parts of their life cycle in the surf zone, since postlarvae, juveniles as well as adult specimens were regularly recorded. If other hyper-, epi- and macrobenthic studies are considered (e.g. Mees 1994, Degraer et al. 1999, Dewicke unpublished), most hyper- and epibenthic residents found, could be expected

in the study area, however, their densities were remarkably high. The value of this study is therefore mainly a first inventory and the description of the distribution patterns of the different species.

'Migrants'. Almost all **hyperbenthic** species indicated as 'migrants' have a planktonic (e.g. jellyfish, copepods) or endobenthic (e.g. most amphipods, polychaetes) lifestyle. Planktonic organisms are probably passively transported toward the coast. Active migration is plausible for species like the chaetognath *Sagitta elegans*, but also for several endobenthic species (e.g the isopod *Eurydice pulchra*), as some of them are mainly found during well-defined periods. Leaving the sediment to swim in the overlaying water may be a strategy related to their reproduction cycle (e.g. Colman & Segrove 1955). The occurrence or absence of **epibenthic** migrants is probably mainly linked to both a seaward migration as water temperature drops below a critical value in winter (e.g. the crabs *Liocarcinus holsatus* and *Cancer pagurus* and the weever *Echiichthys vipera*), and to the use of the surf zone as a nursery and/or transient area during restricted periods when they migrate from the estuary to the open sea (or vice versa) (e.g. juvenile bass *Dicentrarchus labrax* and brill *Scophthalmus rhombus*) (see below). Next to the intensive use of the surf zone by several residential species, the area is obviously temporarily important for a number of early life stages of epibenthic species.

'Sporadics'. Finally, a large number of sporadically occurring species adds to the typical composition of surf zone fauna. Most of the species found have a wide distribution area and can occur in the shallow surf zone as well as in the deeper subtidal region. However, some of the **hyperbenthic** sporadics are known to be restricted to the water column of very shallow water or intertidal areas: the isopod *Idotea granulosa* (Naylor 1955), the amphipods *Corophium insidiosum*, *Corophium acherusicum* and *Hyale nilssoni* (Lincoln 1979). Organisms may be washed out of the nearby estuaries (e.g. the amphipod *Gammarus zaddachi*) or of the higher reaches of the beach (e.g. the isopod *Jaera nordmanni*). Typical intertidal endobenthic organisms can occur in low densities in the water column (e.g. the cumacean *Cumopsis goodsiri*, the isopod *Eurydice affinis*, Jones & Naylor 1967, Jones 1976). Also, species associated with hydroids and/or algae (e.g. most sea spiders, King 1974, the isopod *Idotea metallica*, Naylor 1957) that are frequently transported towards the shore and accumulate into the surf zone are not likely to be caught with a hyperbenthic sledge in deeper waters. This study also indicates that several species are less rare than formerly expected (e.g. the mysid *Siriella armata*, the cnidarian *Margelopsis haeckeli*, see mainly Appendix 3C). Moreover, some species were not yet recorded from the Belgian coast (e.g. the sea spider *Nymphon brevirostris*) (Marc Peeters pers. comm.). **Epibenthic** sporadics are most likely coincidentally caught individuals from deeper waters.

Seasonality in surf zone assemblages

As already discussed above, clear seasonal distribution patterns were observed for both the hyper- and epibenthic communities. Next to general seasonal fluctuations in abundance and species composition of the holo**hyperbenthos**, three recruitment peaks could be observed for the merohyperbenthic organisms: winter, spring and summer-autumn (Chapter IA). Winter was characterised by very low total density and diversity, and by the presence of fish eggs. In spring, total merohyperbenthic densities were highest and postlarvae of the shore crab *Carcinus maenas* dominated, while in summer the merohyperbenthos was dominated by postlarvae of gobies *Pomatoschistus* species. Furthermore, a clear succession could be observed as several postlarval fish species appeared for longer or shorter periods within the surf zone during the year. **Epibenthic** catch densities and numbers of fish species varied considerably between samples and fluctuations in abundance at the different sites were not in phase with one another. However, when the stations were treated as separate communities, clear seasonal patterns could be observed (Chapter IIA). Although the highest number of species (and highest catch density) was found during summer-autumn, a clear dominance of *Crangon crangon* resulted in a low evenness. Indeed, as is often the case, the variation in the epibenthic community largely reflects the variability in numbers of the dominant species (Layman 2000). Several species absent in winter re-appeared in spring. The abundance of intertidal fish species is generally highest in late spring and summer due to the influx of juveniles of both resident and transient species following their breeding seasons (Gibson & Yoshiyama 1999, Layman 2000). In most temperate regions, an offshore migration of fish species in late summer and autumn is observed, which results in a decline of both density and diversity in the community (Gibson 1999). For some species, however, wintertime is the only period in which they occur in the surf zone (e.g. juvenile sea bass *Dicentrarchus labrax*). It seems likely that temperature either directly or indirectly (i.e. by influencing the time of spawning) is the underlying mechanism of seasonal surf-zone dynamics (Layman 2000). Moreover, Clark et al. (1996b) suggest that seasonal fluctuations in the faunal abundance of the surf zone are especially important on beaches in which temperature change exceeds 20°C annually, a criterion that was met in our study. To conclude, the Belgian surf zone is frequented by early life stages of several species during most of the year.

Other influencing factors

Temporal distribution patterns. Although clear temperature-related seasonal distribution patterns were observed, the **hyper**- and **epibenthic** communities of the surf zone can also be influenced severely by hydrodynamic factors and this both by short-term events (e.g. storm) and long-term effects (influence on morphodynamics of the beach). This is not surprising as the surf zone of exposed beaches can be very dynamic and wave action is one of its main characteristics (Chapters I and II). On the other hand, this turbulence may also have affected sampling efficiency. With increasing surf action, sampling becomes more difficult: not only is it harder to move steadily forward at the same sampling speed, but also the net currents perpendicular to the shore line become stronger, thus moving the nets sideways. Although this might have diminished the catch efficiency, it is questionable whether the species present at that moment have the same capabilities to produce escape reactions as in calmer circumstances.

Spatial distribution patterns. Although both hyper- and epibenthic assemblages are susceptible to spatial variation between sites, several differences can be observed. While for the **hyperbenthos**, seasonal patterns were found to be very strong and the same seasonal pattern was found in all stations, temporal variation in the **epibenthos** was greatly masked by spatial differences between sites (Chapters IA and IIA). This may be due to the higher mobility of the epibenthic species, also resulting in a larger variation in catch efficiency. Moreover, and probably most important, densities of the epibenthos are much lower than of the hyperbenthos. A higher sampling effort with replicate sampling is therefore probably necessary. Nevertheless, within each sampling station, clear seasonal patterns were observed.

On a short-term scale, spatial differences were found both in species richness and in density (Chapters IB and IIB). In general, highest hyper- and epibenthic densities were found on flat, wide beaches, but also intermediate sites (relatively in our study area) and sites with a high turbidity were characterised with high densities and a high number of species. A high turbidity might be an important protection, since the mobile and relatively homogenous nature of the substratum on sandy shores means that few refuges are available. Also the protection that organisms gain by occurring on flat, shallow beaches (less predation, less wave exposure) is probably outweighed by increased fluctuations in environmental variables such as salinity and a higher risk of retention on the beach at ebb-tide, resulting in a higher diversity at intermediate sites. Less mobile and more sediment-associated hyperbenthic animals such as cumaceans and several amphipods were more species-specific restricted to certain types of beaches.

All beaches studied were macro-tidal beaches (tidal range > 4 m, Short 1991) open to the sea. They are low-tide bar/rip (LTBR) or ultra-dissipative (UD) beaches according to the modified morphodynamic classification scheme of Masselink & Short (1993) (Short 1996). UD beaches are generally flat and featureless and have very wide intertidal zones. LTBR beaches are beaches with a relatively steep upper intertidal zone, but are fronted by a low-gradient mid-intertidal zone, possibly with swash bars, and then bar and rip morphology around low tide level. This type of beaches has complex morphodynamic signatures and may experience reflective (high tide), intermediate and dissipative (low tide) surf zone conditions through the tidal cycle. The bar and rip morphology only exists on the low tide beach and is active only on either side of low tide. Reflective-type beaches show lower species richness and abundances than dissipative ones (San Vicente & Munilla 2000). In general, other surf zone studies only consider these intertidal beach characteristics. In the present study, an attempt was made to incorporate the adjacent shallow subtidal characteristics, as they may differ substantially from those of the beach and since the 'surf zone', as defined here, also moves towards this area during the tidal cycle. The effect of intertidal slope (and correlated variables) on **hyperbenthic** density is mainly visible in the holohyperbenthos, and especially in the mysid species. In contrast, merohyperbenthic organisms were mainly found on beaches with intermediate subtidal slopes characterised by a high turbidity, and this both in terms of density and in the number of species. These results are not surprising since early life stages of most organisms are more susceptible to water movements and thus to the circumstances further offshore. Inter- and subtidal slope separately were not correlated with the spatial structure of the **epibenthic** assemblages. However, if the combination of both was considered, some patterns were observed. This study indicates that both intertidal and subtidal characteristics should be considered if the (mobile) surf zone fauna is investigated.

Turbulence. The surf zone is a region of high turbulence primarily generated through breaking waves and - to a lesser extent - by shear at the benthic boundary layer. It is widely acknowledged that wave breaking at the surface provides the dominant source of water column turbulence[3]. Despite the strong turbulence characteristic for surf zones of exposed sandy beaches, it is remarkable that active migration and maintenance of position seems to remain possible for several **epi-** and **hyperbenthic** species. While passive transport towards the surf zone is most likely to occur (e.g. polychaete larvae, Chapter IA), active migration (e.g. mysids) and/or retention (e.g. I-group plaice) is suggested for at least some species (Chapters I and IV).

Although not discussed in the previous chapters, vertical distribution patterns of the hyperbenthic species during the 24h-cycles, confirmed these results: several species were found to be able to maintain their vertical position in the water column. As an example, the vertical distribution coefficients ('swimming activity coefficients' K_1 and K_2, Elizalde et al. 1991) of two mysids (*Mesopodopsis slabberi* and *Schistomysis spiritus*) are given in Figure 2.

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[3] source: http://www.agu.org/revgeophys/holman01/node10.html

$$K_1 = N_1/N_t$$
$$K_2 = N_2/N_t$$

with N_1 and N_2 the density of the upper and lower net respectively and N_t the total density.

Mann-Whitney U tests confirm that densities of the upper and lower net of the hyperbenthic sledge differed significantly ($p < 0.05$) for the 2 species. While *M. slabberi* mainly occurs higher in the water column, *S. spiritus* is clearly able to stay in close proximity of the bottom. If hydrodynamic conditions grow worse however (i.e. storm), good swimmers like mysids are capable of leaving the surf zone and avoiding the turbulence (see also Colman & Segrove 1955).

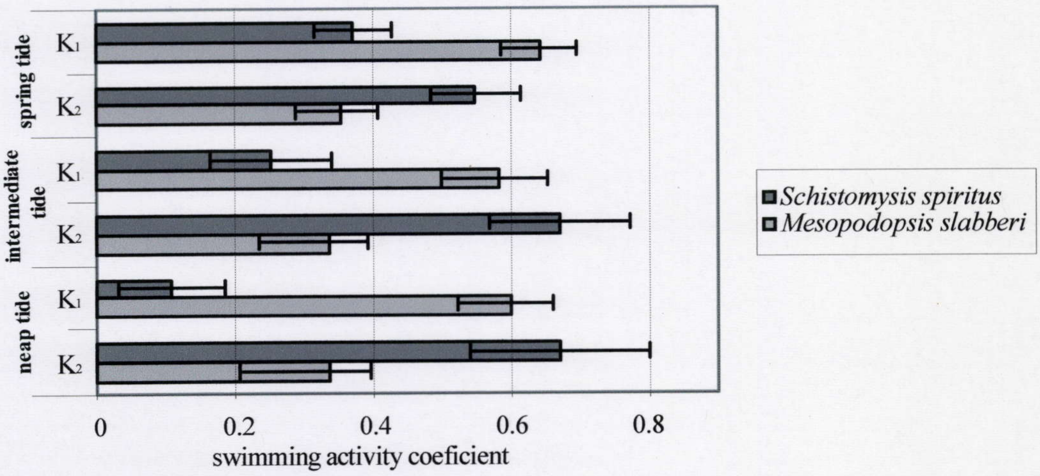

Figure 2. Average swimming activity coefficients ± SE (Elizalde et al. 1991) for the two main mysid species during three 24h-sampling cycles.

Surf zone food web

Trophic relationships amongst the macrofauna of an exposed sandy beach and surf zone in Algoa Bay (South Africa) are illustrated in Figure 3 of McLachlan & Romer (1990). The macrofauna food web is centred in the surf water and is dominated by the phytoplankton-zooplankton-fish pathway. Their high biomass and turnover, their central importance as primary consumers, and their availability as food for higher trophic levels make mysids an important component of the surf-zone fauna. Their extensive vertical and horizontal migrations induce cyclical redistribution of biomass that is of fundamental importance to the trophodynamics of the system. On exposed beaches, a few resident hyperbenthic populations are responsible for most of the global secondary production (Brown & McLachlan 1990). In general, all feeding types in fish display a high degree in opportunism and zooplankton (hyperbenthos) dominates the diets.

In the present study (Chapter III), prey items of all flatfish species indeed included hyperbenthic (e.g. mysids), endobenthic (e.g. polychaetes) and epibenthic (e.g. shrimps) species. Little dietary overlap was observed. If diet overlap did occur, it mainly involved prey species that are dominant in the surf zone of the studied beaches, such as shrimps and mysids. These results confirm the opportunistic utilisation by flatfish of the available food resources in surf zone ecosystems. Although in the present study only flatfishes were investigated, several authors support this hypothesis and prove it to be also valid for other surf zone teleost fish species (e.g. McLachlan & Romer 1990). Such opportunistic utilisation of food resources can be important for teleosts frequenting physically stressed environments such as surf-exposed beaches. The surf zone itself is not only a physically dynamic habitat - many of the associated faunal assemblages are themselves highly dynamic. Short-term variations in wind strength and direction and their subsequent effects on surf conditions probably play a major role in the control and interaction of these assemblages (McLachlan 1983, Lasiak 1984). Furthermore, the suggestion of partitioning of food resources by prey type and size and the spatial (and temporal) separation of foraging habitats shown by these species (also found by Modde & Ross (1983) in a surf zone habitat in the northern Gulf of Mexico) is surprising in view of the apparent physical harshness, low spatial heterogeneity and the temporary use of the habitat.

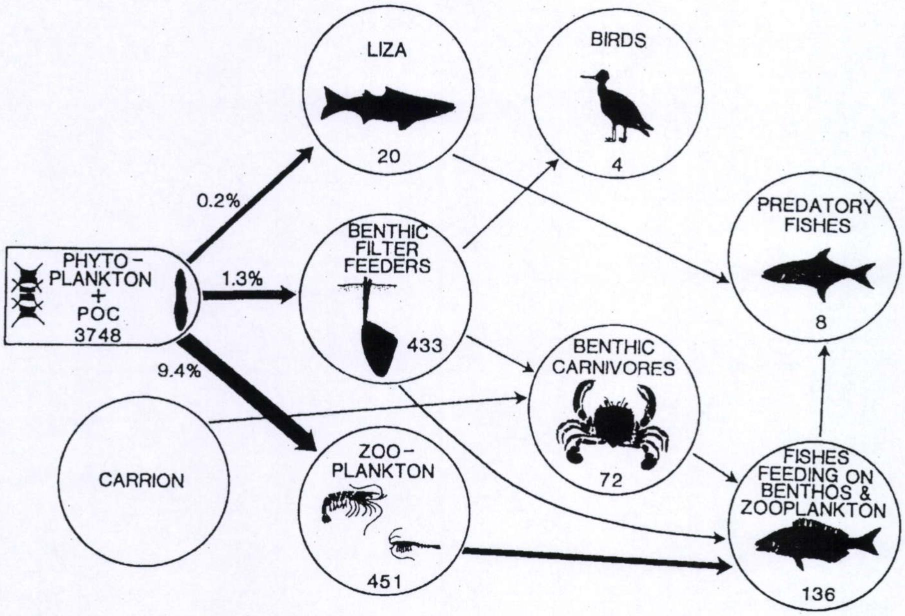

Figure 3. Trophic relationships amongst the macrofauna of an exposed sandy beach and surf zone in Algoa Bay (South Africa) (after McLachlan & Romer 1990). Biomass values in gC^{-1}. Inputs to mullet, filter-feeding benthos and zooplankton as percentages of total available carbon in the ecosystem.

Also, two strategically different feeding habits could be distinguished in the 5 flatfish species. Turbot *Scophthalmus maximus* and brill *Scophthalmus rhombus* mainly fed on large, highly mobile prey (e.g. fish, shrimp and mysids) and had a rather narrow prey-spectrum, whereas plaice *Pleuronectes platessa*, dab *Limanda limanda* and sole *Solea solea* ate more benthic prey (e.g. polychaetes) and had a broader prey-spectrum. The diets of the first two species reveal part of the main interactions between the hyper- and epibenthos, whereas those of the latter three species reveal important links between the epibenthos and the macro-endobenthos within the local surf zone food web.

Tidal and diurnal periodicity

Despite the turbulent conditions of the studied sites, clear tidal (e.g. I-group plaice *Pleuronectes platessa*, the brown shrimp *Crangon crangon*) and diurnal (e.g. juvenile sole *Solea solea*) periodicities were observed in many macrocrustacean and demersal fish species (Chapter IV). Gibson et al. (1998) identified three main reasons for such horizontal migrations: (1) foraging considerations, (2) predator avoidance, and (3) selection of suitable environmental conditions. The former two explanations are probably important in the shallow surf zone.

Although the extremely turbulent conditions of the surf zone possibly have their effect on the behaviour of many species, some species such as I-group plaice are most likely capable of active retention along the water edge during ebb tide and migration on the beach at flood.

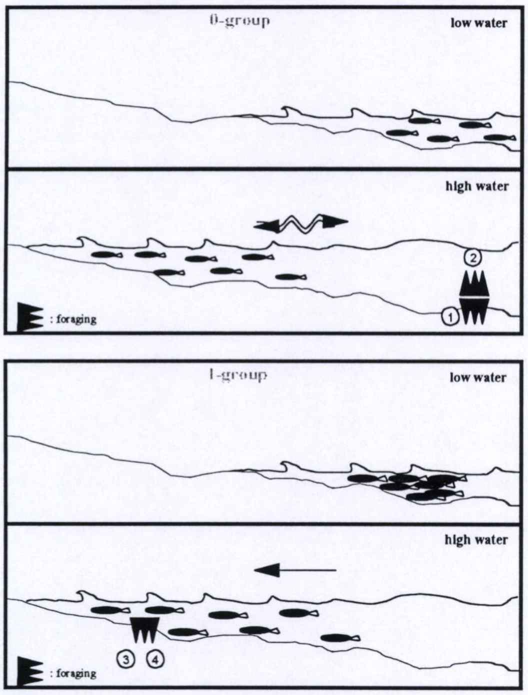

Figure 4. Horizontal distribution patterns during a tidal cycle for 0- and I-group plaice *Pleuronectes platessa*, with indication of their main feeding grounds (1-4: see text).

Furthermore, the Belgian sandy beaches are used as a feeding ground by I-group plaice (Chapters III and IV). An opportunistic utilisation of available food resources is again suggested. I-group plaice clearly migrate high up the beach during flood to disperse in order to profit from the rich macrobenthic area (mainly the polychaete *Scolelepis squamata* (3) and ends of *Arenicola* species (4)), while the 0-group feeds mainly on the most abundant hyper- and macrobenthic organisms from somewhat deeper water (mainly palps of the polychaete *Magelona papillicornis* (1) and cyprid larvae (2)) (Figure 4).

Nursery/transient function of Belgian surf zone

The Belgian surf zone may act as a nursery and/or transient area for at least some species, both for the hyper- and epibenthic stages. A good nursery is characterised by a good **location**; transport of early life stages towards the area should be possible. Also the area should be **rich** enough to sustain sufficient feeding of the young individuals. Ideally, it should further provide a **refuge** for the youngsters to hide from potential predators. All in all, a good nursery enhances the chances of early life stages to survive and recruit to the adult stocks.

The data presented here indicate that high numbers of these early life history stages of both fish and macrocrustaceans are indeed transported towards the surf zone of Belgian sandy beaches during most of the year (Chapters IA and IIA). Monthly average hyperbenthic densities were generally higher in the surf zone than in the Dutch Delta area, including the Westerschelde estuary (Chapter IA, Appendix 10). The same holds true for the catch densities of several epibenthic species (e.g. juvenile plaice *Pleuronectes platessa*) as compared to those reported from the deeper adjacent regions of the Belgian coast (see below). The **location** of the Belgian sandy beaches adjacent to a rich shallow sand bank system in the west and the large estuary of the Westerschelde in the east may enhance the importance of the surf zone as a transient area between both sites or towards the open sea. Many juvenile marine fishes use the Westerschelde estuary as a nursery ground (e.g. De Veen et al. 1979, Cattrijsse et al. 1994, Hostens 2000). In the present study, some of these species were found during well-defined periods in the surf zone (Chapter IIA). Other species were found more sporadically throughout the year (e.g. sole *Solea solea*) or during longer periods (brill *Scophthalmus rhombus*). For example, while juvenile bass *Dicentrarchus labrax* is most abundant in the Westerschelde during October and November (Hostens et al. 1996), it was mainly found in the surf zone in December. The species may use the surf zone as a transient area between the estuary and the open sea.

The nursery function of the Belgian sandy beaches can be illustrated with plaice *Pleuronectes platessa*, as this species is one of the major components of both the hyper- (as postlarvae) and epibenthos (as 0- and I-group juveniles). Postlarval plaice reaches the surf zone in February (Chapter IA). These postlarvae probably concentrate in the surf zone at the onset of their demersal life style, since most organisms were caught just after their metamorphosis was completed (±12 mm). Settlement of larval flatfish in surf zones of sandy beaches has been reported before by Amarullah et al. (1991) and Subiyanto et al. (1993). Kinoshita (1993) demonstrated that surf zones provide a good foraging environment for larval (and juvenile) fishes.

Juvenile individuals remain in the surf zone area for at least one year, since both the 0- and I-group was caught and individuals were present all year round (Chapter IIA). Juvenile plaice is a common member of shallow surf zones (e.g. Wennhage & Pihl 1994 and references herein). However, the species generally prefers more sheltered areas in comparison to other flatfish species such as brill *Scophthalmus rhombus* and turbot *Scophthalmus maximus* (Riley et al. 1981). Juvenile plaice is indeed less abundant at the exposed Belgian coast than in the shallow bays of the surrounding areas of the UK and continental NW Europe (Rogers et al. 1998). The turbulence that characterises Belgian surf zones probably makes it an energetically expensive habitat for juvenile plaice, as is also demonstrated by the preliminary growth data (Chapter IIA). Nevertheless, catch densities are still higher in the surf zone (between 0.9 and 3.5 ind./100m^2 in autumn of 1996), as compared to the adjacent shallow subtidal area of the Belgian coast (between 0 and 0.22 ind./100m^2 in autumn of 1997-1998, see also Table 2). Although sampling device and strategy differed and possible interannual variation might be responsible for these differences, these data can give some indication of the minimum expected densities in both areas. If postlarvae are transported into the area, the surf zone is probably a satisfactory alternative for the more sheltered bays on the other side of the English Channel. It is a relatively **rich** area, at least with respect to macro- (Degraer et al. 1999) and hyperbenthos (Chapter IA), containing the main prey items of juvenile plaice. While the more vulnerable 0-group individuals feed in somewhat deeper water, the I-group individuals profit from the rich intertidal areas as the water covers the beach during flood tide (Chapter IV).

Although no hard data are available, predation by larger predators seems to be unlikely in the shallow surf zone. Although **protection** can be gained by occurring on flat, shallow beaches (less predation, less wave exposure), this is probably outweighed by increased fluctuations in environmental variables such as salinity and higher risks of retention on the beach at ebb-tide (Chapters IB and IIB). Although the turbulence and turbidity may have affected sampling efficiency, the mobile and relatively homogenous nature of the substratum on sandy shores means that few refuges are available and that protection due to higher turbidity may be important. Indeed, the sites with the highest turbidity were characterised by the highest number of species and highest densities. Juvenile plaice, however, could not directly be linked to these patterns. Furthermore, it occurred at all sites along the coast in comparable densities (Chapter IIB). More detailed research is necessary to reveal the influencing factors concerning spatial occurrence of juvenile plaice.

To conclude, as plaice normally prefers more sheltered conditions, the nursery function for this species may not be optimal, but is nevertheless substantial. Van der Veer et al. (2000) state that recruitment to a stock appears to be related to the quantity of juvenile nursery habitats. The Belgian surf zone as an additional nursery for plaice (next to e.g. the Wadden Sea, Fonds 1978, Zijlstra 1978) should therefore not be neglected and investigated further to evaluate the importance of this area for the recruitment of plaice to the adult stock. Furthermore, the nursery value of the Belgian surf zone for other species should be studied in detail. Although the emphasis should lie on early life stages of fish and macrocrustaceans, also gravid animals should not be neglected as they may migrate into the area to spawn or breed (e.g. the shrimp *Philocheras trispinosus*). The Belgian surf zone might therefore be important to many species.

RECOMMENDATIONS FOR FUTURE RESEARCH

This study is a first attempt to study the hyper- and epibenthic fauna of the surf zone of Belgian sandy beaches. Many gaps in the current knowledge still remain. A first task that will be performed is the investigation of tidal, diurnal and semi-lunar periodicity of the surf zone hyperbenthos. Samples for this study were already taken and analysed (see Chapter IV). Although they are not discussed in depth, density and biomass data are presented in Appendices 3C and 4C, respectively.

Future research should include a thorough study of the feeding ecology and behaviour of the brown shrimp *Crangon crangon* as it is the dominant epibenthic species of the study area. Since the species is also commercially important, it is highly recommended to evaluate the nursery function of the Belgian surf zone. A more detailed study on growth and other population parameters of the dominant species, should give more insight into the survival conditions within the study area and thus in the nursery value of the surf zone of Belgian sandy beaches.

Since the food web of surf zones of exposed sandy beaches is dominated by the phytoplankton-zooplankton-fish pathway (McLachlan & Romer 1990), information on the phytoplankton component is of major importance to understand the interactions. However, no information is available on phytoplankton inhabiting the Belgian surf zone. In well-developed dissipative surf zone systems, the major part of the primary production is delivered by 'surf-diatom' populations (Lewin & Schaefer 1983, Wooldridge 1989, McLachlan & Romer 1990). During a study of benthic protists along the Belgian coast (Blondeel 1996), two species (both occurring in high densities) could be identified that are described as typical 'surf-zone diatoms' at the South-African, South-American and South-Australian sandy coasts (Talbot et al. 1990): *Chaetoceros armatum* and *Asterionella glacialis*. Further research is necessary to determine whether these diatoms indeed behave as 'surf-diatoms' and in what way they contribute to the primary production of the surf zone of the Belgian coast. In more dissipative beach systems, 'surf-diatom' production may be higher, whereas at reflective beaches, which lack substantial surf zones, surf zone primary producers are possibly impoverished or absent (Lewin & Schaefer 1983). Also, estimates of secondary production are needed to determine the significance of the studied faunistic groups and to further unravel the local food webs.

To fully understand the surf zone habitat and its inhabitants, the investigation of the shallow troughs at the beach in which the water is retained during ebb tide should not be neglected. Higher species richness and total fish abundance occurred in the shallow water (< 0.4 m) of runnels on a sandy beach at the Virginia barrier islands (Layman 2000). The increased richness and abundance in these low-energy habitats on the backside of small sand bars, suggests a small-scale movement of fishes parallel to the beach face as fishes seek sheltered runnel habitats.

Finally, for a good beach management, it is recommended to investigate the effects of other environmental factors such as tourism and recreational and/or commercial fisheries on the surf zone fauna.

GENERAL CONCLUSIONS

1. This study has demonstrated that the surf zone of sandy beaches is an important habitat within the marine ecosystem of the North Sea. The Belgian surf zone can be seen as an important extension of the shallow sandbank system in front of the coast. A large number of species characterises the area and both densities and biomass of hyper- and epibenthic communities are high.
2. The dominant hyperbenthic species are mysids, mainly *Mesopodopsis slabberi*, *Schistomysis spiritus* and *Schistomysis kervillei* (holohyperbenthos). Other common groups are early life stages of caridean shrimps, brachyuran crabs and fish, small cnidarians, isopods and amphipods. The brown shrimp *Crangon crangon* strongly dominates the epibenthos. Other important species are the shore crab *Carcinus maenas,* juvenile plaice *Pleuronectes platessa*, herring *Clupea harengus* and sprat *Sprattus sprattus*, and the gobies *Pomatoschistus minutus* and *Pomatoschistus lozanoi*. Many juveniles can be found.
3. Next to the early life history stages of many fish and macrocrustacean species, several other organisms migrate seasonally into the surf zone. These migrations can be horizontal (e.g. the swimming crab *Liocarcinus holsatus*) or vertical (e.g. several polychaetes). Although more information is needed on several population dynamical aspects (mainly survival conditions), it can be stated that the study area is used as a nursery and/or transient area by several hyper- and epibenthic species.
4. Water temperature is either directly or indirectly the main underlying structuring factor of seasonal surf-zone dynamics. Other factors such as hydrodynamic conditions, local beach characteristics (e.g. intertidal and subtidal slope) and turbidity are also important. Although the hydrodynamic conditions of the surf zone can have a major influence on the total community composition and the distribution patterns of several faunistic groups, some species have the capacity to withstand turbulent circumstances (at least within 'normal' limits). They are either capable of active migration (e.g. I-group plaice) or vertical (e.g. mysids) or horizontal retention (I-group plaice).
5. Although part of the local surf zone food web has been elucidated, many gaps still remain. Most importantly, estimates of primary and secondary production are necessary, and the feeding ecology of different key species (e.g. shrimp and mysids) remains to be described.

REFERENCES

REFERENCES

ERRATA

Missing references:

Baretta-Bekker, J.G., E.K. Duursma & B.R. Kuipers, 1992. Encyclopedia of Marine Sciences Springer-Verlag, Berlin Heidelberg, 311p.

Bergman, M.J.N., H.W. van der Veer & J.J. Zijlstra, 1988. Plaice nurseries: effects on recruitment. J. Fish Biol. 33, Suppl. A, 201-218.

Aarnio, K., E. Bonsdorff & N. Rosenback, 1996. Food and feeding habits of juvenile flounder *Platichthys flesus* (L.) and turbot *Scophthalmus maximus* L. in the Åland archipelago, northern Baltic Sea. J. Sea Res. 36(3/4), 311-320.

Allen, L.J. & M.H. Horn, 1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitoos Bay, California. Estuar. Coast.Shelf Sci. 3, 371-380.

Amarullah, M., H. Subiyanto, T. Noichi, K. Shigemitsu, Y. Tamamoto & T. Senta, 1991. Settlement of larval japanese flounder (*Paralichthys olivaceus*) along Yanagihama Beach, Nagasaki prefecture. Bull. Fac. Fish. Nag. Univ. 70, 7-12.

Anderson, W.D. Jr., J.K. Dias, R.K. Dias, D.M. Cupka & M.A. Chamberlain, 1977. The macrofauna of the surf zone off Folly Beach, South Carolina. NOAA Tech. Rep. NMFS SSRF-704.

Anonymous, 1995. Hydrometeogegevens jaaroverzicht 1995, deel 2. Statistische verwerkingsresultaten, Golfregistraties. Ministerie van de Vlaamse Gemeenschap, Dep. Leefmilieu en Infrastructuur, Adm. Waterwegen en Zeewezen, Afd. Waterwegen Kust, tabellen.

Anonymous, 1996. Nondirectional and directional wave and data analysis procedures. NDBC Technical Document 96-01. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, 37p.

Ansell, A.D. & R.N. Gibson, 1990. Patterns of feeding and movement of juvenile flatfishes on an open sandy beach. In: Barnes M. & R.N. Gibson (eds.). Tropic relationships in the marine environment. Proc. 24th Europ. Mar. Biol. Symp., 191-207.

Berg, J., 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Mar. Biol. 50, 263-273.

Berghahn, R., 1987. Effects of tidal migration on growth of O-group plaice (*Pleuronectes platessa* L.) in the North Frisian Wadden Sea. Meeresforsch. 31, 209-226.

Beukema, J.J., 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. Neth. J. Sea Res. 10, 236-261.

Beyst, B. & J. Mees, submitted a. Factors influencing the spatial occurrence of surf zone hyperbenthos of Belgian sandy beaches.

Beyst B., A. Cattrijsse & J. Mees, 1999a. Feeding ecology of juvenile flatfishes of the surf zone of a sandy beach. J. Fish Biol. 55, 1171-1186.

Beyst B., D. Buysse, A. Dewicke & J. Mees, in press a. Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns. Est. Coast. Shelf Sci.

Beyst, B., K. Hostens & J. Mees, in press b. Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: temporal variation. J. Sea Res.

Beyst, B., K. Hostens & J. Mees, submitted b. Factors influencing fish and macrocrustacean communities in the surf zone of sandy beaches in Belgium: spatial variation.

Beyst, B., J. Mees & A. Cattrijsse, 1999b. Early postlarval fish in the hyperbenthos of the Dutch Delta (south-west Netherlands). J. Mar. Biol. Ass. U.K. 79, 709-724.

Beyst, B., J. Vanaverbeke, M. Vincx & J. Mees, in press c. Tidal and diurnal periodicity in macrocrustaceans and demersal fish of an exposed sandy beach, with special emphasis on juvenile plaice (*Pleuronectes platessa* L.). Mar. Ecol. Prog. Ser.

Bijl, W., 1997. Impact of wind climate change on the surge in the southern North Sea. Climate Res. 8(1), 45-59.

Blaber, S.J.M., 1981. The zoogeographic affinities of estuarine fishes in south-east Africa. S. Afr. J. Sci. 77, 305-307.

Blaber, S.J.M. & T.G. Blaber, 1980. Factors of affecting the distribution and abundance of juvenile estuarine and inshore fish. J. Fish Biol. 17, 143-162.

Blaber, S.J.M., J.W. Young & M.C. Dunning, 1985. Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of north-western Australia. Austr. J. Mar. Fresh. Res. 36, 247-266.

Blondeel, A., 1996. Systematisch-ecologische studie van intertidale benthische protistengemeenschappen van de Vlaamse kust. Unpublished graduate thesis, Ghent University, 56p.

Boddeke, R., 1976. The seasonal migration of the brown shrimp *Crangon crangon*. Neth. J. Sea Res. 10, 103-130.

Boesch D.F. & R.E. Turner, 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7, 460–468.

Braber, L. & S.J. De Groot, 1973. The food of five flatfish species (Pleuronectiformes) in the southern North Sea. Neth. J. Sea Res. 6(1-2), 163-172.

Bray, J.R. & J.T. Curtis, 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27, 325-349.

Brown, A.C. & A. McLachlan, 1990. Ecology of sandy shores. Elsevier, Amsterdam, 340pp.

Burrows, M. T., 1994. Foraging time strategy of small juvenile plaice: a labatory study of diel and tidal behaviour patterns with Artemia prey and shrimp. Mar. Ecol. Prog. Ser. 115, 31-39.

Burrows, M. T., R. N. Gibson & A. Maclean, 1994. Effects of endogenous rhythms and light conditions on foraging and predator-avoidance in juvenile plaice. J. Fish Biol. 45 (suppl.A), 171-180.

Cattrijsse A. & A. Dewicke, in press. Hyperbenthic biodiversity patterns of the Belgian coastal waters. In: Cattrijsse A. & M. Vincx (eds). Biodiversity of the benthos and the avifauna of the Belgian coastal waters. Federal Office for Scientific, Technical and Cultural Affairs, Brussels

Cattrijsse A. & M. Vincx, in press. Biodiversity of the benthos and the avifauna of the Belgian coastal waters. Federal Office for Scientific, Technical and Cultural Affairs, Brussels

Cattrijsse, A., in press. Epifauna of the Belgian continental shelf. In: Cattrijsse, A. & M. Vincx (eds). Biodiversity of the Benthos and the avifauna of the Belgian coastal waters. Federal Office for Scientific, Technical and Cultural affairs, Brussels, 27-31.

Cattrijsse, A., E.S. Makwaia, H.R. Dankwa, O. Hamerlynck & M.A. Hemminga, 1994. Nekton communities of an intertidal creek of a European estuarine brackish marsh. Mar. Ecol. Prog. Ser. 109, 195-208.

Cattrijsse, A., J. Mees & O. Hamerlynck, 1993 The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde estuary. Cah. Biol. Mar. 34, 187-200.

Clark, B.M., 1997. Variation in surf zone fish community structure across a wave exposure gradient. Est. Coast. Shelf Sci. 44, 659-674.

Clark, B.M., B.A. Bennett, S.J. Lamberth, 1996a. Factors affecting spatial variability in seine net catches of fish in the surf zone of False Bay, South Africa. Mar. Ecol. Prog. Ser. 131, 17-34.

Clark, B.M., B.A. Benneth & S.J. Lamberth, 1996b. Temporal variations in surf zone fish assemblages from False Bay, South Africa. Mar. Ecol. Prog. Ser. 131, 35-47.

Clutter, R. I., 1967. Zonation of nearshore mysids. Ecology 48(2), 200-208.

Colman, J. S. & F. Segrove, 1955. The tidal plankton over stoupe beck sands, Robin Hood's bay (Yorkshire, North Riding). J. Anim. Ecol. 24, 445-462.

Creutzberg, F. & M. Fonds, 1971. The seasonal variation in the distribution of some demersal fish species in the Dutch Wadden Sea. Thalassia Jugosl. 7, 13-23.

Cyrus, D.P., 1983. The influence of turbidity on fish distribution in Natal estuaries. Unpubl. PhD thesis, University of Natal, Pietermaritzburg.

Cyrus, D.P. & S.J.M. Blaber, 1987a. The influence of turbidity on juvenile marine fishes in estuaries. Part 1. Field studies in Lake St. Lucia on the southeastern coast of Africa. J. Exp. Mar. Biol. Ecol. 109, 53-70.

Cyrus, D.P. & S.J.M. Blaber, 1987b. The influence of turbidity on juvenile marine fishes in estuaries. Part 2. Laboratory studies, comparisons with field data and conclusions. J. Exp. Mar. Biol. Ecol. 109, 71-91.

De Groot, S.J., 1971. On the interrelationships between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectiformes). Neth. J. Sea Res. 5, 121-196.

De Veen, J.F., R. Boddeke & K.H. Postuma, 1979. Tien jaar kinderkamer-opnames in Nederland? I Het Zeeuws estuarium. Visserij 32, 3-32.

Degraer, S., 1999. Macrobenthos of shallow marine habitats (Belgian coast) and its use in coastal zone management. Unpublished PhD thesis, Ghent University, Belgium, 156p.

Degraer, S., I. Mouton, L. De Neve & M. Vincx, 1999. Community structure and intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative sandy beach: summer-winter comparison. Estuaries 22(3B), 742-752.

Dexter, D.M., 1990. The effect of exposure and seasonality on sandy beach community structure in Portugal. Cienc. Biol. Ecol. Syst. 10, 31-50.

Ducrotoy, J.P., M. Elliott & V.N. De Jonge, 2000. The North Sea. Mar. Poll. Bull. 41, 5-23.

Edwards, R.L., 1958. Movements of individual members in a population of the shore crab, *Carcinus maenas*, in the littoral zone. J. Anim. Ecol. 27, 37-46.

Edwards, R.R.C. & J.H. Steele, 1968. The ecology of 0-group plaice and dabs at Loch Ewe. I. population and food. J. exp. mar. Biol. Ecol. 2, 215-238.

Eisma, D. & T. Fey, 1982. De kust van Rottum tot Calais. Het Spectrum, Antwerpen.

Eleftheriou, A. & N.A. Holme, 1984. Macrofauna techniques. In Holme, N.A. & A.D. McIntyre (eds.). Methods for the study of marine benthos. Blackwell Scientific, Oxford, 140-216.

Elizalde, M., J.C. Dauvin & J.C. Sorbe, 1991. Les Mysidacés suprabenthiques de la marge sud du canyon du Cap-Ferret (Golfe de Gascogne): répartition bathymétrique et activité natatoire. Ann. Inst. Océan. Paris 67, 129-144.

Elliott, B., S. Degraer, M. Bursey & M. Vincx, 1996. Intertidal zonation of macroinfauna on a dissipative, sandy beach at De Panne (Belgium): a pilot study. Biologisch Jaarboek Dodonea 64, 92-108.

Evans, S., 1983. Production, predation and food niche segragation in a marine shallow soft-bottom community. Mar. Ecol. Prog. Ser. 10, 147-157.

Feller R.J. & R.M. Warwick, 1988. Energetics. In Higgins, R.P. & H. Thiel (eds.). Introduction to the study of meiofauna. Smithsonian Institution Press, London, 181-196.

Field, J.G., K.R. Clarke & R.M. Warwick, 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37-52.

Fincham, A.A., 1970. Amphipods in the surf plankton. J. Mar. Biol. Ass. U.K. 50, 177-198.

Fonds, M., 1978. The seasonal distribution of some fish species in the western Dutch Wadden Sea. In: Dankers, N.M.J.A., W.J. Wolff & J.J. Zijlstra (eds.). Fishes and fisheries of the Wadden Sea. Balkema, Rotterdam, 42-77.

Fonds, M., 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In: Naylor, E. & R.G. Hartnoll (eds.). Cyclic phenomena in marine plants and animals. Proceedings of the 13th EMBS, Pergamon Press, Oxford, 151-156.

Gibson, R.N., 1973. The intertidal movements and distribution of young fish on a sandy beach with special reference to the plaice, *Pleuronectes platessa* L. J. Exp. Mar. Biol. Ecol. 12, 79-102.

Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of flatfishes. Neth. J. Sea Res. 32, 191-206.

Gibson, R.N., 1999. Movement and homing in intertidal fishes. In: Horn, M.H., K.L.M. Martin, & M.A. Chotkowski (eds.). Intertidal fishes: life in two worlds. Academic Press, London, 97-125.

Gibson, R.N. & R.M. Yoshiyama, 1999. Intertidal fish communities. In: Horn, M.H., K.L.M. Martin & M.A. Chotkowski (eds). Intertidal fishes: life in two worlds. Academic Press, London, 264-296.

Gibson, R.N., A.D. Ansell & L. Robb, 1993. Seasonal and annual variations in abundance and species composition of fish and macrocrustacean communities on a Scottish sandy beach. Mar. Ecol. Prog. Ser. 98, 89-105.

Gibson, R. N., L. Pihl, M. T. Burrows, J. Modin, H. Wennhage & L. A. Nickell, 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. Mar. Ecol. Prog. Ser. 165, 145-159.

Gibson, R.N., L. Robb, M.T. Burrows & A.D. Ansell, 1996. Tidal, diel and longer term changes in the distribution of fishes on a Scottish sandy beach. Mar. Ecol. Prog. Ser. 130, 1-17.

Gilhousen, D.B., 1987. A field evaluation of NDBC moored buoy winds. J. Atm. Ocean. Tech. 4, 94-104.

Govaere J.C.R., 1978. Numerieke analyse van het makrobenthos in de Southern Bight. Unpublished PhD thesis, University of Gent, 220pp.

Hall, R.I. & J.P. Smoll, 1992. A weighted - averaging regression and calibration model for inferring total phosphorus concentration from diatoms in British Columbia (Canada) lakes. Freshwater Biol. 27, 417-434.

Hamerlynck, O., 1993. The ecology of *Pomatoschistus minutes* Pallas and *Pomatoschistus lozanoi* de Buen (Pisces, Gobiidae) in the shallow coastal waters and estuaries of the Southern Bight of the North Sea. Unpublished PhD thesis, University of Gent, 187pp.

Hamerlynck, O. & A. Cattrijsse, 1994. The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in Belgian coastal waters, and a comparison with the food of its potential competitor *Pomatoschistus lozanoi*. J. Fish Biol. 44, 753-771.

Hamerlynck, O. & K. Hostens, 1993. Growth, feeding, production and consumption in O-group bib (*Trisopterus luscus* L.) and whiting (*Merlangius merlangus* L.) in a shallow coastal area of the SW Netherlands. ICES J. Mar. Sci. 50(1), 81-91.

Hamerlynck O. & J. Mees, 1991. Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. Oceanol. Acta 11, 205–212.

Hamerlynck, O., C. Heip & F. Redant, 1986. Life history, food consumption and resource partitioning in two sympatric gobies *Pomatoschistus minutus* and *P. lozanoi* in the Belgian coastal waters. Int. Coun. Expl. Sea CM1986/L14, 1-19.

Hamerlynck, O., P. Van De Vyver & C.R. Janssen, 1990. The trophic position of *Pomatoschistus lozanoi* (Pisces: Gobiidae) in the Southern Bight. 'Trophic relationships in the marine environment' Proc. 24th Eur. Mar. Biol. Symp., Aberdeen University Press, Aberdeen, 183-190.

Hamerlynck, O., J. Mees, J.A. Craeymeersch, K. Soetaert, K. Hostens, A. Cattrijsse & P.A. Van Damme, 1993. The Westerschelde estuary: two food webs and a nutrient rich desert. Proc. Belg. Nat. Comm. Ocean., 217-234.

Hanamura, Y., 1999. Seasonal abundance and life cycle of *Archaeomysis articulata* (Crustacea: Mysidacea) on a sandy beach of western Hokkaido, Japan. J. Nat. Hist. 33, 1811-1830.

Harris, S. A. & D.P. Cyrus, 1996. Larval and juvenile fishes in the surf zone adjacent to the St Lucia Estuary Mouth, KwaZulu-Natal, South Africa. Mar. Freshwater Res. 47, 465-482.

Hartmann-Schröder, G., 1971. Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Teil 58: Annelida - Borstenwürmer - Polychaeta. VEB Gustav Fischer Verlag Jena, Hamburg, 894pp.

Hayward, P.J., J.S. Ryland, 1996. Handbook of the marine fauna of north-west Europe. Oxford University Press, Oxford.

Henderson, P.A., R. Seaby & S.J. Marsh, 1990. The population zoogeography of the common shrimp (*Crangon crangon*) in British waters. J. Mar. Biol. Ass. U.K. 70, 89-97.

Hesthagen, I. H., 1973. Diurnal and seasonal variation in the near-bottom fauna-the hyperbenthos-in one of the deeper channels of the Kieler Bucht (Western Baltic). Kieler Meeresforsch. 29(2), 116-140.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54(2), 427-432.

Hill M.O., 1979. TWINSPAN. A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York.

Hillman, R.E., N.W. Davis & J. Wennemer, 1977. Abundance, diversity and stability in shore-zone fish communities in an area of Long Island Sound affected by discharge of a nuclear power station. Est. Coast. Shelf Sci. 5, 355-381.

Holmes, R.A. & R.N. Gibson, 1983. A comparison of predatory behaviour in flatfish. Anim. Beh. 31, 1244-1255.

Hook, J.H., 1991. Seasonal variation in relative abundance and species diversity of fishes in South Bay. Contr. Mar. Sci. 32, 127-141.

Hostens, K., 2000. Spatial patterns and seasonality in the epibenthic communities of the Westerschelde (Southern Bight of the North Sea). J. Mar. Biol. Ass. U.K. 80, 27-36.

Hostens, K., J. Mees, B. Beyst & A. Cattrijsse, 1996. Het vis- en garnaalbestand in de Westerschelde: soortensamenstelling, ruimtelijke verspreiding en seizoenaliteit (periode 1988-1992). Rapport i.o.v. Rijkswaterstaat Direktie Zeeland, Afdeling AXW, Middelburg.

Hunter, J.R. & W.J. Wisby, 1964. Net avoidance behaviour of carp and other species of fish. J. Fish. Res. Bd. Can. 21, 613-633.

Janssen, G. M. & B. R. Kuipers, 1980. On tidal migration in the shrimp *Crangon crangon*. Neth. J. Sea Res. 14(3/4), 339-348.

Jaramillo E., McLachlan A. & P. Coetzee, 1993. Intertidal zonation patterns of macrobenthos over a range of exposed beaches in south-central Chile. Mar. Ecol. Prog. Ser. 101, 105-117.

Jaramillo, E., R. Stead, P. Quijon, H. Contreras & M. Gonzalez, 1996. Temporal variability of the sand beach macroinfauna in south-central Chile. Rev. Chil. Hist. Nat. 69, 641-653.

Jones, A., 1973. The ecology of young turbot, *Scophthalmus maximus* (L.), at Borth, Cardiganshire, Wales. J. Fish Biol. 5, 367-383.

Jones, N.S., 1952. The bottom fauna and the food of flatfish off the Cumberland coast. J. Anim. Ecol. 21, 182-205.

Jones, N.S., 1976. British cumaceans. Arthropoda: Crustacea. Keys and notes for the identification of the species. Academic Press, London, 66pp.

Jones, D.A. & E. Naylor, 1967. The distribution of *Eurydice* (Crustacea: Isopoda) in British waters, including *E. affinis* new to Britain. J. Mar. Biol. Ass. U.K. 47, 373-382.

Keats, D.W. & D.H. Steele, 1992. Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in eastern Newfoundland. J. Northw. Atl. Fish. Sci. 13, 7-14.

King, P.E., 1974. British sea spiders. Arthropoda: Pycnogonida. Keys and notes for the identification of the species. Academic Press, London, 68pp.

Kinoshita, I., 1993. Ecological study on larvae and juveniles of sparine fishes occurring in surf zones of sandy beaches. Bull. Mar. Sci. Fish. Kochi Univ. 13, 21-99.

Klein Breteler, W.C.M., 1976. Migration of the shore crab, *Carcinus maenas*, in the Dutch Wadden Sea. Neth. J. Sea Res. 10, 338-353.

Kramer, K.J.M., U.H. Brockmann & R.M. Warwick, 1994. Tidal estuaries. Manual of sampling and analytical procedures. Published for the European Commission by A.A. Balkema, Rotterdam, 304pp.

Kramp, P.L., 1930. Hydromedusae collected in the south-western part of the North Sea and the eastern part of the Channel in 1903-14. Mém. Mus. Roy. Hist. Nat. Belg. 45, 1-55.

Kruuk, H., 1963. Diurnal periodicity in the activity of the common sole, *Solea vulgaris* Quensel. Neth. J. Sea Res. 2, 1-28.

Kuipers, B., 1973. On the tidal migration of young plaice. Neth. J. Sea Res. 6(3), 367-388.

Kuipers, B.R., B. Maccurrin, J.M. Miller, H.W. van der Veer & J.IJ. Witte, 1992. Small trawls in juvenile flatfish research: their development and efficiency. Neth. J. Sea Res. 29, 109-117.

Lamberth, S.J., B.M. Clark & B.A. Bennett, 1995. Seasonality of beach-seine catches in False Bay, South Africa, and implications for management. S. Afr. J. mar. Sci. 15, 157-167.

Lasenby, D.C. & R.K. Sherman, 1991. Design and evaluation of a bottom-closing net used to capture mysids and other suprabenthic fauna. Can. J. Zool. 69, 783-786.

Lasiak, T.A. & A. McLachlan, 1987. Opportunistic utilization of mysid shoals by surf-zone teleosts. Mar. Ecol. Prog. Ser. 37, 1-7.

Lasiak, T.A., 1981a. Structural aspects of the surf-zone fish assemblage at King's Beach, Algoa Bay: short term fluctuations. Est. Coast. Shelf Sci. 18, 347-360.

Lasiak, T.A., 1981b. Nursery grounds of juvenile teleosts: evidence from the surf zone of King's Beach, Port Elizabeth. S. Afr. J. Sci. 77, 38-390.

Lasiak, T.A., 1982. Structural and functional aspects of the surf zone fish community in the eastern Cape. Unpublished PhD thesis, University of Port Elizabeth, South Africa.

Lasiak, T.A., 1984a. Aspects of the biology of three benthic-feeding teleosts from King's Beach, Algoa Bay. South Afr. J. Zool. 19(1), 51-56.

Lasiak, T.A., 1984b. Structural and functional aspects of the surf zone fish assemblage of King's Beach, Algoa Bay, South Africa: long term fluctuations. Estuar. Coast. Shelf Sci. 18, 459-483.

Lasiak, T.A., 1986. Juveniles, food and the surf zone habitat: implications for teleost nursery areas. South Afr. J. Zool. 21(1), 52-56.

Layman, C.A., 2000. Fish assemblage structure of the shallow ocean surf-zone on the eastern shore of Virginia Barrier Island. Est. Coast. Shelf Sci. 51, 201-213.

Lazzari, M.A., S. Sherman, C.S. Brown, J. King, B.J. Joule, S.B. Chenoweth & R.W. Langton, 1999. Seasonal and annual variations in abundance and species composition of two near-shore fish communities in Maine. Estuaries 22(3A), 636-647.

Le, K.L., 1983. Les phases initiales du cycle biologique (oeufs, larves et jeunes) de *Solea vulgaris* Quensel et *Solea senegalensis* Kaup (Poissons, Pleuronectiformes, Soleidae). Relations avec le bassin de Marennes-Oléron, écosystème estuarien à vocation aquicole. Thése 3ème cycle, Université d'Aix-Marseille II, 136pp.

Legardère, J.P., 1987. Feeding ecology and daily food consumption of common sole, *Solea vulgaris* Quensel, juveniles on the French Atlantic coast. J. Fish Biol. 30, 91-104.

Lewin, J. & C.T. Schaefer, 1983. The role of phytoplankton in surf ecosystems. In: Erasmus, T. & A. McLachlan (eds.). Sandy beaches as ecosystems. Junk, The Hague, 381-389.

Lincoln, R.J., 1979. British marine Amphipoda: Gammaridea. British Museum (Natural History), London, 658pp.

Lloyd, A.J. & C.M. Younge, 1947. The biology of *Crangon vulgaris* (L.) in the Bristol Channel and Severn Estuary. J. mar. biol. Ass. U.K. 26, 626-661.

Lock, K., B. Beyst. & J. Mees, 1999. Circadiel patterns in the tidal plankton of a sandy beach in Zeebrugge (Belgium). Belg. J. Zool. 129(2), 339-352.

Lockwood, S.J., 1973. Weight and length changes of 0-group plaice (*Pleuronectes platessa* L.) after preservation in 4% neutral formalin. J. Cons. Int. Expl. Mer 35(1), 100-101.

Lockwood, S. J., 1984. The daily food intake of O-group plaice (*Pleuronectes platessa* L.) under natural conditions : changes with size and season. J. Cons. Int. Explor. Mer 41, 181-193.

Lyons, J., 1986. Capture efficiency of a beach-seine for seven freshwater fishes in a north-temperate lake. N. Am. J. Fish Manage 6, 288-289.

Macer, C.T., 1967. The food web in Red Wharf Bay (North Wales) with particular reference to young plaice, *Pleuronectes platessa*. Helgolander wiss. Meeresunters. 15, 560-573.

Macquart-Moulin, C., 1977. Le côntrole de l'émergence et des nages nocturnes chez les Péricarides des plages de Méditteranée *Eurydice affinis* Hansen (Isopoda), *Gastrosaccus mediterraneus* Bãcescu, *Gastrosaccus spinifer* (Goës) (Mysidacea). J. Exp. Mar. Biol. Ecol. 27, 61-81.

Mantoura, R.F.C. &. C.A. Llewellyn, 1983. The rapid determination of algall chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. Anal. Chem. Acta 151, 297-314.

Masselink, G. & A.D. Short, 1993. The effect of tide range on beach morphodynamics and morphology: a conceptual beach model. J. Coast. Res. 9(3), 785-800.

Mauchline, J., 1980. The biology of mysids and euphausiids. In: Blaxter, J.H.S., F.S. Russel & M. Yonge (eds.). Advances in Marine Biology 18, Academic Press, London, 681p.

Mauchline, J., 1998. The biology of calanoid copepods. Academic Press, London, 710pp.

McFarland, W.N., 1963. Seasonal change in the number and biomass of fishes from the surf at Mustang Island, Texas. Publs. Inst. Mar. Sci. Univ. Texas 9, 91-105.

McLachlan, A., 1980. Exposed sandy beaches as semi-enclosed ecosystems. Mar. Environ. Res. 4, 59-63.

McLachlan, A., 1983 Sandy beach ecology - A review. In: McLachlan, A. & T. Erasmus (eds.). Sandy Beaches As Ecosystems. Dr W. Junk Publishers, The Hague, 321-380.

McLachlan, A., 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. J. Coast. Res. 6, 57-71.

McLachlan, A., T. Erasmus, A.D. Dye, T. Wooldridge, G. Van Der Horst, G. Rossouw, T.A. Lasiak & L. Gwynne, 1981. Sand beach energetics: an ecosystem approach towards a high energy interface. Est. Coast. Shelf Sci. 13, 11-25.

McLachlan, A. & G. Romer, 1990. Throphic relationships in a high energy beach and surf-zone ecosystem. In: Barnes, M. & R.N. Gibson (eds.). Throphic relationships in the marine environment. Aberdeen University Press, Aberdeen, 356-371.

Mees, J., 1994. The hyperbenthos of shallow coastal waters and estuaries: community structure and biology of the dominant species. Unpublished PhD thesis, Ghent University, Belgium, 212 pp.

Mees J. & O. Hamerlynck, 1992. Spatial community structure of the winter hyperbenthos of the Schelde estuary, The Netherlands, and the adjacent coastal waters. Neth. J. Sea Res. 29(4), 357-370.

Mees, J. & M.B. Jones, 1997. The hyperbenthos. Ocean. Mar. Biol. Ann. Rev. 35, 221-255.

Mees, J., Z. Abdulkerim & O. Hamerlynck, 1994. Life history, growth and production of *Neomysis integer* in the Westerschelde estuary (SW Netherlands). Mar. Ecol. Prog. Ser. 109, 43-57.

Mees, J., A. Cattrijsse & O. Hamerlynck, 1993. Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, southwest Netherlands. Cah. Biol. Mar. 34, 165-186.

Mielke, P.W., K.J. Berry & E.S. Johnson, 1976. Multi-Response Permutation Procedures for a priori classifications. Community statistics - Theory Meth. A5, 1409-1424.

Miller, P.J., 1986. Gobiidae. In: Whitehead, P.J.P., M.-L. Bauchot, J.-C. Hureau, J. Nielsen & E. Tortonese (eds.). Fishes of the North-eastern Atlantic and the Mediterranean. Vol. III, 1019-1085.

Milliken, G.A. & D.E. Johnson (1984). Analysis of messy data: Vol. I. Designed experiments. Van Nostrand Reinhold, Co., New York.

Modde, T. & S.T. Ross, 1981. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. Fish. Bull. 78(4), 911-922.

Modde, T. & S.T. Ross, 1983. Trophic relationships of fishes occurring within a surf zone habitat in the northern Gulf of Mexico. Northeast Gulf Sci. 6(2), 109-120.

Molinero, A. & R. Flos, 1992. Influence of season on the feeding habits of the common sole *Solea solea*. Mar. Biol. 113, 499-507.

Moran, S., 1972. Ecology and distribution of the sand-dwelling mysid crustacean *Gastrosaccus sanctus* (Van Beneden, 1861) along the Mediterranean sandy shore of Israel. Crustaceana (suppl.) 3, 357-361.

Munilla, T. & M.J. Corrales, 1995. Suprabenthos de la plage de Rosas (Gerona, Mediterranea occidental). Orsis 10, 83-90.

Munilla, T., M.J. Corrales & C. San Vicente, 1998. Suprabenthic assemblages from Catalan beaches: zoological groups. Orsis 13, 67-78.

Naylor, E., 1955. The ecological distribution of British species of *Idotea* (Isopoda). J. Anim. Ecol. 24, 270-281.

Naylor, E., 1957. The occurrence of *Idotea metallica* Bosc. in British waters. J. Mar. Biol. Ass. U.K. 36, 599-602.

Naylor, E., 1962. Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. J. Anim. Ecol. 31, 601-609.

Naylor, E., 1972. British Marine Isopods. Keys and notes for the identification of the species. Academic Press, London, 86pp.

Nijssen, H., S.J. De Groot, 1987. De vissen van Nederland. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht, 224pp.

Peters, D.J. & W.G. Nelson, 1987. The seasonality and spatial patterns of juvenile surf zone fishes of the Florida east coast. Biol. Sci. 50, 85-99.

Pierce, C.L., J.B. Rasmussen & W.C. Leggett, 1990. Sampling littoral fish with a seine: corrections for variable catch efficiency. Can. J. Fish. Aquat. Sci. 47, 1004-1010.

Pihl, L., 1982. Food intake of young cod and flounder in a shallow bay on the Swedish West coast. Neth. J. Sea Res. 15 (3/4), 419-432.

Pihl, L., 1986. Exposure, vegetation and sediment as primary factors for mobile epibenthic faunal community structure and production in shallow marine soft bottom areas. Neth. J. Sea Res. 20(1), 75-83.

Pihl, L., 1989. Abundance, biomass and production of juvenile flatfish in southeastern Kattegat. Neth. J. Sea Res. 24(1), 69-81.

Pihl, L. & R. Rosenberg, 1982. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, western Sweden. J. Exp. Mar. Biol. Ecol. 57, 273-301.

Pihl, L. & H.W. van der Veer, 1992. Importance of exposure and habitat structure for the population density of 0-group plaice, *Pleuronectes platessa* L., in coastal nursery areas. Neth. J. Sea Res. 29, 145-152.

Poxton, M.G., 1992. Towards a strategy for the conservation of marine fish in Scotland. Proc. R. Soc. Edinb. 100B, 141-167.

Reina-Hervas, J.A. & P. Serrano, 1987. Structural and seasonal variations of inshore fish populations in Malaga Bay, southeastern Spain. Mar. Biol. 95, 501-508.

Rice A.L., 1961. The responses of certain mysids to changes in hydrostatic pressure. J Exp Biol 38, 391-401.

Riley, J.D, D.J. Symonds & L. Woolner, 1981. On the facors influening the distribution of 0-group demersal fish in coatal waters. Rapp. P-v. Reun. Cons. Int. Explor. Mer 178, 223-228.

Riley, J.D, D.J. Symonds, & L. Woolner, 1981. On the factors influencing the distribution of 0-group demersal fish in coastal waters. Rapp. P-v. Reun. Cons. Int. Explor. Mer 178, 223-228.

Ringler, N.H., 1979. Prey selection by benthic feeders. In Clepper, H. (ed.). Predator-prey systems fisheries management. Sport Fishing Institute, Washington, D.C 219-229.

Robertson, A.I. & R.G.J. Lenanton, 1984. Fish community structure and food chain dynamics in the surf zone of sandy beaches: the role of detached macrophyte detritus. J. Exp. Mar. Biol. Ecol. 84, 265-283.

Rogers, S.I. & R.S. Millner, 1996. Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations: 1973 to 1995. ICES J. Mar. Sci. 53, 1094-1112.

Rogers, S.I., A.D. Rijnsdorp, U. Damm & W. Vanhee, 1998. Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990 to 1995. J. Sea Res. 39, 79-102.

Romer, G.S., 1990. Surf zone fish community and species response to a wave energy gradient. J. Fish Biol. 36, 279-287.

Romer, G.S. & A. McLachlan, 1986. Mullet grazing on surf diatom accumulations. J. Fish Biol. 28, 93-104.

Ross, S.T., 1983. A review of the surf zone ichthyofauna in the Gulf of Mexico. In: Shabica, S.V. & E.W. Cake Jr. (eds.). Proceedings of the northern Gulf of Mexico estuaries and barrier islands research conference, U.S. Department of the Interior, Atlanta, 25-34.

Ross, S.T., R.H. McMichael Jr & D.L. Ruple, 1987. Seasonal and diel variation in the standing crop of fishes and macroinvertebrates from a Gulf of Mexico surf zone. Est. Coast. Shelf Sci. 25, 391-412.

Russel, F.S., 1953. The medusae of the British Isles. University Press, Cambridge, 530pp.

Russel, F.S., 1976 The egs and planktonic stages of British marine fishes. Academic Press, London, 524pp.

Salvat, B., 1962. Faune des sédiments meubles intertidaux du bassin d' Arcachon. Systématic et écologie. Cah. Biol. Mar. 3, 219-244.

San Vicente, C. & T. Munilla, 2000. Misidáceos suprabentónicos de las playas catalanas (Mediterráneo nordoccidental). Orsis 15, 45-55.

San Vicente, C. & J.C. Sorbe, 1993a. Biologie du mysidacé suprabenthique *Schistomysis parkeri* Norman, 1892 dans la zone sud du Golfe de Gascogne (Plage d'Hendaye). Crustaceana 65(2), 222-252.

San Vicente, C. & J.C. Sorbe, 1993b. Estudio comparado del suprabenthos de una playa catalana y otra vasca: metodología y resultados preliminares. Pub. Esp. Inst. Esp. Ocean. 11, 299-304.

San Vicente, C. & J.C. Sorbe, 1999. Spatio-temporal structure of the suprabenthic community from Creixell beach (western Mediterranean). Acta Oecologica 20(4), 377-389.

Sanderson, A.R., 1930. The coelenterate plankton of the Northumbrian coast during the year 1924. J. Mar. Biol. Ass. (N.S.) 17(1), 219-232.

Short, A.D., 1991. Macro-meso tidal beach morphodynamics - An overview. J. Coast. Res. 7(2), 417-436.

Short, A.D., 1996. The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review. Rev. Chil. Hist. Nat. 69, 589-604.

Smaldon, G., 1979. British coastal shrimps and prawns. Keys and notes for the identification of the species. Academic Press, London, 126pp.

Sokal, R.R & F.J. Rohlf, 1981. Biometry. W.H. Freeman and Company, New York, 859pp.

Stickney, A.P., 1972. The locomotor activity of juvenile herring (*Clupea harengus harengus* L.) in response to changes in illumination. Ecology 53, 438-455.

Subiyanto, I. Hirata & T. Senta, 1993. Larval settlement of the japanese flounder on sandy beaches of the Yatsushiro Sea, Japan. Nippon Suisan Gakkaishi 59(7), 1121-1128.

Swenson, W.A., 1978. Influence of turbidity on fish abundance in West Lake Superior. Research Report of the U.S. Environmental Protection Agency, Duluth.

Talbot, M.M., G.C. Bate & E.E. Campbell, 1990. A review of the ecology of surf-zone diatoms, with special reference to *Anaulus australis*. Oceanogr. Mar. Biol. Annu. Rev. 28, 155-175.

Tallmark, B. & S. Evans, 1986. Substrate-related differences in antipredator behaviour in two gobiid fish species and the brown shrimp, and their adaptive value. Mar. Ecol. Prog. Ser. 29, 217-222.

Tattersall, W. M. & O.S. Tattersall, 1951. The British Mysidacea. Ray Society, London, 460pp.

Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167-1179.

Ter Braak, C.J.F., 1988. CANOCO – a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondance analysis (version 2.1). Agricultural Mat. Group. Ministry of Agriculture and Fisheries.

Thijssen, R., A.J. Lever & J. Lever, 1974. Food composition and feeding periodicity of 0-group plaice (*Pleuronectes platessa*) in the tidal area of a sandy beach. Neth. J. Sea Res. 8(4), 369-377.

Vallet, C. & J.C. Dauvin, 1999. Seasonal changes of macrozooplankton and benthic boundary layer macrofauna from the Bay of Sau-int-Brieuc (western English Channel). J. Plankt. Res. 21(1), 35-49.

Van Der Baan, S. M. & L.B. Holthuis, 1971. Seasonal occurence of Mysidacea in the surface plankton of the Southern North Sea near the 'Texel' lightship. Neth. J. Sea Res. 5(2), 227-239.

van der Veer, H.W. & M.J.N. Bergman, 1986. Development of tidally related behaviour of a newly settled O-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 31, 121-129.

van der Veer, H.W., R. Berghahn, J.M. Miller & A.D. Rijnsdorp, 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: progress made by the Flatfish Symposia. ICES J. Mar. Sci. 57, 202-215.

Watkin, E.E., 1939. The pelagic phase in the life-history of the amphipod genus *Bathyporeia*. J. Mar. Biol. Ass. U.K. 23, 467-481.

Watkin, E.E., 1941. Observations on the night tidal migrant Crustacea of Kames Bay. J. Mar. Biol. Ass. U.K 25, 81-96.

Watson, H.G., 1930. The coelenterate plankton of the Northumbrian coast during the year 1925. J. Mar. Biol. Ass. U.K 17, 233-239.

Wennhage, H. & L. Pihl, 1994. Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): impact of benthic microalgae and filamentous macroalgae. Neth. J. Sea Res. 32, 343-351.

Whaley, F.S., 1983. The equivalence of three independently derived permutation procedures for testing the homogeneity of multidimensional samples. Biometrics 39, 741-745.

Whitfield, A.K., S.J.M. Blaber & D.P. Cyrus, 1981. Salinity ranges of some southern African fish species occurring in estuaries. S. Afr. J. Zool. 16, 151-155.

Wooldridge, T., 1983. Ecology of beach and surf zone mysid shrimps in the eastern Cape, South Africa. In: McLachlan, A. & T. Erasmus (eds.). Sandy Beaches As Ecosystems. Dr W. Junk Publishers, The Hague, 449-460.

Wooldridge, T., 1989. The spatial and temporal distribution of mysid shrimps and phytoplankton accumulations in a high energy surf zone. Vie Milieu 39(3/4), 127-133.

Wright, J.M., 1989. Diel variation and seasonal consistency in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. Mar. Biol. 102, 135-142.

Wright, L.D., J. Chapell & B.J. Tom, 1979. Morphodynamics of reflective and dissipative beach and coastal systems: southeastern Australia. Mar. Geol. 32, 105-140.

Wyche C.J. & S.E. Shackley, 1986. The feeding ecology of *Pleuronectes platessa* L., *Limanda limanda* (L.) and *Scophthalmus rhombus* (L.) in Camarthen Bay, South Wales, UK. J Fish Biol 29, 303-311.

Zar, J.H., 1996. Biostatistical analysis. Prentice Hall International Editions, London, 662p.

Zatkutskiy, V.P., 1970. Some biological features of mysids of the hyponeuston in the Black Sea and Sea of Azov. Gidrobiologischeskii Zhurnal 6, 17-22.

Zijlstra, J.J., 1972. On the importance of the Wadden Sea as a nursery area in relation to the conservation of the southern North Sea fishery resources. Symp. Zool. Soc. Lond. 29, 233-258.

Zijlstra, J.J., 1978. The function of the Wadden Sea for the members of its fauna. In: Dankers, N.M.J.A., Wolff, W.J. & Zijlstra, J.J. Fishes and fisheries of the Wadden Sea. Balkema, Rotterdam, 20-25.

Zimmerman, G. M., H. Goetz & P. W. Mielke Jr., 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology 66, 606-611.

APPENDICES

Appendix 1. Environmental variables. (A) Temporal campaign. (B) Spatial campaign. (C) 24-hour cycles.

Appendix 2. Species lists. (A) Hyperbenthos. (B) Epibenthos.

Appendix 3. Hyperbenthic densities. (A) Temporal campaign. (B) Spatial campaign. (C) 24-hour cycles.

Appendix 4. Hyperbenthic biomass. (A) Temporal campaign. (B) 24-hour cycles.

Appendix 5. Epibenthic densities. (A) Temporal campaign. (B) Spatial campaign. (C) 24-hour cycles.

Appendix 6. Epibenthic biomass. (A) Temporal campaign. (B) Spatial campaign.

Appendix 7. Regressions and assigned values used for calculation of biomasses.

Appendix 8. Numerical stomach content analyses. (A) Temporal series flatfish. (B) 24-hour cycle plaice.

Appendix 9. Gravimetrical stomach content analyses. (A) Temporal series flatfish. (B) 24-hour cycle plaice.

Appendix 10. Beyst, B., J. Mees, & A. Cattrijsse (1999). Early postlarval fish in the hyperbenthos of the Dutch Delta (south-west Netherlands). ***Journal of the Marine Biological Association of the United Kingdom*** **79, 709-724.**

Appendix 11. Lock, K., B. Beyst & J. Mees (1999). Circadiel patterns in the tidal plankton of a sandy beach in Zeebrugge (Belgium). ***Belgian Journal of Zoology*** **129(2), 339-352.**

Appendix 1

Environmental variables. (A) Temporal campaign. (B) Spatial campaign. (C) 24-hour cycles

Appendix 1.A. Environmental variables temporal campaign (IT: intertidal, ST: subtidal).

OOSTDUINKERKE

	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
33H wave height (class)	2	1.5	1	1.5	1.5	1.5	1.5	1	2	2	2.5	2	2.5	2
wind direction (see text)	-0.22	0.99	-0.93	0.21	0.98	-0.97	-0.99	-0.85	-0.62	-0.39	0.10	-0.05	0.45	0.42
wind speed (class)	3.5	1.5	2	2.5	1	1.5	1	1.5	3.5	2	1.5	1.5	1.5	1
water temperature IT (°C)	16.0	23.5	22.0	19.5	14.0	11.3	7.0	0.1	6.8	9.3	12.6	17.5	20.8	20.7
salinity IT (psu)	33.0	33.0	32.5	36.0	34.0	35.0	34.4	32.8	34.3	34.6	32.4	34.3	33.2	35.1
water temperature ST (°C)	12.2	15.5	18.5	19.8	14.7	13.7	7.0	0.5	4.2	8.0	9.3	11.9	17.0	18.6
salinity ST (psu)	26.4	31.5	31.4	31.8	32.5	32.3	32.4	30.8	34.0	33.5	33.1	31.8	32.7	30.4
current speed (kn)	0.6	0.6	0.7	0.6	0.6	0.6	0.7	0.6	0.6	0.6	0.6	0.7	0.6	0.6
turbidity (ftu)	102	98	149	59	243	203	193	582	78	51	76	122	226	45
POC water column (%C)	2.9	1.9	4.9	4.2	2.4	1.2	1.2	1.8	0.4	6.6	3.7	4.2	6.9	5.8
median grain size (µm)	191	180	185	189	182	183	184	189	189	190	189	185	186	183
organic matter of the sediment (g/100g dw)	0.77	0.88	1.04	0.93	0.86	0.88	0.77	0.96	0.59	0.68	0.70	0.78	0.83	0.95
oxygen content (mg/l)	9.1	7.5	7.9	8.7	8.1	8.3	9.4	11.3	8.5	8.5	9.3	9.3	9.1	8.0
oxidized nitrogen-N (µmol/l)	26	34	1	4	119	52	87	286	147	6	46	3	82	3
ammonia-N (µmol/l)	51	23	37	37	25	33	61	79	56	33	30	33	625	62
phosphate-P (µmol/l)	16	7	23	41	22	29	8	33	14	8	7	18	257	28
silicium (µmol/l)	13	3	26	34	92	72	166	295	129	20	28	0	232	101
chlorophyll-*a* (µg/l)	15	0	18	41	2	14	0	0	4	5	3	9	143	79
chlorophyll-*c* (µg/l)	2	0	4	5	0	3	0	0	1	1	0	1	21	4
fucoxanthine (µg/l)	6	0	8	16	1	8	0	0	3	3	2	2	78	15

LOMBARDSIJDE

	May'96	Jun'96	Aug'96	Sep'96	Oct'96	Dec'96	Feb'97	Mar'97	Apr'97(1)	Apr'97(2)	May'97(1)	May'97(2)	Jun'97	Jul'97
33H wave height (class)	1.5	1.5	1.5	1.5	1	1	2	1	0.5	2.5	1.5	1.5	2.5	2.5
wind direction (see text)	0.17	0.99	0.53	0.97	-0.85	-0.85	-0.62	-0.94	0.93	0.14	-0.36	0.48	0.28	0.28
wind speed (class)	1.5	1.5	2	1	1.5	1.5	3.5	0.5	1	1	1.5	1	2	1
water temperature IT (°C)	16.0	22.5	24.0	14.0	13.1	5.0	5.9	9.1	11.8	11.0	15.6	15.2	18.9	20.9
salinity IT (psu)	34.0	32.0	35.0	33.5	35.5	35.5	34.0	34.1	34.3	34.2	34.0	31.6	32.9	34.1
water temperature ST (°C)	10.0	15.5	20.0	14.8	13.7	6.0	4.1	7.1	9.0	9.2	13.3	13.4	17.1	19.0
salinity ST (psu)	26.2	31.9	30.5	32.5	32.2	31.5	34.0	34.3	33.2	33.3	32.0	32.4	32.4	30.3
current speed (kn)	0.65	0.6	0.6	0.6	0.6	0.4	0.6	0.55	0.4	0.6	0.45	0.7	0.6	0.6
turbidity (ftu)	110	151	121	167	244	207	209	161	30	69	124	257	193	61
POC water column (%C)	6.8	6.4	5.2	5.5	6.6	1.9	3.7	4.7	4.2	2.1	4.5	4.3	5.7	4.2
median grain size (µm)	193	185	191	191	190	185	185	184	185	186	191	185	187	186
organic matter of the sediment (g/100g dw)	0.17	0.24	0.60	0.25	0.27	0.21	0.26	0.25	0.21	0.19	0.09	0.10	0.10	0.09
oxygen content (mg/l)	8.1	8.0	7.4	8.1	8.3	9.8	9.5	9.2	9.9	8.5	8.2	8.5	7.4	7.2
oxidized nitrogen-N (µmol/l)	114	174	5	178	118	652	371	169	1	30	2	302	50	150
ammonia-N (µmol/l)	152	138	28	54	106	1178	95	64	16	53	44	67	625	79
phosphate-P (µmol/l)	18	37	64	32	50	84	23	18	12	7	33	52	257	13
silicium (µmol/l)	92	74	37	196	190	728	188	94	17	18	0	26	232	20
chlorophyll-*a* (µg/l)	2	10	23	4	13	17	2	3	15	5	23	55	49	15
chlorophyll-*c* (µg/l)	0	2	3	1	2	1	0	0	3	1	4	11	8	2
fucoxanthine (µg/l)	1	4	9	2	7	7	1	1	6	2	13	33	27	7

WENDUINE

	May'96	Jun'96	Aug'96	Sep'96	Oct'96	Dec'96	Jan'97	Mar'97	May'97	Jun'97	Jul'97
33H wave height (class)	2.5	2	2	1	2	1.5	1	1.5	1.5	3.5	1.5
wind direction (see text)	0.21	0.80	-0.05	-0.74	-0.85	-1.00	-1.00	1.00	0.62	0.44	0.75
wind speed (class)	0.5	1	1	1.5	3.5	1.5	1.5	1	1	2	1
water temperature IT (°C)	13.0	16.0	16.5	14.7	12.7	5.8	0.3	10.6	15.5	18.0	22.3
salinity IT (psu)	33.0	35.0	36.0	33.0	33.5	34.5	34.0	33.2	31.5	31.2	31.7
water temperature ST (°C)	11.9	15.5	19.0	15.0	13.6	6.0	0.5	7.9	12.4	17.1	18.8
salinity ST (psu)	26.8	31.5	31.5	32.0	32.0	30.9	30.8	32.9	31.5	32.5	30.8
current speed (kn)	0.6	0.4	0.6	0.4	0.5	0.6	0.6	0.6	0.6	0.6	0.6
turbidity (ftu)	179	40	72	63	388	278	1610	65	147	27	67
POC water column (%C)	3.8	5.7	4.1	3.7	4.5	0.1	3.7	2.9	6.8	2.5	7.3
median grain size (µm)	241	251	257	251	273	251	262	302	275	263	269
organic matter of the sediment (g/100g dw)	0.16	0.21	0.20	0.22	0.24	0.19	0.16	0.18	0.07	0.72	0.07
oxygen content (mg/l)	9.0	7.5	6.7	8.1	7.9	9.8	10.8	8.5	8.0	7.3	8.5
oxidized nitrogen-N (µmol/l)	137	73	69	210	232	766	658	239	249	185	10
ammonia-N (µmol/l)	101	103	121	110	82	206	331	51	240	132	335
phosphate-P (µmol/l)	18	15	119	57	66	138	238	25	47	64	47
silicium (µmol/l)	69	80	137	82	236	865	716	90	81	171	106
chlorophyll-*a* (µg/l)	6	2	29	10	5	6	3	5	14	14	60
chlorophyll-*c* (µg/l)	1	0	3	1	1	0	1	1	1	3	7
fucoxanthine (µg/l)	4	1	19	5	2	0	11	3	4	12	16

KNOKKE

	May'96	Jun'96	Aug'96	Sep'96	Oct'96	Dec'96	Jan'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
33H wave height (class)	2.5	2	1.5	1.5	1.5	1.5	1	1.5	2.5	1.5	3.5	1.5
wind direction (see text)	-0.02	0.98	0.16	0.99	-0.99	-0.95	-1.00	0.67	0.24	0.48	0.74	0.16
wind speed (class)	1.5	1.5	1.5	1	2.5	1.5	1.5	1	1.5	1	1.5	1
water temperature IT (°C)	13.0	17.0	20.0	15.6	12.1	5.7	0.5	9.4	9.0	14.6	18.4	21.3
salinity IT (psu)	33.0	35.0	33.0	31.1	31.4	31.5	30.5	31.5	31.8	31.1	31.1	31.4
water temperature ST (°C)	11.8	15.2	19.0	14.9	13.5	6.0	-0.5	7.9	9.2	12.3	17.0	18.5
salinity ST (psu)	30.0	31.5	31.5	32.0	31.4	31.2	30.8	31.2	31.7	31.8	30.5	30.4
current speed (kn)	1.3	0.6	1.3	1.3	1.3	1.35	1.35	1.3	1.3	1.3	0.6	1.35
turbidity (ftu)	56	55	83	18	78	71	132	92	21	61	27	29
POC water column (%C)	1.9	2.6	2.6	1.9	2.4	2.1	1.8	2.1	1.9	4.4	1.8	5.6
median grain size (µm)	359	344	368	382	349	383	354	366	267	360	310	289
organic matter of the sediment (g/100g dw)	0.65	0.60	0.69	0.48	0.59	0.70	0.51	0.51	0.51	0.50	0.69	0.64
oxygen content (mg/l)	9.0	7.5	7.9	8.4	8.0	9.5	10.9	8.5	9.3	8.1	7.2	8.5
oxidized nitrogen-N (µmol/l)	231	110	50	252	324	546	409	722	183	200	234	137
ammonia-N (µmol/l)	80	88	18	56	68	152	71	91	59	142	170	61
phosphate-P (µmol/l)	31	23	21	56	44	142	23	47	19	28	762	40
silicium (µmol/l)	40	108	40	150	296	976	408	530	92	50	137	126
chlorophyll-*a* (µg/l)	1	1	3	1	2	2	1	2	7	1	10	13
chlorophyll-*c* (µg/l)	0	0	1	0	0	0	0	0	1	0	2	1
fucoxanthine (µg/l)	1	0	1	1	1	1	0	1	4	1	5	4

Appendix 1.B. Environmental variables spatial campaign (IT: intertidal, ST: subtidal).

	BD	**DP**	**Oo**	**Ni**	**Lo**	**Mi**	**Ma**	**Br**	**DH**	**Bl**	**Ze**	**Kn**
33% wave height (class)	1.5	1.5	1.5	1.5	1	1.5	0.5	0.5	1.5	1.5	4.5	1
wind direction (see text)	-0.37	0.79	0.29	0.47	0.53	0.98	-0.05	-0.05	0.21	0.29	0.54	1.00
wind speed (class)	1.5	1.0	2.0	1.5	1.5	1.5	3.0	1.0	1.5	2.0	3.5	1.5
water temperature IT (°C)	9.5	12.5	14.0	18.0	12.0	12.0	12.5	12.0	11.5	10.0	10.0	14.0
salinity IT (psu)	32.1	26.4	35.4	34.6	29.6	28.4	28.7	31.8	30.6	30.2	31.0	27.9
water temperature ST (°C)	9.8	10.0	8.0	10.0	8.0	10.0	7.8	7.8	7.9	7.9	10.0	9.8
salinity ST (psu)	28.5	28.5	29.0	28.5	29.0	29.0	31.8	31.8	29.4	29.5	30.0	29.8
turbidity (ftu)	310	15	76	320	112	49	31	274	80	292	140	27
POC water column (%C)	0.4	2.3	2.7	3.6	5.2	2.2	4.0	3.9	3.0	5.6	4.6	1.9
median grain size (low tide) (μm)	179	181	181	180	181	301	304	244	288	246	232	294
organic material of sediment (g/100g dw)	0.843	2.449	0.799	0.803	0.837	1.128	0.586	0.473	0.880	0.614	0.805	0.661
oxidized nitrogen-N (μmol/l)	0.591	0.000	0.616	1.009	0.141	0.000	0.527	12.665	10.575	14.446	15.318	3.829
ammonia-N (μmol/l)	2.821	0.190	8.214	2.537	1.980	0.705	46.000	3.852	14.579	2.509	4.591	1.464
phosphate-P (μmol/l)	0.794	0.462	0.569	0.496	0.746	0.429	0.256	0.223	1.298	0.306	0.339	0.543
silicium (μmol/l)	0.978	0.715	1.614	1.338	0.978	0.000	0.000	2.351	1.023	0.000	0.414	0.677
chlorophyll-*a* (μg/l)	48.65	8.38	20.09	23.32	12.88	13.48	72.51	50.07	49.97	25.76	21.58	5.43
chlorophyll-*c* (μg/l)	4.50	1.48	2.70	3.70	1.53	2.06	5.84	3.91	6.11	5.39	1.95	0.80
fucoxanthine (μg/l)	28.23	4.40	11.03	12.81	7.20	6.45	41.72	34.38	25.69	14.70	12.83	2.43

Appendix 1.C. Environmental variables: 24-hours cycles (hours in CET) (IT: intertidal) (for hydrodynamic variables see Chapter IV, Figure 2).

SPRING TIDE

	15:00	17:00	19:00	21:00	23:00	1:00	3:00	5:00	7:00	9:00	11:00	13:00	15:00
light intensity	100	62	10	0	0	0	0	0	15	65	97	42	52
water temperature IT (°C)	11.6	11.6	10.3	10.0	9.9	8.8	8.8	8.8	9.1	9.8	11.2	11.1	11.9
salinity IT (psu)	32.6	32.5	32.5	32.4	32.4	32.5	32.4	32.5	32.6	32.4	32.4	32.4	32.4
turbidity (ftu)	29	46	52	81	43	42	38	35	57	24	8	26	37
median grain size (μm)	212	202	191	191	204	214	208	214	189	181	188	215	204
oxygen content (mg/l)	8.3	8.6	8.5	8.6	8.8	9.0	8.0	8.2	8.2	8.8	8.6	8.8	7.8
oxidized nitrogen-N (μmol/l)	0.4	3.4	1.6	0.3	0.1	0.1	0.3	0.6	0.9	0.9	0.4	0.4	0.3
ammonia-N (μmol/l)	5.2	4.8	5.5	2.2	2.9	4.0	2.2	2.2	3.0	3.0	4.4	2.7	2.4
phosphate-P (μmol/l)	0.1	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.3	0.1	0.1	0.1	0.0
silicium (μmol/l)	1.6	2.1	3.0	1.2	0.5	0.9	0.8	0.4	0.3	0.5	0.4	0.7	0.9
chlorophyll-*a* (μg/l)	9	14	9	27	8	7	8	10	26	39	46	12	9
chlorophyll-*c* (μg/l)	2	3	2	8	2	2	2	2	7	9	12	3	3
fucoxanthine (μg/l)	7	9	8	22	7	5	6	7	20	25	33	9	8

INTERMEDIATE TIDE

	15:00	17:00	19:00	21:00	23:00	1:00	3:00	5:00	7:00	9:00	11:00	13:00
light intensity	71	20	8	0	0	0	0	0	12	9	28	130
water temperature IT (°C)	13.3	13.2	12.2	11.1	10.6	10.5	10.3	10.3	10.5	10.9	11.3	12.2
salinity IT (psu)	32.4	32.5	32.5	32.5	32.5	32.5	29.9	32.4	29.7	32.4	32.4	32.3
turbidity (ftu)	39	37	37	50	90	104	37	36	65	35	82	99
median grain size (μm)	213	211	200	191	186	190	211	218	206	192	188	188
oxygen content (mg/l)	8.3	8.7	8.6	8.2	8.2	8.2	8.4	8.7	8.6	8.4	8.4	8.0
oxidized nitrogen-N (μmol/l)	1.2	0.5	0.5	0.8	0.8	0.9	0.6	0.6	0.4	1.2	1.4	2.3
ammonia-N (μmol/l)	5.8	4.5	6.0	7.4	5.9	6.5	5.8	6.4	4.1	7.6	7.7	8.2
phosphate-P (μmol/l)	0.2	0.2	0.2	0.3	0.2	0.3	0.1	0.2	0.1	0.2	0.3	0.2
silicium (μmol/l)	1.9	1.9	2.1	2.2	2.1	2.2	2.2	0.0	1.2	1.7	1.8	1.6
chlorophyll-*a* (μg/l)	17	16	16	20	22	21	10	15	19	25	39	28
chlorophyll-*c* (μg/l)	4	5	4	5	6	5	3	4	5	7	10	6
fucoxanthine (μg/l)	14	13	12	15	16	17	9	13	17	24	34	24

NEAP TIDE

	15:00	17:00	19:00	21:00	23:00	1:00	3:00	5:00	7:00	9:00	11:00	13:00	15:00
light intensity	127	68	15	0	0	0	0	0	0	97	114	120	121
water temperature IT (°C)	13.7	14.4	13.6	12.8	11.8	11.1	10.0	10.5	10.5	11.4	13.0	13.7	15.0
salinity IT (psu)	33.6	33.7	33.6	33.6	33.6	33.6	29.5	33.6	33.5	33.5	33.4	33.5	33.6
turbidity (ftu)	16	14	8	11	25	28	14	8	5	11	7	13	20
median grain size (μm)	189	201	213	199	188	186	192	198	211	212	194	188	190
oxygen content (mg/l)	8.2	8.2	8.3	8.3	7.8	8.1	8.2	10.2	7.8	9.0	8.6	9.1	8.6
oxidized nitrogen-N (μmol/l)	0.2	0.1	0.2	0.1	0.0	0.0	0.2	0.4	0.1	0.1	0.0	0.0	0.4
ammonia-N (μmol/l)	4.5	1.5	0.9	2.0	2.8	4.0	4.6	5.0	2.8	2.3	4.1	2.5	2.4
phosphate-P (μmol/l)	0.4	0.2	0.3	0.3	0.2	0.1	0.1	0.1	0.0	0.1	0.1	0.0	0.1
silicium (μmol/l)	0.7	0.6	0.5	0.8	0.5	0.5	0.6	0.9	0.9	1.2	1.0	0.7	1.5
chlorophyll-*a* (μg/l)	12	16	10	8	13	11	9	8	15	14	9	15	22
chlorophyll-*c* (μg/l)	2	3	2	2	3	3	2	1	2	3	2	3	6
fucoxanthine (μg/l)	6	7	5	5	8	8	7	4	7	7	5	9	19

Appendix 2.

Species lists. (A) Hyperbenthos. (B) Epibenthos.

Appendix 2.A. Species list: hyperbenthos (pl: postlarva, juv: juvenile, a: adult, *: excluded from analyses).

Taxon		**Stage**	**Code**	**Remarks**
Phylum Cnidaria				
Classis Hydrozoa	Hydrozoa species	polyp	Hydrop	*
	Aequoria forskalea		Aequfo	
	Bougainvillia brittanica		Bougbr	
	Bougainvillia principis		Bougpr	
	Bougainvillia species		Bougsp	
	Eucheilota maculata		Euchma	
	Eutonina indicans		Eutoin	
	Hybocodon prolifer		Hyboco	
	Margelopsis haeckeli		Margha	
	Phialella quadrata		Phiaqu	
	Phialidium hemisphaericum		Phiahe	
	Sarsia cfr. *tubulosa*		sarcfr	
	Sarsia tubulosa		Sarstu	
	Hydrozoa species	ephyra	Cnidep	
	Hydrozoa species	juv-a	Cnidar	
Classis Scyphozoa	*Aurelia aurita*		Aureau	*
	Cyanea lamarckii	ephyra	Cyanep	*
		juv	Cyanla	*
Classis Anthozoa	Anthozoa species	juv	Anthsp	*
Phylum Ctenophora				
Classis Tentaculata	*Beroë gracilis*		Berogr	
	Pleurobrachia pileus		Pleupi	
Phylum Nematoda	Nematoda species		Nemasp	*
Phylum Annelida				
Classis Polychaeta	*Anaitides maculata*		Anaima	
	Anaitides species		Anaisp	
	Arenicola marina		aremar	
	Eteone species		Eteosp	
	Eulalia pusillus		Eulapu	
	Eumida sanguinea		Eumisa	
	Lanice species	larva	Lanila	
		juv-a	Lanisp	
	Nephtys cirrosa		Nephci	
	Nephtys species		Nephsp	
	Nereis species		Neresp	
	Ophelia rathkei		Ophera	
	Polydora species		Polydo	
	Pygospio elegans		pygele	
	Scolelepis squamata		Scolsq	
	Spio species		Spiosp	
	Spiophanes bombyx		Spiobo	
	Typosyllis armillaris		typarm	
	Typosyllis species		Typhsp	
	Spionidae species		Spioni	
	Capitellidae species		Capite	
	Polynoidae species		Polyno	
	Phyllodocidae species		Phyllo	
	Polychaeta species		Polych	
Nemertinea species			Nemert	
Phylum Arthropoda				
Subphylum Crustacea				
Classis Copepoda	*Anomalocera patersoni*		Anompa	
	Calanus helgolandicus		Calahe	
	Centropages hamatus		Centha	
	Pseudocalanus elongatus		Pseuel	
	Temora longicornis		Temolo	
	Copepoda species		Copepo	
	parasitic Copepoda		parCop	*
Classis Cirripedia	*Elminius modestus*	juv	Elmimo	*
	Cirripedia species	juv	Cirrsp	*

Classis Malacostraca				
Superordo Eucarida				
Ordo Euphausiacea	*Nyctiphanes couchi*		Nyctco	
Ordo Decapoda				
Infraordo Caridea	*Crangon crangon*	zoea	Cranzo	
		pl	Cranpl	
		a	Cranad	*
	Hippolyte varians	pl	Hippva	
	Hippolyte species	zoea	Hippzo	
	Palaemon cf spec1	pl	Palas1	
	Palaemon cf spec4	pl	Palas4	
	Palaemon cf. *longirostris*	pl	Palalo	
	Palaemonidae species	pl	Palasp	
	Pandalus montagui	a	Pandmo	*
	Philocheras trispinosus	pl	Philpl	
		a	Philad	*
	Processidae species	a	Proces	*
Infraordo Anomura	*Acheus cranchii*	pl	Achapl	
		juv	Achaju	
	Diogenes pugilator	pl	Diogpl	
		juv	Diogju	
	Majidae species	juv	Majida	
	Pagurus bernhardus	zoea	Paguzo	
		pl	Pagupl	
	Paguridae species	pl	Paguri	
	Pisidia longicornis	pl	Pisipl	
		a	Pisilo	
	Porcellana platycheles	pl	Porcpl	
	Porcellana species1	pl	Porcsp	
Infraordo Brachyura	*Carcinus maenas*	zoea	Carczo	
		pl	Carcpl	
		juv	Carcju	
		a	Carcad	*
	Corystes cassivelaunus	pl	Corypl	
	Ebalia tuberosa	pl	Ebalpl	
	Liocarcinus holsatus	zoea	Lioczo	
		pl	Liocpl	
		juv	Liocju	
		a	Liocad	*
	Necora puber	pl	Necopl	
	Pilumnus hirtellus	pl	Pilupl	
	Pinnotheres pisum	a	Pinnpi	
	Portumnus latipes	pl	Portpl	
		juv	Portju	
		a	Portad	*
	Brachyura species	zoea	Braczo	
		pl	Bracpl	
		juv	Bracju	
		a	Bracad	*
	Brachyura species 9	pl	Brasp9	
Superordo Peracarida				
Ordo Mysidacea	*Anchialina agilis*		Anchag	
	Gastrosaccus spinifer		Gastsp	
	Mesopodopsis slabberi		Mesosl	
	Mysidopsis gibbosa		Mysigi	
	Neomysis integer		Neomin	
	Praunus flexuosus		Praufl	
	Schistomysis kervillei		Schike	
	Schistomysis spiritus		Schisp	
	Siriella armata		Siriar	
	Siriella clausii		Siricl	
	Siriella jaltensis		Sirija	
	Siriella species		Sirrisp	
	Mysidacea species		Mysida	*
Ordo Cumacea	*Bodotria scorpioides*		Bodosc	
	Cumopsis fagei		Cumofa	
	Cumopsis goodsiri		Cumogo	
	Diastylis bradyi		Diasbr	
	Diastylis laevis		Diasla	
	Diastylis lucifera		Diaslu	
	Diastylis rathkei		Diasra	

Ordo Isopoda	*Eurydice affinis*		Euryaf	
	Eurydice pulchra		Eurypu	
	Idotea baltica		Idotba	
	Idotea granulosa		Idotgr	
	Idotea linearis		Idotli	
	Idotea metallica		Idotme	
	Idotea pelagica		Idotpe	
	Idotea species		Idotsp	
	Jaera 'albifrons' group		Jaeral	
	Jaera nordmanni		Jaerno	
	Sphaeroma serratum		spaser	
	Zenobiana primatica		Zenopr	*
Ordo Amphipoda				
Subordo Gammaridea	*Ampelisca spinipes*		ampspi	
	Aora typica		aortyp	
	Apherusa ovalipes		Apheov	
	Atylus falcatus		Atylfa	
	Atylus guttatus		Atylgu	
	Atylus swammerdami		Atylsw	
	Bathyporeia pilosa		Bathpi	
	Bathyporeia sarsi		Bathsa	
	Bathyporeia species		Bathsp	
	Calliopus laeviusculus		Callla	
	Corophium acherusicum		Coroac	
	Corophium arenarium		Coroar	
	Corophium insidiosum		Coroin	
	Corophium species		Corosp	
	Corophium volutator		Corovo	
	Gammarellus angulosus		gamang	
	Gammarus crinicornis		Gammcr	
	Gammarus insensibilis		Gammin	
	Gammarus lousta		Gammlo	
	Gammarus zaddachi		Gammza	
	Haustorius arenarius		Haustar	
	Hyale nilssoni		Hyalni	
	Hyperia galba		Hypega	
	Jassa cf *marmorata*		Jasscm	
	Jassa cf. *falcata*		Jasscf	
	Jassa falcata		Jassfa	
	Jassa marmorata		Jassma	
	Jassa species		Jasssp	
	Melita dentata		Melide	
	Melita hergensis		Melihe	
	Melita obtusata		Meliob	
	Melita palmata		Melipa	
	Melita species		Melisp	
	Melita species3		Melis3	
	Orchomene nana		Orchna	
	Pontocrates altamarinus		Pontal	
	Pontocrates arenarius		Pontar	
	Stenothoë marina		Stenma	
	Synchelidium maculatum		Syncma	
	Urothoë marina		Urotma	
	Urothoë poseidonis		Urotpo	
	Gammaridae species		Gammar	
	Ischyroceridae species		Ischyr	
	Amphipoda species		Amphip	
Subordo Caprellidea	*Caprella linearis*		Caprli	
	Pariambus typicus		Parity	
	Phtisica marina		Phtima	
	Pseudoprotella phasma		Pseupr	
Phylum Pycnogonida				
	Callipallene brevirostris		Callib	
	Nymphon brevirostre		Nympbr	
	Nymphon rubrum		Nympru	
	Nymphon species		Nympsp	
	Phoxichilidium tubulariae		Phoxtu	
Phylum Mollusca				
Classis Gastropoda	*Eubranchus exiguus*	juv	Eubrex	

	Nassarius reticulatus	juv	Nassre	
	Opistobranchia species	juv	Opisto	
Classis Bivalvia	*Mytilus edulis*	juv	Mytied	*
	Bivalvia species	spat	Bivasp	
Classis Cephalopoda	*Sepiola atlantica*	juv	Sepiat	
Phylum Bryozoa	Bryozoa species		Bryozo	*
Phylum Chaetognatha	*Sagitta elegans*		Saggel	
	Sagitta setosa		Saggse	
	Sagitta species		Saggsp	
Phylum Echinodermata				
Classis Asteroidea	*Asterias rubens*	juv	Asteju	
Classis Ophiuroidea	Ophiuridae species	juv	Ophiur	
Phylum Chordata				
Subphylum Vertebrata				
Classis Osteichthyes	*Agonus cataphractus*	juv	Agonju	
	Ammodytes tobianus	pl	Ammopl	
		juv	Ammoju	
	Anguilla anguilla	juv	Anguju	
	Belone belone	pl	Belopl	
	Buglossidium luteum	pl	Bugllu	
	Chelon labrosus	pl	Chelpl	
	Ciliata mustela	juv	Cilimu	
	Clupea harengus	juv	Clupha	
	Clupeidae species	pl	Cluppl	
		juv	Clupju	
	Dicentrarchus labrax	pl	Dicepl	
		juv	Diceju	
	Gasterosteus aculeatus	a	Gastad	*
	Hyperoplus lanceolatus	a	Hypela	*
	Merlangius merlangus	pl	Merlpl	
		juv	Merlju	
	Mugilidae species	pl	Mugilpl	
	Myoxocephalus scorpius	pl	Myoxpl	
	Pleuronectes flesus	pl	Platpl	
	Pleuronectes platessa	pl	Pleupl	
		juv	Pleuju	
		a	Pleua	*
	Pomatoschistus lozanoi	a	Pomalo	*
	Pomatoschistus microps	a	Pomamc	*
	Pomatoschistus minutus	a	Pomami	*
	Pomatoschistus species	pl	Pomapl	
		a	Pomasp	*
	Solea solea	pl	Solepl	
		juv	Soleju	
	Sprattus sprattus	juv	Sprasp	
	Syngnathus rostellatus	pl	Syngpl	
		juv	Syngju	
	Taurulus bubalis	pl	Taurpl	
	Trisopterus minutus	pl	Trispl	
	Pisces species	eggs	Pisceg	
		pl	Pisces	
Total number of hyperbenthic functional species		**207**		
Total number of hyperbenthic biological species		**180**		

Appendix 2.B. Species list: epibenthos (pl: postlarva, juv: juvenile, a: adult, *: excluded from analyses).

Taxon		**Stage**	**Code**	**Remarks**
Phylum Cnidaria	Cnidaria species	juv-a	cnid spec	
	Aurelia aurita	juv-a	aure auri	
	Cyanea lamarckii	juv-a	cyan lama	
Phylum Ctenophora				
Classis Tentaculata	*Pleurobrachia pileus*		pleu pile	*
Phylum Arthropoda				
Subphylum Crustacea				
Classis Malacostraca				
Superordo Eucarida				
Ordo Decapoda				
Infraordo Caridea	*Crangon crangon*	juv	cran juve	
		a	cran cran	
	Palaemon longirostris	a	pala long	
	Palaemon serratus	a	pala serr	
	Palaemon species	a	pala spec	
	Philocheras trispinosus	juv	phil juve	
		a	phil tris	
Infraordo Anomura	Anomura species	juv	rept spec	
Infraordo Brachyura	*Cancer pagurus*	a	canc pagu	
	Carcinus maenas	juv	carc juve	
		a	carc maen	
	Eriocheir sinensis	a	erio sine	
	Liocarcinus holsatus	juv	lioc juve	
		a	lioc hols	
	Liocarcinus species	a	lioc spec	
	Portumnes latipes	juv	port juve	
		a	port lati	
	Brachyura species	a	brac spec	
Superordo Peracarida				
Ordo Mysidacea	*Gastrosaccus spinifer*		gast spin	*
	Mesopodopsis slabberi		meso slab	*
	Neomysis integer		neom inte	*
	Praunus flexuosus		prau flex	*
	Schistomysis kervillei		schi kerv	*
	Schistomysis spiritus		schi spir	*
Ordo Isopoda	*Idotea linearis*		idot line	*
Ordo Amphipoda				
Subordo Gammaridea	*Gammarus crinicornis*		gamm crin	*
Phylum Pycnogonida	*Nymphon gracile*		nymp grac	*
Phylum Mollusca				
Classis Gastropoda	Opistobranchia species	juv-a	opis spec	*
Classis Cephalopoda	*Sepiola atlantica*	juv-a	sepi atla	
Phylum Echinodermata				
Classis Asteroidea	*Asterias rubens*	a	aste rube	
Phylum Chordata				
Subphylum Vertebrata				
Classis Osteichthyes				
Ordo Clupeiformes	*Clupea harengus*	juv	clup hare	
	Sprattus sprattus	juv	spra spra	
	Clupeidae species	pl	clup post	*
		juv	clup spec	
Ordo Gadiformes	*Ciliata mustela*	juv-a	cili must	
Ordo Atheriniformes	*Atherina presbyter*	juv	athe pres	
Ordo Gasterosteiformes	*Gasterosteus aculeatus*	a	gast acul	
Ordo Syngnathiformes	*Syngnathus rostellatus*	juv-a	syng rost	
Ordo Scorpaeniformes	*Agonus cataphractus*	juv	agon cata	
Ordo Perciformes	*Ammodytes tobianus*	pl	ammo post	*

		juv-a	ammo tobi	
	Echiichthys vipera	a	echi vipe	
	Pomatoschistus lozanoi	a	poma loza	
	Pomatoschistus microps	a	poma micr	
	Pomatoschistus minutus	a	poma minu	
	Pomatoschistus species	pl	poma spec	*
	Zoarces viviparus	juv-a	zoar vivi	
Ordo Pleuronectiformes	*Limanda limanda*	juv	lima lima	
	Pleuronectes flesus	juv	pleu fles	
	Pleuronectes platessa	juv	pleu plat	
	Scophthalmus maximus	juv	scop maxi	
	Scophthalmus rhombus	juv	scop rhom	
	Solea solea	juv	sole sole	

Total number of epibenthic functional species	**39**
Total number of epibenthic biological species	**34**

Appendix 3.

Hyperbenthic densities. (A) Temporal campaign. (B) Spatial campaign. (C) 24-hour cycles.

Appendix 3.A. Catch densities of the hyperbenthos (ind./100m²): temporal campaign (*: no sampling).

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Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	* **Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Cnidar	2		32						15			0			
Sarstu	8										2	0			
Phiahe															
Phiaqu															
Margha															
Eutoin	17														
Euchma			224	78	4				55					7	0
Bougsp			754	1	2									2	0
Aequfo															
Berogr															
Pleupi	5								0						
Polych					0										
Spioni															
Phyllo															
Polyno												0			
Eulapu	0														
Spiosp												0			
Spiobo															
Scolsq						0									
Typhsp															
Lanila															
Lanisp															
Nephsp			6	0											
Neresp															
Polydo												0			
Eteosp		0												0	
Ophera															
Anaisp										0					
Calahe										4					
Centha															
Anompa															
Temolo															
Nyctco	0										4				
Cranpl	14	107	120	40	68	23			0	1	6	13	27	8	6
Cranzo	38		2	3	0	0				0	11			0	1
Hippzo											0				
Hippva			0			0		0							
Philpl			1	1	0										
Palalo			11	0		0									1
Palas1			1	2											0
Palas4			1	6											2
Palasp			0	0											

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	* Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Proces			0												
Pagupl	1		0	0											
Paguzo	0														
Diogju				0											
Diogpl			0												0
Paguri															
Achapl				0											
Achaju															
Majida			0												
Porcpl			4												0
Porcsp			3												
Pisilo				5											
Pisipl				1											1
Bracju	1	13	9	4	1								0	4	1
Bracpl															0
Braczo	0														
Carcju	0	20	2	1	0	0									0
Carcpl	58	615	28	18	4	1							53	106	89
Carczo															
Corypl															
Liocju			0	1										0	
Liocpl	0			0											0
Lioczo	1										1				0
Portju		1	3	0	0										0
Portpl			2	1	0										
Pilupl				1	0										
Ebalpl						0									
Necopl															0
Anchag											11				
Gastsp	1	4	10	13	3	6		2		1	11	1	1	8	7
Mesosl	149	546	149	182	34	98		1		53	263	168	1282	42	1856
Neomin			2		2	19		3	0	1					0
Praufl			0		0			0		28	12	0			0
Schike	2	139	65	173	208	2503		776	2	11	44	0	53	12	16
Schisp	67	2	42	116	10	95		135	6	2	986	0	5359	313	1049
Mysigi															
Siricl															
Sirija															
Siriar			0			0					1				0
Mysida															
Cumogo								0			0	0	1	0	
Diasbr															
Diasra										0				1	
Diasla															
Euryaf															
Eurypu	5	2	0		0					0		0	1		

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	* Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Idotgr															
Idotli		46	146	3	29	27		4				0		17	13
Idotpe															
Idotba												4			
Idotsp															
Idotme		0													
Idotema												0			
Jaerno															
Nympru															
Nympbr															
Nympsp															
Callib															
Phoxtu															
Parity															
Caprli															
Phtima															
Amphip									0		0				
Atylfa						0								0	
Atylgu															
Atylsw	60	53	1	0	1	3		0			0	1	1	8	
Bathsa	1		0		0				3	2	0	1	0	1	0
Bathpi									0						
Bathsp						0			1	1	0	0		0	
Callla									0						
Coroac											0				
Coroin															
Corosp															
Gammar		14													
Gammcr	7	500	5	2	387	11		3	1	3	0	0	1	36	11
Gammin															
Gammlo	0														
Gammza															
Haustar															
Ischyr												0			
Jassfa															
Jassma					0						0		0	0	
Jasssp															
Pontal	38	1	0	1		25		1					4	13	5
Pontar															
Stenma															
Urotpo									0						
Urotma															
Hyalni															
Melis3															
Melipa															
Melide										0					

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	* Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Melihe									0						
Meliob										0					
Melisp											0				
Orchna			0												
Hypega			2	0										0	
Opisto															
Sepiat															
Bivasp		2													
Ophiur															
Asteju															
Saggel															
Saggse	0				3	1		1	4	1				0	
Ammoju	2	0			0					2	1				1
Ammopl	1							0		1					1
Anguju											0				
Clupha	0				0							0			
Cluppl	244	28	6		0						28	5	16	1	1
Clupju	0	0													
Myoxpl															
Platpl	22										0	18	13		
Pleuju		5	0		1	1									
Pleupl	0									7	0	0			
Pomapl	200	5	205	104	1	1							2		95
Solepl	10										0		1		
Soleju		1	0												
Bugllu															
Sprasp															
Syngpl			1	0											1
Syngju			1	2	1	22					1				2
Trispl															
Dicepl			6	1											1
Diceju															
Belopl															
Agonju		0			0										
Ciliju				0											
Mugipl					0										
Pisces															
Pisceg	8	2								0	4	7	0		
TOTAL	**966**	**2105**	**1848**	**762**	**764**	**2838**		**928**	**88**	**117**	**1390**	**222**	**6814**	**580**	**3163**

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			*				*		*								
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97(1)**	**Apr'97(2)**	**May'97(1)**	**May'97(2)**	**Jun'97**	**Jul'97**
Cnidar					0	0											
Sarstu	2																
Phiahe		4															
Phiaqu																	
Margha	0	1												0	44	9	
Eutoin	2													1			
Euchma				7	2	1										26	9
Bougsp		15		0	2	0								2	3	1	3
Aequfo																	
Berogr																	
Pleupi	2															0	
Polych																1	
Spioni				0													
Phyllo																	
Polyno						0				0			0		0	0	
Eulapu																	
Spiosp																	
Spiobo																	
Scolsq											0			0			
Typhsp						0										1	
Lanila																3	
Lanisp																	
Nephsp				0													0
Neresp																	
Polydo		0													0	7	0
Eteosp															0		0
Ophera																	
Anaisp		0								0						0	
Calahe	1									0	9	0		0			
Centha															0		
Anompa		0															
Temolo											0						
Nyctco																	
Cranpl	4	17		6	21	17					6	2	12	14	29	25	5
Cranzo	1	0			0										1		0
Hippzo																	
Hippva					0												
Philpl																	
Palalo				0		1											0
Palas1																	
Palas4																	3
Palasp																	
Proces																	
Pagupl	0													0			
Paguzo														0			

			*				*		*								
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97(1)**	**Apr'97(2)**	**May'97(1)**	**May'97(2)**	**Jun'97**	**Jul'97**
Diogju																	
Diogpl																	
Paguri																	
Achapl																	
Achaju																	
Majida																	
Porcpl																	1
Porcsp					0												
Pisilo																	
Pisipl																	1
Bracju	0	14			2	1							0	10	42	16	0
Bracpl																	
Braczo																	
Carcju		9			2	0								3	7	3	
Carcpl	1	101			0	1								223	180	271	67
Carczo		0															
Corypl	0																
Liocju	0					0								0	2		1
Liocpl	0	1												1			
Lioczo	0													0			
Portju					0												
Portpl																	
Pilupl																	
Ebalpl																	
Necopl	0																
Anchag											1	0	0				
Gastsp		0		0	1	0				1	23		0	0	2	2	1
Mesosl	127	678		1560	585	401				5		4	26	1702	9	26	757
Neomin		1			1	17		75		0		0					
Praufl								3		20	3	3		0			
Schike	0	2		9	22	386		63		4	166	0		30	3	1	7
Schisp	1	2		1	71	281		0		4	378	7	0	6497	15	8	39
Mysigi																	
Siricl											0						
Sirija												0					
Siriar		0												4			
Mysida								0		0			0				
Cumogo	0										0	0	1	1	2	0	
Diasbr						0											
Diasra								0		0	2	0	0		19	0	0
Diasla																	
Euryaf																	
Eurypu	1	0				0						0		0			
Idotgr																	
Idotli		3		0	5	44						0				3	1
Idotpe											0						0

Taxon	May'96	Jun'96	* Jul'96	Aug'96	Sep'96	Oct'96	* Nov'96	Dec'96	* Jan'97	Feb'97	Mar'97	Apr'97(1)	Apr'97(2)	May'97(1)	May'97(2)	Jun'97	Jul'97
Idotba													1				
Idotsp																	
Idotme																	
Idotema																	
Jaerno																0	
Nympru						0											
Nympbr																	
Nympsp																	
Callib																	
Phoxtu															0		
Parity																	
Caprli																	
Phtima																	
Amphip																	
Atylfa		0													1	1	0
Atylgu																	
Atylsw	1	4		0	2			0				0		0	2	18	
Bathsa	0									0		0		0	1	0	
Bathpi																	
Bathsp										0	0	0	0		0	0	
Callla																	
Coroac													0			0	0
Coroin		0													0	1	
Corosp																	
Gammar																	
Gammcr	0	24		1	67	18		5				1	0	0	34	157	7
Gammin													0				
Gammlo																	
Gammza										0							
Haustar																	
Ischyr																	
Jassfa		1									0						
Jassma		1			0	0					0		0		0	2	
Jasssp																0	
Pontal	1	1		0	5	38		0			0	1	1	1	2	38	3
Pontar																	
Stenma																	
Urotpo																	
Urotma	0																
Hyalni																	
Melis3																	
Melipa						0											
Melide																	
Melihe																	
Meliob																	
Melisp	0																

			*				*		*								
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97(1)**	**Apr'97(2)**	**May'97(1)**	**May'97(2)**	**Jun'97**	**Jul'97**
Orchna																	
Hypega															0	0	
Opisto																0	
Sepiat														1			
Bivasp		2													1	5	
Ophiur																	
Asteju															1	0	
Saggel																	
Saggse	0					1				0					0	1	
Ammoju										0	0			0			0
Ammopl											0			0			
Anguju										0							
Clupha																	
Cluppl	26	10		0								4	1	8	2	1	1
Clupju	0																
Myoxpl																	
Platpl	9												12	1	1		
Pleuju					0			2								0	
Pleupl										2	4	0		1			
Pomapl	4	2		7	0	1				5	0			5	0	0	9
Solepl	1										0			0			
Soleju												0					
Bugllu																	
Sprasp		0															
Syngpl				0													2
Syngju				1	0	1											
Trispl										0							
Dicepl		1		0												0	1
Diceju																	
Belopl																	
Agonju																	
Ciliju																	
Mugipl					2												
Pisces				0							0		0				
Pisceg	7										4	10	5		0		
TOTAL	**195**	**898**		**1594**	**792**	**1211**		**150**		**44**	**599**	**35**	**61**	**8507**	**404**	**629**	**920**

WENDUINE

			*				*			*		*			
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Cnidar		0			3	1			57		0		0		
Sarstu	1														
Phiahe					0				51						
Phiaqu															
Margha	0	40											869	1	
Eutoin	2														
Euchma				2	3	0									
Bougsp		0		6	1	1							0		1
Aequfo															
Berogr															
Pleupi	2								0				1		
Polych	0	1						0	0						
Spioni													0		0
Phyllo															
Polyno	0							0			1				
Eulapu															
Spiosp	0														
Spiobo									0						
Scolsq								0	0						
Typhsp								0	0		4				
Lanila	0	1													0
Lanisp	0														
Nephsp									0						
Neresp	0														
Polydo	73	8											0	1	
Eteosp											0				
Ophera															
Anaisp						1					0				
Calahe	3					0					0				
Centha															
Anompa		0													
Temolo															
Nyctco											0				
Cranpl	66	124		52	2	6					5		68	14	3
Cranzo						0							0		
Hippzo															
Hippva											0				
Philpl															
Palalo				2		0									1
Palas1				10	1										0
Palas4				1											3
Palasp				1											0
Proces															
Pagupl													0		
Paguzo		0													

			*				*			*		*			
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Diogju															
Diogpl															
Paguri	0														
Achapl															
Achaju				0											
Majida															
Porcpl															
Porcsp															
Pisilo															
Pisipl															
Bracju	0	8		1		0							3	8	9
Bracpl															
Braczo															
Carcju		4		2		1							2	5	5
Carcpl	2	174		85	0	7							17	292	97
Carczo		10													
Corypl															
Liocju				0		0									
Liocpl															
Lioczo		0													
Portju															
Portpl															
Pilupl															
Ebalpl															
Necopl				0											
Anchag											1				
Gastsp		0		1	13	0		1			13				1
Mesosl	15	3		3133	1743	46		1			4		149	1	3355
Neomin		1			2	40		92	2		1				0
Praufl		0		0	0			10			3		0		1
Schike		0		13	11	93		173			3				0
Schisp				9		4		1	0		40		0		
Mysigi						0									
Siricl											0				
Sirija															
Siriar											0				
Mysida															
Cumogo	0	0												0	
Diasbr													0		
Diasra				0	0	0		0			4		0		
Diasla						0									
Euryaf									0						
Eurypu	1	2			0						0		0		
Idotgr															
Idotli		3		0	1	0		1			3		0	1	17
Idotpe															

			*				*			*		*			
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Idotba		1													2
Idotsp															0
Idotme															
Idotema															
Jaerno		0													
Nympru					0						0				
Nympbr											1				
Nympsp								0							
Callib													0		
Phoxtu															
Parity	0										0				
Caprli											1				0
Phtima											0				
Amphip					0										
Atylfa															
Atylgu		0									2				
Atylsw	3	14		0				1			13		1	0	0
Bathsa		1						0	0		3			0	
Bathpi															
Bathsp	0	0				0		1	2		0		0	1	2
Callla															
Coroac				0				0			0				
Coroin	1	1									0			0	
Corosp															
Gammar															
Gammcr	2	64		5	0	15		305			3		6	11	63
Gammin															
Gammlo															
Gammza															
Haustar															
Ischyr														1	
Jassfa															0
Jassma	0	1						0			1		0	3	1
Jasssp															
Pontal	0					4		3			1		2	3	31
Pontar		0			0			3			1		0		1
Stenma	0	0									0				
Urotpo	0														
Urotma															
Hyalni		0													
Melis3											1				
Melipa								0							
Melide															
Melihe															
Meliob															
Melisp															

			*				*			*		*			
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Orchna															
Hypega						0								33	1
Opisto											0		0		
Sepiat															
Bivasp		0									0		1	2	0
Ophiur											0				
Asteju		0									0				
Saggel	1												0		
Saggse					0	0		1							0
Ammoju	1	0			0	0							0		0
Ammopl	0	1												0	0
Anguju															
Clupha	0	0						1							
Cluppl	1	10				0							11	1	2
Clupju		0													
Myoxpl															
Platpl	7										0		40		
Pleuju	0					0		1							
Pleupl											2				
Pomapl	0			79	2	7		3					2	1	12
Solepl													0		
Soleju															
Bugllu													0		
Sprasp	0														1
Syngpl	0			0											
Syngju	0			44	1	3					0				4
Trispl															
Dicepl				2										0	4
Diceju				0											
Belopl		0													
Agonju															
Ciliju															
Mugipl															
Pisces					0										
Pisceg	8										36				
TOTAL	**197**	**478**		**3452**	**1785**	**233**		**601**	**114**		**155**		**1177**	**382**	**3620**

KNOKKE

			*				*			*					
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Cnidar	0	2		8	62										1
Sarstu	3														
Phiahe		5		8	11	16								1	
Phiaqu		1													
Margha		0											1	0	
Eutoin											0				
Euchma				99	29			0							8
Bougsp				3							0		0		2
Aequfo					0										
Berogr		0													
Pleupi	1	12		0	1						2		4		1
Polych	0														
Spioni															
Phyllo									0						1
Polyno		0										3			
Eulapu															
Spiosp															
Spiobo															
Scolsq												0			
Typhsp															
Lanila						0								1	
Lanisp															
Nephsp															
Neresp															
Polydo	34	2										0		0	0
Eteosp															
Ophera												0			
Anaisp												0			
Calahe	0										2				
Centha											0				
Anompa															
Temolo															
Nyctco															
Cranpl	6	4			0	1		0				7	45	5	6
Cranzo	1			0									0		
Hippzo															
Hippva															
Philpl															
Palalo				1											0
Palas1				21	1										
Palas4														0	
Palasp				1											0
Proces															
Pagupl													0		
Paguzo															

			*				*			*					
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Diogju															
Diogpl															
Paguri															
Achapl															
Achaju															
Majida															
Porcpl															
Porcsp															
Pisilo						0									
Pisipl															
Bracju	0	1		0								8	1	30	3
Bracpl															
Braczo		0													
Carcju		0			0							1	0	9	3
Carcpl	0	34		3	0	3							7	214	32
Carczo		19													
Corypl															
Liocju						0									
Liocpl														0	
Lioczo															
Portju															
Portpl															
Pilupl															
Ebalpl															
Necopl															
Anchag															
Gastsp	0				0						1			0	
Mesosl	3	4		140	207	1504		0			0	1	149	0	65
Neomin		9			0	8		1	1					0	
Praufl	0			0	1			2			2		0		3
Schike	0			1	0	4		6	3		3		0		1
Schisp	0				0	1		6	0		7	0	6	0	
Mysigi															
Siricl															
Sirija															
Siriar													2		1
Mysida	2					0									
Cumogo															
Diasbr						0									
Diasra								0			1				
Diasla															
Euryaf															
Eurypu	24										0		0	1	
Idotgr					0									0	
Idotli					0	1		0						0	4
Idotpe															

			*				*			*					
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Idotba					0							225			
Idotsp															
Idotme												5			
Idotema															
Jaerno												0			
Nympru															
Nympbr															
Nympsp															
Callib															
Phoxtu															
Parity															0
Caprli												0			
Phtima															
Amphip															
Atylfa															
Atylgu															
Atylsw	0	1			0	0					0	6		1	0
Bathsa					0							0	1		0
Bathpi	0													0	
Bathsp											0	3		3	
Callla															
Coroac	0	0													0
Coroin		0												0	
Corosp														0	
Gammar															
Gammcr		2			1	1					0	5	0	13	25
Gammin															
Gammlo															
Gammza															
Haustar											0	0			
Ischyr															
Jassfa								0							
Jassma		1		0	0						0	5	0	0	0
Jasssp		0													1
Pontal						0									0
Pontar					2			0			1	1	1	0	
Stenma												0			
Urotpo		0													
Urotma															
Hyalni											0			0	
Melis3															
Melipa															
Melide															
Melihe															
Meliob															
Melisp															

Taxon	**May'96**	**Jun'96**	* **Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	* **Nov'96**	**Dec'96**	**Jan'97**	* **Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Orchna															
Hypega														6	1
Opisto															
Sepiat													0		
Bivasp											0	0		0	
Ophiur															
Asteju															0
Saggel													0		
Saggse						0									
Ammoju	2			0	3	1							2	0	0
Ammopl	0														
Anguju															
Clupha						0					0				
Cluppl	10	0									0		5	0	
Clupju															
Myoxpl	0														
Platpl	25											0	9		
Pleuju						0		0							
Pleupl											6				
Pomapl				9	1	2									2
Solepl	0														
Soleju															
Bugllu															
Sprasp															
Syngpl															
Syngju				0		0									2
Trispl															
Dicepl				1											1
Diceju															
Belopl		1												0	
Agonju															
Ciliju															
Mugipl															
Pisces															
Pisceg	0										2	10			
TOTAL	**115**	**100**		**298**	**323**	**1545**		**17**	**5**		**30**	**283**	**235**	**289**	**164**

Appendix 3.B. Catch densities of the hyperbenthos (ind./100m²): spatial campaign.

Taxon	BD	DP	Oo	Ni	Lo	Mi	Ma	Br	DH	Bl	Ze	Kn
Sarstu	29	12	1	1	0	6	9	2	3	0	3	1
Hyboco							4					
Cnidsp	2		2	5		8	9					
Eutoin	29	45	9	3					1			
Cnidep	0	2	0	1		1	0					
Pleupi	143	3	21	3			91	1	31	3	2	24
Berogr	5	2	1	0		0	43	1				
Lanila					0	45	1	0		2	2	0
Polydo					28	3				3	1	1
Polych												0
Calahe	3		6	0	0	1	13	277	0	8	2	
Centha	1		4	0			3	29		20	0	
Temolo								5	0	4	28	
Copepo								0			1	
Nyctco	1	0	0			0	0	0				
Cranpl	332	88	159	55	21	18	7	43	3	144	7	11
Cranzo	1	2	2			2		2		8	1	6
Philpl								0				
Hipppl			0					2			0	
Hippzo											0	
Caripl											0	
Paguzo	0							0			0	
Pagupl	2			0						0	0	0
Porcpl						0						
Pinnpi	1											
Carcju		1			3	1					0	
Carcpl	4	8	6		1	1		1			1	
Liocpl	3	4	0			0	1	4				
Liocju								0				
Lioczo	2							0				
Braczo						0	0	2				
Bracpl						0	0			0		
Bracju	5		2	1		1		1		1		
Gastsp	10	1	1	0	10	3	3	7	0	12	3	0
Mesosl	940	2880	800	396	216	501	143	129	1018	499	6	273
Schike	420	211	10	2	1	0	5	189	2	897		8
Schisp	156	171	110	48	0	1	1	11	6	19		1
Neomin	1	1	0		1	2	0	2	1	25	1	2
Praufl	2	2	1	0	0	2		2	1	2		7
Anchag						0		0				
Cumogo	0		0			0					0	
Diasra	1						0	1		3		
Diasbr								0		1		
Bodosc										0	0	
Diaslu								0				
Eurypu	1	6	0	1		0	0	0	1	0	8	0

Taxon	**BD**	**DP**	**Oo**	**Ni**	**Lo**	**Mi**	**Ma**	**Br**	**DH**	**Bl**	**Ze**	**Kn**
Euryaf			0						0			
Idotli	1				0	0						
Idotgr												0
Idotpe						0		0		0		
Jaera					0							
Atylsw	10		3	2	8	1	2	19	0	3	0	
Atylfa	7		1					0				
Atylgu	0											
Pontal	1	2		0	1	1				0	1	
Pontar										1	1	0
Gammcr	0	0	0			0	0			0		
Apheov			0					1				
Syncma									0			
Bathsp	1	0			0			0	0	0	5	0
Coroin						0	0					
Coroac	1				2	0	0	0		1		
Coroar											3	
Corovo					0					1		
Jassfa	0											
Jasscm					0	0	0			0		
Hausar					0							
Stenoma								0				
Gammar	0						0			0	0	
Gammlo	0											
Melipa										0		
Ischsp		0										
Parity			2		2	0		0		0		
Pseuph								0				
Sagisp	1	1							0	0	0	0
Syngju	0	0	0									
Cluppl	116	1	85	15	7	9	35	184	21	129		57
Pomapl							0	1				
Merlju								0				
Merlpl	1		3	0		1	1	37		0		0
Solepl	12	0	1	0								
Pleuju						0						
Pleupl	9	2	4	0	0	1	3	10	0	14	4	3
Platpl	738	281	108	61	74	56	83	451	20	91	200	14
Ammoju		0	1			0	0	0	1		0	
Clupju	0	5	0					0				
Taurpl			0									
Anguju							0	0				
Myoxpl		0			1	0	0	0		3		
Trispl							0					
Spraju								2		0		
Pisces			0					0	0	0		0
Peggs	82	131	488	136	86	86	510	1371	86	1407	49	95
TOTAL	**3077**	**3864**	**1834**	**731**	**465**	**754**	**971**	**2796**	**1199**	**3303**	**333**	**507**

Appendix 3.C. Catch densities of the hyperbenthos (ind./100m²): 24-hour cycles (hours in CET, *: no sampling).

SPRING TIDE

Taxon	**15:00**	**17:00**	**19:00**	**21:00**	**23:00**	**1:00**	**3:00**	**5:00**	**7:00**	**9:00**	**11:00**	**13:00**	**15:00**
Ephyra													
Sartub	0		0	0			0			1			
Sarspe				0		0							
Sarcfr	0		0			0	0		0				0
Eutind			0	0		0				0	0		0
Marhae													
Phihem													
Cnidsp													
Plepil	64	39	45	16	36	101	70		1	6	44	451	116
Bergra			0							0			
Polspe			0	0	0	1	1				0		
Nepcir					0								
Pygele											0		
Scosqu		0									0		
Spionid													
Spiosp													
Lanlar	1	6		0	0					2	0		
Typarm													
Polych													
Temlon													
Cenham													
Calhel	1	0	0			0	1	0	0	2	0		
Bodsco											0		
Cumgoo			1	1	2	0			1	2	4		
Cumfag													
Diarat		0	1	2			0	1	1	1			
Dialae													
Gasspi			0	10	5	1	0	2	2		0	0	
Ancagi									0	1	0		
Prafle		0		2	1					0		0	
Schspi		1	3	153	77	37	46	90	74	187	37	1	1
Schker			0	198	33	3	0	7	45	148	16	0	
Messla	47	383	490	2790	825	297	135	655	492	2020	4671	454	1008
Neoint													
Sirarm				0				0		1	1		
Idolin				0				0	0				
Idobal	0	1	2	2						0		0	
Idopel	0	1	0	1									
Eurpul	6	8	1	1	1	40	31	25	1		1	3	3
Spaser													
Partyp													
Corvol	0	0				0					0		
Corare		0				0						0	
Corins													
Ponalt				8	0				1	9			
Orcnan									0				
Stemar													
Atyswa		0	1	6	3	1	0		0	1			
Atygut				1	0					0			
Hyanil		0											
Jasfal					0							0	
Jasmar				0									
Jasspe						0							
Gamcri			1	3	0	0			3	4	0		
Ampspi													
Batpil	5	4	0		0	25	45	10	1		0	2	3
Batsar	1	4		0	1	6	6	7	0		0	1	1
Batspe	1	0				2	2	0		0		0	0
Uropos													
Melher													
Aortyp													
Gamang													
Ampspe		0					0						
Nyccou	0									1			0

Taxon	**15:00**	**17:00**	**19:00**	**21:00**	**23:00**	**1:00**	**3:00**	**5:00**	**7:00**	**9:00**	**11:00**	**13:00**	**15:00**
Cranpl	2	34	24	159	54	57	73	82	121	624	108	4	0
Cranzo	2	3	20	31	17	16	1	2	3	14	4		0
Phitri													
Palapl													
Hipvpl				0					0	1			
Pagber													
Pagzoë													
Corzoë													
Carmeg	0		0		0	0							
Carzoë		0							0				
Porzoë													
Liomeg													
Liozoë	0	0	0			0				1			
Liojuv													
Brajuv								0		1	0		
Terter													
Bivspa													
Sagele										0			
Sagset													
Astjuv													
Angjuv				0							0		
Cluppl	0	4	2	2	0	1	0	9	20	110	40	18	18
Trilpl										0			
Synros				1	0			0	0	2	1		
Synrpl				0						0			
Myospl						0					0		
Phogpl			0	2	0	0	0		0	0			
Ammjuv				0								0	0
Ammopl					0						0	0	
Pomspl				0						0			
Lizram													
Ttaubub													
Platpl	58	56	17	27	6	5	2	24	62	264	138	16	18
Pleupl	1	0	0	6	2	2	1	3	3	2	1		
Solsol													
Pisegg	18	20	12	16	12	10	8	23	19	61	14	15	11
spec1													
spec2													
spec3													
spec8													
TOTAL	209	567	624	3442	1079	609	424	943	852	3467	5084	968	1180

INTERMEDIATE TIDE

Taxon	15:00	17:00	19:00	21:00	23:00	1:00	3:00	5:00	7:00	9:00	11:00	13:00	* 15:00
Ephyra		0	9			0					36	24	
Sartub	0									4		2	
Sarspe	2	2	4	3	1	25	12	27	15		2		
Sarcfr													
Eutind	2	0	3	1	0	7	11	18	17	14	140	136	
Marhae							0			0	40	15	
Phihem											0	2	
Cnidsp							0					3	
Plepil	26	2	20				226	362	59	32	13	17	
Bergra							2	4	2	0	1	4	
Polspe				0			0	0	0	1	1		
Nepcir				0									
Pygele													
Scosqu							0	0					
Spionid													
Spiosp													
Lanlar		0	124	162	170	20	1	61	138	248	548	618	
Typarm													
Polych								0					
Temlon										1		2	
Cenham										6		2	
Calhel	2	0	6	2		17	17	32	3	6	3	6	
Bodsco		0											
Cumgoo			0		0	2			0	7	0	2	
Cumfag													
Diarat				2	2	0		0	1	1	4		
Dialae					0								
Gasspi			14	18	10	35	2	0	10	4	8	6	
Ancagi											0		
Prafle		0	0		1	0		0					
Schspi	0	0	8	4	5	9	3	10	4	1	1	0	
Schker			3	36	703	43	1	0	0	2	20	0	
Messla	165	339	356	132	248	317	153	220	81	48	48	6	
Neoint													
Sirarm	0	0	1		2	2	1	4	2		0		
Idolin													
Idobal	0	0			0					1			
Idopel					0								
Eurpul	10	5	1		1	0	49	37	3	0	4	0	
Spaser		0											
Partyp													
Corvol	0						0	0					
Corare													
Corins					0							1	
Ponalt				0	15	2				0	3		
Orcnan													
Stemar											0		
Atyswa				1	2	0		0	0	1	2		
Atygut								0					
Hyanil													
Jasfal						0							
Jasmar						0					0	0	
Jasspe													
Gamcri			0	1	2	0				1	3	0	
Ampspi							0						
Batpil	8	4	0		1		44	26	5			0	
Batsar	0	0	4			1	2	4	3	0	0		
Batspe	2	1		0	2	0	6	3	0				
Uropos					2	0	0	1					
Melher													
Aortyp											0		
Gamang													
Ampspe	0	0							0				
Nyccou						0				0	1	0	
Cranpl	0	2	208	224	470	144	71	58	230	134	152	68	
Cranzo		0	10				2	0	1	9	1	1	
Phitri					0					0	0		
Palapl				0					0		0	0	

													*
Taxon	**15:00**	**17:00**	**19:00**	**21:00**	**23:00**	**1:00**	**3:00**	**5:00**	**7:00**	**9:00**	**11:00**	**13:00**	**15:00**
Hipvpl										1			
Pagber						0		0		0		0	
Pagzoë										0			
Corzoë													
Carmeg			0							1	0		
Carzoë													
Porzoë								0					
Liomeg		0	2			1	1	2	2	1	10	4	
Liozoë	1	1	1	0		2	9	12	8	4	6	6	
Liojuv							0		1	1	2	1	
Brajuv								0	0	1	5	0	
Terter		0	1								0	1	
Bivspa													
Sagele			0										
Sagset					0	1		0					
Astjuv													
Angjuv					1	0	0				0	0	
Cluppl	50	41	138	48	71	58	7	93	73	26	10	1	
Trilpl					0								
Synros			0		0	1							
Synrpl					0								
Myospl													
Phogpl					1			0	0	0			
Ammjuv				0	4	0				1	1		
Ammopl													
Pomspl							0			0			
Lizram													
Ttaubub											0		
Platpl	25	51	66	20	40	28	24	37	18	18	57	24	
Pleupl			3	2	26	4	0	1	15	4	7	1	
Solsol			0			0			0				
Pisegg	56	74	249	68	190	174	92	152	97	132	233	252	
spec1													
spec2													
spec3													
spec8													
TOTAL	351	528	1232	726	1971	896	740	1167	790	715	1366	1206	

NEAP TIDE

Taxon	**15:00**	**17:00**	**19:00**	**21:00**	**23:00**	**1:00**	**3:00**	**5:00**	**7:00**	**9:00**	**11:00**	**13:00**	**15:00**
Ephyra							1	0		0	0		
Sartub							0	1	0		0	0	1
Sarspe													
Sarcfr													
Eutind		0	1		0	3	1	1	4	1	5	2	8
Marhae		1	1		1	996	3		0		5	5	2
Phihem									0				
Cnidsp													
Plepil	1	0	1					0	1	1	3	2	1
Bergra									0		0		
Polspe	2	0		1	2	2	1					0	
Nepcir													
Pygele													
Scosqu					0								
Spionid							0						
Spiosp												0	
Lanlar	2	2	1	0	72	568	400	16	12	2	61	55	174
Typarm						1							
Polych													
Temlon					0	0							
Cenham					0	0	0			0	0		
Calhel	0	1	1	1	5	3	4	2	0	1	1	1	1
Bodsco							0						
Cumgoo	6	0		1	8	4	3	0			7	0	1
Cumfag					0								
Diarat		0				0						0	
Dialae													
Gasspi	0	0		5	9	23	72	2			1	2	8
Ancagi								0					
Prafle			0	0		0	0	0		0	0		0
Schspi				1		0	0				0	1	1
Schker					5	33	0						
Messla	32	9	7	184	18	42	16	30	1	2	265	389	1155
Neoint	0						0						
Sirarm	0				0	3	0	0			1	1	0
Idolin						3						1	
Idobal			0	0	0		0			0		0	0
Idopel								0					
Eurpul	0	0	8	9	3	5	4	2	7	6			
Spaser													
Partyp							0						
Corvol		0	0										
Corare													
Corins							0						
Ponalt					0	28	6	0				2	3
Orcnan													
Stemar						1						0	
Atyswa				0	1	6		0				0	
Atygut					1	1						0	
Hyanil													
Jasfal	0												0
Jasmar		0		0			0		0				
Jasspe													
Gamcri				0	2	38	1	0				1	0
Ampspi													
Batpil			1	4	1		0	0	2	2	1		
Batsar	0	1	2	4	1		0	0	0	2			
Batspe		0	0	0	1	2	1		0	1	0	0	0
Uropos				1	1		0						
Melher					0								
Aortyp													
Gamang					0								
Ampspe								0					
Nyccou						0							
Cranpl	19	1	2	24	100	152	115	18	0	0	20	76	44
Cranzo	0												0
Phitri							1						
Palapl													

Taxon	**15:00**	**17:00**	**19:00**	**21:00**	**23:00**	**1:00**	**3:00**	**5:00**	**7:00**	**9:00**	**11:00**	**13:00**	**15:00**
Hipvpl											0		
Pagber	0			0	0	0	0	0					
Pagzoë													
Corzoë									0				
Carmeg		0	0	0	0			1	0	0	0	0	0
Carzoë													
Porzoë													
Liomeg					0		0	0					
Liozoë													
Liojuv													
Brajuv						0						0	
Terter						1					0		
Bivspa					1								
Sagele					0		0				0		
Sagset							0				0		
Astjuv											0		
Angjuv						0							
Cluppl	78	33	42	5	5	36	53	78	79	9	8	11	43
Trilpl													
Synros				0	0	6	0					0	
Synrpl						2							
Myospl													
Phogpl				0		1		0					
Ammjuv	0				2	0	4				0		
Ammopl						6						0	1
Pomspl					0	1			0	0			
Lizram					0								
Ttaubub													
Platpl	31	3	14	63	38	36	48	38	15	18	43	30	48
Pleupl				0	1	4	3	0				1	
Solsol								0					
Pisegg	18	9	12	10	73	290	176	58	38	21	62	82	105
spec1		0	0			1						9	
spec2						0							
spec3												4	0
spec8											2		
TOTAL	192	63	97	316	356	2299	918	252	163	68	488	679	1599

Appendix 4.

Hyperbenthic biomass. (A) Temporal campaign. (B) 24-hour cycles.

Appendix 4.A. Catch biomass of the hyperbenthos (mg AFDW/100m², w/o adult polychaetes): temporal campaign (*: no sampling).

OOSTDUINKERKE

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	* Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Cnidar	0		0						0			0			
Sarstu	0										0	0			
Phiahe															
Phiaqu															
Margha															
Eutoin	0														
Euchma			0	0	0				0					0	0
Bougsp			2	0	0									0	0
Aequfo															
Berogr															
Pleupi	0								0						
Lanila															
Calahe										0					
Centha															
Anompa															
Temolo															
Nyctco	0										2				
Cranpl	7	26	102	8	30	9			0	0	3	6	34	6	2
Cranzo	9		0	1	0	0				0	3			0	0
Hippzo											0				
Hippva			0			0		0							
Philpl			1	1	0										
Palalo			4	0		0									0
Palas1			0	1											0
Palas4			0	2											1
Palasp			0	0											
Proces			0												
Pagupl	1		0	0											
Paguzo	0														
Diogju				1											
Diogpl			0												0
Paguri															
Achapl				0											
Achaju															
Majida			1												
Porcpl			3												0
Porcsp			2												
Pisilo				3											
Pisipl				1											1
Bracju	5	1	17	1	0								2	10	3
Bracpl															0
Braczo	0														

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Carcju	5	31	12	0	1	0									0
Carcpl	5	50	2	1	0	0							4	9	7
Carczo															
Corypl															
Liocju			4	4										3	
Liocpl	0			0											0
Lioczo	0										0				0
Portju		13	22	0	3										0
Portpl			0	0	0										
Pilupl				0	0										
Ebalpl						0									
Necopl															0
Anchag											6				
Gastsp	2	4	5	9	1	4		6		1	28	3	4	5	4
Mesosl	209	615	182	162	31	90		1		41	269	222	2164	45	1008
Neomin			2		2	16		5	1	2					0
Praufl			1		2			6		339	193	4			0
Schike	2	182	127	90	59	785		797	3	10	45	0	48	8	7
Schisp	178	3	88	87	4	46		285	2	1	1618	0	12389	189	275
Mysigi															
Siricl															
Sirija															
Siriar			0			2					5				1
Mysida															
Cumogo								0			0	0	0	0	
Diasbr															
Diasra										0				1	
Diasla															
Euryaf															
Eurypu	1	0	0		0					0		0	0		
Idotgr															
Idotli		36	202	2	14	133		4				0		3	25
Idotpe															
Idotba												5			
Idotsp															
Idotme		3													
Jaerno															
Nympru															
Nympbr															
Nympsp															
Callib															
Phoxtu															
Parity															
Caprli															
Phtima															
Amphip									0		0				

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Atylfa						0								0	
Atylgu															
Atylsw	17	14	0	0	0	1		0			0	0	0	2	
Bathsa	0		0		0				1	0	0	0	0	0	0
Bathpi									0						
Bathsp						0			0	0	0	0		0	
Callla									0						
Coroac											0				
Coroin															
Corosp															
Gammar		24													
Gammcr	8	611	6	1	244	6		2	0	2	0	0	2	65	12
Gammin															
Gammlo	1														
Gammza															
Haustar															
Ischyr												0			
Jassfa															
Jassma					0						0		0	0	
Jasssp															
Pontal	19	0	0	0		5		0					1	2	1
Pontar															
Stenma															
Urotpo									0						
Urotma															
Hyalni															
Melis3															
Melipa															
Melide										0					
Melihe									0						
Meliob										0					
Melisp											0				
Orchna			0												
Hypega			0											0	
Opisto															
Sepiat															
Bivasp		0													
Ophiur															
Asteju															
Saggel															
Saggse	0				0	0		0	0	0				0	
Ammoto	537	10			14			5		193	278				96
Angu											1				
Clupha	27				49							13			
Cluppl	5012	257	22		4						194	98	247	4	6
Clupju	82	82													

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Myox															
Platpl	21										0	20	13		
Pleuju		2098	206		1383	1046									
Pleupl	21									326	6	10			
Pomapl	603	7	1416	199	3	1							6		102
Solepl	3										0		1		
Soleju		400	274												
Bugllu															
Sprasp															
Syngro	14	280	13	14	544	637		48			99	7		18	16
Trispl															
Dicela			26	5											3
Belopl															
Agonju		16			59										
Ciliju				7											
Mugipl					1										
Pisces															
Pisceg	0	0								0	0	0	0		
TOTAL	**6789**	**4762**	**2745**	**602**	**2450**	**2782**		**1160**	**10**	**918**	**2750**	**391**	**14915**	**373**	**1569**

KNOKKE

			*				*			*					
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
Cnidar	0	0		0	0										0
Sarstu	0														
Phiahe		0		0	0	0								0	
Phiaqu		0													
Margha		0											0	0	
Eutoin											0				
Euchma				0	0			0							0
Bougsp				0							0		0		0
Aequfo					0										
Berogr		0													
Pleupi	0	0		0	0						0		0		0
Lanila						0								0	
Calahe	0										0				
Centha											0				
Anompa															
Temolo															
Nyctco															
Cranpl	3	4			0	1		1				3	16	1	2
Cranzo	0			0									0		
Hippzo															
Hippva															
Philpl															
Palalo				0											0
Palas1				7	0										

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Palas4														0	
Palasp				0											0
Proces															
Pagupl													0		
Paguzo															
Diogju															
Diogpl															
Paguri															
Achapl															
Achaju															
Majida															
Porcpl															
Porcsp															
Pisilo						0									
Pisipl															
Bracju	0	0		0								79	0	615	0
Bracpl															
Braczo		0													
Carcju		0			0							2	0	22	14
Carcpl	0	3		0	0	0							1	17	3
Carczo		1													
Corypl															
Liocju						4									
Liocpl														0	
Lioczo															
Portju															
Portpl															
Pilupl															
Ebalpl															
Necopl															
Anchag															
Gastsp	2				0						3			0	
Mesosl	2	4		46	32	33		0			1	1	73	1	45
Neomin		6			1	11		1	1					0	
Praufl	4			1	6			22			29		4		16
Schike	0			0	0	1		2	2		1		0		0
Schisp	0				0	0		2	0		5	0	0	0	
Mysigi															
Siricl															
Sirija															
Siriar													13		5
Mysida	2					1									
Cumogo															
Diasbr						0									
Diasra								2			4				
Diasla															

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Euryaf															
Eurypu	3										0		0	0	
Idotgr					0									0	
Idotli					0	1		0						1	4
Idotpe															
Idotba					0							703			
Idotsp															
Idotme												20			
Jaerno												0			
Nympru															
Nympbr															
Nympsp															
Callib															
Phoxtu															
Parity															0
Caprli												0			
Phtima															
Amphip															
Atylfa															
Atylgu															
Atylsw	0	0			0	0					0	2		0	0
Bathsa					0							0	0		0
Bathpi	0													0	
Bathsp											0	1		1	
Callla															
Coroac	0	0													0
Coroin		0												0	
Corosp														0	
Gammar															
Gammcr		3			0	0					1	10	0	9	16
Gammin															
Gammlo															
Gammza															
Haustar											0	0			
Ischyr															
Jassfa								0							
Jassma		0		0	0						0	2	0	0	0
Jasssp		0													0
Pontal						0									0
Pontar					0			0			0	0	0	0	
Stenma												0			
Urotpo		0													
Urotma															
Hyalni											0			0	
Melis3															
Melipa															

Taxon	May'96	Jun'96	Jul'96	Aug'96	Sep'96	Oct'96	Nov'96	Dec'96	Jan'97	Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
Melide															
Melihe															
Meliob															
Melisp															
Orchna															
Hypega														2	1
Opisto															
Sepiat													2		
Bivasp											0	0		0	
Ophiur															
Asteju															0
Saggel													0		
Saggse						0									
Ammoto	189			59	489	166							384	6	15
Angu															
Clupha						126					57				
Cluppl	206	2									5		61	1	
Clupju															
Myox	10														
Platpl	22											0	7		
Pleuju						117		55							
Pleupl											12				
Pomapl				10	0	1									2
Solepl	0														
Soleju															
Bugllu															
Sprasp															
Syngro				8		34									13
Trispl															
Dicela				3											3
Belopl		0												0	
Agonju															
Ciliju															
Mugipl															
Pisces															
Pisceg	0										0	0			
TOTAL	**444**	**25**		**136**	**531**	**496**		**86**	**3**		**120**	**823**	**562**	**679**	**138**

Appendix 4.B. Catch biomass of the hyperbenthos (mg AFDW/100m²): 24-hour cycles (hours in CET).

SPRING TIDE

Taxon	15:00	17:00	19:00	21:00	23:00	1:00	3:00	5:00	7:00	9:00	11:00	13:00	15:00
Sartub	0		0	0			0			0			
Sarspe				0		0							
Sarcfr	0		0			0	0		0				0
Eutind			0	0		0				0	0		0
Plepil	0	0	0	0	0	0	0		0	0	0	2	1
Bergra			0							0			
Polspe			0	0	0	0	0				0		
Nepcir					0								
Pygele											0		
Scosqu		0									0		
Lanlar	0	1		0	0					0	0		
Calhel	0	0	0			0	0	0	0	1	0		
Bodsco											0		
Cumgoo			0	0	1	0			0	1	1		
Diarat		2	3	17			1	0	3	2			
Gasspi			1	52	32	3	3	14	12		1	2	
Ancagi									0	0	0		
Prafle		6		31	14					5		7	
Schspi		1	9	305	127	65	150	346	169	592	89	5	1
Schker			0	364	74	15	3	7	51	174	18	3	
Messla	52	473	588	3544	1006	365	169	1240	656	2759	7203	630	1395
Sirarm				3				4		8	4		
Idolin				1				1	0				
Idobal	0	1	1	3						1		3	
Idopel	0	0	0	0									
Eurpul	1	1	0	0	0	6	5	4	0		0	1	0
Corvol	0	5				0					0		
Corare		0				0						0	
Ponalt				2	0				0	2			
Orcnan									0				
Atyswa		0	0	4	2	0	0		0	1			
Atygut				1	0					0			
Hyanil		0											
Jasfal					0							0	
Jasmar				0									
Jasspe						2							
Gamcri			0	1	0	0			1	1	0		
Batpil	2	1	0		0	9	15	3	0		0	1	1
Batsar	0	1		0	0	2	2	2	0		0	0	0
Batspe	2	2				13	15	0		3		0	0
Ampspe		2					3						
Nyccou	1									1			0
Cranpl	1	12	14	64	31	26	63	46	83	245	51	2	0
Cranzo	2	3	20	32	18	17	1	2	3	14	4		0
Hipvpl				0					0	2			
Carmeg	0		0		0	0							
Carzoë		0							0				
Liozoë	0	0	0			0				0			
Brajuv								0		1	271		
Sagele										0			
Angjuv				0							0		
Cluppl	3	47	12	20	2	6	7	82	196	1088	375	181	179
Trilpl										2			
Synros				33	13			20	14	93	41		
Synrpl				6						3			
Myospl						0					0		
Phogpl			5	21	3	2	1		1	3			
Ammjuv				0								0	0
Ammopl					35						6	43	
Pomspl				2						2			
Platpl	50	48	14	24	5	4	2	23	54	239	126	15	16
Pleupl	3	1	1	18	4	4	2	11	5	6	1		
Pisegg	2	2	1	2	1	1	1	3	2	7	2	2	1
TOTAL	**120**	**653**	**961**	**10561**	**3859**	**775**	**912**	**2711**	**2102**	**6786**	**9535**	**911**	**1644**

Appendix 5.

Epibenthic densities. (A) Temporal campaign. (B) Spatial campaign. (C) 24-hour cycles.

Appendix 5.A. Catch densities of the epibenthos (ind./100m²): temporal campaign (*: no sampling).

OOSTDUINKERKE

			*				*								
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
cran cran	1	213		181	224	89		48		6	218	5	178	178	1894
phil tris	0	7		0											3
pala spec															
rept spec															
brac spec					0										2
Carc spec	0	1			0									0	
lioc hols		4		1	0	3								0	14
port lati	1	0			0							0	0	0	2
canc pagu															
loli vulg						0									
sepi atla															
syng rost	1	2			0										3
osme eper															
echi vipe				0											
zoar vivi		1													
scop rhom															
scop maxi					0										
poma micr		0						0							3
poma minu		0		0	0	4		2			0	0			1
poma loza		1		0	0	4		0			1				
poma spec		0													
cili must															
sole sole		6		0							0				
lima lima					0	0									
clup hare										1					
clup spec	53														
pleu plat	0	8		1	3	1		2			0	1	1	1	1
plat fles															
athe pres															
dice labr															
gast acul															
agon cath		0													
ammo tobi															
liza rama											1				
myox ceph															
spra spra		5		2	0	3		3		1			0		2
taur buba					0										
TOTAL	**57**	**250**		**185**	**230**	**106**		**55**		**7**	**221**	**7**	**180**	**179**	**1925**
TOTAL w/o cran cran	**56**	**37**		**4**	**5**	**17**		**7**		**1**	**3**	**1**	**2**	**1**	**31**

LOMBARDSIJDE

			*				*		*								
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97(1)**	**Apr'97(2)**	**May'97(1)**	**May'97(2)**	**Jun'97**	**Jul'97**
cran cran	10	25		587	484	13		42		139	8	153	46	264	151	312	413
phil tris																	
pala spec																	
rept spec																	
brac spec				1				0		1		0			0	0	1
Carc spec	1	4		6	4	0		0			1	1		3	1	3	2
lioc hols				1	0	1					1					2	3
port lati	2	1			0			0									
canc pagu																	
loli vulg						2											
sepi atla		1															
syng rost	0																
osme eper	1																
echi vipe	1			1		0						0					
zoar vivi	1													0	1	0	
scop rhom		1			0											0	1
scop maxi					1												
poma micr				2				0									
poma minu				2		3		3		1	2	0				0	
poma loza				0		1				1	2	0					
poma spec																	
cili must				1													
sole sole		0						1			0						
lima lima					1			0									
clup hare	1	6		3	2	1		0						1		0	2
clup spec																	
pleu plat	3	0		4	1	1		6		0	0	0	0	2		3	
plat fles										1							
athe pres													0				
dice labr								0		1							
gast acul										1							
agon cath																	
ammo tobi																	
liza rama																	
myox ceph																	
spra spra																	
taur buba																	
TOTAL	**20**	**38**		**608**	**494**	**23**		**54**		**145**	**14**	**154**	**47**	**271**	**153**	**320**	**421**
TOTAL w/o cran cran	**10**	**13**		**20**	**10**	**9**		**12**		**6**	**6**	**1**	**1**	**7**	**2**	**8**	**9**

WENDUINE

			*				*			*		*			
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**	**Jul'97**
cran cran	65	153		112	698	575		67	0		65		98	92	26
phil tris															
pala spec								0							
rept spec											0				
brac spec		0						0						0	0
Carc spec	1	1		1	1	0					1			0	
lioc hols	0	0		3	0	1							0		
port lati	0				0				0					0	
canc pagu	0	0													
loli vulg															
sepi atla															
syng rost											0				
osme eper															
echi vipe	0														
zoar vivi															
scop rhom				0				0							
scop maxi					0										
poma micr															
poma minu				1	1	2		1			0				0
poma loza						1		0	0						0
poma spec															
cili must						0		1							
sole sole				0											0
lima lima						0									
clup hare	7	1		8	0	0		1					0		2
clup spec															
pleu plat	8	0		1	3	1		3			1		0		1
plat fles															
athe pres															
dice labr				1				0							
gast acul															
agon cath															
ammo tobi															
liza rama															
myox ceph															
spra spra				0											6
taur buba															
TOTAL	**82**	**157**		**126**	**705**	**580**		**74**	**1**		**66**		**98**	**93**	**36**
TOTAL w/o cran cran	**18**	**3**		**14**	**7**	**5**		**7**	**0**		**2**		**1**	**1**	**10**

KNOKKE

Taxon	May'96	Jun'96	* Jul'96	Aug'96	Sep'96	Oct'96	* Nov'96	Dec'96	Jan'97	* Feb'97	Mar'97	Apr'97	May'97	Jun'97	Jul'97
cran cran	24	64		694	115	368		94	0		16	33	38	27	263
phil tris															
pala spec															
rept spec															
brac spec		0													
Carc spec	0	0		6	1	5		0	0		0	2	0	1	11
lioc hols		0		3		0									3
port lati												0			
canc pagu															
loli vulg															
sepi atla															
syng rost															
osme eper															
echi vipe		0													
zoar vivi															
scop rhom															1
scop maxi															
poma micr								0							1
poma minu				0		1		0							
poma loza						0									
poma spec															
cili must															
sole sole				1		0		0							
lima lima						0		0							
clup hare				2				2	0		0				
clup spec						0									
pleu plat	3	0		2	2	2		3	0		1		0	1	2
plat fles															
athe pres															
dice labr								0							
gast acul															
agon cath															
ammo tobi	0														
liza rama															
myox ceph								0							
spra spra				1	0	1					0				19
taur buba															
TOTAL	**28**	**65**		**709**	**118**	**377**		**100**	**0**		**18**	**35**	**38**	**29**	**300**
TOTAL w/o cran cran	**3**	**1**		**15**	**3**	**9**		**6**	**0**		**2**	**2**	**0**	**1**	**37**

Appendix 5.B. Catch densities of the epibenthos (ind./100m²): spatial campaign.

	BD	**DP**	**Oo**	**Ni**	**Lo**	**Mi**	**Ma**	**Br**	**DH**	**Bl**	**Ze**	**Kn**
sepi atla						0						
nymp grac			0									
pala long										0		
pala serr							0			0		
cran cran	130	153	248	67	262	482	82	95	63	508	69	29
cran juve						0	1	1		1		
phil tris		2	2		2	4		0		0	0	0
phil juve							0	0				
brac spec					0							
canc pagu					0							
lioc hols	3		0					0		0		
lioc spec						0						
carc maen	0	0			3	1		0		1	2	0
carc juve					4	1				0		
port lati		0	0		0	0		0	1	0	0	
port juve		0	0	0				0	0			
erio sine					0							
gast spin							1	0	0			
prau flex	1	1	0	1		1	0	1	1	3		9
schi spir		0							2			
schi kerv	0	1	0	0		0	0	16	1	40		6
meso slab		0								0		0
neom inte									1	4		0
gamm crin							0					
idot line		0		0	0							
aste rube											1	
clup post	0		1	8	2	5	49	3	7	6	0	78
clup spec				0	0	0			1			
clup hare						0			0			
spra spra				1		0	0	0	1	0		
syng rost	0									0		
agon cata								0		0		
zoar vivi						0						
echi vipe	0											
ammo tobi				0	0				0			1
poma loza	9		0				0	11		0		
poma micr			0	0	0		0	0		1		0
poma minu	14	0	1					0				
poma spec						0		0				
scop rhom							0		0			0
scop maxi	0											
lima lima	0											
pleu fles						0						
pleu plat	6	0	2	3		1	15	0	0	1	4	1
sole sole	0											
TOTAL	**165**	**159**	**254**	**80**	**274**	**495**	**151**	**130**	**77**	**565**	**76**	**124**
TOTAL w/o cran cran	**35**	**6**	**7**	**13**	**12**	**13**	**68**	**35**	**14**	**58**	**7**	**95**

Appendix 5.C. Catch densities of the epibenthos (ind./100m²): 24-hour cycles (hours in CET, *: no sampling).

SPRING TIDE

Taxon	**16:00**	**18:00**	**20:00**	**22:00**	**0:00**	**2:00**	**4:00**	**6:00**	**8:00**	**10:00**	**12:00**	**14:00**
cnid spec												
cyan lama			1							1		
aure auri												
opis spec												
sepi atla			1	1								
pala serr					1					1		
cran cran	1	2	4	4	2	2	2	3	4	4	3	1
lioc hols				1					1			
carc maen	1	1	1	1					1	1	1	
clup hare											1	
spra spra											1	2
cili must				1								
athe pres												1
syng rost								1	1			
zoar vivi												
echi vipe			1						1			
ammo tobi											1	
ammo post												
poma loza				1			1		1			
poma micr												
poma minu				1	1	1	1		1	1		
poma spec												
scop maxi												
plat fles			1									
pleu plat	1	1	1	1	1	1	1	1	1	1	1	1
sole sole				1				1				
TOTAL	**2**	**4**	**9**	**11**	**5**	**4**	**4**	**5**	**10**	**8**	**7**	**4**

INTERMEDIATE TIDE

Taxon	**16:00**	**18:00**	**20:00**	**22:00**	**0:00**	**2:00**	**4:00**	**6:00**	**8:00**	**10:00**	**12:00**	**14:00**
cnid spec			1	1					1			
cyan lama			1		1							
aure auri							1					
opis spec												
sepi atla			1	1								
pala serr												
cran cran	1	2	3	4	4	3	2	2	3	3	3	2
lioc hols					1							
carc maen		1	1	1	1	1			1	1	1	
clup hare	2	2	2	1	1		1	1		1		
spra spra		1										
cili must					1							
athe pres	1							1				
syng rost			1		1							
zoar vivi				1	1							
echi vipe												
ammo tobi		1	1	1	1				1			
ammo post												
poma loza			1	1	1		1					
poma micr								1				
poma minu				1	1							
poma spec				1	1							
scop maxi	1											
plat fles									1			
pleu plat		1	1	1	1	1	1	1	1	1	2	1
sole sole			1	1	1		1	1				
TOTAL	**4**	**7**	**11**	**12**	**15**	**5**	**6**	**5**	**6**	**6**	**5**	**3**

NEAP TIDE

Taxon	**16:00**	**18:00**	**20:00**	**22:00**	**0:00**	**2:00**	**4:00**	**6:00**	**8:00**	**10:00**	**12:00**	**14:00**
cnid spec												
cyan lama		1	1	1	1	2	1		1			1
aure auri				1								
opis spec											1	
sepi atla						1						
pala serr												
cran cran	1	1	2	3	3	4	3	1	1	1	2	4
lioc hols					1	1						1
carc maen	1			1	1	1	1			1	1	1
clup hare	1							1	1	1	1	1
spra spra												
cili must						1						
athe pres												
syng rost												
zoar vivi												
echi vipe						1						
ammo tobi	1							1				1
ammo post	1			1								
poma loza												
poma micr									1			
poma minu												
poma spec												
scop maxi		1										
plat fles						1	1					
pleu plat	1	1	1	1	1	1	1	1	1	1	1	1
sole sole				1	1	1						1
TOTAL	**4**	**3**	**4**	**8**	**8**	**12**	**5**	**3**	**4**	**3**	**5**	**9**

Appendix 6.

Epibenthic biomass. (A) Temporal campaign. (B) Spatial campaign.

Appendix 6.A. Catch biomass of the epibenthos (g AFDW/100m²): temporal campaign (*: no sampling).

OOSTDUINKERKE

			*				*		*					
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**
loli vulg						0.0								
cran cran	0.5	37.9		14.5	20.3	9.2		5.9		0.5	17.3	3.8	21.6	13.5
phil tris	0.0	0.1		0.0										
brac spec														
brac juve					0.0									
lioc juve		0.0												
lioc hols		0.6		1.1	0.5	5.9								0.3
carc maen	0.0	3.0			0.1									0.0
carc juve														
port lati	0.0				0.0							0.0		0.1
port juve	0.0	0.0											0.0	
prau flex								0.0		0.1	0.1			
clup spec	3.2													
clup post	25.2	0.2											0.1	
clup hare										1.1				
spra spra		1.1		0.7	0.1	1.4		1.5		0.7			0.1	
spra post														
syng rost	0.1	0.2			0.0									
myox scor														
taur buba						0.0								
agon cata		0.0												
dice labr														
liza rama											0.1			
zoar vivi		0.5												
echi vipe				1.3										
ammo juve														
poma spec		0.0												
poma post				0.0										
poma loza		0.3		0.0	0.0	1.2		0.0			0.1			
poma micr		0.0						0.0						
poma minu		0.0		0.1	0.1	12.4		0.5			0.1	0.1		
scop maxi					0.0	0.0								
lima lima					0.0	0.1								
pleu plat	0.0	1.4		0.3	1.3	0.5		1.2			0.2	0.6	0.7	0.2
sole sole		0.4		0.0							0.3			
TOTAL	**29**	**46**		**18**	**23**	**31**		**9**		**2**	**18**	**5**	**22**	**14**
TOTAL w/o cran cran	**29**	**8**		**3**	**2**	**22**		**3**		**2**	**1**	**1**	**1**	**1**

KNOKKE

			*				*			*				
Taxon	**May'96**	**Jun'96**	**Jul'96**	**Aug'96**	**Sep'96**	**Oct'96**	**Nov'96**	**Dec'96**	**Jan'97**	**Feb'97**	**Mar'97**	**Apr'97**	**May'97**	**Jun'97**
loli vulg														
cran cran	11.6	4.3		33.0	7.5	27.0		9.3	0.1		1.6	3.0	3.4	1.4
phil tris														
brac spec														
brac juve		0.0												
lioc juve		0.0												
lioc hols				2.0		0.3								
carc maen	0.4	0.1		12.6	2.2	6.5		0.4	0.4		0.0	0.2	0.4	0.0
carc juve	0.0											0.0		0.0
port lati												0.1		
port juve														
prau flex								0.0			0.1		0.0	
clup spec						0.1								
clup post	0.1												0.0	
clup hare				0.8				0.7	0.1		0.0			
spra spra				0.3	0.0	0.3					0.1			
spra post														
syng rost														
myox scor								0.6						
taur buba														
agon cata														
dice labr								0.2						
liza rama														
zoar vivi														
echi vipe		0.1												
ammo juve	0.0													
poma spec														
poma post														
poma loza						0.0								
poma micr								0.0						
poma minu				0.1		0.3		0.1						
scop maxi														
lima lima						0.0		0.1						
pleu plat	1.3	0.2		2.0	1.4	1.9		3.8	0.0		1.1		0.0	0.6
sole sole				0.2		0.1		0.2						
TOTAL	**13**	**5**		**51**	**11**	**37**		**15**	**1**		**3**	**3**	**4**	**2**
TOTAL w/o cran cran	**2**	**0**		**18**	**4**	**10**		**6**	**1**		**1**	**0**	**0**	**1**

Appendix 6.B. Catch biomass of the epibenthos (g AFDW/100m²): spatial campaign.

Taxon	**BD**	**DP**	**Oo**	**Ni**	**Lo**	**Mi**	**Ma**	**Br**	**DH**	**Bl**	**Ze**	**Kn**
sepi atla						0.0						
pala long										0.0		
pala serr							0.0			0.0		
carn cran	15.2	14.8	21.9	3.9	24.0	38.6	4.8	7.4	6.1	31.6	12.9	2.9
cran juve						0.0	0.0		0.0	0.0		
phil tris		0.2	0.0		0.0	0.0			0.0	0.0	0.0	0.0
phil juve							0.0		0.0			
brac spec					0.2							
canc pagn					0.0							
lioc hols	3.3		0.1						0.0	0.1		
lioc spem						0.0						
carc maen	0.9	0.3			2.8	1.3			0.6	0.7	2.3	0.1
carc juve					0.1	0.0				0.0		
port lati		0.0	0.0		0.0	0.1		0.1	0.0	0.0	0.0	
port juve		0.0	0.0	0.0				0.0	0.0			
erio sinm					0.4							
prau flex	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.1		0.2
aste rube											1.3	
clup post	0.0		0.0	0.2	0.0	0.1	1.1	0.2	0.1	0.2	0.0	1.6
clup spec				0.0	0.1	0.3		0.1				
clup hare						0.0		0.0				
spra spra				0.0		0.1	0.1	0.2	0.1	0.0		
syng rost	0.0									0.0		
agon cata									0.0	0.0		
zoar vivi						0.0						
echi vipe	2.2											
ammo tobi				0.0	0.0			0.1				0.3
poma loza	3.0		0.0				0.0	0.0	1.9	0.0		
poma micr			0.0	0.0	0.0		0.0	0.0	0.0	0.2		0.0
poma minu	3.7	0.1	0.2					0.0	0.0			
poma spec									0.0			
scop rhom							0.2	0.2				0.6
scop maxi	0.5											
lima lima	0.1											
pleu fles						0.0						
pleu plat	15.2	0.2	0.4	0.1		0.1	2.6	0.0	0.0	0.0	13.2	1.2
sole sole	0.5											
TOTAL	**45**	**16**	**23**	**4**	**28**	**41**	**9**	**8**	**9**	**33**	**30**	**7**
TOTAL w/o cran cran	**29**	**1**	**1**	**0**	**4**	**2**	**4**	**1**	**3**	**1**	**17**	**4**

Appendix 7.

Regressions and assigned values used for calculation of biomasses.

Appendix 7. Regressions and assigned values used for calculation of biomasses (ADW in mg) (L: length; S: standard; W: width; V: volume; C: carapax; A: antenna; TE: telson; a: adult; pl: postlarva; juv: juvenile

	Formula		**Source**
Foraminifera species	**0.001**		Hamerlynck & Cattrijsse 1994
Hydrozoa species	**V (nl) = L (mm) * W^2 (mm) * 385**	from Foraminifera	Feller & Warwick 1988
	DW (ng) = (V * 1.13) / 4	from Nematoda	
	ADW = DW - 10%		
Cnidaria species adult	**1**		(this study)
Eutonina indicans	**0.002**	gewogen waarde	(this study)
Sarsia tubulosa	**0.002**	cf. *Eutonina indicans*	(this study)
Margelopsis haeckeli	**0.0002**		(this study)
Pleurobrachia pileus	**0.001**		(this study)
Nematoda species	**0.003**		Mees 1994
Magelona papillicornis palp	**0.008**		(this study)
Polychaeta species palp	**0.008**	from *Magelona papillicornis* palp	(this study)
Arenicola species tail	**weighed value**		
Eteone longa	**ln ADW = -5.717+1.524 ln L**		Govaere1978
Magelona papillicornis	**ln ADW = -5.916+1.847 ln L**		Govaere1978
Nephtys cirrosa	**ln ADW = -7.139+2.489 ln L**	from *Nephtys hombergii*	Govaere1978
Nereis species	**ln ADW = -7.139+2.489 ln L**	from *Nephtys hombergii*	Govaere1978
Polychaeta species1	**ln ADW = -6.029+1.831 ln L**	from *Spio filicornis*	Govaere1978
Polychaeta species2	**ln ADW = -7.139+2.489 ln L**	from *Nephtys hombergii*	Govaere1978
Pygospio elegans	**ln ADW = -6.029+1.831 ln L**	from *Spio filicornis*	Govaere1978
Scolelepis species	**ln ADW = -5.912+2.137 ln L**	from *Scolelepis bonnieri*	Govaere1978
Spio species	**ln ADW = -6.029+1.831 ln L**	from *Spio filicornis*	Govaere1978
Spionidae species	**ln ADW = -6.029+1.831 ln L**	from *Spio filicornis*	Govaere1978
Spiophanes bombyx	**ln ADW = -6.621+2.069 ln L**		Govaere1978
Polynoidae species	**ln ADW = -6.017+2.769 ln L**		Govaere1978
Lanice conchilega	**ln ADW = -6.918+2.181 ln L**		Govaere1978
Harmothoë species	**ln AFDW = -6.017+2.769 ln L**	regr. Polynoidae	Govaere1979
Bivalvia species juv.	**ln ADW = -4.052+2.817 ln L**		Mees 1994
Bivalvia species siphon1	**0.017**		(this study)
Bivalvia species siphon2	**ln ADW = +0.815+0.043 ln L**		Hamerlynck & Cattrijsse 1994
Ostracoda species	**0.014**		Hamerlynck & Cattrijsse 1994
Temora longicornis	**0.089**	from *Calanus helgolandicus*	Dewicke unpub.
Centropages hamatus	**0.089**	from *Calanus helgolandicus*	Dewicke unpub.
Pseudocalanus elongatus	**0.089**	from *Calanus helgolandicus*	Dewicke unpub.
Calanoida species	**0.089**	from *Calanus helgolandicus*	Dewicke unpub.
Harpacticoida species	**0.002**		Hamerlynck et al. 1986
Cirripedia species	**0.014**		Hamerlynck et al. 1986
Cirripedia species nauplius	**0.014**		Hamerlynck et al. 1986
Cirripedia species exuvia	**ln ADW = -5.857+2.863 ln SL**	from *Gammarus salinus*	Hamerlynck 1993
Elminius modestus	**0.089**	from *Calanus helgolandicus*	(this study)
Philocheras trispinosus	**ln ADW = -5.379+2.903 ln SL**	from *Crangon crangon*	Hamerlynck et al. 1986
allometric regression		from *Crangon crangon*	Hamerlynck et al. 1986
Crangon crangon pl+a	**ln ADW = -5.379+2.903 ln SL**		Hamerlynck et al. 1986
allometric regression	**ln SL = 1.2420+1.0438 ln CL**	pl	(this study)
	ln SL = 1.5504+0.8874 ln TE	pl	(this study)
	ln Sl = 1.7591+0.8780 ln AL	pl	(this study)
	SL-Uropod	from SL-TE	(this study)
Crangonidae species zoa	**0.2261**		Dewicke unpub.
Pagurus bernhardus pl	**0.669**		Dewicke unpub.
Pagurus bernhardus juv	**ln ADW = -3.967+3.164 ln CW**	from *Carcinus maenas*	Dewicke unpub.
Diogenes pugilator juv	**ln ADW = -3.967+3.164 ln CW**	from *Carcinus maenas*	Dewicke unpub.
Brachyura species juv	**ln ADW = -3.967+3.164 ln CW**	from *Carcinus maenas*	Dewicke unpub.
Carcinus maenas juv	**ln ADW = -3.967+3.164 ln CW**		Mees 1994
Liocarcinus holsatus pl	**0.189**		Mees 1994
Liocarcinus holsatus a	**ln ADW = -4.489+3.247 ln CW**		Mees 1994
(3-5 mm)	**0.5131**		Dewicke unpub.
(5-7 mm)	**2.806**		Dewicke unpub.
Schistomysis kervillei	**ln ADW = -5.898+2.931 ln SL**		Mees 1994
allometric regression	**SL = 0.0801+2.9282 CL**	from *Neomysis integer*	(this study)
	SL= 0.591+5.6298 TE	from *Neomysis integer*	(this study)
	SL= 0.836+3.37 AL	from *Neomysis integer*	(this study)
	SL-Uropod	from SL-TE	(this study)
Anchialina agilis	**0.1989**	cf. *Mysidopsis gibbosa*	Dewicke unpub.
Bodotriidae species	**0.0868**		Dewicke unpub.
Cumopsis goodsiri	**0.0659**		(this study)
Diastylidae species	**ln DW = -5.775+2.8708 ln SL**	from *Diastylis bradyi*	Dewicke unpub.

	ADW = DW - 10%		
Pseudocuma species	**0.0449**		Dewicke unpub.
Eurydice pulchra	**ln ADW = -5.910+2.8073 ln TL**	from *Idotea linearis*	Dewicke unpub.
Bathyporeia species	**ln ADW = -5.857+2.863 ln SL**	from *Gammarus salinus*	Mees 1994
Hausorius arenarius	**ln ADW = -5.857+2.863 ln SL**	from *Gammarus salinus*	Mees 1994
Stenothoë marina	**0.0663**		Dewicke unpub.
Micropotopus maculatus	**0.025**		Dewicke unpub.
Amphipoda species	**ln ADW = -5.857+2.863 ln SL**	from *Gammarus salinus*	Mees 1994
Pontocrates species	**ln ADW = -5.857+2.863 ln SL**	from *Gammarus salinus*	Mees 1994
Atylus species	**ln ADW = -5.857+2.863 ln SL**	from *Gammarus salinus*	Mees 1994
Sepiola atlantica	**6.892**	cf. *Loligo* species	Dewicke unpub.
Solea solea pl			
(4-6 mm)	**0.2489**		(this study)
(6-8 mm)	**0.4301**		(this study)
(8-10 mm)	**0.7424**		Dewicke unpub.
(10-12 mm)	**1.3825**		Dewicke unpub.
(12-14 mm)	**2.4687**		Dewicke unpub.
(14-16 mm)	**3.5046**		Dewicke unpub.
(16-18 mm)	**5.7571**		Dewicke unpub.
(18-20 mm)	**8.7922**		Dewicke unpub.
Pleuronectes platessa 0+ and I	**ln ADW = -6.4275+3.0855 ln SL**		(this study)
Pleuronectidae species pl	**ln ADW = -6.4275+3.0855 ln SL**	from *Pleuronectes platessa*	(this study)
Pleuronectes flesus pl	**ln ADW = -6.4275+3.0855 ln SL**	from *Pleuronectes platessa*	(this study)
(6-8 mm)	**0.8855**		(this study)
(8-10 mm)	**1.1932**		(this study)
Limanda limanda pl (10.2mm)	**1.2**		(this study)
Hippoglossoides platessoides pl	**ln ADW = -6.4275+3.0855 ln SL**	from *Pleuronectes platessa*	(this study)
Clupeidae species pl	**ln ADW = -10.2+3.816 ln SL**		Mees 1994
Callionymus lyra pl	**ln ADW = -7.851+3.46 ln SL**	from *Pomatoschistus* species pl	Dewicke unpub.
Pomatoschistus species pl			
(4-6 mm)	**0.359**		(this study)
(6-8 mm)	**0.5944**		(this study)
(8-10 mm)	**0.9549**		Dewicke unpub.
(10-12 mm)	**1.8063**		Dewicke unpub.
(12-14 mm)	**2.8319**		Dewicke unpub.
(14-16 mm)	**5.2772**		Dewicke unpub.
(16-18 mm)	**8.0867**		Dewicke unpub.
(18-20 mm)	**13.9485**		Dewicke unpub.
Pomatoschistus species a	**ln ADW = -7.851+3.46 ln SL**	from *Pomatoschistus minutus*	Hamerlynck et al. 1986
Merlangius merlangus pl			
(10-12 mm)	**1.4691**		(this study)
Ammodytes tobianus juv	**ln ADW = -16,122+3,491 ln SL**		(this study)

Appendix 8.

Numerical stomach content analyses. (A) Temporal series flatfish. (B) 24-hour cycle plaice.

Appendix 8A. Numerical stomach/gut content analyses: temporal campaign (pl: plaice *Pleuronectes platessa,* so: sole *Solea solea,* da: dab *Limanda limanda,* tu: turbot *Scophthalmus maximus,* br: brill *Scophthalmus rhombus,* *: empty stomach/gut, n.i.: not identifiable) (a: adult, pl: postlarva, juv: juvenile, n: nauplius larva, cl: cyprid larva, s: siphon, p: palp, e: exuvia) (parasites: N:nematode, T: trematode, W: tapeworm, C: copepode).

PLAICE-MAY 1996

Standard length (mm)	69	74	66	85	66	75	82	78	69	72	69	78	67	73	75	78	68	70	66	68	62	60
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Foraminifera species																						
Hydrozoa species																				1		
Nematoda species				4	1	1	24				1	2				1						1
Magelona papillicornis p																					2	
Polychaeta species p2																						
Polychaeta species p7																						
Polychaeta species px																					3	6
Arenicola species end						1	1								1		1					
Eteone longa		3										1		1			1					
Magelona papillicornis																						
Nephtys cirrosa																						
Nereis species																						
Polychaeta species					4	1	1		1		1					1						
Pygospio elegans																						
Scolelepis species															1		1		1			
Scolelepis squamata			1	5				4				2		4								
Spio filicornis														1								
Spio species																						
Spionidae species			1		2			1														3
Spionidae species 3	1	2	5			2	2	7	2	2		19		19	4	2	4	10	2		4	
Spiophanes bombyx																						
Harmothoë species								1														
Bivalvia species spat																						
Bivalvia species s1																1					1	
Temora longicornis	1638	32	351	20		19	15	26	11	43	1	537	1	307	15	4	82	115	3	8		1
Centropages hamatus	70	7	22	9	2	4		3	1	6		35		36	7	1	4	12	4	4	1	1
Pseudocalanus elongatus	22	2	16	5		1	2	8		8		16		11	9		1	3			1	
Calanoida species												2						2		1		
Harpacticoida species															2							
Cirripedia species cl	1	1	2	25		1		20				14		38	1	1	3	3				
Cirripedia species e														1				2				
Elminius modestus																						
Philocheras trispinosus											1											
Crangon crangon pl								1														
Crangonidae species zoea																						
Pagurus bernhardus pl																						
Carcinus maenas juv																						
Liocarcinus holsatus ?	2																					
Schistomysis kervillei	1																1					

Bodotriidae species																						
Cumopsis goodsiri																						
Diastylis species																						
Pseudocuma longicornis																						
Eurydice pulchra								2						2								
Bathyporeia species				1				1				1		3		1						
Bathyporeia pilosa		3	2									1		8								
Bathyporeia sarsi																						
Stenothoë marina														1								
Amphipoda species																						
Pontocrates altamarinus																						
Pontocrates species																						
Atylus falcatus																						
Solea solea pl																						
Limanda limanda pl																						
Clupeidae species pl																						
fish eye																						
eggs					1																	
Nassarius reticulatus eggs																						
species 6																						
species 11																						
n.i.										1											2	
TOTAL	**1735**	**50**	**400**	**69**	**10**	**30**	**45**	**74**	**15**	**60**	**4**	**630**	**1**	**432**	**40**	**12**	**98**	**147**	**10**	**14**	**14**	**12**
parasite abdomen (nematode)						1			1	2	2	3	1			1			2	1	1 n.i.	
parasite stomach (trematode)																						

PLAICE-JUN 1996

Standard length (mm)	38	34	38	35	38	40	36	33	29	33	32	37	35	32	33	28	31	32	43	44
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species			1																	
Hydrozoa species																				
Nematoda species																			1	
Magelona papillicornis p	8		8		1	1				6	10	1	2			4	1			16
Polychaeta species p2																				
Polychaeta species p7																				
Polychaeta species px			3																	
Arenicola species end																				
Eteone longa			1																	
Magelona papillicornis																				1
Nephtys cirrosa																				3
Nereis species																				
Polychaeta species	1	1	3		1				1			2				1			1*	1
Pygospio elegans																				
Scolelepis species																				
Scolelepis squamata																				
Spio filicornis			1																	

Spio species																				
Spionidae species			4																	
Spionidae species 3					1														4	
Spiophanes bombyx																				
Harmothoë species																				
Bivalvia species spat			1					1												1
Bivalvia species s1	8	1	8	5	3	1		6	2	2	8		1			8+3	5	4	3	8
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species			20													1				
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																				
Philocheras trispinosus																				
Crangon crangon pl	3	1	5		5	2	11	9	2	3	10	2		6	4	4	1	4		
Crangonidae species zoea													1							
Pagurus bernhardus pl																				
Carcinus maenas juv																				
Liocarcinus holsatus ?																				
Schistomysis kervillei													1							
Bodotriidae species																				
Cumopsis goodsiri			1		1															
Diastylis species									1											
Pseudocuma longicornis																				
Eurydice pulchra																				
Bathyporeia species																				
Bathyporeia pilosa																				
Bathyporeia sarsi																				
Stenothoë marina																				
Amphipoda species																				
Pontocrates altamarinus					1				1							1				
Pontocrates species																				1
Atylus falcatus					1															
Solea solea pl			1		2					3										
Limanda limanda pl					1															
Clupeidae species pl					1															
fish eye																1				
eggs																				
Nassarius reticulatus eggs																				
species 6																				
species 11																				
n.i.																	2			
TOTAL	**20**	**3**	**57**	**5**	**18**	**4**	**11**	**16**	**7**	**14**	**28**	**5**	**5**	**6**	**4**	**12**	**9**	**8**	**8**	**31**
parasite abdomen (nematode)		1									1	2	1	1						

parasite stomach (trematode)					1						1								1	

PLAICE-JUL 1996

Standard length (mm)	42	43	39	42	43	42	44	43	43	41	41	42	41	41	40	41	40	39	39	39
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species																				
Magelona papillicornis p	1		1					1		4	1	2				3			1	3
Polychaeta species p2					1					9		1								
Polychaeta species p7					4								5	7						
Polychaeta species px						2				1				3	2				3	5
Arenicola species end								4												
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa																				
Nereis species																				
Polychaeta species			1	1				1	1	2	1		1	7		1		2		
Pygospio elegans	7																			
Scolelepis species							1	1												
Scolelepis squamata											3									
Spio filicornis																				
Spio species	1																			
Spionidae species	1+4						2					2			6	2				
Spionidae species 3									1		2	2	1	2	2				1	6
Spiophanes bombyx																				
Harmothoë species																				
Bivalvia species spat			1		1						1									
Bivalvia species s1	2			1		1			2		3			2		1				
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species	1																			
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																				
Philocheras trispinosus																				
Crangon crangon pl	2		2					1			1				1			1		
Crangonidae species zoea																				
Pagurus bernhardus pl																				
Carcinus maenas juv	1																			
Liocarcinus holsatus ?																				
Schistomysis kervillei																				
Bodotriidae species																				
Cumopsis goodsiri											1									
Diastylis species																				

Pseudocuma longicornis		1																		
Eurydice pulchra																				
Bathyporeia species																				
Bathyporeia pilosa																				
Bathyporeia sarsi			1																	
Stenothoë marina																				
Amphipoda species													1							
Pontocrates altamarinus																				
Pontocrates species																				
Atylus falcatus																1				
Solea solea pl																				
Limanda limanda pl																				
Clupeidae species pl																				
fish eye																				
eggs																				
Nassarius reticulatus eggs																		1		
species 6																				
species 11																				
n.i.								1				1		3	2					2
TOTAL	**15**	**1**	**6**	**2**	**6**	**3**	**3**	**9**	**4**	**16**	**13**	**8**	**8**	**24**	**13**	**8**	*****	**4**	**5**	**16**
parasite abdomen (nematode)	1					2					1				1					
parasite stomach (trematode)							2					1						1		

PLAICE-AUG (1) 1996

Standard length (mm)	40	40	40	40	40	40	39	40	40	39	40	39	40	40	40	40	40	40	39	40
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species																				
Magelona papillicornis p									5								2			
Polychaeta species p2																	8			
Polychaeta species p7																	1			
Polychaeta species px	1			2		1			2			3								5
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa																				
Nereis species																				
Polychaeta species			7	4	1	1		6	7			6	1		1	2	1		1	7
Pygospio elegans																				
Scolelepis species																				
Scolelepis squamata																				
Spio filicornis																				
Spio species																				
Spionidae species																				
Spionidae species 3	1				2			2	5	1		1							1	2

Spiophanes bombyx																				
Harmothoë species			1																	
Bivalvia species spat							2					1				1				
Bivalvia species s1	1					1	2		1			2				1			1	
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species																				
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																				
Philocheras trispinosus																				
Crangon crangon pl				1		1	3		1				1		3	5		1	1	
Crangonidae species zoea																				
Pagurus bernhardus pl																				
Carcinus maenas juv																				
Liocarcinus holsatus ?																				
Schistomysis kervillei																				
Bodotriidae species																				
Cumopsis goodsiri																				1
Diastylis species																				
Pseudocuma longicornis																				
Eurydice pulchra																				
Bathyporeia species																				
Bathyporeia pilosa																				
Bathyporeia sarsi																				
Stenothoë marina																				
Amphipoda species																				
Pontocrates altamarinus																				
Pontocrates species																				
Atylus falcatus																				
Solea solea pl																				
Limanda limanda pl																				
Clupeidae species pl																				
fish eye																				
eggs																				
Nassarius reticulatus eggs																				
species 6																				
species 11																				
n.i.										2										
TOTAL	**3**	*****	**8**	**7**	**3**	**4**	**7**	**8**	**21**	**3**	*****	**13**	**2**	*****	**4**	**9**	**12**	**1**	**4**	**15**
parasite abdomen (nematode)							1													
parasite stomach (trematode)																				

PLAICE-AUG (2) 1996

Standard length (mm)	44	43	45	43	44	43	44	43	45	43	41	42	42	41	42	46	45	43	45	45
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species				2				1												
Magelona papillicornis p	1				2			1				5								
Polychaeta species p2																				
Polychaeta species p7																				
Polychaeta species px			2									4								
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa																				
Nereis species																				
Polychaeta species	1		6	30	1	1	1	17			1	5			1	1		1		
Pygospio elegans																				
Scolelepis species																				
Scolelepis squamata																				
Spio filicornis																				
Spio species																				
Spionidae species								1							1				2	12
Spionidae species 3			5	10				5	1			3			1					3
Spiophanes bombyx																				
Harmothoë species																				
Bivalvia species spat			1	1					1			2				1				
Bivalvia species s1				5	7			1					3	1	1					3
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species	1				1	8														
Cirripedia species cl	1										1									
Cirripedia species e																				
Elminius modestus																				
Philocheras trispinosus																				
Crangon crangon pl	2	7	1		8	5	7	1	3	4	3	4	5	3	1	3	6	2	3	1
Crangonidae species zoea																				
Pagurus bernhardus pl							1													
Carcinus maenas juv																				
Liocarcinus holsatus ?																				
Schistomysis kervillei																				
Bodotriidae species																				
Cumopsis goodsiri																				
Diastylis species																				
Pseudocuma longicornis																				
Eurydice pulchra																				
Bathyporeia species																				

Bathyporeia pilosa																				
Bathyporeia sarsi																				
Stenothoë marina																				
Amphipoda species																				
Pontocrates altamarinus																				
Pontocrates species																				
Atylus falcatus																				
Solea solea pl																				
Limanda limanda pl																				
Clupeidae species pl																				
fish eye					1															
eggs																				
Nassarius reticulatus eggs																				
species 6																				
species 11																				
n.i.																				1
TOTAL	**6**	**7**	**15**	**48**	**20**	**14**	**9**	**27**	**5**	**4**	**5**	**23**	**8**	**4**	**5**	**5**	**6**	**3**	**5**	**20**
parasite abdomen (nematode)								2									1			
parasite stomach (trematode)		1																		

PLAICE-SEP 1996																				
Standard length (mm)	50	49	49	50	50	46	46	45	45	46	47	47	47	47	48	47	47	48	49	49
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species		1																		
Magelona papillicornis p		2					1													
Polychaeta species p2																				
Polychaeta species p7	2																			
Polychaeta species px										2										
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa																				
Nereis species																				
Polychaeta species															2					
Pygospio elegans																				
Scolelepis species																				
Scolelepis squamata																				
Spio filicornis																				
Spio species																				
Spionidae species																				
Spionidae species 3		1									1									
Spiophanes bombyx											1									
Harmothoë species																				
Bivalvia species spat																				

Bivalvia species sl		3													3					
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species	1											2								
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus															1					
Philocheras trispinosus																				
Crangon crangon pl																				
Crangonidae species zoea																				
Pagurus bernhardus pl																				
Carcinus maenas juv																				
Liocarcinus holsatus ?																				
Schistomysis kervillei																				
Bodotriidae species			2																	
Cumopsis goodsiri																				
Diastylis species																				
Pseudocuma longicornis																				
Eurydice pulchra																				
Bathyporeia species																				
Bathyporeia pilosa																				
Bathyporeia sarsi																				
Stenothoë marina																				
Amphipoda species																				
Pontocrates altamarinus																				
Pontocrates species																				
Atylus falcatus																				
Solea solea pl																				
Limanda limanda pl																				
Clupeidae species pl																				
fish eye																				
eggs																				
Nassarius reticulatus eggs																				
species 6																				
species 11																				
n.i.		2	1			2			6			2				2		3		
TOTAL	**3**	**9**	**3**	*****	*****	**2**	**1**	*****	**6**	**2**	**2**	**4**	*****	*****	**6**	**2**	*****	**3**	*****	*****
parasite abdomen (nematode)			1																	
parasite stomach (trematode)		1																		

PLAICE-OCT 1996

Standard length (mm)	49	50	50	51	50	49	50	50	50	50	49	50	49	49	50	49	49	49	50	50
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				

Hydrozoa species																				
Nematoda species	1																	1		
Magelona papillicornis p				1								2		2						
Polychaeta species p2		4																		
Polychaeta species p7					4															
Polychaeta species px					1				3	3			1							
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa		1	2							1										
Nereis species										1										
Polychaeta species						1				2	1	1		1			1			
Pygospio elegans																				
Scolelepis species																				
Scolelepis squamata	1					7	4													
Spio filicornis																				
Spio species																				
Spionidae species																				
Spionidae species 3				1	3					1						4				
Spiophanes bombyx									1	1		1								
Harmothoë species														1						
Bivalvia species spat					2											2				
Bivalvia species s1					1					3		1						1		
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species	2			1	1			2		2	2		5			4	1			1
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																				
Philocheras trispinosus																				
Crangon crangon pl				1																
Crangonidae species zoea																				
Pagurus bernhardus pl																				
Carcinus maenas juv																				
Liocarcinus holsatus ?																				
Schistomysis kervillei			1																	
Bodotriidae species																				
Cumopsis goodsiri									1				1	2						
Diastylis species																				
Pseudocuma longicornis																				
Eurydice pulchra						1														
Bathyporeia species																				
Bathyporeia pilosa						1														
Bathyporeia sarsi						1														
Stenothoë marina																				

Amphipoda species																				
Pontocrates altamarinus																				
Pontocrates species																				
Atylus falcatus																				
Solea solea pl																				
Limanda limanda pl																				
Clupeidae species pl																				
fish eye																				
eggs																				
Nassarius reticulatus eggs																				
species 6																				
species 11																				
n.i.		2			1						1			1				1		
TOTAL	**4**	**7**	**3**	**4**	**13**	**11**	**4**	**2**	**5**	**14**	**4**	**5**	**7**	**7**	*****	**10**	**2**	**3**	*****	**1**
parasite abdomen (N)	2																	1		
parasite stomach (T)	1						1				1									

PLAICE-DEC 1996

Standard length (mm)	57	62	61	55	59	55	55	53	55	50	51	48	50	52	50	43	46	49	44	43
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species																				
Magelona papillicornis p											2	11			1		2	3		
Polychaeta species p2																				2
Polychaeta species p7																				
Polychaeta species px													2				2	2		2
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa														1						
Nereis species																				
Polychaeta species												1	6							
Pygospio elegans																				
Scolelepis species																				
Scolelepis squamata																				
Spio filicornis																				
Spio species														2						
Spionidae species																				
Spionidae species 3																	1			
Spiophanes bombyx																				
Harmothoë species																				
Bivalvia species spat																				
Bivalvia species s1											3	3	3			1	1			
Temora longicornis																				
Centropages hamatus																				

Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species																				
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																				
Philocheras trispinosus																				
Crangon crangon pl																				
Crangonidae species zoea																				
Pagurus bernhardus pl																				
Carcinus maenas juv																				
Liocarcinus holsatus ?																				
Schistomysis kervillei																				
Bodotriidae species																			1	
Cumopsis goodsiri												1								
Diastylis species																				
Pseudocuma longicornis																				
Eurydice pulchra																				
Bathyporeia species																				
Bathyporeia pilosa																				
Bathyporeia sarsi																				
Stenothoë marina																				
Amphipoda species																				
Pontocrates altamarinus																				
Pontocrates species																				
Atylus falcatus																				
Solea solea pl																				
Limanda limanda pl																				
Clupeidae species pl																				
fish eye																				
eggs																				
Nassarius reticulatus eggs																				
species 6																				
species 11																				
n.i.												3								
TOTAL	*	*	*	*	*	*	*	*	*	*	**5**	**19**	**11**	**3**	**1**	**1**	**6**	**5**	**1**	**4**
parasite abdomen (nematode)		1			1			1					1					2		1
parasite stomach (trematode)											1									

SOLE-MAY 1996

Standard length (mm)	118	121	131	123	116	119	116	116	91	128	123	123	118	124	125	127	115	126	115	107	110	113	108	132
	so1	**so2**	**so3**	**so4**	**so5**	**so6**	**so7**	**so8**	**so9**	**so10**	**so11**	**so12**	**so13**	**so14**	**so15**	**so16**	**so17**	**so18**	**so19**	**so20**	**so21**	**so22**	**so23**	**so24**
Foraminifera species																								
Hydrozoa species																								
Nematoda species							1			8														
Magelona papillicornis p																	6	1						
Arenicola species end	3		2			1	2			1	1		1		6		3	1	1			1		5
Lanice conchilega																				1		1		
Nephthys cirrosa									1					2						2		2	1	
Scolelepis squamata																								
Polychaeta species	1		2	1		1	1				1	3	2		1		4			1			6	
Spiophanes bombyx																								
Pygospio elegans ?																								
species 3																	1							
Spionidae species																							50	
Bivalvia species spat																						1		
Bivalvia species s1									1								1			2				
Bivalvia species s2																							1	
Temora longicornis	5	1		1	4	8	10	3	2	9	1		1		10		3	1		2			2	4
Centropages hamatus	3	1	2	1	1		7			3					7			2				1	2	
Pseudocalanus elongatus															3									1
Calanoida species							1	1				2				1	1						1	
Harpacticoida species																				1				
Ostracoda species																								
Cirripedia species cl					1	2			1	23									2			1	4	
Cirripedia species n	1																							
Elminius modestus																								
Cirripedia species e										1													1	
Philocheras trispinosus																								
Crangon crangon a										2													1	
Crangon crangon pl	4		6	16	2	6	24	1	22	18	3	6	9	2	31	2	11	1	11	51	5	15	29	15
Diogenes pugilator																								
Paguridae species																								
Brachyura species	1		5		2								1									1		1
Carcinus maenas pl																								
Schistomysis species															1									
Schistomysis kervillei				1																				
Cumopsis goodsiri																								
Cumacea species																				1				
Diastylis species																								
Pseudocuma longirostris																								
Pseudocuma gilsoni									2															
Pseudocuma species											1													
Eurydice pulchra									1															
Idotea pelagica																								
Stenothoë marina																								

Amphipoda species	1					2														1				
Pontocrates altamarinus				2		1				1									1	1				
Microprotopus maculatus									1			1												1
Bathyporeia sarsi																								
Bathyporeia species																								
Atylus falcatus																			1			1		
Atylus swammerdami				7													2		2	1		1		
Gammarus crinicornis?	1																							
Jassa species?																								
Haustorius arenarius							1				1				1							1	2	
Crustacea species																								
Pomatoschistus species?				1																			2	
Callionymus lyra									2													2		
Solea solea							1													2		2	3	
Pleuronectes platessa			1						1						2							1		
Pleuronectidae species											1						1							
Limanda limanda																								
Hippoglossoides platesso									2	2							1							
Pisces species nd				1										1	2					1	1		1	
empty capsule									1			1	1				1		1					
gelatinous capsule																								4
egg			1													1								
n.i.							1																	
TOTAL	**20**	**2**	**19**	**31**	**10**	**21**	**49**	**5**	**37**	**68**	**9**	**13**	**15**	**5**	**64**	**4**	**35**	**6**	**19**	**67**	**6**	**31**	**106**	**31**
parasite abdomen (N)						1																		
parasite stomach (T)														1						1		3		
parasite stomach (N)											1													
parasite stomach (C?)		1																						
parasite gut (T)									1			2 n.i.					1			1			1	
parasite gut (N)											3													

SOLE-JUN 1996								**SOLE-AUG (1) 1996**				**SOLE-AUG (2) 1996**												
Standard length (mm)	105	123	122	103	128	122		53	52	47		60	55	48	61	56	52	53	59	55	59	54	75	67
	so1	**so2**	**so3**	**so4**	**so5**	**so6**		**so7**	**so8**	**so9**		**so1**	**so2**	**so3**	**so4**	**so5**	**so6**	**so7**	**so8**	**so9**	**so10**	**so11**	**so12**	**so13**
Foraminifera species													1											
Hydrozoa species																								
Nematoda species																								
Magelona papillicornis p																								
Arenicola species end						2																		
Lanice conchilega																								
Nephthys cirrosa				1								2						3	3					2
Scolelepis squamata																								
Polychaeta species	1																		2					1
Spiophanes bombyx																								
Pygospio elegans ?																								
species 3									1															

Spionidae species																								
Bivalvia species spat										3									2					
Bivalvia species s1																								
Bivalvia species s2																								
Temora longicornis								1	1				1											
Centropages hamatus																								
Pseudocalanus elongatus																								
Calanoida species																								
Harpacticoida species								2	2	272				1										1
Ostracoda species																								
Cirripedia species cl					2																			
Cirripedia species n																								
Elminius modestus																								
Cirripedia species e																			1					
Philocheras trispinosus																								
Crangon crangon a																								
Crangon crangon pl	20			10	27	3		3	14			5		1				6	1	3			6	1
Diogenes pugilator																								
Paguridae species														1										
Brachyura species	2				12																			
Carcinus maenas pl																								
Schistomysis species																								
Schistomysis kervillei																								
Cumopsis goodsiri								2	1					1				1						
Cumacea species									1											1				
Diastylis species																								
Pseudocuma longirostris																								
Pseudocuma gilsoni																								
Pseudocuma species					1																			
Eurydice pulchra																								
Idotea pelagica																								
Stenothoë marina																								
Amphipoda species					2				1	1		1												
Pontocrates altamarinus										1													1	
Microprotopus maculatus																								
Bathyporeia sarsi																		1						
Bathyporeia species													1											
Atylus falcatus																								
Atylus swammerdami																								
Gammarus crinicornis?																								
Jassa species?																								
Haustorius arenarius																								
Crustacea species														1										
Pomatoschistus species?																								
Callionymus lyra																								
Solea solea																								
Pleuronectes platessa																								

Pleuronectidae species																								
Limanda limanda																								
Hippoglossoides platesso																								
Pisces species nd					1																			
empty capsule			1																1					
gelatinous capsule																								
egg																								
n.i.					1					2									1					
TOTAL	**23**	*****	**1**	**11**	**46**	**5**		**8**	**21**	**279**		**8**	**3**	**5**	*****	*****	*****	**11**	**11**	**4**	*****	*****	**7**	**5**
parasite abdomen (N)	2																							
parasite stomach (T)																								
parasite stomach (N)			1																					
parasite stomach (C?)																								
parasite gut (T)																								
parasite gut (N)			1			1																		

								SOLE-SEP 1996							**SOLE-OCT 1996**		
Standard length (mm)	53	51	51	64	57	51		59	65	54	62	55	57		83	77	66
	so14	**so15**	**so16**	**so17**	**so18**	**so19**		**so1**	**so2**	**so3**	**so4**	**so5**	**so6**		**so1**	**so2**	**so3**
Foraminifera species																	
Hydrozoa species																	
Nematoda species									2		2						
Magelona papillicornis p								22			1						
Arenicola species end																	
Lanice conchilega																	
Nephthys cirrosa											2						
Scolelepis squamata									5		5						
Polychaeta species			2	2	1	1			5								4
Spiophanes bombyx									1								
Pygospio elegans ?								7	7				3				
species 3																	
Spionidae species																	
Bivalvia species spat																	
Bivalvia species s1								8	1				1				
Bivalvia species s2																	
Temora longicornis																	
Centropages hamatus																	
Pseudocalanus elongatus																	
Calanoida species																	
Harpacticoida species			2					1		1							
Ostracoda species																	1
Cirripedia species cl																	
Cirripedia species n																	
Elminius modestus																	
Cirripedia species e																	
Philocheras trispinosus																	1

Crangon crangon a																	
Crangon crangon pl	1		2	3	3	1				3		2	4		1		
Diogenes pugilator	1																
Paguridae species																	
Brachyura species																	
Carcinus maenas pl			1														
Schistomysis species																	
Schistomysis kervillei																	
Cumopsis goodsiri										2							
Cumacea species																	
Diastylis species																	
Pseudocuma longirostris																	
Pseudocuma gilsoni										1							
Pseudocuma species					1										1		
Eurydice pulchra																	
Idotea pelagica									1								
Stenothoë marina																	
Amphipoda species										1							
Pontocrates altamarinus								3		2			2		3		3
Microprotopus maculatus																	
Bathyporeia sarsi																	
Bathyporeia species																	
Atylus falcatus																	
Atylus swammerdami																	
Gammarus crinicornis?																	
Jassa species?					1												
Haustorius arenarius																	
Crustacea species																	
Pomatoschistus species?																	
Callionymus lyra																	
Solea solea																	
Pleuronectes platessa																	
Pleuronectidae species																	
Limanda limanda																	
Hippoglossoides platesso																	
Pisces species nd																	
empty capsule				1					1		1						
gelatinous capsule																	
egg								1									
n.i.									2			1				1	
TOTAL	**2**	*****	**7**	**6**	**6**	**2**		**42**	**25**	**10**	**11**	**3**	**10**		**5**	**1**	**9**
parasite abdomen (N)								1									
parasite stomach (T)																	
parasite stomach (N)																	
parasite stomach (C?)					1												
parasite gut (T)												1					

DAB-MAY 1996			**DAB-SEP 1996**																			
Standard length (mm)	57	59	37	37	43	38	37	37	43	37	37	43	43	43	37	43	43	43	42	44	38	37
	da1	**da2**	**da1**	**da2**	**da3**	**da4**	**da5**	**da6**	**da7**	**da8**	**da9**	**da10**	**da11**	**da12**	**da13**	**da14**	**da15**	**da16**	**da17**	**da18**	**da19**	**da20**
Hydrozoa species	1	1						1							2			1				
Magelona papillicornis																						
Bivalvia species spat																		1				
Temora longicornis	1																					
Centropages hamatus	1																					
Harpacticoida species	1		2	1				1		3	1				2			2	1		2	
Cirripedia species cl	1	1																				
Crangon crangon pl		1	1																			
Diogenes pugilator pl													3									
Cumopsis goodsiri																				1		
Cumacea species		1																				
Atylus swammerdami		1																				
Gammarus species																						
Pontocrates altamarinus														1		1						1
Microprotopus maculatu																1						
Amphipoda species								1														
Crustacea species																		1				
fish scale						1			6											1		
n.i.																			1			1
TOTAL	**5**	**5**	**3**	**1**	*****	**1**	*****	**3**	**6**	**3**	**1**	*****	**3**	**1**	**4**	**2**	*****	**5**	**2**	**2**	**2**	**2**
parasite abdomen (N)	1												1									
parasite stomach (T)																						
parasite gut (T)									1													

DAB-OCT 1996												
Standard length (mm)	44	39	47	46	39	38	41	39	38	43	38	39
	da1	**da2**	**da3**	**da4**	**da5**	**da6**	**da7**	**da8**	**da9**	**da10**	**da11**	**da12**
Hydrozoa species			1							1		
Magelona papillicornis										1		
Bivalvia species spat												
Temora longicornis												
Centropages hamatus												
Harpacticoida species		1				1			1			
Cirripedia species cl												
Crangon crangon pl				1						1		
Diogenes pugilator pl										4		
Cumopsis goodsiri												
Cumacea species												
Atylus swammerdami												
Gammarus species							1					
Pontocrates altamarinus					1					1	1	
Microprotopus maculatu												
Amphipoda species												

Crustacea species							1					
fish scale												
n.i.												
TOTAL	*****	**1**	**1**	**1**	**1**	**1**	**2**	*****	**1**	**8**	**1**	*****
parasite abdomen (N)				2						2		
parasite stomach (T)				2								
parasite gut (T)				2					1+1 n.i.			

TURBOT-MAY 1996

Standard length (mm)	58	58	58	58	58	53	63	58	78	73	73	78	73	78	78	78	78	78	78	78
	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
Nematoda species																				
Polynoidae species?																				
Scolelepis squamata ?																				
Spionidae species																				
Polychaeta species																				
Temora longicornis							7			1			2				2	10	1	8
Acartia species																				
Centropages species							2											1		
Copepoda species			8				1											8		
Pseudocalanus elongatus ?																				
Harpacticoida species												90								
Cirripedia species cl							1										1		1	1
Cirripedia species e																				
Crangon crangon			1					1	2											
Philocheras trispinosus																				
Caridea species1																				
Caridea species zoea?																1				
Brachyura species juv		1																		
Brachyura species pl?																				
Schistomysis kervillei		2	1							3			1	2	1					
Schistomysis spiritus																				
Mysidacea species larva?																				
Mysidacea species?																				
Eurydice pulchra			2				3													
Bathyporeia species				2			4													
Gammarus crinicornis																				
Amphipoda species																				
Crustacea species n							1													
Crustacea species egg	1															1	1			
Clupeidae species pl									1				3					1		
Ammodytidae species pl																				
Ammodytidae species juv																				
Pomatoschistus species pl																				
Pomatoschistus species															1		1			1
Pleuronectidae species																				
Pisces species pl	1		1				1			1		1								
n.i.																1		2		
TOTAL	**2**	**3**	**13**	**2**	*	*	**20**	**1**	**3**	**5**	*	**91**	**6**	**2**	**2**	**3**	**5**	**22**	**2**	**10**
parasite body (C)									1											
parasite abdomen (N)			2				1	3			1			1						
parasite stomach (T)		5	3		1	1	3		2		1		2	2	4	1	4		7	1
parasite stomach (W)									1						1					
parasite stomach (N)																				

	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
parasite stomach (n.i.)																				
parasite gut (W)																				

TURBOT-JUN 1996

Standard length (mm)	73	58	63	73	68	68	78	78	78	73	63	63	78	73	83	88	83	63	73	48
	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
Nematoda species					1		2													
Polynoidae species?																				
Scolelepis squamata ?																				
Spionidae species																				
Polychaeta species																				
Temora longicornis	1		6		12							4		4	45			1	10	
Acartia species					24										3				8	
Centropages species					6							4			2				6	
Copepoda species		1	24		1									2	22			1	1	
Pseudocalanus elongatus ?			1																	
Harpacticoida species																	1			
Cirripedia species cl					1							3							4	
Cirripedia species e												1								
Crangon crangon	1							2		1							1	1		3
Philocheras trispinosus											1									
Caridea species1			1	3																
Caridea species zoea?																				
Brachyura species juv											1									
Brachyura species pl?										2										
Schistomysis kervillei	2	4					1	3		2				1	3					
Schistomysis spiritus																				
Mysidacea species larva?																				
Mysidacea species?					1															
Eurydice pulchra																				
Bathyporeia species												2								
Gammarus crinicornis																				
Amphipoda species					1															
Crustacea species n															1					
Crustacea species egg															1					
Clupeidae species pl	4	2	2	2	2	2	2	4			1	1	4	2	1	1		1	1	
Ammodytidae species pl																1				
Ammodytidae species juv																1				
Pomatoschistus species pl																				
Pomatoschistus species																				
Pleuronectidae species		2																		
Pisces species pl																				
n.i.									1								1			
TOTAL	**8**	**9**	**34**	**5**	**49**	**2**	**5**	**9**	**1**	**5**	**3**	**15**	**4**	**9**	**78**	**3**	**3**	**4**	**30**	**3**

parasite body (C)

	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
parasite abdomen (N)				1	1	2	1	2				2			1			2		1
parasite stomach (T)	4	2	8		6	2	7	1	3	3	1	7	7	3	4	2	3	2	1	
parasite stomach (W)									1											
parasite stomach (N)			2				1								1					
parasite stomach (n.i.)															1					
parasite gut (W)															1	1			1	

TURBOT-AUG (2) 1996				**TURBOT-SEP 1996**													
Standard length (mm)	33	28	23	53	48	43	43	33	28	28	33	43	43	43	43	43	53
	tu1	**tu2**	**tu3**	**tu1**	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**
Nematoda species																	
Polynoidae species?	2																
Scolelepis squamata ?	1																
Spionidae species	3																
Polychaeta species	1	1															
Temora longicornis																	
Acartia species																	
Centropages species																	
Copepoda species																	
Pseudocalanus elongatus ?																	
Harpacticoida species																	
Cirripedia species cl																	
Cirripedia species e																	
Crangon crangon	3	1															
Philocheras trispinosus																	
Caridea species1																	
Caridea species zoea?																	
Brachyura species juv				1													
Brachyura species pl?																	
Schistomysis kervillei			10														
Schistomysis spiritus																	
Mysidacea species larva?																	
Mysidacea species?																	
Eurydice pulchra																	
Bathyporeia species																	
Gammarus crinicornis																	1
Amphipoda species																	
Crustacea species n																	
Crustacea species egg																	
Clupeidae species pl		1															
Ammodytidae species pl																	
Ammodytidae species juv																	
Pomatoschistus species pl	4																
Pomatoschistus species																	
Pleuronectidae species																	
Pisces species pl																	

	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
n.i.											1									
TOTAL	**14**	**3**	**10**		**1**	*	*	*	*	*	**1**	*	*	*	*	*	*	**1**		
parasite body (C)																				
parasite abdomen (N)						1				2		4					1			
parasite stomach (T)						1				1										
parasite stomach (W)																				
parasite stomach (N)																				
parasite stomach (n.i.)																				
parasite gut (W)																				

TURBOT-OCT 1996

Standard length (mm)	33	38	38	43	43	48	43	68	58
	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**
Nematoda species									
Polynoidae species?									
Scolelepis squamata ?									
Spionidae species									
Polychaeta species							2		
Temora longicornis									
Acartia species									
Centropages species									
Copepoda species									
Pseudocalanus elongatus ?									
Harpacticoida species									
Cirripedia species cl									
Cirripedia species e									
Crangon crangon					1			1	1
Philocheras trispinosus									
Caridea species1									
Caridea species zoea?									
Brachyura species juv									
Brachyura species pl?									
Schistomysis kervillei					3			5	
Schistomysis spiritus									
Mysidacea species larva?					1				
Mysidacea species?									
Eurydice pulchra									
Bathyporeia species		1					2		
Gammarus crinicornis									
Amphipoda species									
Crustacea species n									
Crustacea species egg									
Clupeidae species pl									
Ammodytidae species pl									
Ammodytidae species juv									

	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
Pomatoschistus species pl																				
Pomatoschistus species																				
Pleuronectidae species																				
Pisces species pl																				
n.i.																				
TOTAL	*****	**1**	*****	*****	**5**	*****	**4**	**6**	**1**											
parasite body (C)																				
parasite abdomen (N)	2	4	5						1											
parasite stomach (T)		2	1			1														
parasite stomach (W)																				
parasite stomach (N)																				
parasite stomach (n.i.)																				
parasite gut (W)																				

BRILL-AUG (1) 1996

Standard length (mm)	61	54	54	33	34	31
	br1	**br2**	**br3**	**br4**	**br5**	**br6**
Cirripedia species cl	1					
Crangon crangon a				1		
Crangon crangon pl		2	1	2		1
Liocarcinus holsatus pl	1					
Schistomysis kervillei		2				2
Amphipoda species	1					
Pomatoschistus minutus						
Pomatoschistus species	2	1	1			
Pisces species		1	1		1	
TOTAL	**5**	**6**	**3**	**3**	**1**	**3**
parasite abdomen (N)		2				
parasite stomach (T)	2					1

BRILL-AUG (2) 1996

Standard length (mm)	77	59	50	31	30	26	25
	br1	**br2**	**br3**	**br4**	**br5**	**br6**	**br7**
Cirripedia species cl							
Crangon crangon a		1					
Crangon crangon pl			1	1	1		
Liocarcinus holsatus pl							
Schistomysis kervillei	4	5	17	10	12	4	1
Amphipoda species		1					
Pomatoschistus minutus							
Pomatoschistus species	3						
Pisces species		1					
TOTAL	**7**	**8**	**18**	**11**	**13**	**4**	**1**
parasite abdomen (N)	1	3					
parasite stomach (T)							

BRILL-SEP 1996

Standard length (mm)	66	76	75	80
	br1	**br2**	**br3**	**br4**
Cirripedia species cl				
Crangon crangon a				
Crangon crangon pl				
Liocarcinus holsatus pl				
Schistomysis kervillei				1
Amphipoda species			1	
Pomatoschistus minutus	1			
Pomatoschistus species			1	
Pisces species				1
TOTAL	**1**	*****	**2**	**2**
parasite abdomen (N)				
parasite stomach (T)			1	1

BRILL-OCT 1996

Standard length (mm)	60	93	81
	br1	**br2**	**br3**
Cirripedia species cl			
Crangon crangon a			
Crangon crangon pl	1		
Liocarcinus holsatus pl			
Schistomysis kervillei			6
Amphipoda species			
Pomatoschistus minutus			
Pomatoschistus species			
Pisces species			
TOTAL	**1**	*****	**6**
parasite abdomen (N)			1
parasite stomach (T)		1	

Appendix 8B. Numerical stomach content analyses of 0- and I-group plaice *Pleuronectes platessa* : 24-hour cycle (pl: plaice, *: empty stomach, l: postlarva, p: palp, s: siphon, cl: cypris larva, e: exuvia, hours in CET)

0-GROUP

Standard length (mm)	34	37	43	35	33	33	30	27	35	33	32	28	44	35	33	30	35	29	41	26	35
	18h pl1	**20h pl1**	**22h pl1**	**22h pl2**	**22h pl3**	**22h pl4**	**22h pl5**	**22h pl6**	**0h pl1**	**0h pl2**	**0h pl3**	**0h pl4**	**2h pl1**	**2h pl2**	**4h pl1**	**4h pl2**	**4h pl3**	**4h pl4**	**9h pl1**	**9h pl2**	**8h pl1**
Nematoda species																					
Anthozoa species		1																			
Bivalvia species s										1							1				
Bivalvia species																					
Polychaeta species		1							1												
Polychaeta empty capsule																					
Scolelepis squamata +eggs																					
Scolelepis squamata																					1
eggs																					
Pygospio elegans		1		4	5										1						
Polydora species																	3				
Spio filicornis																					
Spiophanes bombyx																					
Spio species		1	1			1			1	6	3						3				
Eteone longa																	1				
Arenicola species																					
Arenicola species end																					
Polychaeta species p																					
Magelona papillicornis p		5	28			1				1					1						8
Harmothoë species																					
Lanice conchilega			1																		
Nereis species																					
species 2															2						
Crangon crangon																					
Pisidia longicornis l																					
Cumacea species																					
Cumopsis goodsiri																					
Bathyporeia species											1	1									
Bathyporeia pilosa													1								
Bathyporeia pilosa ?																					
Bathyporeia sarsi	1			1																	
Corophium insidiosum																					
Corophium acherusicum																					
Corophium species																					
Ischyroceridae species																	1				
Pontocratues altamarinus																					
Calanus species																					
Centropages hamatus																2	2				
Centropages species																	4				
Harpacticoida species						1											2				
Temora longicornis																	5				
species 6																	1				

Eurydice pulchra																					
Cirripedia species n																2					
Cirripedia species cl																1	20				
Elminius modestus																					
Cirripedia species e																					
Chironomidae species larva																					
species 7																					
n.i.																					
TOTAL	**1**	**9**	**30**	**5**	**5**	**3**	*****	*****	**2**	**8**	**4**	**1**	**1**	*****	**4**	**5**	**43**	*****	*****	*****	**9**

Standard length (mm)	27	29	28	23	19	42	32	32
	8h pl2	**8h pl3**	**8h pl4**	**8h pl5**	**8h pl6**	**12h pl1**	**12h pl2**	**12h pl3**
Nematoda species								
Anthozoa species								
Bivalvia species s								
Bivalvia species								
Polychaeta species								
Polychaeta empty capsule								
Scolelepis squamata +eggs								
Scolelepis squamata								
eggs								
Pygospio elegans				1		1	4	
Polydora species								
Spio filicornis								
Spiophanes bombyx								
Spio species		1						
Eteone longa								
Arenicola species								
Arenicola species end								
Polychaeta species p							8	
Magelona papillicornis p								
Harmothoë species								
Lanice conchilega								
Nereis species								
species 2								
Crangon crangon								
Pisidia longicornis l								
Cumacea species								
Cumopsis goodsiri								
Bathyporeia species								
Bathyporeia pilosa								
Bathyporeia pilosa ?								
Bathyporeia sarsi								
Corophium insidiosum								
Corophium acherusicum								
Corophium species								
Ischyroceridae species								
Pontocratues altamarinus								

Calanus species								
Centropages hamatus								
Centropages species								
Harpacticoida species								
Temora longicornis								
species 6								
Eurydice pulchra								
Cirripedia species n								
Cirripedia species cl								
Elminius modestus								
Cirripedia species e								
Chironomidae species larva								
species 7								
n.i.								
TOTAL	*****	**1**	*****	**1**	*****	**1**	**12**	*****

I-GROUP

Standard length (mm)	78	69	72	73	57	69	80	64	74	75	76	80	74	86	73	63	63	57	64	84	65
	16h pl1	**16h pl2**	**18h pl1**	**18h pl2**	**18h pl3**	**20h pl1**	**20h pl2**	**20h pl3**	**20h pl4**	**20h pl5**	**20h pl7**	**20h pl8**	**20h pl9**	**20h pl10**	**20h pl11**	**20h pl12**	**20h pl13**	**20h pl14**	**20h pl15**	**22h pl1**	**22h pl2**
Nematoda species	8		6				3		13				3				2				
Anthozoa species																					
Bivalvia species s	2	1	1	3			2	2	3				1	2		1	3	1			1
Bivalvia species																				1	
Polychaeta species							3		1					2		1	1	1	1		
Polychaeta empty capsule																					
Scolelepis squamata +eggs																		1		2	
Scolelepis squamata	3	2	3	5	3		1		1			1	3					1		3	
eggs																					
Pygospio elegans			2	2	1		2	3					2	1			1		1		
Polydora species						149	1		1		484								1		
Spio filicornis												1	1								
Spiophanes bombyx																					
Spio species					1		1												3	1	3
Eteone longa							1	1	1								1	1			
Arenicola species							2	1					1								
Arenicola species end		1	3				3		1						1						
Polychaeta species p																					2
Magelona papillicornis p				2	2			2				2						4		1	1
Harmothoë species				1									1								
Lanice conchilega																					
Nereis species											1										
species 2							1														
Crangon crangon											1					1					
Pisidia longicornis 1																					
Cumacea species				1																	
Cumopsis goodsiri									1												
Bathyporeia species		1	2						1				1				1	1			
Bathyporeia pilosa	4						2		1							2		1			2

Bathyporeia pilosa ?									1												
Bathyporeia sarsi																1	2				
Corophium insidiosum											13										
Corophium acherusicum											2										
Corophium species																					
Ischyroceridae species																					
Pontocratues altamarinus																					
Calanus species																					
Centropages hamatus																					
Centropages species			1																		
Harpacticoida species																					
Temora longicornis																					
species 6																					
Eurydice pulchra	1		1						3												
Cirripedia species n																					
Cirripedia species cl	6			5			1	1	6				2			1	1	1		5	1
Elminius modestus									1											1	
Cirripedia species e																					
Chironomidae species larva																					
species 7																					
n.i.																					
TOTAL	**24**	**5**	**19**	**19**	**7**	**149**	**23**	**10**	**35**	*****	**501**	**4**	**15**	**5**	**1**	**7**	**12**	**12**	**6**	**14**	**10**
Standard length (mm)	68	77	64	77	62	68	65	65	68	77	80	77	77	75	63	85	85	69	70	83	78

	22h pl3	**22h pl4**	**22h pl5**	**22h pl6**	**22h pl7**	**22h pl8**	**22h pl9**	**22h pl10**	**22h pl11**	**22h pl12**	**22h pl13**	**22h pl14**	**22h pl15**	**22h pl16**	**22h pl18**	**22h pl19**	**22h pl20**	**0h pl1**	**0h pl2**	**0h pl3**	**0h pl4**
Nematoda species				3		6							1							1	
Anthozoa species																					
Bivalvia species s		1			2					2			1								
Bivalvia species			3	17		8														1	
Polychaeta species		1	1							1		1			2		1			2	
Polychaeta empty capsule																					
Scolelepis squamata +eggs						1							1								
Scolelepis squamata				6		2						2								1	
eggs																					
Pygospio elegans		6	11	2		2				4	1	3	12	1			4				
Polydora species													1								
Spio filicornis			1	1						1											
Spiophanes bombyx																					
Spio species				2							1				1						
Eteone longa													2				2				
Arenicola species												1								1	
Arenicola species end										1										2	
Polychaeta species p											8										
Magelona papillicornis p		2	3	3		4				2	5	8	11		4		1				
Harmothoë species																					
Lanice conchilega												1	1								
Nereis species																					
species 2																					

Crangon crangon					1																
Pisidia longicornis 1													1								
Cumacea species																					
Cumopsis goodsiri																					
Bathyporeia species	1		1														1				
Bathyporeia pilosa																					
Bathyporeia pilosa ?																					
Bathyporeia sarsi			2										1								
Corophium insidiosum																					
Corophium acherusicum																					
Corophium species																					
Ischyroceridae species																					
Pontocratues altamarinus																					
Calanus species																					
Centropages hamatus																					
Centropages species																					
Harpacticoida species																					
Temora longicornis																					
species 6																					
Eurydice pulchra																					
Cirripedia species n																					
Cirripedia species cl		1	5	6		3							1							1	
Elminius modestus																					
Cirripedia species e						2						2									
Chironomidae species larva																					
species 7																					
n.i.																					
TOTAL	**1**	**11**	**27**	**40**	**3**	**28**	*****	*****	*****	**11**	**15**	**18**	**33**	**1**	**7**	*****	**9**	*****	*****	**9**	*****
Standard length (mm)	80	63	66	79	65	70	80	83	76	62	61	80	65	80	74	71	80	85	70	74	75
	0h pl5	**0h pl7**	**0h pl8**	**0h pl11**	**2h pl2**	**2h pl3**	**2h pl4**	**2h pl5**	**2h pl6**	**2h pl7**	**2h pl8**	**4h pl1**	**4h pl2**	**6h pl1**	**6h pl2**	**6h pl3**	**6h pl4**	**6h pl5**	**6h pl6**	**6h pl7**	**8h pl1**
Nematoda species	2		1			4		40									1			28	
Anthozoa species																					
Bivalvia species s					1																
Bivalvia species	1																				
Polychaeta species																	2				1
Polychaeta empty capsule															1						
Scolelepis squamata +e	1					2		1							1						
Scolelepis squamata	1		2		3									1						10	
eggs	1																				
Pygospio elegans	1					1				1				1		4	2	2			
Polydora species			1															1			
Spio filicornis	1																			1	
Spiophanes bombyx																					
Spio species	2				1	5							1	1					2		
Eteone longa					1																
Arenicola species	1																				1
Arenicola species end					1		1								1				1		

Polychaeta species p								1													7
Magelona papillicornis	3					7											2				4
Harmothoë species																					
Lanice conchilega																					1
Nereis species																					
species 2						2		4		2			1								
Crangon crangon														1							
Pisidia longicornis	1																				
Cumacea species																					
Cumopsis goodsiri																					
Bathyporeia species						1		1					1							1	
Bathyporeia pilosa					3																
Bathyporeia pilosa ?																					
Bathyporeia sarsi			1			1															
Corophium insidiosum																					
Corophium acherusicum																					
Corophium species																					
Ischyroceridae species																					
Pontocratues altamarinus																					
Calanus species																1					
Centropages hamatus																					
Centropages species																					
Harpacticoida species																1					
Temora longicornis																					
species 6																					
Eurydice pulchra																					
Cirripedia species n																					
Cirripedia species cl			1					1							2	1	2			6	
Elminius modestus																					
Cirripedia species e								1													
Chironomidae species larva																					
species 7																					
n.i.																	1				
TOTAL	**14**	*****	**6**	*****	**10**	**23**	**1**	**49**	*****	**3**	*****	*****	**3**	**4**	**5**	**7**	**9**	**3**	**3**	**46**	**14**
Standard length (mm)	71	73	66	68	81	68	78	81	70	71	71	65	54	82	75	72	73	66	61	88	65
	8h pl2	**8h pl3**	**8h pl4**	**8h pl5**	**8h pl6**	**8h pl7**	**8h pl8**	**8h pl9**	**8h pl10**	**8h pl11**	**8h pl13**	**8h pl14**	**8h pl17**	**10h pl1**	**10h pl2**	**10h pl3**	**10h pl4**	**10h pl5**	**10h pl6**	**10h pl7**	**10h pl8**
Nematoda species				12	22									4			6	2			
Anthozoa species																					
Bivalvia species s						1			2		1							1			
Bivalvia species									2												
Polychaeta species		2		1		2		3										1			
Polychaeta empty capsule																					
Scolelepis squamata +eggs		1		1	1									1		1	1				
Scolelepis squamata eggs				6	3					1				2	1	1	3	7	1		3
Pygospio elegans		1	1		1			1		1	1			1	1	1					
Polydora species					1				205		1										

Spio filicornis											2			2							
Spiophanes bombyx														1							
Spio species				1						2			4	2	1		4				1
Eteone longa		1							2												
Arenicola species									8						2						
Arenicola species end					1																
Polychaeta species p	1			7											2						
Magelona papillicornis	15	7				2							8			1	4		7		15
Harmothoë species																					
Lanice conchilega													1	1							1
Nereis species									3												
species 2																	2	1			
Crangon crangon			1						1						1			2			
Pisidia longicornis 1																					
Cumacea species																					
Cumopsis goodsiri		1																1			
Bathyporeia species																	1	1			
Bathyporeia pilosa					2												1	1			
Bathyporeia pilosa ?										2											
Bathyporeia sarsi					4																
Corophium insidiosum									3												
Corophium acherusicum																					
Corophium species									1												
Ischyroceridae species									1												
Pontocratues altamarin	1																				
Calanus species									1												
Centropages hamatus																					
Centropages species																					
Harpacticoida species																					
Temora longicornis									1								1				
species 6																					
Eurydice pulchra																					
Cirripedia species n																					
Cirripedia species cl		1		2										10		3	2	1			
Elminius modestus																					
Cirripedia species e				1										1							
Chironomidae species larva									1												
species 7											1										
n.i.																					
TOTAL	**17**	**14**	**2**	**31**	**35**	**5**	*****	**4**	**231**	**6**	**6**	*****	**13**	**25**	**8**	**7**	**25**	**18**	**8**	*****	**20**

Standard length (mm)	74	89	75	70	66	70	68	65	82	67
	10h pl9	**12h pl1**	**12h pl2**	**12h pl3**	**12h pl4**	**12h pl5**	**12h pl6**	**12h pl7**	**14h pl1**	**14h pl2**
Nematoda species								1	1	
Anthozoa species										
Bivalvia species s										
Bivalvia species		1				1				
Polychaeta species						1				

Polychaeta empty capsule										
Scolelepis squamata +e	1							1		
Scolelepis squamata						1		2		
eggs										
Pygospio elegans		1		2	1	3		6	2	
Polydora species										
Spio filicornis		1	1							
Spiophanes bombyx										
Spio species				3		1			2	
Eteone longa			1						1	
Arenicola species						1		1		
Arenicola species end										
Polychaeta species p										
Magelona papillicornis p										
Harmothoë species										
Lanice conchilega						1				
Nereis species										
species 2									2	
Crangon crangon	1									
Pisidia longicornis 1										
Cumacea species										
Cumopsis goodsiri										
Bathyporeia species										1
Bathyporeia pilosa									4	1
Bathyporeia pilosa ?										
Bathyporeia sarsi										
Corophium insidiosum										
Corophium acherusicum										
Corophium species										
Ischyroceridae species										
Pontocratues altamarinus										
Calanus species										
Centropages hamatus										
Centropages species										
Harpacticoida species										
Temora longicornis										
species 6										
Eurydice pulchra										1
Cirripedia species n										
Cirripedia species cl								2		
Elminius modestus								1		
Cirripedia species e										
Chironomidae species larva										
species 7										
n.i.										
TOTAL	**2**	**3**	**2**	**5**	**1**	**9**	*****	**14**	**12**	**3**

Appendix 9.

Gravimetrical stomach content analyses. (A) Temporal series flatfish. (B) 24-hour cycle plaice.

Appendix 9A. Gravimetrical stomach/gut content analyses (mg AFDW): temporal campaign (pl: plaice *Pleuronectes platessa,* so: sole *Solea solea,* da: dab *Limanda limanda,* tu: turbot *Scophthalmus maximus,* br: brill *Scophthalmus rhombus,* *: empty stomach/gut, n.i.: not identifiable) (a: adult, pl: postlarva, juv: juvenile, n: nauplius larva, cl: cyprid larva, s: siphon, p: palp, e: exuvia).

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Standard length (mm)	69	74	66	85	66	75	82	78	69	72	69	78	67	73	75	78	68	70	66	68	62	60
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Foraminifera species																				0.03		
Hydrozoa species										0.01												
Nematoda species				0.01	0.00	0.00	0.07				0.00	0.01				0.00						0.00
Magelona papillicornis p																					0.02	
Polychaeta species p2																						
Polychaeta species p7																						
Polychaeta species px																					0.02	0.05
Arenicola species end						2.61	2.61								2.61		2.61					
Eteone longa		0.01										0.01		0.01			0.06					
Magelona papillicornis																						
Nephtys cirrosa																						
Nereis species																						
Polychaeta species					0.07	0.02	0.02		0.02		0.02					0.02	0.02					
Pygospio elegans																						
Scolelepis squamata				23.96				19.17				9.58		19.17	4.79				4.79			
Spio species																						
Spionidae species			0.04		2.85			0.05						0.02								0.04
Spionidae species 3	0.01	0.01	0.03			0.01	0.01	0.04	0.01	0.01		0.10		0.10	0.02	0.01	0.02	0.05	0.01		0.01	
Spiophanes bombyx																						
Harmothoë species								0.02														
Bivalvia species spat																						
Bivalvia species s1																						
Temora longicornis																0.09					0.09	
Centropages hamatus	145.78	2.85	31.24	1.78		1.69	1.34	2.31	0.98	3.83	0.09	47.79	0.09	27.32	1.34	0.36	7.30	10.24	0.27	0.71		0.09
Pseudocalanus elongatus	6.22	0.62	1.96	0.80	0.18	0.36		0.27	0.09	0.53		3.12		3.20	0.62	0.09	0.36	1.07	0.36	0.36	0.09	0.09
Calanoida species	1.98	0.18	1.42	0.45		0.09	0.18	0.71		0.71		1.42		0.98	0.80		0.09	0.27			0.09	
Harpacticoida species												0.00						0.00		0.00		
Cirripedia species cl															0.03							
Cirripedia species e	0.01	0.01	0.03	0.35		0.01		0.28				0.20		0.53	0.01	0.01	0.04	0.04				
Elminius modestus														0.09				0.18				
Philocheras trispinosus											6.63											
Crangon crangon pl								3.62														
Crangonidae species zoea								0.23														
Pagurus bernhardus pl																						
Carcinus maenas juv																						
Liocarcinus holsatus ?	0.74																					
Schistomysis kervillei	0.10																0.06					
Bodotriidae species	0.09																0.09					
Cumopsis goodsiri																						

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Diastylis species																						
Pseudocuma longicornis																						
Eurydice pulchra								0.39						0.24								
Bathyporeia species		0.50	0.39	0.23				0.35				0.32		2.46		0.27						
Stenothoë marina				0.07				0.07				0.07		0.20		0.07						
Amphipoda species																						
Pontocrates species																						
Atylus falcatus																						
Solea solea pl																						
Limanda limanda pl																						
Clupeidae species pl																						
TOTAL	**154.9**	**4.2**	**35.1**	**27.6**	**3.1**	**4.8**	**4.2**	**27.5**	**1.1**	**5.1**	**6.7**	**62.6**	**0.1**	**54.3**	**10.2**	**0.9**	**10.6**	**11.8**	**5.4**	**1.1**	**0.3**	**0.3**

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Standard length (mm)	38	34	38	35	38	40	36	33	29	33	32	37	35	32	33	28	31	32	43	44
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species			0.00																	
Hydrozoa species																				
Nematoda species																			0.00	
Magelona papillicornis p	0.06		0.06		0.01	0.01				0.05	0.08	0.01	0.02			0.03	0.01			0.13
Polychaeta species p2																				
Polychaeta species p7																				
Polychaeta species px			0.02																	
Arenicola species end																				
Eteone longa			0.01																	
Magelona papillicornis																				0.86
Nephtys cirrosa																				4.06
Nereis species																				
Polychaeta species	0.01	0.02	0.05		0.03				0.02			0.01				0.06			0.03	0.05
Pygospio elegans																				
Scolelepis squamata																				
Spio species			0.00																	
Spionidae species																				
Spionidae species 3					0.04														0.02	
Spiophanes bombyx																				
Harmothoë species																				
Bivalvia species spat			0.02					0.02												0.03
Bivalvia species s1	0.14	0.02	0.14	0.09	0.05	0.02		0.10	0.03	0.03	0.14		0.02			0.19	0.09	0.07	0.05	0.14
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species			0.04													0.00				
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																				

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Philocheras trispinosus																						
Crangon crangon pl	1.68	0.34	1.70		2.67	0.96	4.89	3.72	1.28	1.79	6.21	0.90		3.83	1.60	1.74	0.36	1.54				
Crangonidae species zoea													0.23									
Pagurus bernhardus pl																						
Carcinus maenas juv																						
Liocarcinus holsatus ?																						
Schistomysis kervillei													0.69									
Bodotriidae species																						
Cumopsis goodsiri			0.07		0.07																	
Diastylis species									0.01													
Pseudocuma longicornis																						
Eurydice pulchra																						
Bathyporeia species																						
Stenothoë marina																						
Amphipoda species																						
Pontocrates species					0.53				0.02							0.01				0.02		
Atylus falcatus					0.13																	
Solea solea pl			0.43		0.86					1.42												
Limanda limanda pl					1.20																	
Clupeidae species pl					0.30																	
TOTAL	**1.9**	**0.4**	**2.6**	**0.1**	**5.9**	**1.0**	**4.9**	**3.8**	**1.4**	**3.3**	**6.4**	**0.9**	**0.9**	**3.8**	**1.6**	**2.0**	**0.5**	**1.6**	**0.1**	**5.3**		

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Standard length (mm)	42	43	39	42	43	42	44	43	43	41	41	42	41	41	40	41	40	39	39	39
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species																				
Magelona papillicornis p	0.01		0.01					0.01		0.03	0.01	0.02				0.02			0.01	0.02
Polychaeta species p2					0.01					0.07		0.01								
Polychaeta species p7					0.03								0.04	0.06						
Polychaeta species px						0.02				0.01				0.02	0.02				0.02	0.04
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa																				
Nereis species																				
Polychaeta species			0.02	0.01				0.08	0.02	0.01	0.06	0.00	0.03		0.02					
Pygospio elegans	0.06																			
Scolelepis squamata								0.02			0.02									
Spio species	0.26						0.26													
Spionidae species	0.04										0.03	0.05			0.02	0.14				
Spionidae species 3												0.01	0.01	0.01	0.01				0.01	0.05
Spiophanes bombyx																				
Harmothoë species																				
Bivalvia species spat			0.00		0.02						0.03									

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Bivalvia species sl	0.03			0.02		0.02			0.03		0.05			0.03		0.02						
Temora longicornis																						
Centropages hamatus																						
Pseudocalanus elongatus																						
Calanoida species																						
Harpacticoida species	0.00																					
Cirripedia species cl																						
Cirripedia species e																						
Elminius modestus																						
Philocheras trispinosus																						
Crangon crangon pl	1.47		1.03					0.56			0.74				1.36			0.88				
Crangonidae species zoea																						
Pagurus bernhardus pl																						
Carcinus maenas juv	0.09																					
Liocarcinus holsatus ?																						
Schistomysis kervillei																						
Bodotriidae species																						
Cumopsis goodsiri											0.07											
Diastylis species																						
Pseudocuma longicornis		0.04																				
Eurydice pulchra																						
Bathyporeia species			0.02																			
Stenothoë marina																						
Amphipoda species													0.37									
Pontocrates species																						
Atylus falcatus																0.09						
Solea solea pl																						
Limanda limanda pl																						
Clupeidae species pl																						
TOTAL	**2.0**	**0.0**	**1.1**	**0.0**	**0.1**	**0.0**	**0.3**	**0.7**	**0.1**	**0.1**	**1.0**	**0.1**	**0.4**	**0.1**	**1.4**	**0.3**	*	**0.9**	**0.0**	**0.1**		

PLAICE-AUG (1) 1996

Standard length (mm)	40	40	40	40	40	40	39	40	40	39	40	39	40	40	40	40	40	40	39	40
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species																				
Magelona papillicornis p									0.04								0.02			
Polychaeta species p2																	0.06			
Polychaeta species p7																	0.01			
Polychaeta species px	0.01			0.02		0.01			0.02			0.02								0.04
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa																				
Nereis species																				

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Polychaeta species			0.07	0.00	0.02	0.02		0.01	0.02			0.01	0.00		0.00	0.02	0.02		0.06	0.03		
Pygospio elegans																						
Scolelepis squamata																						
Spio species																						
Spionidae species																						
Spionidae species 3	0.01				0.02			0.01	0.02	0.01		0.00							0.02	0.01		
Spiophanes bombyx																						
Harmothoë species			0.00																			
Bivalvia species spat							0.03					0.01				0.01						
Bivalvia species s1	0.02					0.02	0.03		0.02			0.03				0.02			0.02			
Temora longicornis																						
Centropages hamatus																						
Pseudocalanus elongatus																						
Calanoida species																						
Harpacticoida species																						
Cirripedia species cl																						
Cirripedia species e																						
Elminius modestus																						
Philocheras trispinosus																						
Crangon crangon pl				0.71		0.78	1.45		0.78				0.78		2.20	2.37		2.83	0.78			
Crangonidae species zoea																						
Pagurus bernhardus pl																						
Carcinus maenas juv																						
Liocarcinus holsatus ?																						
Schistomysis kervillei																						
Bodotriidae species																						
Cumopsis goodsiri																				0.07		
Diastylis species																						
Pseudocuma longicornis																						
Eurydice pulchra																						
Bathyporeia species																						
Stenothoë marina																						
Amphipoda species																						
Pontocrates species																						
Atylus falcatus																						
Solea solea pl																						
Limanda limanda pl																						
Clupeidae species pl																						
TOTAL	**0.0**	*****	**0.1**	**0.7**	**0.0**	**0.8**	**1.5**	**0.0**	**0.9**	**0.0**	*****	**0.1**	**0.8**	*****	**2.2**	**2.4**	**0.1**	**2.8**	**0.9**	**0.1**		

PLAICE-AUG (2) 1996

Standard length (mm)	44	43	45	43	44	43	44	43	45	43	41	42	42	41	42	46	45	43	45	45
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species				0.01				0.00												

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Magelona papillicornis p	0.01				0.02			0.01				0.04										
Polychaeta species p2																						
Polychaeta species p7																						
Polychaeta species px			0.02									0.03										
Arenicola species end																						
Eteone longa																						
Magelona papillicornis																						
Nephtys cirrosa																						
Nereis species																						
Polychaeta species	0.01		0.03	0.28	0.02	0.02	0.02	0.08			0.03	0.05			0.05	0.04		0.01				
Pygospio elegans																						
Scolelepis squamata																						
Spio species																						
Spionidae species															0.01				0.05	0.05		
Spionidae species 3			0.01	0.21				0.04	0.10			0.03			0.02					0.01		
Spiophanes bombyx																						
Harmothoë species																						
Bivalvia species spat			0.03	0.02					0.03			0.01				0.01						
Bivalvia species s1				0.09	0.12			0.02					0.05	0.02	0.02					0.05		
Temora longicornis																						
Centropages hamatus																						
Pseudocalanus elongatus																						
Calanoida species																						
Harpacticoida species	0.00				0.00	0.02																
Cirripedia species cl	0.01										0.01											
Cirripedia species e																						
Elminius modestus																						
Philocheras trispinosus																						
Crangon crangon pl	1.82	4.88	0.36		3.75	2.68	3.69	0.23	1.69	3.50	2.00	1.61	4.61	0.99	0.53	2.69	4.58	1.38	1.68	0.73		
Crangonidae species zoea																						
Pagurus bernhardus pl							0.67															
Carcinus maenas juv																						
Liocarcinus holsatus ?																						
Schistomysis kervillei																						
Bodotriidae species																						
Cumopsis goodsiri																						
Diastylis species																						
Pseudocuma longicornis																						
Eurydice pulchra																						
Bathyporeia species																						
Stenothoë marina																						
Amphipoda species																						
Pontocrates species																						
Atylus falcatus																						
Solea solea pl																						
Limanda limanda pl																						

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Clupeidae species pl																						
TOTAL	**1.9**	**4.9**	**0.4**	**0.6**	**3.9**	**2.7**	**4.4**	**0.4**	**1.8**	**3.5**	**2.0**	**1.8**	**4.7**	**1.0**	**0.6**	**2.7**	**4.6**	**1.4**	**1.7**	**0.8**		

PLAICE-SEP 1996

Standard length (mm)	50	49	49	50	50	46	46	45	45	46	47	47	47	47	48	47	47	48	49	49
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species		0.00																		
Magelona papillicornis p		0.02					0.01													
Polychaeta species p2																				
Polychaeta species p7	0.02																			
Polychaeta species px										0.02										
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa																				
Nereis species																				
Polychaeta species															0.08					
Pygospio elegans																				
Scolelepis squamata																				
Spio species																				
Spionidae species																				
Spionidae species 3		0.00									0.00									
Spiophanes bombyx											0.00									
Harmothoë species																				
Bivalvia species spat																				
Bivalvia species s1		0.05													0.05					
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species	0.00											0.00								
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																0.09				
Philocheras trispinosus																				
Crangon crangon pl																				
Crangonidae species zoea																				
Pagurus bernhardus pl																				
Carcinus maenas juv																				
Liocarcinus holsatus ?																				
Schistomysis kervillei																				
Bodotriidae species			0.17																	
Cumopsis goodsiri																				
Diastylis species																				

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Pseudocuma longicornis																						
Eurydice pulchra																						
Bathyporeia species																						
Stenothoë marina																						
Amphipoda species																						
Pontocrates species																						
Atylus falcatus																						
Solea solea pl																						
Limanda limanda pl																						
Clupeidae species pl																						
TOTAL	**0.0**	**0.1**	**0.2**	*	*	**0.0**	**0.0**	*	**0.0**	**0.0**	**0.0**	**0.0**	*	*	**0.1**	**0.1**	*	**0.0**	*	*		

PLAICE-OCT 1996

Standard length (mm)	49	50	50	51	50	49	50	50	50	50	49	50	49	49	50	49	49	49	50	50
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species	0.00																	0.00		
Magelona papillicornis p				0.01								0.02		0.02						
Polychaeta species p2		0.03																		
Polychaeta species p7					0.03															
Polychaeta species px					0.01				0.02	0.02			0.01							
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa		0.91	3.89							0.03										
Nereis species										0.00										
Polychaeta species						0.19				0.03	0.02			0.01						
Pygospio elegans																				
Scolelepis squamata	0.08					2.91	0.75													
Spio species																				
Spionidae species																				
Spionidae species 3				0.02	0.05					0.01						0.03				
Spiophanes bombyx									0.00	0.00		0.01								
Harmothoë species														0.00						
Bivalvia species spat					0.02											0.01				
Bivalvia species s1					0.02					0.05		0.02						0.02		
Temora longicornis																				
Centropages hamatus																				
Pseudocalanus elongatus																				
Calanoida species																				
Harpacticoida species	0.00			0.00	0.00			0.00		0.00	0.00		0.01			0.01	0.00			0.00
Cirripedia species cl																				
Cirripedia species e																				
Elminius modestus																				
Philocheras trispinosus																				

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Crangon crangon pl				0.78																		
Crangonidae species zoea																						
Pagurus bernhardus pl																						
Carcinus maenas juv																						
Liocarcinus holsatus ?																						
Schistomysis kervillei			0.22																			
Bodotriidae species																						
Cumopsis goodsiri									0.07				0.07	0.13								
Diastylis species																						
Pseudocuma longicornis																						
Eurydice pulchra						0.04																
Bathyporeia species						0.60																
Stenothoë marina																						
Amphipoda species																						
Pontocrates species																						
Atylus falcatus																						
Solea solea pl																						
Limanda limanda pl																						
Clupeidae species pl																						
TOTAL	**0.1**	**0.9**	**4.1**	**0.8**	**0.1**	**3.7**	**0.8**	**0.0**	**0.1**	**0.1**	**0.0**	**0.0**	**0.1**	**0.2**	*	**0.0**	**0.0**	**0.0**	*	**0.0**		

PLAICE-DEC 1996

Standard length (mm)	57	62	61	55	59	55	55	53	55	50	51	48	50	52	50	43	46	49	44	43
	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**
Foraminifera species																				
Hydrozoa species																				
Nematoda species																				
Magelona papillicornis p											0.02	0.09			0.01		0.02	0.02		
Polychaeta species p2																				0.02
Polychaeta species p7																				
Polychaeta species px													0.02				0.02	0.02		0.02
Arenicola species end																				
Eteone longa																				
Magelona papillicornis																				
Nephtys cirrosa														0.07						
Nereis species																				
Polychaeta species												0.00	0.06							
Pygospio elegans																				
Scolelepis squamata																				
Spio species																				
Spionidae species																				
Spionidae species 3														0.03			0.12			
Spiophanes bombyx																				
Harmothoë species																				
Bivalvia species spat																				
Bivalvia species s1											0.05	0.05	0.05			0.02	0.02			

	pl1	**pl2**	**pl3**	**pl4**	**pl5**	**pl6**	**pl7**	**pl8**	**pl9**	**pl10**	**pl11**	**pl12**	**pl13**	**pl14**	**pl15**	**pl16**	**pl17**	**pl18**	**pl19**	**pl20**	**pl21**	**pl22**
Temora longicornis																						
Centropages hamatus																						
Pseudocalanus elongatus																						
Calanoida species																						
Harpacticoida species																						
Cirripedia species cl																						
Cirripedia species e																						
Elminius modestus																						
Philocheras trispinosus																						
Crangon crangon pl																						
Crangonidae species zoea																						
Pagurus bernhardus pl																						
Carcinus maenas juv																						
Liocarcinus holsatus ?																						
Schistomysis kervillei																						
Bodotriidae species																			0.09			
Cumopsis goodsiri												0.07										
Diastylis species																						
Pseudocuma longicornis																						
Eurydice pulchra																						
Bathyporeia species																						
Stenothoë marina																						
Amphipoda species																						
Pontocrates species																						
Atylus falcatus																						
Solea solea pl																						
Limanda limanda pl																						
Clupeidae species pl																						
TOTAL	*	*	*	*	*	*	*	*	*	*	**0.1**	**0.2**	**0.1**	**0.1**	**0.0**	**0.0**	**0.2**	**0.0**	**0.1**	**0.0**		

SOLE-MAY 1996

Standard length (mm)	118	121	131	123	116	119	116	116	91	128	123	123	118	124	125	127	115	126	115	107	110	113	108	132
	so1	**so2**	**so3**	**so4**	**so5**	**so6**	**so7**	**so8**	**so9**	**so10**	**so11**	**so12**	**so13**	**so14**	**so15**	**so16**	**so17**	**so18**	**so19**	**so20**	**so21**	**so22**	**so23**	**so24**
Foraminifera species																								
Nematoda species							0.00			0.02														
Magelona papillicornis p																	0.05	0.01						
Arenicola species end	2.62		13.96			0.75	18.60			4.02	0.00		5.34		41.62		14.99	28.03	2.12			9.17		25.60
Lanice conchilega																				9.99		4.16		
Nephthys cirrosa									2.06					39.35						36.37		53.53		
Scolelepis squamata																								
Polychaeta species	2.63		2.49				0.21				6.91	30.12	0.38		0.56		1.42			0.08			21.21	
Spiophanes bombyx																								
species 3																								
Spionidae species																							0.50	
Bivalvia species spat									0.02								0.02			0.03				
Bivalvia species s1																								
Bivalvia species s2																							0.51	
Temora longicornis	0.45	0.09		0.09	0.36	0.71	0.89	0.27	0.18	0.80	0.09		0.09		0.89		0.27	0.09		0.18			0.18	0.36
Centropages hamatus	0.27	0.09	0.18	0.09	0.09		0.62			0.27					0.62			0.18				0.09	0.18	
Pseudocalanus elongatus															0.27									0.09
Calanoida species							0.09	0.09				0.18				0.09	0.09						0.09	
Harpacticoida species																				0.00				
Ostracoda species																								
Cirripedia species cl					0.01	0.03			0.01	0.32									0.03			0.01	0.06	
Cirripedia species n	0.01																							
Elminius modestus																								
Cirripedia species e										0.01													0.05	
Crangon crangon	1.98		10.52	10.52	1.32	7.73	13.54	0.58	10.36	20.38	1.21	2.48	5.63	0.86	24.48	1.42	5.20	0.37	4.73	27.27	2.46	6.39	17.85	6.25
Philocheras trispinosus																								
Paguridae species																								
Brachyura species	0.54		4.02		1.06								0.72									0.49		0.76
Schistomysis kervillei				5.78																				
Schistomysis species															0.05									
Cumopsis goodsiri																								
Cumacea species																				0.07				
Pseudocuma longirostris																								
Pseudocuma gilsoni									0.09															
Pseudocuma species											0.04													
Eurydice pulchra									0.28															
Idotea pelagica																								
Stenothoë marina																								
Amphipoda species						0.16														1.40				
Pontocrates altamarinus				0.18		0.48				0.07									0.63	0.54				
Microprotopus maculatus									0.03			0.03												0.03
Bathyporeia species																								
Atylus species				3.28													0.55		1.74	0.49		0.41		
Gammarus species	0.40																							

Jassa species?																								
Haustorius arenarius							0.29				0.10				0.12							0.23	0.40	
Crustacea species																								
Pomatoschistus species? pl				8.09																			2.76	
Callionymus lyra									1.70													1.35		
Solea solea							3.50													1.48		1.48	2.24	
Pleuronectes platessa			1.19						1.19													4.88		
Pleuronectidae sp ecies															11.18		2.98							
Hippoglossoides platessoi									18.81	15.48	9.18						11.59							
Pisces species nd														4.70	8.83					3.51	3.51		3.22	
empty capsule									0.21			0.08											0.29	
gelatinous capsule																								0.12
egg			0.00													0.00								
n.i.							0.00																	
TOTAL	**8.9**	**0.2**	**32.4**	**28.0**	**2.8**	**9.9**	**37.7**	**0.9**	**34.9**	**41.4**	**17.5**	**32.9**	**12.2**	**44.9**	**88.6**	**1.5**	**37.1**	**28.7**	**9.2**	**81.4**	**6.0**	**82.2**	**49.5**	**33.2**

SOLE-JUN 1996								**SOLE-AUG (1) 1996**				**SOLE-AUG (2) 1996**												
Standard length (mm)	105	123	122	103	128	122		53	52	47		60	55	48	61	56	52	53	59	55	59	54	75	67
	so1	**so2**	**so3**	**so4**	**so5**	**so6**		**so1**	**so2**	**so3**		**so1**	**so2**	**so3**	**so4**	**so5**	**so6**	**so7**	**so8**	**so9**	**so10**	**so11**	**so12**	**so13**
Foraminifera species													0.00											
Nematoda species																								
Magelona papillicornis p																								
Arenicola species end						22.69																		
Lanice conchilega																								
Nephthys cirrosa				27.43														13.70	4.63					2.41
Scolelepis squamata																								
Polychaeta species	6.65								0.00			2.37							1.24					0.06
Spiophanes bombyx																								
species 3																								
Spionidae species																								
Bivalvia species spat										0.09									0.11					
Bivalvia species s1																								
Bivalvia species s2																								
Temora longicornis								0.09	0.09				0.09											
Centropages hamatus																								
Pseudocalanus elongatus																								
Calanoida species																								
Harpacticoida species								0.00	0.00	0.54				0.00										0.00
Ostracoda species																								
Cirripedia species cl					0.03																			
Cirripedia species n																								
Elminius modestus																								
Cirripedia species e																			0.06					
Crangon crangon	11.81			6.04	18.36	2.71		2.21	6.04			3.35		0.60				2.68	0.71	0.34			3.08	0.39
Philocheras trispinosus																								
Paguridae species														0.02										
Brachyura species	0.99				6.44																			

Schistomysis kervillei																							
Schistomysis species																							
Cumopsis goodsiri							0.13	0.07					0.07				0.07						
Cumacea species								0.07											0.07				
Pseudocuma longirostris																							
Pseudocuma gilsoni																							
Pseudocuma species					0.04																		
Eurydice pulchra																							
Idotea pelagica																							
Stenothoë marina																							
Amphipoda species					0.90			0.20	0.17		0.02												
Pontocrates altamarinus									0.03													0.14	
Microprotopus maculatus																							
Bathyporeia species												0.70					0.22						
Atylus species																							
Gammarus species																							
Jassa species?																							
Haustorius arenarius																							
Crustacea species					0.09								0.09										
Pomatoschistus species? pl																							
Callionymus lyra																							
Solea solea																							
Pleuronectes platessa																							
Pleuronectidae species																							
Hippoglossoides platessoi																							
Pisces species nd																							
empty capsule			0.20																				
gelatinous capsule																							
egg																							
n.i.																		0.01					
TOTAL	**19.4**	*	**0.2**	**33.5**	**25.9**	**25.4**	**2.4**	**6.5**	**0.8**		**5.7**	**0.8**	**0.8**	*	*	*	**16.7**	**6.8**	**0.4**	*	*	**3.2**	**2.9**

							SOLE-SEP 1996							**SOLE-OCT 1996**									
Standard length (mm)	53	51	51	64	57	51	59	65	54	62	55	57		83	77	66							
	so14	**so15**	**so16**	**so17**	**so18**	**so19**	**so1**	**so2**	**so3**	**so4**	**so5**	**so6**		**so1**	**so2**	**so3**							
Foraminifera species																							
Nematoda species									0.01		0.01												
Magelona papillicornis p								0.18			0.01												
Arenicola species end																							
Lanice conchilega																							
Nephthys cirrosa											1.50												
Scolelepis squamata									3.62		2.66												
Polychaeta species			0.49	0.51		0.09			0.73		8.67		0.01				0.40						
Spiophanes bombyx									0.00														
species 3				0.00																			
Spionidae species									0.22														
Bivalvia species spat																							

Bivalvia species s1									0.14	0.02				0.02				
Bivalvia species s2																		
Temora longicornis																		
Centropages hamatus																		
Pseudocalanus elongatus																		
Calanoida species																		
Harpacticoida species			0.00						0.00		0.00							
Ostracoda species																		0.01
Cirripedia species cl																		
Cirripedia species n																		
Elminius modestus																		
Cirripedia species e																		
Crangon crangon	0.47		1.81	1.48	0.96	0.61					1.26		1.45	1.49		4.07		
Philocheras trispinosus																		1.31
Paguridae species	0.01																	
Brachyura species																		
Schistomysis kervillei																		
Schistomysis species																		
Cumopsis goodsiri											0.13							
Cumacea species																		
Pseudocuma longirostris																		
Pseudocuma gilsoni											0.04							
Pseudocuma species					0.04											0.04		
Eurydice pulchra																		
Idotea pelagica										0.03								
Stenothoë marina																		
Amphipoda species											0.03							
Pontocrates altamarinus									0.19		0.16			0.14		0.28		0.22
Microprotopus maculatus																		
Bathyporeia species																		
Atylus species																		
Gammarus species																		
Jassa species?					0.01													
Haustorius arenarius																		
Crustacea species																		
Pomatoschistus species? pl																		
Callionymus lyra																		
Solea solea																		
Pleuronectes platessa																		
Pleuronectidae sp ecies																		
Hippoglossoides platessoi																		
Pisces species nd																		
empty capsule				0.11						0.01								
gelatinous capsule																		
egg									0.00									
n.i.													0.00				0.00	
TOTAL	**0.5**	*****	**2.3**	**2.1**	**1.0**	**0.7**			**0.5**	**4.6**	**1.6**	**12.8**	**1.4**	**1.7**		**4.4**	**0.0**	**1.9**

DAB-MAY-1996			**DAB-SEP 1996**																			
Standard length (mm)	57	59	37	37	43	38	37	37	43	37	37	43	43	43	37	43	43	43	42	44	38	37
	da1	**da2**	**da1**	**da2**	**da3**	**da4**	**da5**	**da6**	**da7**	**da8**	**da9**	**da10**	**da11**	**da12**	**da13**	**da14**	**da15**	**da16**	**da17**	**da18**	**da19**	**da20**
Hydrozoa species	0.02	0.30						0.02							0.09			0.01				
Magelona papillicornis p																						
Bivalvia species spat																		0.51				
Temora longicornis	0.09																					
Centropages hamatus	0.09																					
Harpacticoida species	0.00		0.00	0.00				0.00		0.01	0.00				0.00			0.00	0.00		0.00	
Cirripedia species cl	0.01		0.03	0.01				0.01		0.04	0.01				0.03			0.03	0.01		0.03	
Crangon crangon pl		3.77	0.48																			
Diogenes pugilator pl													0.05									
Cumopsis goodsiri																				0.07		
Cumacea species		0.07																				
Atylus swammerdami		1.13																				
Gammarus species																						
Pontocrates altamarinus														0.05		0.17						0.05
Micropotopus maculatus																0.03						
Amphipoda species								0.01														
Crustacea species																		0.09				
fish scale						0.00			0.01											0.00		
n.i.																			0.00			0.00
TOTAL	**0.2**	**5.3**	**0.5**	**0.0**	*****	**0.0**	*****	**0.0**	**0.0**	**0.0**	**0.0**	*****	**0.0**	**0.0**	**0.1**	**0.2**	*****	**0.6**	**0.0**	**0.1**	**0.0**	**0.1**

DAB-OCT-1996												
Standard length (mm)	44	39	47	46	39	38	41	39	38	43	38	39
	da1	**da2**	**da3**	**da4**	**da5**	**da6**	**da7**	**da8**	**da9**	**da10**	**da11**	**da12**
Hydrozoa species			0.04							0.03		
Magelona papillicornis p										0.01		
Bivalvia species spat												
Temora longicornis												
Centropages hamatus												
Harpacticoida species		0.00				0.00			0.00			
Cirripedia species cl		0.01				0.01			0.01			
Crangon crangon pl				0.55						0.57		
Diogenes pugilator pl										0.35		
Cumopsis goodsiri												
Cumacea species												
Atylus swammerdami												
Gammarus species							0.03					
Pontocrates altamarinus					0.01					0.08	0.12	
Microprotopus maculatus												
Amphipoda species												
Crustacea species							0.09					
fish scale												
n.i.												
TOTAL	*****	**0.0**	**0.0**	**0.5**	**0.0**	**0.0**	**0.1**	*****	**0.0**	**1.0**	**0.1**	*****

TURBOT-MAY 1996

Standard length (mm)	58	58	58	58	58	53	63	58	78	73	73	78	73	78	78	78	78	78	78	78
	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
Nematoda species																				
Polynoidae species?																				
Scolelepis squamata ?																				
Spionidae species																				
Polychaeta species																				
Crangon crangon			3.98					3.43	18.40											
Philocheras trispinosus																				
Caridea species1																				
Caridea species zoea?																0.23				
Liocarcinus holsatus																				
Carcinus maenas		0.43																		
Brachyura species pl?																				
Schistomysis kervillei		8.89	6.20							16.64			1.00	9.10	5.55					
Schistomysis spiritus																				
Mysidacea species larva?																				
Mysidacea species?																				
Eurydice pulchra			0.97				0.90													
Bathyporeia species				1.29			1.34													
Gammarus crinicornis																				
Amphipoda species																				
Clupeidae species pl									26.00				116.53					26.00		
Ammodytidae species																				
Pomatoschistus species pl																				
Pomatoschistus species															284.91		239.87			164.69
Pleuronectidae species																				
Pisces species pl	26.00		26.00				26.00			26.00		26.00								
n.i.																0.09		0.18		
TOTAL (-prey)	**26.0**	**9.3**	**37.2**	**1.3**	*	*	**28.2**	**3.4**	**44.4**	**42.6**	*	**26.0**	**117.5**	**9.1**	**290.5**	**0.3**	**239.9**	**26.2**	*	**164.7**

TURBOT-JUN 1996

Standard length (mm)	73	58	63	73	68	68	78	78	78	73	63	63	78	73	83	88	83	63	73	48
	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**	**tu15**	**tu16**	**tu17**	**tu18**	**tu19**	**tu20**
Nematoda species					0.00		0.01													
Polynoidae species?																				
Scolelepis squamata ?																				
Spionidae species																				
Polychaeta species																				
Crangon crangon	8.52							16.47		4.18							92.22	14.08		13.44
Philocheras trispinosus											6.79									
Caridea species1			4.52	32.06																
Caridea species zoea?																				
Liocarcinus holsatus											0.28									
Carcinus maenas																				
Brachyura species pl?										0.16										

Schistomysis kervillei	2.85	11.67					0.68	10.69		2.73				2.19	7.84					
Schistomysis spiritus										2.55										
Mysidacea species larva?																				
Mysidacea species?					2.76															
Eurydice pulchra																				
Bathyporeia species												0.67								
Gammarus crinicornis																				
Amphipoda species					0.97															
Clupeidae species pl	105.77	46.33	51.26	44.18	33.62	66.42	51.86	48.22			30.41	26.00	130.62	55.67	43.38	33.85		23.19	42.39	
Ammodytidae species																9.96				
Pomatoschistus species pl																				
Pomatoschistus species																				
Pleuronectidae species		2.08																		
Pisces species pl								26.00												
n.i.									0.00								0.09			
TOTAL (-prey)	**117.1**	**60.1**	**55.8**	**76.2**	**37.4**	**66.4**	**52.6**	**101.4**	**0.0**	**9.6**	**37.5**	**26.7**	**130.6**	**57.9**	**51.2**	**43.8**	**92.3**	**37.3**	**42.4**	**13.4**

TURBOT-AUG 1996				**TURBOT-SEP 1996**													
Standard length (mm)	33	28	23	53	48	43	43	33	28	28	33	43	43	43	43	43	53
	tu1	**tu2**	**tu3**	**tu1**	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**	**tu10**	**tu11**	**tu12**	**tu13**	**tu14**
Nematoda species																	
Polynoidae species?	1.98																
Scolelepis squamata ?	0.64																
Spionidae species	0.37																
Polychaeta species	0.28																
Crangon crangon	0.89	0.58															
Philocheras trispinosus																	
Caridea species1																	
Caridea species zoea?																	
Liocarcinus holsatus																	
Carcinus maenas				1.45													
Brachyura species pl?																	
Schistomysis kervillei			2.58														
Schistomysis spiritus																	
Mysidacea species larva?																	
Mysidacea species?																	
Eurydice pulchra																	
Bathyporeia species																	
Gammarus crinicornis																	1.07
Amphipoda species																	
Clupeidae species pl		0.68															
Ammodytidae species																	
Pomatoschistus species pl	7.40																
Pomatoschistus species																	
Pleuronectidae species																	
Pisces species pl																	
n.i.										0.00							

TOTAL (-prey)	**11.6**	**1.3**	**2.6**		**1.4**	*	*	*	*	*	**0.0**	*	*	*	*	*	*	**1.1**

TURBOT-OCT 1996

Standard length (mm)	33	38	38	43	43	48	43	68	58
	tu1	**tu2**	**tu3**	**tu4**	**tu5**	**tu6**	**tu7**	**tu8**	**tu9**
Nematoda species									
Polynoidae species?									
Scolelepis squamata ?									
Spionidae species									
Polychaeta species									
Crangon crangon					0.79			31.22	24.89
Philocheras trispinosus									
Caridea species1									
Caridea species zoea?									
Liocarcinus holsatus									
Carcinus maenas									
Brachyura species pl?									
Schistomysis kervillei					2.32			4.10	
Schistomysis spiritus									
Mysidacea species larva?									
Mysidacea species?									
Eurydice pulchra									
Bathyporeia species		0.31					0.41		
Gammarus crinicornis									
Amphipoda species									
Clupeidae species pl									
Ammodytidae species									
Pomatoschistus species pl									
Pomatoschistus species									
Pleuronectidae species									
Pisces species pl									
n.i.									
TOTAL (-prey)	*	**0.3**	*	*	**3.1**	*	**0.4**	**35.3**	**24.9**

BRILL-AUG (1) 1996							**BRILL-AUG (2) 1996**							**BRILL-SEP 1996**				**BRILL-OCT 1996**		
Standard length (mm)	61	54	54	33	34	31	77	59	50	31	30	26	25	66	76	75	80	60	93	81
	br1	**br2**	**br3**	**br4**	**br5**	**br6**	**br1**	**br2**	**br3**	**br4**	**br5**	**br6**	**br7**	**br1**	**br2**	**br3**	**br4**	**br1**	**br2**	**br3**
Cirripedia species cl	0.01																			
Crangon crangon a		2.76	0.47	5.16		0.18		7.84	0.68	0.27	1.50							1.17		
Liocarcinus holsatus pl	0.19																			
Schistomysis kervillei		2.82				2.43	4.50	8.53	16.97	8.19	2.08	1.14	0.96				2.30			9.32
Gammarus crinicornis																1.43				
Amphipoda species	0.09							0.38												
Pomatoschistus minutus														49.58						
Pomatoschistus species	118.79	15.12	20.42				82.60	40.26								89.67				
Pisces species a		40.26			3.99												26.38			
Pisces species pl			40.26																	
TOTAL	**119.1**	**61.0**	**61.2**	**5.2**	**4.0**	**2.6**	**87.1**	**57.0**	**17.6**	**8.5**	**3.6**	**1.1**	**1.0**	**49.6**	*****	**91.1**	**28.7**	**1.2**	*****	**9.3**

Appendix 9B. Gravimetrical stomach content analyses of 0- and I-group plaice *Pleuronectes platessa* (mg AFDW): 24-hour cycle (pl: plaice, *: empty stomach, hours in CET)

0-GROUP

Standard length (mm)	34	37	43	35	33	33	30	27	35	33	32	28	44	35	33	30	35	29	41	26	35
	18h pl1	**20h pl1**	**22h pl1**	**22h pl2**	**22h pl3**	**22h pl4**	**22h pl5**	**22h pl6**	**0h pl1**	**0h pl2**	**0h pl3**	**0h pl4**	**2h pl1**	**2h pl2**	**4h pl1**	**4h pl2**	**4h pl3**	**4h pl4**	**9h pl1**	**9h pl2**	**8h pl1**
Nematoda species																					
Anthozoa species		2.61																			
Bivalvia species s										0.02							0.02				
Bivalvia species																					
Polychaeta species		0.01							0.02												
Polychaeta empty capsule																					
Scolelepis squamata																					0.30
eggs																					
Pygospio elegans		0.01		0.08	0.10										0.00						
Polydora species																	0.02				
Spio filicornis																					
Spiophanes bombyx																					
Spio species		0.01	0.00			0.00			0.01	0.18	0.04						0.06				
Eteone longa																	0.00				
Arenicola species																					
Arenicola species end																					
Polychaeta species p																					
Magelona papillicornis p		0.04	0.22			0.01				0.01					0.01						0.06
Harmothoë species																					
Lanice conchilega			0.01																		
Nereis species																					
species 2															0.02						
Crangon crangon																					
Pisidia longicornis l																					
Cumacea species																					
Cumopsis goodsiri																					
Bathyporeia species	0.22			0.35							0.54	0.22	0.32				0.00				
Calanus species																					
Centropages hamatus																0.18	0.18				
Centropages species																	0.36				
Harpacticoida species						0.00											0.00				
Temora longicornis																	0.45				
species 6																	0.00				
Eurydice pulchra																					
Cirripedia species n																0.03					
Cirripedia species cl																0.01	0.28				
Elminius modestus																					
Cirripedia species e																					
Chironomidae species larva																					
species 7																					
n.i.																					
TOTAL	**0.2**	**2.7**	**0.2**	**0.4**	**0.1**	**0.0**	*	*	**0.0**	**0.2**	**0.6**	**0.2**	**0.3**	*	**0.0**	**0.2**	**1.4**	*	*	*	**0.4**

Standard length (mm)	27	29	28	23	19	42	32	32
	8h pl2	**8h pl3**	**8h pl4**	**8h pl5**	**8h pl6**	**12h pl1**	**12h pl2**	**12h pl3**
Nematoda species								
Anthozoa species								
Bivalvia species s								
Bivalvia species								
Polychaeta species								
Polychaeta empty capsule								
Scolelepis squamata								
eggs								
Pygospio elegans				0.01		0.02	0.05	
Polydora species								
Spio filicornis								
Spiophanes bombyx								
Spio species		0.00						
Eteone longa								
Arenicola species								
Arenicola species end								
Polychaeta species p							0.06	
Magelona papillicornis p								
Harmothoë species								
Lanice conchilega								
Nereis species								
species 2								
Crangon crangon								
Pisidia longicornis l								
Cumacea species								
Cumopsis goodsiri								
Bathyporeia species								
Calanus species								
Centropages hamatus								
Centropages species								
Harpacticoida species								
Temora longicornis								
species 6								
Eurydice pulchra								
Cirripedia species n								
Cirripedia species cl								
Elminius modestus								
Cirripedia species e								
Chironomidae species larva								
species 7								
n.i.								
TOTAL	*	**0.0**	*	**0.0**	*	**0.0**	**0.1**	*

I-GROUP

Standard length (mm)	78	69	72	73	57	69	80	64	74	75	76	80	74	86	73	63	63	57	64	84	65
	16h pl1	**16h pl2**	**18h pl1**	**18h pl2**	**18h pl3**	**20h pl1**	**20h pl2**	**20h pl3**	**20h pl4**	**20h pl5**	**20h pl7**	**20h pl8**	**20h pl9**	**20h pl10**	**20h pl11**	**20h pl12**	**20h pl13**	**20h pl14**	**20h pl15**	**22h pl1**	**22h pl2**
Nematoda species	0.02		0.02				0.01		0.04				0.01				0.01				
Anthozoa species																					
Bivalvia species s	0.03	0.02	0.02	0.05			0.03	0.03	0.05				0.02	0.03		0.02	0.05	0.02			0.02
Bivalvia species																				0.00	
Polychaeta species							0.04		0.02					0.07		0.00	0.13	0.02	0.01		
Polychaeta empty capsule																					
Scolelepis squamata	56.15	0.07	1.06	2.72	1.08		0.62		0.88			0.13	1.96					0.27		4.49	
eggs																					
Pygospio elegans			0.16	0.03	0.01			0.01					0.07	0.00			0.02		0.02		
Polydora species						2.45	0.01		0.03		7.76								0.01		
Spio filicornis												0.03	0.06								
Spiophanes bombyx																					
Spio species							0.01												0.03	0.01	0.07
Eteone longa							0.02	0.05	0.06								0.01	0.02			
Arenicola species							0.14	0.01					0.06								
Arenicola species end		2.90	3.36				10.45		2.61						3.42						
Polychaeta species p																					0.02
Magelona papillicornis p				0.02	0.01			0.02				0.02						0.03		0.01	0.01
Harmothoë species													0.02								
Lanice conchilega																					
Nereis species											0.00										
species 2							0.01														
Crangon crangon											1.31					0.81					
Pisidia longicornis l																					
Cumacea species				0.08																	
Cumopsis goodsiri									0.07												
Bathyporeia species	0.91	0.02	0.38				0.06		0.61		1.00		0.22			0.88	0.86	0.34			0.74
Calanus species																					
Centropages hamatus																					
Centropages species			0.09																		
Harpacticoida species																					
Temora longicornis																					
species 6																					
Eurydice pulchra	0.04		0.04						0.09												
Cirripedia species n																					
Cirripedia species cl	0.08			0.07			0.01	0.01	0.08				0.03			0.01	0.01	0.01		0.07	0.01
Elminius modestus									0.09											0.09	
Cirripedia species e																					
Chironomidae species larva																					
species 7																					
n.i.																					
TOTAL	**57.2**	**3.0**	**5.1**	**3.0**	**1.1**	**2.4**	**11.4**	**0.1**	**4.6**	*	**10.1**	**0.2**	**2.5**	**0.1**	**3.4**	**1.7**	**1.1**	**0.7**	**0.1**	**4.7**	**0.9**

Standard length (mm)	68	77	64	77	62	68	65	65	68	77	80	77	77	75	63	85	85	69	70	83	78
	22h pl3	**22h pl4**	**22h pl5**	**22h pl6**	**22h pl7**	**22h pl8**	**22h pl9**	**22h pl10**	**22h pl11**	**22h pl12**	**22h pl13**	**22h pl14**	**22h pl15**	**22h pl16**	**22h pl18**	**22h pl19**	**22h pl20**	**0h pl1**	**0h pl2**	**0h pl3**	**0h pl4**
Nematoda species				0.01		0.02							0.00							0.00	
Anthozoa species																					
Bivalvia species s		0.02			0.03					0.03			0.02								
Bivalvia species			0.00	0.01		0.01														0.00	
Polychaeta species		0.11	0.20							0.23					0.05		0.11			0.10	
Polychaeta empty capsule																					
Scolelepis squamata				7.21		3.14						0.35	0.03							0.10	
eggs																					
Pygospio elegans		0.13	0.17	0.05		0.03				0.11	0.01	0.06	0.22	0.01			0.04				
Polydora species													0.01								
Spio filicornis			0.12	0.14						0.14											
Spiophanes bombyx																					
Spio species				0.05							0.01				0.00						
Eteone longa													0.03				0.03				
Arenicola species												0.04								0.05	
Arenicola species end										1.61										3.81	
Polychaeta species p											0.08										
Magelona papillicornis p		0.02	0.02	0.02		0.03				0.02	0.04	0.06	0.09		0.03		0.01				
Harmothoë species																					
Lanice conchilega												0.03	0.02								
Nereis species																					
species 2																					
Crangon crangon					0.02																
Pisidia longicornis l													0.62								
Cumacea species																					
Cumopsis goodsiri												0.07									
Bathyporeia species	0.22		0.86										0.07				0.22				
Calanus species																					
Centropages hamatus																					
Centropages species																					
Harpacticoida species																					
Temora longicornis																					
species 6																					
Eurydice pulchra																					
Cirripedia species n																					
Cirripedia species cl		0.01	0.07	0.08		0.11							0.01							0.01	
Elminius modestus																					
Cirripedia species e						0.00						0.00									
Chironomidae species larva																					
species 7																					
n.i.																					
TOTAL	**0.2**	**0.3**	**1.4**	**7.6**	**0.1**	**3.3**	*	*	*	**2.1**	**0.1**	**0.6**	**1.1**	**0.0**	**0.1**	*	**0.4**	*	*	**4.1**	*

Standard length (mm)	80	63	66	79	65	70	80	83	76	62	61	80	65	80	74	71	80	85	70	74	75
	0h pl5	**0h pl7**	**0h pl8**	**0h pl11**	**2h pl2**	**2h pl3**	**2h pl4**	**2h pl5**	**2h pl6**	**2h pl7**	**2h pl8**	**4h pl1**	**4h pl2**	**6h pl1**	**6h pl2**	**6h pl3**	**6h pl4**	**6h pl5**	**6h pl6**	**6h pl7**	**8h pl1**
Nematoda species	0.01		0.00		0.01	0.01		0.12									0.00			0.08	
Anthozoa species																					
Bivalvia species s					0.02																
Bivalvia species	0.00																				
Polychaeta species																	0.06				0.15
Polychaeta empty capsule															0.07						
Scolelepis squamata	0.64		1.69		0.11	0.89		6.60						0.05	1.34					18.86	
eggs	0.00																				
Pygospio elegans	0.01					0.00				0.01				0.01		0.08	0.05	0.08			
Polydora species			0.01															0.00			
Spio filicornis	0.03																			0.10	
Spiophanes bombyx																					
Spio species	0.04				0.01	0.06							0.03	0.01					0.01		
Eteone longa					0.05																
Arenicola species	0.04																				0.05
Arenicola species end					0.73		1.09								0.54				1.44		
Polychaeta species p								0.01													0.06
Magelona papillicornis p	0.02					0.06											0.02				0.03
Harmothoë species																					
Lanice conchilega																					0.03
Nereis species																					
species 2						0.02		0.03		0.02			0.01								
Crangon crangon														0.28							
Pisidia longicornis 1																					
Cumacea species																					
Cumopsis goodsiri																					
Bathyporeia species			0.27		0.71	0.39		0.02					0.02							0.25	
Calanus species																0.09					
Centropages hamatus																					
Centropages species																					
Harpacticoida species																0.00					
Temora longicornis																					
species 6																					
Eurydice pulchra																					
Cirripedia species n																					
Cirripedia species cl			0.01					0.01							0.03	0.01	0.03			0.08	
Elminius modestus																					
Cirripedia species e								0.00													
Chironomidae species larva																					
species 7																					
n.i.																	0.00				
TOTAL	**0.8**	*****	**2.0**	*****	**1.6**	**1.4**	**1.1**	**6.8**	*****	**0.0**	*****	*****	**0.1**	**0.3**	**2.0**	**0.2**	**0.2**	**0.1**	**1.5**	**19.4**	**0.3**

Standard length (mm)	71	73	66	68	81	68	78	81	70	71	71	65	54	82	75	72	73	66	61	88	65
	8h pl2	**8h pl3**	**8h pl4**	**8h pl5**	**8h pl6**	**8h pl7**	**8h pl8**	**8h pl9**	**8h pl10**	**8h pl11**	**8h pl13**	**8h pl14**	**8h pl17**	**10h pl1**	**10h pl2**	**10h pl3**	**10h pl4**	**10h pl5**	**10h pl6**	**10h pl7**	**10h pl8**
Nematoda species				0.04	0.07									0.01			0.02	0.01			
Anthozoa species																					
Bivalvia species s						0.02			0.03		0.02							0.02			
Bivalvia species									0.00												
Polychaeta species		0.16		0.03		0.01		0.14										0.01			
Polychaeta empty capsule																					
Scolelepis squamata		0.07		13.73	6.52					1.63				7.52	0.18	0.89	0.93	3.30	0.02		0.64
eggs																					
Pygospio elegans		0.01	0.00		0.01			0.01		0.02	0.01			0.02	0.02	0.02					
Polydora species					0.02				2.17		0.00										
Spio filicornis											0.36			0.13							
Spiophanes bombyx														0.02							
Spio species				0.01						0.06			0.03	0.11	0.01		0.24				0.00
Eteone longa		0.03							0.04												
Arenicola species									0.39						0.04						
Arenicola species end					0.83																
Polychaeta species p	0.01			0.06											0.02						
Magelona papillicornis p	0.12	0.06				0.02							0.06			0.01	0.03		0.06		0.12
Harmothoë species																					
Lanice conchilega													0.04	0.02							0.02
Nereis species									0.02												
species 2																	0.02	0.01			
Crangon crangon			0.81						0.58						0.12			1.54			
Pisidia longicornis l																					
Cumacea species																					
Cumopsis goodsiri		0.07																0.07			
Bathyporeia species	0.12				2.32				0.50	0.75							0.43	0.79			
Calanus species									0.09												
Centropages hamatus																					
Centropages species																					
Harpacticoida species																					
Temora longicornis									0.09								0.09				
species 6																					
Eurydice pulchra																					
Cirripedia species n																					
Cirripedia species cl		0.01		0.03										0.14		0.04	0.03	0.01			
Elminius modestus																					
Cirripedia species e				0.00										0.00							
Chironomidae species larva									0.02												
species 7											0.02										
n.i.																					
TOTAL	**0.2**	**0.4**	**0.8**	**13.9**	**9.8**	**0.0**	*****	**0.2**	**3.9**	**2.5**	**0.4**	*****	**0.1**	**8.0**	**0.4**	**1.0**	**1.8**	**5.8**	**0.1**	*****	**0.8**

Standard length (mm)	74	89	75	70	66	70	68	65	82	67
	10h pl9	**12h pl1**	**12h pl2**	**12h pl3**	**12h pl4**	**12h pl5**	**12h pl6**	**12h pl7**	**14h pl1**	**14h pl2**
Nematoda species								0.00	0.00	
Anthozoa species										
Bivalvia species s										
Bivalvia species		0.00				0.00				
Polychaeta species						0.12				
Polychaeta empty capsule										
Scolelepis squamata	0.21					0.38		1.30		
eggs										
Pygospio elegans		0.01		0.04	0.05	0.09		0.07	0.02	
Polydora species										
Spio filicornis		0.02	0.00							
Spiophanes bombyx										
Spio species				0.14		0.07			0.06	
Eteone longa			0.02						0.02	
Arenicola species						0.05		0.12		
Arenicola species end										
Polychaeta species p										
Magelona papillicornis p										
Harmothoë species										
Lanice conchilega						0.01				
Nereis species										
species 2									0.02	
Crangon crangon	0.60									
Pisidia longicornis 1										
Cumacea species										
Cumopsis goodsiri										
Bathyporeia species									1.28	0.10
Calanus species										
Centropages hamatus										
Centropages species										
Harpacticoida species										
Temora longicornis										
species 6										
Eurydice pulchra										0.06
Cirripedia species n										
Cirripedia species cl								0.03		
Elminius modestus								0.09		
Cirripedia species e										
Chironomidae species larva										
species 7										
n.i.										

Appendix 10.

Beyst, B., J. Mees, & A. Cattrijsse (1999). Early postlarval fish in the hyperbenthos of the Dutch Delta (south-west Netherlands). Journal of the Marine Biological Association of the United Kingdom 79, 709-724.

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Early postlarval fish in the hyperbenthos of the Dutch Delta (south-west Netherlands)

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Early (post)larval fish constitute a significant part of the temporary hyperbenthos, i.e. of the fauna living in the lower reaches of the water column close to the substratum. Information on the densities and spatial and temporal variations of these stages, as well as on their lengths at the moment of occurrence, can be an important contribution to the knowledge of their dispersion, migrations and to the identification of possible bottlenecks in their recruitment. Therefore the hyperbenthos of the Voordelta, a shallow coastal zone in front of the Dutch Delta, as well as that of the subtidal channels and the intertidal brackish marsh creeks of the Westerschelde Estuary, was sampled monthly during one year by means of a sledge and a stow net. A total of 37 taxa were recorded from 410 samples. Densities often exceeded 400 ind 1000 m^{-2} in the Voordelta and 300 ind 1000 m^{-2} in the Westerschelde, including the tidal marshes of Waarde and Saeftinghe. The dominant taxa were clupeid larvae (predominantly herring *Clupea harengus* and sprat *Sprattus sprattus*), *Pomatoschistus* spp. (a mixture of sand goby *P. minutus* and Lozano's goby *P. lozanoi*), common goby *Pomatoschistus microps*, *Syngnathus* spp. (probably almost exclusively Nilsson's pipefish *S. rostellatus*), plaice *Pleuronectes platessa*, sole *Solea solea* and flounder *Pleuronectes flesus*. Most species were found at a larger size in the Westerschelde (and in the tidal marshes) suggesting migration from the shallow coastal area into the estuary. Several species utilize the tidal marshes in the brackish reaches of the Westerschelde. The nursery value of these areas however, is restricted to specific early life history stages of a few species, especially flounder, bass *Dicentrarchus labrax* and the common goby. The estuary itself seems to function as a nursery for other species like sole and plaice. The hyperbenthic sledge was found to sample specific life history stages of postlarval flatfish (early settlement stages at the onset of asymmetry), which are not easy to sample with other types of sampling gear.

INTRODUCTION

Shallow coastal areas and estuaries have long been acknowledged as providing nurseries for marine teleosts (e.g. Gunter, 1961; Creutzberg & Fonds, 1971; Blaber, 1987). The distribution of larval fish towards these areas is controlled by both active behaviour and passive transport mechanisms, resulting from a combination of biotic and abiotic factors (Norcross & Shaw, 1984). Variability in abundance of early life stages can have important consequences for the dynamics of nekton populations and communities in estuarine and shallow near-shore environments (Kneib, 1997). Nekton that reside in estuaries and nearshore habitats often produce demersal eggs and young (Haedrich, 1983) that are unlikely to be affected by mortality factors operating within the pelagic environment. Variability during the early life stages of these species however, has not received much attention, particularly in estuaries. Permanent resident species often reside in shallow vegetated habitats, and so they and their young may not be well represented in trawl or plankton samples taken in deeper estuarine waters. As a result, they are often ignored components of the estuarine nekton assemblage (Kneib, 1997).

This study focuses on the distribution and abundance of (post)larval fish in the shallow coastal area in front of the mouth of the rivers Rhine, Meuse and Schelde (the Voordelta) and of the Westerschelde Estuary. Already in the early 1970s, the Westerschelde was, besides the Wadden Sea and some other estuaries, recognized as a nursery area for the North Sea populations of flatfish, clupeids and gadoids (Creutzberg & Fonds, 1971; Zijlstra, 1972). At the end of the seventies, the nursery function for commercially important species such as sole *Solea solea*, dab *Limanda limanda*, plaice *Pleuronectes platessa* and shrimp *Crangon crangon*, was emphasized (De Veen et al., 1979).

More specifically, the focus is on the so-called 'hyperbenthic' phase of fish. The hyperbenthos is a term applied to the association of small animals living in the water layer close to the substratum (Mees & Jones, 1997). Permanently hyperbenthic animals spend variable periods of their adult life in the hyperbenthos, while temporary hyperbenthic species (merohyperbenthos; Hamerlynck & Mees, 1991) spend only part of their early life history in the hyperbenthal. Teleost fish have been found to be a prominent member of the merohyperbenthos (e.g. Hesthagen, 1973; Jahn & Lavenberg, 1986; Hamerlynck & Mees, 1991; Cattrijsse et al., 1994). The hyperbenthos of soft bottoms is usually sampled with sledges. The fish larvae present in such samples are rarely studied as such. Still, since the hyperbenthic sledges seem to sample specific life history stages of postlarval (flat)fish which are not easy to sample with other types of sampling gear (see below), information on the densities and spatial and temporal variations of these stages can be an important contribution to the knowledge of their dispersion, migrations and to the identification of possible bottlenecks in their recruitment. To understand interannual recruitment variability, it is necessary to focus on early life history stages that are subject to intense mortality (Hjort, 1914; May, 1974; Blaxter, 1988; Bailey & Houde, 1989). The importance of mortality occurring in later larval stages and early juveniles has been stressed by several authors (e.g. Sissenwine, 1984; Smith, 1985; Folkvord & Hunter, 1986; Peterman et al., 1988). Larger fish larvae have been shown to be especially abundant in the near-bottom water layers; the fine-scale zonation patterns and depth distribution of fish larvae are discussed in Brewer & Kleppel (1986) and Jahn & Lavenberg (1986).

In order to assess horizontal seasonal migrations and recruitment patterns, the spatial and temporal variability and the length–frequency distributions of the dominant species are investigated. The possible nursery function of the estuary and its tidal marshes is discussed.

MATERIALS AND METHODS

Study area

The Voordelta is the shallow coastal area that stretches from the Dutch–Belgian border in the south to the Hoek van Holland in the north. Offshore, the area is arbitrarily defined by the mean tidal level (MTL)—15 m depth contour. The study area only covers the central part of the Voordelta at the mouth of the former Grevelingen (closed in 1971) and Oosterschelde estuaries. The Grevelingen now is a closed brackish lake separated by a dam from the open sea, while the Oosterschelde is a marine bay which has an open connection with the Voordelta through a storm surge barrier. The abiotic environment of the Voordelta is discussed in Louters et al. (1991).

The Westerschelde Estuary is the lower seaward part of the River Schelde. The maritime zone of the tidal system is about 70 km long from the North Sea (Vlissingen) to the Dutch–Belgian border near Bath. The Westerschelde is the last remaining true estuary in the Delta area and is characterized by a marked salinity gradient. The abiotic environment is discussed in Van Eck et al. (1991) and Heip (1988, 1989).

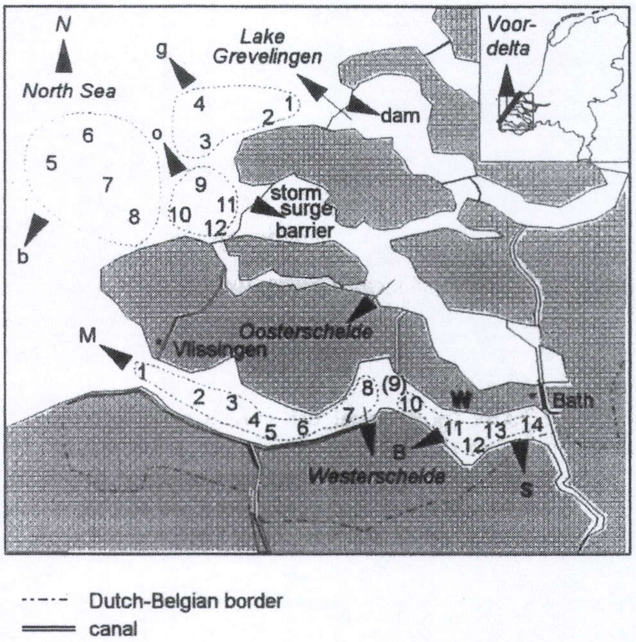

Figure 1. Study area with the sampling localities: g, ebb-tidal delta of the Grevelingen (VD G); o, ebb-tidal delta of the Oosterschelde (VD O); b, Banjaard area (VD B); M, marine part of the Westerschelde (WS M); B, brackish part of the Westerschelde (WS B); W, tidal marsh of Waarde (TM W), S, tidal marsh of Saeftinghe (TM S).

Two tidal marshes of the Westerschelde were sampled. The tidal marsh of Waarde (107 ha) is an elongated marsh situated on the right bank of the estuary. It is drained by one major creek that runs parallel to the main channel of the estuary. The tidal marsh of Saeftinghe (2760 ha), situated on the left bank north of the harbour of Antwerp, is one of the largest brackish marshes of

Table 1. *Sampling dates per area (VD, Voordelta; WS, Westerschelde; TM W, tidal marsh of Waarde; TM S, tidal marsh of Saeftinghe).*

Year	Area	J	F	M	A	M	J	J	A	S	O	N	D
1988	VD								*	*		*	*
	WS												
	TM W												
	TM S												
1989	VD	*	*	*	*	*	*	*					
	WS												
	TM W												
	TM S												
1990	VD												
	WS				*	*	*	*	*	*	*	*	*
	TM W		*	*	*	*	*	*	*		*	*	*
	TM S		*	*	*	*	*	*	*		*	*	*
1991	VD												
	WS	*	*	*	*								
	TM W	*	*	*	*	*	*		*				
	TM S	*		*	*	*	*	*	*				

*, sampling.

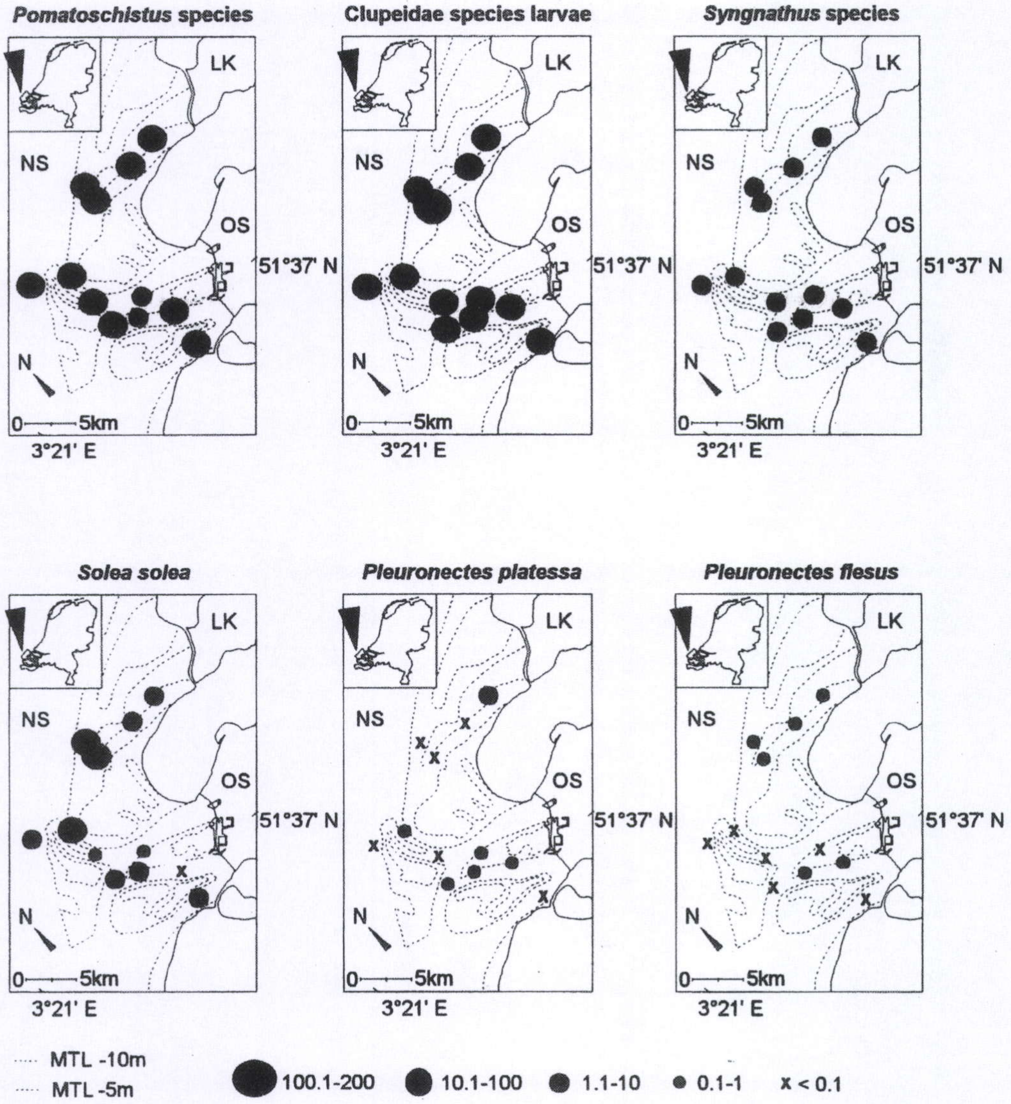

Figure 2. Geographical distribution of the dominant species for the Voordelta (NS, North Sea; LK, Lake Grevelingen; OS, Oosterschelde). Densities are yearly averages of the numbers of individuals caught per trawl (ind 1000 m^{-2}).

Europe. It is drained by several large creeks that run perpendicular to the main estuarine channel.

Sampling sites and sampling regime

Between August 1988 and July 1989, eleven surveys were conducted at approximately monthly intervals in 12 localities in the Voordelta: stations 1–4 in the ebb-tidal delta of the Grevelingen, stations 8–12 in the ebb-tidal delta of the Oosterschelde and stations 5–7 in the more seaward Banjaard area in-between both ebb-tidal deltas (Figure 1). At each station two samples were taken: one in the gully at a depth of about MTL (10 m) and one on the sandbank slope at a depth of about MTL (5 m), thus yielding 24 samples per sampling campaign (Table 1). As no consistent differences were found between these two depth strata, the numbers of individuals caught in both samples were pooled and divided by two for the purpose of this paper. In the Westerschelde 13 surveys were conducted from April 1990 to April 1991. On each occasion 14 stations were sampled along the salinity gradient (Mees et al., 1993a). All samples were taken in the subtidal channels. Where possible, the MTL (10 m) isobath was followed. Besides the subtidal surveys, monthly samples were taken at two intertidal stations in the tidal marshes of Saefthinge and Waarde (S and W in Figure 1) from March 1990 to November 1990. In Waarde, samples were taken in the main creek, while in Saeftinghe the easternmost major creek was selected (Cattrijsse et al., 1994). An overview of all sampling dates is presented in Table 1.

All samples were taken during daytime. The subtidal samples in the Voordelta and the Westerschelde were collected with a hyperbenthic sledge (Hamerlynck & Mees, 1991) according to Mees et al. (1993a). The tidal marsh samples were taken passively with a fyke net according to Cattrijsse et al. (1994). The use of different sampling techniques and the different sampling periods should be kept in mind when comparison between the regions are made.

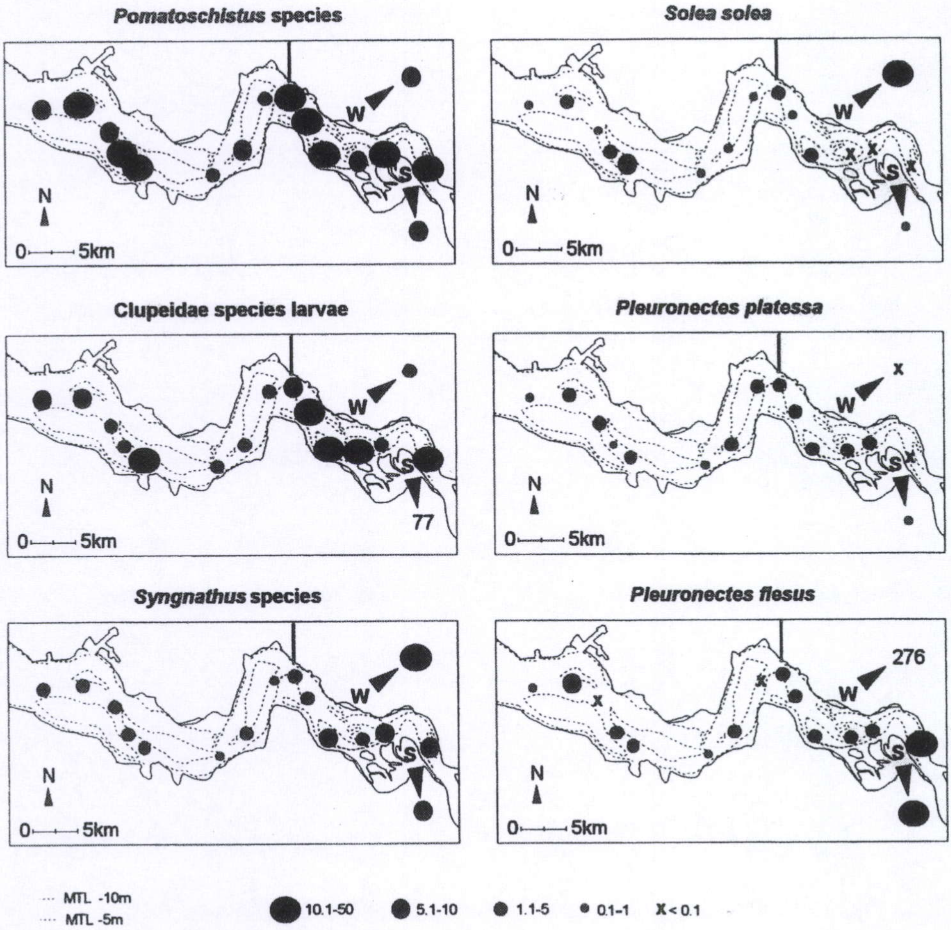

Figure 3. Geographical distribution of the dominant species for the Westerschelde, including tidal marshes of Saeftinghe (S) and Waarde (W). Densities are yearly averages of the numbers of individuals caught per trawl (ind 1000 m^{-2}).

All samples were immediately preserved in a buffered formaldehyde solution, 7% final concentration. During sampling, temperature and salinity of the water were measured near the bottom. For temperature and salinity values we refer to Hamerlynck & Mees (1991) for the Voordelta, Mees et al. (1993b, in press) for the Westerschelde and Cattrijsse et al. (in press) for the tidal marshes.

Treatment of samples and data analysis

In the laboratory all fish were sorted, identified, counted and measured (standard length (SL): the distance between the tip of the lower jaw and the end of the notochord). Shrinkage caused by formalin preservation was not taken into account, but all samples were preserved for at least 1 y prior to analysis in order to stabilize the shrinkage process. Shrinkage can thus be assumed to be equal for all individuals of the same species. The nomenclature proposed by Wheeler (1992) was followed. Most organisms were identified to species level, except the (post)larvae of Clupeidae (probably a mixture of herring *Clupea harengus* and sprat *Sprattus sprattus*), *Pomatoschistus* spp. (a mixture of sand goby *P. minutus* and Lozano's goby *P. lozanoi*) and *Syngnathus* spp. (probably exclusively Nilsson's pipefish *S. rostellatus*; possibly some greater pipefish *S. acus*). The identification keys of Nichols (1971, 1976), Russell (1976) and Nijssen & De Groot (1987) were used. Gobies were identified according to Hamerlynck (1990). All gobies smaller than 20 mm and all clupeids smaller than 40 mm (metamorphosis of herring takes place around 48–50 mm and that of sprat around 32–41 mm; Russell, 1976) were not identified to species level (except for *Pomatoschistus microps*) and were grouped as 'larvae'. Information available about the species composition of the demersal fish fauna of the Voordelta and the Westerschelde (Hamerlynck et al., 1992, 1993; Hostens & Hamerlynck, 1994; Hostens, in press) facilitated the identification process and allowed for the (hypothetical) characterization of the amalgam 'species groups' described above. Length–frequency distributions are only reported when more than 30 individuals were measured.

Other faunal components of the hyperbenthos included mysids, euphausiids, amphipods, larval decapods, fish eggs, isopods, cumaceans, chaetognaths and a variety of other less abundant groups. For full species lists of the hyperbenthos of the Voordelta, the Westerschelde and the tidal marshes, we refer to Hamerlynck & Mees (1991), Mees & Hamerlynck (1992), Mees et al. (1993b, in press) and Cattrijsse et al. (1994, in press). The distribution patterns of several crustacean groups (Mysidacea, Euphausiacea, Amphipoda and Isopoda) are discussed in detail in Cattrijsse et al. (1993) and Mees et al. (1993a).

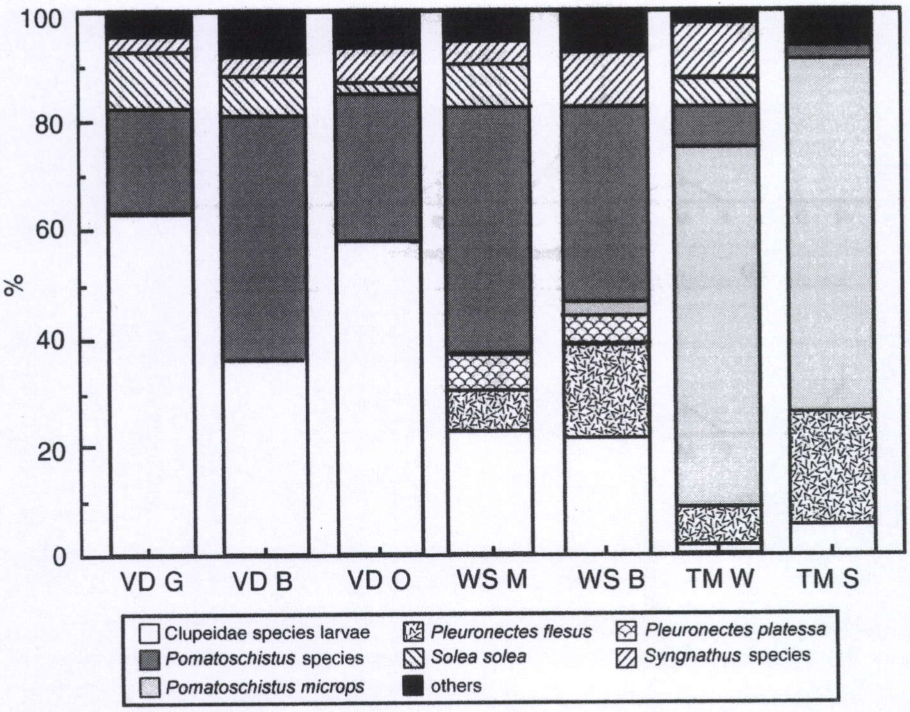

Figure 4. Community composition per subarea (VD G, ebb-tidal delta of the Grevelingen; VD B, Banjaard area; VD O, ebb-tidal delta of the Oosterschelde; WS M, marine part of the Westerschelde; WS B, brackish part of the Westerschelde; TM W, tidal marsh of Waarde; TM S, tidal marsh of Saeftinghe).

Reported densities in each station are the average numbers of individuals per sample taken in that station (ind 1000 m^{-2}) averaged over the whole study period. For the tidal marsh samples, densities were calculated for each hourly sample. Both the cumulative densities of the flood samples and the tidal flood volume were used to estimate an overall abundance present in the marsh at the moment of high water. Applying the same procedure with the ebb samples provided another estimate of the densities present at high water. Both results were subsequently averaged and used as the reported density for a particular sampling date. For more information about hourly temporal trends we refer to Cattrijsse (1994).

The temporal patterns in the densities of the fish populations are presented as the variation of average densities over all stations per area (Voordelta, Westerschelde) per sampling campaign. In order to further describe the migrations and seasonal patterns, both environments are divided into a total of seven regions (three in the coastal marine environment of the Voordelta, two in the estuarine channel environment of the Westerschelde and the two tidal marshes) based on descriptive multivariate community analyses in previous work (both classification and direct ordination techniques: Hamerlynck & Mees, 1991; Mees & Hamerlynck, 1992; Cattrijsse et al., in press; Mees et al., 1993b, in press). The Voordelta is divided into three regions, each comprising four stations: the ebb-tidal delta of the Grevelingen (stations 1–4), the Banjaard area (stations 5–8) and the ebb-tidal delta of the Oosterschelde (stations 9–12). The main channel of the Westerschelde Estuary is divided into a western and eastern part. The marine channel region of the estuary (west) comprises the eight downstream stations and the brackish channel region (east) comprises stations 10–14. Station 9 represents a transitional situation between the two communities and was eliminated for the purpose of this analysis. The seasonal variations in abundance in the tidal marshes of Waarde and Saeftinghe are also presented separately.

RESULTS

Species composition

A total of 37 taxa of teleost fish were recorded from the 410 hyperbenthos samples analysed for this study (Appendix 1). Total densities often exceeded 400 ind 1000 m^{-2} in the Voordelta (maximum of 4430 ind 1000 m^{-2} in station 3 in June) and 300 ind 1000 m^{-2} in the Westerschelde (maximum of 456 ind 1000 m^{-2} in station 14 in April) including the marshes (maximum of 4979 ind 1000 m^{-2} in the marsh of Saeftinghe in April).

Several species were restricted to one or more subarea(s) (Appendices 1 & 2). Of the species that were only found in the Westerschelde (including the marshes), thick-lipped grey mullet *Chelon labrosus*, zander *Stizostedion lucioperca*, nine-spined stickleback *Pungitius pungitius* and bleak *Alburnus alburnus* were restricted to the tidal marsh of Saeftinghe (*C. labrosus* also occurred in the marsh of Waarde). Of the species that occurred in the Westerschelde, lampern *Lampetra fluviatilis*, cod *Gadus morhua*, bib *Trisopterus luscus*, bull-rout *Myoxocephalus scorpius*, sea-snail *Liparis liparis*, butterfish *Pholis gunnellus*, *Hyperoplus lanceolatus*, dragonet *Callionymus lyra* and dab *Limanda limanda*

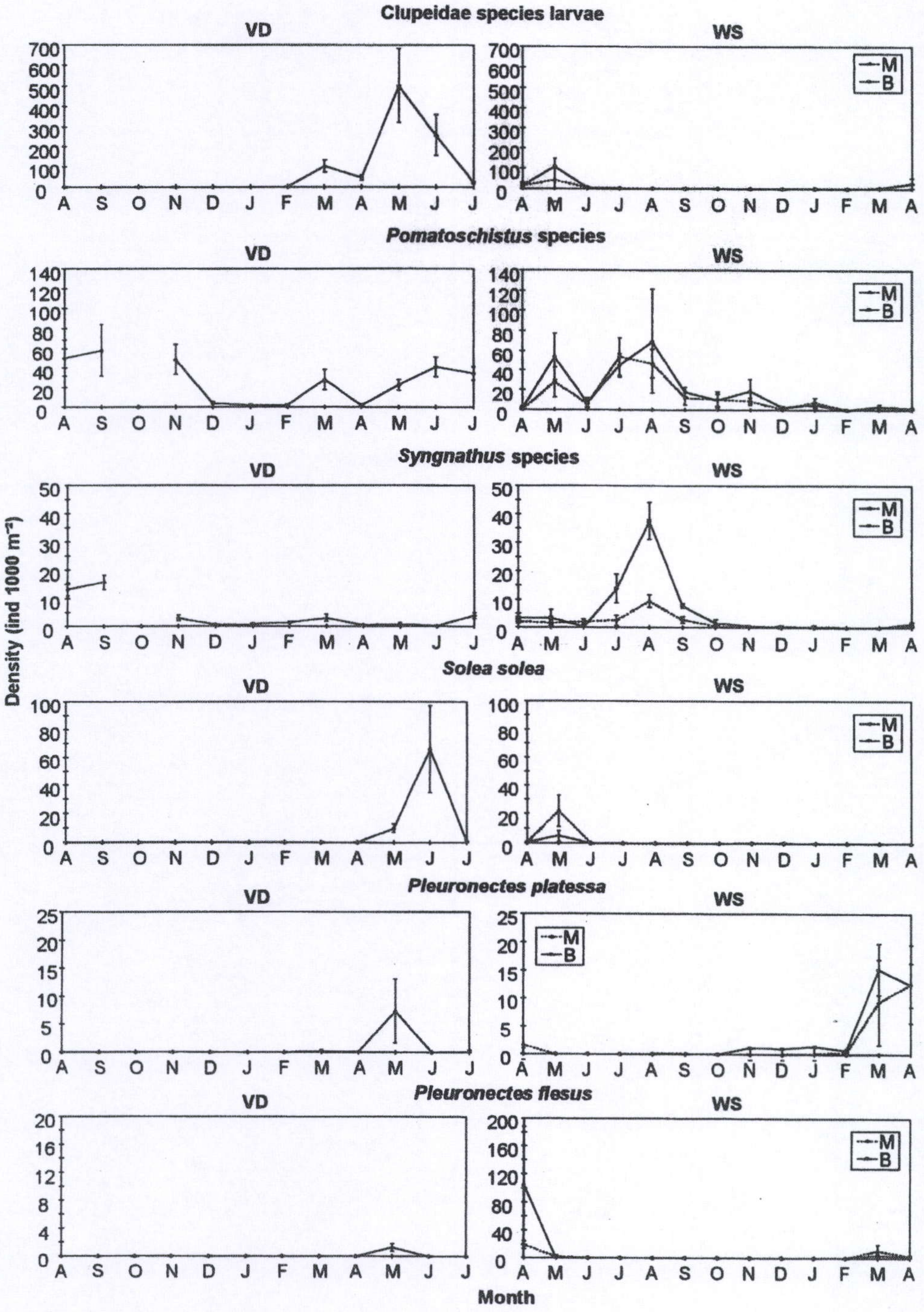

Figure 5. Seasonal variation of the numbers of individuals (average ±SE over all stations per month) of the dominant species for the Voordelta (VD) and the Westerschelde (WS) (M, marine part of the Westerschelde; B, brackish part of the Westerschelde).

were never recorded from the marshes. The bulk of the species however occurred in every region, although most were only present in certain seasons or showed clear preferences for specific regions.

The dominant taxa (mean densities >5% of the total community in one or several of the regions) were: (1) Clupeidae spp. larvae; (2) *Pomatoschistus* spp. larvae; (3) *Syngnathus* spp.; (4) common goby *P. microps* and the flatfish (5) sole *Solea solea*; (6) plaice *Pleuronectes platessa* and (7) flounder *Pleuronectes flesus*. Only these species will be discussed further (data of the common goby are not figured).

Geographical distribution and abundance

The geographical distribution and densities of the dominant species are presented separately for the Voordelta (Figure 2) and the Westerschelde (Figure 3), the community composition of each region (yearly averages) in Figure 4.

In the Voordelta (Figures 2 & 4), total average densities per station were never higher than 400 ind $1000\,m^{-2}$. Densities were significantly higher in the more sheltered area of the ebb-tidal delta of the Grevelingen and lower in the more dynamic ebb-tidal delta of the Oosterschelde

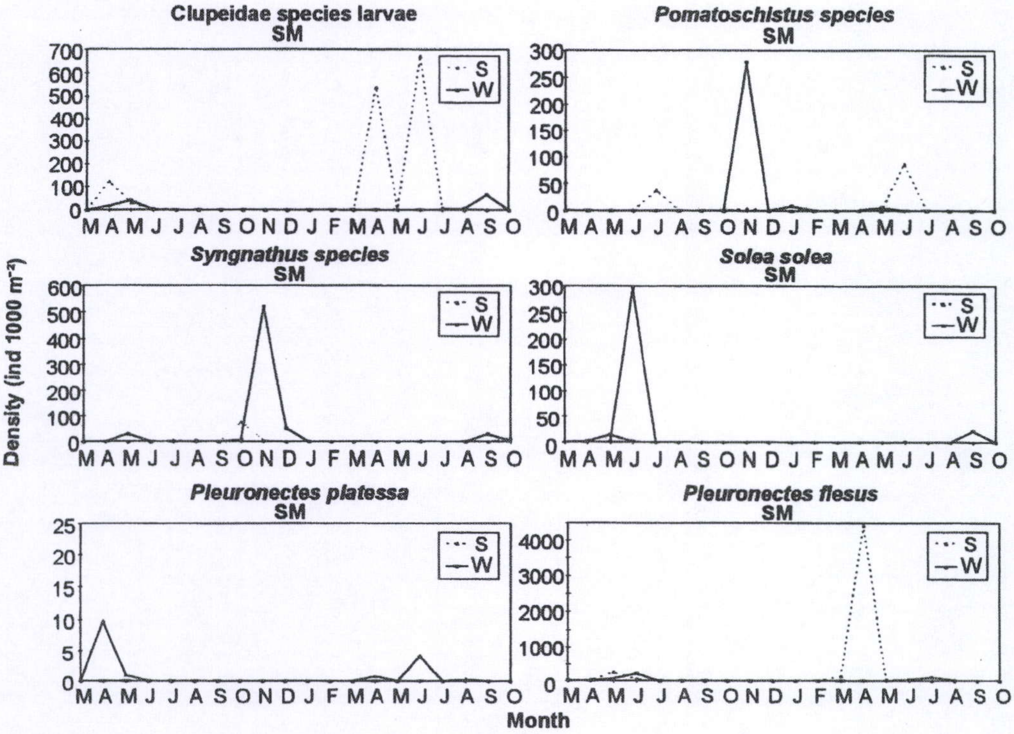

Figure 6. Seasonal variation of the numbers of individuals (monthly average of the estimated numbers present at ebb and flood tide, see also material and methods) of the dominant species for the tidal marshes. SM, salt marsh; S, marsh of Saeftinghe; W, marsh of Waarde.

(Appendix 2). Since the data were not normally distributed, testing for differences between total average densities was done with a Kruskal–Wallis Test ($P<0.05$), and subsequent multiple comparison tests according to Conover (1980) (without accumulation of α-error). The Banjaard stations were characterized by intermediate densities. Clupeid larvae was the most abundant taxon (45 ±13 ind $1000\,m^{-2}$), followed by *Pomatoschistus* spp. (21 ±3 ind $1000\,m^{-2}$) and sole (7 ±4 ind $1000\,m^{-2}$). The three taxa had overlapping geographical distributions. The common goby did not occur in the Voordelta. In all three regions of the Voordelta (Figure 4), clupeid larvae and *Pomatoschistus* spp. represented >80% of the fish communities.

Total average densities per station of the Westerschelde were never higher than 150 ind $1000\,m^{-2}$. In the five most downstream stations (marine channel region) and in the six most upstream stations (brackish channel region) of the estuary, total densities were on average higher than in the three remaining stations in the middle reaches. *Pomatoschistus* spp. and clupeid larvae were the most important organisms (densities of 15 ±3 and 9 ±2 ind $1000\,m^{-2}$, respectively) (Figures 3 & 4). They had comparable geographical distributions: high densities were recorded in the marine channel region and in the brackish channel region, while in stations 6–8 densities were much lower. *Syngnathus* spp. and the common goby seemed to prefer the more brackish part of the Westerschelde, while sole was more abundant in the marine reaches. In both the marine and brackish parts of the Westerschelde (Figure 4), *Pomatoschistus* spp. dominated the community (45.1% in the marine part and 32.5% in the brackish part), followed by clupeid larvae (23.2 and 20.3% respectively).

In the tidal marshes (Figures 3 & 4) the common goby was the most abundant species (533±17 ind $1000\,m^{-2}$), followed by flounder (151±17 ind $1000\,m^{-2}$). *Pomatoschistus* spp., *Syngnathus* spp. and sole occurred in higher densities in the tidal marsh of Waarde than in the marsh of Saefthinghe, while this was the opposite for the other species. Plaice were absent from the marsh of Waarde and only occurred in low densities in the marsh of Saeftinghe (0.89 ind $1000\,m^{-2}$). The communities of both marshes were dominated by the common goby (±65% of the community) (Figure 4).

Temporal distribution patterns

In spring, plaice appeared first, with maximal densities in March in the Westerschelde and in May in the Voordelta (Figures 5 & 6). Then flounder was recorded with a peak in April (Westerschelde), followed by sole and clupeid larvae, with maximal abundances in May in the Westerschelde and in June in the Voordelta. *Syngnathus* spp. had their peak of abundance in August in the Westerschelde and in August–September in the Voordelta. Two peaks were observed for *Pomatoschistus* spp.: one (smaller) peak in May and one in June–August.

Length–frequency distributions

With a few exceptions, all flatfish caught were early (post)larval stages (Figure 7). Individuals just before or at the onset of asymmetry were clearly dominant. Hardly any planktonic yolk-sac larvae nor post-settlement demersal stages were caught. Monthly length–frequency distribution patterns of *Pomatoschistus* spp. revealed two peaks (not figured): one in May/July and one in August/October

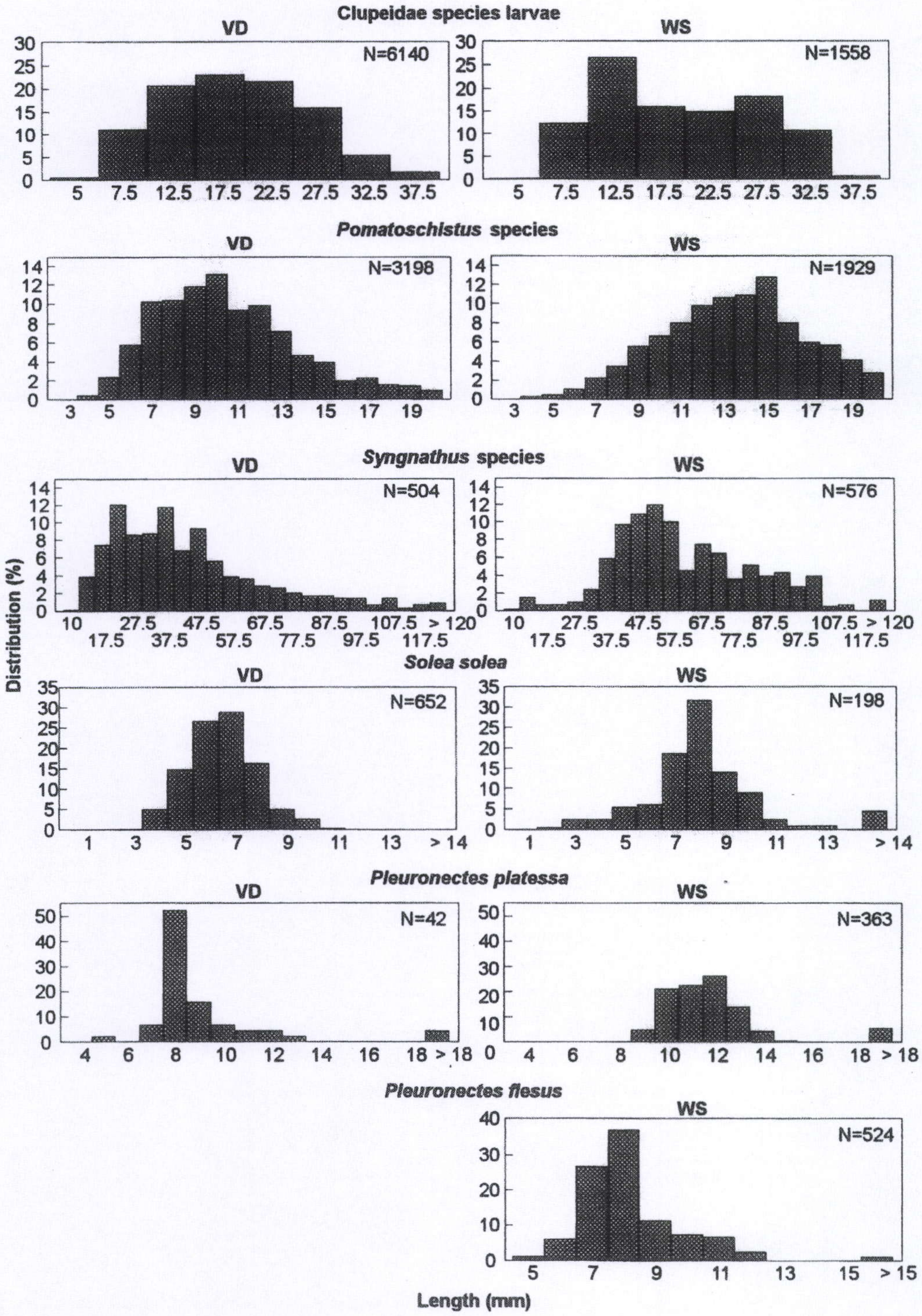

Figure 7. Length–frequency distributions of the dominant species for the Voordelta (VD) and the Westerschelde (WS) (N, total number of individuals measured).

(both around 10 mm SL in the Voordelta, while in the Westerschelde the modal length-class in May/July was 14 mm SL and in August/October two modal length classes were observed of respectively 15 mm SL and 18 mm SL). Monthly length–frequency distributions of *Syngnathus* spp. (not figured) revealed that from May through July individuals measured 22.5 mm in the Voordelta and 42.5 in the Westerschelde. During August/October the length–frequency distributions showed bimodal patterns: modal length-classes were found at 37.5 and 47.5 mm respectively in the Voordelta, while in the Westerschelde the modal length was 55 mm SL and a large number of individuals measured between 65 and 105 mm SL. In general, larger individuals were captured in the tidal marshes (Figure 8).

Mean lengths per month

Monthly length–frequency distributions were very narrow for most species, especially for the flatfish species sole, plaice and flounder (Appendix 3). Clear differences between months could be observed. Mean lengths of clupeid larvae revealed two possible recruitment peaks:

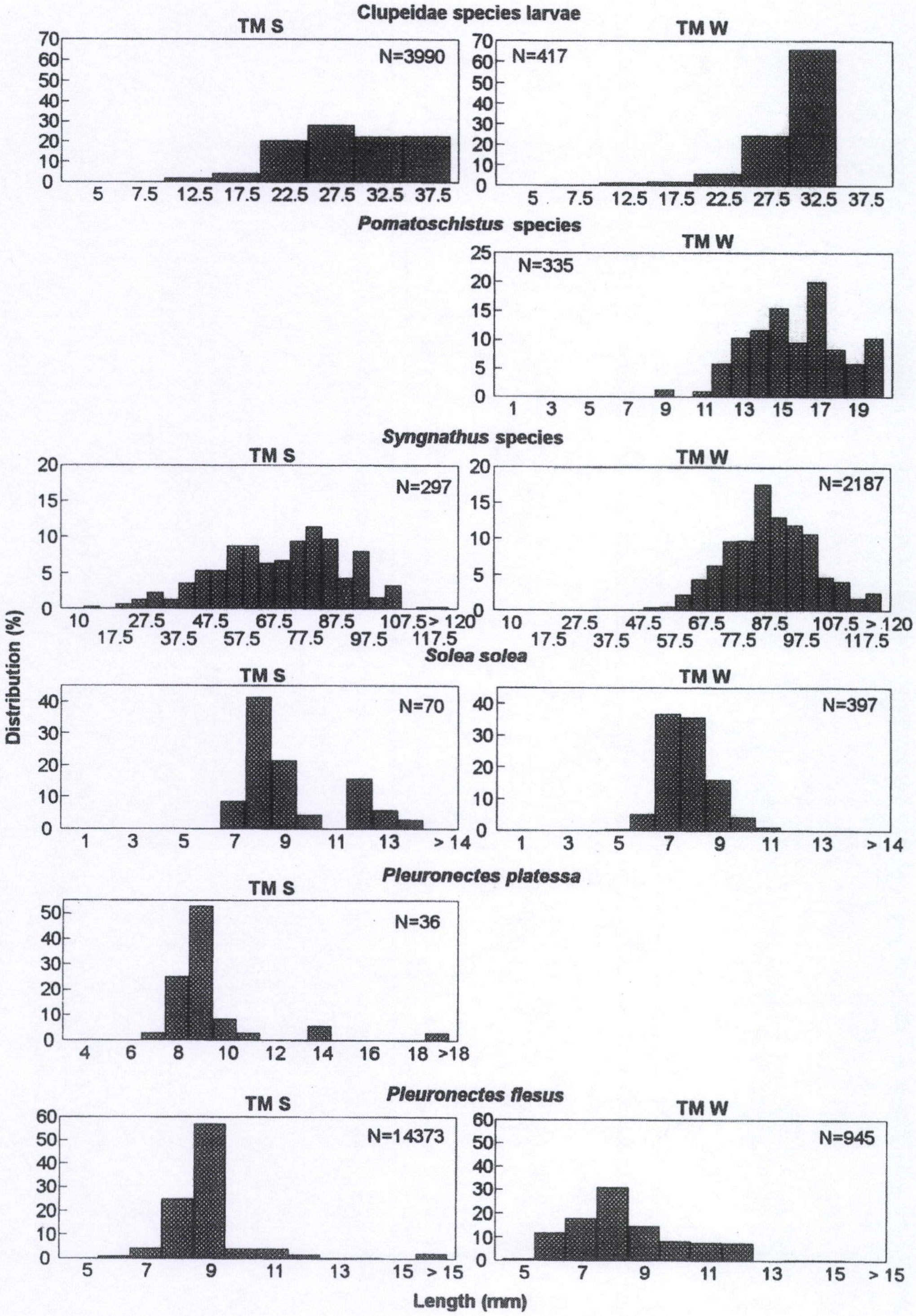

Figure 8. Length–frequency distributions of the dominant species for the tidal marshes (TM S, tidal marsh of Saeftinghe; TM W, tidal marsh of Waarde) (N, total number of individuals measured).

one before March and one in May (Westerschelde) and June (Voordelta) (14.13±0.15 and 13.67±0.09 mm SL, respectively). The same pattern was found for *Syngnathus* species: a first recruitment peak was observed before February and a second one in July (53.28±1.62 mm SL in the Westerschelde and 24.32±0.86 mm SL in the Voordelta). For most species, mean lengths were somewhat greater in the Westerschelde than in the Voordelta.

DISCUSSION

Spatial patterns

In general, average densities were higher in the shallow coastal environment than in the estuary, but also within these areas differences could be found. In the Voordelta, densities were significantly higher in the sheltered region (ebb-tidal delta of the Grevelingen) and lower in the dynamic ebb-tidal delta of the Oosterschelde. The

Banjaard stations were characterized by intermediate densities. These higher densities in the ebb-tidal delta of the Grevelingen can be explained by local current patterns and the higher primary production in this area (Hamerlynck & Mees, 1991). The area seems to act as a sink for passively transported material, e.g. silt, decaying phytoplankton, macrobenthic larvae and fish eggs with near neutral buoyancy. This creates a rich and varied benthic life that sustains high densities of demersal fish. Fish larvae and postlarvae may actively migrate to the area to profit from the high abundance of food (Creutzberg et al., 1978). Although the Banjaard has a rich epibenthic fauna, wave conditions there prevent sedimentation and preclude the establishment of rich macrobenthic communities. Despite being sheltered from the wave action, the ebb-tidal delta of the Oosterschelde has a poorer hyperbenthic fauna than the Grevelingen. The richer water masses of the Banjaard (and offshore) do not reach the area because they are flushed outwards at low tide by the relatively oligotrophic water from the Oosterschelde. Moreover, the high current velocities as attested by high seston loads, prevent sedimentation in the ebb-tidal delta of the Oosterschelde (Hamerlynck & Mees, 1991).

In the Westerschelde, densities were on average lower in the middle reaches than either downstream (marine) or upstream (brackish). This bimodal density pattern was also reported for a wide variety of ecosystem compartments and processes (primary production, zooplankton, macrobenthos, hyperbenthos and epibenthos; e.g. Hamerlynck et al., 1993; Soetaert et al., 1994). In the brackish part, the food web depends on the input of large amounts of organic matter from the land side (heterotrophic food chain), while the area close to the mouth of the estuary is characterized by a food chain based on local primary production (photoautotrophic food chain) (Hummel et al., 1988). Both subsystems also seem to support high densities at the higher trophic levels. The middle reaches of the estuary have been described as a 'nutrient rich desert', where most functional units display low biomass levels. The same (largely unexplained) pattern was observed for the fish larvae in this study (Hamerlynck et al., 1993).

Densities of several fish species were seasonally higher in the tidal marshes than in the main estuarine channel. Two hypotheses are commonly used to explain the high densities of species in tidal marshes: (1) the marsh creeks are used as foraging areas; and (2) function as predator refugia (Boesch & Turner, 1984). The exact reasons why metamorphosing stages of flatfish use the marshes as a nursery still remain unclear.

Most demersal fish species that are common in the adjacent reaches of the Westerschelde are absent from the marshes (Hostens, in press). The common goby spends the major part of its life cycle in the tidal creeks. Bass *Dicentrarchus labrax* and flounder were very abundant in the marshes and seem to utilize these habitats as a nursery (Cattrijsse, 1994). Of all other species recorded from the Westerschelde, only few were occasionally recorded in Waarde or Saeftinghe. The dominance of a small number of generalist species is a common feature of the fish fauna of tidal marshes (e.g. Cain & Dean, 1976; Haedrich, 1983; Weinstein & Brooks, 1983; Kneib, 1987; Sogard & Able, 1991).

The composition of the fish fauna of the tidal marsh of Waarde was quite different from that of Saeftinghe. In Waarde, 13 taxa were recorded. The common goby, *Syngnathus* spp., *Pomatoschistus* spp., flounder and sole dominated the fauna (>5%). In Saeftinge, 20 taxa were recorded. The common goby, flounder and clupeid larvae were the dominant taxa. When salinities increase in summer, typical marine species migrate into the estuary (Mees et al., 1993b). These species were hardly ever recorded from the tidal marsh of Saeftinghe, but some of them were present (sometimes even in high numbers) in the tidal marsh of Waarde (e.g. sole). Except for the obvious difference in salinity (salinity ranged between 15.5 and 26.1 psu in Waarde and between 3.4 and 16.1 psu in Saeftinghe), the different distance of both marshes to the main channel of the estuary can determine the accessibility for certain species (Figure 1). There seems to be a maximal distance that some species are willing to bridge to enter the marsh from the subtidal areas (Rozas, 1993). Good swimmers such as bass can probably resist the strong currents in the subtidal channel—which is very close to the marsh of Saeftinghe—and enter the creeks. In contrast, the presence of an extensive sandbank in front of the marsh of Waarde can give better possibilities to enter the marsh for species that prefer shallow and calmer waters (Cattrijsse, 1994).

Temporal patterns

In all regions, marked seasonal patterns were observed in the densities of the most common species: maximal numbers were recorded in spring and minimal numbers from late summer until late winter. Exceptions were *Syngnathus* (peak in late summer) and *Pomatoschistus* spp. (two peaks: one in spring and one in summer). The low numbers observed from summer onwards are probably mainly due to the absence of the specific life history stages that are sampled efficiently by the sledge and the fyke net: as the fish grow, their swimming capacities improve and they either migrate out of the area or recruit to the demersal, benthic or pelagic stocks.

Our results are in general agreement with current knowledge about the biology of the North Sea populations of the dominant species. Plaice is a winter spawner: eggs and larvae appear from December until March with peaks in January and early February. Postlarvae can generally be found until May (Russell, 1976). Still, some postlarvae were observed in June (Saeftinghe) and July (Voordelta). Flounder spawns from mid January until April in the southern parts of the North Sea and until July in the northern parts (Simpson, 1949). Off Plymouth, spawning took place from February until April (Clark, 1920) and postlarvae occurred from March to June (especially in April and May) (Clark, 1914; Russell, 1935). Spawning of sole occurs in the North Sea between April and August, especially in May (Russell, 1976). Postlarvae off Plymouth appeared in March to June with maxima in April and with the earliest observation in February (Russell, 1940). The clupeid larvae recorded in this study are probably a mixture of herring *Clupea harengus* and sprat *Sprattus sprattus*. The time of year at which postlarval herring are most abundant depends on whether the local stocks are spring or autumn spawners. In northern areas, the number of postlarvae generally increases in late spring and summer, while more to the south they mainly occur during late winter and early spring. The main spawning period of sprat occurs earlier in the south than in the north. Eggs have been recorded from January to July (Russell, 1976). De Silva (1973), in a study of the reproductive biology of the sprat on the west coast of Scotland, found that spawning lasted for five to six months starting in February to March. Most *Syngnathus* spp. recorded in this study are probably Nilsson's pipefish *S. rostellatus*. The eggs of greater pipefish *S. acus* appear from May until July, those of Nilsson's pipefish from June to August. The young of greater pipefish take immediately to a bottom life upon release from the parent, while those of Nilsson's pipefish are pelagic for a short period (a few weeks) (Russell, 1976), increasing their catchability with a sledge type gear. *Pomatoschistus* spp. are a mixture of sand goby *P. minutus* and Lozano's goby *P. lozanoi*, both of which are very abundant in the study area (Hamerlynck et al., 1993). The different recruitment periods of sand and Lozano's goby can largely explain the rather erratic abundance pattern observed in the Voordelta and the Westerschelde. In the Belgian coastal area, spawning periods are spring (March to June) and mid-summer (June to August) (Fonds, 1973; Hamerlynck et al., 1986), for sand and Lozano's goby respectively. Juveniles of both species are common in estuaries, even occurring at salinities as low as 5 psu (O. Hamerlynck, unpublished data) and only migrating to the sea in winter when temperatures drop below 2.5°C. If temperatures rise again above 3°C, they return to the estuary (Fonds, 1973). This might explain the low numbers observed in February in the Westerschelde.

It is striking that maximal abundance peaks always occurred earlier in the Westerschelde than in the Voordelta, except for clupeids. This is probably due to the fact that the two environments were sampled in different years (interannual variability).

Length–frequency distributions

For most species, individuals were smaller in the subtidal of the Voordelta than in the Westerschelde, suggesting either migrations from the coastal marine environment to the estuary, where the marshes and other intertidal areas are probably chosen as a habitat before recruiting to the subtidal population, or slower growth. For several species (e.g. clupeid larvae, *Pomatoschistus* and *Syngnathus* spp.), individuals were larger in the tidal marshes than in the other regions.

The hyperbenthic sledge and the fyke net obviously sampled predominantly specific pre-settlement stages of all three flatfish species: individuals just before or at the onset of asymmetry are clearly over-represented in the hyperbenthos. Recent evidence suggests that metamorphosis may play a significant role in modifying recruitment potential for some marine fish. In numerous fish species and especially flatfish, this period of metamorphosis may be characterized by extensive morphological, physiological, ecological and behavioural changes (Youson, 1988). There also appears to be a period of intense mortality associated with the completion of metamorphosis and settlement in several species of marine fish. Metamorphosis represents thus an important period with respect to recruitment (Keefe & Able, 1993).

The mean length of young flounders was larger in March (10–11 mm) than in April and May (around 8 mm) which suggests prolonged recruitment. Monthly length–frequency distributions of clupeid larvae were quite irregular. This may also result from several or prolonged recruitment periods and/or from the fact that we are dealing with a mixture of several species. Only one peak was observed in the Voordelta (June) at a mean length of about 14 mm. This was also reflected in the unimodal length–frequency distribution pattern of the pooled data (Figure 7). In contrast, two peaks were visible in the Westerschelde: one before March and one in May, which was again reflected in the pooled length–frequency distributions. In the Voordelta, two clear recruitment periods of *Pomatoschistus* species were revealed: one around June and one in August–September. This probably reflects the different spawning periods of sand and Lozano's goby. In the Westerschelde, this pattern is less obvious because of the smaller differences in mean length per month. Most of the smallest pipefish measured between 10 and 15 mm. Since greater and Nilsson's pipefish hatch at lengths of respectively 25–35 mm and 13–14 mm (Russel, 1976), this again confirms that they were most likely larvae of Nilsson's pipefish. The rather erratic patterns of the length–frequency distributions can again be due to the fact that more than one species was sampled. Further, it should be mentioned that—in contrast to most other species treated in this study—not only 'early postlarvae' of *Syngnathus* spp. were sampled: the length–frequency distributions show that a significant part of the population consisted of subadult (and even some adult) individuals.

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REFERENCES

Bailey, K.M. & Houde, E.D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, **25**, 1–83.

Blaber, S.J.M., 1987. Factors affecting recruitment and survival of mugilids in estuaries and coastal waters of southeastern Africa. *American Fisheries Society Symposia*, **1**, 507–518.

Blaxter, J.H.S., 1988. Pattern and variety in development. In *Fish physiology*, vol. XIA (ed. W.S. Hoar and D.J. Randall), pp. 1–58. New York: Academic Press.

Boesch, D.F. & Turner, R.E., 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries*, 7, 460–468.

Brewer, G.D. & Keppel, G.S., 1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. *Marine Ecology Progress Series*, **27**, 217–226.

Cain, R.L. & Dean, J.M., 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. *Marine Biology*, **36**, 369–379.

Cattrijsse, A., 1994. *Schorkreken in het brakke deel van het Westerschelde estuarium als habitat voor vissen en macrocrustacea.* PhD thesis, University of Gent, Belgium.

Cattrijsse, A., Makwaia, E.S., Dankwa, R.H., Hamerlynck, O. & Hemminga, M.A., 1994. Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Marine Ecology Progress Series*, **109**, 195–208.

Cattrijsse, A., Mees, J. & Hamerlynck, O., 1993. The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde Estuary. *Cahiers de Biologie Marine*, **34**, 187–200.

Cattrijsse, A., Mees, J., Hostens K. & Makwaia, E.S., in press. The aquatic fauna of two intertidal salt marsh creeks in the Westerschelde Estuary. *Belgian Journal of Zoology.*

Clark, R.S., 1914. General report on the larval and postlarval teleosteans in Plymouth waters. *Journal of the Marine Biological Association of the United Kingdom*, **10**, 327–394.

Clark, R.S., 1920. The pelagic young and early bottom stages of teleosteans. *Journal of the Marine Biological Association of the United Kingdom*, **12**, 159–240.

Conover, W.J., 1980. *Practical nonparametric statistics.* New York: John Wiley & Sons.

Creutzberg, F., Eltink, A.T. & Noort, G.J. van, 1978. The migration of plaice larvae *Pleuronectes platessa* into the Western Wadden Sea. In *Physiology and behaviour of marine organisms* (ed. D.S. McLusky and A.J. Berry), pp. 243–251. Oxford: Pergamon Press.

Creutzberg, F. & Fonds, M., 1971. The seasonal variation in the distribution of some demersal fish species in the Dutch Wadden Sea. *Thalassia Jugoslavica*, **7**, 13–23.

De Silva, S.S., 1973. Aspects of the reproductive biology of the sprat, *Sprattus sprattus* (L.), in inshore waters of the west coast of Scotland. *Journal of Fish Biology*, **5**, 689–705.

De Veen, J.F., Boddeke, R. & Postuma, K.H., 1979. Tien jaar kinderkamer-opnames in Nederland. I. Het Zeeuwse estuarium. *Visserij*, **32**, 3–23.

Folkvord, A. & Hunter, J.R., 1986. Size-specific vulnerability of northern anchovy, *Engraulis mordax*, to predation by fishes. *Fishery Bulletin. National Oceanic and Atmospheric Administration, Washington, DC*, **84**, 859–869.

Fonds, M., 1973. Sand gobies in the Dutch Wadden Sea (*Pomatoschistus*, Gobiidae, Pisces). *Netherlands Journal of Sea Research*, **6**, 417–478.

Gunter, G., 1961. Some relations of estuarine organisms to salinity. *Limnology and Oceanography*, **6**, 182–190.

Haedrich, R.L., 1983. Estuarine fishes. In *Ecosystems of the world.* Vol. 26. *Estuaries and enclosed seas* (ed. B.H. Ketchum), pp. 183–207. Amsterdam: Elsevier Scientific Publishing Company.

Hamerlynck, O., 1990. The identification of *Pomatoschistus minutus* (Pallas) and *Pomatoschistus lozanoi* (de Buen) (Pisces, Gobiidae). *Journal of Fish Biology*, **37**, 723–728.

Hamerlynck, O., Heip, C. & Redant, F., 1986. Life history, food consumption and food partitioning in two sympatric gobies *Pomatoschistus minutus* and *Pomatoschistus lozanoi* in the Belgian coastal waters. *International Council for the Exploration of the Sea (CM Papers and Reports)*, CM 1986/L:14, 19 pp.

Hamerlynck, O., Hostens, K., Mees, J., Arellano, R.V., Cattrijsse, A., Van de Vijver, P. & Craeymeersch, J.A., 1992. The ebb tidal delta of the Grevelingen: a man-made nursery for flatfish? *Netherlands Journal of Sea Research*, **30**, 191–200.

Hamerlynck, O. & Mees, J., 1991. Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. *Oceanologica Acta*, **11**, 205–212.

Hamerlynck, O., Mees, J., Craeymeersch, J.A., Soetaerts, K., Hostens, K., Cattrijsse, A. & Van Damme, P.A., 1993. The Westerschelde Estuary: two food webs and a nutrient rich desert. In *Progress in Belgian oceanographic research* (ed. J.C.J. Nihoul), pp. 217–234. Brussels: Institute of Marine Research and Air Sea Interaction.

Heip, C., 1988. Biota and abiotic environment in the Westerschelde Estuary. *Hydrobiological Bulletin*, **22**, 31–34.

Heip, C., 1989. The ecology of the estuaries Rhine, Meuse and Scheldt in the Netherlands. In *Topics in marine biology* (ed. J.D. Ross), pp. 457–463. [Scientia Marina, vol. no. 53.]

Hesthagen, I.H., 1973. Diurnal and seasonal variations in the near-bottom fauna—the hyperbenthos—in one of the deeper channels of the Kieler Bucht (western Baltic). *Kieler Meeresforschungen*, **26**, 1–10.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe. *Rapports et Procès-Verbaux des Réunions Conseil International Exploration de la Mer*, **20**, 1–227.

Hostens, K., in press. Spatial patterns and seasonality in the epibenthic communities of the Westerschelde (Southern Bight of the North Sea). *Belgian Journal of Zoology.*

Hostens, K. & Hamerlynck, O., 1994. The mobile epifauna of the soft bottoms in the subtidal Oosterschelde Estuary: structure, function and impact of the storm-surge barrier. *Hydrobiologia*, **282/283**, 479–496.

Hummel, H., Moerland, G. & Bakker, C., 1988. The concomitant existence of a typical coastal and a detritus food chain in the Westerschelde Estuary. *Hydrobiological Bulletin*, **22**, 35–41.

Jahn, A.E. & Lavenberg, R.J., 1986. Fine-scale distribution of nearshore, suprabenthic fish larvae. *Marine Ecology Progress Series*, **31**, 223–231.

Keefe, M. & Able, K.W., 1993. Patterns of metamorphosis in summer flounder, *Paralichthys dentatus*. *Journal of Fish Biology*, **42**, 713–728.

Kneib, R.T., 1987. Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology*, **68**, 379–386.

Kneib, R.T., 1997. Early life stages of resident nekton in intertidal marshes. *Estuaries*, **20**, 214–230.

Louters, T., Mulder, J.P.M., Postma, R. & Hallie, F.P., 1991. Changes in coastal morphological processes due to the closure of tidal inlets in the SW netherlands. *Journal of Coastal Research*, **7**, 635–652.

May, R.C., 1974. Larval mortality in marine fishes and the critical period concept. In *The early life history of fish* (ed. J.S. Blaxter), pp. 3–19. New York: Springer-Verlag.

Mees, J., Cattrijsse, A. & Hamerlynck, O., 1993a. Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, southwest Netherlands. *Cahiers de Biologie Marine*, **34**, 165–186.

Mees, J., Dewicke, A., Cattrijsse, A., Fockedey, N. & Hostens, K., in press. Seasonality in hyperbenthic communities of the Westerschelde Estuary. *Belgian Journal of Zoology.*

Mees, J., Dewicke, A. & Hamerlynck, O., 1993b. Seasonal composition and spatial distribution of hyperbenthic communities along estuarine gradients in the Westerschelde. *Netherlands Journal of Aquatic Ecology*, **27**, 359–376.

Mees, J. & Hamerlynck, O., 1992. Spatial community structure of the winter hyperbenthos of the Schelde Estuary, the Netherlands, and the adjacent coastal waters. *Netherlands Journal of Sea Research*, **29**, 357–370.

Mees, J. & Jones, M.B., 1997. The hyperbenthos: a review. *Oceanography and Marine Biology. Annual Review*, **35**, 221–255.

Nichols, J.H., 1971. Peuronectidae. *Fiches d'Identification des Oeufs et Larves de Poissons*, **4/6**, 1–18.

Nichols, J.H., 1976. Soleidae of the eastern North Atlantic. *Fiches d'Identification du Zooplancton*, **150/151**, 1–10.

Nijssen, H. & De Groot, S.J., 1987. *De vissen van Nederland.* Utrecht: Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging.

Norcross, B.L. & Shaw, R.F., 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of the American Fisheries Society*, **113**, 153–165.

Peterman, R.M., Bradford, M.J., Lo, N.C.H. & Methot, R.D., 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 8–16.

Rozas, L.P., 1993. Nekton use of salt marshes of the southeast region of the United States. Coastal Zone '93. *Proceedings of the Eighth Symposium on Coastal and Ocean Management*, 528–537.

Russell, F.S., 1935. The seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the ring-trawl in offshore waters in the Plymouth area. Part II. *Journal of the Marine Biological Association of the United Kingdom*, **20**, 147–179.

Russell, F.S., 1940. On the seasonal abundance of young fish VII. The year 1939, January to August. *Journal of the Marine Biological Association of the United Kingdom*, **24**, 265–270.

Russell, F.S., 1976. *The eggs and planktonic stages of British marine fishes*. London: Academic Press.

Simpson, A.C., 1949. Notes on the occurrence of fish eggs and larvae in the Southern Bight of the North Sea during the winter of 1947–48. *Annales Biologique*, **5**, 90–97.

Sissenwine, M.P., 1984. Why do fish populations vary? In *Exploration of marine communities* (ed. R.M. May), pp. 59–94. New York: Springer-Verlag.

Smith, P.E., 1985. Year-class strength and survival of 0-group clupeids. *Canadian Journal of Fisheries and Aquatic Science*, **42**, supplement 1, 69–82.

Soetaert, K., Herman, P.M.J. & Kromkamp, J., 1994. Living in the twilight: estimating net phytoplankton growth in the Westerschelde estuary (The Netherlands) by means of an ecosystem model (MOSES). *Journal of Plankton Research*, **16**, 1277–1301.

Sogard, S.M. & Able, K.A., 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine and Coastal Shelf Science*, **33**, 501–519.

Van Eck, G.T.M., De Pauw, N., Van Den Langenbergh, M. & Verreet, G., 1991. Emmissies, gehalten, gedrag en effecten van, micro-verontreinigingen in het stroomgebied van de Schelde en het Schelde-estuarium. *Water*, **60**, 164–181.

Weinstein, M.P. & Brooks, H.A., 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. *Marine Ecology Progress Series*, **12**, 15–27.

Wheeler, A., 1992. A list of the common and scientific names of fishes of the British Isles. *Journal of Fish Biology*, **41**, 1–37.

Youson, J.H., 1988. First metamorphosis. In *Fish physiology*, vol. XIB (ed. W.S. Hoar and D.J. Randall), pp. 135–196. New York: Academic Press.

Zijlstra, J.J., 1972. On the importance of the Waddensea as a nursery area in relation to the conservation of the southern North Sea fishery resources. *Symposia of the Zoological Society of London*, **29**, 233–258.

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Appendix 1. *List of species recorded, with indication of their distribution and average density in the different subareas and seasons (see also text).*

Order	Species and stage	Area	Month	Density	Remarks
Petromyzontiformes	*Lampetra fluviatilis* (Linnaeus, 1758)	WSB	Mar	—	
Anguilliformes	*Anguilla anguilla* (Linnaeus, 1758)	VDO/WSM, WSB/TMW, TMS	Feb/occ/all	—/—/—	peak in spring
Clupeiformes	*Clupeidae* spp. larvae	VDG > VDB, VDO/WSM < WSB/TMW < TMS	Mar–Jul	***/*/***	peaks in May/June
	Clupea harengus (Linnaeus, 1758)	WSM < WSB/TMW ≪ TMS	all	—/**	
	Sprattus sprattus (Linnaeus, 1758)	WSM < WSB/TMS	all	+/**	
Cypriniformes	*Alburnus alburnus* (Linnaeus, 1758)	TMS	Mar	—	freshwater species
Gadiformes	*Ciliata mustela* (Linnaeus, 1758)	VDB	Jul	—	
	Gadus morhua (Linnaeus, 1758)	WSM < WSB	May	—	
	Merlangius merlangus (Linnaeus, 1758)	VDG, VDB, VDO/WSM/TMS	Apr–Jul	—/—/—	
	Pollachius pollachius (Linnaeus, 1758)	VDG	May	—	
	Trisopterus luscus (Linnaeus, 1758)	VDG > VDB, VDO/WSM, WSB	May–Jul/occ	—/—	peak in June
	Trisopterus minutus (Linnaeus, 1758)	VDB	May	—	
Atheriniformes	*Atherina presbyter* (Cuvier, 1829)	VDG/WSB/TMW, TMS	Sep–Nov	—/—/—	
Gasterosteiformes	*Gasterosteus aculeatus* (Linnaeus, 1758)	VDO/WSM, WSB/TMW > TMS	Jul/occ/all	—/—/+	
	Pungitius pungitius (Linnaeus, 1758)	TMS	occ	—	freshwater species

(*Continued*).

Appendix 1. *(Continued).*

Order	Species and stage	Area	Month	Density	Remarks
Syngnathiformes	*Syngnathus* spp.	VDG > VDB, VDO/ WSM < WSB/ TMW > TMS	all	+/+/***	peak in Aug/Sep (Nov in marshes)
Scorpaeniformes	*Myoxocephalus scorpius* (Linnaeus, 1758)	VDG, VDO/WSB	Mar–May	—/—	
	Agonus cataphractus (Linnaeus, 1758)	VDG, VDO	May–Sep	—	
	Liparis liparis (Linnaeus, 1766)	VDG, VDB/WSM, WSB	Apr–Jun	—/—	
Perciformes	*Dicentrarchus labrax* (Linnaeus, 1758)	WSM < WSB/TMW ≪ TMS	occ/all	—/*	
	Stizostedion lucioperca (Linnaeus, 1758)	TMS	occ	—	freshwater species
	Trachurus trachurus (Linnaeus, 1758)	VDG, VDB, VDO	Jul–Aug	—	peak in July
	Chelon labrosus (Risso, 1826)	TMW, TMS	Oct–Dec	—	
	Liza ramada (Risso, 1826)	WSM, WSB/TMW, TMS	occ	—/—	
	Pholis gunnellus (Linnaeus, 1758)	VDO/WSM	Feb/Apr	—/—	
	Echiichthys vipera (Cuvier, 1829)	VDB	Jul	—	
	Ammodytes tobianus (Linnaeus, 1758)	VDG, VDB, VDO/WSM, WSB/ TMS	occ	—/—/—	
	Hyperoplus lanceolatus (Le Sauvage, 1824)	WSM, WSB	occ	—	
	Callionymus lyra (Linnaeus, 1758)	VDG > VDB > VDO/WSM	Jun–Jul/May	+/—	peak in June
	Aphia minuta (Risso, 1810)	VDG > VDB > VDO	Nov–May	—	
	Pomatoschistus microps (Kröyer, 1838)	WSM < WSB/TMW < TMS	all	—/533	
	Pomatoschistus spp. Larvae (comprising *P. minutus* and *P. lozanoi*)	all	all	***/**/***	peaks in May and June/August (November in marshes)
Pleuronectiformes	*Scophthalmus rhombus* (Linnaeus, 1758)	VDG, VDO	Jun–Jul	—	
	Limanda limanda (Linnaeus, 1758)	VDG > VDB > VDO/ WSM < WSB	occ	—/—	
	Pleuronectes flesus (Linnaeus, 1758)	VDG > VDB, VDO/ WSM < WSB/TMW < TMS	Mar–Jun	—/+/150	peak in June (Voordelta and marshes) and May (estuary)
	Pleuronectes platessa (Linnaeus, 1758)	VDG > VDB, VDO/WSM, WSB/TMS	Mar–Jul/ Nov–Apr/Apr	—/+/—	peak in April in marshes
	Solea solea (Linnaeus, 1758)	VDG > VDB > VDO/ WSM > WSB/TMW > TMS	May–Jun/ Apr–Jun/Apr	*/+/*	peaks in March/ April in the estuary and in May in the Voordelta

VDG, ebb-tidal delta of the Grevelingen; VDB, Banjaard area; VDO, ebb-tidal delta of the Oosterschelde; WSM, marine region of the Westerschelde; WSB, brackish region of the Westerschelde; TMW tidal marsh of Waarde; TMS, tidal marsh of Saeftinghe; occ, occasionally; –, 0–1 ind 1000 m^{-2}; +, 1.1–5 ind 1000 m^{-2}; *, 5.1–10 ind 1000 m^{-2}; **, 10.1–20 ind 1000 m^{-2}; ***, 20.1–50 ind 1000 m^{-2}.

Appendix 2. *Mean ±SE densities (ind 1000 m^{-2}) per subarea for each 'species'.*

	Mean ±SE						
	VDG	VDB	VDO	WSM	WSB	TMW	TMS
Lampetra fluviatilis	—	—	—	—	0.06 ±0.05	—	—
Anguilla anguilla	—	—	0.01 ±0.01	0.02 ±0.02	0.27 ±0.11	—	0.06 ±0.02
Anguilla juveniles						2.95 ±0.40	1.48 ±0.29
Clupea harengus	—	—	—	0.02 ±0.03	0.31 ±0.10	0.08	33.54 ±6.41
Sprattus sprattus	—	—	—	0.53 ±0.16	2.08 ±0.64	—	25.14 ±3.13
Clupeidae spp. larvae	86.02 ±33.48	19.82 ±4.84	23.43 ±4.87	4.18 ±2.02	11.23 ±3.44	7.21 ±1.09	76.64 ±9.66
Alburnus alburnus	—	—	—	—	—	—	0.02 ±0.00
Ciliata mustela	—	0.01 ±0.01	—	—	—	—	—
Gadus morhua	—	—	—	0.00 ±0.02	0.06 ±0.06	—	—
Merangius merlangus	0.02 ±0.02	0.04 ±0.02	0.08 ±0.04	0.00 ±0.05	—	—	0.02
Pollachius pollachius	0.01 ±0.01	—	—	—	—	—	—
Trisopterus luscus	0.83 ±0.46	0.23 ±0.13	0.16 ±0.08	0.02 ±0.04	0.03 ±0.03	—	—
Trisopterus minutus	—	0.01 ±0.01	—	—	—	—	—
Atherina presbyter	0.01 ±0.01	—	—	—	0.03 ±0.03	0.14 ±0.02	0.12 ±0.07
Gasterosteus aculeatus	—	—	0.01 ±0.01	0.02 ±0.02	0.02 ±0.02	2.53 ±0.18	0.43 ±0.02
Pungitius pungitius	—	—	—	—	—	—	0.04
Syngnathus spp.	4.10 ±0.69	1.88 ±0.56	2.69 ±0.87	0.85 ±0.35	5.61 ±1.46	35.92 ±5.08	6.06 ±0.66
Myoxocephalus scorpius	0.01 ±0.01	0.00 ±0.00	0.01 ±0.01	—	0.03 ±0.03	—	—
Agonus cataphractus	0.01 ±0.01	—	0.05 ±0.03	—	—	—	—
Liparis liparis	0.08 ±0.03	0.08 ±0.05	0.00 ±0.00	0.02 ±0.04	0.03 ±0.03	—	—
Dicentrarchus labrax	—	—	—	0.00 ±0.02	0.02 ±0.02	0.03	11.09 ±0.31
Stizostedion lucioperca	—	—	—	—	—	—	0.03 ±0.01
Trachurus trachurus	0.72 ±0.47	1.01 ±0.67	1.29 ±0.74	—	—	—	—
Chelon labrosus	—	—	—	—	—	0.80	0.69 ±0.10
Liza ramada	—	—	—	0.01 ±0.02	0.06 ±0.05	0.55 ±0.39	0.05 ±0.02
Pholis gunnellus	—	—	0.01 ±0.01	0.01 ±0.01	—	—	—
Echiichthys vipera	—	0.89 ±0.66	—	—	—	—	—
Ammodytes tobianus	0.14 ±0.08	0.09 ±0.05	0.10 ±0.04	0.15 ±0.12	0.50 ±0.18	—	0.23 ±0.17
Hyperoplus lanceolatus	—	—	—	0.02 ±0.02	0.03 ±0.03	—	—
Calionymus lyra	3.33 ±1.50	1.84 ±0.73	1.03 ±0.35	0.04 ±0.11	—	—	—
Aphia minuta	0.48 ±0.18	0.14 ±0.06	0.02 ±0.01	—	—	—	—
Pomatoschistus spp.	26.22 ±5.28	23.93 ±7.55	10.95 ±1.99	8.14 ±2.59	17.97 ±5.14	26.58 ±1.65	35.53 ±3.26
Pomatoschistus microps	—	—	—	0.10 ±0.07	1.32 ±0.46	229.78 ±9.68	836.27 ±31.23
Scophthalmus rhombus	0.01 ±0.01	—	0.01 ±0.01	—	—	—	—
Limanda limanda	0.57 ±0.21	0.22 ±0.11	0.023 ±0.02	0.07 ±0.06	0.21 ±0.10	—	—
Pleuronectes flesus	0.05 ±0.03	0.01 ±0.01	0.01 ±0.01	1.41 ±0.94	9.13 ±7.11	25.57 ±2.33	276.22 ±48.66
Pleuronectes platessa	0.31 ±0.31	0.09 ±0.06	0.11 ±0.07	1.00 ±0.55	2.57 ±1.00	—	0.89 ±0.18
Solea solea	14.65 ±9.39	3.73 ±2.18	0.70 ±0.27	1.45 ±1.00	0.37 ±0.26	17.78 ±9.48	1.21 ±0.25

Appendix 3. *Mean ±SE lengths per months (in mm) of the dominant species for the Voordelta (A), the Westerschelde (B) and the tidal marshes of Waarde (C) and Saeftinghe (D). For sampling dates per study area, see Table 1.*

A. Voordelta	A	S	O	N	D	J	F	M	A	M	J	J
Clupeidae spp. larvae								27.1 ±0.2	28.7 ±0.1	21.9 ±0.1	13.7 ±0.1	15.7 ±0.2
Pomatoschistus spp.	9.4 ±0.1	9.8 ±0.2			14.7 ±0.3					12.0 ±0.2	7.4 ±0.1	9.1 ±0.1
Syngnathus spp.	33.7 ±0.7	40.3 ±1.3	81.4 ±2.7				67.7 ±2.7	77.1 ±3.4				24.3 ±0.9
Solea solea										7.6 ±0.2	6.2 ±0.1	
Pleuronectes platessa										8.1 ±0.2		

B. Westerschelde	A	M	J	J	A	S	O	N	D	J	F	M	A
Clupeidae spp.	28.7 ±0.3	14.1 ±0.1	15.1 ±0.6									24.1 ±1.5	27.9 ±0.2
Pomatoschistus spp.		14.0 ±0.1	11.7 ±0.2	12.6 ±0.2	13.9 ±0.2	13.3 ±0.5							
Syngnathus spp.				53.3 ±1.6	61.7 ±1.1	73.1 ±3.1							
Solea solea	8.1 ±0.2	7.4 ±0.2											
Pleuronectes platessa												10.6 ±0.1	12.0 ±0.1
Pleuronectus flesus	7.6 ±0.0											10.5 ±0.1	7.6 ±0.2

C. Tidal marsh of Waarde	M	A	A	M	J	J	A	S	O	O	N	D	J	F	M	A	M	J	J	A
Clupeidae spp. larvae		28.4 ±0.4	28.7 ±0.4																34.0 ±0.3	
Pomatoschistus spp.				14.6 ±0.1	18.2 ±0.2													17.3 ±0.2		
Syngnathus spp.			99.4 ±2.0			109.0 ±3.1			90.6 ±0.4	94.3 ±1.5								90.7 ±1.0		
Solea solea				7.8 ±0.1														7.7 ±0.1		
Pleuronectes platessa																				
Pleuronectes flesus			8.0 ±0.1	8.1 ±0.1											10.8 ±0.1	8.1 ±0.1				

D. Tidal marsh of Saeftinghe	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O
Clupeidae spp. larvae		30.7 ±0.1	30.5 ±0.7											34.9 ±0.1		24.2 ±0.1				
Syngnathus spp.								76.7 ±1.1												
Solea solea			9.0 ±0.2																	
Pleuronectes platessa		11.7 ±0.1																		
Pleuronectes flesus	11.7 ±0.2	8.2 ±0.1	8.9 ±0.0	21.5 ±0.2									11.0 ±0.0	8.7 ±0.1	8.4 ±0.2	10.8 ±0.2				

Appendix 11.

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CIRCADIEL PATTERNS IN THE TIDAL PLANKTON OF A SANDY BEACH IN ZEEBRUGGE (BELGIUM)

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Abstract. The intertidal fauna of a Belgian sandy beach was sampled on an hourly basis with a hand-pushed sledge to study circadiel patterns in species composition. Four assemblages could be distinguished with classification and ordination techniques. A first division separated the samples taken during daytime from the night samples. Both assemblages were subsequently divided into an ebbtide and a floodtide situation. Light intensity and tidal height were the most important variables explaining the variation in the Canonical Correspondence Analysis.

Key words : tidal plankton, circadiel patterns, Belgium.

INTRODUCTION

Since the study by RUSSELL (1925) of the diurnal vertical movements of macro-plankton, there have been several papers reporting vertical movements in intertidal waters. Early plankton collections using tow nets at the edge of sandy beaches showed that certain species of amphipods swim to the surf zone during the night (ELMHIRST, 1932 ; WATKIN, 1939 ; 1941). A distinction can be made between local endobenthic species that actively perform nocturnal vertical migrations, and tidal migrants carried in from sublittoral habitats by the tide. A very detailed study of the so-called tidal plankton was carried out on a sandy beach in Robin Hood's Bay (Great Britain) by COLMAN & SEGROVE (1955). In addition to a distinction between sand-inhabiting species and immigrants, they also found that the zonation of the sand-inhabiting species corresponded very closely to the range occupied by the same species in the sand. However, only a very small proportion of the sand-dwelling animals known to be present in the sand was caught in the water column. The tidal plankton (mainly Amphipoda, Mysidacea and Decapoda) was much more abundant near the bottom of the water column than at the surface. During rough weather, a number of species were carried between the tide marks by the turbulence of the water movements, but good swimmers like mysids avoided the surf zone in such conditions. In addition, FINCHAM (1970) reported semi-lunar and annual fluctuations in amphipod densities. Also, over rocky shores (JANSSON & KÄLLADER, 1968 ; SETRAN, 1992) and seagrass beds (LEDOYER, 1964), a variety of taxa are known to perform vertical migrations into the surf at night.

However, information about structural characteristics of the assemblages of the benthic boundary layer of intertidal areas (species composition, density, biomass, diversity, ...) is very scarce (MEES & JONES, 1997). To date, no attempt has been made to describe the circadiel patterns of the tidal plankton as a whole. In this study the intertidal fauna was sampled hourly during 25 hours, and subsequently the samples were clustered into assemblages.

MATERIAL AND METHODS

Study area and sampling

The study was performed on a homogenous sandy beach in Zeebrugge (Belgium) where the intertidal area has recently enlarged enormously, due to the expansion of the harbour of Zeebrugge in which a long jetty causes a lot of sedimentation (Fig. 1). The study area was chosen because in Zeebrugge, the tidal plankton reached the highest density of all stations that were sampled along the Belgian coast in the summer of 1995 (unpublished data).

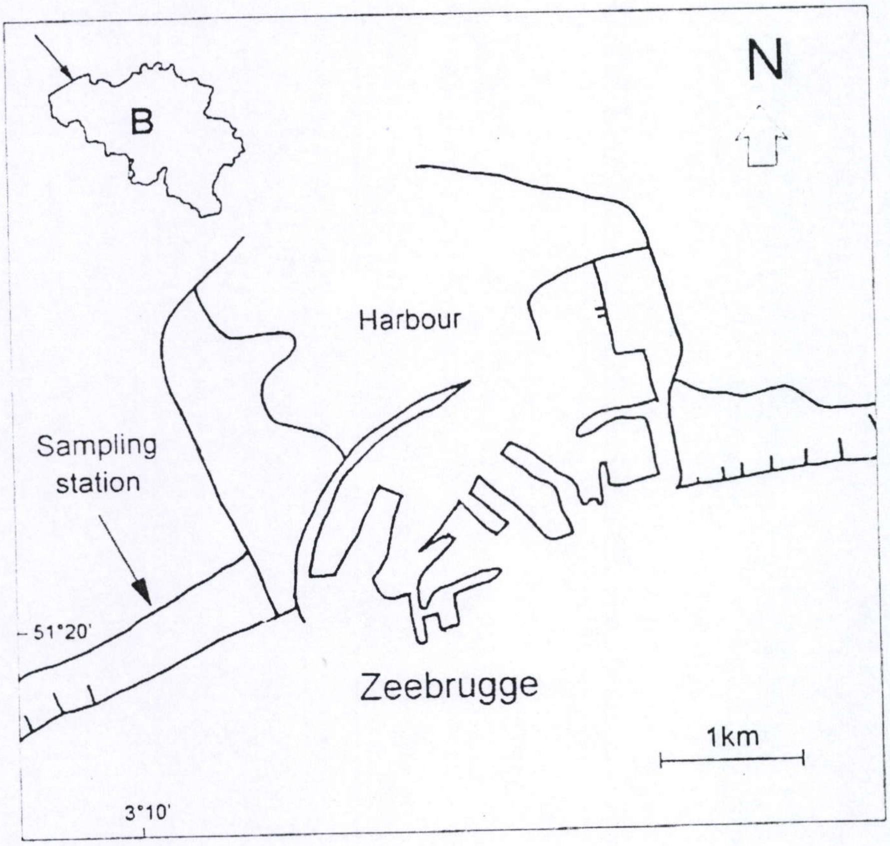

Fig. 1. – Study area, with indication of the sampling site.

On 2 and 3 November 1995, samples were collected with a 50 cm wide, hand-pushed sledge which sampled the lowest 20 cm of the water column. The net had a length of 90 cm and a mesh size of 1 x 1 mm. The total area of the mouth of the net was 0.1 m^2. The samples were immediately rinsed over a 1 mm sieve and preserved in a formalin solution, 7% final concentration. Rose Bengal was added to facilitate sorting of the organisms. On each occasion, the sledge was pushed over a distance of 50 m. Sampling depth ranged from 50 to 100 cm. In order to have an idea of the variability, each hour three successive samples were taken at the same depth. Hourly, the temperature of the sea water and the light intensity were measured, and a watersample was taken for the quantification of nitrate, nitrite, ammonium, phosphate and silicon in the laboratory with the HPLC-method (MANTOURA & LLEWELLYN, 1983). The tidal height at each hour is shown in Fig. 5.

Processing of samples and data analysis

In the laboratory all animals were sorted, identified, when possible to species level, and counted. The amphipod species of the genus *Bathyporeia* and the polychaete species of the genus *Harmothoe* could not be identified to species level. Different developmental stages of decapods were treated as separate ecological species. All individuals of each species were measured (standard length : distance from base of the rostral tip to the end of the last abdominal segment for crustaceans ; from the tip of the nose to the base of the caudal fin for fishes), and their biomass was derived from length - ash-free dry weight regressions (MEES, 1994). All density and biomass data are presented as numbers of individuals (N) and mg ash-free dry weight (AFDW) per 100 m^2 ; these values correspond to a volume of 20 m^3 water filtered through the net.

Species that were caught less than 10 times during the whole sampling period were excluded from classifications and ordinations because these species are so rare they do not show a clear pattern and they do not have any influence on the analysis (DAY *et al.*, 1971). The density differences between day and night or between high and low water were tested for the dominant species with a Kruskal-Wallis ANOVA.

Diversity was calculated as Hill's diversity numbers (HILL, 1973). This set of indices incorporates the most widely used diversity measures in a continuum of indices of the orders $-\infty$ to $+\infty$. The indices differ in their tendency to include or to ignore the relatively rarer species : the impact of dominance increases and the influence of species richness decreases with an increasing order of the diversity number. Of particular interest are :

$N_0 = S$ with S = the number of species
$N_1 = e^H$ with H = Shannon-Wiener index
$H = -\sum p_i \ln(p_i)$ (p_i = the relative abundance of the i^{th} dominant species)
$N_2 = SI^{-1}$ with SI = Simpson's dominance index
$SI = \sum p_i^2$
$N_\infty = p_1^{-1}$ with p_1 = the relative abundance of the most abundant species.

To quantify the similarity between the three replicates taken per hour on the one hand, and the similarity between the samples of the subsequent hours on the other hand, a group-average sorting cluster analysis with Bray-Curtis similarities (BRAY & CURTIS, 1957) was performed on the fourth root transformed density and biomass data.

The samples were classified into clusters according to species composition, using the classification program TWINSPAN (Two-Way INdicator SPecies ANalysis) (HILL, 1979). TWINSPAN also yields indicator species characterising the various assemblages. The cut levels used in the analysis were 0, 1, 2, 5, 20 and 40 for the density data and 0, 0.1, 0.3, 0.9, 5 and 40 mg for the biomass data. These cut levels correspond with the densities and the biomass of the data pooled per hour, which are measures of the amount of animals per 75 m^2. To check the stability of the TWINSPAN results, the Canonical Correspondence Analysis

(CCA) option from the program package CANOCO (Ter Braak, 1988) was applied on the fourth root transformed data. A Correspondence Analysis (CA) was applied on the same data in order to see if the parameters used in the CCA explained the variation in the data.

RESULTS

Exploration of the data matrix

A total of 44 ecological species was recorded (Table 1). These included species generally referred to as mesozooplankton, macrozooplankton, macrobenthos or hyperbenthos. The dominant taxa were Mysidacea (6 species, 38 % of the total number of individuals caught) and Cnidaria (1 species, 25 %). Isopoda (2 species, 9.6 %), Decapoda (7 species, 8.9 %), Cumacea (1 species, 7.8 %), Copepoda (4 species, 4.3 %) and Amphipoda (12 species, 3 %) were also common. Fishes (4 species, 1.5 %), Chaetognatha (1 species, 1.4 %), Polychaeta (5 species, 0.5 %) and Ctenophora (1 species, 0.4 %) were rare.

The temporal variation in the densities of the most abundant species can be related to the waterlevel (Fig. 5) and the light regime. Night fell at 19 h and lasted until 9 h the next morning. Dusk and dawn only lasted for one hour before and after the night respectively.

Planktonic species like *Mitrocomella polydiademata* (Cnidaria) (Fig. 2a) and *Pleurobrachia pileus* (Ctenophora) showed no clear pattern of occurrence. Despite the fact that calanoid copepods cannot be sampled efficiently with a 1 mm mesh net, *Calanus helgolandicus* (Fig. 2b), *Centropages typicus* and *Temora longicornis* were caught regularly. They all reached highest densities during the night, but only for *C. helgolandicus* was this difference significant (Kruskal-Wallis ANOVA, $p<0.05$).

The cumacean *Cumopsis goodsiri* (Fig. 2c) was most abundant during ebbtide ($p<0.001$); the species was, however, most abundant in the midlitoral. The mysid *Mesopodopsis slabberi* (Fig. 2d) was mainly found during the day ($p< 0.001$). It was by far the most abundant species (densities upto 1333 individuals per 100 m^2). Another mysid species, *Neomysis integer* (Fig. 2e) was mainly found during the night ($p < 0.01$) and during high water ($p<0.05$). The isopod *Eurydice pulchra* (Fig. 2f) was predominantly found during the night ($p<0.001$) and at floodtide ($p<0.001$). The amphipods were the most diverse group during the sampling period : 12 species were recorded. Most of them were, however, very rare. Only *Gammarus crinicornis* once reached a density of more than 10 animals per 100 m^2. This species was most abundant during the night ($p<0.05$). Adult *Crangon crangon* (Fig. 2g), as well as its postlarva, were most abundant during the night (both $p<0.01$). This shrimp was the most important species in terms of biomass, with a maximum of 2067 mg AFDW per 100 m^2. *Pomatoschistus microps* (Fig. 2h) was the only fish that was caught regularly. It was most common during the night ($p<0.05$).

TABLE 1

List of species with indication of the used abbreviations and the classification

Name and stage	Abbreviation	Classification
Cnidaria		
Mitrocomella polydiademata (Romanes, 1876)	Mitr poly	Macrozooplankton
Ctenophora		
Pleurobrachia pileus (Müller, 1776)	Pleu pile	Macrozooplankton
Polychaeta		
Harmothoe species	Harm Spec	Hyperbenthos
Lanice conchilega (Pallas, 1766)	Lani conc	Macrobenthos
Lanice conchilega (Pallas, 1766) (aulophorelarva)	Lani Aulo	Macrozooplankton
Scolelepis squamata (Müller, 1789)	Scol squa	Macrobenthos
Spio filicornis (Müller, 1766)	Spio fili	Macrobenthos
Crustacea		
Copepoda		
Calanus helgolandicus (Claus, 1863)	Cala helg	Mesozooplankton
Centropages typicus (Kröyer, 1849)	Centr typi	Mesozooplankton
Labidocera wollastoni (Lubbock, 1857)	Labi woll	Mesozooplankton
Temora longicornis (Müller, 1792)	Temo long	Mesozooplankton
Cumacea		
Cumopsis goodsiri (van Beneden, 1851)	Cumo good	Hyperbenthos
Mysidacea		
Gastrosaccus spinifer (Goës, 1864)	Gastr spin	Hyperbenthos
Mesopodopsis slabberi (van Beneden, 1861)	Meso slab	Hyperbenthos
Neomysis integer (Leach, 1814)	Neom inte	Hyperbenthos
Praunus flexuosus (Müller, 1776)	Prau flex	Hyperbenthos
Schistomysis kervillei (Sars, 1885)	Schi kerv	Hyperbenthos
Schistomysis spiritus (Norman, 1860)	Schi spir	Hyperbenthos
Isopoda		
Eurydice pulchra (Leach, 1815)	Eury pulc	Hyperbenthos
Idotea pelagica (Leach, 1815)	Idot pela	Hyperbenthos
Amphipoda		
Bathyporeia species	Bath Spec	Hyperbenthos
Corophium acherusicum (Costa, 1851)	Coro ache	Hyperbenthos
Corophium insidiosum (Crawford, 1937)	Coro insi	Hyperbenthos
Gammarus crinicornis (Stock, 1966)	Gamm crin	Hyperbenthos
Haustorius arenarius (Slabber, 1769)	Haus aren	Hyperbenthos
Jassa marmorata (Holmes, 1903)	Jass marm	Hyperbenthos
Microprotopus maculatus (Norman, 1867)	Micr macu	Hyperbenthos
Pariambus typicus (Kröyer, 1845)	Pari typi	Hyperbenthos
Perioculodes longimanus (Bate & Westwood, 1868)	Peri long	Hyperbenthos
Pontocrates altamarinus (Bate & Westwood, 1862)	Pont alta	Hyperbenthos
Pontocrates arenarius (Bate, 1858)	Pont aren	Hyperbenthos
Stenothoe marina (Bate, 1856)	Sten mari	Hyperbenthos
Decapoda		
Carcinus maenas (L., 1758) (zoea)	Carc Zoea	Mesozooplankton
Carcinus maenas (L., 1758) (megalopa)	Carc Mega	Mesozooplankton
Crangon crangon (L., 1758)	Cran cran	Hyperbenthos
Crangon crangon (L., 1758) (postlarva)	Cran Post	Hyperbenthos
Diogenes pugilator (Roux, 1828) (megalopa)	Diog Mega	Mesozooplankton
Portumnus latipes (Pennant, 1777)	Port lati	Hyperbenthos
Portumnus latipes (Pennant, 1777) (megalopa)	Port Mega	Mesozooplankton
Chaetognatha		
Sagitta setosa (Müller, 1847)	Sagi seto	Mesozooplankton
Pisces		
Ammodytes tobianus (L., 1758)	Ammo tobi	Hyperbenthos
Chelon labrosus (Risso, 1962)	Chel labr	Hyperbenthos
Pleuronectes platessa (L., 1758)	Pleu plat	Hyperbenthos
Pomatoschistus microps (Kröyer, 1838)	Poma micr	Hyperbenthos

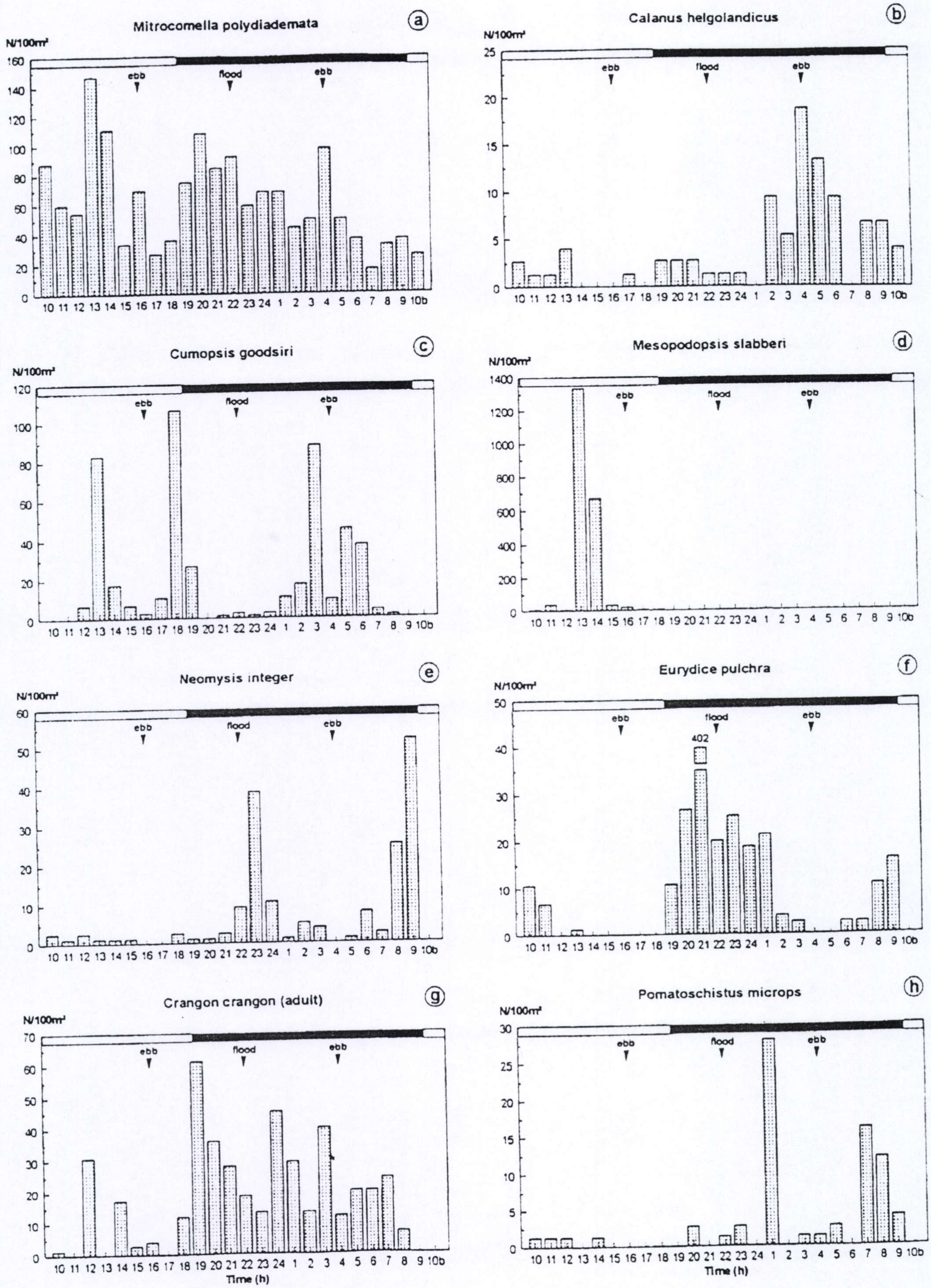

Fig. 2. – The abundance of some intertidal animals during the course of the cycle.

Analysis of the temporal patterns

The cluster analyses with the density data, as well as with the biomass data, separated the day samples from the night samples. The samples that were taken at a similar tidal height were often clustered together. However, the similarity between the three successive samples taken each hour was not much greater than the similarity between samples taken at approximately the same tidal height. Therefore the three replicates per hour were pooled for TWINSPAN and for the ordinations.

The result of the TWINSPAN of the density data is presented in Fig. 3. In the first division, the samples taken during daytime were separated from the samples taken at night. Indicator species for the night samples were *Calanus helgolandicus* (cut level 2), *Crangon crangon* (cut level 3), *Pomatoschistus microps* (cut level 2), *Eurydice pulchra* (cut level 2) and *Gammarus crinicornis* (cut level 2). The indicator species for the day samples was *Mesopodopsis slabberi* (cutlevel 2). Both the clusters of day and night were subsequently divided into groups of flood- and ebbtide samples. At night, the indicator species for the flood cluster was *Eurydice pulchra* (cut level 3), while *Cumopsis goodsiri* (cut level 3) was the indicator species for the ebb cluster. Also during the day, the indicator species for the ebb cluster was *C. goodsiri* (cut level 1). The analysis with the biomass data yielded the same four clusters (not figured).

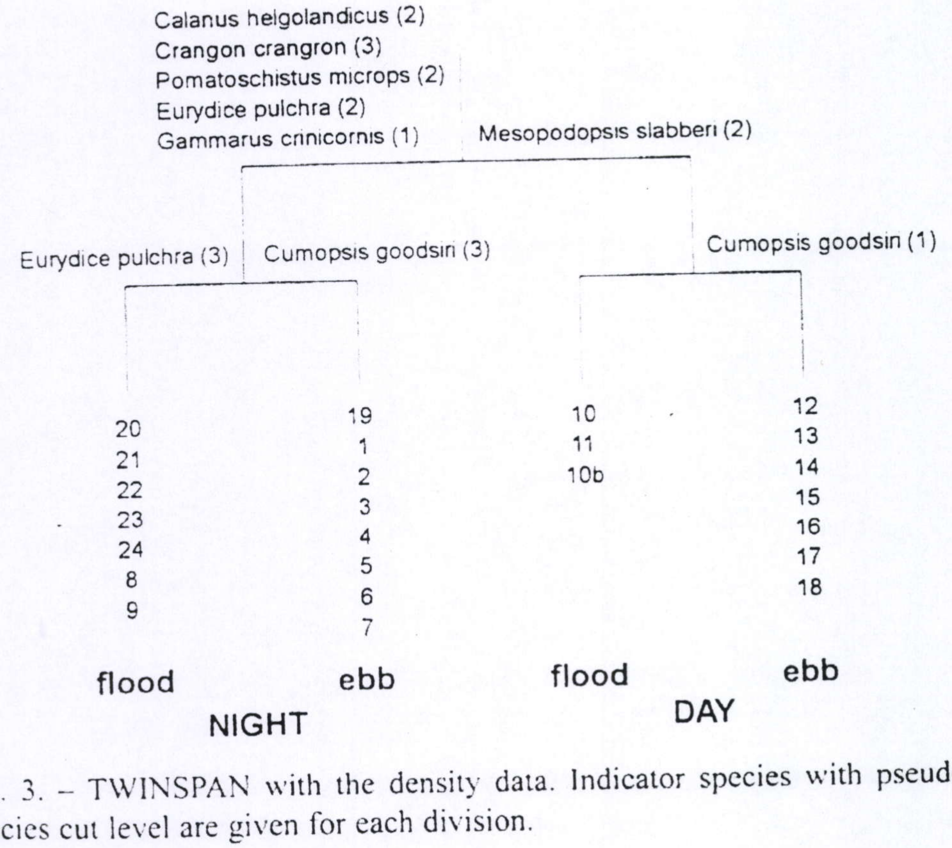

Fig. 3. – TWINSPAN with the density data. Indicator species with pseudospecies cut level are given for each division.

The direct gradient analysis of the fourth root transformed density data was in general agreement with the classification: the four clusters identified by TWINSPAN could also be identified in the ordination plane formed by the first (eigenvalue 0.12) and the second (eigenvalue 0.06) axes (Fig. 4, right). The eigenvalues for the third axis were much lower (0.03), and yielded no additional information. Along the first and most important axis, the

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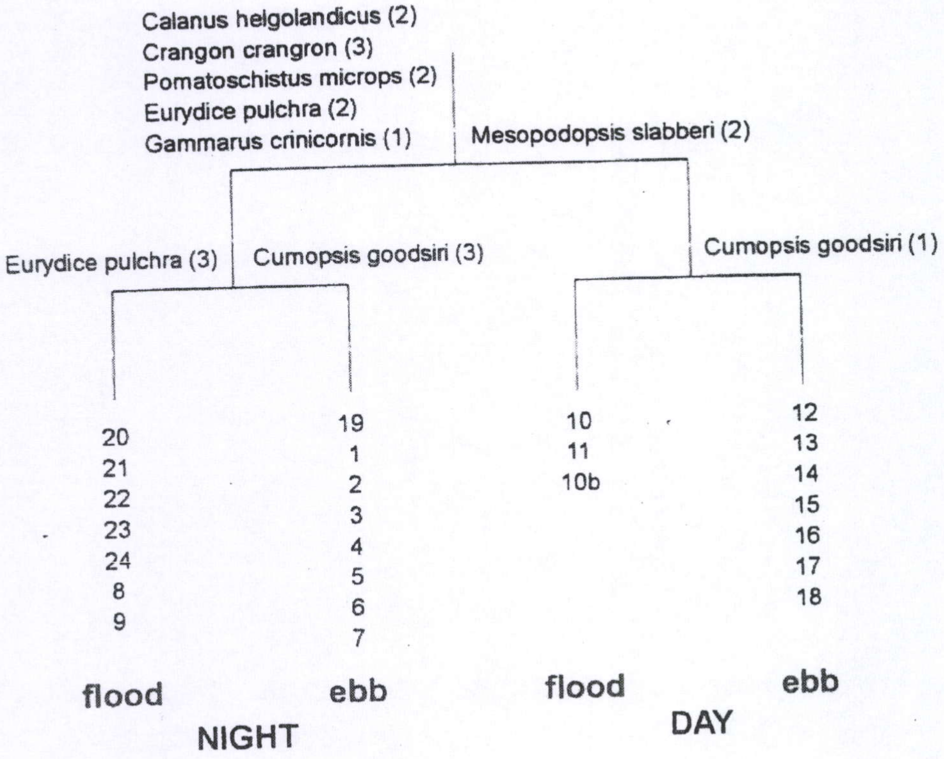

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For the indirect gradient analysis of the density data, the first axis (eigenvalue 0.15) was plotted against the third axis (eigenvalue 0.07) (Fig. 4). When the first axis was plotted against the second axis (eigenvalue 0.08), the samples from low and high water were not clearly separated from each other. Just as for the direct gradient analysis, the

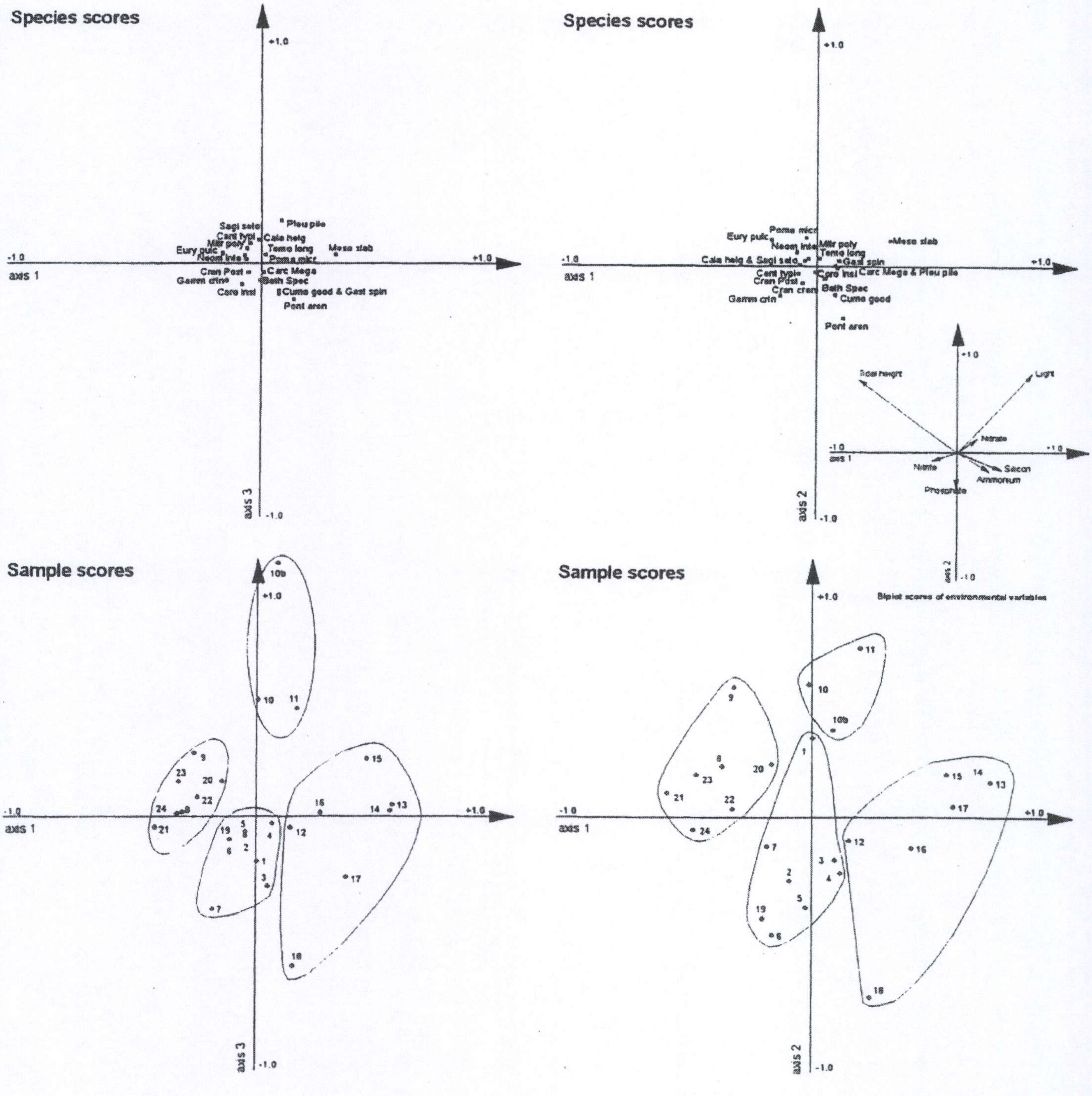

Fig. 4. – Correspondence Analysis (left) and Canonical Correspondence Analysis (right) of the fourth root transformed density data.

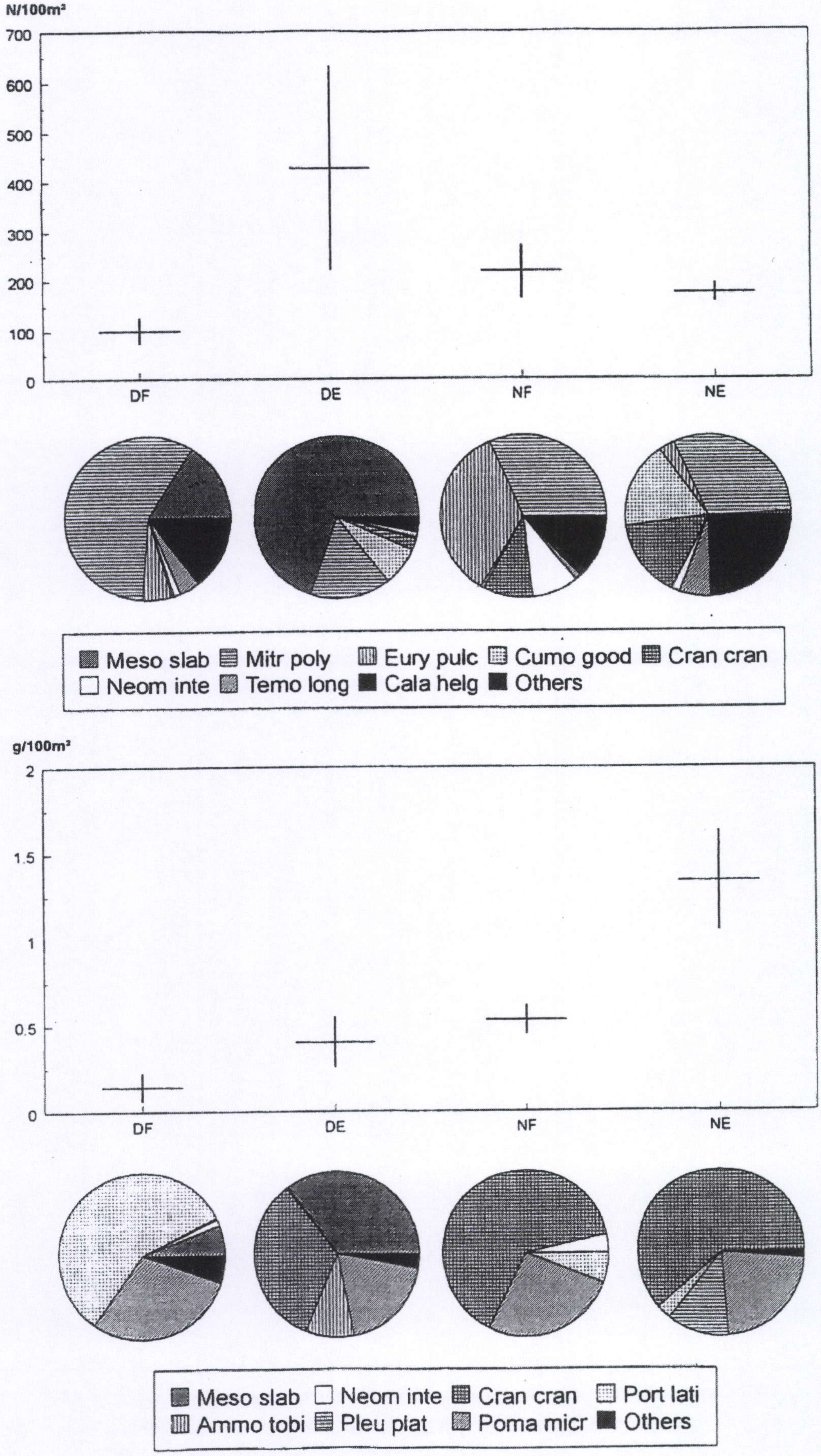

Fig. 6. – Average density and biomass of the four assemblages, as identified by the multivariate analyses with indication of the standard error. The species composition of each assemblage is shown in the pie charts below each graph.

During the day flood tide, the fauna was dominated by *Mitrocomella polydiademata*, *Mesopodopsis slabberi* and, to a lesser extent, *Eurydice pulchra*. Biomass on the other hand, was mainly made up of *Portumnus latipes*, *Pomatoschistus microps* and *Mesopodopsis slabberi*. The mean density, as well as the biomass, was very low in comparison with the other assemblages.

The ebbtide situation of the day was characterised by very high densities of *Mesopodopsis slabberi*, but also of *Mitrocomella polydiademata* and *Cumopsis goodsiri*. *Mesopodopsis slabberi*, *Crangon crangon*, *Pomatoschistus microps* and *Ammodytes tobianus* were most important in terms of biomass.

At night and flood tide, *Eurydice pulchra*, *Mitrocomella polydiademata*, *Cumopsis goodsiri* and *Neomysis integer* were the most important taxa, while the biomass was made up almost exclusively of *Crangon crangon* and *Pomatoschistus microps*.

The ebbtide situation of the night was most diverse, and *Mitrocomella polydiademata*, *Crangon crangon*, *Cumopsis goodsiri*, *Temora longicornis* and *Calanus helgolandicus* all contributed considerably to the density. The biomass of this assemblage was much higher than that of the other assemblages. This was mainly because of *Crangon crangon*, *Pomatoschistus microps* and *Pleuronectes platessa*.

The average Hill's diversity numbers per assemblage are presented in Table 2. For all diversity indices, the night samples had higher values than the day samples. Within those night samples, the diversity was higher during ebbtide.

TABLE 2

Mean Hill's diversity numbers of the four assemblages, as identified by the multivariate analysis, with indication of the standard error

	DF	DE	NF	NE
N_0	11,67 (2,72)	11,29 (0,80)	14,71 (0,72)	17,38 (1,33)
N_1	3,93 (0,49)	3,68 (0,46)	5,68 (0,61)	7,91 (0,49)
N_2	2,49 (0,29)	2,50 (0,28)	3,86 (0,48)	5,30 (0,40)
N_∞	1,73 (0,18)	1,76 (0,16)	2,38 (0,25)	3,12 (0,27)

DISCUSSION

This is a first attempt to quantify the tidal plankton of a sandy beach in the Southern Bight of the North Sea. We concentrated on the macro-component of the zooplankton (animals larger than 1 mm). A community approach, though often used in studies of the subtidal hyperbenthos (*e.g.* MEES, 1994) has not yet been applied to intertidal assemblages. In this pilot study, a high number of species has been found to utilise the beach habitat at specific times of the tidal cycle or day. The fauna mainly consisted of fast swimming species like mysids. These typically live subtidally in the benthic boundary layer or hyperbenthal (MAUCHLINE, 1980; MEES & JONES, 1997; ZOUHIRI *et al.*, 1998), and their densities are notoriously difficult to estimate. Many species are known to form aggregations (MAUCHLINE, 1980) and, especially in intertidal areas, it is difficult to distinguish between increases in population numbers resulting from immigration and those resulting from a disaggregated population aggregating or swarming in a small area. We tried to avoid this problem by taking three replicates per hour. Also, the biomass data presented in this study should be interpreted with care, since incidentially caught large epibenthic animals (mainly adult crabs and fish) sometimes contributed significantly to the total biomass. The present study covers only one situation and does not include seasonal or semi-lunar patterns. Further research is needed to determine and to understand the impact of this and other factors on the tidal plankton communities.

Despite the extreme conditions in the intertidal, a lot of species occur between the tide-marks. Decreased predation pressure and optimal feeding conditions are the most obvious factors. In this study *Eurydice pulchra* (JONES & NAYLOR, 1967) and *Cumopsis goodsiri* (JONES, 1976) are good examples of sand-dwelling species that clearly have a restricted range in the intertidal, and are only rarely found in subtidal areas (HAMERLYNCK & MEES, 1991 ; MEES & HAMERLYNCK, 1992 ; CATTRIJSSE *et al.*, 1993). Some other species are typically estuarine, like *e.g. Neomysis integer* (TATTERSALL & TATTERSALL, 1951) or *Pomatoschistus microps* (NIJSSEN & DE GROOT, 1987 ; ELLIOTT & DEWAILLY, 1995). Both species are euryhaline, with a wide range of salinity tolerance and considerable powers of adaptation to the changing salinity of the waters they frequent. MAUCHLINE (1971) has often found *N. integer* in the intertidal, whereas according to NIJSSEN & DE GROOT (1987), *P. microps* is common and abundant in the shallow gullies (0.2-2 m) of the Wadden Sea.

The intertidal fauna clearly showed circadiel and tidal distribution patterns. Each situation (day-flood, day-ebb, night-flood, night-ebb) was characterised by a different faunal assemblage. Moreover, the floodtide situation during the day was characterised by both the lowest densities and biomasses in comparison with the other periods, whereas the ebbtide situation during the night was the most diverse. Circatidal activity rhythms of planktonic organisms in the intertidal area have hardly been studied as such. Most studies only cover rocky shores (*e.g.* JANSSON & KÄLLANDER, 1968 ; SAWARA, 1992), or concentrate on only one taxonomic group (*e.g.* COLMAN & SEGROVE, 1955 : amphipods ; TAKAHASHI & KAWAGUCHI, 1997 : three mysid species), and mostly they discuss only sand-burrowing species (*e.g.* COLMAN & SEGROVE ; DE RUYCK *et al.*, 1991 ; TAKAHASHI & KAWAGUCHI, 1997). However, the activity rhythms of most species were in general agreement with the available literature. *Eurydice pulchra* for example, emerges from the sand as the tide comes in and re-buries after high tide (a.o. ALHEIT & NAYLOR, 1976). *Neomysis integer* is known to avoid light in seawater (TATTERSALL & TATTERSALL, 1951). MAUCHLINE (1971) often found the species in the intertidal at high water. Also in this study, *N. integer* was mainly found during the night during high water.

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REFERENCES

ALHEIT, J. & E. NAYLOR (1976) – Behavioural basis of intertidal zonation in *Eurydice pulchra* Leach. *J. Exp. Mar. Biol. Ecol.*, **23** : 135-144.

BRAY, J.R. & J.T. CURTIS (1957) – An ordination of the upland forest communites of southern Wisconsin. *Ecol. Monogr.*, **27** : 325-349.

CATTRIJSSE, A., J. MEES & O. HAMERLYNCK (1993) – The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde estuary. *Cah. Biol. Mar.*, **34** : 187-200.

COLMAN, J.S. & F. SEGROVE (1955) – The tidal plankton over stoupe beck sands, Robin Hood's Bay (Yorkshire, North Riding). *J. Anim. Ecol.*, **24** : 445-462.

DAY, J.H., J.G. FIELD & M.P. MONTGOMERY (1971) – The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. *J. Anim. Ecol.*, **40** : 93-126.

DE RUYCK, A.M.C., T.E. DONN Jr. & A. MCLACHLAN (1992) – Distribution of three intertidal cirolanid isopods (Flabellifera : Cirolanidae) on a South African sandy beach. *Cah. Biol. Mar.*, **33** : 147-168.

ELLIOTT, M. & F. DEWAILLY (1995) – The structure and components of European estuarine fish assemblages. *Neth. J. Aquat. Ecol.*, **39** : 397-417.

ELMHIRST, R. (1932) – Quantitative studies between tide-marks. *Glasgow Nat.*, **10** : 56-62.

FINCHAM, A.A. (1970) – Amphipods in the surf plankton. *J. mar. biol. Ass. U.K.*, **50** : 177-198.

HAMERLYNCK, O. & J. MEES (1991) – Temporal and spatial structure in the hyperbenthic community of a shallow coastal area and its relation to environmental variables. *Oceanologica Acta*, **11** : 205-212.

HILL, M.O. (1973) – Diversity and eveness : a unifying notation and its consequences. *Ecology*, **54** : 427-432.

HILL, M.O. (1979) – A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and systematics. Cornell University Ithaca, New York (66 pp).

JANSSON, B.O. & C. KÄLLANDER (1986) – On the diurnal activity of some littoral peracarid crustaceans in the Baltic Sea. *J. exp. mar. Biol. Ecol.*, **2** : 24-36.

JONES, N.S. (1976) – British Cumaceans (Arthropoda : Crustacea), Identification of the Species. Synopsis of the British Fauna (New Series) 7, The Linnean Society of London, Academic Press, London and New York (66 pp).

JONES, D.A. & E. NAYLOR (1967) – The distribution of *Eurydice* (Crustacea : Isopoda) in Bristish waters, including E. Affinis new to Britain. *J. Mar. Biol. Ass. UK*, **47** : 373-382.

LEDOYER, M. (1964) – Les migrations nycthémérales de la faune vagile aux sein des herbiers de *Zostera marina* de la zone intertidale en Manche et comparaison avec les migrations en Méditerranée. *Rec. Trav. St. Mar. End. Bull.*, **34** : 241-247.

MANTOURA, R.F.C & C.A. LLEWELLYN (1983) – The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. *Analytica Chemica Acta*, **151** : 297-314.

MAUCHLINE, J. (1971) – Seasonal occurrence of mysids (Crustacea) and evidence of social behaviour. *J. mar. biol. Ass. U.K.*, **51** : 809-825.