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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).

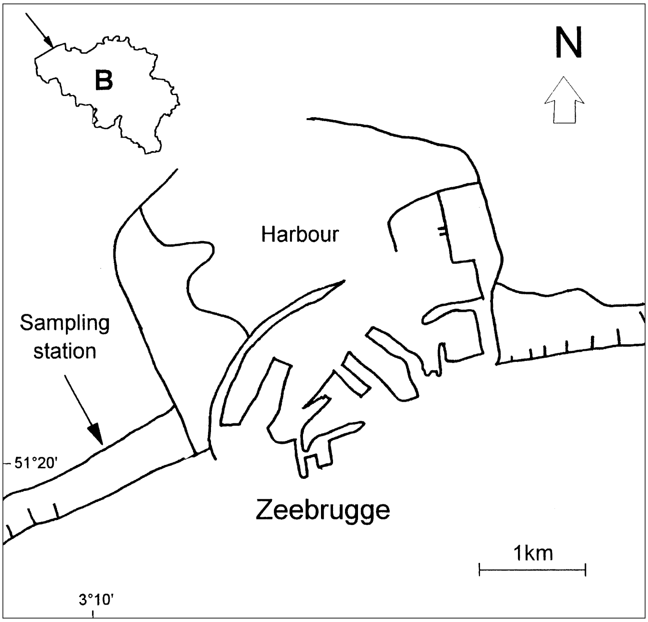


Fig. 1. – Study area, with indication of the sampling site.

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
$H = -\sum p_1 \ln(p_i)$ (p_1 = the relative abundance of the i^{th} dominant species)
$N_2 = SI^{-1}$ with SI = Simpson's dominance index
$SI = \sum p_1^2$
$N_\infty = p_1^{-1}$ 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.

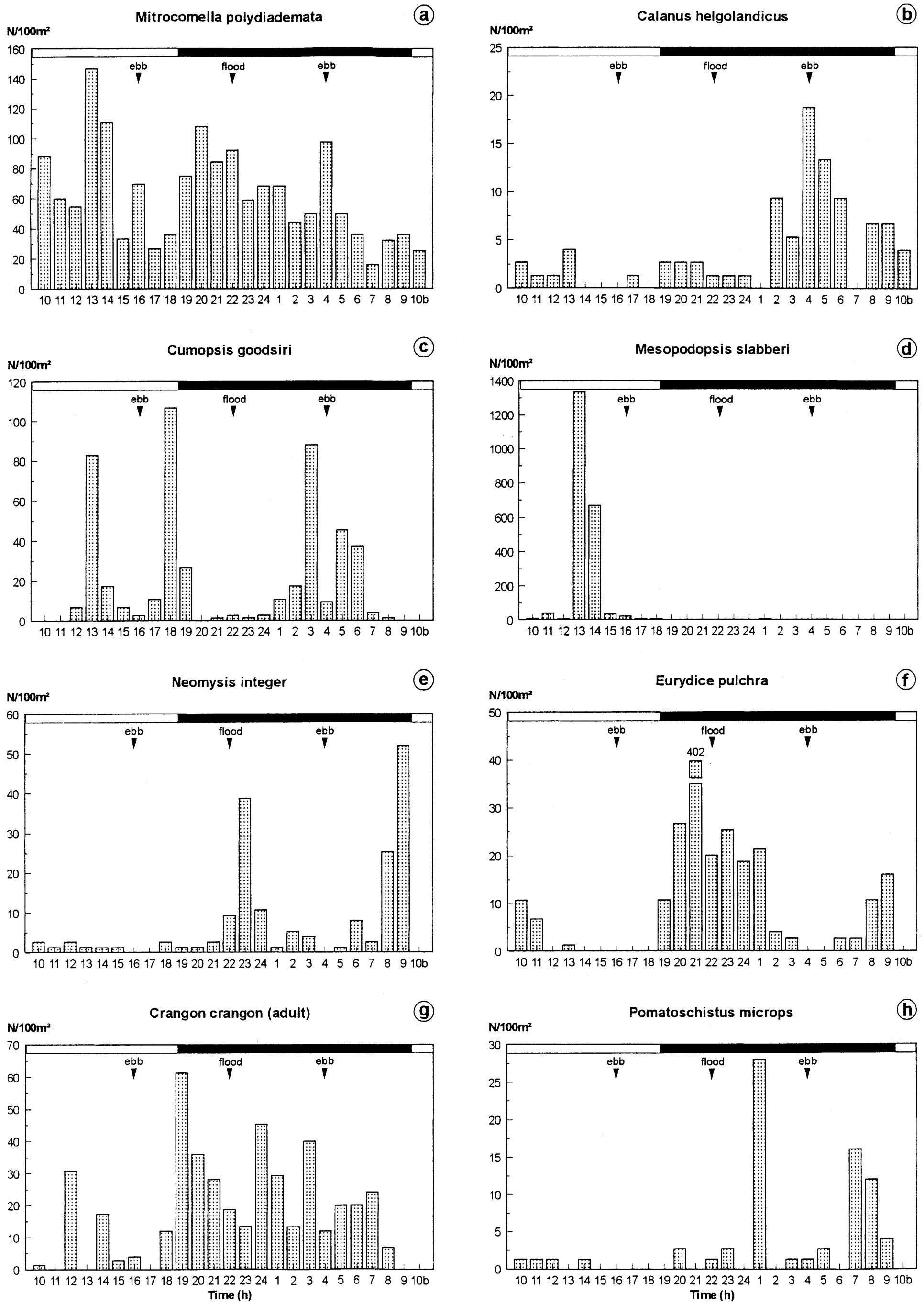
Planktonic species like *Mitrocomella polydiademata* (Cnidaria) (Fig. 2a) and *Pleurobrachia pileus* (Ctenophora) showed no clear pattern of occurrence. Despite the fact that calanoid copepods cannot be sampled efficiently with a 1 mm mesh net, *Calanus helgolandicus* (Fig. 2b), *Centropages typicus* 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



Mitrocomella polydiademata ⓐ

Calanus helgolandicus ⓑ

Cumopsis goodsiri ⓒ

Mesopodopsis slabberi ⓓ

Neomysis integer ⓔ

Eurydice pulchra ⓕ

Crangon crangon (adult) ⓖ

Pomatoschistus microps ⓗ

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).

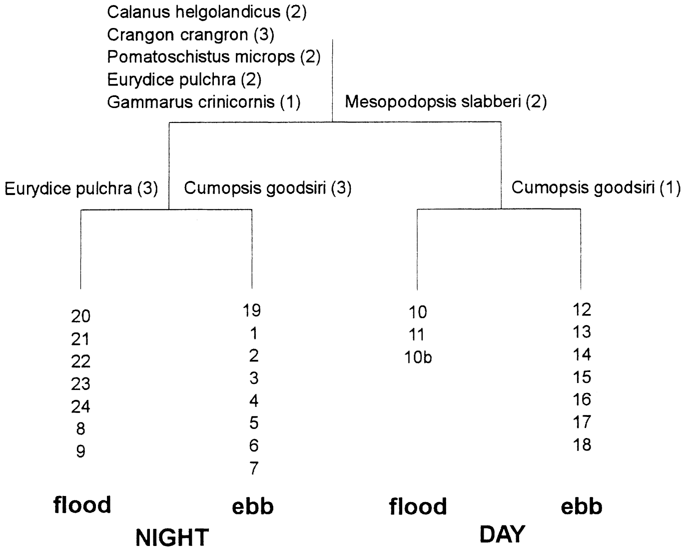


Fig. 3. – TWINSPAN with the density data. Indicator species with pseudospecies cut level are given for each division.

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 day and night samples were spatially segregated. Along the second axis, the samples taken at low and at high water were segregated. The tidal height and the light intensity were the largest vectors, which explained most of the variation in the ordination plane. The other parameters explained only a little of the variation between the different samples.

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

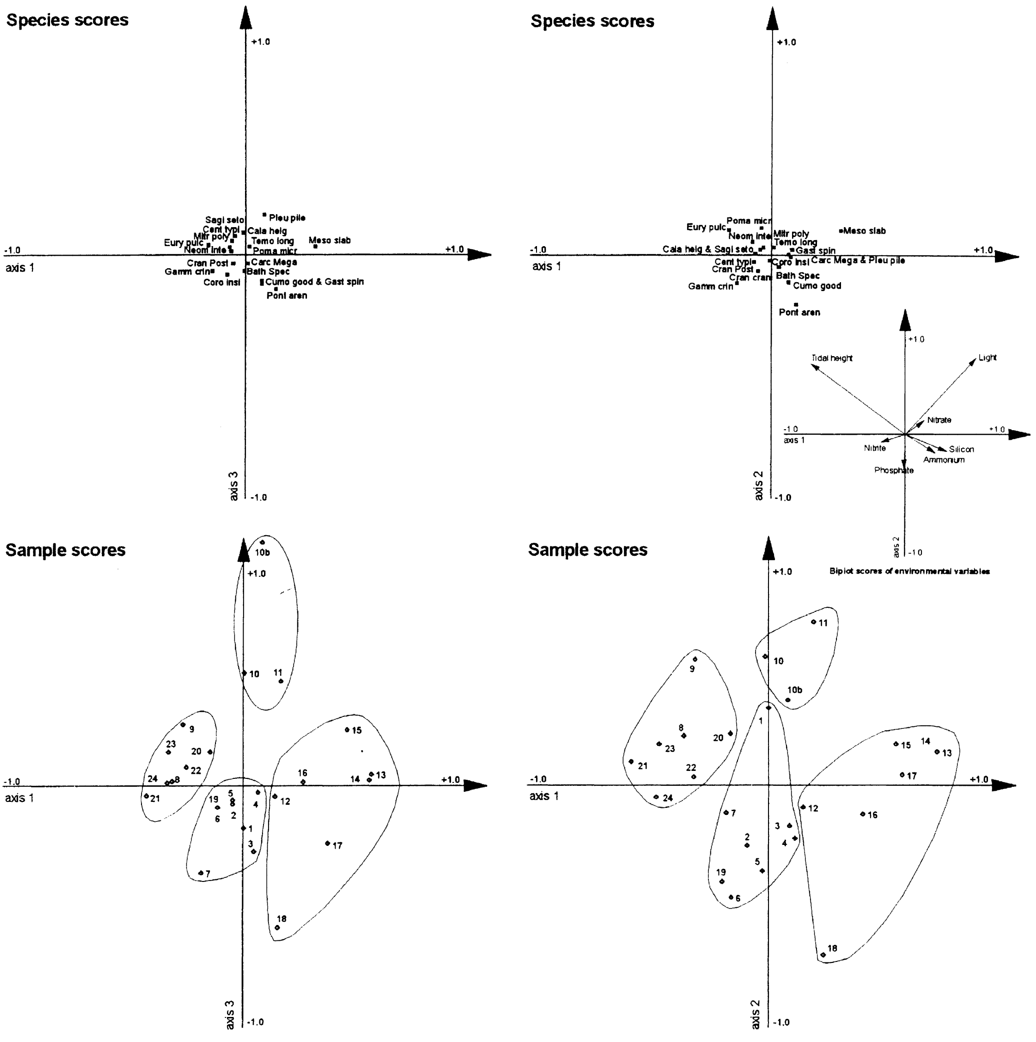


Fig. 4. – Correspondence Analysis (left) and Canonical Correspondence Analysis (right) of the fourth root transformed density data.

TWINSPAN clusters were clearly separated in the ordination plane formed by the first and the third axis (Fig. 4). The similarity between the sample scores from the direct and the indirect gradient analysis indicates that the most important environmental parameters were measured. The light intensity and the tidal height were indeed shown to be the most important parameters in the explanation of the circadiel patterns of the intertidal fauna.

The direct and the indirect gradient analysis of the biomass data gave the same pattern after removing the outliers *Pomatoschistus microps* and *Gammarus crinicornis* (not presented).

As can be seen in Fig. 5, the identified assemblages were separated very well into a day versus a night situation. The same held true for the differentiation between the floodtide and the ebbtide situation: the edge between those assemblages was found to be at a tidal height of approximately 3 m above ELWS.

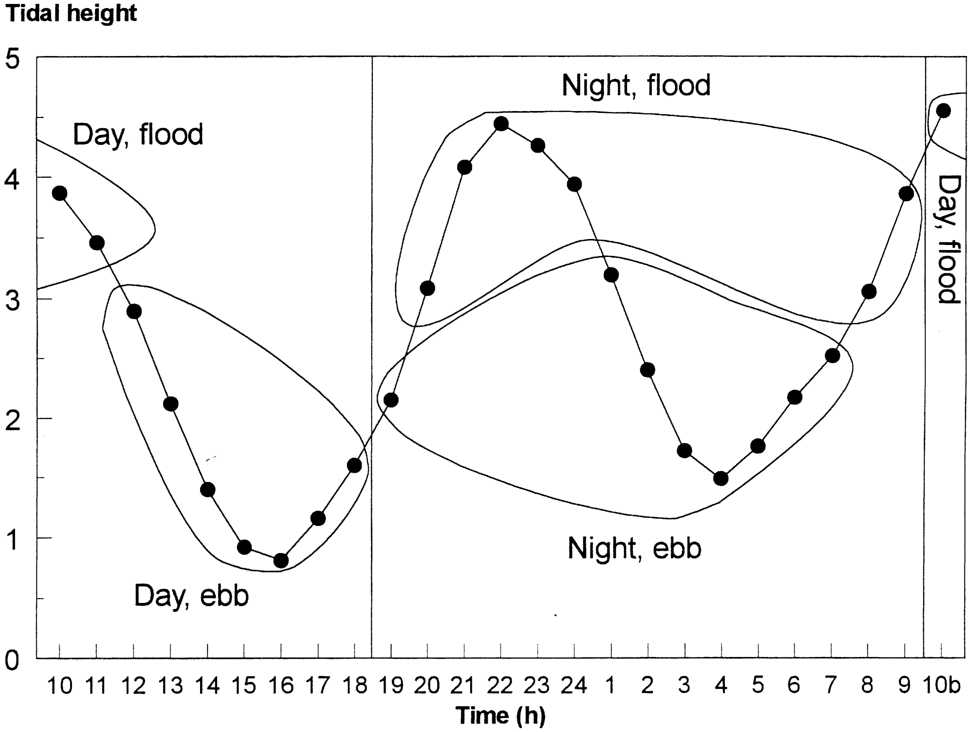


Fig. 5. – The waterlevel per hour with indication of the distinguished assemblages.

Characterisation of the assemblages

The average abundance and biomass of the different assemblages, as identified by TWINSPAN and confirmed by the ordination, are shown in Fig. 6. In the pie charts, the faunistic composition of each cluster is shown.

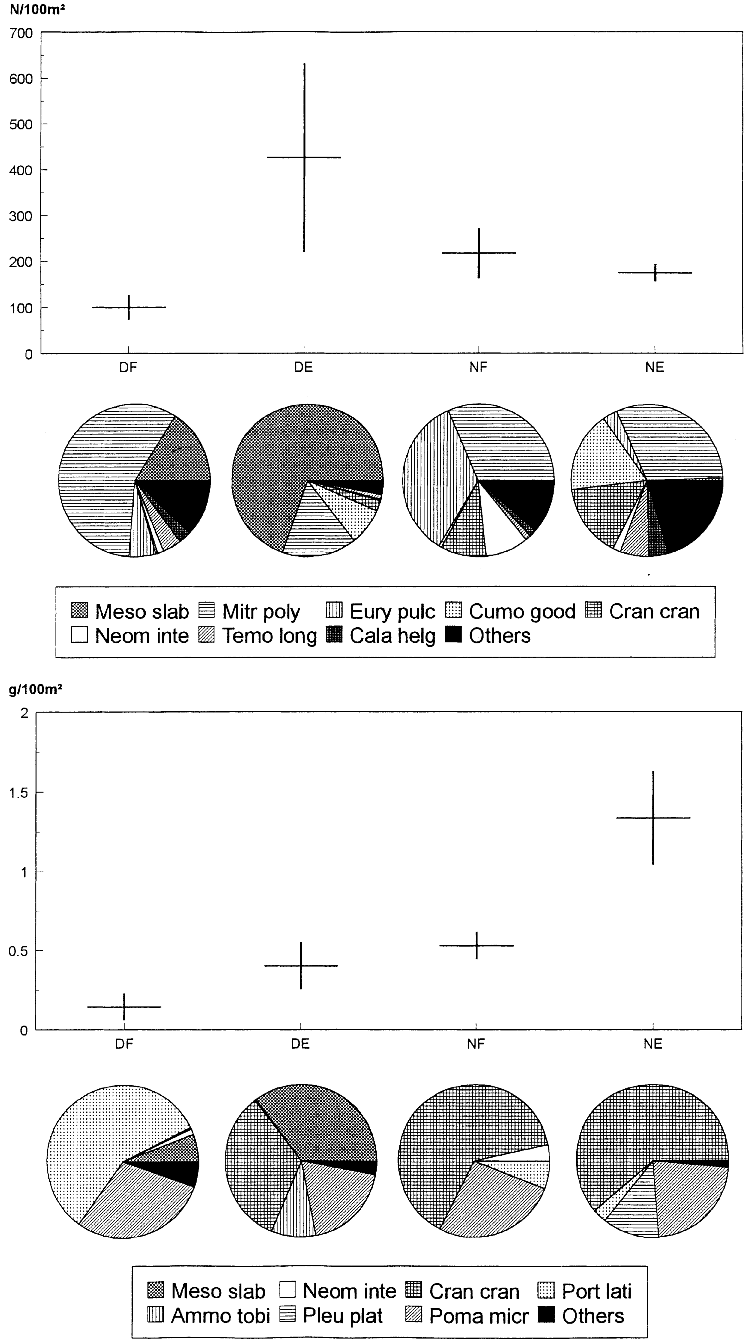


Fig. 6. – Average density and biomass of the four assemblages, as identified by the multivariate analyses with indication of the standard error. The species composition of each assemblage is shown in the pie charts below each graph.

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 tidemarks. 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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