

RECRUITMENT OF MEROPLANKTONIC LARVAE
IN THE SOUTHERN BIGHT OF THE NORTH SEA

A. Belgrano ¹, M. Vincx ¹, J.M. Dewarumez ², A. Richard ²,
J. Craeymeersch ³ & C. Heip ³.

¹ Institut de Zoologie, section de biologie marine, Université d'Etat de Gand,
Ledeganckstraat, 35, B 9000 Gand, Belgique

² Station Marine, B.P. 80, 28, avenue Foch, F 62930 Wimereux

³ Delta Instituut voor Hydrobiologisch Onderzoek, Vierstraat 28,
N 4401 EA, Yerseke, The Netherlands.

Key-words: North Sea, recruitment, meroplankton, macrobenthos, meiobenthos.

Mots-clés: mer du Nord, méroplancton, macrobenthos, méiobenthos.

Abstract

The density distribution of meroplanktonic larvae is compared with the density distribution of adults in the benthos, at five coastal stations in the Southern Bight of the North Sea (*Abra alba* community).

Plankton communities were sampled during one tidal cycle, along a buoy traject or at a fixed point; southern and northern locations, 250 m from each central sampling point, have been investigated too. Benthos samples were taken only at the central points of this traject. Meroplankton consisted of polychaete larvae (9 families) and bivalve and echinoderm larvae. The highest density values of these larvae (6,400 ind./0.25 m²) are found on the southern sites of each traject (closest to the coastline).

The highest meroplankton densities are found where the macrobenthos and meiobenthos density values are low.

Results suggest the existence of a larval flux established by specific water bodies running parallel to the coastline. Higher meroplankton densities are present after high water and just before low water. The picture which emerges from this preliminary survey of recruitment shows the important influence of hydrodynamics on biological processes. The meroplankton density distribution pattern at the different locations shows a clear effect of short-term tidally induced variability.

Résumé

**Recrutement de larves méroplanctoniques
dans le Bight Sud de la mer du Nord**

La densité des populations larvaires méroplanctoniques est comparée avec la densité des populations benthiques sous-jacentes dans la baie Sud de la mer du Nord (communauté à *Abra alba*). Les communautés planctoniques ont été étudiées, pendant un cycle de marée, en suivant les dérives de bouées ainsi qu'en point fixe, en plusieurs stations. Des prélèvements à 250 m au nord et au sud des dérives ont permis d'étudier la dispersion latérale des populations larvaires. Les populations benthiques ont également été échantillonnées tout au long des dérives des bouées.

Le méroplancton est constitué essentiellement de larves d'Annélides polychètes (9 familles), de bivalves et d'échinodermes. La densité de ces larves est toujours la plus forte (6400 ind./0,25 m²) aux stations échantillonnées au sud des dérives, c'est-à-dire aux stations les plus côtières, et ce malgré les renverses de courant.

Les plus fortes densités larvaires sont trouvées au-dessus de populations d'adultes à faible densité, après la marée et juste avant la marée basse.

Les résultats suggèrent l'existence de la canalisation des flux larvaires au sein de veines d'eau qui circulent parallèlement à la côte.

Le fait qui ressort de cette étude préliminaire est l'influence à court terme des processus hydrodynamiques, générés par des facteurs courantologiques et météorologiques, sur les phénomènes biologiques.

INTRODUCTION

Most members of the macrobenthos have a planktonic larval phase; the recruitment of these larvae depends mainly on their distribution in the water column during the pelagic phase, a successful settlement, and the survival of the postlarvae as temporary meiobenthos within the sediment. The majority of benthic studies do not mention the pelagic and early juveniles stages of macrofaunal animals, but only the interaction between adults. Thorson (1966) suggested that recruitment and early-life stages play an important role in bottom population dynamics. Muus (1973), Woodin (1976), Peterson (1977) and Highsmith (1982) pointed out that interactions between species in the early-life stages of their complex life cycle may reflect some of the biological processes occurring between benthic communities during their life history. Eckman (1983) emphasized the fact that hydrodynamic and other physical phenomena are very important in the recruitment of marine invertebrates: substrate selection, predation or disturbance are greatly influenced by hydrodynamic processes. Butman (1987) distinguished clearly between the different events in the life-cycle : metamorphosis, settlement and recruitment. The following phenomena are discussed in this paper: a) hydrodynamic processes affecting the recruitment of benthic organisms, b) existence of possible pollution-induced effects on recruitment, c) effect of meiofauna on settling macrofauna.

The coastal area (Fig.1) of the Southern Bight of the North Sea is characterized by high densities of macrobenthic species, as reported in a number of studies on the French coast by Dewarumez *et al.*, 1978, Dewarumez, 1979, Souplet & Dewarumez, 1980 and Souplet *et al.*, 1980; and on the Belgian coast by Govaere *et al.*, 1980, Vanosmael *et al.*, 1982, Willems *et al.*, 1982 and Vermeulen & Govaere, 1983.

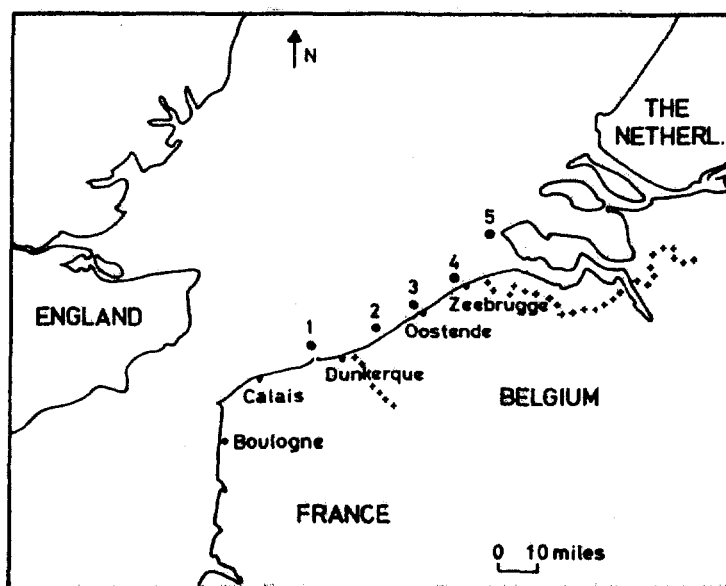


Fig. 1 - Zone d'étude : localisation des cinq sites.
- Study area : location of the five sampling sites.

MATERIAL AND METHODS

Study area

The hydrodynamic regime of the Southern Bight of the North Sea is characterized by strong northeasterly mesoscale currents produced by tides, concomitant with residual currents generated by the flow through the North Sea of the two branches of the North Atlantic current (Nihoul & Runday 1975, Nihoul 1975, 1980; Nihoul & Runfala 1981); the main pattern of the residual circulation in the Southern Bight of the North Sea is described here, and the existence along the Belgian coast of a southbound coastal current accompanied by the residual coastal gyre off Zeebrugge is demonstrated. Long-wave residue models are reproduced by the Mesoscale Reynolds Stress Models (Runday and Nihoul 1978, 1979; Backhaus 1982), which in mathematical terms try to solve the time-dependent hydrodynamic equations which describe the macroscale and mesoscale processes related to the residual circulation pattern in the Southern Bight of the North Sea. The five stations sampled are shown in Fig. 1; the coordinates of each location as well as the date of sampling are indicated in Table 1.

DATE	STATION	COORDINATES
15.06.88	GRAVELINES STATION 1	51°01'10'' N 2°04'50'' E
19.06.88	NIEUWPOORT STATION 2	51°10'04'' N 2°35'02'' E
30.06.88	OOSTENDE STATION 3	51°17'30'' N 2°55'03'' E
20.06.88	ZEEBRUGGE STATION 4	51°18'26'' N 2°56'72'' E
2.07.88	OOSTERSCHELDE STATION 5	51°38'06'' N 3°36'63'' E

Table 1 - Sampling date and coordinates of the five sampling stations.
- *Dates de prélèvement et coordonnées des cinq sites d'étude.*

Sampling at sea

Sampling took place from 12 June to 2 July 1988. Two different sampling designs have been used and named : a) tidal cycle and b) fixed point.

Tidal cycle

During one tidal cycle (13h), a buoy has been followed at three different sampling sites: Gravelines (station 1), Nieuwpoort (station 2) and Zeebrugge (station 4). The occurrence of High and Low water at each location for each sampling day is reported in Table 2. Samples were taken according to the sampling plan outlined in Fig. 2, meroplankton samples were taken with a plankton net model WP2 (UNESCO 1968) equipped with a 80 micron mesh size for a

DATE	STATION	TIME	
		H.W	L.W
15.06.88	GRAVELINES	2.03	9.03
	STATION 1	14.23	21.24
19.06.88	NIEUWPOORT	4.47	11.57
	STATION 2	17.07	0.17
20.06.88	ZEEBRUGGE	6.17	13.25
	STATION 4	18.36	1.44

Table 2 - Sampling date and time of High and Low water of three sampling stations.

- Date de prélèvement et heure des marées pour trois sites étudiés.

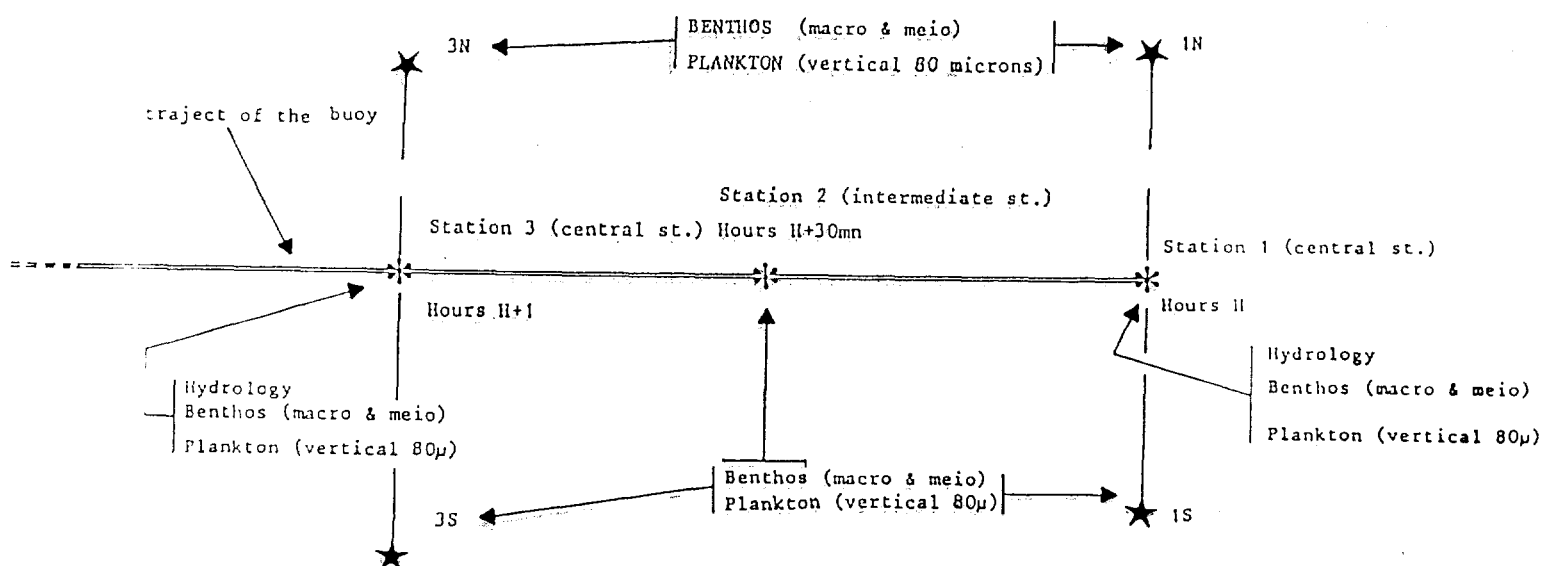


Fig. 2 - Sampling method along the buoy trajectory during a tidal cycle.

- Méthode d'échantillonnage le long du trajet de la bouée pendant un cycle de marée.

surface area equivalent to 0.25 m². At each location respectively 10, 30 and 15 samples were taken. In order to investigate the lateral larval dispersion, two stations located respectively north and south of the central station, at a distance of 250 m from the trajectory of the buoy, were sampled. One additional intermediate station was sampled at approximately 30 minutes from each central station; this was necessary in order to verify the presence of adult benthic populations along the trajectory of the buoy and to envisage a possible larval flux transported by the previous water body sampled.

To complete the pelagic study on benthic populations (juveniles and adults) at Nieuwpoort, ten macrobenthos grab samples and ten meiobenthos core samples were taken respectively at each central station, using a Van Veen grab. The Reineck box corer for

meiobenthos sampling (although more suitable) was not used owing to bad sea conditions. The meroplankton, macrobenthos, and meiobenthos samples were fixed with 10% per volume of formalin (4% formaldehyde). Temperature, dissolved oxygen and salinity were measured using a sonde. The N.T.U (Nephelometric Turbidity Unit) measurements were performed on board using a nephelometer with a Tyndall effect (DRT 1000, HF Instrument).

Fixed point

At two other stations, the boat stationed at the same location for one tidal cycle (13h), and samples were taken every hour at these stations (Oostende, station 3, Oosterschelde, station 5). A total of 11 and 13 meroplankton samples were taken respectively at each location.

Treatment of the samples in the laboratory

In order to determine the content of each meroplankton sample, it is necessary to reduce the total volume of the container from 1,500 ml to 500 or to 100 ml, according to the richness of the sample itself. This was done by removing excess liquid from the container while the meroplankton remained in the sediment at the bottom of the container. Small aliquots of approximately 0.5 ml were counted using a Dollfus dish and with the aid of a stereoscopic microscope. The samples were sorted according to the method outlined by Blin (1988).

The macrofauna samples were treated on a sieve of mesh size 0.5 mm. Extraction of the meiofauna from the sediment was performed by using the method described in Heip *et al.*, 1985.

RESULTS

Meroplankton

The general taxa distribution of the meroplanktonic larvae at the five stations is presented in Table 3. Polychaetes, bivalves, and echinoderms are identified respectively at the family, class, and superfamily level. Impoverishment is evident from Gravelines (12 taxa) to the Oosterschelde (5 taxa) with a minimum of only 3 taxa at Zeebrugge. Amongst the Polychaetes, Spionidae and Terebellidae are found at the five sites; while Aphroditidae and Owenidae are only found at Gravelines. Sabellidae are only present at Nieuwpoort. Bivalves are present at every location and echinoderms are only absent at Zeebrugge.

Data on Gravelines are reported in Blin (1987-1988), data concerning Nieuwpoort and Zeebrugge are discussed in this paper.

Table 4 and Fig. 3 show the distribution of the mean number of individuals per station for each main taxon studied: Polychaeta, Bivalvia, and Echinodermata. The same decreasing trend was recorded and Zeebrugge (station 4) turned out to be the poorest site in terms of meroplankton density distribution and a recruitment rate of a mean total of 544 ind./0.25 m² in comparison with the highest values at Gravelines (station 1) (mean total of 64,970 ind./0.25 m²).

The echinoderms occur in high numbers only in the southwestern stations (1 and 2) and are almost absent from Oostende (station 3) northwards. Polychaetes follow the same decreasing trend from southwest to northeast. The bivalves do not tend to decrease: the Oosterschelde region (station 5) has the second highest density values (3106 ind./0.25 m²) after Gravelines (25,548 ind./0.25 m²).

The buoy trajectories of station 2 (Nieuwpoort) and station 4 (Zeebrugge) are described in more detail.

LOCATIONS					
TAXA	GRAVELINES	NIEUWPOORT	OOSTENDE	ZEEBRUGGE	OOSTERSCHELDE
Aphroditidae	*	-	-	-	-
Owenidae	*	-	-	-	-
Spionidae	*	*	*	*	*
Pectinariidae	*	*	*	-	-
Terebellidae	*	*	*	*	*
Magelonidae	*	*	*	-	*
Nereidae	*	*	-	-	-
Nephtyidae	*	*	*	-	-
Sabellidae	-	*	-	-	-
Phyllodocidae	*	*	-	-	-
Ophiuroidea	*	*	-	-	-
Echinoidea	*	*	*	-	*
Bivalvia	*	*	*	*	*
Total	12	11	7	3	5

Table 3 - Macrobenthic larvae of the meroplankton at the five sampling locations (* = presence; - = absence).

- *Présence (*) ou absence (-) des larves méroplanctoniques aux cinq sites étudiés.*

Density (ind./0.25 m ² ± se) of the meroplankton						
	Polychaeta		Bivalvia		Echinodermata	
Station 1 (n=10)	8954	± 723	25548	± 2724	30468	± 4031
Station 2 (n=30)	1085	± 130	759	± 181	314	± 37
Station 3 (n=11)	790	± 148	2665	± 594	2	± 2
Station 4 (n=15)	15	± 7	529	± 238	0	± 0
Station 5 (n=13)	80	± 11	3106	± 614	11	± 4

Table 4 - Density (ind./0.25 m² ± standard error) of meroplankton at the five sampling stations.

- *Densité (ind./0,25 m² ± erreur standard) des larves méroplanctoniques aux cinq sites étudiés.*

meroplankton density (ind./0.25 m²)

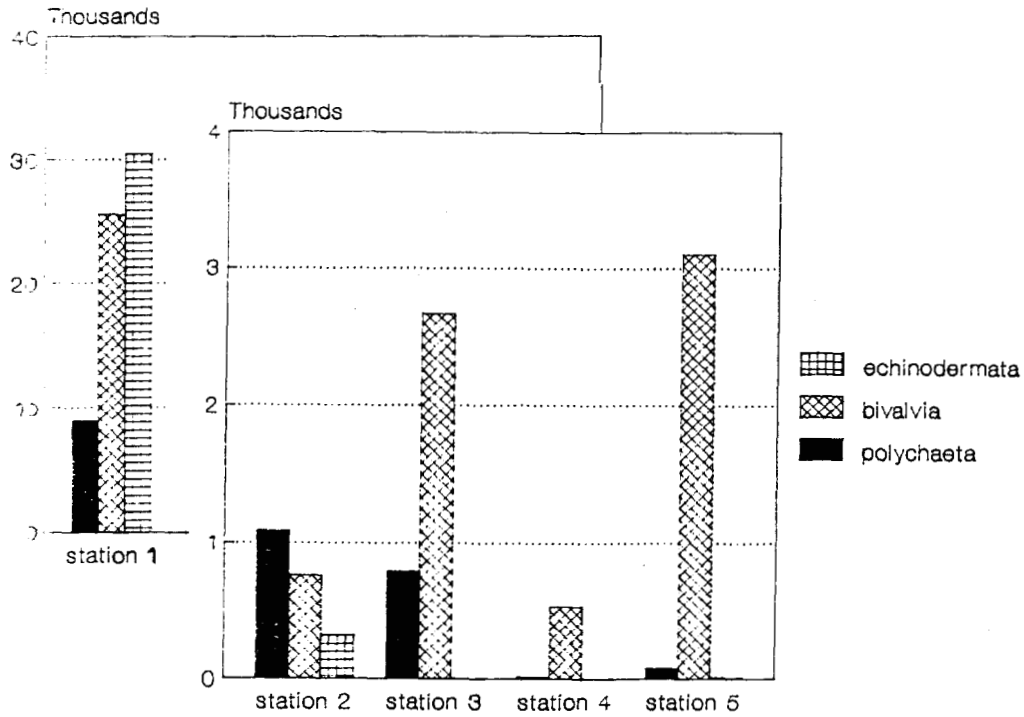


Fig. 3 - Density of meroplankton at the five sampling sites.
- *Densité des populations méroplanctoniques aux cinq sites étudiés.*

Nieuwport

The buoy trajectory obtained during one tidal cycle, as shown in Fig. 4, demonstrated that the ebb tide current ran in the opposite direction to the prevailing northeasterly watermasses flowing from the English Channel and generated by the flow of the North Atlantic current through the Straits of Dover. The association of mesoscale tidal and velocity currents, residual velocities and wind-induced currents with meteorological changes throughout the year seems to contribute to the establishment of a residual circulation pattern. The Belgian coastal area is characterized by the Zeebrugge gyre which, according to the current measurement along the Northern Belgian coast (Ronday and Nihoul 1978, 1979) is responsible for the generation of a south-bound coastal current turning westward at Oostende. The ebbing and flooding channels of the Scheldt estuary, bearing respectively south and north off the Belgian coast, also determine changes in the physico-chemical characteristics of the coastal water masses, and in particular increase the input of plume coming from the Scheldt estuary along the Belgian coast.

The density of the meroplankton has been determined from the southern, central and northern location of the 10 sites on the buoy trajectory (see Fig. 4, sites n. 1 to 23). The southern locations always are close to the coastline throughout the period of one tidal cycle; the northern stations are always farther off shore than the corresponding southern location.

The first sampling was performed at 8.13 a.m. (site 1) and the last one at 19.33 p.m. (site 23). Low water was at 11.57 a.m. just after site 7, high water was at 17.07 p.m. between site 17 and 19.

The meroplankton density values vary between 410 ind./0.25 m² and 6,400 ind./0.25 m² (Table 5). The density values during the morning ebb tide decreased drastically and became

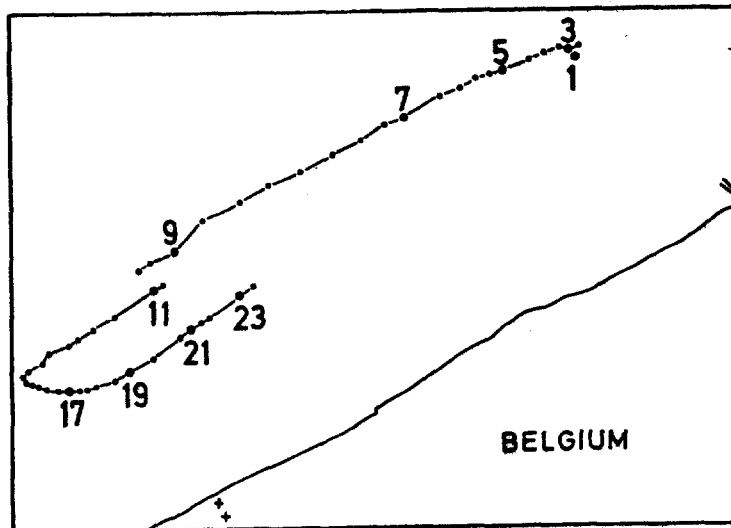


Fig. 4 - Traject of the buoy during a tidal cycle at station 2 (Nieuwpoort).

- Trajet de la bouée pendant un cycle de marée à Nieuwpoort.

Meroplankton density (ind./0.25 m ²)				
site	time	north	central	south
1	8.13	3240	3340	4510
3	9.07	2190	2960	6400
5	10.10	3970	4600	3340
7	11.10	1800	1500	1860
9	13.11	2030	1170	3180
11	13.46	410	440	2630
17	16.36	1180	500	2080
19	17.36	1190	540	1880
21	18.33	1260	880	1840
23	19.33	940	440	2340

Table 5 - Density (ind./0.25 m²) of meroplankton at station 2 (Nieuwpoort) in the northern, central and southern sampling points of each site, including the time of sampling.

- Densité (ind./0,25 m²) des larves méroplanctoniques aux stations nord, centre et sud du site de Nieuwpoort.

more or less stable during the flood tide (Fig. 5). With the ebb tide in the evening meroplankton densities again tend to increase at the southern sampling points along the buoy trajet. Unfortunately the sampling time available was too short to have these patterns confirmed for the whole period of the evening ebb tide.

The comparison between the Central, South and North Bight as reported in Figs. 5 & 6, shows a clear difference between north and south, but no major differences in density values between the North and Central Bight (see trend-line analysis in Fig. 5). The density values for the three major taxa (polychaetes, bivalves, echinoderms) at each sampling point, south, central, and north for the 10 sites are presented in Fig. 7. The sampling sites 1, 3, and 5 have the highest density values concomitant to the ebbing tide, while sampling site 17 and 19 have the lowest density approaching the High water time.

The larvae of the echinoderms show a more or less constant density value along the buoy trajet, but the southern stations have the highest values in 8 out of the 10 sites. The polychaetes of sites 1 to 5 (North + Central + South) are significantly higher than in the other sites, with no constant differences between north, central and south. The bivalves are extremely abundant in sites 1 to 9, with a very patchy distribution (large difference between the southern and the other stations) in sites 1 and 3.

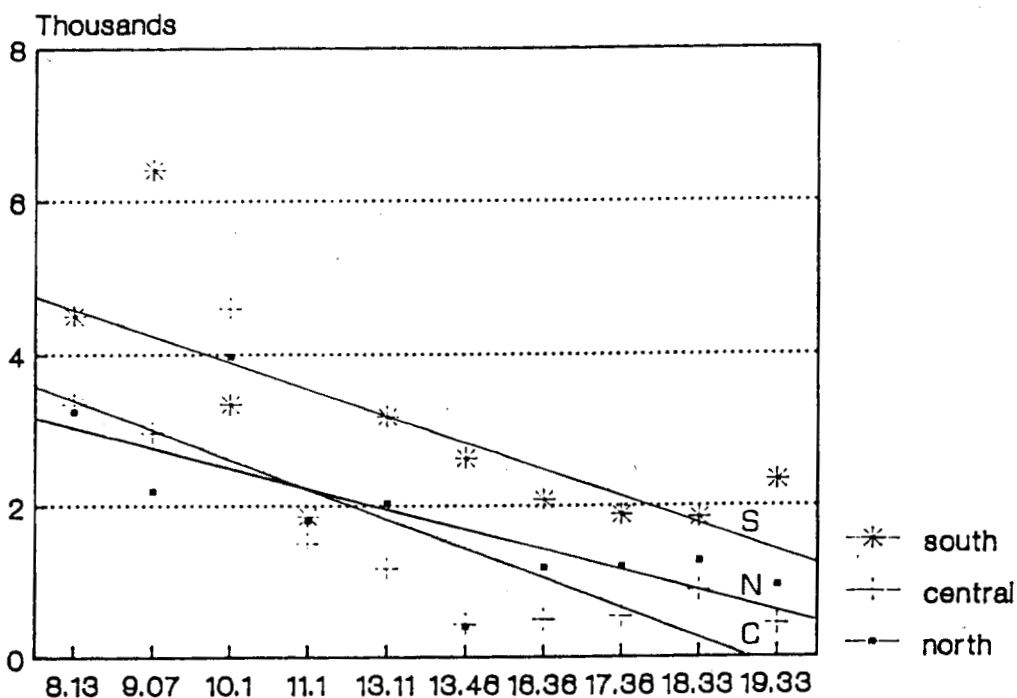


Fig. 5 - Density (ind./0.25 m²) of meroplankton at the northern, central and southern position of the ten sampling sites (Nieuwpoort, station 2) (abscissa values indicate the time of sampling) and trend-line for each set of samples.

- Densité (ind./0,25 m²) du méroplancton aux stations nord, sud et centre (Nieuport, station 2) (les valeurs en abscisses indiquent les heures de prélèvement) et tendance pour chaque série.

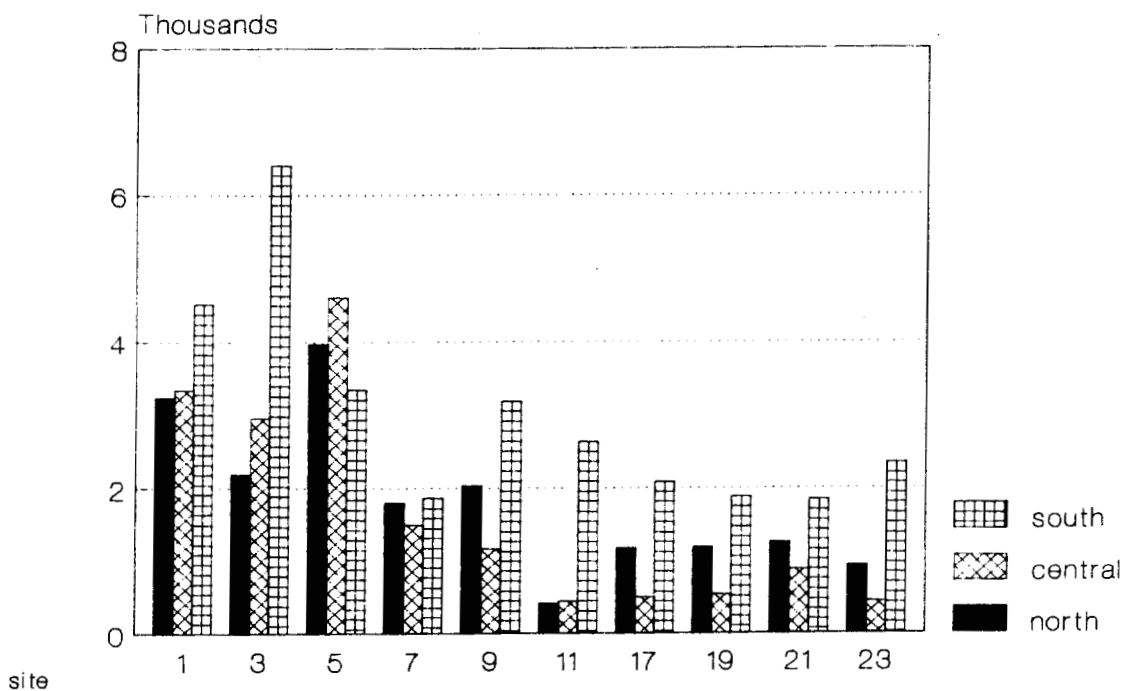


Fig. 6 - Density (ind./0.25 m²) of meroplankton at the northern, central and southern position of the ten sampling sites (Nieuwpoort, station 2).

- Densité (ind./0,25 m²) du méroplancton aux stations nord, sud et centre (Nieuport, station 2).

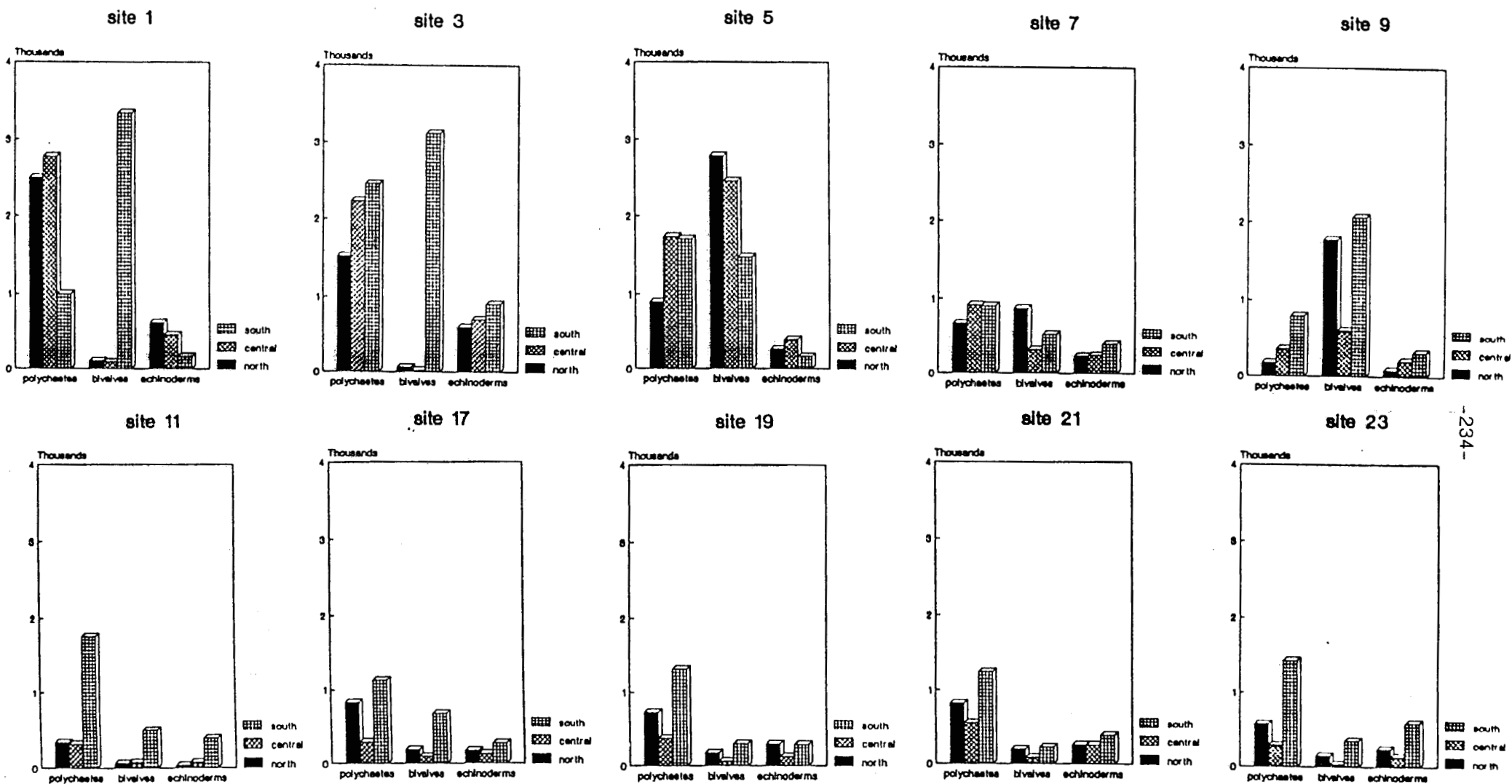


Fig. 7 - Density (Ind./0.25 m²) of polychaetes, bivalves and echinoderms at the ten sampling sites in Nieuwpoort in the southern, central and northern locations of each site.

- Densité (ind./0,25 m²) des polychètes, des bivalves et des échinodermes aux stations nord, sud et centre du trajet Nieuwpoort.

The benthos samples were analysed for each central station and compared with the meroplankton of these stations. Macrobenthic densities are very different between the ten sites (Table 6) ; values range between 8 ind./0.1 m² (site 17) and 192 ind./0.1 m² (site 19). Nine polychaete families are found; the Nephtyidae and the Terebellidae are the most important ones with a frequency of 90% and 60% respectively; amongst the bivalves the Tellinidae and the Scrobicularidae are the dominant families with a frequency of 90% and 60% respectively; the echinoderms are present with a frequency of 30% for the Ophiuroidea and Echinoidea.

NIEUWPOORT MACROBENTHOS											
NUMBER OF INDIVIDUALS PER 0.1 m ²											
TAXA	SITE	1	3	5	7	9	11	17	19	21	23
Spionidae		1	-	1	-	2	5	-	1	-	-
Pectinariidae		3	-	-	-	-	-	-	-	-	-
Terebellidae		-	-	3	-	14	27	-	135	2	17
Magelonidae		-	-	-	-	7	-	-	12	3	-
Nereidae		-	-	-	-	-	-	-	-	-	-
Nephtyidae		12	2	5	7	-	10	3	4	8	5
Cirratulidae		-	-	2	-	4	3	-	1	2	-
Glyceridae		-	-	1	2	-	3	-	1	1	1
Maldanidae		3	-	-	-	-	-	-	-	-	-
Nemertini		-	-	-	-	-	1	-	-	-	-
Oligochaeta		-	-	-	-	-	1	-	-	-	-
Tellinidae		55	2	19	3	19	41	4	32	-	1
Scrobicularidae		32	5	2	-	2	3	-	2	-	-
Myacea		2	-	-	-	-	-	-	-	-	-
Maत्रacea		2	-	1	-	-	2	-	1	-	-
Mytilacea		-	-	-	1	-	-	-	-	-	-
Veneracea		1	-	-	-	-	-	-	-	-	-
Naticidae		2	2	-	-	-	-	-	-	-	-
Anthozoa		17	-	-	-	-	16	-	3	1	-
Ophiuroidea		3	-	1	-	-	5	-	-	-	-
Echinoidea		-	-	5	-	3	-	1	-	-	-
TOTAL		133	11	40	13	51	117	8	192	17	24

Table 6 - Density (ind./0.1 m²) of the macrobenthic taxa at the ten sampling sites in the Nieuwpoort (station 2) sampling area.

- Densité (ind./0.1 m²) du macrobenthos aux dix stations du site de Nieuwpoort.

Meiobenthic density values range between 214 ind./10 cm² (site 7) and 1,624 ind./10 cm² (site 11) (Table 7); nematodes and copepods are found at each site and are the most important components. It is interesting to note the presence within the meiofauna of newly settled macrobenthic larvae, such as the polychaete families Pectinariidae, Terebellidae, Magelonidae, and Phyllodocidae, but in very low numbers; newly settled bivalves larvae were found at each site; newly settled echinoderm larvae were only found once.

NIEUWPOORT MEIOBENTHOS											
NUMBER OF INDIVIDUALS PER 10 cm ²											
TAXA	SITE	1	3	5	7	9	11	17	19	21	23
Nematoda		827	337	253	143	873	1,435	578	1,386	421	389
Copepoda		18	12	2	44	21	31	24	30	19	34
Isopoda		-	-	-	-	-	-	-	1	-	-
Halacaroida		-	-	1	3	2	9	4	8	1	-
Spionidae		-	-	-	-	-	3	-	-	-	-
Pectinariidae		-	-	-	-	-	1	-	-	-	1
Terebellidae		-	-	-	-	-	-	-	-	2	-
Magelonidae		-	-	-	1	1	1	-	1	-	2
Phyllodocidae		1	-	-	-	-	-	-	-	1	-
Cirratulidae		1	2	-	-	1	-	-	-	-	-
Bivalvia		14	2	-	4	3	20	2	4	1	3
Ophiuroidea		-	-	1	-	-	-	-	-	-	-
Other Meiofauna		48	12	30	19	27	124	13	32	8	46
TOTAL		909	365	287	214	928	1,624	621	1,462	453	475

Table 7 - Density (ind./10 cm²) of the meiobenthic taxa at the ten sampling sites in the Nieuwpoort (station 2) sampling area.

- *Densité (ind./10 cm²) du méiobenthos aux dix stations du site de Nieuwpoort.*

The meroplankton, macrobenthos, and meiobenthos density distributions are represented in Fig.8. The highest meroplankton density distribution was found concomitant to low macrobenthos and meiobenthos density values.

As it is an important macrobenthic component, we compare the densities of the Terebellidae both in the water column and in the sediment. At sampling sites 1 and 3 a high density of Terebellidae larvae with a range between 90 and 1,300 ind./0.25 m², (Table 8) are present in the absence of adult Terebellidae in the macrobenthos; at sampling point 19, a low density of Terebellidae larvae is found (170 ind./0.25 m²), concomitant to the highest number of adult Terebellidae in the macrobenthos 135 ind./0.1 m².

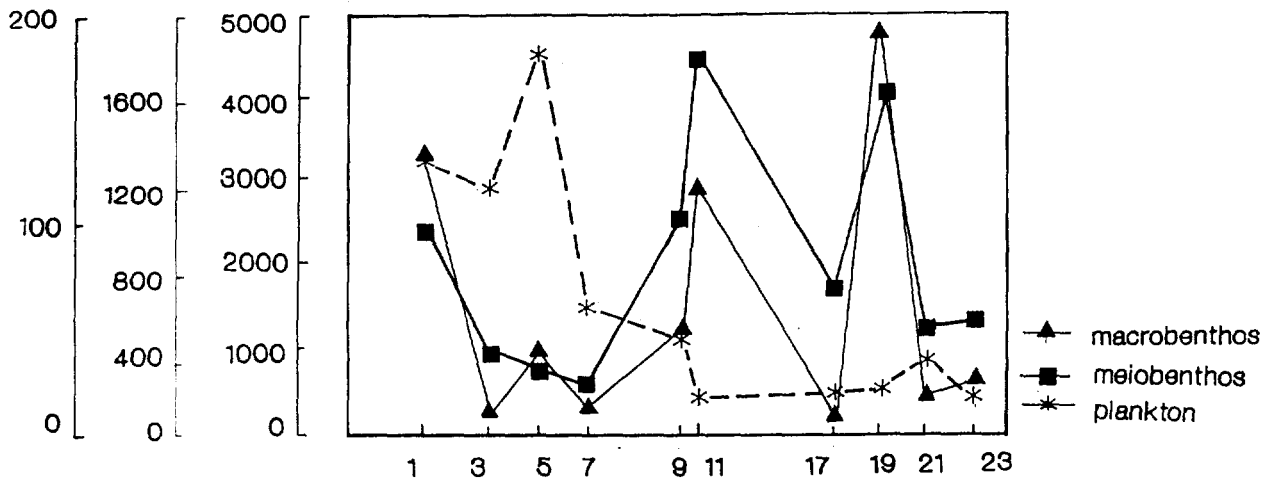


Fig. 8 - Density of macrobenthos (ind./0.1 m²), meiobenthos (ind./10 cm²) and meroplankton (ind./0.25 m²) at the ten sites in station 2, Nieuwpoort.
 - Densité du macrobenthos (ind./0,1 m²), du méiobenthos (ind./10 cm²) et du méroplankton (ind./0,25 m²) au cours du trajet Nieuwpoort.

NIEUWPOORT MEROPLANKTON											
NUMBER OF INDIVIDUALS PER 0.25 m ²											
TAXA	SITE	1	3	5	7	9	11	17	19	21	23
Spionidae		580	320	200	60	80	40	30	20	50	30
Pectinariidae		500	390	190	140	90	50	60	120	170	80
Terebellidae		1,280	1,300	920	560	100	180	140	170	280	90
Magelonidae		350	120	180	100	30	20	30	30	20	60
Nereidae		30	10	20	20	—	—	—	—	—	—
Nephtyidae		40	90	220	40	60	10	20	20	30	20
Bivalvia		90	20	2,460	330	610	70	90	60	80	30
Ophiuroidea		180	260	90	40	20	20	20	30	50	20
Echinoidea		290	450	320	210	180	50	110	90	200	110
TOTAL		3,340	2,960	4,600	1,500	1,170	440	500	540	880	440

Table 8 - Density (ind./0.25 m²) of the meroplankton taxa at the ten sampling sites in the Nieuwpoort (station 2) sampling area.
 - Densité (ind./0,25 m²) du méroplankton aux dix stations du site de Nieuwpoort.

Owing to the characteristic planktotrophic larval development of the Terebellidae, we suggest that the meroplanktonic larvae of the Terebellidae present at sampling points 1 and 3 may have been generated from the adult population present at sampling point 19.

The data available are not sufficient to formulate a more precise hypothesis concerning the recruitment rate and dispersion range of the Terebellidae larvae. The meiofauna data were insufficient to consider any possible effect of meiofauna on the settling of macrofauna and this aspect of the research needs to be specifically investigated by experimental techniques. At this early stage of the work, it is not possible to have any experimental approach to the problem until a preliminary research study such as this one is undertaken. According to the time of High water and Low water at all locations (see Table 2), the overall results obtained for Nieuwpoort showed that the highest density values are found after High water and before Low water (see Fig. 6) presumably at the highest tidal current speed. Thus dispersion seems to be affected by short-term tidally-induced variability.

Zeebrugge

At Zeebrugge, thanks to the same sampling technique as at Nieuwpoort, it is possible to compare the north, central and south sampling points (Figs. 9 & 10 and Table 9). The meroplankton samples at the five sampling sites at Zeebrugge (station 4) are characterized by high densities of bivalves which, in 10 out of the 15 sampling sites, were the only animals present in the plankton. Polychaetes are represented by Spionidae (5 stations) and Terebellidae (1 station). When comparing the northern, central and southern sites at each sampling point, a clear increase in bivalve density is found from north to south, the central point having an intermediate value. This trend is confirmed in Fig. 10 too (trend-line analysis of the density values of bivalves). The densities are higher at sites 1 and 3 (ebb tide) than at the three other sites (5-7-9).

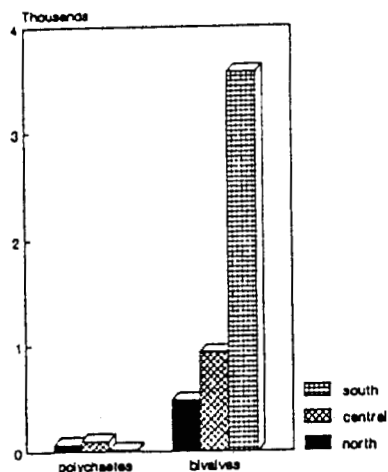
DISCUSSION

The picture which emerges from this preliminary survey of the recruitment of meroplanktonic larvae in the Southern Bight of the North Sea reveals the important influence of hydrodynamics on the biological processes. Results suggest the existence of a larval flux established by specific water bodies running parallel to the coastline at Nieuwpoort and Zeebrugge. Higher meroplankton density distribution occurred, except for the Oosterschelde, after High water and before Low water.

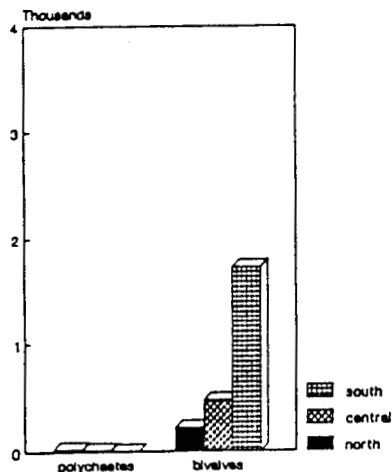
The results obtained for the buoy trajectory during a complete tidal cycle (see Figs. 7 and 9) and the meroplankton density distribution pattern at the different locations, show a clear effect of short-term tidally-induced variability on meroplankton recruitment. Likewise a clear increase in meroplankton density is found in the watermasses towards the coast at both stations. In work by White *et al.* (1988), the hydrodynamic and meteorological processes were investigated in relation to the recruitment behaviour of the *Nephrops norvegicus* (L) larvae; they concluded that geostrophic current patterns can be related to the transport of the larvae; they also suggested the need to relate larval recruitment more carefully to advection mixing and meteorological processes. Advection and suspension by currents as postulated by Uncles and Joint (1983) seem to be among the major forces determining the availability of phytoplankton concentrations to zooplankton, in turbid coastal areas such as the one studied here.

The effect of short-term tidally-induced variation on pelagic larvae dispersion has been observed by Levin (1986); she recorded a distinct bimodal abundance pattern related to the time of occurrence of High water and Low water. Okubo (1971) suggested that pelagic larvae disperse horizontally by oceanic diffusion, for approximately 100 km over a period of one

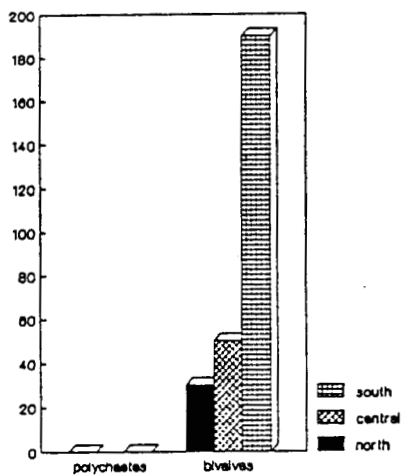
zeebrugge - station 4
site 1



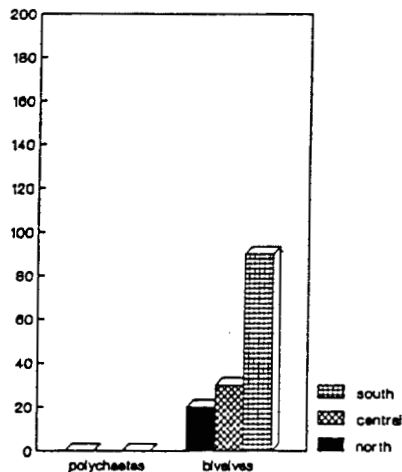
zeebrugge - station 4
site 3



site 5



site 7



site 9

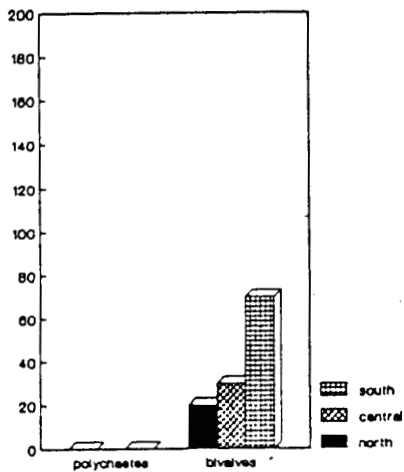


Fig. 9 - Density of meroplankton (ind./0.25 m²) at the five sampling sites at Zeebrugge in the southern, central and northern locations at each site.

- Densité (ind./0,25 m²) du méroplancton aux stations nord, sud et centre du trajet "Zeebrugge".

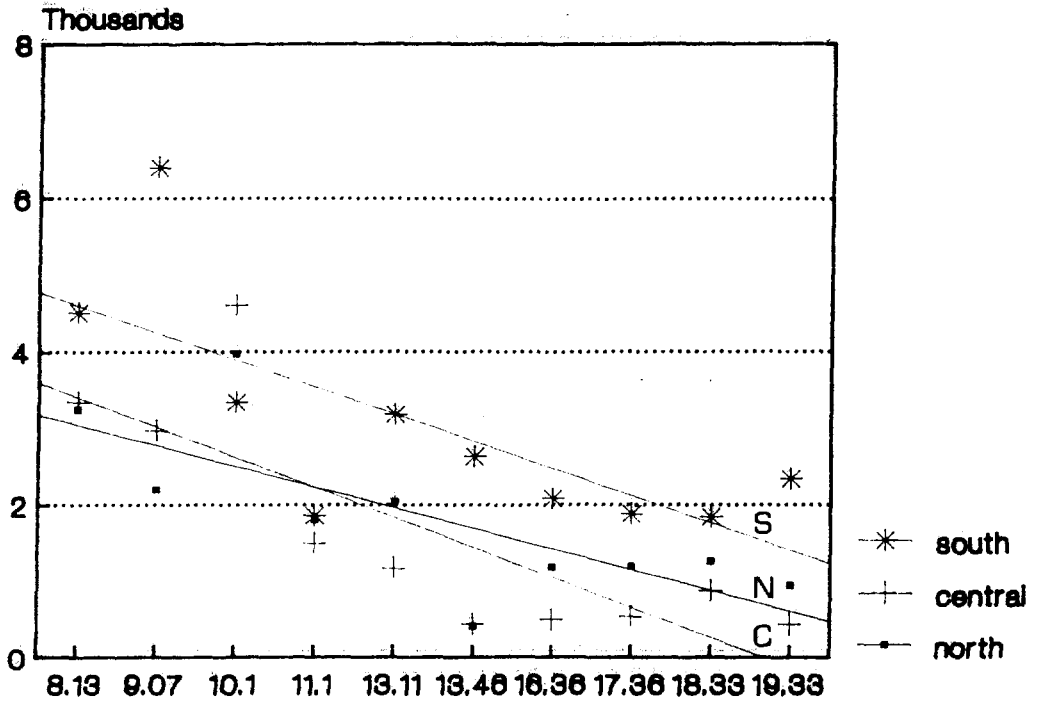


Fig. 10 - Density of meroplankton (ind./0.25 m²) in station 4 (Zeebrugge) in the southern, central and northern location of each site (abscissa values indicate the time of sampling).

- Densité (ind./0,25 m²) du méroplancton aux stations nord, sud et centre du trajet "Zeebrugge" (les valeurs en abscisse indiquent les heures de prélèvement) et tendance pour chaque série.

ZEBRUGGE MEROPLANKTON																
NUMBER OF INDIVIDUALS PER 0.25 m ²																
TAXA	SITE	1N	1C	1S	3N	3C	3S	5N	5C	5S	7N	7C	7S	9N	9C	9S
Spionidae		50	100	20	20	10	-	-	-	-	-	-	-	-	-	-
Terebelliidae		20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bivalvia		480	930	3,570	220	480	1,730	30	50	190	20	30	90	20	30	
TOTAL		550	1,030	3,590	240	490	1,730	30	50	190	20	30	90	20	30	

Table 9 - Density (ind./0,25 m²) of the meroplankton taxa at the five sampling sites (including the northern and southern sampling points) in the Zeebrugge (station 4) sampling area.

- Densité (ind./0,25 m²) du méroplancton aux cinq stations du site de Zeebrugge.

month. The description of the characteristics of the bottom boundary-layer flow, and the near-bed flow regime needed also to be taken into consideration, in order to relate the hydrodynamics of sedimentation processes to habitat selection during larval settlement (Butman 1987).

The preliminary consideration and results concerning the hydrodynamic regime of the study area suggest that biological processes such as the recruitment of meroplankton are directly linked to hydrodynamic and meteorological processes; more emphasis on the physical interaction on biological processes may therefore be needed, in order to avoid a deterministic approach which undoubtedly would result in a misunderstanding of the recruitment problem in relation to benthic population dynamics.

The complete set of results obtained for Nieuwpoort led to possible dispersion behaviour of the pelagic larvae belonging to the Terebellidae family being envisaged. The high abundance of Terebellidae larvae at sampling points 1 and 3 (see Table 8) corresponds to the absence of adults in the macrobenthos at the same sampling locations (see Table 6), thus suggesting that they might have been generated by the adult population present at sampling point 19. This result also suggested that the Terebellidae larvae found at sampling points 1 and 3 covered a distance of approximately 10 miles from sampling point 19 to sampling points 1 and 3. However, owing to long-lived planktotrophic larval development strategy exhibited by the Terebellidae, the so-called teleplanic larvae (Scheltema 1971, and Hines 1986), it is not possible to determine exactly the amount of time spent by the larvae in the water column, prior to being caught by the net.

According to Scheltema (1986), long-lived planktotrophic larvae can spend up to two months in the water column as temporary holoplankton, suggesting a possible interaction within the foraging activity of the holoplankton on the phytoplankton biomass. The results obtained for Nieuwpoort were not sufficient to formulate a more precise hypothesis concerning food partitioning resources within the benthic/pelagic component.

Our results do not allow us to draw any conclusions concerning the genetic-adaptive strategies hypothesis formulated in recent years by Sanders (1968), Grassle (1967), Bretsky and Lorenz (1970). They claimed that physically controlled communities seem to possess a high genetic variability, presumably generated by environmental heterogeneity. Environmental instability generates genetic variability through lateral selection, whereas coastal and estuarine environment are primarily heterogeneous and unpredictable. Species of these communities therefore possess high genetic variability to ensure the survival of the species. The main problem with this hypothesis is to explain how genetic variability can be associated with communities that are continuously under stressful conditions (Kinne 1975).

The high density values of larvae found at the southern sampling site at Nieuwpoort and Zeebrugge closer to the coastline can be regarded as the result of the influence of local tidal and residual current patterns in the opposite direction to the prevailing northeasterly current, contributing to a retention of meroplanktonic larvae close to coastal adult populations.

The southbound current running parallel to the northern part of the Belgian coast, generated by the ebb channel of the Scheldt estuary, may also contribute to the transport south of some larvae of macrobenthic species normally not found in large numbers in such a location (e.g. *Spicula subtruncata* at Gravelines, Blin 1988).

A biological interchange in terms of a succeeding pattern in the species composition of benthic communities may exist in the coastal area studied from north to south and vice versa. It seems to be determined by short-term changes in the global hydrodynamic regime of the study area and by mesoscale changes imposed by seasonal meteorological changes.

Acknowledgements

This research programme is part of the RENORA project (Recrutement en Mer du Nord de la Communauté de l'*Abra alba*), subsidized by COST 67 (Coastal Benthic Ecology), in the framework of the EEC environmental policy, and is also part of the FKFO programme (2.0086.88) from the National Science Foundation Belgium and of the PNDR from France (Programme national sur le déterminisme du recrutement). The authors are grateful to the crew of the French ships *Pluteus* (Roscoff), *Sepia* (Wimereux) and the Dutch ship *Lucktor* (DIHO, Yerseke). We should also like to thank colleagues from the marine biology section of the State University of Gent, the Station marine de Wimereux and DIHO, Yerseke, for their help during sampling at sea.

Bibliography

- Backhaus J., 1982. - Model experiments on the North Sea circulation with emphasis on the Norwegian coastal current. - NATO Coastal Oceanography Workshop, Os, Norway June 6-11.
- Bhaud M., 1987. - Description and identification of Polychaeta larvae, their implications in current biological problems. - *Océanis* 13, 6: 160 pp.
- Blin F., 1988. - Suivi de transit de larves planctoniques dans la partie sud de la mer du Nord. - Rapport de stage de fin d'études. Station marine Wimereux, Inst.Univ.de Tech.de Tours, Dép. biol. app. opt. Génie de l'Environnement, 44 pp.
- Bretsky P.W. & Lorenz D.M., 1970. - An essay on genetic-adaptive strategies and mass extinctions. - *Bull. Geol. Soc. Am.* 81 : 2449-2456.
- Butman C.A., 1987. - Larval settlement of soft-sediment invertebrates the spatial scales of pattern explained by active habit at selection and the emerging role of hydrodynamical processes. - *Oceanogr. Mar. Biol. Ann. Rev.*, 25 : 113-165.
- Dewarumez J.M., Smigielski F. & Richard A., 1978. - *Abra alba* (Mollusque lamelibranche), sa location en zone littorale de la mer du Nord. - *Haliotis*, 7 : 13-19.
- Dewarumez J.M., 1979. - Etude biologique d'*Abra alba* (Wood), mollusque lamelibranche du littoral de la mer du Nord. - Thèse de 3e cycle, Univ. de Lille : 139 pp.
- Eckman J.E., 1983. - Hydrodynamic processes affecting benthic recruitment. - *Limnol. Oceanogr.* 28 (2) : 241-257.
- Grassle J.F., 1967. - Influence of environmental variation on species diversity in benthic communities. - *Univ. microfilms*. Ann Arbor, Michigan.
- Govaere J.C.R., Van Damme D., Heip C. & De Coninck L.A.P., 1980. - Benthic communities in the Southern Bight of the North Sea and their use in ecological monitoring. - *Helgolander Meeresunters.*, 33 : 507-521.
- Heip C, Vincx M. & Vranken G., 1985. - The Ecology of marine Nematodes. - *Oceanogr. Mar. Biol. Ann. Rev.*, 23 : 399 - 489.
- Highsmith R.C., 1982. - Induced settlement and metamorphosis of sand dollar (*Dendraster excentricus*) larvae in predator-free sites : adult sand dollar beds. - *Ecology*, 63 : 329-337.
- Hines A.H., 1986. - Larval problems and perspectives in life histories of marine invertebrates. *Bull. Mar. Sci.* 39 : 506-525.
- Kinne O., 1975. - Marine Ecology.vol.II, Physiology Mechanisms, part I : 386-400. - John Wiley & Sons.
- Levin L.A., 1986. - The influence of tides on larval availability in shallow water overlying a mudflat. *Bull. Mar. Sci.* 39 (2) : 224-230
- Muus K., 1973. - Settling, growth and mortality of young bivalves in the Aresund. - *Ophelia*, 12 : 79-116.
- Nihoul J.C.J., 1975. - Modelling of marine systems. - Elsevier, Oceanography, Series, 10, Amsterdam, Oxford, New York, 272 : 16-21.
- Nihoul J.C.J., 1980. - Residual circulation, long waves and mesoscale eddies in the North Sea. - *Oceanologica Acta* 3 : 309-316.
- Nihoul J.C.J. & Runday F.C., 1975. - The influence of the tidal stress on the residual circulation. - *Tellus*, 29 : 484-490.
- Nihoul J.C.J. & Runfola Y., 1981. - The residual circulation in the North Sea. In : *Ecohydrodynamics*.-(J.C.J.Nihoul,ed.) : 219-271. Amsterdam: Elsevier.
- Okubo A., 1971. - Oceanic diffusion diagrams. - *Deep Sea. Res.* 18 : 789-802.

- Peterson C.H., 1977. - Competitive organisation of the soft-bottom macrobenthic communities of southern California lagoons. - *Mar. Biol.* 43 : 343-359.
- Ronday F.C. & Nihoul J.C.J., 1978. - Matematisch model van de zeewaartse uitbouw van de Haven van Zeebrugge. - Deelkontrakt 3 Dep. for. Publ. Works. Brussels, Mod. 382. 1, 262 pp.
- Ronday F.C. & Nihoul J.C.J., 1979. - Mathematisch model van de zeewaartse uitbouw van de haven van Zeebrugge. - Deelkontrakt 3 Dep. for. Publ. Works, Brussels, Mod. 382. 3, 147 pp.
- Sanders H.L., 1968. - Marine benthic diversity : a comparative study. - *Am. Nat.* 102 : 243-282.
- Scheltema R.S., 1971. - Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water benthic marine gastropods. - *Biol. Bull.* 140 : 284-322.
- Scheltema R.S., 1986. - On dispersal and planktonic larvae of benthic invertebrates : an eclectic overview and summary of problems. - *Bull. Mar. Sci.* 39 : 290-322.
- Souplet A. & Dewarumez J.M., 1980. - Les peuplements benthiques du littoral de la région de Dunkerque. - *Cah. Biol. Mar.* Tome XXI : 23-29.
- Souplet A., Glaçon R., Dewarumez J.M. & Smiglieski F., 1980. - Distribution des peuplements benthiques littoraux en mer du Nord du Cap Blanc Nez à la frontière de Belgique. - *C. R. Acad. Sci. Paris.* 29 : 627-630.
- Thorson G., 1966. - Some factors influencing the recruitment and establishment of marine benthic communities. - *Neth. J. Sea. Res.* 3 : 267-293.
- Uncles R.V. & Joint I.R., 1983. - Vertical mixing and its effect on phytoplankton growth in turbid estuary. - *Can. J. Fish. aquat. sci.* 40 (suppl.), :221-228.
- Unesco., 1968. - Monographs on Oceanographic Methodology (2). Zooplankton sampling. - pp : 154-155, Publ. Unesco Paris
- Vanosmael C., Willems K.A., Claeys D., Vincx M. & Heip C., 1982. - Macrobenthos of a sublittoral sandbank in the Southern Bight of the North Sea. - *J. Mar. Biol. Ass. UK.*, 62 : 521-534.
- Vermeulen Y.M. & Govaere J., 1983. - Distribution of benthic macrofauna in the Western Schelde Estuary. - *Cah. Biol. Mar.*, Tome XXIV : 297-308.
- White R.G, Hill A.E. & Jones D.A., 1988. - Distribution of *Nephrops norvegicus* (L) larvae in the western Irish Sea : an example of advective control on recruitment. - *Journal of Plankton Research*, vol 10. No. 4 : 735-747.
- Willems K.A., Vanosmael C., Claeys D., Vincx M. & Heip C., 1982. - Benthos of a sublittoral sandbank in the Southern Bight of the North Sea : general consideration. - *J. Mar. Biol. Ass U.K.*, 62 : 549-557.
- Woodin S.A., 1976. - Adult larval interactions in dense infaunal assemblages : patterns of abundance. - *J. Mar. Res.*, 34 : 25-41.