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THE MEROPLANKTON COMMUNITY IN THE SOUTHERN BIGHT OF THE NORTH SEA : SPATIAL PATTERNS AND ECOLOGICAL ANALYSIS

LA COMMUNAUTE MEROPLANCTONIQUE DANS LA BAIE SUD DE LA MER DU NORD : REPARTITION SPATIALE ET ANALYSE ECOLOGIQUE

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To Nino, Irina, Elisabeth

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Abstract

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Résumé

Abstract

The majority of the macrobenthic species has a larval pelagic phase, the meroplanktonic larvae could be dispersed over a period of time which varies from one week to one month.

The present work is part of the RENORA program (REcrutement en Mer du NORd dans le peuplement à Abra alba). The aim of RENORA was to assess the spatial hetereogenity of the meroplankton community structure in relation to hydrodynamic and environmental processes in order to understand the mechanisms involved in the larval dispersion and the complex biological fluxes existing in the coastal waters between the English Channel and the Southern Bight of the North Sea. The coastal locations studied are characterized by the presence of a Abra alba community which forms a large continuum, subjected to seasonal and yearly fluctuations.

The first step in the research carryied out in 1988 was to try to relate larval dispersion of benthic organisms to the tide-induced variability. The horizontal drift of meroplankton is determined by tides, residual currents and the horizontal turbulence field. These physical processes are important because they impose some spatial constraints during the planktonic phase of the majority of the benthic invertebrates resulting in migration-induced motion which allows the organisms to move between different shelf circulation regimes, which will then affect their distribution over larger space and time scales.

The first results showed that advection and suspension by tidal currents was the major force determining the changes in the density distribution of meroplankton larvae in the two locations studied at Oostende and at the Oosterschelde in the Southern Bight of the North Sea. Polydora spp., Lanice conchilega and the bivalves were strongly correlated with the tide and with salinity (Spearman's r_s, $p<0.01$). The results suggested that the distribution of the meroplankton in the upper part of the water column can be regarded as patches moving in response to tidal currents. The hydrodynamic processes in these locations controled quite considerably the larval density distribution at different scales. Path analysis showed the strenght of the causal relationship between meroplankton, tide and the environment.

The second phase of the RENORA project in 1989-1990 allowed to measure the impact, on the species data, of the effects of the environmental conditions and of the spatial structure present along the two transect studied.

In 1989 the environmental descriptors such as salinity and temperature showed that the Westerschelde played a considerable role in the input of less saline waters, which could be transported with the effect of the North-East wind southward, reaching the French coast as far as Gravelines and further.
This circulation pattern was enhanced by the North-East wind, is inverse to the general water circulation pattern in the South-West-North-East direction. The establishment of salinity fronts along the transect showed that these structure were related to specific larval patches. The echinoids larvae were related to the higher salinity values on the French part of the transect, suggesting that the larvae were generated by the adult population of Echinocardium cordatum present in the subtidal macrobenthos community in front of Gravelines and Dunkerque. The bivalves larvae distribution pattern were associated with low salinity value located on the Belgian part of the transect near Oostende. The spatial distribution of Polydora spp. *showed two distinct density peaks located before and after the salinity front, suggesting that the larvae were generated by two distinct adult population, one characterizing the French coast (Cap Griz-Nez and Cap Blanc-Nez) and one the Belgian coast (Oostende). The larval dispersion of this polychaete under different wind conditions, can bring changes in the spatial distribution and spatial structure of the adult macrobenthic population. The presence of Pectinaria koreni and Lanice conchilega larvae was concomitant with the salinity fronts and these two species were present in the adult macrobenthic community in the subtidal area of these locations. The results showed that the polychaetes, echinoids, and bivalves spatial distributions were mainly explained by the salinity-density gradient and the by the tidal-induced variability.*

In 1990 the spatial distribution of the taxonomic group in relation to the environmental descriptors showed that the polychaetes larvae of Lanice conchilega, Pectinaria koreni, Magelona mirabilis, Ampharetidae, *and the echinoids larvae were associated with higher salinity-density value. The polychaetes larvae of Polydora* spp., *Nephtys* spp., *and the bivalves larvae were associated with the tide, and the ophiuroids larvae were found in nutrient-rich waters coming form the Westerschelde and Oosterschelde. Most of the variance in the species distribution was explained by the salinity-density gradient which reflected more the spatial structure in the environment. The temperature and fluorometry gradient perpendicular to the salinity-density gradient indicated a lack of correlation between these two gradients, and reflected more the environmental temporal variation. These results indicated that the spatially* *distinct peaks in the meroplankton could be determined by the spatial-temporal shifting boundaries in the spatially structure environment along the transect. The spatial structuring of natural communities implies a better understanding of the relative contribution of the different abiotic and biotic factors in determining the distribution and interaction between organisms.*

In order to investigate the validity of these results, the data were subjected to different multivariate statistical analysis and to a method based on canonical correspondence analysis (CCA), which allows to measure the amount of variation as a sum of canonical eigenvalues for the species matrix which can be explained by the environmental variables. In most cases the environmental variables alone are not able to explain fully the amount of variation observed in the species community structure. The need to compare the set of biotic and abiotic data with the spatial coordinates or distances between the samples become extremely important to better understand the concept of spatial hetereogeneity, which can be regarded as functional in ecosystems.

The spatial component of the community structure was isolated from the species-environment component to detect whether the environmental control model can explain the variation observed. The application of this method to marine ecological data set is presented here by considering the associated statistical problem of spatial autocorrelation across geographic space. The spatial autocorrelation of plankton community can be used to quantify community dissimilarity. In this case, space was used as an explanatory variables in the CCA.

The data for the CCA analyses were divided into three matrices : (a) species densities, (b) environmental variables, (c) geographic locations of the samples (spatial component). The geographic coordinates of the sampling locations were used to perform a cubic trend surface regression in order to ensure the extraction of more complex structure such as patches, and not only the linear gradient pattern in the species matrix.

The three data sets were analysed using canonical correspondence analysis (CCA), using alternatively the spatial matrix and the environmental matrix as covariables. Running two canonical ordinations constrained by a set of explanatory variables (covariables) allows us to measure the impact, on the species data, of the environmental conditions and of the spatial structure.

Aware of the fact that in some cases, the species and the environmental variables share the same spatial structure, the degree of variation in the species data due to the spatial structure has been partialled out by the use of the covariables. The probability values for each analysis were determined by Monte

Carlo permutation test. The Mantel test and partial Mantel tests associated to path analyses were computed to correlate and link the ecological structure with the spatial gradient present in the environment.

The PCA was a good departure point for the explanatory analysis of the results, but the species-environment relationships was imposed, by using the environmental descriptors as added explanatory variables in a way that can be described as an indirect analysis. The results, however, indicated that the stations along the transect were grouped according to the environmental descriptors and that the species distribution was dependent on the environmental descriptors, furthermore, the results showed that the data were spatially structured and suggested the importance to compare these results with those of other methods.

The chronological clustering method gave a very good indication of the division occuring at a species-environment level along the transect. The division clearly illustrated the importance of the geographical location of the station according to both the biotic and abiotic descriptors. These divisions were confirmed by the results of the Bray-Curtis dissimilarity measure and by the non-metric multidimensional scaling (MDS). Furthermore, chronological clustering and MDS showed that the influence of the environmental variables can be identify at the whole community level as well as at the species level. The comparison of the results obtained by the chronological clustering and the Bray-Curtis non-metric MDS proved to be a valuable tool for the analysis of this type of data set. The presence of more division in the chronological clustering based on the environmental-matrix were detected by the Bray-Curtis dissimilarity measure and MDS at a taxonomic level.

The results obtained in this study showed the importance of considering the spatial component to describe the distribution of pelagic organisms. The innovative CCA-based method quantified the percentage of the variation in the species matrix accounted by the different fractions of variance considered.

The use of covariables in a partial ordination method allows to partial out the environmental and spatial variation to test the meroplankton successional patterns. However the purely environmental fraction a may largely reflect site-scale ecological patterns determined by local environmental factors. The spatially covarying environment component b may be related more to regional-scale ecological processes influenced by environmental variables that covaried geographically when the space component is regarded as a cubic trend-surface regression. Fraction c, the purely spatial, might have reflected spatial population or community based processes, unmeasured abiotic environmental factors, or some past events (historical dynamic) that are reflected today in the spatial *structure of fraction c. Considering fraction d, the unexplained variation, it will be interesting to map this fraction as the "site ordination score", based in this case on the meroplankton residual variation that is unexplained by the available spatial and environmental variables.*

The complementary use of the Mantel statistics and path analysis contributed quite considerably to the understanding of some of the causes establishing the complex biological fluxes in the coastal waters between the French-Belgian coast and the Schelde Estuary region. The computed Mantel statistics and path analysis shows that the path between Geography (Space) and Environment, and between Environment and Species were all very highly significant, while the path between Geography (Space) and Species resulted non significant.

The conclusion was clearly that in all four transect considered the spatial pattern of the species comes from the spatial pattern of the environmental variables, and is almost completely explained away by them, so that no significant spatial pattern remains in the species data after controlling the effect of the environmental variables. The spatial structure in the species data considered in this work always comes from a spatial structuring of the environmental variables, according to the environmental control model (ECM).

The theoretical causal relationships between environmental variables representing processes and community structure indicates how the different fraction explaining the percentage of the total variation in a species assemblage or community can be associated to different causal factors, processes, and effects. The main sources of causal variation may be related to the environmental control model (ECM), and the biotic control model (BCM), the presence of some other factors such as anthropogenic events can be referred to as historical dynamics (HD).

Analyses of the spatial-temporal shift in the larval distribution in relation to frontal structures or distinct water masses are important to further understand factors affecting dispersal and recruitment in benthic studies.

Résumé

La plupart des espèces macrobenthiques possèdent une phase larvaire pélagique, les larves méroplanctoniques peuvent donc être soumises à des dérives considérables pendant leur présence au sein de la masse d'eau qui peut aller de une semaine à un mois.

Le travail présenté ici fait partie du programme RENORA (REcrutement en mer du NORd dans les peuplements à Abra alba*). Le but de RENORA était de comprendre les mécanismes mis en jeu dans la dispersion des larves méroplanctoniques et dans leur recrutement benthique. La compréhension de ces mécanismes passait par une meilleure connaissance des communautés méroplanctoniques, de leur hétérogénéité supposée, des rôles respectifs de l'hydrodynamisme et des facteurs environnementaux sur le devenir des populations larvaires au cours de la phase pélagique (ce travail) et des mécanismes mis en jeu au cours de la sédentarisation benthique à différentes échelles d'observation (thèse de Ch. Luczak).*

Le phénomène est étudié en une zone côtière de la baie sud de la mer du Nord (entre Calais et le delta de l'Escaut) caractérisée par la présence de la communauté à Abra alba qui forme un très vaste continuum et qui présente de très importantes fluctuations annuelles et saisonnières que les études précédentes ont liées aux phénomènes du recrutement.

Grace à ces acquis et à ceux enregistrés dans le cadre de l'étude du fleuve côtier en Manche orientale, il deviendrait possible de mieux appréhender les flux complexes existant entre la Manche orientale et la mer du Nord.

La première étape de ce travail fut en 1988 de relier la dispersion larvaire des organismes benthiques avec la variabilité induite par la marée. La dérive horizontale les populations méroplanctoniques est déterminée par les marées, le courant résiduel et le champ de turbulence horizontale. Ces processus physiques sont importants car ils imposent des contraintes spatiales pendant la phase de vie planctonique des invertébrés benthiques. Ils provoquent des mouvements migratoires passifs parfois considérables et peuvent permettre aux organismes d'être repris dans différents régimes de circulation côtière, ce qui influence grandement leur distribution spatiale et temporelle (les larves planctoniques peuvent être considérées comme des horloges qui permettent de dater les masses d'eaux où elles se trouvent).

Les premiers résultats montrent que l'advection et la dispersion par les courants de marée sont les facteurs principaux déterminant les changements de distribution de densité des larves meroplanctoniques sur les deux sites étudiés : au large d'Ostende et dans l'Escaut oriental. Polydora spp, Lanice conchilega *et les bivalves sont fortement corrélés avec la marée et la salinité (r de Spearman, $p<0.01$). Ces résultats suggèrent que les larves meroplanctoniques sont distribuées dans la partie supérieure de la colonne d'eau sous forme de tâches se déplaçant sous l'action des courants de marée. L' analyse des coefficients de direction (path analysis) prouve la forte relation causale entre le meroplancton, la marée et les variables environnementales.*

La deuxième phase de ce travail (1989-1990) a permis de mesurer l'impact des conditions environnementales et des structures spatiales mises en évidence sur les données de densité, le long de deux transects étudiés.

Lors de l'étude 1989, les descripteurs environnementaux comme la température et la salinité montrent le rôle important joué par l'Escaut occidental du fait des eaux moins salées qu'il injecte dans la baie sud de la mer du Nord. Si la dérive normale de ces eaux est dirigée vers le nord après leur reprise dans le gyre d'Ostende-Blankenbergue, elles peuvent être entraînées vers le sud pendant des conditions météorologiques anticycloniques génératrices de vents de nord-est pour atteindre Dunkerque, Gravelines voire des zones situées encore plus au sud. Ce type de circulation, généré par des vents de nord-est, est inverse par rapport à la dérive normale des masses d'eaux dans la zone d'étude. La descente des masses d'eaux originaires de l'Escaut entraîne la formation de fronts de salinité qui séparent des populations larvaires différentes. Les larves d'échinoides sont présentes dans les eaux à forte salinité de la partie française du transect, suggérant que les larves sont produites par les populations d'Echinocardium cordatum *présentes dans les peuplements benthiques situés au large de Gravelines ou de Dunkerque. Les larves de bivalves sont plutôt associées aux eaux à faible salinité de la partie belge du transect. La distribution des larves de* Polydora spp., *montre deux pics de densité avant et après le front de salinité, ce qui suggère que les populations larvaires émanent de deux populations d'adultes différentes, situées pour l'une vers les caps Gris Nez et Blanc Nez et pour l'autre sur les brise-lames de la côte belge. Les zones de présence de* Pectinaria koreni *et de* Lanice conchilega *correspondent aux fronts de salinité et ces deux espèces sont abondantes dans la communauté benthique sous-jacente.*

Ces résultats démontrent que la distribution spatiale des polychètes, des échinoides et des bivalves sont souvent expliquées par les gradients de salinité et de densité et par la variabilité induite par la marée.

En 1990, l'analyse de la distribution spatiale des groupes taxonomiques en relation avec les descripteurs environnementaux a permis d'associer les larves de polychètes Lanice conchilega, *Magelona mirabilis,* Ampharetidae spp, *et les larves d'échinoides avec les eaux à forte salinité. Les larves de* Polydora spp, Nephtys spp *et les larves de bivalves étaient plutôt associées à la marée, tandis que les larves d'ophiures n'ont été trouvées que dans les eaux provenant de l'Escaut Occidental et de l'Escaut oriental. La plus grande partie de la variance de la distribution des espèces est expliquée par le gradient de salinité-densité qui reflète le plus la structuration de l'environnement. Les gradients de température et de fluorimétrie sont perpendiculaires au gradient de salinité ce qui indique une absence de corrélation entre ces deux groupes de gradients. La température et la fluorimétrie reflètent plus l'évolution temporelle que l'évolution spatiale de l'environnement. Ces résultats indiquent donc que les pics d'abondance spatialement distincts du meroplancton peuvent être déterminés par des changements spatio-temporels des limites dans la structure spatiale de l'environnement le long du transect . L'étude de la structuration spatiale de communautés naturelles nécessite une meilleure compréhension de la contribution relative des facteurs abiotiques et biotiques dans la détermination de la distribution des organismes et des interactions qu'ils établissent.*

Les données brutes ont été soumises à plusieurs analyses multivariées dans le but de tester la validité des résultats. Une méthode basée sur l'analyse canonique des correspondances a été utilisée, elle permet de mesurer la fraction de la variance en tant que somme des valeurs propres (eigenvalues) canoniques pour la matrice des espèces qui peut être expliquée par les variables environnementales. Dans la majorité des cas, les variables environnementales seules ne peuvent pas expliquer complètement la variance observée dans la structure de la communauté. Le besoin de comparer l'ensemble des données biotiques et abiotiques avec les coordonnées spatiales ou les distances entre les échantillons devient cruciale pour mieux comprendre le concept d'hétérogénéité spatiale.

La composante spatiale de la structure de la communauté méroplanctonique a été isolée de la composante espèces-environnement pour vérifier si le modèle de contrôle environnemental *peut expliquer la variation observée. L'utilisation de cette méthode sur des données écologiques marines est présentée ici en considérant le problème statistique de l'autocorrélation spatiale à travers un espace géographique. L'autocorrélation spatiale de communautés planctoniques peut être utilisée pour quantifier la dissimilarité. Dans ce cas, l'espace est utilisé comme variable explicative dans l'analyse canonique des correspondances.*

Les données pour ces analyses ont été divisées en trois matrices: densité des espèces, données environnementales et position géographique des echantillons (composante spatiale). Les coordonnées géographiques des positions des stations d'echantillonnage ont été utilisées, et les termes de l'équations du 2eme et du 3eme degré calculés sur ces cordonnés, dans le but de pouvoir extraire des structures complexes comme des taches et pas uniquement des gradients linéaires de la matrice d'espèces.

Les trois séries de données ont été traitées en utilisant l'analyse canonique des correspondances et en utilisant alternativement la matrice spatiale et la matrice environnementale. Le fait de pratiquer deux ordinations canoniques contraintes par un ensemble de variables explicatives (covariables) nous permet de mesurer l'impact sur les espèces des conditions environnementales et de la structure spatiale.

Connaissant le fait que, dans certains cas, les espèces et les variables environnementales partagent la même structure spatiale, le degré de variation dans les données spécifiques dû à la structure spatiale a été déterminée par l'utilisation des covariables. Les valeurs de probabilité pour chaque analyse ont été déterminées par des test de permutation de Monte Carlo. Le test de Mantel et le test partiel de Mantel associés à l'analyse des coefficients de direction (path analysis) ont été pratiqués pour corréler et lier le structure écologique avec le gradient spatial présent dans l'environnement.

L'analyse en composantes principales constituait un bon point de départ pour l'analyse explicative des résultats, mais les relations entre espèces et environnement s'imposa par l'utilisation de descripteurs environnementaux en variables explicatives supplémentaires de manière à ce que cela puisse être considéré comme un méthode indirecte. Les résultats ont indiqué que les stations sont groupées le long des transects en fonction des descripteurs environnementaux et que la distribution des espèces dépend de ces descripteurs. En outre, les résultats ont montré que les données étaient structurées spatialement et qu'il fallait donc comparer ces résultats avec ceux obtenus par d'autres méthodes.

La méthode du groupement chronologique a donné une très bonne indication de la division apparaissant le long du transect au niveau espèces-environnement. La division illustre clairement l'importance de la position géographique des stations en fonction des descripteurs biotiques et abiotiques. Ces divisions sont confirmées par les résultats obtenus à l'aide de la mesure de dissimilarité de Bray-Curtis et du cadrage multidimensionnel non-metrique (non-metric MDS). En outre, le groupement chronologique et la MDS ont montré que l'influence des variables environnementales peut être identifiée tant au niveau de la communauté qu'à celui des espèces qui la composent. La comparaison des résultats obtenus par le groupement chronologique; la dissimilarité de Bray-Curtis et la MDS semble être un bon outil pour les analyses de ce type de données. La présence de divisions plus nombreuses dans le groupement chronologique effectué sur les données environnementales a été détectée par la dissimilarité de Bray-Curtis et la MDS au niveau taxonomique.

Les résultats obtenus dans cette étude ont montré qu'il est important de considérer la composante spatiale pour décrire la distribution des organisme pélagiques.La méthode innovatrice basée sur l'analyse canonique des correspondances a permis de quantifier le pourcentage de variation dans la matrice des espèces apporte par les différentes partition de variance considérées.

L'utilisation de covariables dans une méthode d'ordination partielle permet de séparer les variations environnementales et spatiales pour tester les modèles de succession du méroplancton.. La fraction a, purement environnementale, reflète largement les « patterns » écologiques à l'échelle du site déterminés par les facteurs environnementaux. La composante b (espace-environnement) se rapporte plus à des processus écologiques à l'échelle régionale influencés par des variables environnementales qui covarient géographiquement quand la composante spatiale est considéré comme une surface explicative ajustée par une fonction cubique. La fraction c, purement spatiale peut refléter les processus basés sur les populations et les communautés, les facteurs environnementaux non mesurés ou des événements passés qui apparaissent dans la structure spatiale. Pour ce qui est de la fraction d (la variation inexpliquée) il serait intéressant de la cartographier en se basant sur la variation résiduelle du méroplancton qui n'est pas expliquée par les variables sptatiales et environnementales dont nous disposons.

L'utilisation complémentaire des statistiques de Mantel et de l'analyse des coefficients de direction (path analysis) ont considérablement contribué à la compréhension de quelques *unes des causes qui établissent les flux biologiques complexes des eaux côtières entre la côte franco-belge et le delta de l'Escaut. Ces méthodes ont montré que les relations entre la GEOGRAPHIE et l'ENVIRONNEMENT et entre l'ENVIRONNEMENT et les ESPECES étaient toutes hautement significatives.*

La conclusion est que dans les quatre cas considérés la répartition spatiale des espèces est conditionnée par la répartition spatial des variables environnementales. La structure spatiale des données spécifiques considérée dans ce travail provient toujours d'une structuration spatiale des variables environnementales en relation avec le modèle de contrôle environnemental (ECM).

Les relations causales théoriques entre les variables environnementales représentant les processus et la structure de la communauté indiquent comment les différentes fractions expliquant le pourcentage de la variance totale dans un assemblage d 'espèces ou une communauté peuvent être associées à différents facteurs, processus ou effets. La source principale de variation causale doit être reliée au modèle de contrôle environnemental et au modèle de contrôle biotique. La présence de certains autres facteurs comme une action anthropique doit être rapportée à une dynamique historique.Les analyses de déplacements spatio-temporels dans la distribution larvaire en relation avec des structures frontales ou des masses d'eaux distinctes sont importantes pour la compréhension future des facteurs affectant la dispersion et le recrutement dans les études relatives au recrutement benthique.

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Introduction

INTRODUCTION

The RENORA program

The research presented here is a part of the RENORA program (Recrutement en Mer du Nord dans le peuplement à *Abra alba*) founded by the PNDR (Programme National sur le Déterminisme du Recrutement) and closely related to the international research program GLOBEC (Global Ocean Ecosystem Dynamics). These programs deal with the study of the interactions between physical and biological processes, in order to understand the respective importance of pelagic larval processes and benthic settlement in the induction of quantitative interannual variability of the adult populations.

The coastal locations studied in the Southern Bight of the North Sea within the framework of this Program are characterized by the presence of a benthic continuum dominated by the bivalve *Abra alba.* The species composition of the macrobenthos has been reported in a number of studies on the French coast by Dewarumez (1976; 1979) and Souplet & Dewarumez (1980) and on the Belgian-Dutch coast by Govaere *et al.,* (1980), Vermeulen & Govaere (1983) and Craeymeersch *et al.,* (1990).

The main species of this community are *Abra alba, Tellina fabula, Lanice conchilega, Spiophanes bombyx, Nephtys hombergii, Mysella bidentata.* In spite of important changes in the total density from year to year, due to changes in the sediment structure as well as in the recruitment of most species (Dewarumez *et al.,* 1978; Dewarumez *et al.,* 1986; Dewarumez *et al.,* 1992), this community can be regarded as very stable (Dewarumez *et al.,* 1986) and the interchange in species composition along a South-North-East-South gradient plays an important role in structuring the macrobenthos. According to Fromentin & Ibanez (1994) the analysis of a time series data set (1977-1992) in relation to changes in the meteorological features on the French coastal area near Dunkerque, shows that the *Abra alba* maximal densities always occur with mild winters, whereas cold winters are always characterized by very low densities. Some of the mechanisms involved in the observed fluctuations in the macrobenthos were suspected to be related to recruitment processes, and more precisely to the pelagic dispersal of benthic larvae

Hydrodynamic, wind effect, water masses movement, environmental and geographical variables.

The hydrodynamic regime of the Southern Bight of the North Sea i characterized by strong mesoscale currents produced by tides and winds concomitant with the residual currents generated by the flow through the Nort Sea and the English Channel of the two branches of the North Atlantic curren (Nihoul *et al.*, 1989). The general South-West-North-East water circulatio pattern can be inversed by the circulation pattern enhanced by the frequen North-East wind (Nihoul & Ronday, 1975; Salomon, 1993). A biologica interchange, marked by succeding patterns in the species composition of benthi communities, can be established from North to South and *vice versa*, followin tidally-induced variability and wind stress on the surface water (Belgrano *et al.* 1990).

Relating the effects of wind on the intensity of water masses movements to the distribution of marine macrobenthic larvae in the Southern Bight of th North Sea (Dewarumez *et al.*, 1991), showed that the planktonic larval phase i critical in the life histories and population dynamics of benthic organisms because it is the primary dispersal stage and thus is responsible for colonizin new habitat or replenishing established populations (Butman, 1994). The change in the environmental descriptors such as salinity, or wind stress, during th pelagic transport of meroplankton larvae, can have a drastic consequence on thei distribution and settlement (Fromentin & Ibanez, 1994). Monitoring thes changes at a pelagic level can give a good indication of the external forcing factor involved within the area of larval input.

State of the art in species-environmental relationships.

In marine systems, the distributional pattern of meroplankton are mostl linked to abiotic processes. Environmental variables such as temperatur salinity, density, fluorometry, depth, tide height are among the major factor explaining the structuring of pelagic systems (Pinel-Alloul, 1995). The geographi variables can be regarded as the way to express the spatial structure of th environmental variables as a linear combination of the geographic coordinates o the sampling stations, or by a matrix of geographic distances among samples. Th use of both environmental and geographical variables is important to stud spatially distributed data and spatially continuous phenomena (Legendre, 1990).

It is important to describe briefly the previous work on plankton ecology and the developments of recent statistical and multivariate techniques aimed to investigate species-environment relationships. The complexities involved in the interpretation of the effects of localised wind-driven advection transport on the water masses movements, in relation to the changes in the distribution and abundance of meroplankton and holoplankton in this area, have been discussed by many authors (Colebrook 1978; Colebrook & Taylor 1984; Belgrano *et al.*, 1990; Dewarumez *et al.*, 1991). The larvae of benthic marine invertebrates are dispersed at a variety of spatial and temporal scales (Scheltema, 1986). Previous studies on larvae dispersion considered extensively the benthic boudary layer (Butman, 1987, Butman *et al.*, 1988), but only few studies of dispersal considered the processes that might influence the density distribution of larvae in the upper water column (Levin, 1990). The studies on passive transport and behaviour of larvae in estuarine conditions (Wolf, 1974), and in a marine bay (Banse, 1986), suggested that hydrodynamical and physico-chemical processes are responsible for the retention of the larvae within restricted and identifiable water masses. Early observations by Levin (1983; 1986) show the importance of relating the density distribution of pelagic larvae to the time of occurence of high and low water. Epifanio *et al.*, (1988), and Mann (1988) stressed the importance of relating hydrographic measurements and larval distribution to salinity discontinuities.

The patchy distribution of benthic organisms in marine soft sediments and in plankton studies has been recognised for a long time (Barry & Dayton, 1991; Mackas, 1984; Colebrook, 1978). Patchiness in the distribution of benthic invertebrates have been related to physical and environmental factors which are believed to determine large-scale patterns of distribution (Thorson, 1957, Gray 1974; Warwick & Davies, 1977; Barry & Dayton, 1991). Spatial autocorrelation has been used to examine and describe patterns of distribution occuring at small spatial scale (Jumars *et al.*, 1977; Volckaert, 1987; McArdle & Blackwell, 1989; Trush *et al.*, 1989).

When studying ecological processes, a large part of the species variability is not only directly controlled by environmental variables, bottom-up process, but also by other factors such as historical events or by top-down ecological processes (Carpenter *et al.*, 1985; Legendre, 1990; Rudstam, 1994). In the study of benthic communities bottom-up processes such as competition, predation, reproduction, turbulence occuring at the *benthic boudary layer* (BBL) are important during larval settlement (Fréchette *et al.*, 1993); while top-down processes such as wind forcing, horizontal and vertical advection transport, tidal currents and the variability of abiotic variables such as temperature, salinity, fluorometry are important during the pelagic phase of meroplanktonic larvae.

To compare and contrast the coupling of physical-biological processes, one should recognize that the description of a system under study will vary with the choice of scales used; and more important, that, rather than trying to determine the correct scale, one should understand how the system description changes across scales (Levin, 1995). For individuals, the scale of observations can vary from millimeters to meters. For populations, we can have a scale defined biologically in terms of area occupied by reproductive units, or statistically, as the largest spatial scale within which variations in population structure exhibit coherence (Steele, 1995). In a conceptual framework for the study of the pelagic system, like in the present study, one should consider the effect of scale in the size scale regime between 100 m and 100 km in determining the biotic and abiotic forces such as fronts acting on the community compositional structure, to produce different patterns of species composition and distribution (Tonn *et al.*, 1990; Pinel-Alloul, 1995; Steele, 1995). However there is no *single* correct scale at which to view ecosystems (Levin, 1995); and a community or ecosystem can be regarded as an arbitrary subdivision of a continuous gradation of local species assemblages (Whittaker, 1956; McIntosh, 1991). This explains why there is an increasing interest in ecology in the theory of fractals (Mandelbrot, 1977; Frontier, 1986; Sugihara & May, 1990) which emphasizes both the scale dependence of the data and the description of phenomena showing the possible existence of scaling laws (Levin, 1995). As a first step an understanding of biology at the level of interacting species is critical in ecology, and there is the need to understand further how species partition space (Powell, 1995).

Spatial structure.

The importance of spatial heterogeneity comes from its central role in ecological theories (May, 1984). In aquatic environments the spatial heterogeneity of the physical environment generates a diversity in communities as well as in the biological and ecological processes that can be observed at various points in space (Allen & Starr, 1982; Legendre & Fortin, 1989; 1993; Dutilleul & Legendre, 1993). Understanding and predicting natural variability in benthic populations is a fundamental problem in biological oceanography. The spatial variation in larval dispersal is one of the aspects least understood and it requires a highly interdisciplinary approach.

The spatial structure of the physical and biological environment is important in determining the range and temporal rate of change of environmental conditions experienced by organisms, living in and moving through that environment. The various physical and biological processes contributing to an observed biological pattern will also differ by the range of spatial scales over which they are effective (Mackas, 1984). The form and scale dependence of spatial autocorrelation is important to identify and interpret the mechanisms which control the pattern formation (Legendre & Fortin, 1989). The spatial component present in the environmental descriptors plays an important role in the interpolation and interpretation of the spatial structure of an ecological process and this is one of the reason why detecting the spatial arrangements of populations and communities is interesting. It is important to provide with a sufficient degree of quantitative exactness, the taxonomic compositional structure of a community and to be able to give some initial indication of the over-all patterns of interaction between biological and physical phenomena. Ecological processes involving the spatial structure of interactions between the taxa of the community are best studied by examining the pattern of multivariate data.

Data analysis.

Different analytical techniques can be used to study the complex suite of variables describing the forces acting on recruitment of benthic population by pelagic larvae, and to understand the mechanisms involved in meroplankton dispersion. This was particularly necessary in our study, knowing the complex biological fluxes existing in the coastal waters between the Calais-Dover strait and the Southern Bight of the North Sea (Luczak *et al.*, 1993).

Multivariate analyses such as *Principal Components Analysis* (PCA), *Correspondence Analysis* (CA), *Detrended Correspondence Analysis* (DCA), and *Non-Metric Multidimensional Scaling* (MDS) are among the techniques mostly used in ecological studies. In recent years, new techniques have been developed to analyse species-environment relationships. *Canonical Correspondence Analysis* (CCA) can be used to bring out that part of the species variability that can be accounted for by the environmental variables. CCA is related to multiple regression as well as to ordination. The analysis selects as the first ordination axis the linear combination of the environmental variables that maximizes the dispersion of the species scores when a second data table contains the geographic coordinates of the data points; the ordination of the species data can be

Fraction	Causal factor	Process	Effect
(a)	Environmental factor	ECM	Community structure
(a)*	Non-spatially structured factor not included in the analysis	ECM	Env. variable in the analysis Non-spatial community var.
	Historical events without spatial structure at the study scale	HD	Env. variable in the analysis Non-spatial community var.
(b)	Env. factor with spatial structure	ECM	Community spatial structure
(b)*	Spatially structured env. factor not included in the analysis	ECM	Env. variable in the analysis Community spatial structure
	Spatially structured historical events	HD	Env. variable in the analysis Community spatial structure
(c)*	Spatially structured factors not icluded in the analysis	ECM	Community spatial structure
	Spatially structured historical events	HD	Community spatial structure
	Predation, competition, etc.	BCM	Community spatial structure
(d)*	Factor not included in the analysis, not spatially structured (at study scale)	ECM	Non-explained community variation
	Biotic control factors not spatially structured (at study scale)	BCM	Non-explained community variation
	Random variation, sampling error, turbulence, fractal dimension, etc.	Noise	Non-explained community variation

Table. 1. Theoretical causal relationships between environmental variables and community structure. ECM = Environmental control model. BCM = Biotic control model. HD = Historical dynamics. Asterisks (*) indicate factors not explained or hidden in the model (after Borcard & Legendre 1994).

constrained to be consistent with the geographic distribution of the samples. CCA then allows to perform constrained ordination (Borcard *et al.,* 1992) to partition the variation of species abundance data into four additive components:

- a) local environmental effects
- b) environmental gradient effects
- c) pure spatial biological structure effects
- d) undetermined variance

The information contained in these fractions can provide a better insight into the spatial structure of the data and generate new hypotheses to be tested for integrating space as a predictive variable into ecological models (Legendre & Troussellier, 1988).

The spatial structure in the species distribution patterns can be explained by the spatial structuring of the environmental variables with reference to two classical conceptual models: the *environmental control model* (ECM), where the environmental variables are responsible for the observed variations in the species distribution (Whittaker, 1956; Bray & Curtis, 1957; Hutchinson, 1957); the *biotic control model* (BCM), where competition and predation are considered to be the primary factors structuring the communities (Lindeman, 1942; Southwood, 1987) and by the presence of some other factors such as anthropogenic events regarded as historical dynamics (HD) (Borcard & Legendre, 1994).

In Table. 1. the theoretical causal relationships between environmental variables representing processes and community structure indicate how the different fractions explaining the percentage of the total variation in a species assemblage or community can be associated to different causal factors, processes, and effects. These causal relationships can be tested with the use of *path analysis* and the complementary *Mantel test* and *partial Mantel test* (Legendre & Troussellier, 1988). The use of these techniques can provide a measure of the strength of the association between species-environment sharing the same spatial gradient and produce a possible model of causal relationships (Legendre & Troussellier, 1988).

Present study.

As stated above the first objective of the RENORA program was to investigate in more detail the meroplankton dispersal in relation to environmental factors, before studying, in a second phase, the processes involved in larval settlement and the interactions with the existing meiofauna.

The different campaigns within the framework of the RENORA program permitted to study, at different structural scales, the meroplankton community. The use of the statistical tools described allowed to understand better the physical and biological processes involved in the coastal area located within two different ecosystems: the Eastern part of the English Channel, influenced by the input from the Seine estuary, and the North Sea, influenced by input from the Rheine-Meuse-Scheldt delta region.

The first part of this study was related to the retention hypothesis (Iles & Sinclair, 1982) and the member/vagrant hypothesis (Sinclair, 1988) concerning population variability and life-cycle continuity by considering the effectiveness of retention and the spatial constraints exerted upon marine organisms by physical environmental processes such as advection-diffusion transport. The aim was to show how meroplanktonic larvae are dispersed over a tidal cycle at two coastal locations characterized by more or less strong tidal currents, and to attempt to understand the possible consequences of such dispersal in relation to different abiotic parameters. The relative strenghts of direct and indirect interactions among variables was determined by *path analysis* (Wootton, 1994).

The second part of the research focused on the analysis of the relationship between meroplankton, environmental variables and geography to quantify the spatial heterogeneity of the meroplankton community structure in relation to hydrodynamic and environmental processes. The observed variation in the species abundance was analysed in detail in order to partition it into components that could and could not be explained in terms of environmental variables taking into account the important effect of spatial structure in the dispersion of larvae.

The final step of this research was to produce a *causal model* to see if the spatial structure in the species data was always generated by the spatial structuring of the environmental variables or by fractions not generated by the spatial structure present in the environmental data.

Chapter I.
Materials and Methods

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1.1. Study area and communities

The study area was located in the Southern Bight of the North Sea (Fig. 1.). The transport of the water masses coming from the English Channel and entering the North Sea at Calais are very much influenced by meteorological factors and the mean transport velocity can change from an estimate of 1 km per day for the English channel to 5 km per day for the Dover-Calais strait (Pingree *et al.*, 1975; Pingree & Maddock 1977; Prandle 1978). The general circulation pattern tends to be in a North-Easterly direction but the wind can change and reverse this general trend (Djenidi *et al.*, 1986; Dewarumez *et al.*, 1991).

The Belgian coast is characterized by the presence of a residual gyre at Zeebrugge interacting with the general circulation pattern (Nihoul & Ronday 1975; Nihoul & Runfala 1981).

The Westerschelde estuary ebb-tide channel (ETC), running parallel to the Northern Belgian coast reaching Oostende, and the flood-tide channel (FTC), running parallel to the Dutch coast at Vlissingen, are responsible for the dilution of the Westerschelde estuary waters with the open sea (Nihoul *et al.*, 1989).
The Oosterchelde estuary is characterized by a strong tidal current and can be regarded as a well-mixed zone (Dronkers & Zimmerman, 1982). The closure of two storm surge barriers in 1986 and 1987 (Wetsteyn *et al.*, 1990) resulted in the reduction of the amount of water exchange with the North Sea by approximately 28% (Leewis & Waardenburg, 1990).

The subtidal benthic communities in the study area are influenced by the strength of tidal currents, reaching a maximum at the Calais-Dover strait and decreasing in the Southern Bight of the North Sea. The tidal currents also directly influence the sediment composition which vary from flint pebbles between Gris Nez and the Calais area to dominant sandy-muddy sediment from Dunkerque to the Belgian-Dutch coast. The decrease of the strength of tidal currents to the North-East has an effect on the subtidal benthic community in reducing the density of some epifauna species e.g. *Ophiotrix fragilis*, and increasing the density of infauna species e.g. *Ophiura albida* (Davoult *et al.*, 1988).

The largest subtidal benthic community present in the study area is characterized by the presence of *Abra alba* at a depth of 10 metres as a result of

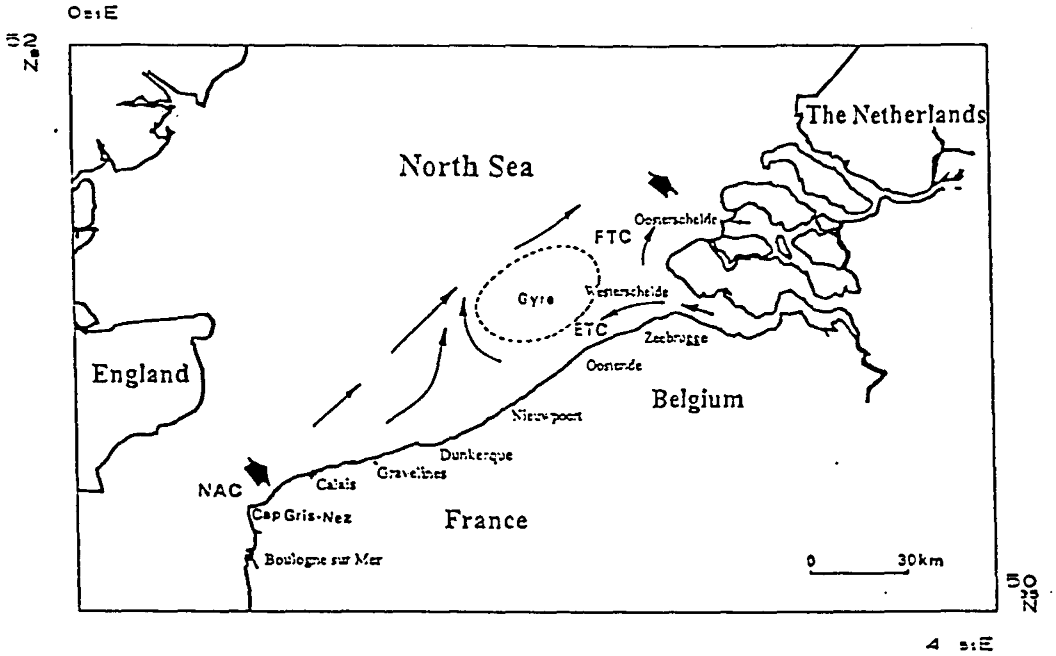


Fig. 1. The map of the study area, showing the residual circulation induced by the residual gyre and the outflow of the Westerschelde estuary superimposed on the north-bound flow of the North Atlantic current (NAC). ETC and FTC indicates the ebb-tide channel, and the flood-tide channel of the Westerschelde (after Nihoul *et al.*, 1989).

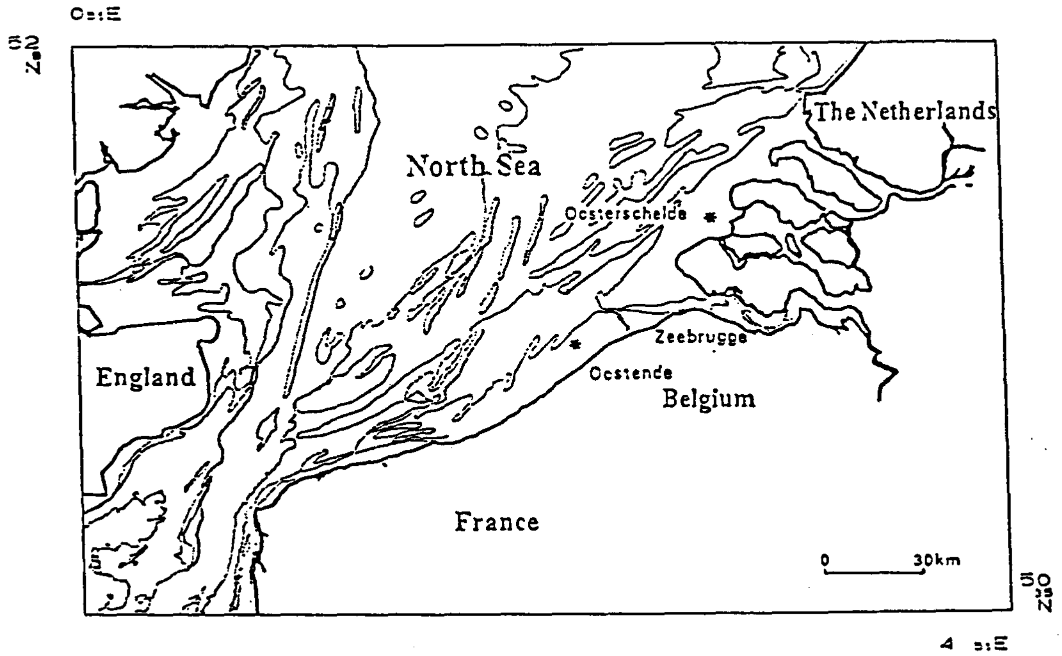


Fig. 2. * indicates the locations of the sampling stations in the Southern Bight of the North Sea. Depth countour indicates the 20 m margin.

changes in the sediment composition along a coastal-off-shore gradient (Davoult *et al.,* 1988).

The *Abra alba* community shows unpredictable changes according to years, which affect the bionomical structure of the community in terms of species composition. In spite of variable recruitment periods and yearly fluctuations since 1978 in the recruitments of *Abra alba, Tellina fabula, Lanice conchilega,* this community can be regarded as particularly stable (Dewarumez *et al.,* 1986). In June 1991 high numbers of post-larvae of *Ensis directus* was recorded for the first time along the French coast in the Southern Bight of the North Sea (Luczak *et al.,* 1993). Their findings indicated that the recruitments of this species occured after a period of northerly winds, as a clear indication that the settled larvae originated from adult populations along the Belgian-Dutch coast.

The macrobenthos communities present along the Belgian-Dutch transect have been recently studied by Craeymeersch *et al.,* (1990) and previously by Govaere (1978) and Govaere *et al.,* (1980). The species composition has been divided into 6 different clusters representing different species assemblages in different geographical areas. At the northern part of the Belgian coast and at Wielingen the macrobenthos is characterized by the presence of *Polydora ciliata, Pectinaria koreni, Spisula subtruncata, Abra alba.* When moving towards the mouth of the Westerschelde at Vlissingen, *Lanice conchilega, Nepthys cirrosa, Nepthys hombergii, Spiophanes bombyx, Echinocardium cordatum,* and *Ophiura albida* are found. From the Dutch coast towards the Oosterschelde *Spisula subtruncata, Spio filicornis, Spiophanes bombyx, Magelona mirabilis, Ophiura albida* are among the species present in these locations.

The majority of the macrobenthos species present in the study area have a planktonic larval phase which is affected by hydrodynamic processes. The study of the dispersal and spatial distribution of meroplankton larvae is important for a better understanding and for the prediction of natural variability in benthic populations. An interdisciplinary approach was required during the RENORA program because larvae are vulnerable to physical transport and changes in the abiotic descriptors while they are in the water column and when they settle onto the sediment.

1.2. Data

The RENORA project was conducted over a three year period. The first phase in 1988 was designed to study the tidally-induced larval dispersion using two different sampling procedure: one following a drifting buoy during a complete tidal cycle (Belgrano et al., 1990) and a second phase concerning the study of the effects of tidally-induced variability on meroplankton at fixed locations. The results of 1988 provided new information about meroplankton dispersion to prepare more extensive investigations in 1989 and 1990 along the French-Belgian-Dutch coast from Gravelines to the Oosterschelde.

1.2.1. Sampling procedure

In order to observe the effect of tidally-induced variability on the meroplanktonic larvae distribution, for the 1988 campaign two sampling stations were located in the Southern Bight of the North Sea (Fig. 2). Meroplankton vertical haul samples were taken every hour from a stationary boat, at 3 m depth, during one tidal cycle (12 hours at Oostende and 13 hours at the Oosterschelde) using a 80 µm mesh size plankton net model WP2 (UNESCO 1968). Meroplankton samples were preserved in 10% per volume of formalin (4% formaldehyde). The filtered volume was controlled by a flowmeter TSK (Tsurimi-Seiki-Kosakusho, Japan). The tide excursion was monitored by the use of an ANDERAA currentmeter. Temperature, salinity were measured using a CTD probe (SEABIRD), dissolved oxygen with the Winkler method, and the turbidity N.T.U (Nephelometric Turbidity Unit) was recorded with a nephelometer with a Tyndall effect (DRT 1000, HF Instrument).

In order to study in detail the influence of hydrodynamical processes and abiotic factors on the spatial distribution of meroplanktonic larvae, it was necessary to take continuous samples along a planned transect. The 1989 and 1990 sampling campaigns were conducted respectively, during the late spring of 1989 along a transect from Gravelines (France) to Middelkerke (Belgium), corresponding to 35 nautical miles (Fig. 3.), and during the late spring of 1990 along a transect from Zeebrugge (Belgium) to the Oosterschelde estuary (The Netherlands) corresponding to 40 nautical miles in the Southern Bight of the North Sea (Fig. 4.).

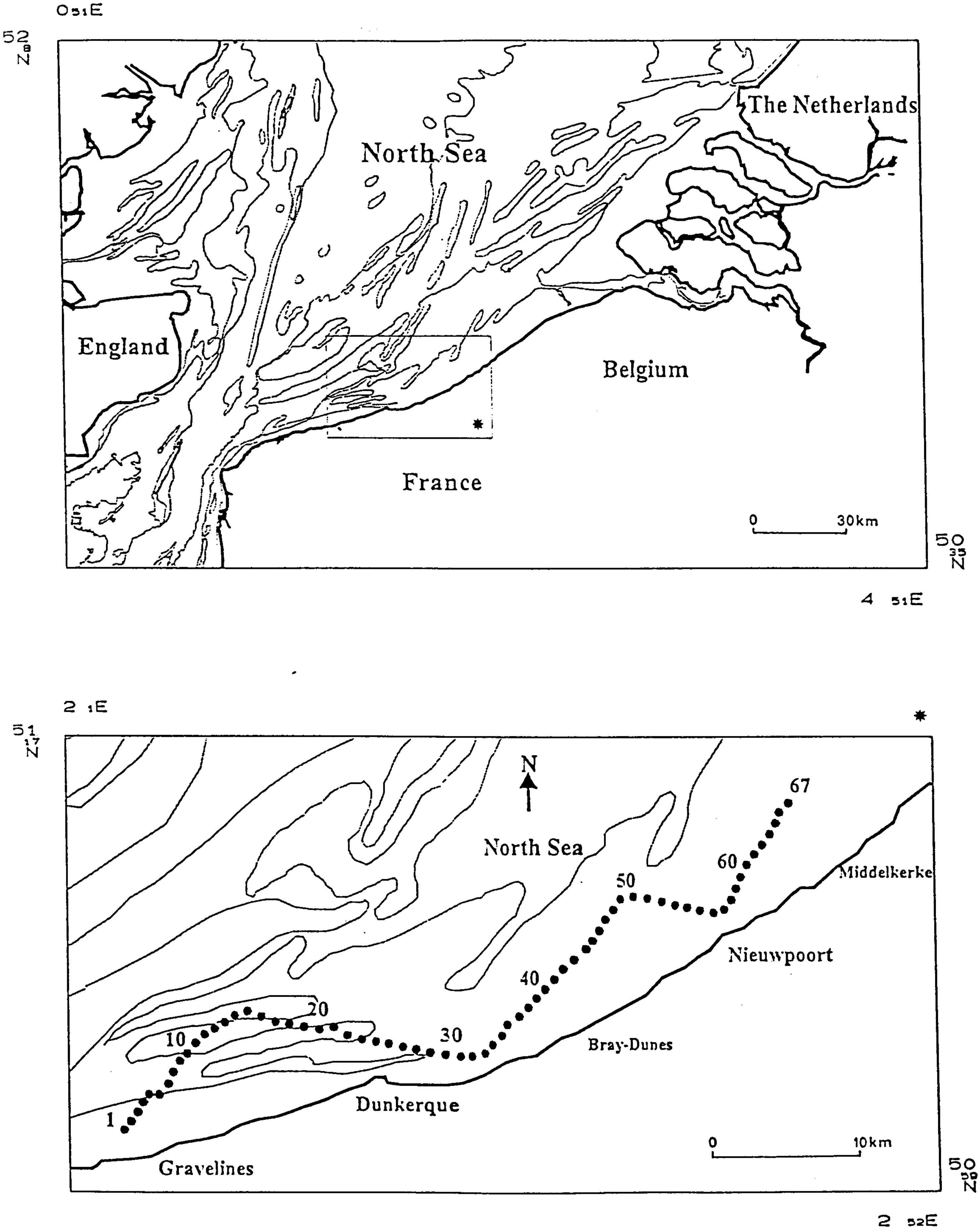


Fig. 3. Schematic map of the geographical location of the study area for RENORA 1989. The sampling transect along the coastline is presented by a dotted line. Depth countour indicates the 20m margin.

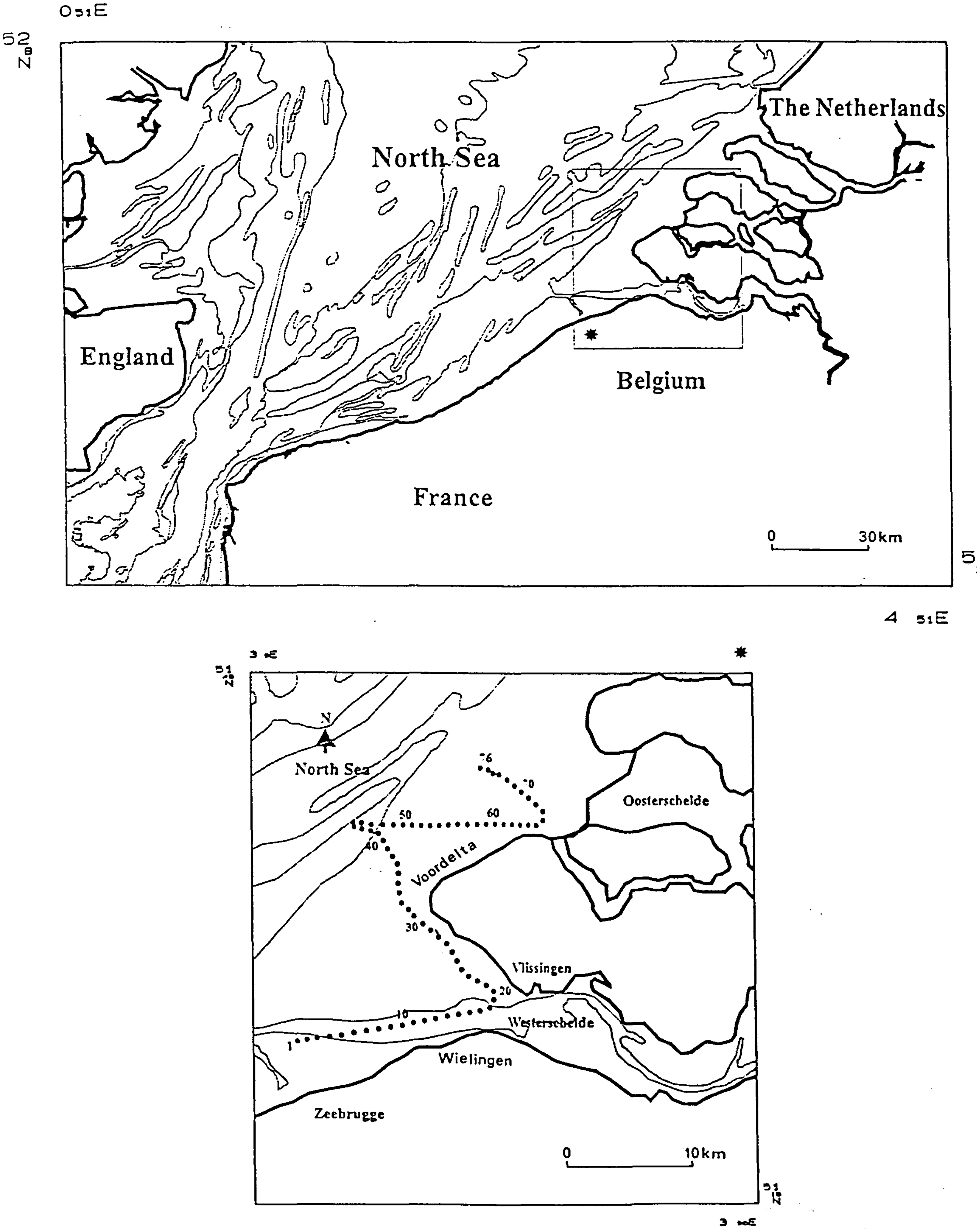


Fig. 4. Schematic map of the geographical location of the study area for RENORA 1990. The sampling transect along the coastline is presented by a dotted line. Depth contour indicates the 20m margin.

Temperature, salinity, density and fluorometry (1990 only) were measured at 0.5 s intervals by a hydrological probe CTD (SEABIRD). Depth and corrected depth were measured by the Color Echo Sounder (Raytheon V 800) on board.

For 1989, 64 and 67 meroplankton samples were collected during the two cruises at 3 m depth by a volumetric pump (PCM Moineau, 200 l/min). Each sample corresponded to 5 mn (1000 l) continuous pumping, at a constant boat velocity of 6 knots, corresponding to 0.5 nautical miles. Samples were filtered on board using a 80 µm mesh size plankton net attached to the pumping system. The meroplankton samples were preserved in 10% per volume of formalin (4% formaldehyde).

The wind direction and velocity data were obtained from the Meteorological station at Dunkerque, (France).

During the 1990 campaign 70 and 76 meroplankton samples were collected during the two cruises using an identical sampling procedure as in 1989. The surface temperature and the total suspended matter distribution were monitored by the aid of satellite images (NOAA-AVHRR) provided by KNMI (Royal Netherlands Meteorological Institute), in conjunction with the wind direction and velocity during the whole period of the RENORA campaign (May-June 1990).

1.2.2. Treatment of the samples

Meroplankton samples were counted according to the method proposed by Frontier (1969, 1972): a fraction of the sample (1/10, 1/20, 1/30... according to the plankton abundance) was removed from the sample after being well mixed. Each fraction was counted using a Dollfus dish and the aid of a stereoscopic microscope. A second replicate was counted when the number of the larvae was less than 100 individuals (Lagadeuc, 1992). The meroplanktonic larve were sorted to a species level when possible.

1.3. Data analysis

The data analysis methods described are covering a range of classical multivariate methods such as PCA, and new methods now available for analysing the spatial structure of ecological communities and their interactions with the environment. The use of different methods was needed in order to illustrate the spatial structure of the meroplankton community. The classical inferential statistical analysis implies as a fundamental assumption the independence of the observations neglecting the fact that the existence of spatial structure within the sample space implies that this assumption is not satisfied and the observations at neighbouring points are not independent from one another (Legendre & Fortin 1989). The series of methods used are following an increasing refinement that was necessary to describe the underlying spatial phenomenon in the data sets and to test interrelation models that include space as an explanatory variable.

1.3.1. Transformation of variables and PCA

Clifford & Stephenson (1975) discussed a number of methods of transformation and standarization, one of the differences being that transformation alters the score for each species in each sample without reference to the range of scores in the rest of the data (Dutilleul & Legendre, 1993).

A number of transformations are commonly used on species abundance, the commonest being the logarithmic transformation:

$$Y_{ij} = \log (X_{ij} + 1) \qquad \text{(eq. 1.)}$$

where X_{ij} = abundance of the ith species in the jth sample; Y_{ij} = the transformed variable.

According to Field *et al.*, (1982) in most cases transformation of the data is necessary to approach a statistical normality: species density data invariably show a skewed distribution with many rare species and few ones extremely abundant. A simultaneous result is often that the mean and standard deviation are strongly correlated. Transformation performs at the same time the normalisation and the homoscedasticity of variates (Field & McFarlane 1967; Clifford & Stephenson 1975).

For the 1988 investigation the species density data were first transformed to their natural logarithm. Homogeneity of variances after transformation was tested by the use of the Barlett test (Sokal & Rohlf, 1981) since the equality of variances or homoscedasticity in the set of samples was an important precondition for the statistical tests that were performed.

For the 1989 and 1990 campaign the species density data and the abiotic variables where root-root (√√) transformed according to Field *et al.*, (1982) for the PCA, chronological clustering, MDS, CCA, and constrained CCA. This transformation has a similar effect as the log transformation in reducing the weighting of abundant species, but in addition has the advantage that, when similarity is assesed the similarity coefficient is invariant to a scale change. For all the transformed data normality was not rejected at the 1% level by the Kolmogorov-Smirnov test of goodness-of-fit, (Sokal & Rohlf, 1981), as modified by Lilliefors (1967).

The PCA was used on the data of the 1989 and 1990 campaign as a first exploratory tool in order to find any correlation between species assemblages and stations. The hierarchical flexible clustering strategies described by Lance & Williams (1967), Legendre & Legendre (1984), with ß = - 0.3 on a matrix of Euclidean distances among observation vectors was used. For the 1989 campaign the two set of data were respectively of 64 and 67 stations and 8 species, and for the 1990 campaign of 70 and 76 stations and 9 species.

1.3.2. Nonparametric method

For the data of the 1988 campaign nonparametric procedures (Ardisson *et al.*, 1990), were used since the meroplankton mean densities departed significantly from a normal distribution (Kolmogorov-Smirnov test, $P<0.001$). The Spearman's test (Castonguay *et al.*, 1992), was used to test the existence of any correlations between species data and environmental descriptors.

For the data of the 1989 and 1990 campaign the Kruskal-Wallis H test (Siegel, 1956; Sokal & Rohlf 1981; Legendre & Legendre, 1984) was performed on the environmental variables measured along the transect within the group of stations defined by the chronological clustering to test for statistical significance.

Furthermore, in order to interpret the taxonomic group clusters using the environmental variables, and conversely interpret the environmental data clusters using the taxonomic groups, an ANOVA was used with the taxonomic and environmental clusters as the classification criterion, and each quantitative environmental variable in turn as the variable to be analysed. These Anova were used to detect the environmental variables responsible for the taxonomic groups being different in the clusters, and to see what taxonomic groups corresponded to the environmental clusters.

1.3.3. Cumulated function

For the data collected during the summer 1988 the cumulated function method proposed by Ibanez *et al.,* (1993) was used to detect the general trend of the meroplankton density distribution in relation to the tide excursion. This method can be applied to any chronological series with data x (t) sampled at each t varying between 1 and N and with reference value k. In this case, k was the mean of the series. After subtracting k from all the data we added these residuals to obtain the cumulated function:

$$S_1 = (x_1 - k)$$
$$S_2 = (x_1 - k) + (x_2 - k) = S1 + (x_2 - k) = x_1 + x_2 - 2k$$

$$S_p = \sum_{i=1}^{p} x_i - pk$$

(eq. 2. after Ibanez *et al.,* 1993)

This cumulated function is very sensitive to the changes of the mean value of the series and is therefore a useful tool for detecting any trends in the original data.

1.3.4. Chronological Clustering

The "chronological clustering" method was developed and used by Legendre *et al.* (1985) to describe discontinuities occurring during an ecological succession and to associate them with corresponding shifts in the environmental structure (Allen *et al.,* 1977). In the present study, this form of time-constrained clustering was used as a starting point to define the spatial structure of the data sets, taking into account the spatio-temporal continuity of the transects, and to describe disjunctions occurring along the space-and-time data series. The main difference between "chronological clustering" and other clustering methods is that it allows to identify breakpoints in a space or time series of multispecies biological samples, collected as a time series or along a transect, taking into account the space or time sequence itself (or, in the present study, the space-and-time sequence) of the samples.

This method presents the additional advantage that it may pinpoint aberrant samples, resulting for instance from random events that may temporarily perturb the sequence of the series of samples. These random events can include for example temporary shifts of water masses at a fixed station in a marine ecosystem, where it is not certain that in the field one actually always samples the same water mass. These external forcing events are very common when studying shallow-water pelagic organisms.

The data for these analyses were divided first into two matrices, one representing the number of each taxonomic group for each station (8 taxa for 1989 and 9 taxa for 1990), and one representing the environmental variables (5 for 1989 and 6 for 1990) measured at each station along the succession of samples in chronological order. Each matrix was transformed into a symmetric distance matrix by calculating similarity indices.

The choice of the appropriate indices of similarity was based on the reviews by Gower (1984) and Legendre and Legendre (1983; 1984). For the environmental data, the Gower similarity coefficient (Gower, 1971) was used; the measure of variability is measured as the range of variation of each variable in all samples under study. For the species data, the Steinhaus coefficient was used as suggested by Legendre and Legendre (1984). This coefficient is asymmetrical and does not consider double zeros as an indication of resemblance. Gower and Legendre (1986) showed its reliability for measuring both high and low similarities with the same fidelity. Following Legendre *et al.*, (1985), the degree of connectedness or cluster fusion (Co) was set to 50% and the probability level $\alpha=$ 0.20 to obtain the partition of each data series. The similarity matrices were computed using programme SIMIL (Legendre and Vaudor, 1991). From the similarity matrices, the chronological clustering was computed using the CHRONO programme from "The R Package" (Legendre and Vaudor, 1991).

1.3.5. Non-metric Multi-Dimensional Scaling (MDS) and Bray-Curtis dissimilarity measure

Following the results obtained from PCA and chronological clustering the spatial structure of the data sets was double checked using MDS. The non-metric multi-dimensional scaling MDS (Kruskal & Wish, 1978) differs from PCA in the sense that a specified number of new axes is found to preserve some relationship among the between-sample distances. The attraction of non-metric MDS lies in its dependence on rank rather than quantitative values in the between-sample dissimilarity matrix, and its ability to construct a map of the samples in 2 dimensions which attempts to satisfy all such conditions. The extent to which this has been achieved is given by stress statistics (Field *et al.*, 1982). Stress may be thought of as the distortion involved in compressing the data to a small number of dimensions. If the stress is large, the current map matches poorly with the observed dissimilarities, conversely, low stress indicates that the sample relationship can be well represented by a station map in the specified dimensionality.

The non-metric MDS is an interative procedure more computationally demanding than PCA. The non-metric MDS was performed on a Bray-Curtis dissimilarity matrix (Bray & Curtis, 1957). This dissimilarity coefficient avoids the problem often occuring in the presence of sparse matrices, where many species are jointly absent from any 2 samples whose similarity is being calculated, resulting in an unsatisfactory correlation.

The Bray-Curtis dissimilarity can be defined as the absolute differences between the transformed species count for two samples, summed over all species, and then divided by the total count over both samples and all species. The Bray-Curtis and non-metric MDS were performed according to Field *et al.*, (1982) using the statistical package SYSTAT (Macintosh, Version 5.2, 1992).

1.3.6. Canonical Correspondence Analysis method (CCA)

In order to interpret species assemblages variations by environmental variables, a direct gradient analysis technique was necessary. Canonical Correspondence Analysis (CCA) preserves the chi-square distance, like standard Correspondence Analysis (CA) and is related to both multiple regression and ordination. The main difference with PCA is that CCA does not rely on *a posteriori* correlations to associate environmental characteristics to species ordination axis. The Canonical Correspondence Analysis (ter Braak, 1986; 1988 a; 1988 c) was used to identify factors contributing to the spatial variability of the meroplankton because CCA performs well with skewed species distributions, with quantitative noise in species abundance data, with samples taken from unusual sampling design, with highly intercorrelated environmental variables, and especially with situations where not all the factors determining species composition are known (Palmer, 1993).

The technique of canonical correspondence analysis (CCA) selects as the first ordination axis the linear combination of environmental variables that maximizes the dispersion of the species scores; the species scores remain weighted averages of the sites scores, and the first eigenvalue measures the dispersion of the species along the axis. The second and further axes also select linear combinations of environmental variables that are maximally related to the species data, subject to the constraint. This protocol ensures that the canonical ordination axes are optimally related to the supplied environmental descriptors.

The analysis provides then two sets of sample scores: the sample scores that are weighted averages of the species scores, and the sample scores that are linear combinations of environmental variables.

By means of CCA, species, samples and environmental variables can be arranged in a 2-dimensional space such that similar entities are far apart. The arrows in a CCA biplot represent environmental variables such that their size indicates their explanatory power.

The angle between the arrows representing the environmental variables indicates correlation between factors: 0° indicates strong positive, 180° strong negative, 90° indicates no correlation. The occurrence of a species can be related to the environmental variables by perpendicular projecting their position on the environmental axes in the same plot, called a biplot.

The sample scores are weighted averages of species scores and the combination of the sample and species positions in the plot yields an insight into what species are responsible for a certain position of the sample (Jongman *et al.*, 1987; ter Braak, 1988a).

1.3.7. Partial Canonical Correspondence Analysis and the use of covariables

The partial version of CCA (ter Braak, 1990) allows removing, by multiple linear regression, the effect of known variables before computing the constrained ordination. These ordination techniques allow to measure the amount of variation as a sum of canonical eigenvalues for the species matrix which can be explained by the environmental variables. In most cases the environmental variables alone are not able to fully explain the amount of variation observed in the species community structure. The need to compare the set of biotic data (species) and abiotic data (environmental variables), as suggested by ter Braak (1987), is very important to understand further the spatial structure in community studies (Legendre & Fortin, 1989).

The data for the CCA analyses were divided into three matrices : a) species densities, b) environmental variables, c) geographic locations of the samples (spatial component). Following Legendre (1990) and Borcard *et al.*, (1992), the geographic coordinates of the sampling locations were used to perform a cubic trend surface regression to ensure the extraction of more complex structure such as patches and not only the linear gradient pattern in the species matrix. The three data sets were analysed using canonical correspondence analysis (CCA), alternatively with the spatial matrix and the environmental matrix as covariables (Table 2). The geographic coordinates, x and y, of the sampling stations along the path of the boat were used, by adding all terms, for a cubic trend surface regression (Legendre, 1990):

$$z = b_1x + b_2y + b_3y^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \qquad \text{(eq. 3.)}$$

where z is the quantitative variable to be estimated and the terms b_1, b_2 ... are the coefficient parameters in the rgression equation. This type of regression allows not only the linear gradient patterns in the species data to be extracted, but also more complex features such as patches, which require the quadratic and cubic terms of the coordinates and their interactions to be correctly described. In this case there was no need for an intercept term (b_0) since the species data are centered on the origin in the correspondence analysis (Borcard *et al.*, 1992). The nine terms of the equation were submitted to a multivariate extension of the stepwise regression method in the CANOCO program (Borcard *et al.*, 1992). The following terms of the equation were retained for the analysis:

$$z = b_1x + b_2y + b_4xy + b_5y^2 + b_9y^3 \qquad \text{(eq. 4.)}$$

The three data matrices were transformed into distance matrices before the CCA tests; euclidean distances among sampling locations were used to form the spatial distance matrix.

CCA Input	Species Matrix	Covariables Matrix	Environmental Matrix	Spatial Matrix
Step (1)	*	-	*	-
Step (2)	*	-	-	*
Step (3)	*	Spatial matrix	*	-
Step (4)	*	Environmental matrix	-	*

Table 2. Each step of the four canonical correspondence analyses (CCA) is shown, the asterisk (*) indicates the data matrix input, and the trait (-) indicates no input. Covariables are used in steps (3) and (4).

The use of constrained canonical ordination (ter Braak, 1988a) allowed to measure the impact on the species data of both the environmental condition and the spatial structure. Aware of the fact that in some cases the species and the environmental variables share the same spatial structure, the degree of variation in the species data, due to the spatial structure, has been partialled out by the use of the covariables.

Using this method we consider the case where a set of explanatory variables is subdivided in two sets, one set of p covariables and one set of q variables. It is possible to obtain an ordination diagram of the unimodal relationship between the response variables and the q variables of interest after eliminating the effect of the p covariables. The four steps in Table 2. represent the four fractions of the variation:

- (a) the species variation that can be explained by the environmental descriptors independently from the spatial structure.

- (b) the spatial structure in the species data shared by the environmental descriptors.

- (c) the spatial structure in the species data not shared by the environmental descriptors.

- (d) the species variation not explained neither by the spatial structure nor by the environmental descriptors.

Each of these fraction was calculated as suggested by Borcard *et al.,* (1992). For example, if the four analyses gave the following results:

Step (1) CCA - sum of all canonical eigenvalues = 0.152

Step (2) CCA - sum of all canonical eigenvalues = 0.168

Step (3) CCA - sum of all canonical eigenvalues = 0.128

Step (4) CCA - sum of all canonical eigenvalues = 0.044

and the sum of all eigenvalues, or total inertia, of the species matrix = 0.291 then the percentage of the total variation for each step can be calculated as follows:

$$\text{Step (1)} : 0.152 \cdot 100/0.291 = 52.2\%$$

$$\text{Step (2)} : 0.168 \cdot 100/0.291 = 57.7\%$$

$$\text{Step (3)} : 0.028 \cdot 100/0.291 = 9.6\%$$

$$\text{Step (4)} : 0.044 \cdot 100/0.291 = 15.1\%$$

The whole amount of explained variation as a percentage of the total variation of the species matrix is calculated by summing the results of step (1) and step (4), or those of step (2) and step (3), this is equal to 67.3%

The overall variation of the species matrix can be divided in four fractions:

- (a) the nonspatial environmental variation, step (3) = 9.6%

- (b) the spatially structured environmental variation, step (1) - step (3), or step (2) - step (4) = 42.6%

- (c) the spatial-species variation that is not shared by the environmental descriptors, step (4) = 15.1%

- (d) the unexplained variation and the stochastic fluctuations, which is either the sum of step (1) and (4), or the sum of step (2) and (3).

This method allows to quantify and divide in term of percentages the whole variation of the species matrix in relation to environmental and spatial-structuring processes.

1.3.8. Monte Carlo permutation test

The Monte Carlo permutation test was used to test the significance of the CCA results. The Monte Carlo permutation of samples determines classes of sample within which samples are randomly permuted 999 times (in this case).

For example, the species data and covariable data of the samples will be linked in a particular permutation to, for example, the environmental data of the samples respectively. In this way classes are permuted, and a random dataset is obtained, then the differences between the permutation and the measured trace statistics or the first eigenvalue are compared.

In this particular case the Monte Carlo test used the permutations of the residuals of the species after fitting covariables and environmental variables (ter Braak, 1990). The p-value equal to the exact Monte Carlo significance level will be, for example, $p = 0.05$. This means that the first ordination axis is just significant at the 5% significance level.

The Monte Carlo permutation test and the multivariate anlyses were performed using the CANOCO ™ program (ter Braak, 1988 b; 1990).

The results of the significance tests where subjected to the so-called Bonferroni's correction method for multiple tests. This type of testing is the central step of inferential statistics (Legendre, pers. comm.) and it allows to generalize one's findings to some reference population that the observations were drawn from and are supposed to represent.

The Bonferroni's correction method for k independent tests, computes a corrected significance level $\alpha' = \alpha/k$. This α' can be used in two different ways. One can check whether any of the probability values p_i remains significant at that level, which constitutes a global test of significance (Legendre, pers. comm.). It is also possible to decide to make all the individual tests more conservative and interpret only those that remain significant at the alpha' level (Cooper, 1968; Miller, 1977).

1.3.9. Path analysis

Path analysis can be regarded as a sequence of multiple regression and correlations according to an *a priori* hypothesis, and as a promising statistical technique for assessing covariation among species in the investigation of community structure (Wootton, 1994). Path analysis can be used to test if for example assumed significant correlations between species-environment are real or spurious implying a common spatial gradient (Legendre & Troussellier, 1988). Path analysis was carried out on the data collected in summer 1988 using three correlation matrices based on Pearson correlation coefficients corresponding to the physical forcing (tide height and tidal current velocity), environment (abiotic factors), and biology (meroplankton density) using the program Piste (Vaudor, 1992).

In this particular case the causal links to be tested were the direct and indirect effect of the tide and the environment on the meroplankton density distribution. The tests of significance in the program Piste are based on the usual tests of significance of multiple regression and they assume that the coefficients used for the data imput are Pearson coefficients and that the relations are linear. The computed results are reported as direct causal covariance regression values with the corresponding levels of probabilities, since the path analysis used for the 1988 data was standard and not based on Mantel statistics, the significance tests of path coefficients were used for interpretation (Nantel & Neumann, 1992).

For the data collected in the summer 1989 and 1990 a path analysis was computed from the simple Mantel statistic values and the significance tests of the path coefficient were confirmed by the partial Mantel test (Nantel & Neumann, 1992). The use of Path analysis in combination with Mantel statistic and related computational technique are explained in more detail in the next section.

1.3.10. Mantel and partial Mantel tests for spatial autocorrelation and causal modelling

The Mantel and partial Mantel tests (Mantel, 1967, Smouse *et al.*, 1986) are very useful methods to look for spatial trend in data corresponding to some form of diffusive process (Legendre & Troussellier, 1988).

Mantel proposed to represent the spatial relationship among sampling localities by a matrix **A** of geographic distances among all pairs of geographic points or coordinates. This matrix is referred to as space. Mantel's tests looks for a relationship between this matrix of geographic distances and some other distance matrix **B** which is meaningful for the problem at hand. The trend in the data may be linear, in which case geographic distances are used directly for testing. The Mantel statistics can be regarded as the sum of the cross-products of the corresponding values in the two matrices **A** and **B** under investigation (for instance the geographic distance and the species distribution, or the geographic distance and the environmental variables).

The Mantel test hypothesis are set up in the following way: the null hypothesis (H_o): distances among points in matrix **B** are not linearly related to the corresponding distances in matrix **A**. When **A** represents geographic distances (space), H_o reads as follows: the variable (or multivariate data) in **B** are not autocorrelated as a gradient. (H_1) reads as: distances among points in matrix **B** are correlated to the corresponding distances in matrix **A**.

The three matrices corresponding to the space (geographic distances among sampling stations matrix **A**), environment (environmental variables matrix **B**), and biology (species density matrix C), were compared as suggested by Legendre & Trousselier (1988). The Mantel statistic is identical to a linear correlation between two vectors of distance when the values within each distance matrix are standardised. To eliminate the linear relationship between distance spaces, also the partial Mantel test was computed as suggested by Smouse *et al.*, (1986).

As a first step one computes the three matrices **A**, **B** and **C**, then one computes **B'** which contains the residuals of the regression of the values in **C** on the values in **A**; finally the standardised Mantel statistic is computed between the values in **B'** and those in **C'** which contains the residuals of the regression of the values in **C** on the values in **A**; finally the standardized Mantel statistic was computed between the values in **B'** and those in **C'**. This is basically a standard way to compute a partial correlation coefficient for two variables b and c while controlling the effect of a third variable a. Finally the probability associated with this partial Mantel statistics was determined by Monte Carlo permutation test.

As suggested by Legendre & Troussellier (1988) the results of Path analysis combined with the Mantel statistics can be used to produce a synthetic model of causal relationships able to elucidate whether the observed relationships between species and environmental variables are causal, or simply the result of sharing the same common spatial gradient in both set of variables.

The partial Mantel tests were used for causal modelling, as described by De Neufville & Stafford (1971), Legendre & Legendre (1984) and by Legendre & Troussellier (1988). This type of predictive models are based on causal relations (not only correlative) between the different descriptors used in the analysis. These informations are based on causal analysis which makes prediction involving the values of the simple correlations (Mantel test) and of partial correlation (Partial Mantel test). The result of actual computations indicates which predictions are realized.

The Mantel statistic is computed as a product-moment correlation coefficient while the partial Mantel statistic is computed as a partial correlation coefficient. The use of Mantel statistics in causal analysis shows that it is possible to have an estimation of the proportion of spatial variation present in the data and to explain the theoretical causal relationship between environmental variables representing processes and community structure.

In community analysis there are a multiplicity of potential causal paths in the observed structures, acting at different spatial and temporal scales.

This can help the field ecologist to try to identify, for example, whether the observed changes of some environmental variables have an effect on the biotic variables and, if the answer is yes, to what extent this prediction can be used to build an hypothetical predictive causal model. The Mantel and partial Mantel tests were computed using the RPackage : Multidimensional analysis, spatial analysis (Legendre & Vaudor, 1991).

Chapter II.

Results

CHAPTER II. Results

2.1. The influence of tidal-induced variability on the distribution of meroplankton larvae in the Southern Bight of the North Sea, 1988 campaign.

2.1.1. Hydrographic parameters

The results of the ANDERAA currentmeter for Oostende (Fig. 5. A) shows the excursion of the tide from 9h00 to 22h00 running parallel to the coastline. At low water occuring at 9h06 min the tide moves northward, turning southward at 12h30 min, while approaching the high water time at 14h10 min, and turning northward again while reaching the second low water time at 21h36 min. This was an indication that the residual tidal drift transport was in the North-East direction, also enhanced by the South-West wind at mean velocity of 3.5 m. s-1.

The tidal components are reported in Fig. 5. B. The highest tidal current velocity at 650 mm/sec was found at high water running at 225 degrees East. The tidal component (North-East) are plotted in more details in Fig. 5. C.

The ANDERAA readings obtained for the Oosterschelde station shows the excursion of the tide (Fig. 6. A). At low water at 10h15 min the tide turns Northward in the direction of the North Sea, leaving the Oosterschelde estuary and reaching high water at 16h25 min. The tide turns again at 19h45 min, approaching the second low water time at 23h05 min, entering the Oosterschelde estuary at 90°C. The tidal components measurements (Fig. 6. B) shows that the highest current velocity at 580 mm/sec was found at the ebbing of the tide, approaching the second low water margin at 90° degrees. The tidal component (North and East) are plotted in Fig. 6. C showing the looping circulation pattern in front of the storm surge barrier at the Oosterschelde. The wind conditions were inversed from Oostende to a North-East wind with a mean velocity of 2.5 m.s^{-1}.

2.1.2. Abiotic descriptors

The temperature range distribution at Oostende (Fig. 7. A) was from 16.5°C to 17.5 °C; showing an increase from 17°C to 17.5°C during the ebbing of the tide, the lowest temperature value 16.5°C was found at 12h00, just after the first low water margin at 11h00. The salinity range distribution (Fig. 7. B) shows the lowest value 30.5 p.p.t. between 13h00-14h00, and the highest value 32.25 p.p.t. between

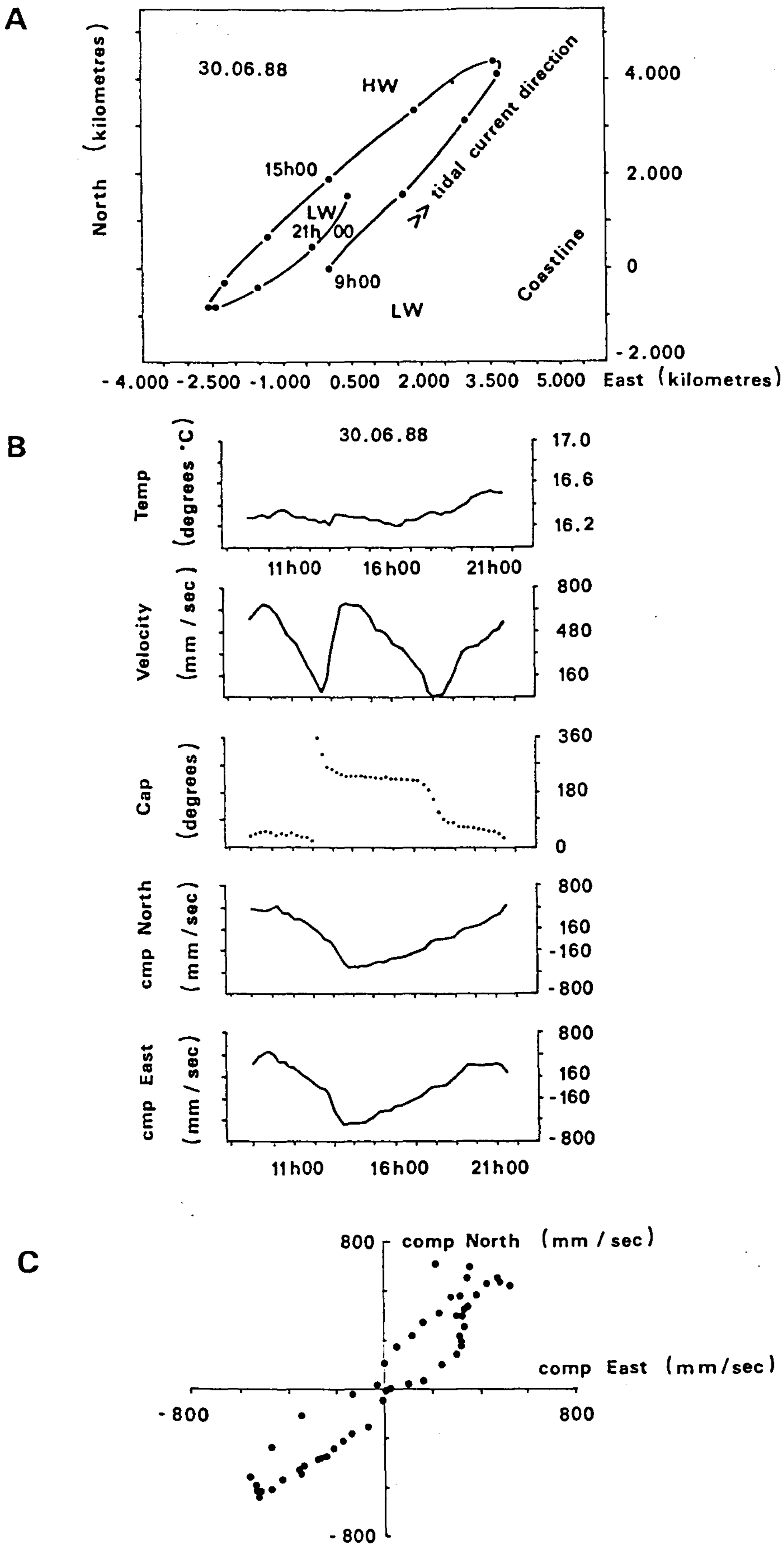


Fig. 5. (A) ANDERAA currentmeter traject at Oostende showing the movement of the tide, and th occurence of low water (L.W) and high water (H.W). (B) From top to bottom are reported th ANDERAA readings of temperature (°C), current velocity (mm:sec), current direction (degrees), an the tidal component North and East (cmp). (C) The plot result of the tidal component North an East (comp).

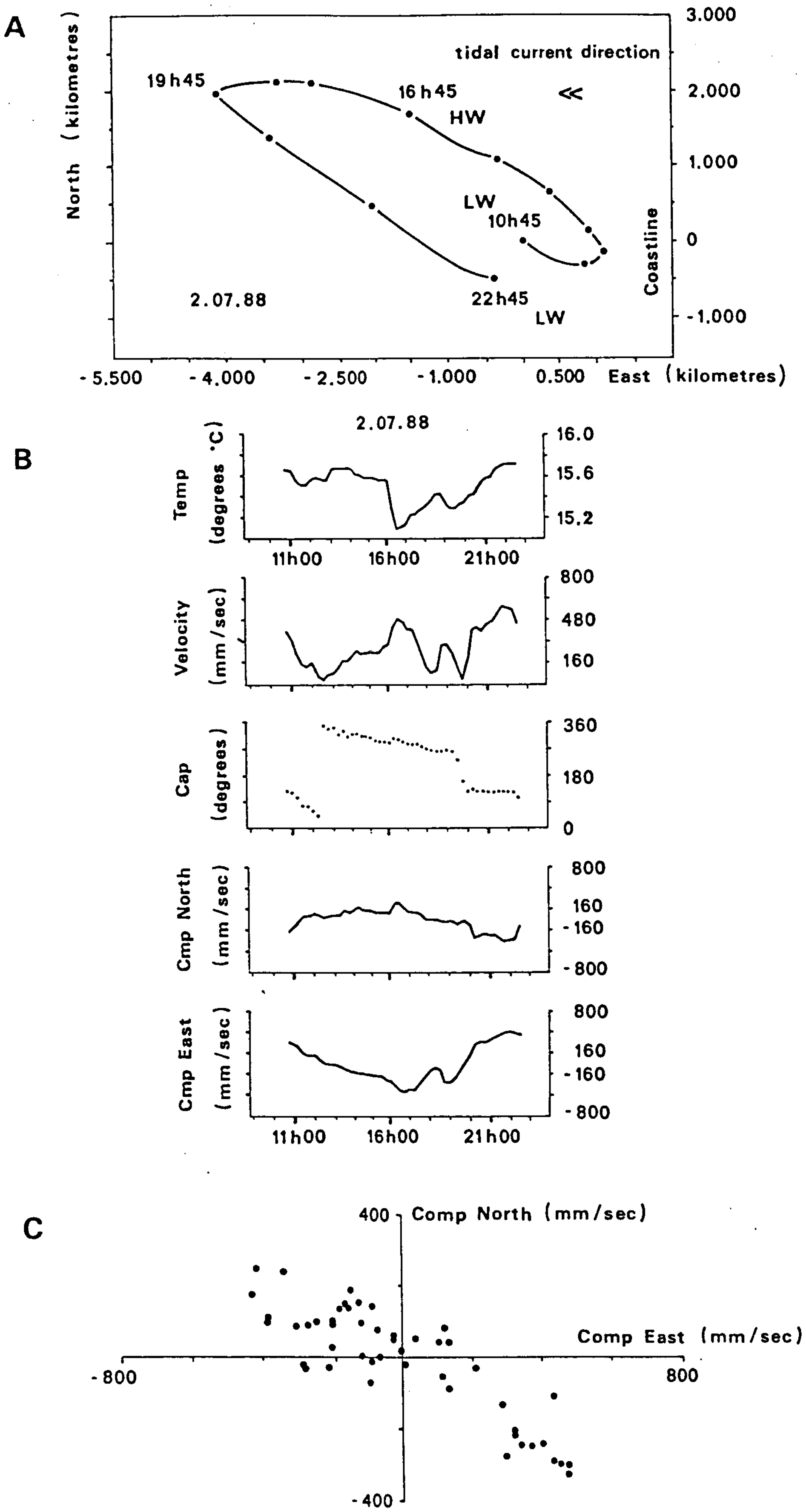


Fig. 6. (A) ANDERAA currentmeter traject at the Oosterschelde showing the movement of the tide, and the occurence of low water (L.W) and high water (H.W). (B) From top to bottom are reported the ANDERAA readings of temperature (°C), current velocity (mm:sec), current direction (degrees), and the tidal component North and East (cmp). (C) The plot result of the tidal component North and East (comp).

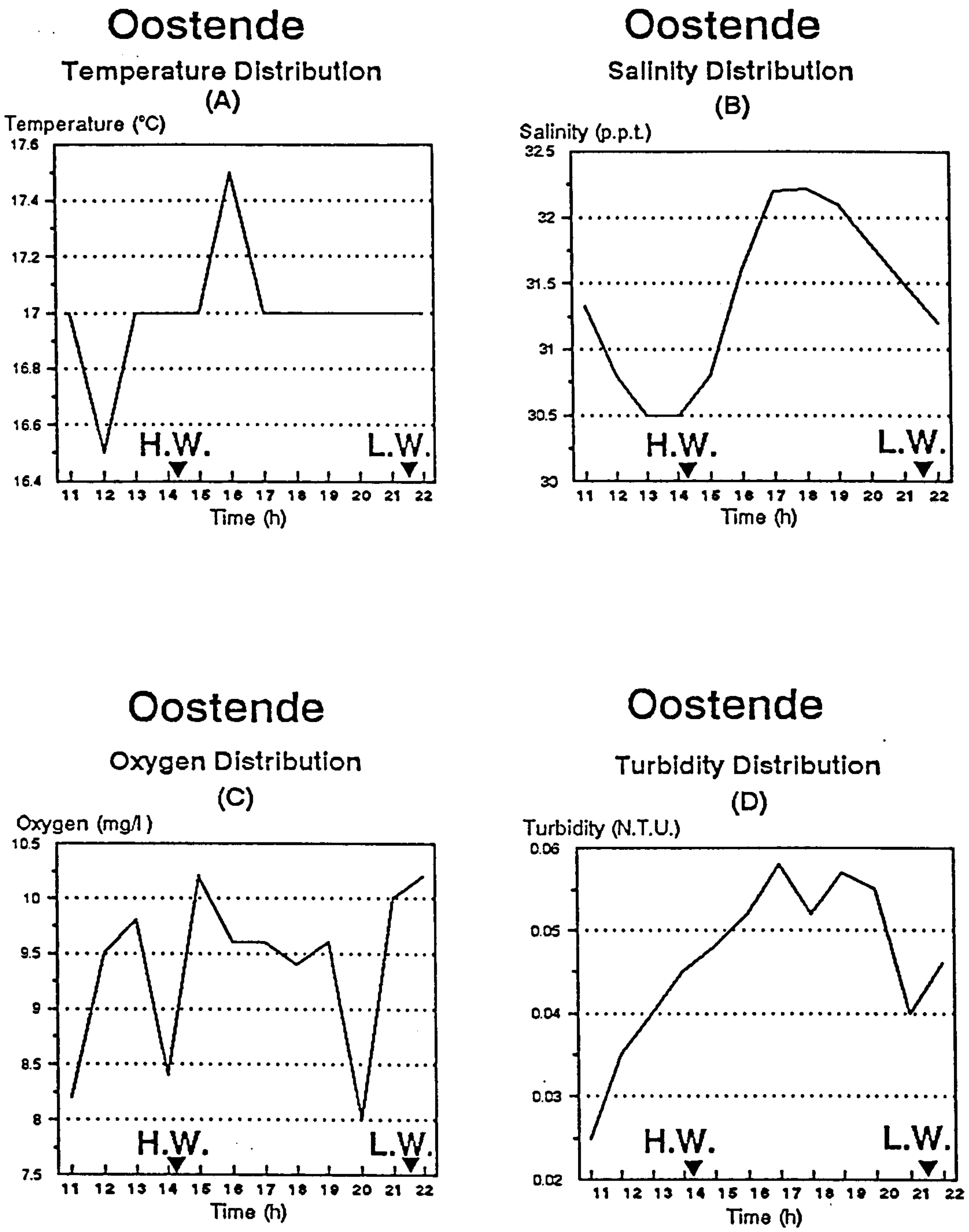


Fig. 7. Abiotic variables at Oostende (A) Temperature, (B) Salinity, (C) Oxygen, (D) Turbidity. H.W. and L.W. indicates the time of occurence of high water and low water.

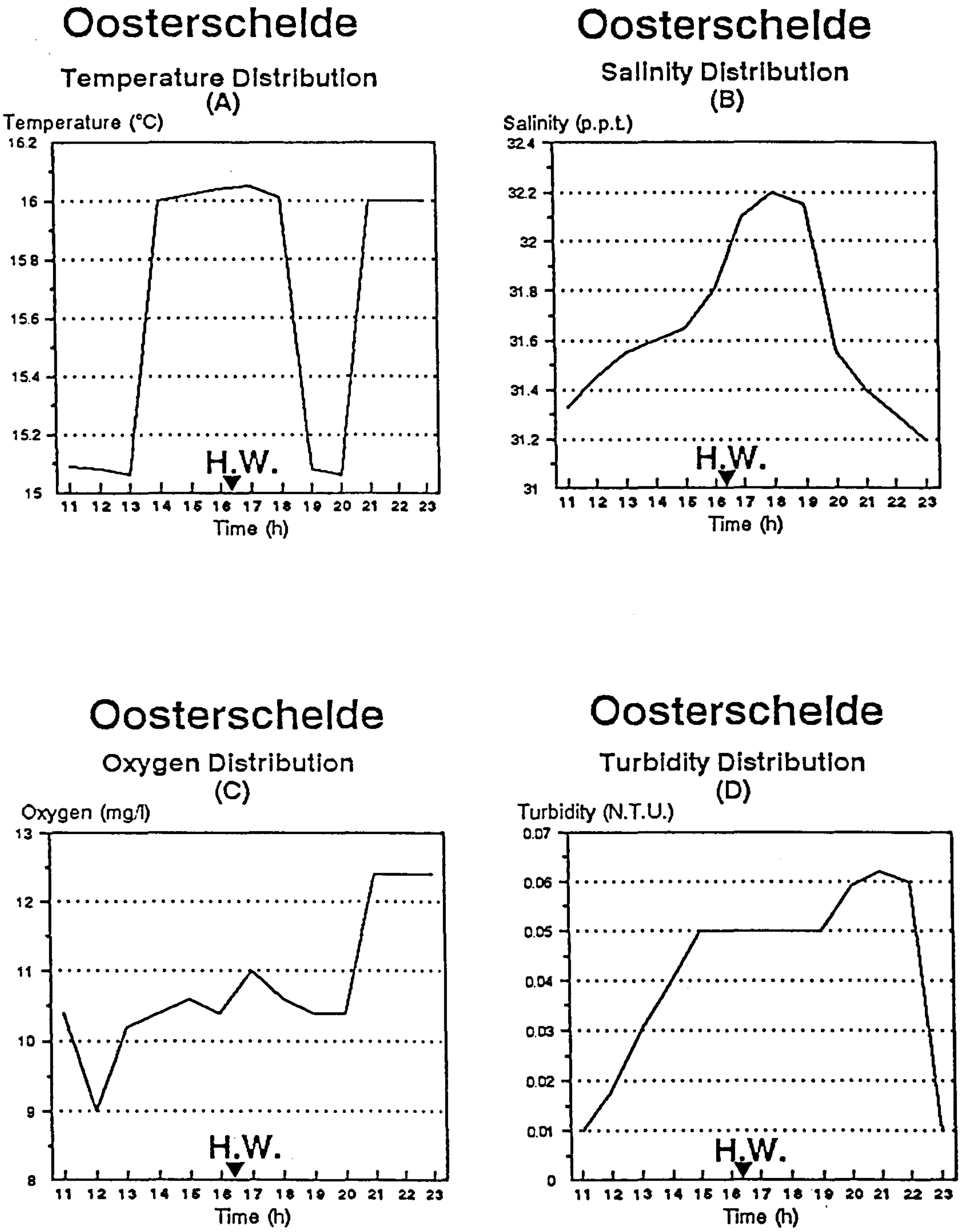


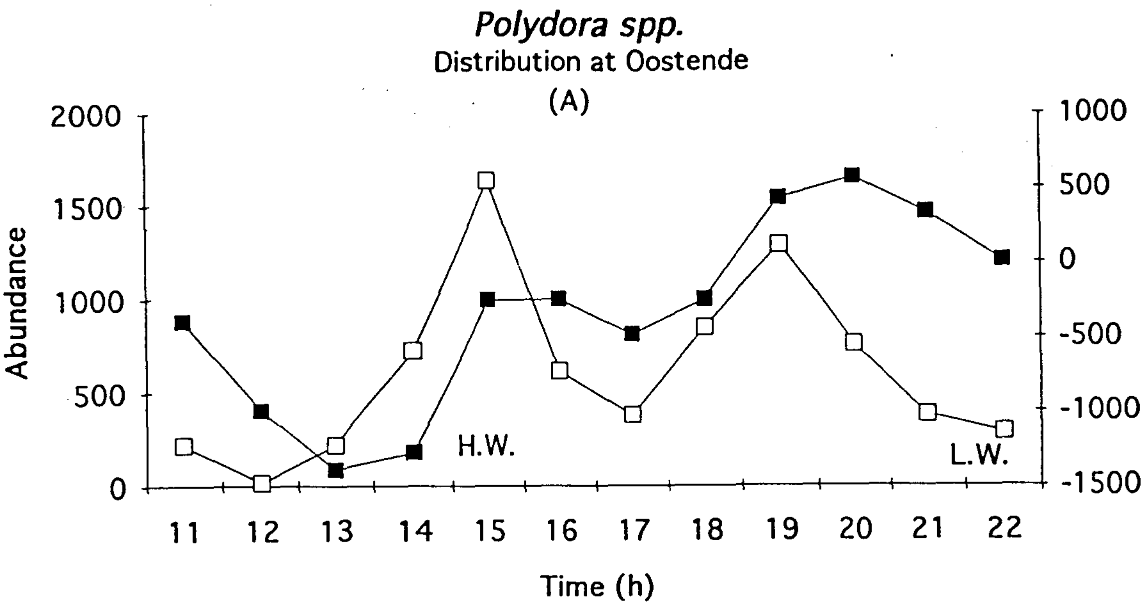
Fig. 8. Abiotic variables at the Oosterschelde (A) Temperature, (B) Salinity, (C) Oxygen, (D) Turbidity. H.W. indicates the time of occurence of high water.

18h00-19h00. The oxygen distribution (Fig. 7. C) shows the highest values of 10.25 mg/l were found at 15h00 and 22h00. The lowest oxygen value 8 mg/l was found at 20h00. The turbidity distribution (Fig. 7. D) shows a clear increase after low water at 11h00 through the high water time until 17h00 with values ranging from 0.02 to 0.058 N.T.U. The turbidity increase maybe, was due to the effect of the tidal current which enhanced sediment resuspension at the benthic boundary level (BBL).

The temperature distribution at the Oosterschelde (Fig. 8. A) shows a bimodal pattern following the tide with the highest values at 17h00 pm with 16.1°C, and at 23h00 with 16.0°C. The lowest values were found at 13h00 and 20.00 pm with 15.1°C. The salinity distribution (Fig. 8. B) reaches its highest value at 18h00 with 32.2 p.p.t. after the high water time at 16h25 min. The oxygen distribution (Fig. 8. C) shows an increase in the oxygen concentration concomitant with the ebbing of the tide at 21h00 at a value of 12.5 mg/l. The lowest value of 9 mg/l was found at 12h00. The turbidity distribution (Fig. 8. D) shows a clear increase from the ebbing of the tide at 12h00 am with 0.01 N.T.U. until 15h00 with 0.05 N.T.U.; the highest value however was found at 21h00 with 0.062 N.T.U. concomitant with the second ebbing of the tide approaching the low water margin at 23h05 and with the highest tidal current velocity.

2.1.3. Biotic descriptors

The meroplankton taxa present at Oostende were the larvae of *Polydora spp.* and the larvae of bivalves. The density curve and the cumulated distribution function was calculated and plotted respectively in Figs. 9. A & 9. B. The *Polydora spp.* larvae reached the highest density value at 15h00 after the high water at 14h10 min with 1,650 ind. m^{-3}. The cumulated sum curve (black square line), showed more clearly the differences in density value between the two flooding periods with the two density peaks at 15h00 and 20h00. The bivalves distribution shows a clear peak at 16h00, after the high water time at 14h10 min, with a density value of 9,500 ind. m^{-3}. The cumulated sum curve (black square line), showed the decreasing density value following the tidal excursion. The results obtained were subjected to Spearman's correlation test between taxa and physical factors. Both *Polydora spp.* and the bivalves were strongly positively correlated with the tide (Spearman's $r_{s(t)}$, $P<0.01$), with turbidity (Spearman's $r_{s(tr)}$, $P<0.05$), and with salinity (Spearman's $r_{s(s)}$, $P<0.01$).



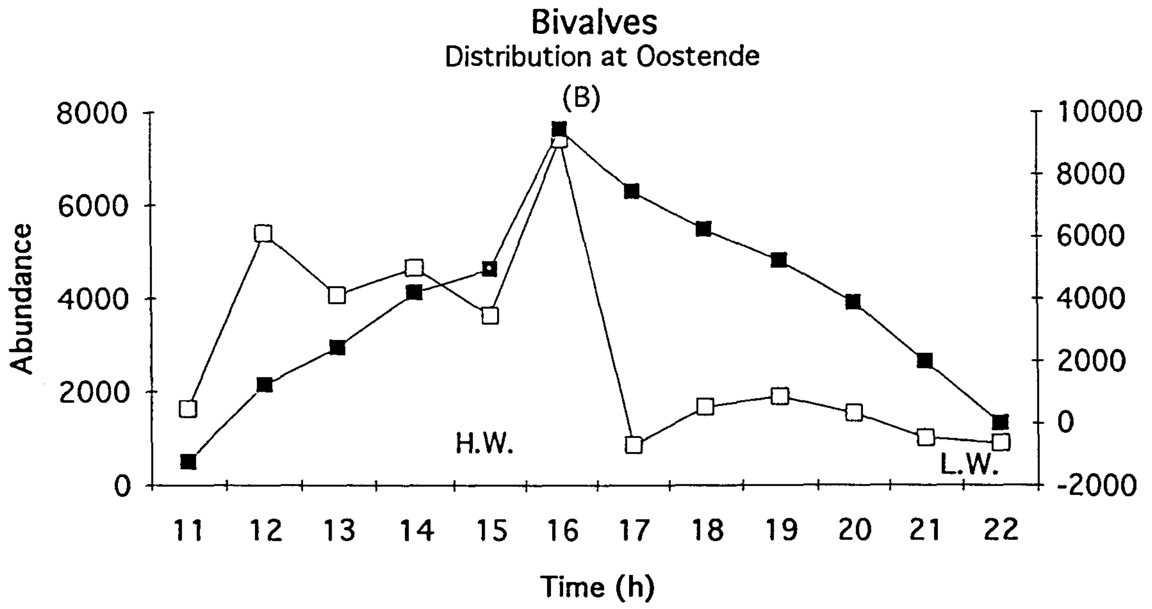


Fig. 9. (A) *Polydora spp.* and (B) bivalves larvae distribution at Oostende, white square line showing the density values not transformed, black square line showing the density values transformed to cumulated function. H. W. and L. W. indicates the time of occurence of high and low water.

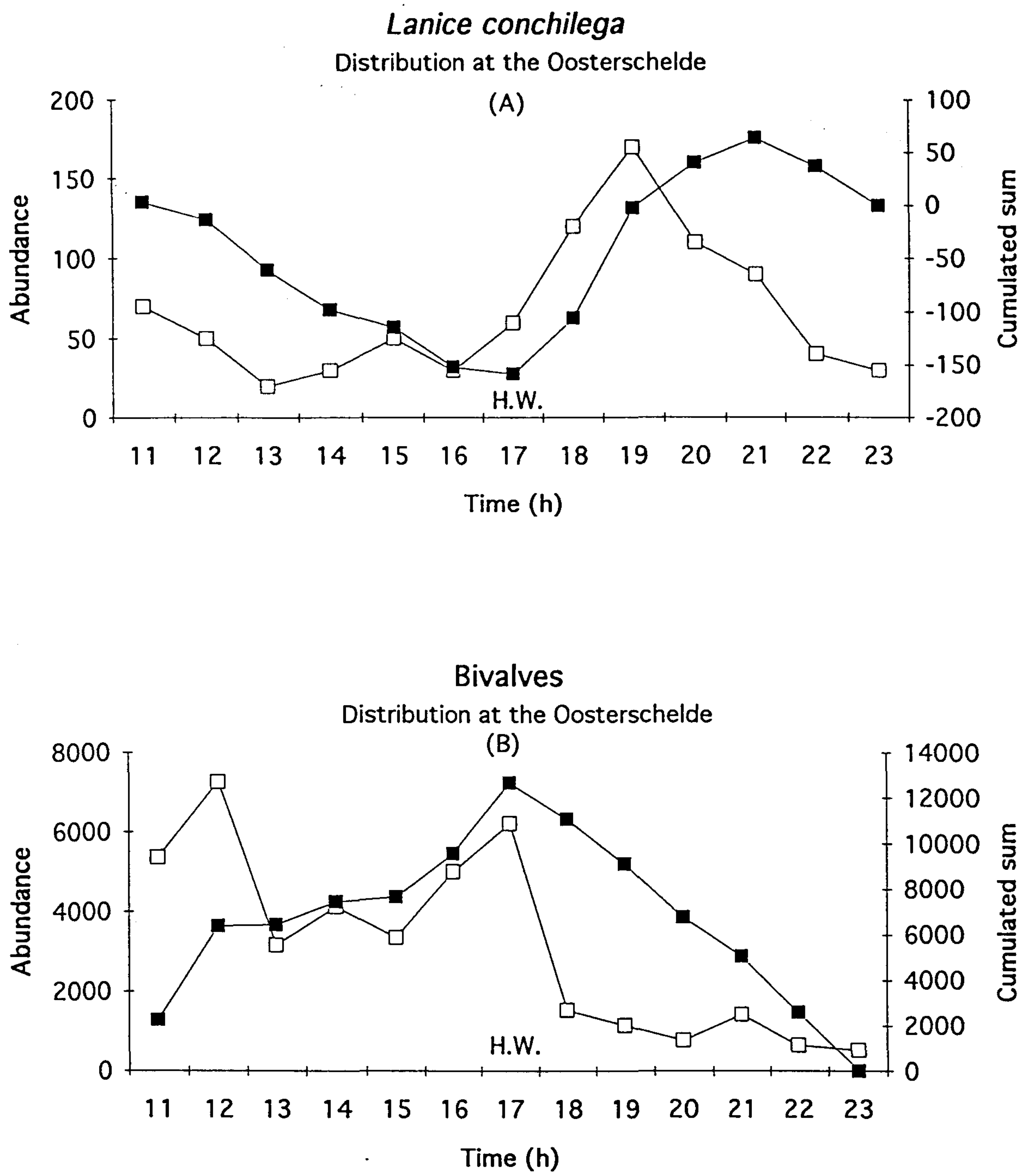


Fig. 10. (A) *Lanice conchilega* and (B) bivalves larvae distribution at the Oosterschelde white square line showing the density values not transformed, black square line showing th density values transformed to cumulated function. H. W. indicates the time of occurence of hig water.

At the Oosterschelde station the meroplankton taxa present were the larvae of *Lanice conchilega* and the bivalves larvae. The results shows for *Lanice conchilega* (Fig. 10. A) a first density peak at 19h00 with 155 ind. m^{-3} during the ebbing of the tide. The cumulated sum (black square line) estimated much better the increase of larvae density concomitant with the ebbing of the tide. The bivalves (Fig. 10. B) show a unimodal pattern with a distinct peak at 17h00, with a density value of 12,500 ind. m^{-3}. For both taxa the cumulated sum shows that the highest density value was found after the high water time at 17h00. Both taxa were strongly positively correlated with the tide (Spearman's $r_{s(t)}$, $P<0.01$), salinity (Spearman's $r_{s(s)}$, $P<0.01$); and turbidity (Spearman's $r_{s(tr)}$, $P<0.05$).

2.1.4. *Path analysis*

The results of the path analysis are represented in a form of path diagrams (Fig. 11.). For Oostende the direct path coefficient from the Tide towards the Species (0.344) and the indirect path coefficient from the Environment towards the Species (0.362) are highly significant at a statistically significant level of ($0.05 \geq p > 0.01$). The direct path coefficient from the Tide towards the Environment (0.134) was also significant at a statistically significant level of ($0.01 \geq p > 0.005$).

For the Oosterschelde the direct path coefficient from the Tide towards the Species (0.350) and the indirect path coefficient from the Environment towards the Species (0.403) are highly significant at a statistically significant level of ($0.05 \geq p > 0.01$). The direct path coefficient from the Tide towards the Environment (0.178) was also significant at a statistically significant level of ($0.01 \geq p > 0.005$).

The expected correlation between tide and meroplankton for Oostende in (Fig. 11.) is the direct path between tide and environment added to the indirect path from the environment to meroplankton and the path from tide to meroplankton ($0.134 + (0.344 \times 0.362) = 0.258$). The expected correlation between environment and meroplankton is the path from environment to meroplankton plus the paths from tide to environment and tide to meroplankton ($0.362 + (0.134 \times 0.344) = 0.408$). For the Oosterschelde the expected correlation between tide and environment is 0.319 and the expected correlation between environment and meroplankton is 0.465.

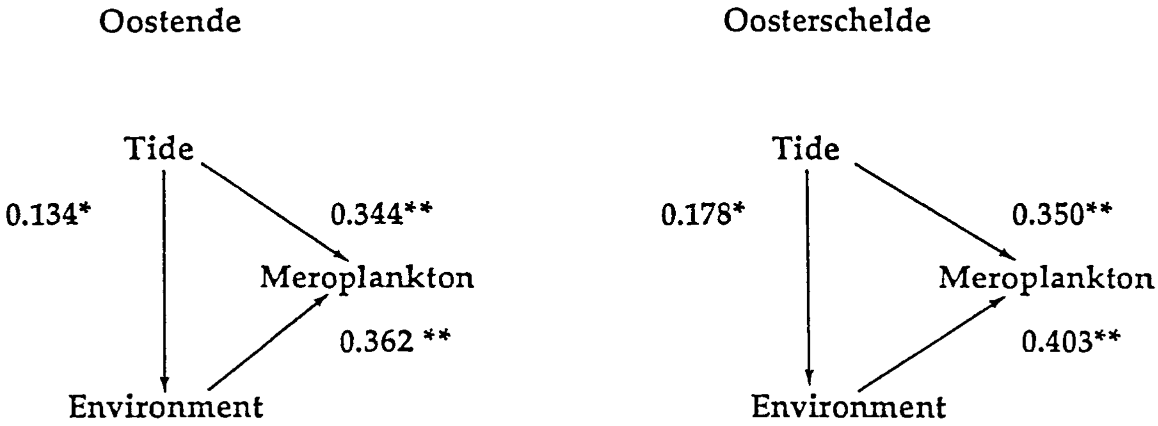


Fig. 11. Path diagrams for Oostende and the Oosterschelde. Arrows designate the direction of the causal links, number next to arrows represent the estimated path coefficients. The ** indicates the probabilities level of the regression coefficients for $0.05 \geq p > 0.01$ and * indicates the probabilities level for $0.01 \geq p > 0.005$.

2.1.5. Discussion and Conclusion

Advection and suspension by tidal currents as postulated by Uncles and Joint (1983), seems to be a major force determining concentration of planktonic organisms in turbid coastal areas. The bimodal pattern in the observed meroplankton density distribution confirm the early observation by Levin (1986; 1990). Carriker (1951), found that younger stages of oyster larvae ebb and flow in a passive way with the tide. Wood and Hargis (1971), found that the density maxima of bivalves larvae coincided with an increase in salinity concomitant to the flood of the tide.

The results obtained here confirmed the importance to consider the tide-coupled environmental factors as processes regulating the dispersion and retention of the early stages of invertebrates larvae in estuaries and coastal locations. Provenzano *et al.* (1983), found that the majority of early stages of zoeae larvae were sychronized with the nighttime slack tides in order to assure the transport of the larvae to the mouth of the estuary Chesapeake Bay, concomitant with salinities values required for the development of the zoeae.

The correlations found with salinities and turbidity ($r_{S(s)}$ $P<0.01$; $r_{S(tr)}$ $P<0.05$) can be regarded as a consequence of the tidally-induced variability. From these observations we confirmed that the larvae studied acted as either passive particles with a similar behaviour as sediment particles, or like neutrally buoyant objects. These results supported the early hypothesis by Levin (1983; 1986), and Banse (1986), concerning the spatial and temporal distribution of larvae as moving patches in response to tidal currents in the North Sea (Wyatt, 1973), and as related to water masses defined by the T-S diagram. The tidal excursion pattern at Oostende confirmed the observation reported by Nihoul (1975), and showed the drift of the water masses in the North-East enhanced by the South-west wind. This circulation pattern may be responsible for the transport of meroplankton larvae in the North-East direction. The tidal component (North and East) at the Oosterschelde confirmed the looping circulation pattern described by Kohsiek *et al.* (1989) showing that this area can be regarded as a retention zone for macrobenthic larvae within the Oosterschelde estuary, allowing a possible larval input to the North Sea under a North-East wind regime.

The passive use of tidal currents by pelagic stages of benthic invertebrates can allow the larvae to remain close to the adult population or on the other hand to be a larval supply to neighbouring benthic communities (Roughgarden et al., 1987). Though pelagic larvae of benthic invertebrates have the capacity to be selective in the use of currents (Butman, 1987; Levin, 1983), the results suggested that hydrodynamic processes controled quite considerably the distribution of the larvae near the surface causing aggregation of passive larvae patches at different scales.

The distribution of *Polydora* spp. and Bivalves at Oostende and of *Lanice conchilega* and Bivalves at the Oosterschelde further supported the hypothesis that larval dispersal can be regarded to be a passive process controlled by oceanic circulation. The different tidal regime of the two locations studied suggested that the observed difference in the local density distribution of the larvae may be the result of active or passive redistribution of larvae in near-bottom water and of hydrodynamical events occuring at the benthic boudary layer (BBL) as reported by Fréchette *et al.*, (1993).

At the Oosterschelde, due to the effect of the storm-surge barrier in reducing the water exchange with the North Sea and the freshwater load by 1% of the tidal volume, the system has changed from an estuary to a tidal bay (Smaal & Nienhuis, 1992). Hence the distribution of the larvae can be regarded, to some extent, to be controlled by the looping circulation sytem of the tide. This results further reinforce the hypothesis that at the Oosterschelde the adult benthic population can be regarded as self-sustaining (Scholten *et al.*, 1990), and their reproductive effort is favoured by the hydrodynamical processes which characterise this location, that can be regarded as a retention area for macrobenthic larvae (Hamerlynck *et al.*, 1992).

The use of path analysis showed the importance to assess the various direct and indirect paths between variables and gave an indication of the strength of the causal links between the tide, environment , and meroplankton. Since the data used represented a portion of the geograhic space sampled, the correlations found by path analysis are likely to have been generated by variables which are autocorrelated, as in most environmental studies (Legendre & Troussellier, 1988).

The spatial structure of the data suggested the need to collect more informations and to use partial Canonical Correspondence Analysis (ter Braak 1988; Borcard *et al.*, 1992), and the partial Mantel statistics (Smouse *et al.*, 1986; Legendre and Fortin, 1989) in order to test if the causal relations between variables are spurious or real, and to propose a possible model of causal relationships.

However in order to understand further the meroplankton distribution in coastal and estuarine locations in relation to tidal-induced variability and its effect on meroplankton, it is necessary to achieve a detailed knowledge of both hydrography and the seasonal changes in the rate and direction of advection related to wind forcing (Hill, 1994 & 1995). A main question still need to be answered : Are larvae taken away from the area of release, or can they return to it ? If we consider that the mechenisms for transport away larvae from the parental stocks are : (a) advection and (b) tidal dispersion then the orders of magnitude of both processes could be obtained from more detailed hydrodynamical descriptions, and compared to the pelagic life-time of the larvae. Alternatively an attemt to estimate the degree of dispersion in the larval plume and compare it to the patchiness of the adults should be made.

Ecological conclusion

The observed patterns in larval distribution are not generated by geographical constraint alone, but by physical geographic regional structure that allows life-cycle closure. Meroplankton larvae can in fact be found within the distributional limits of the adult macrobenthic community.

Different populations can share, during the time of recruitment, a common distributional area. Since the majority of macrobenthic species spend part of their life cycle away from the benthic region, as temporary pelagic species, their chance of survival depends primarily on physical processes such as residual circulation and wind conditions to maintain the larvae within favourable settling benthic habitat.

In this ecological context the observed population patterns can be regarded as species-specific life cycles in relation to an appropriate geographical location. The species absolute abundance can be physically defined in relation to the spatial scale of the geographic region associated with life-cycle continuity.

Changes in the physical environment can provide either new infrastructure for the settling of new species, such as the case on Ensis directus *on the French coast of the North Sea (Luczak* et al., *1993), or unfavourable habitat causing the collapse of species life-cycle-closure.*

The spatial scale and coherence of observations of the planktonic phase of the life cycle of macrobenthic species in relation to physical processes defines the degree of species richness. The persistence of larvae distribution in a favourable settling area such as the Oosterschelde at a time scales of weeks to one month can be regarded as the key factor to life-cycle continuity and species richness.

2.2. Spatial structure and ecological variation of meroplankton data. Southern Bight of the North Sea: French-Belgian coast, two late spring 1989 campaigns.

2.2.1. Spatial variations of the physical and biological data and PCA

The first cruise in 1989 on the 10 June was characterized by a South-West wind with a mean velocity of 3.9 m. s^{-1}. High and low water occured, with reference to Dunkerque (between station 16-17, Fig. 3.) at 6 h 10 min. with 5.15 m amplitude and at 13 h 03 min. with 1.30 m amplitude.

During the second cruise in 1989 on the 21 June with a North-East wind with a mean wind velocity of 5.3 m. s^{-1}. The tide low and high water as a reference to Dunkerque (between station 50-51, Fig. 3.) occured at 9 h 49 min. with 0.80 m amplitude and at 15 h 08 min. with 5.45 m amplitude.

The list of the environmental variables and the name of the taxonomic groups are reported in Table 3 below.

Taxonomic group	**Environmental variables**
Lanice conchilega	Salinity (psu)
Pectinaria koreni	Temperature (°C)
Magelona mirabilis	Density (Kg.m^{-3})
Polydora spp.	Corrected depth (m)
Nephtys spp.	Tide height (m)
Ampharetidae	
Bivalves	
Echinoids	

Table 3. Taxonomic group and set of environmental variables.

The "corrected depth" indicates the depth measurement corrected according to the changes of tide height during the transect. The tide height represents the changes in the tide level along the transect from station 1 to 67; this change in tide height was subtracted from the depth measurement on board to obtain the corrected depth.

The temperature distribution shows (Fig. 12 A) for the first cruise a clear input of warm water (18.70 °C) before station 5, concomitant with Gravelines Power Station activity during the ebbing of the tide. The mean temperature value was 15.20 °C. Under the influence of the South-West wind, the colder water masses coming from the Dover-Calais strait could reach the Belgian coast as far as Middelkerke.

The second cruise in 1989 on the 21 June (Fig. 12B) shows the effect of the North-East wind on the temperature distribution. The warmer water from the Belgian coast are transported southward reaching the French coast. The mean temperature value was 17.85 °C decreasing to a minimum value of 16.65 °C at the coastal station 11. These oscillations in temperature variation can be regarded as the exchange between coastal and off-shore water.

The salinity distribution in Fig. 13A, shows for the 10 June the presence of three salinity fronts : one between stations 2 and 7 of 0.6 (psu), which can be regarded as an anomaly mainly due to the presence of the Gravelines Power Station and the freshwater input from the river l'Aa during ebbing, one between stations 30 and 40 and one between station 52 and 60.

For the second cruise of the 21 June (Fig. 13B), the salinity distribution shows the presence of two salinity fronts : one from station 34 to station 40 and one from station 48 to station 52. The presence and persistence of these salinity front at the same locations may vary according to hydrological processes, meteorological events and seasons. The low salinity value between station 50 to 67 indicates quite clearly that the surface water coming from the Westerschelde estuary can reach under the North-East wind condition the French coast.

Concerning the spatial distribution of the meroplankton, the density values of the most representative taxa are presented here togheter with the temperature and salinity distributions. The adults of *Polydora spp.* are present in the macrobenthos as two distinct populations, one characterizing the French coast at Boulogne sur Mer (Lagadeuc & Brylinski, 1987) and the other in the Gravelines - Dunkerque region (Souplet & Dewarumez, 1980; Souplet *et al.*, 1980). On the Belgian coast, adult *Polydora spp.* are present in the Oostende coastal region (Daro & Polk, 1973).

The larval dispersion of this polychaete under different wind conditions, can bring changes in the spatial distibution and spatial structure of the population. The highest densities values of *Polydora spp.* were found, for the 10 June (Fig. 14A), at station 4, with 160 ind.m^{-3}, concomitant with the highest

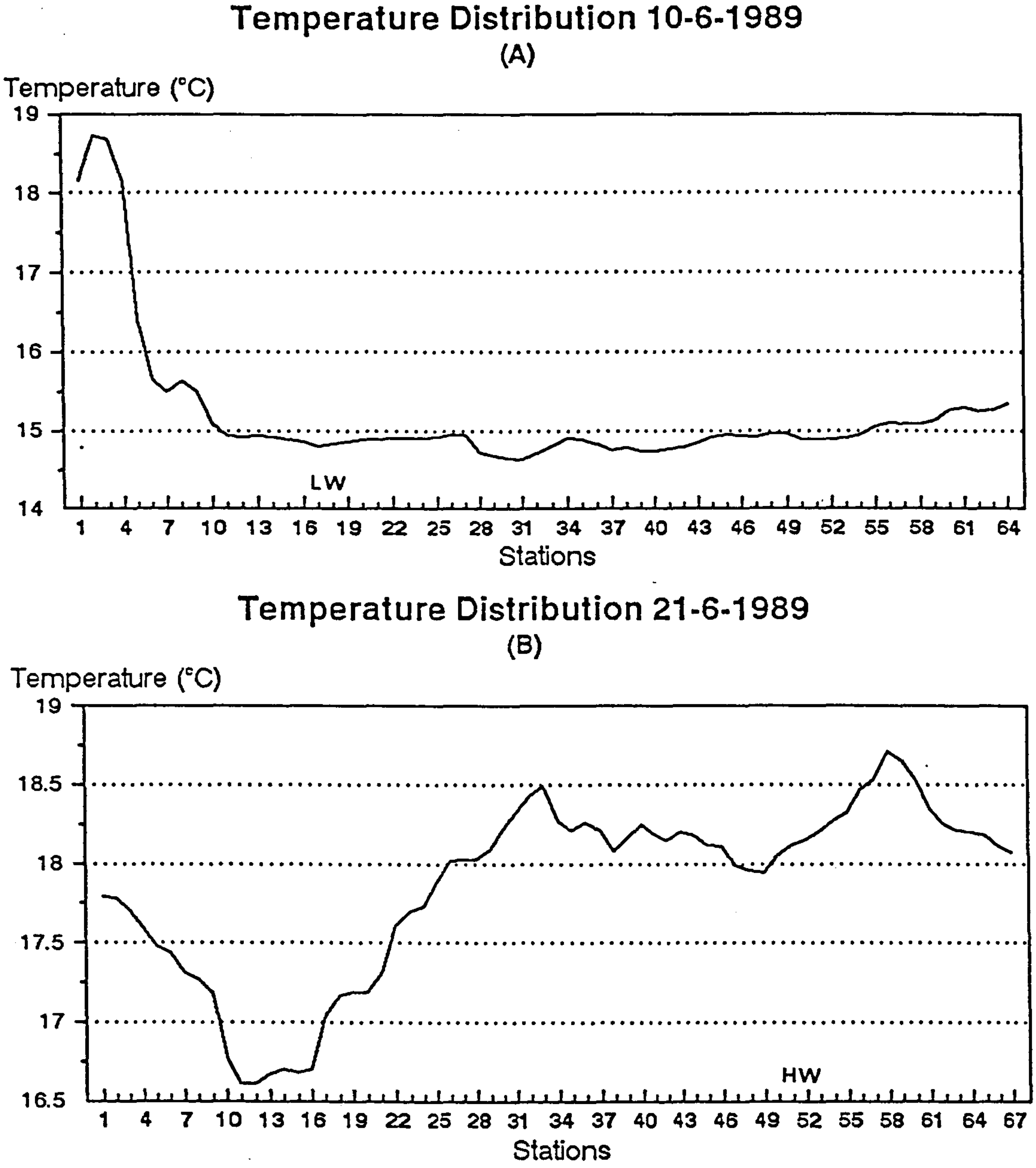
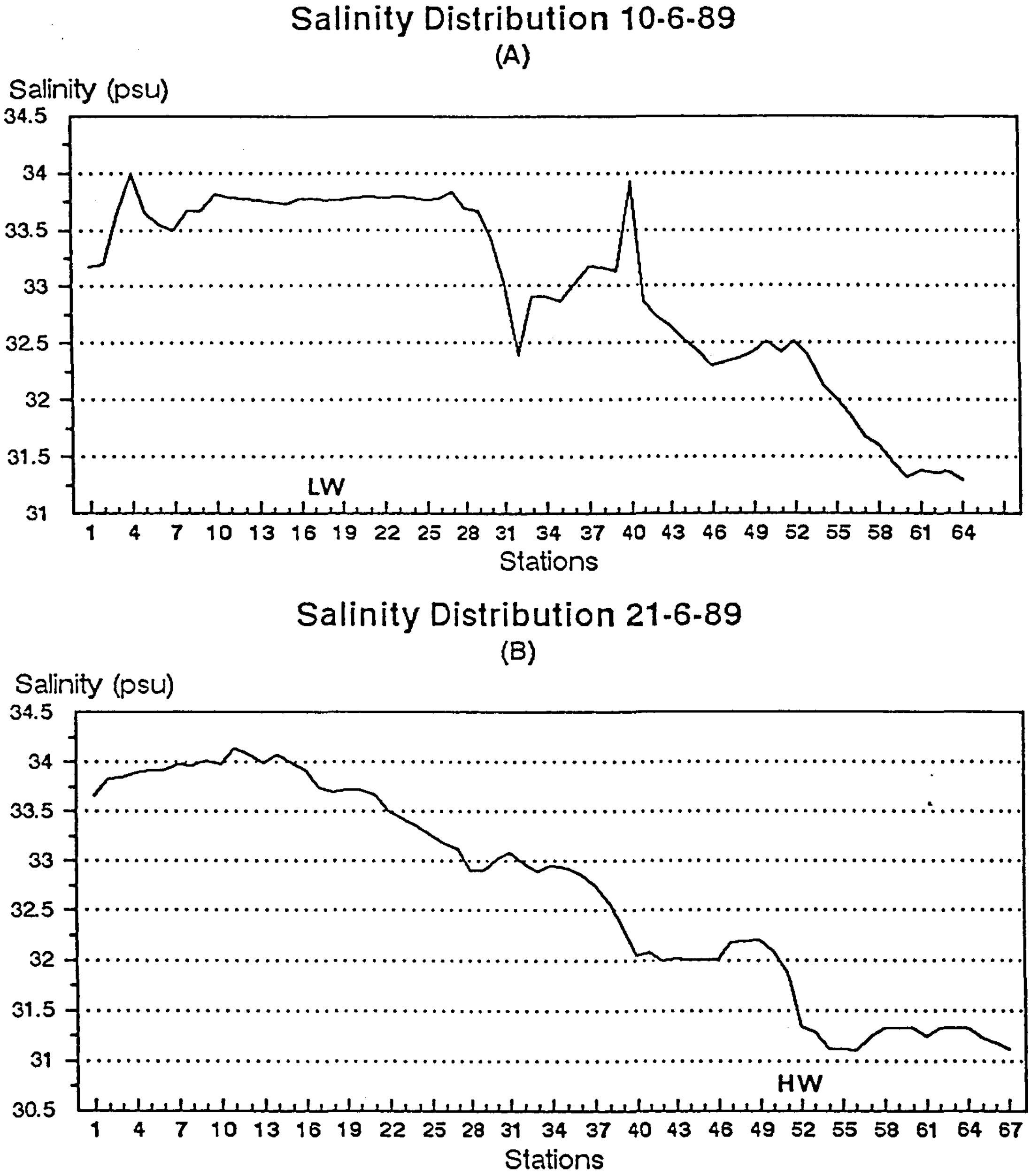


Fig. 12. (A) Temperature distribution for the first cruise shows an increase in temperature at station 4 (Gravelines Power station), and the general lower temperature values coming from the Calais-Dover strait under the influence of the South-West wind. (B) Temperature distribution for the second cruise shows the warmer water coming from the Belgian coast (station 67), reaching the coastal location (station 16), along the French coast under the influence of the North-East wind. H.W. and L.W. indicates the time of occurence of high and low water.



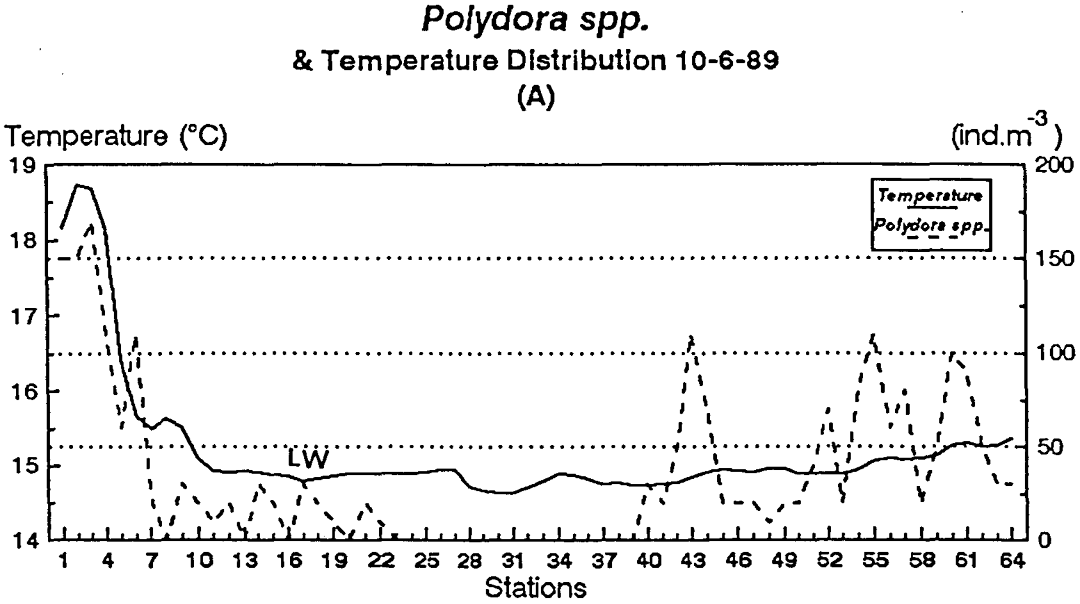
Salinity Distribution 10-6-89

(A)

Salinity Distribution 21-6-89

(B)

Fig. 13. (A) Salinity distribution for the first sampling date shows the presence of salinity fronts between (station 2 and 7 Gravelines Power station; 30 and 40; 52 and 60). (B) Salinity distribution for the second sampling date shows the presence of two salinity fronts between (station 38 and 40; 48 and 52), the effect of the North-East wind enhance the transport of less saline water coming from the Westerschelde estuary and reaching the French coast. H.W. and L.W. indicates the time of occurence of high and low water.



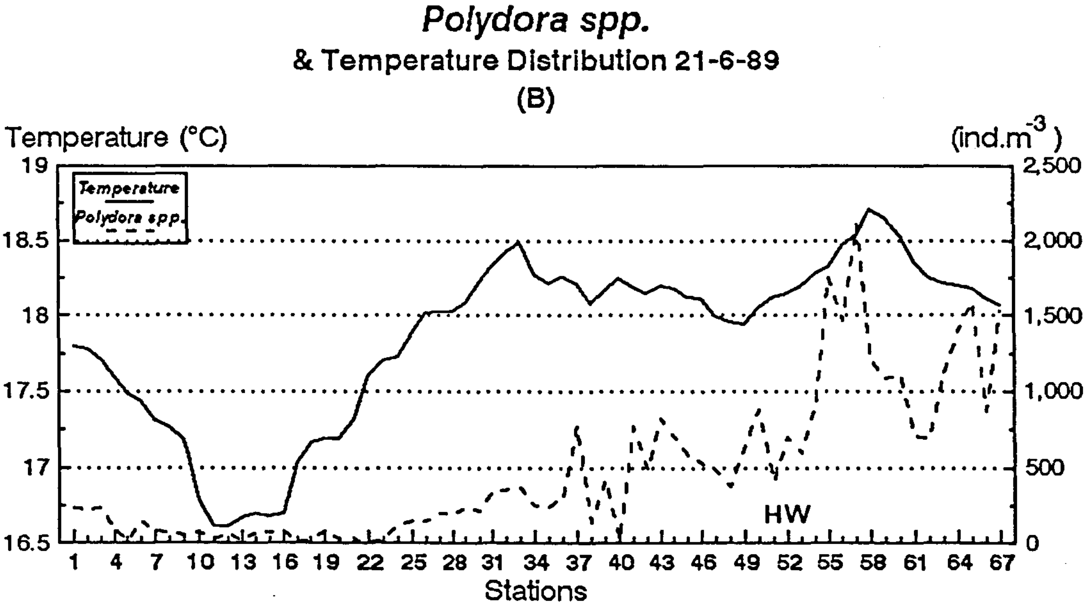


Fig. 14. (A) *Polydora* spp. density distribution and temperature for the 10 June shows two distinct populations one from station 1 to 23 (French coast), and one from station 39 to 64 (French-Belgian coast). (B) *Polydora* spp. density distribution and temperature for the 21 June, due to the North-East wind effect more larvae are transported southward. H.W. and L.W. indicates the time of occurence of high and low water.

temperature value of 18.7 °C, and at station 55, with 110 ind.m^{-3}. For the second cruise on the 21 June (Fig. 14 B) the density of *Polydora spp.* was much higher than during the first cruise and the highest density value with 2,080 ind.m^{-3} was found at station 57 concomitant with temperature values (18.6 °C).

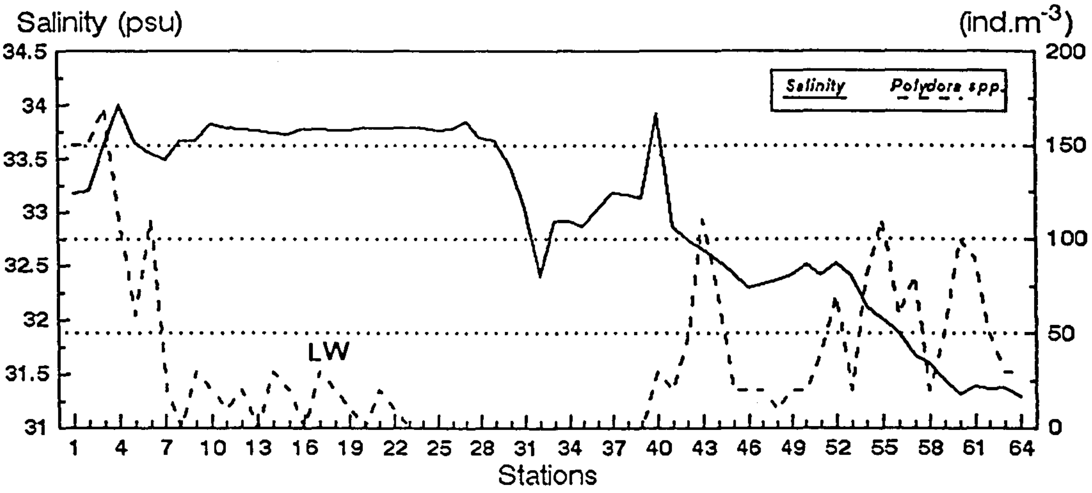
For the first cruise on the 10 June the larvae distribution in relation to salinity (Fig. 15 A), shows that higher densities were located before and after the salinity front, (stations 3, 4 and 43, 55). For the second cruise on the 21 June higher densities were found on the Belgian part of the transect from station 50 to 67. For the first cruise was possible to detect two distinct larval patches: one on the French part of the transect probably originated from the adult population present in front of the river l'Aa and at Dunkerque West and East harbours, and the other on the Belgian part, originated from the adult population present in the subtidal area at Oostende. During this second cruise, the observed effect of the North-East wind on the surface waters proved that the larvae of *Polydora spp.* can be transported South along the Belgian coast reaching the French coast as far as station 25.

The larvae of *Lanice conchilega* are presented in relation to the salinity distribution. For the first sampling date (Fig. 16 A) two density peaks are present: one concomitant with station 1 with a density value of 250 ind.m^{-3} and the second at station 36 with a density value of 100 (ind.m-3). For the second sampling transect, ten days later, the presence of *Lanice conchilega* larvae (Fig. 16 B) is much higher with the highest density value at station 31 (810 ind.m^{-3}) before the salinity front between stations 34 and 40.

The presence of *Pectinaria koreni* larvae for the 21 June (Fig. 17 A) shows a similar pattern to the *Lanice conchilega* larvae with the highest density value at station 37 (220 ind.m^{-3}) associated with the salinity front from station 34 to 40. These polychaetes larvae were most probably generated by the adult macrobenthic community present in the subtidal area of the locations crossed by the transect from Gravelines to Dunkerque and further (Davoult *et al.*, 1988).

The Echinoids larvae were present only on the 21 June. Their distribution pattern (Fig. 17 B) shows that the highest density (20,500 ind.m^{-3}) was associated with high salinity values at station 16 closer to the French coast suggesting that the larvae were generated from the adult population of *Echinocardium cordatum* present in the subtidal macrobenthos community located on the off-shore sand bancs in front of Gravelines (Davoult *et al.*, 1988).

Polydora spp.
& Salinity Distribution 10-6-89
(A)



Polydora spp.
& Salinity Distribution 21-6-89
(B)

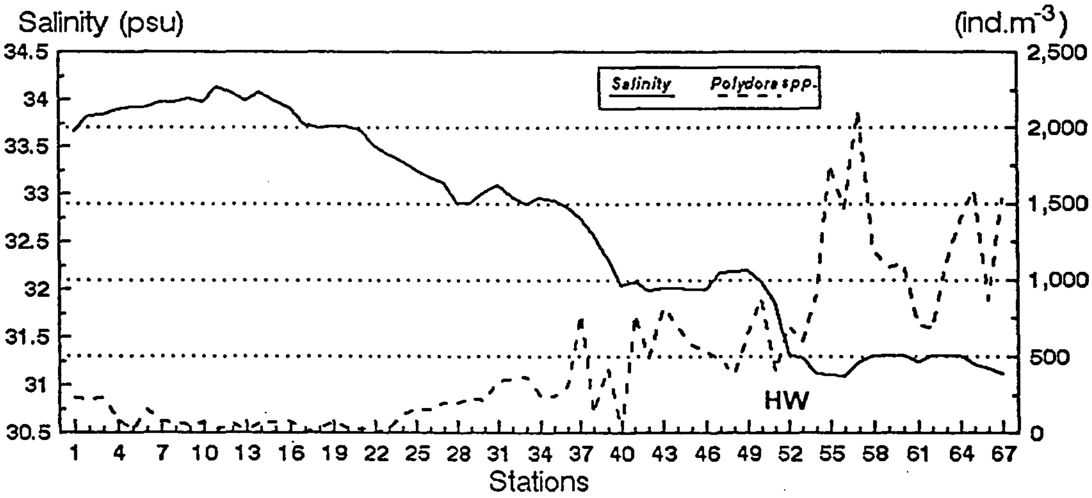


Fig. 15. (A) *Polydora* spp. density distribution and salinity for the 10 June. (B) *Polydora* spp. density distribution and salinity for the 21 June. Higher densities of larvae are found before or after a salinity front. H.W. and L.W. indicates the time of occurence of high and low water.

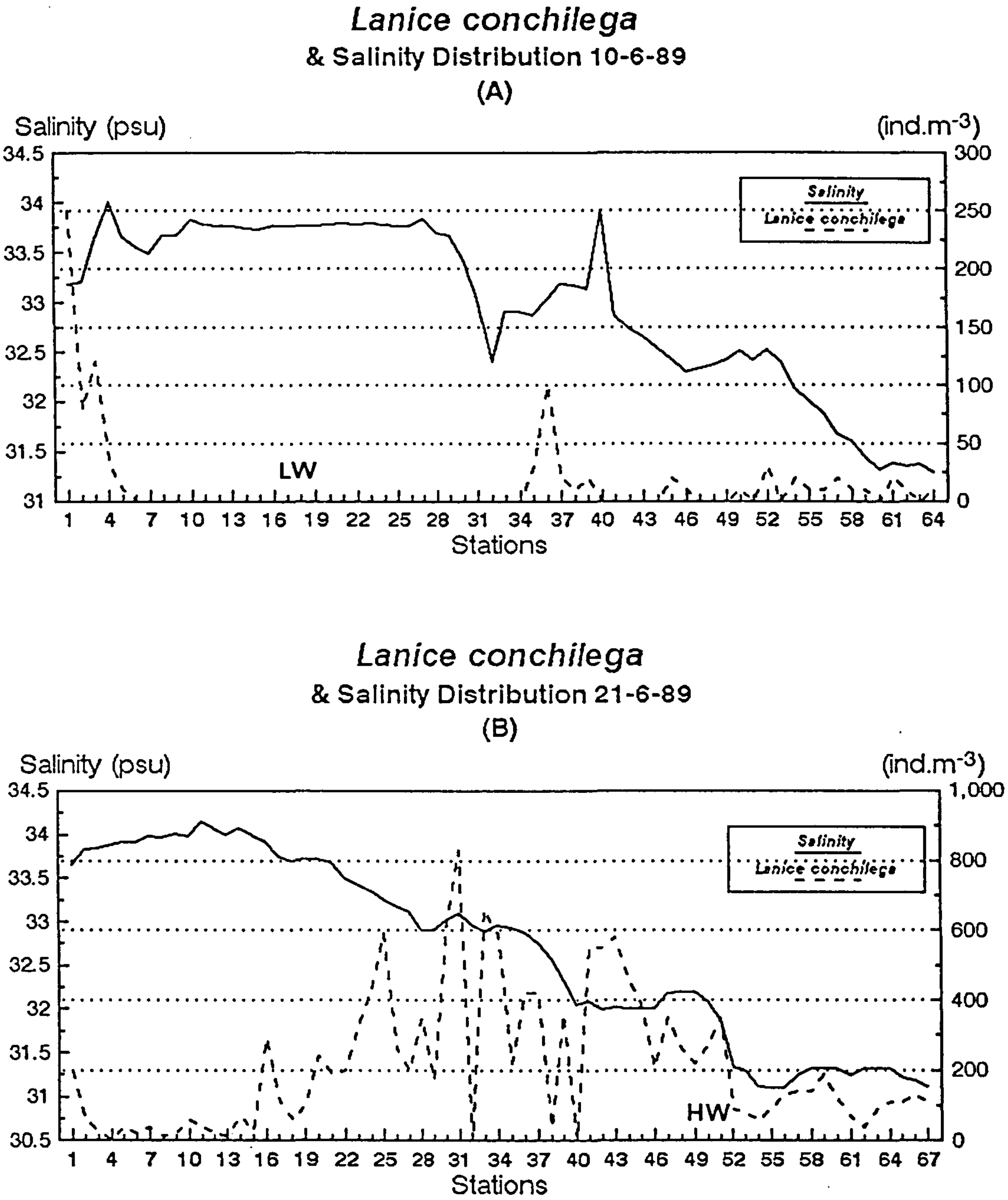
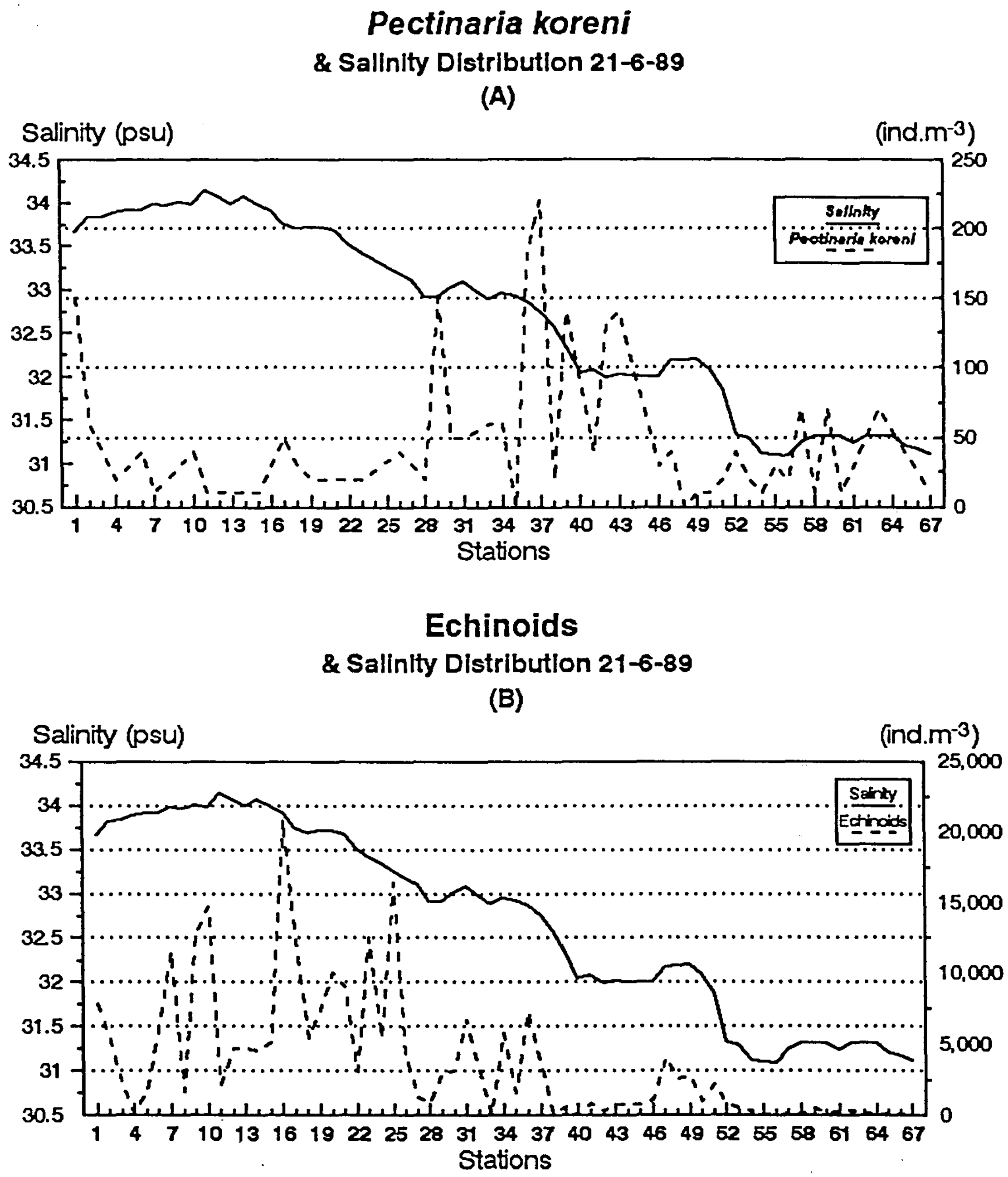


Fig. 16. (A) *Lanice conchilega* density distribution and salinity for the 10 June. (B) *Lanice conchilega* density distribution and salinity for the 21 June. Higher densities of larvae are found in the area of the salinity front between station 38 to 40. H.W. and L.W. indicates the time of occurence of high and low water.



Pectinaria koreni
& Salinity Distribution 21-6-89
(A)

Echinoids
& Salinity Distribution 21-6-89
(B)

Fig. 17. (A) *Pectinaria koreni* density distribution and salinity for the 21 June shows that high density of larvae are located within the salinity front between station 38 to 40. (B) Echinoids density distribution and salinity for the 21 June. Higher densities of larvae are found before the area of the salinity front on the French coast. H.W. and L.W. indicates the time of occurence of high and low water.

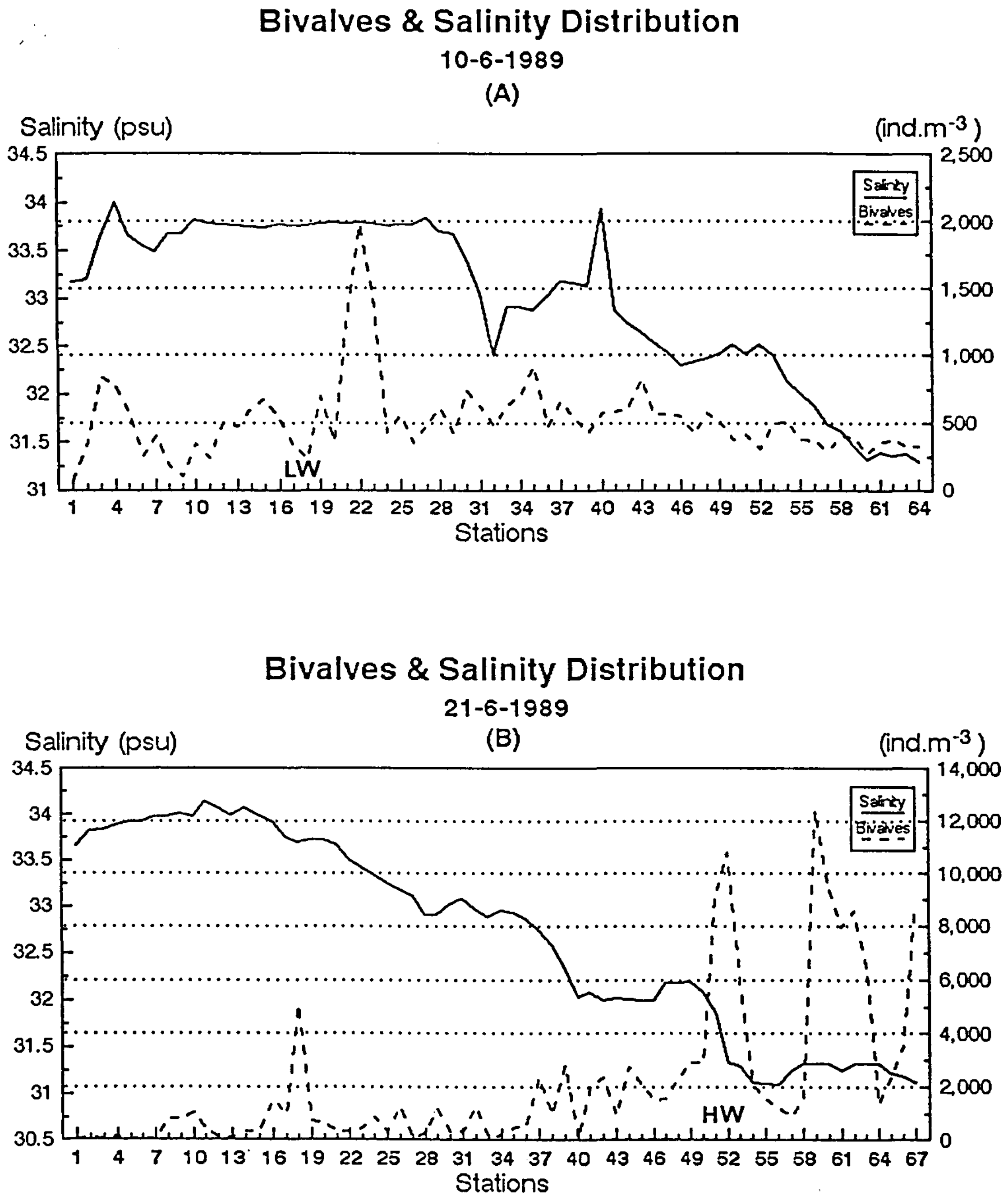


Fig. 18. (A) Bivalves density distribution and salinity for the 10 June shows that the larvae are spread along the transect due to the effect of the South-West wind. (B) Bivalves density distribution and salinity for the 21 June. Higher densities of larvae are found after the area of the salinity front (station 38 to 40) on the Belgian coast. H.W. and L.W. indicates the time of occurence of high and low water.

The Bivalves larvae distribution pattern shows for the 10 June (Fig. 18 A) a density peak of 2,000 ind.m^{-3} at station 22 and the presence of the bivalves larvae along the whole transect. For the 21 June with the inverse wind condition the bivalves larvae were associated with the low salinity value on the Belgian part of the transect (Fig. 18 B) at a density of 12,000 ind.m^{-3} was six times higher than during the first cruise. These results also showed the differences within 11 days in the density of larvae present in the water column as an indication of the periodicity of larval release from the macrobenthos. For both dates the highest densities were found during the ebbing of the tide suggesting a possible drift of larvae southward opposite to the nothward drift during flooding.

The PCA results from the correlation matrix among stations based on the $\sqrt{\sqrt{}}$ transformed species density (representing the 8 taxonomic group in Table. 3.). The PCA shows in Fig. 19A & 19B the scaling of the 64 and 67 observations on the first principal plane (axes 1 and 2) respectively for the first and second cruise on the 10 and 21June 1989. Three major group of stations were identified: the salinity front stations (SF) the coastal stations (CS) and the off-shore station (OFF). For the 10 June the first axis accounts for 32% of the total variance, the second for 25% (together 57%). For the 21 June the first axis accounts for 33% of the total variance, the second for 19% (together 52%). The results showed the presence of a coastal water mass which drifted nearshore separated from the off-shore part of the transect by the formation of salinity fronts along a coastal-off-shore gradients.

2.2.2. *Abiotic and biotic boundaries through Chronological Clustering Analysis*

The PCA analyses did not take sufficiently into account the continuity of samples along the transect and the spatial structure of the data set. The use of Chronological clustering was the first step that allowed to investigate the spatial distribution of both the taxonomic groups and the environmental descriptors, taking into account the sequence of the stations along the transect. The results of the chronological clustering are reported for the species matrix and for the environmental matrix.

For the 10 June the station-species matrix results in Fig. 20 A shows that in term of species composition the transect was divided into two major groups and

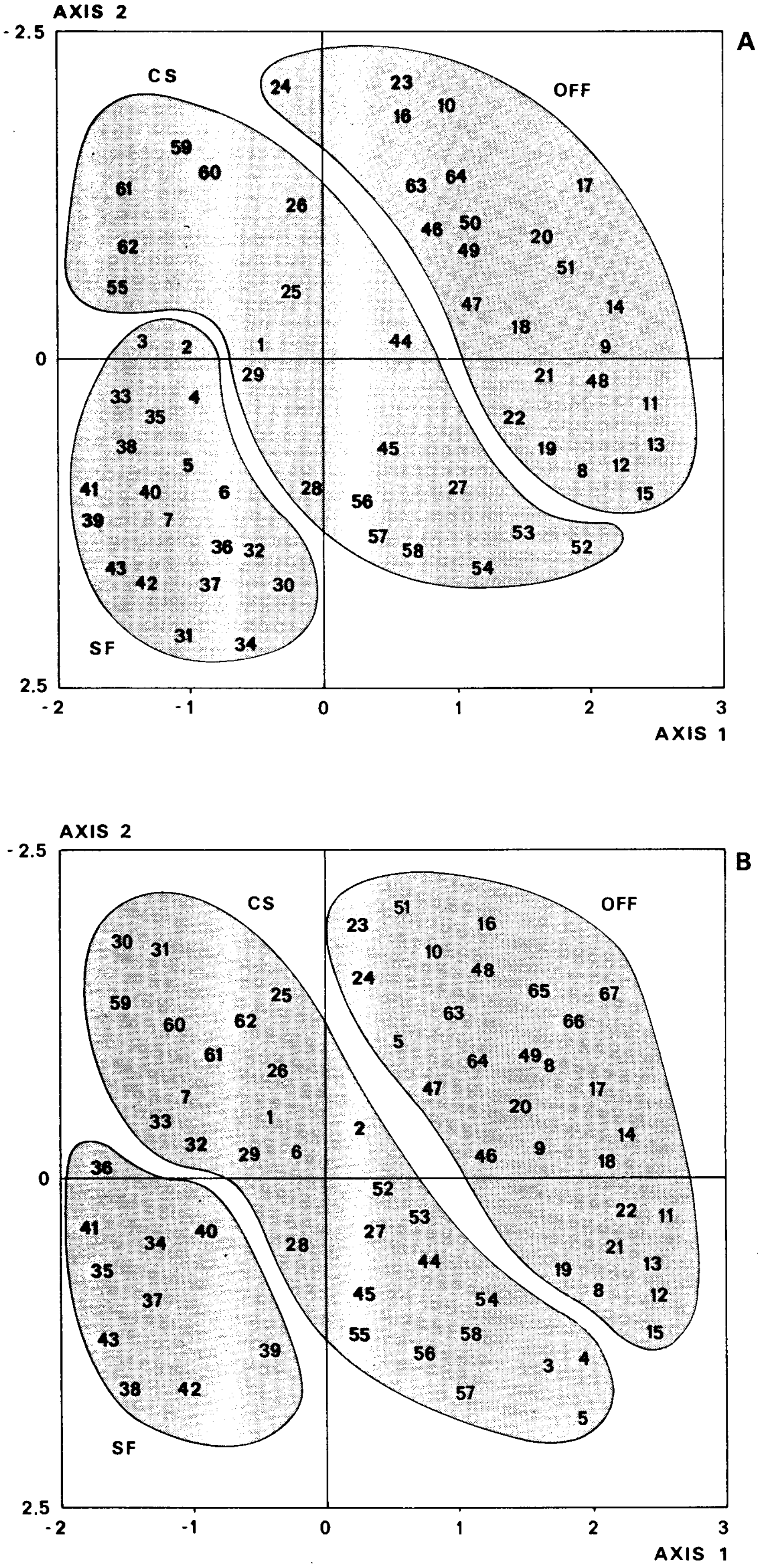


Fig. 19. (A) PCA for the 10/6/89: scaling of the 64 observations. (B) PCA for the 21/6/89: scaling of the 67 observations. Classification results are represented by envelopes. Salinity front sations (SF), coastal stations (CS), and off-shore stations (OFF).

the division occurred at station 35 at the salinity front caused by the two distinct patch of *Polydora spp.* larvae (Figs. 14A & 15A).
For the station-environmental matrix, Fig. 20 B shows that the stations were divided into two groups: one from station 1 to 24 including the first salinity front between stations 2 to 7 and one group from station 25 to 64 including the stations within and after the two salinity fronts (Fig. 13 A). This division can be regarded as an indication of the differences in the salinity distribution on the surface water due to the water masses movement in a North-East direction enhanced by the South-West wind condition.

For the 21 June the station-species matrix results in Fig. 21 A show that in terms of species composition the transect was divided again into two major groups and the division occurred at station 38 within the salinity front. The Echinoids larvae defined the first part of the transect, while the second part from station 38 to 67 was defined by the bivalves and *Polydora spp.* larvae.
For the station-environmental matrix in Fig. 21 B shows that the stations were also divided into two groups: one from station 1 to 42 including the first salinity front between stations 34 to 40, and one group from station 43 to 67 including the stations 48 to 52 of the second salinity front. The breakpoint in the data series corresponds to the major hydrological events positioned around station 43 showing the lower salinity waters coming from the Westerschelde estuary reaching the French coast. This suggested that the North-East wind condition enhanced a movement of the surface water masses southward.

The ANOVA on the taxonomic clusters in terms of the environmental variables showed that for both transects the differences in salinity and tide height between the French and French-Belgian coast were significant ($p<0.001$), the differences in density and depth were significant with ($p<0.005$). Temperature was not significant. The ANOVA on the environmental clusters in terms of the meroplankton composition showed for both transects that the differences between the French and French-Belgian coast were significant for *Polydora spp.* and the Echinoids ($p<0.001$) and for the Bivalves ($p<0.005$).

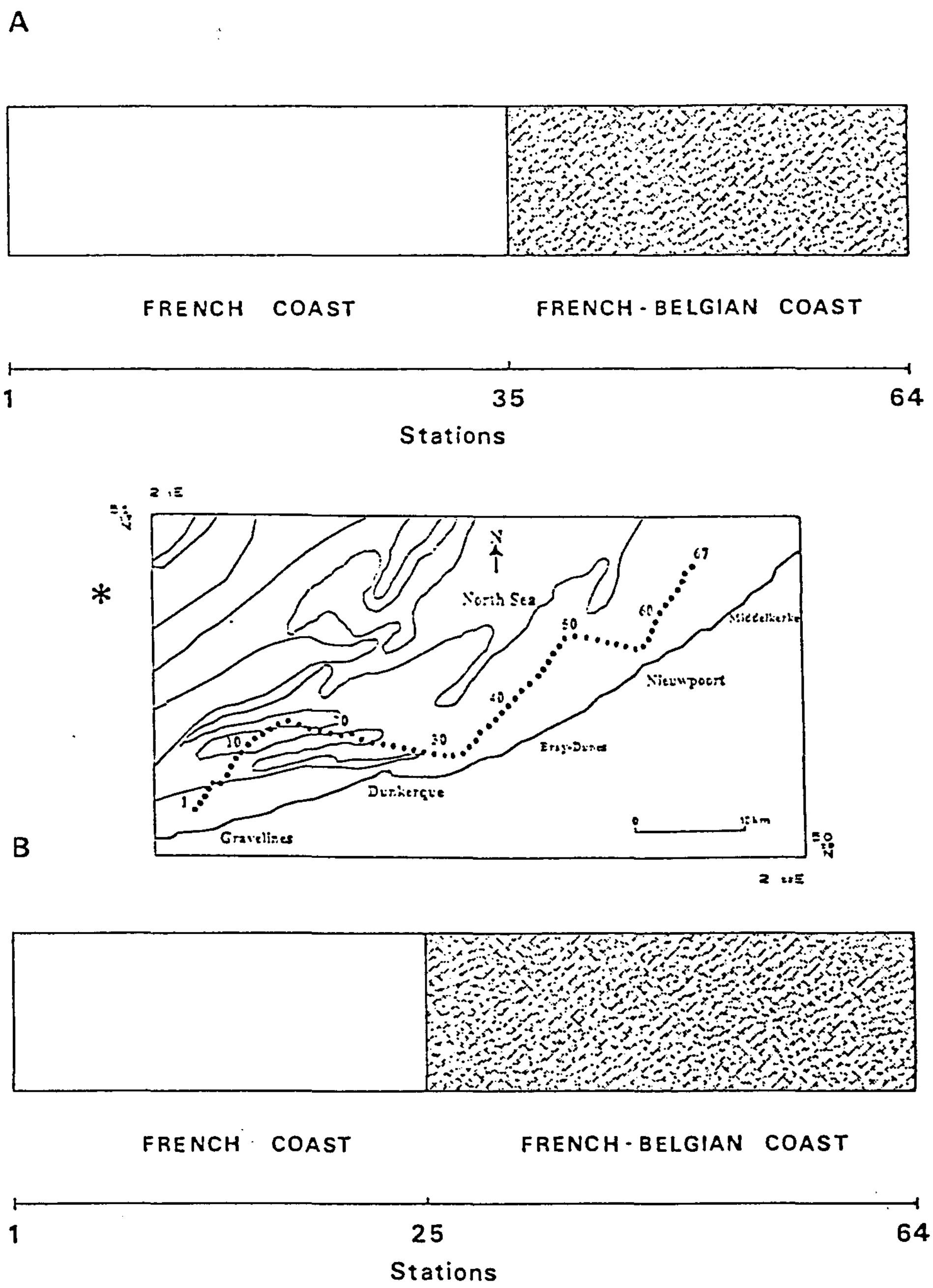


Fig. 20. Schematic representation of the chronological clustering for the 10/6/89. (A) Species matrix chronological clustering. (B) Environmental matrix chronological clustering. Connectedness level Co is 50% and the group expansion test are shown for a significance level $\alpha = 0.20$.

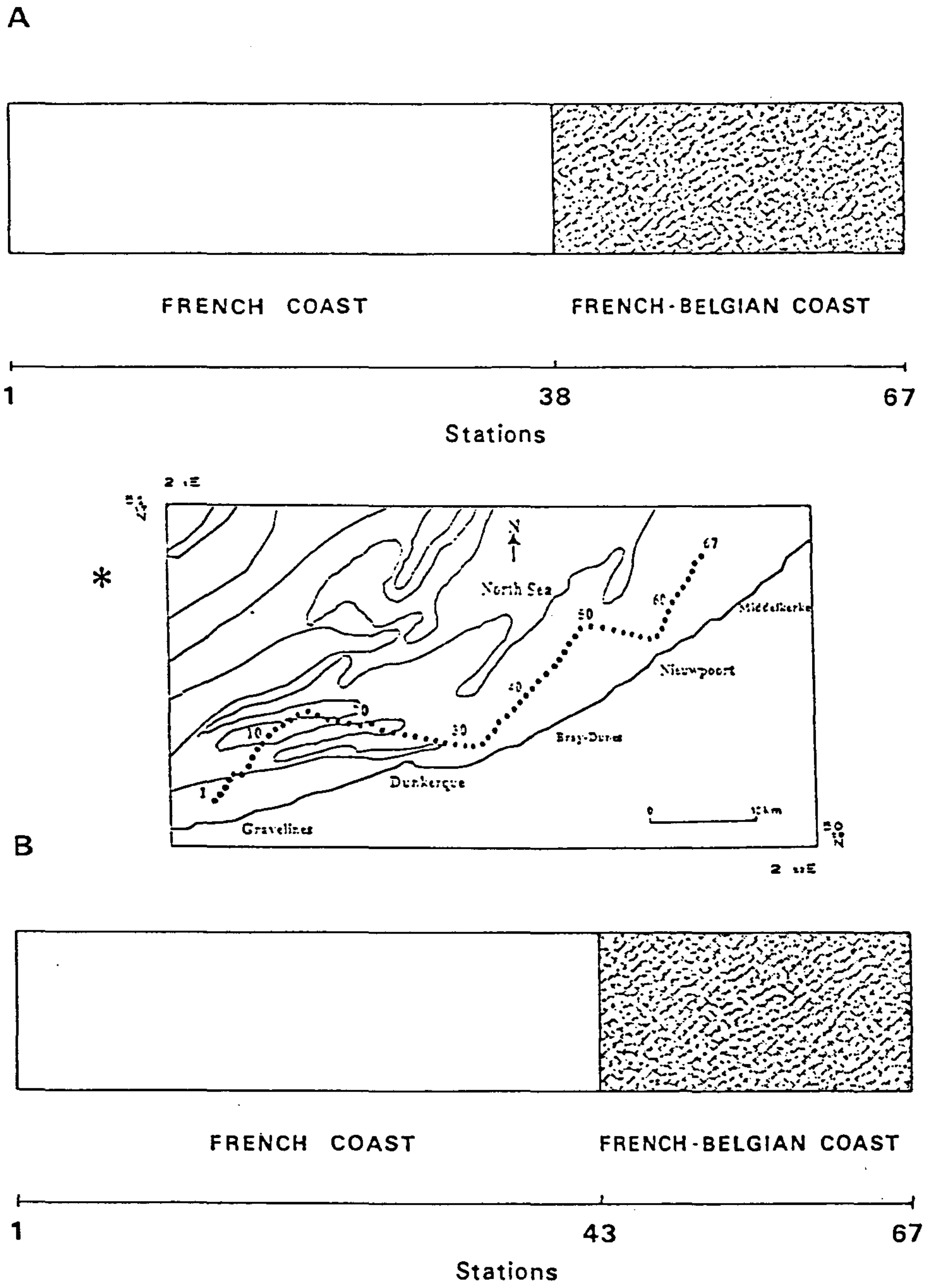


Fig. 21. Schematic representation of the chronological clustering for the 21/6/89. (A) Species matrix chronological clustering. (B) Environmental matrix chronological clustering. Connectedness level Co is 50% and the group expansion test are shown for a significance level $\alpha = 0.20$.

2.2.3. Relations with the environment

The Kruskal-Wallis H test, complementary to the ANOVA, was performed using the measured variables for the separate stations in the biologically defined communities, showed significant differences in salinity, density, depth and tide height between the groups defined by the chronological clustering as reported in Table 4 below.

Abiotic variables	**10 June 89**	**21 June 89**
Salinity	$p<0.001$	$p<0.001$
Temperature	NS	NS
Density	$p<0.005$	$p<0.005$
Depth	$p<0.005$	$p<0.005$
Tidal height	$p<0.001$	$p<0.001$

Table 4. List of the environmental variables tested for differences between the two groups defined in both campaigns by the chronological clustering. The significance level of the Kruskal-Wallis H test are reported for each cruise.

In conclusion, changes in the salinity-density distribution can be regarded as a major factor determining the distribution of planktonic animals and this seems to be an important factor defining the two subareas. Temperature changes were not significant over the whole area studied. The co-occurence of a certain community and a set of (not strictly independent) environmental variables, can be used to suggest any existing causal relation.

The significance level for depth indicated that depth may play a minor role in the distribution of meroplankton as confirmed in an earlier study by Belgrano *et al.,* (1991). The significance level for the tide height indicated that the effect of the tide on meroplanktonic larvae could induce a horizontal transport which could be significant over a variety of time-scales. If we consider the ocean as a diffusive environment in which the horizontal drift of planktonic organisms is determined by tides, residual currents and the horizontal turbulence field is important for understanding the spatial constraints imposed by the requirement for larvae to reach a specific location. These processes may transport organisms between different shelf circulation regime, which in turn will affect their spatial distribution over large areas.

2.2.4. Scaling of the observations through non-metric Multidimensional Scaling (MDS)

The use of the Non-metric Multidimensional Scaling (MDS) was used in order to verify the results obtained with the chronological clustering. The results summarized by the MDS plots (Fig. 22.) indicated quite well that the observations were divided into two major groups of stations. The MDS uses statements of the form: "sample A is more similar to sample B than it is to sample C", and on this bases a two dimensional map is constructed. An ANOSIM test on the whole data was unneccessary since the groups of stations stand out as clearly different (Clarke & Green 1988). The final stress of the configurations are low: between 0.04 and 0.05, indicating a good fit (Field *et al.*, 1982).

For the first transect in Fig. 22 A the stations were grouped in one cluster (FC) representing the French coast, and a second cluster (F-BC) representing the French-Belgian coast. The sequence of the stations distribution showed again the continuity of the transect from station 1 to 28 on the (FC) cluster and from station 29 to 64 on the (F-BC) cluster. This succession also indicated that with presence of a South-West wind there was a progressive drift in the North-East direction. The alternation in the stations sequence (zig-zagging of the hack line) might have been the result of the fact that the sampling transect crossed sand-banks and channels where larval density can change considerably (Belgrano *et al.*, 1990).

For the second transect in Fig. 22 B the stations were also divided into two major groups representing the French coast (FC) and the French-Belgian coast (F-BC). The sequence of the station in the (FC) cluster showed that under the North-East wind condition stations 29 to 40 were found in the (F-BC) cluster during the first cruise (Fig. 22A), moved to the (FC) cluster as an indication of the inversion of the drift transport from a North-East direction to a South-West direction. This results confirmed the earlier observations by Belgrano *et al.*, (1990) concerning this possible inversion which can enhance an exchange in species composition.

From station 26 to 27 there was a shift back close to station 1 continuing towards station 33 before joining again stations 34 to 40 at the bottom of the diagram in the (FC) cluster. In ecological terms it may be that concomitant with

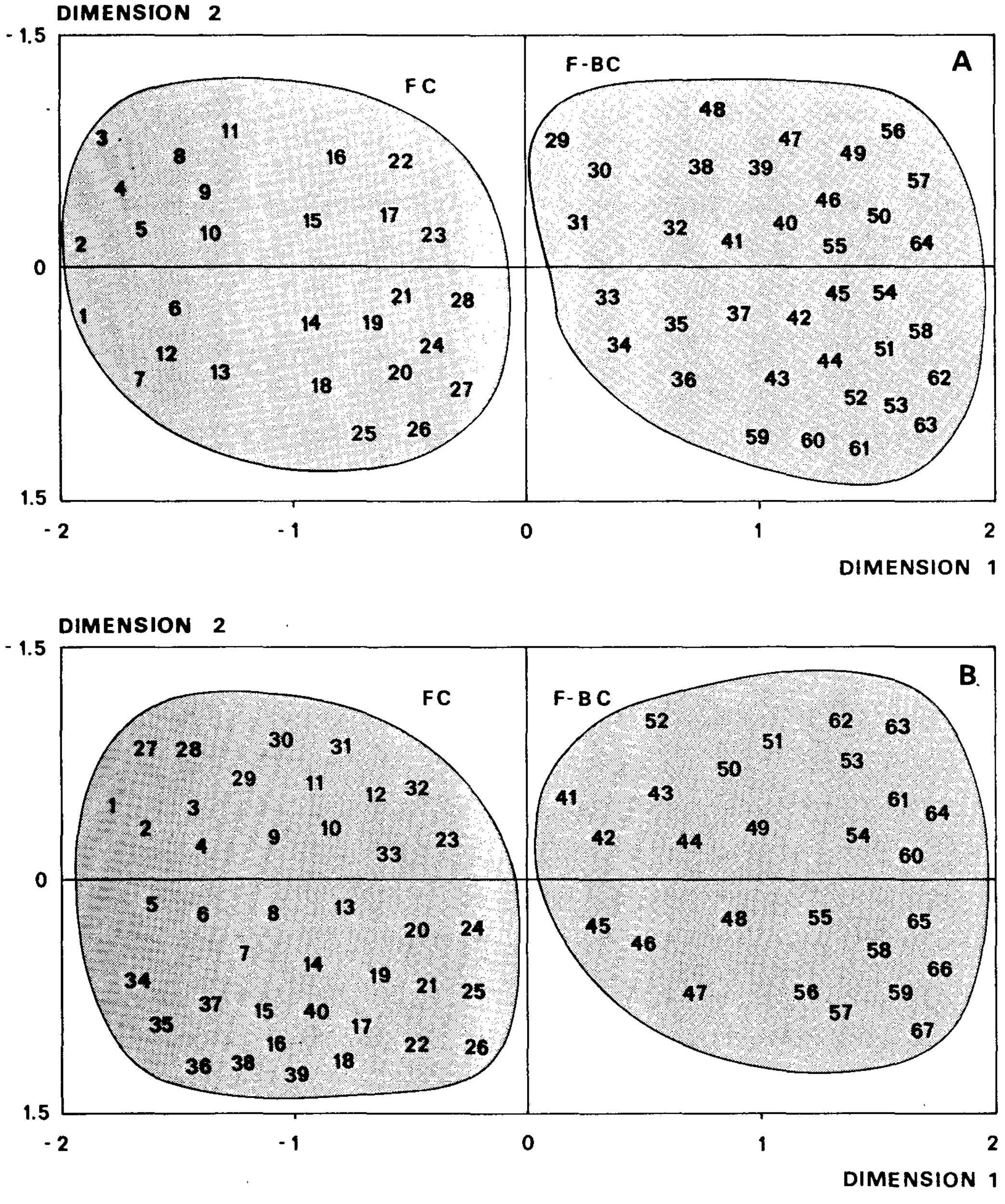


Fig. 22. Non-metric multi-dimensional scaling (MDS) plot in 2 dimensions for meroplankton data. (A) results for the 10/6/89 (B) results for the 21/6/89. Species abundances were √√-transformed and between-sample similarities calculated with the Bray-Curtis coefficient. Stress for the MDS is low, between 0.03 and 0.05. Classification results are represented by envelopes. (FC) French coast and (F-BC) French & Belgian coast are abbreviations denoting the different groups in the MDS.

stations 27 and 28 there was an increase in the density of *Pectinaria koreni* concomitant with a decrease of the echinoids larvae and with the presence a salinity front. These changes were detected by the MDS analysis. The succession from station 40 in the (FC) cluster to station 41 in the (F-BC) cluster shows that the increase in the density distribution of *Polydora spp.* and the decreasing in the echinoids larvae towards the Belgian coast was well detected by the analysis.

The dimension 1 in the plot shows mainly the succesion of the station along the transect, whereas dimension 2 untangles the heterogeneity of the frontal zone between station 30 to 40. Frontal circulation can have important effects on the meroplankton because the convergent surface currents may carry organisms from either side of the front to the region of downwelling. The organisms that are buoyant or that tend to swim upward in the water column may be concentrated at the surface near the front line.

The formation of the salinity fronts observed in the two transect may be regarded as a consequence of a large influx of low salinity water from the Westerschelde spreading over a more saline layer coming from the Dover strait. The MDS and the chronological clustering both defined this frontal situation occuring around station 40. These results indicated further the presence of an underlying spatial structure in the data and the need to quantify the specie-environment relationship in more details.

2.2.5. *Species-environment relationships through Canonical Correspondence Analysis (CCA)*

The Canonical Correspondence Analysis (CCA) showed in more details the importance of underlying factors involved in the species-environmental relationship. Here only the first two canonical axes (axes 1 and 2) are represented and commented upon.

The CCA results for the two campaigns on the 10 and 21 June 1989 are presented in Figs. 23 A & 23 B. For the first cruise the first axis accounted for 42% of the total variance and the second axis for 21% (together 63%), for the second cruise the first axis accounted for 47% of the total variance and the second axis for 19% (together 66%).

For both transects two important environmental gradients are obvious in the biplot. The largest axis, explaining most of the variance, represents the salinity-density gradient opposite to the tide while almost perpendicular to this gradient, and correlated factors, the temperature-depth gradient indicates the lack

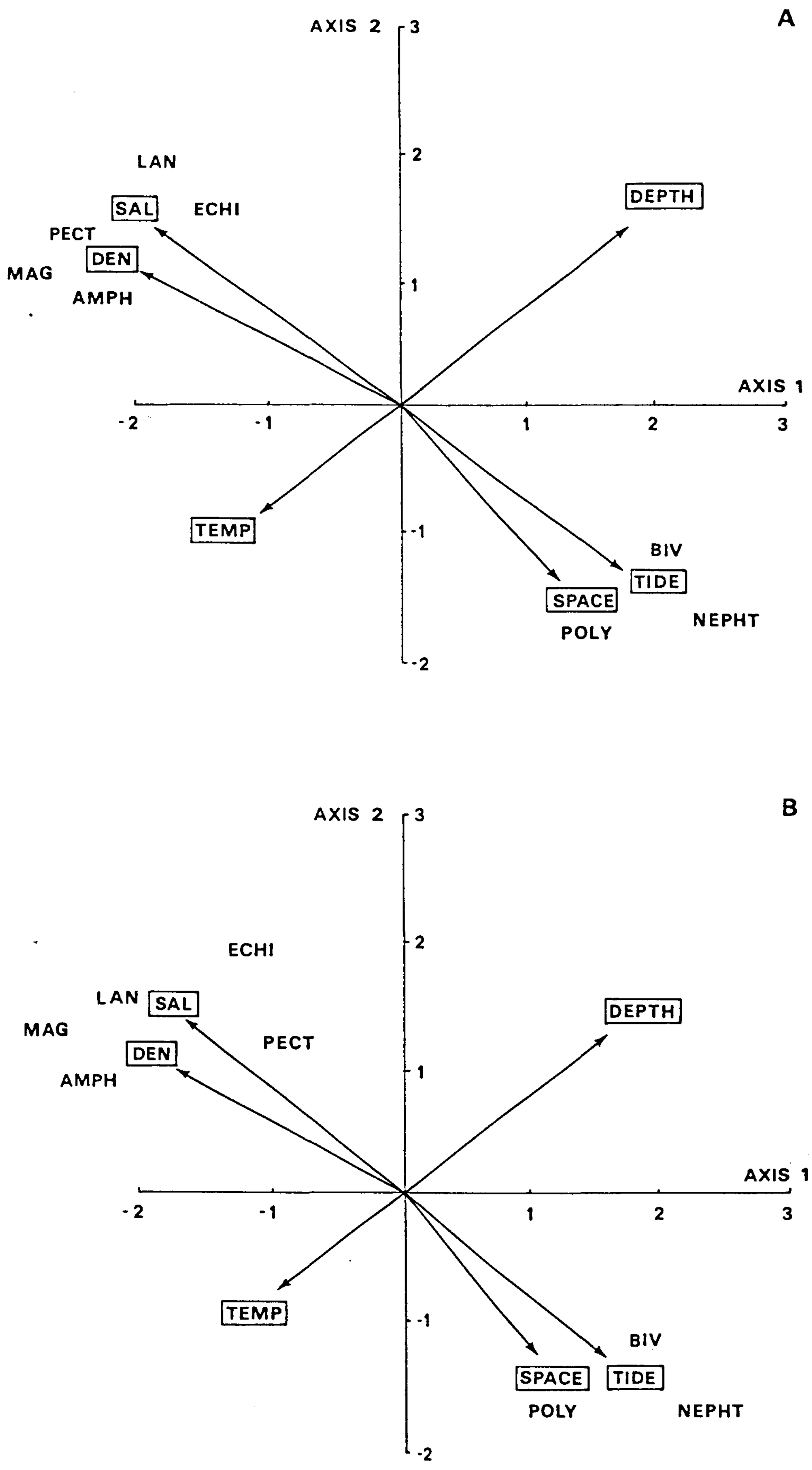


Fig. 23. Biplot based on canonical correspondence analysis (CCA) of meroplankton with respect to 5 environmental variable and space. (A) results for the 10/6/89 (B) results for the 21/6/89. The first two axes in the CCA ordination are presented. The salinity-density gradient (mainly spatial) explained most of the variance.

of correlation between these two gradients. In fact the salinity-density gradient reflects more the spatial structure in the environment, while the temperature gradient reflects more a temporal variation. However is important to remind that the use of space in these analyses highlighted the presence of autocorrelation and these results were influenced by the presence of local deviations from the general trend. Less important in explaining the meroplankton community structure was depth which showed a weak correlation with the other variables and plays a minor role in explaining community structure.

For both dates in 1989 the polychaetes *Pectinaria koreni* (PECT), *Lanice conchilega* (LAN), *Magelona mirabilis* (MAG), *Ampharetidae* (AMPH) and the echinoids were associated with the salinity-density gradient. The polychaetes *Polydora* spp. (POLY), *Nephtys* spp (NEPHT) and the bivalves larvae (BIV) were associated with the tide. The variable tide really reflects some oscillatory function of space. Ecologically showed that these larvae were somehow influenced by the alternation of high and low water. It was not possible due to the pecularity of the sampling campaigns to relate larvae abundance with a specific phase of the tide. The ordination results revealed that no species were present in the centre of the ordination diagram, this can be regarded as a possible indication that none of the meroplankton species present in the samples can be associated with the entire range of environmental conditions measured along the transect (Soetaert & Van Rijswijk, 1993). The CCA results suggested the need to investigate further the species-environment relationship by decomposing the species-abundance data into four independent additive component: (a) representing the nonspatial environmental variation, (b) the spatially structured environmental variation, (c) the spatial species variation not shared by the environmental variables, (d) the unexplained variation, to quantify the site-scale ecological pattern determined by the environmental factors and by the space (geographic coordinates) as shown further.

2.2.6. Partitioning the species variation through Partial Canonical Correspondence Analysis (partial CCA)

The results obtained from the four constrained partial CCA analyses are reported in Table. 5. The percentage of the total variation of the species matrix accounted for by each step of the analysis was obtained as suggested by Borcard *et al.*, (1992) and Borcard & Legendre (1994).

Data	SE	SS	SE/S	SS/E	Total inertia
10-6-89	0.152	0.168	0.028	0.044	0.291
21-6-89	0.634	0.607	0.119	0.091	1.07

PERCENTAGE OF THE VARIATION

CCA 10-6-89	CCA 21-6-89
Step (1) : 0.152 · 100/0.291 = 52.2%	Step (1) : 0.634 · 100/1.07 = 59.2%
Step (2) : 0.168 · 100/0.291 = 57.7%	Step (2) : 0.607 · 100/1.07 = 56.7%
Step (3) : 0.028 · 100/0.291 = 9.6%	Step (3) : 0.119 · 100/1.07 = 11.1%
Step (4) : 0.044 · 100/0.291 = 15.1%	Step (4) : 0.091 · 100/1.07 = 8.5%
Total explained variation = 67.3%	Total explained variation = 67.7%

Table 5. The results of the constrained CCA analyses are reported as the amount of canonica inertia explained by the SE (species-environment matrices), SS (species-space matrices), SE/ (species-environment matrices constrained by the space matrix), SS/E (species-space matrice constrained by the environment matrix). Total inertia indicates the sum of all unconstraine eigenvalues. The overall amount of explained variation as a percentage of the total variation of th species-matrix expressed by fractions (a,b,c) for the 10-6-89 was 67.3% obtained by summing step (1 and step (4), or step (2) and step (3), and partitioned as : (a) nonspatial environmental variatio (step 3) : 9.6%; (b) spatially structured environmental variation (step 1 - step 3, or step 2 - step 4) 42.6%; (c) spatial species variation that is not shared by the environmental variables (step 4) 15.1%; (d) unexplained variation and stochastic fluctuations : 100 - 67.3 = 32.7%. For the 21-6-89 th total explained variation was 67.7% and partitioned as : (a) 11.1%, (b) 48.1%, (c) 8.5%, (d) 32.3%.

For the cruise of the 10 June the whole variation of the species matrix (Fig. 24 A) explained by fractions (a), (b) and (c) was 67.3% and the overall variation including the unexplained fraction (d) was divided as follows :

- fraction (a) representing the nonspatial environmental variation accounted for 9.6%

- fraction (b), which can be regarded as the spatially structered environmental variation accounted for 42.6%

- fraction (c), representing the spatial species variation that is not shared by the environmental variables accounted for 15.1% of the total variation

- fraction (d), can be regarded as the expression of the unexplained variation and the possible stochastic fluctuations was equal to 32.7%.

For the 21 June the whole variation of the species matrix (Fig. 24 B) was 67.7% and was explained in the following same fractions :

- fraction (a) 11.1%

- fraction (b) 48.1%

- fraction (c) 8.5%

- fraction (d) 32.3%

The Monte Carlo permutation tests on the trace statistics for both set of analyses were significant at a Bonferroni-corrected level of 0.05/4 = 0.0125.

The change in the environmental conditions resulted in an increase of fraction (a) and fraction (b) for the 21 June.

(b) - In ecological terms for both transects, fraction (b) explaining the spatial structure in the species data that is shared by the environmental descriptors was quite high. During the first cruise the effect of the South-West wind maintained the general water circulation pattern along the coastal locations sampled in the

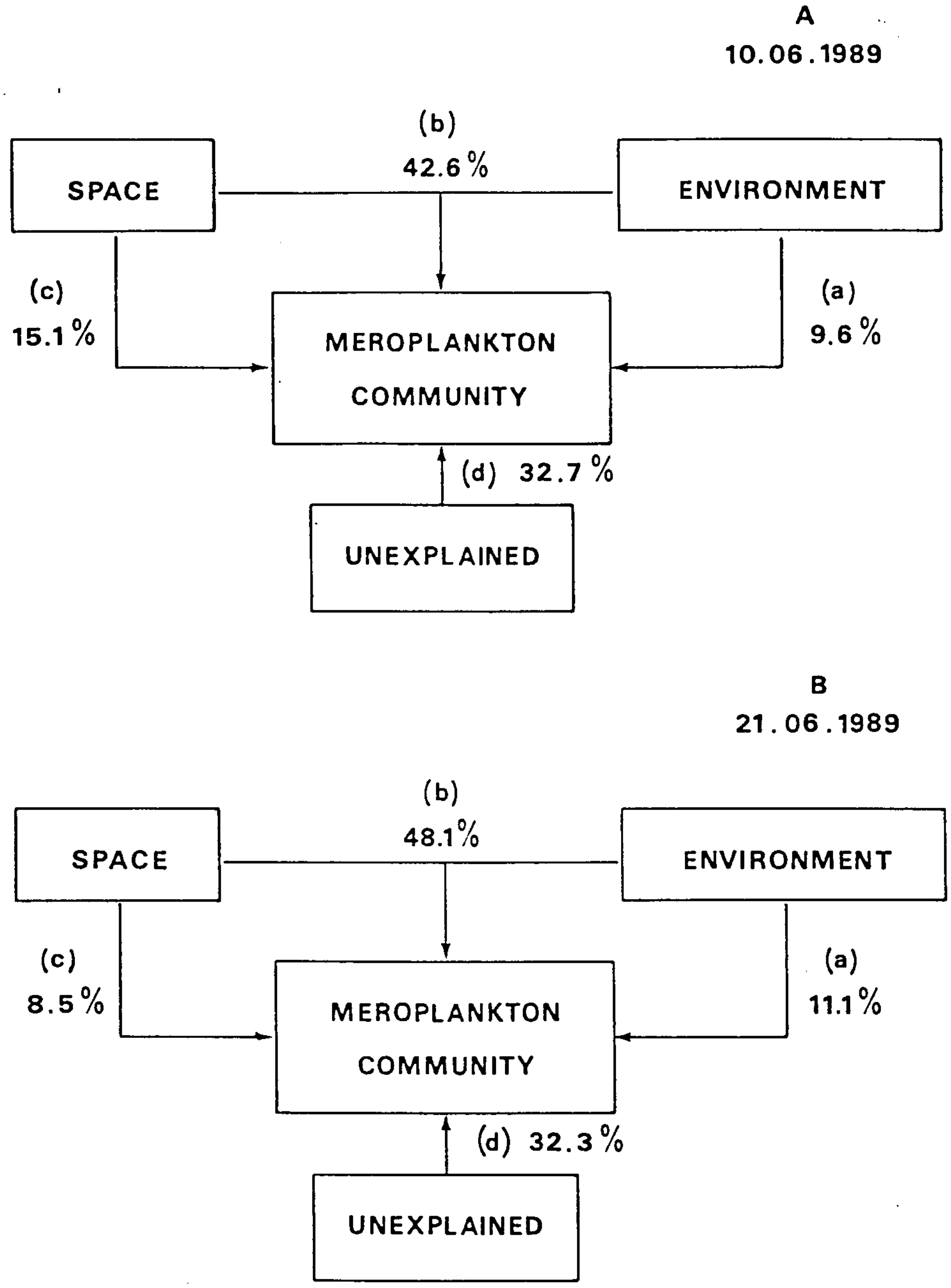


Fig. 24. Model-like representation of the variation partitioning of the meroplankton community data matrix based on constrained partial canonical correspondence analysis (CCA). (A) for the 10/6/89 (B) for the 21/6/89.

South-North-East direction, and the mixing with water masses coming from the Westerschelde estuary occured only on the Belgian coast at stations 61 to 64.

During the second cruise the North-East wind conditions inversed the general trend of the water circulation pattern inducing more mixing with the water masses coming from the Westerschelde estuary.

(a) - The variation in the species matrix due to the influence of the environment was 1.5% higher than during the first campaign, as well as the influence of the environment together with the spatial component (5.5% increase).

(c) - The amount of the strictly spatial variation in fraction c that remains unexplained by the environmental variables was 6.6% higher during the first cruise suggesting that under the South-West wind condition the space component is stronger. This result concerning fraction (c) shows that specific geographical location such as the Oosterschelde may be regarded as an area of larval retention, where larval survival is maintained by the site structure itself and by its environmental characteristics. It may also be that changes in the wind conditions has impel up the water masses, thus reducing the spatial structuring. In the inverse wind condition fraction (c) was reduced from 15.1% to 8.5% showing more the importance of the change in the environmental conditions rather than the purely spatial.

(d) - The undetermined variation, fraction (d), was very similar for both cruises suggesting that this amount of variation can be regarded as the effect of local effects such as short term tidally induced variability, and mesoscale changes in the residual current pattern. Furthermore the available explanatory variables can not explain all the spatial structure of a living community data set since for example processes related to the population dynamics of the species involved, such as predator-prey interactions, food-partitioning, are very likely to generate measurable spatial structures. However it was very important that the results identified and quantified this information.

In conclusion the recruitment of macrobenthic larvae in the coastal location crossed by the transect is correlated to a large extent with the spatial gradient present in the environmental variables, and changes in the spatial structure of the environmental variables do influence the meroplankton community structure. The model-like representation of the results in Figs. 24 A and 24 B were a useful departure point to evaluate a possible causal model using the different fractions extracted from the constrained CCA analysis. This way of interpreting the partial CCA result can be used to list the various cause-to-effect relations that can be contained in each fraction from (a) to (d) (Borcard & Legendre, 1994). The next step was to verify if the causal model compatible with these observations was : Space ⇒ Environment ⇒ Meroplankton, through a path analysis.

2.2.7. Causal Modelling and spatial autocorrelation through Path Analysis, Mantel and partial Mantel tests

The Mantel test among the three matrices considered (1: geographic distance matrix; 2: environmental variables matrix; 3: species matrix) for the two sampling dates gave the following correlations :

(10-6-89)	**(21-6-89)**
$R_{1,2} = 0.498$ ($p<0.001$)	$R_{1,2} = 0.560$ ($p<0.001$)
$R_{1,3} = 0.389$ ($p<0.001$)	$R_{1,3} = 0.315$ ($p<0.001$)
$R_{2,3} = 0.512$ ($p<0.001$)	$R_{2,3} = 0.589$ ($p<0.001$)

For both sets of calculations the null hypothesys (H_o), stating that the multivariate data are not autocorrelated as a gradient was rejected at the 1% significance level according to the test of significance of the Mantel statistics (Mantel, 1967; Legendre & Fortin, 1989; Fromentin *et. al.*, 1993).

The partial Mantel tests for the two campaigns gave the following correlations :

(10-6-89)	**(21-6-89)**
$R_{1,2} = 0.377$ ($p = 0.00001$)*	$R_{1,2} = 0.488$ ($p = 0.00000$)*
$R_{1,3} = 0.179$ ($p = 0.04592$) N. S.	$R_{1,3} = -0.022$ ($p = 0.05612$) N. S.
$R_{2,3} = 0.398$ ($p = 0.00001$)*	$R_{2,3} = 0.524$ ($p = 0.00000$)*

The partial Mantel tests for the two transect shows that the computed partial correlation between the geography (space) matrix and the species (meroplankton) matrix ($R_{1,3}$) were non-significant.

The correlation between geography (space) matrix and the environment ($R_{1,2}$); and between the environment and the species (meroplankton, $R_{2,3}$) were highly significant (*) at a Bonferroni-corrected probability level of 0.05/4 = 0.0125. This result shows that the structure in the meroplankton distribution comes from the structuring of the environmental variable.

It is very important here to note what 'space' means in these analyses. Any Mantel correlation with the geography matrix means that there is a nearly linear, or monotonically increasing or decreasing correlation along the sampling line.

This is fundamentally different from the meaning of 'space' in the CCA analyses, where the variable 'space' was an adjusted full cubic polynomial. The latter can have many shapes, depending on the parameters, and is not necessarily monotonic. For this reason both analyses have to be compared with caution.

If we compare the two sampling campaigns, the Mantel statistics describing the influence of the environment on the meroplankton community structure for the 10 June, is reduced from 0.512 to 0.398 when controlling for the effect of space but remains very highly significant. The specific influence of the environment is therefore 0.398 while the difference 0.254 (0.498 · 0.512 = 0.254), can be regarded as the influence of the spatial structure inbedded in the environment on the species distribution.

For the 21 June the Mantel statistics describing the influence of the environment on the meroplankton was reduced from 0.589 to 0.524 when controlling for the effect of space. The influence of the environment is 0.524, and the difference 0.329 (0.589 · 0.560 = 0.329), corresponds to the influence on the species distribution exerted by the spatial structure present in the environment.

The simple Mantel test statistic values where used to compute a pat analysis for each case. The results are reported in Table 6.

10 June 1989	**Environment**	**Taxonomic groups**
Geography	0.498* p < 0.0001	0.178 p = 0.0459 N. S.
Environment	-----	0.423* p < 0.0001

21 June 1989	**Environment**	**Taxonomic groups**
Geography	0.560* p < 0.0001	−0.021 p = 0.0561 N.S.
Environment	-----	0.601* p < 0.0001

Table 6. Transect 1, campaigns of 1989. Path coefficients (i.e., standard partial regressio coefficients), computed from simple Mantel correlations, represent direct causal covarianc Significance is assessed using partial Mantel tests: (*) significant, (N. S.) non significant at th Bonferroni-corrected probability level of 0.05/3 = 0.01667

The paths between *Geography* and *Environment* are about 0.4 to 0.5 an all very significant. The paths between *Geography* and *Species* are near 0 for th second transect (actually -0.021) except in the case of the first transect where th path coefficient was 0.178, one might expect that some possible spatial structure present in the species data after removing the spatial structure of th environmental variables. However both results were non-significant on the bas of the partial Mantel tests. The paths correlation between *Environment* an *Species* are between 0.4 to 0.6 and all very highly significant.

This confirmed that the spatial structure in the taxonomic group data ca in all cases, be attributed to the influence of the spatially-structure environmental variables, and do not reflect a spatial structuring of the taxonom groups themselves, separate from the spatial structure in the environment variables. Table 7 lists the predictions of the model in terms of the values and significance of the Mantel and partial Mantel correlation coefficients among all three matrices (Legendre and Troussellier, 1988; Legendre and Legendre, 1996).

Model	**Predictions of the model if the model is true**	**Computed results (all 2 transects)**
Space	$R_{1,2}$ signif. $\neq 0$	yes
⇓	$R_{2,3}$ signif. $\neq 0$	yes
	$\lvert R_{1,2} \rvert \geq \lvert R_{1,3} \rvert$	yes
Environment	$\lvert R_{2,3} \rvert \geq \lvert R_{1,3} \rvert$	yes
⇓	$R_{1,2 \cdot 3}$ signif. $\neq 0$	yes
	$R_{2,3 \cdot 1}$ signif. $\neq 0$	yes
Meroplankton	$R_{1,3 \cdot 2}$ not signif.	yes
	$\lvert R_{1,2 \cdot 3} \rvert \leq \lvert R_{1,2} \rvert$	yes
	$\lvert R_{2,3 \cdot 1} \rvert \leq \lvert R_{2,3} \rvert$	yes
	$R_{1,2} \times R_{2,3} \approx R_{1,3}$	yes

Table 7. Predictions of the model of causal relationship supported by the results in Tables 1 and 2. Matrix 1 = "Geography", matrix 2 = "Environment", matrix 3 = "Meroplankton". $R_{1,2}$ is the Mantel correlation between matrices 1 and 2, etc. ; $\lvert R_{1,2} \rvert$ is the absolute value of a correlation coefficient. '$R_{1,2}$ signif. $\neq 0$' means that the correlation is significantly different from zero; '$R_{1,3 \cdot 2}$ not signif.' means that the correlation is not significantly different from zero at the pre-selectected significance level.

The results obtained during both sampling campaigns in 1989 support this model, which states that the spatial gradient present in the environmental variables can explain the variation observed in the spatial distribution of the meroplankton. This shows that changes in the spatial structure of the environmental variables do influence the meroplankton community structure; this is in agreement with the environmental control model (ECM).

2.2.8. Discussion and Conclusion

The first objective of the 1989 campaign was the analysis of the relationship between meroplankton, environmental descriptors, and geography, to quantify the spatial heterogeneity of the meroplankton community structure in relation to hydrodynamic and environmental processes. The second objective was to try to relate the results obtained to recruitment processes and propose a model of causal relationship, in order to provide a measure of the strenght of the association between species and environment sharing the same spatial gradient.

The results presented here are considering events taking place during a short period of time of a few weeks during the recruitment of macrobenthic species and suggested the importance to consider *a priori* the presence of spatial autocorrelation in the data and to regard this as a departure point for any ecological research. As suggested by Mackas (1984), it is important to measure to which extent the samples in different locations are dependent on their separation.

The spatial structuring of natural communities implies a better understanding of the relative contribution of the different abiotic and biotic factors in determining the distribution and interaction between organisms (Hudon & Lamarche, 1989; Christopher *et al.*, 1987). The results suggested the importance to consider the physiographic characteristics of the study area in order to tests the effects of climatic and hydrographic factors on the advection and survival of planktonic larvae and the need to relate dispersal events to settlement processes and on-site experimental study. More precisely: the spatial distribution of the abiotic and biotic variables confirmed the importance of the influence of meteorological conditions on the water masses ciculation and exchange between the English Channel and the North Sea. The oscillation in the temperature and salinity distribution confirmed the presence of a nearshore drift which separate the coastal and off-shore waters establishing two gradients: a coastal-off-shore gradient and a South-West-North-East gradient (Belgrano *et al.*, 1990) similar to the observations in the Eastern English Channel(Brylinski *et al.*, 1991). The South-West-North-East gradient can be reversed in the presence of a North-East wind (Salomon & Breton, 1993) and as confirmed by other RENORA campaigns (Dewarumez *et al.*, 1992). The changes in the wind conditions explained the possible transport of meroplankton in the opposite direction to the prevailing North-Easterly residual tidal current (Belgrano *et al.*, 1990), allowing a South-Westerly dispersal (Luczack *et al.*, 1993). Monitoring the dispersal of meroplankton species at a pelagic level can be extremely useful as biological tracer of water masses, and to quantify the availability of larvae to the adult benthic community in relation to recruitment processes. The presented partially redundant but overall complementary multivariate statistical methods can provide a better and more statistical interpretation of marine ecological data.

The PCA produced an initial picture of the scaling of the observation and allowed to define three different groups of stations indicating a separation between coastal, frontal and off-shore environments, from the salinity front stations. The PCA results suggested the need to further the analysis of the data, in order to have more specific informations related to the sequence of the sample and the existing spatial structure.

The chronological clustering method described one discontinuity in the multivariate series of biological samples along the transects. The main division was based on the presence of a salinity front, whose position can change due to shifts in the environmental descriptors induced by external forcing such as wind-induced horizontal water movements and residual tidal currents, as also reported by Salomon *et al.* (1993). Meroplankton was subjected to dispersal and its distribution was directly associated with variations in regional hydrological phenomena confirming the observations by Hecq *et al.* (1992) concerning the existence of a spatial-temporal scale specific to each environmental parameters related to the distribution of pelagic communities. The species distribution confirmed the earlier observation by Belgrano et al., (1990) in defining the presence of two distinc populations of *Polydora spp.*, and the differences of larvae density within weeks as an indication of the periodicity of the release of larvae from the adult population.

Echinoids larvae may act like passive particles subjected to the hydrodynamic control associated with surface waters (Pedrotti and Fenaux, 1992). For this reason, these larvae can be regarded as a possible marker of surface water displacement, coming from the Calais area and the off-shore sand bancs in front of Gravelines drifting to the North-East, according to regional meteorological events.

The presence of a high a density of bivalve larvae in the water column was an indication of the possible supply of young recruits to the adult macrobenthos community crossed by the transects and characterized by a benthic continuum dominated by the bivalve *Abra alba* (Dewarumez *et al.*, 1992), as an indication that the *Abra alba* community can be regarded as self-sustaining. Changes in the meteorological features and alternation of cold and mild winters along the French coastal area studied, will have an effect on the recrutiment and survival of this bivalve species (Fromentin & Ibanez, 1994).

The chronological analyses showed the importance of the spatial-temporal shift in the larval distribution in relation to frontal structures or distinct water masses affecting dispersal and recruitment in benthic studies, as pointed out earlier by Banse (1986). In ecological terms, the divisions obtained with the chronological clustering method indicated the main differences in both taxonomic composition and environmental characteristics along the coastal locations sampled.

The MDS analyses were complementary to the chronological clustering in showing the scaling of the stations corresponding to the major hydrological events. They showed especially for the second cruise the shift from station 26 to 27 (Fig. 22) concomitant with the presence of a salinity front and an increase in the density of *Lanice conchilega, Polydora spp.* and bivalves, and a decrese in the echinoids density. Since all the stations concerning these shifts were located in the coastal area the MDS indicated that major processes regulating the recruitment of these species are taking place close to the coast and not in the off-shore regions. The retention of larvae in coastal location close to the adult community increase the rate of survival of the larvae and prevent them to be vagrant to the retention area. The coastal part of the transect and the alternation of sand banks and channels can be regarded as a retention area for meroplanktonic larvae, as confirmed earlier by (Belgrano et al., 1990). The off-shore stations may be regarded, under specific meteorological conditions, as a possible source of larval supply from off-shore macrobenthic community allowing the recruitment of new species, as for example *Ensis directus* on the French coast within the *Abra alba* community (Luczack *et al.,* 1993).

The CCA analyses provided a summary of the species-environment relationship taking into account the spatial gradient present in the data set (ter Braak & Prentice, 1988; Palmer, 1993). The salinity-density gradient opposite to the tide-space gradient explained, for both campaigns, the major part of the meroplankton variance. The changes in salinity distribution and the related cicadian occurence of the tide high and low water have a clear effect on the meroplankton distribution. The CCA showed that hydrodynamic and physico-chemical processes are responsible for the retention of larvae within a restricted and identifiable water mass. The larvae of *Lanice conchilega, Pectinaria koreni,* were found during the second campaign in the transition zone of the transect between the French-Belgian coast, were salinity tended to change considerably under the effect of the wind. The persistence of these larvae in this location as previously pointed out by Belgrano *et al.,* (1990) was a good indication of the physiological adaptabilities of these polychaetes to a very fluctuating environment.

The echinoids were related to higher salinity values as an indications that this larvae were characteristic of the French part of the transect. Salinity *per se* plays a decisive role in restricting the distribution of echinoderms. There are only two study (Brattström, 1941; Ursin, 1960) that relate species distribution of echinoderms in a large area in relation to salinity changes, and one study by Rees (1954) on the distribution of echinoderms and other larvae in the North Sea.

The observations of the 1989 campaign confirmed the earlier results on echinoderms larvae and further pointed out the lack of informations on this subject. The bivalves, *Polydora spp.*, and *Nephtys spp.* larvae were associated directly with the circadian tidal movement, and to *space* describing the geographical component present in the data set.

These results further supported the hypothesis tested in 1988 concerning the influence of tidal-induced variability on the distribution of meroplankton larvae. The number of larvae present during the second cruise was much higher than in the first cruise, suggesting that the majiority of larvae were just recently be recruited in the plankton. This sets the first time scale in the order of 10 days. If we consider as a second time scale the residual transport than : How long doest it take, on average, for a larvae to move out of the parental patch by the residual current and tidal dispersion ? The RENORA campaigns showed that larvae can be moved out from the parental patch during a complete tidal cycle suggesting that either a spatial shift or retention mechanisms are active. On the contrary if larvae need more than 10 days to move out from the parental patch, their distribution may be expected to reflect the parental distribution. However this hypothesis needs to be tested further with more field studies, and the data in hand could not provide a full proof.

The combinations of tidal-environmental processes and *space* can be regarded as the major factors regulating the pelagic phase of the recruitment processes of marine invertebrates, resulting in the importance to quantify these regulating factors by constrained partial CCA (ter Braak, 1987; Michin, 1987; Økland, 1986).

The constrained partial CCA offered the possibility to factor out the covariables, in this case the environmental variables and the geographic distance between samples, in a partial ordination (ter Braak, 1987), and to test the variation occuring between samples along a succesional pattern (Palmer, 1993).

The inclusion of space in the form of a spatial distance matrix allowed to quantify the amount of variability associated with a precise spatial structure. This variability, which is expressed by the fraction (c), can be either explained or not explained by the environmental variables considered, and can also suggest the importance to use other environmental variables to explain the observed spatial variability.

This fraction (c) was higher during the first cruise, when more mixing occured due to the South-West wind. This suggested that, when more mixing occurs in the water column the distribution of the environmental variables such as salinity is affected, and larvae are more subjected to dispersal by wind-advection processes.

As a result regional spatial features such as sand bank and channels are 'natural barriers' important for retention processes and this can be quantified by fraction (c). Fraction (a), representing the nonspatial environmental variation, decreases as fraction (c) increases.

The environmental variation itself thus contributed more in explaining the meroplankton variation during the second cruise, with less wind action of the surface waters. For both transect in 1989, fraction (b) representing the spatially structured environmental variation explained most of the meroplankton variation. Fraction (d) can be related to unexplained stochastic processes. In ecological terms, the analysis showed that the spatial structuring of the environmental variables explained quite considerably the spatial structure in the species distribution patterns.

Furthermore, the partitioning of the meroplankton variation into these four fractions gave the possibility to test the *environmental control model* (ECM), and to verify that environmental variables are responsible for the observed variations in the species distribution of meroplankton (Whittaker, 1956; Bray & Curtis, 1957; Hutchinson, 1957).

The results of the path analyses for both campaigns and the corresponding partial Mantel test supported the (ECM) model. The spatial gradient present in the environmental varibles can explain the variation observed in the spatial distribution of the meroplankton, and that changes in the spatial structure of the environmental variables do influence the meroplankton community structure.

Ecological conclusion

The structural forces intrinsic to the meroplankton community, as well as the community composition, change following modifications of the environmental variables; this paradigm is known as the environmental control model (ECM). The discontinuities occurring in the two multispecies time series of biological samples collected along the transect in the French-Belgian coast of the Southern Bight of the North Sea showed the existence of two ecological boudaries representing the French coast and the French-Belgian coast. These *boundaries can shift northward or southward due to changes in the spatial distribution of the environmental variables enhanced by meteorological forcing.*

The results of Path Analysis, combined with Mantel and partial Mantel tests, were used to produce a synthetic model of causal relationships. Its aim was to test whether the observed relationships (correlations) between species and environmental variables were causal, or simply resulted from the presence of a common spatial gradient in both sets of variables. In both cases, the spatial pattern of the species can be fully attributed to the spatial pattern of the environmental variables, and is completely 'explained away' by them; no significant spatial pattern remains in the species data after controlling for the effect of the environmental variables. The only causal model compatible with these observations is then: Space ⇒ Environment ⇒ Meroplankton.

2.3. Spatial structure and ecological variation of meroplankton data. Southern Bight of the North Sea: Belgian-Dutch coast, two late spring 1990 campaigns

2.3.1. Spatial variations of the physical and biological data and PCA

The composite NOAA-AVHRR images from the end of May to mid June 1990 are clearly showing the major spatial differences in the sea surface temperature (Fig. 25 A), and suspended matter distribution (Fig. 25 B). Temperatures values were ranging from 15 °C close to the coast to 13 °C in the waters surrounding the Schelde estuarine system. The suspended matter distribution shows that the major inputs is coming from the Westerschelde. The list of the environmental variables and the name of the taxonomic groups are reported in Table 8 below.

Taxonomic group	**Environmental variables**
Lanice conchilega	Salinity (psu)
Pectinaria koreni	Temperature (°C)
Magelona mirabilis	Density (Kg.m^{-3})
Polydora spp.	Corrected depth (m)
Nephtys spp.	Tide height (m)
Ampharetidae	Fluorometry (Chl-a µg.l^{-1})
Bivalves	
Echinoids	
Ophiuroids	

Table 8. Taxonomic group and set of environmental variables.

The first cruise during spring 1990 on the 5 June was carried out after a week of strong South-West wind with gust up to 30 m.s^{-1}. During sampling the South-West wind velocity decreased to 7 m.s^{-1} . The low and high water as a reference to Vlissingen occured at 7h16 min. with 0.73 m and at 13h18 min. with 4.41 m between station 17-18. The second cruise during spring 1990 on the 11 June was subjected to a North-East wind with an estimated wind velocity of 5.5 m.s^{-1}. The tide low and high water as a reference to Vlissingen occured at 10h55 min. with 0.79 m and at 16h36 min. with 4.57 m between station 62-63.

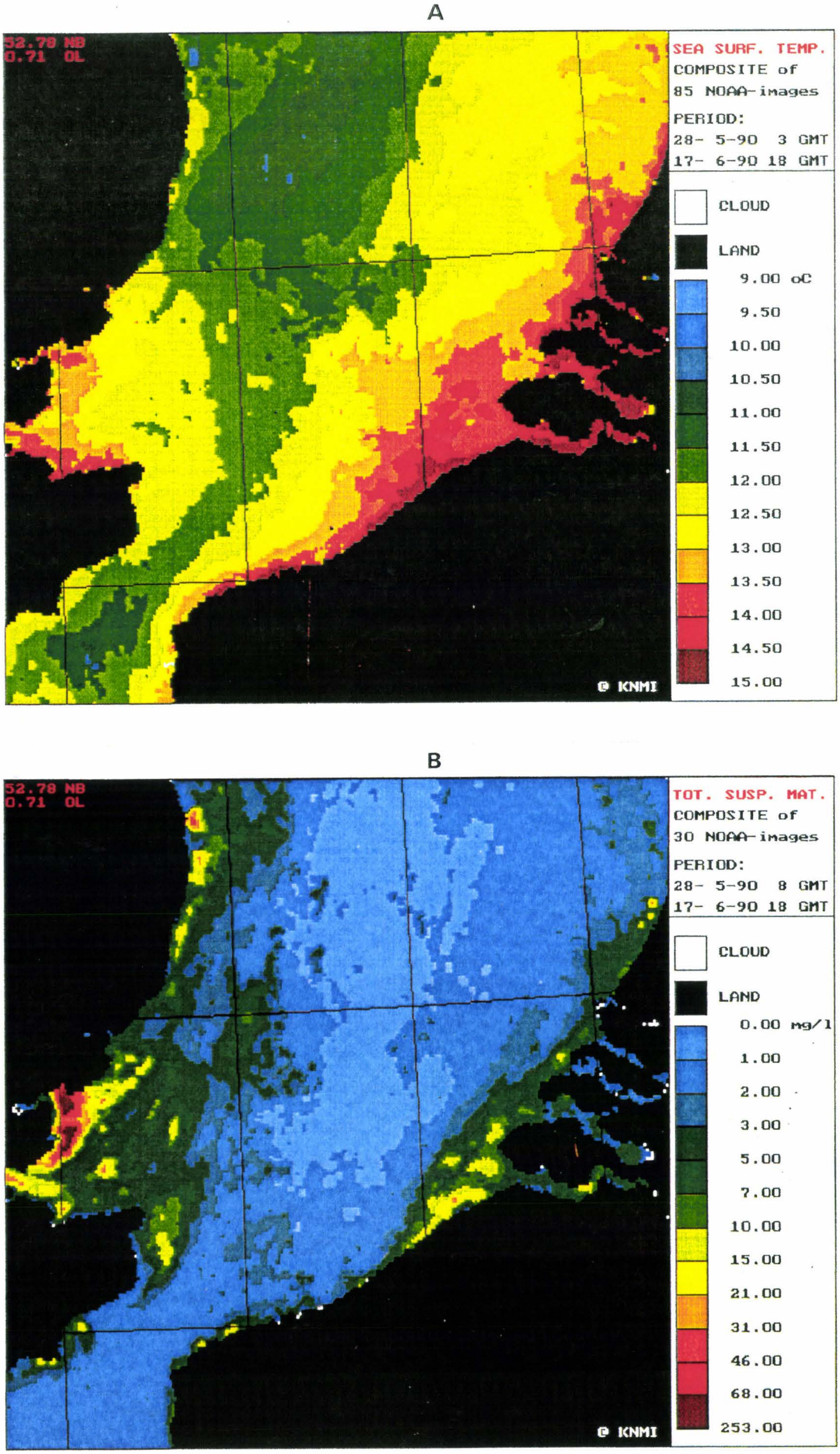


Fig. 25. NOOAA-AVHRR satellite composite image (KNMI, 1990), showing (A) the sea surface temperature distribution and (B) the total suspended matter distribution for the period 28 May to 17 June 1990.

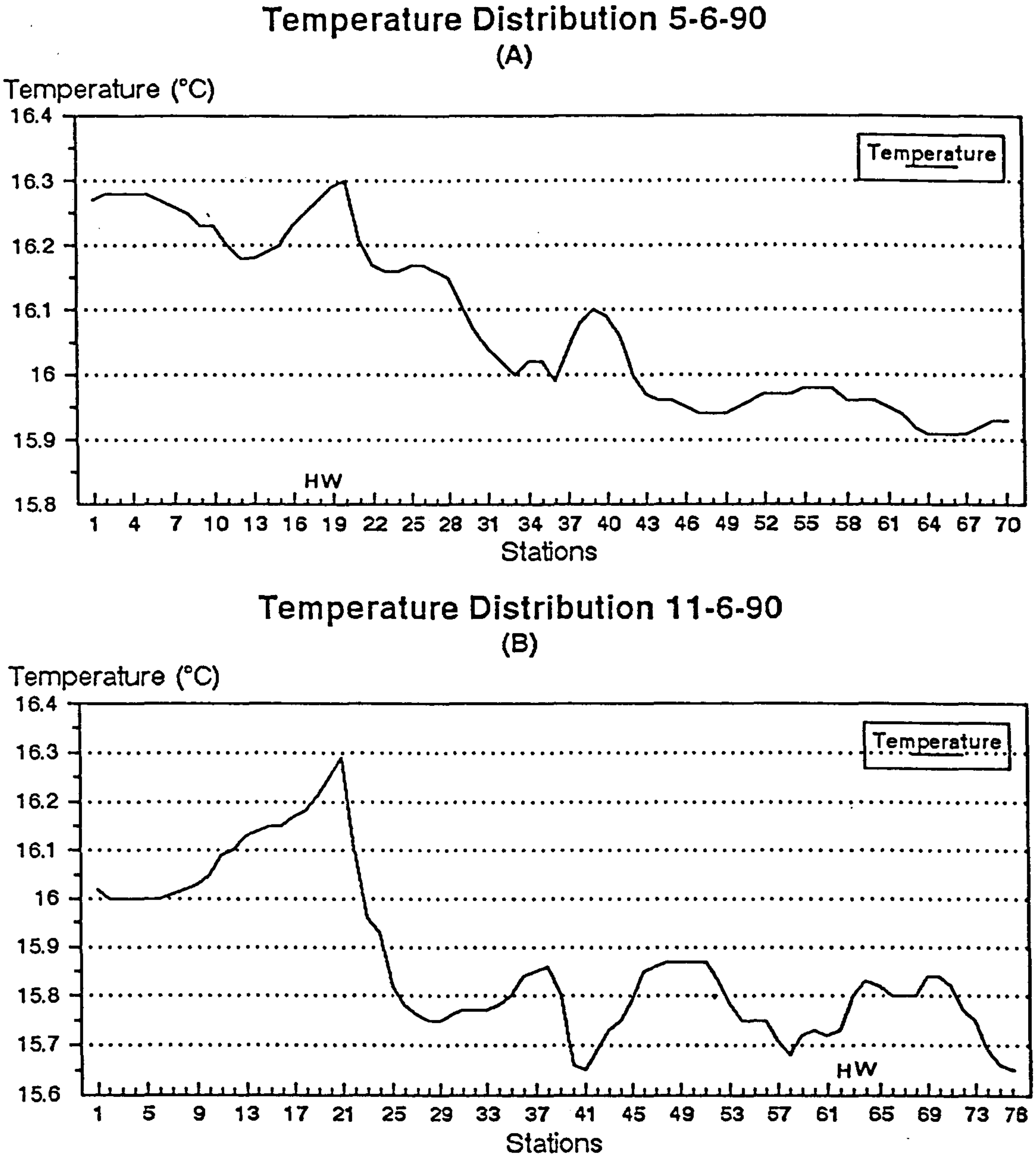


Fig. 26. (A) Temperature distribution for the first cruise influenced by the South-West wind. (B) Temperature distribution for the second cruise influenced by a fable North-East wind. H.W. indicates the time of occurence of high water.

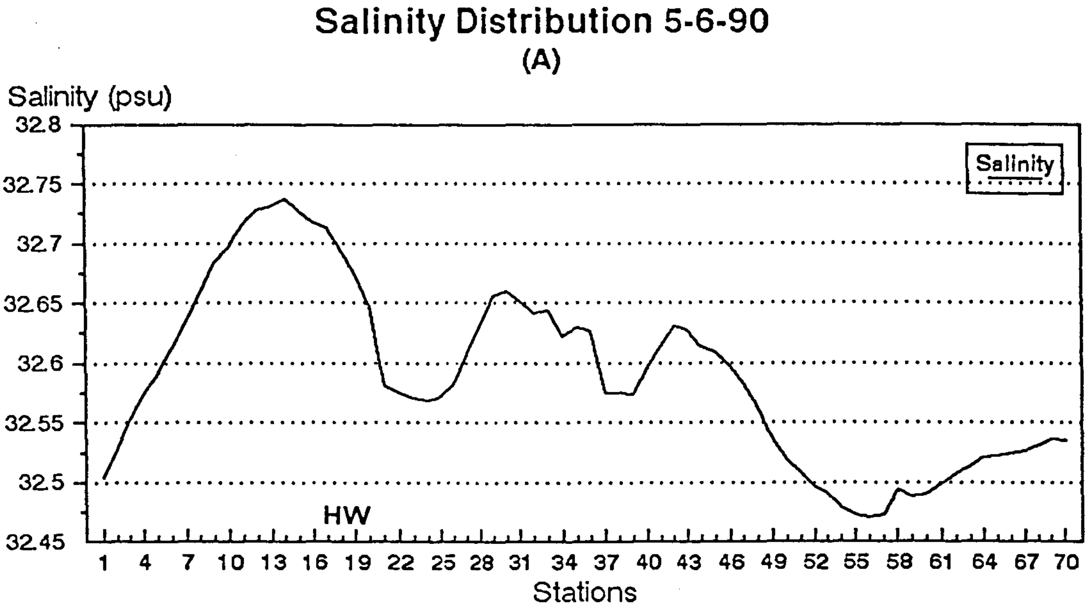
The temperature distribution for the 5 June (Fig. 26 A), shows the highest value of 16.3 °C at station 20 at the mouth of the Westerschelde, than decreasing towards the Oosterschelde reaching the lowest value of 15.91 °C at station 64. During the second cruise the temperature distribution (Fig. 26 B), shows clearly the input of warmer water coming from the Westerschelde with the highest value of 16.29 °C at station 21.

The salinity distribution for the 5 June (Fig. 27 A), shows that the highest salinity value of 32.73 (psu) was found at station 15 on the Northern Belgian coast, and decreasing towards the Westerschelde (station 20), and along the Dutch coast (Stations 30 to 40), the lowest salinity value of 32.47 (psu) was found in the proximity of the Oosterschelde at station 55. For the 11 June the salinity distribution (Fig. 27 B), shows clearly the presence of the Westerschelde with the lowest value of 30.10 (psu) at station 21. The highest salinity value was found at station 41 along the Dutch coast with a value of 32.95 (psu)

The fluorometry distribution, as a measure of Chlorophyll-a, shows for the 5 June (Fig. 28 A), the highest value of 20 Chl-a $\mu g.l^{-1}$ at station 22 and 28 at the mouth of the Westerschelde. The fluorometry ditribution decreases as we moved along the Dutch coast, reaching the lowest value of 7.0 Chl-a $\mu g.l^{-1}$ at station 54. During the second cruise, the fluorometry distribution (Fig. 28 B), shows the input of nutrient-rich waters (22.05 Chl-a $\mu g.l^{-1}$), coming from the Westerschelde along the flood-tide channel running parallel to the Dutch coast from station 21 to 30. At the Oosterschelde (station 70), the fluorometry value was 17.2 Chl-a $\mu g.l^{-1}$.

For the spatial distribution of the taxonomic group, is presented here the distribution of the Ophiuroids togheter with tempeature, salinity, and fluorometry distribution. The Ophiuroids density distribution with temperature (Fig. 29 A), shows for the first cruise the highest density value of 120 ind.m^{-3} at station 60 concomitant with a temperature value of 16 °C. For the 11 June (Fig. 29 B), the Ophiuroids density distribution shows two distinct input points, respectively between stations 26 and 31 (500 ind.m^{-3}), at the mouth of the Westerschelde, and between stations 64 and 76 (590 ind.m^{-3}), at the Oosterschelde.

For the first transect the highest density values of Ophiuroids was associated with a lower salinity value of 32.51 (psu) (Fig. 30 A), at sation 60, for the second cruise (Fig. 30 B), the highest density was found at station 69 at a salinity value of 32.92 (psu). When considering the Ophiuroids distribution in respect to fluorometry, we found for the 5 June (Fig. 31 A), the highest density values of



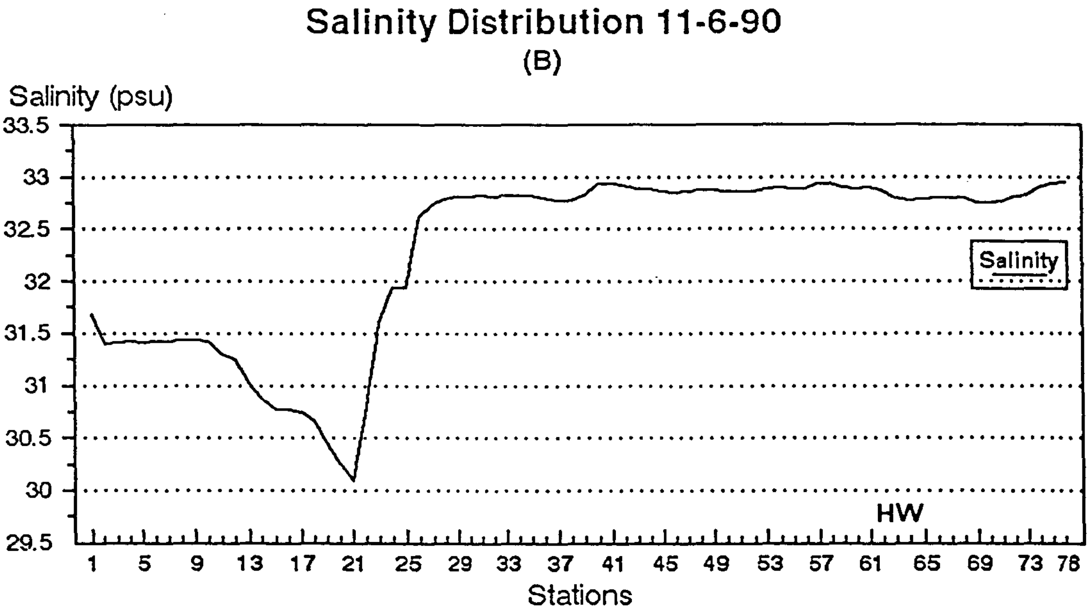


Fig. 27. (A) Salinity distribution for the 5 June; (B) salinity distribution for the second sampling date showing the presence of the Westerschelde at station 21. H.W. indicates the time of occurence of high water.

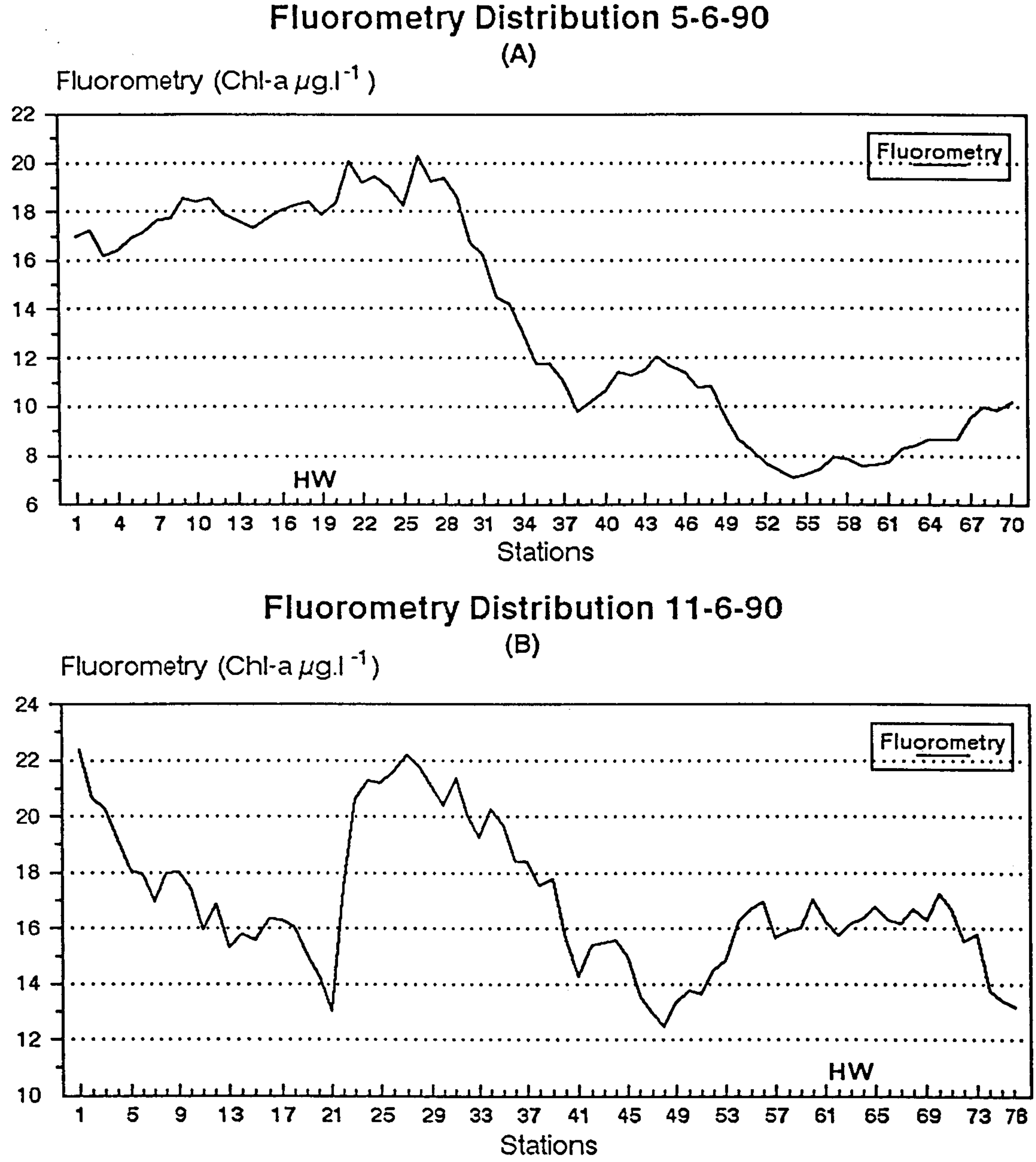
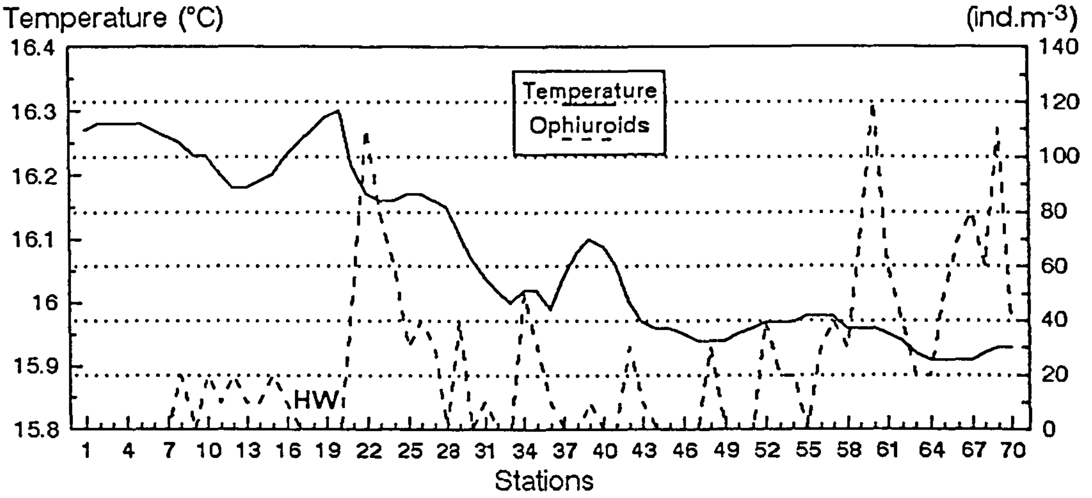


Fig. 28. (A) Fluorometry distribution for the first cruise, showing more mixing occuring due to the effect of the South-West wind; (B) fluorometry distribution for the second cruise with fable North-East wind conditions, the presence of the nutrient-rich waters coming from the Westerschelde (stations 21 to 23), and the input from the Oosterschelde (stations 61 to 76) are clearly visible. H.W. indicates the time of occurence of high water.

Ophiuroids
& Temperature Distribution 5-6-90
(A)



Ophiuroids
& Temperature Distribution 11-6-90
(B)

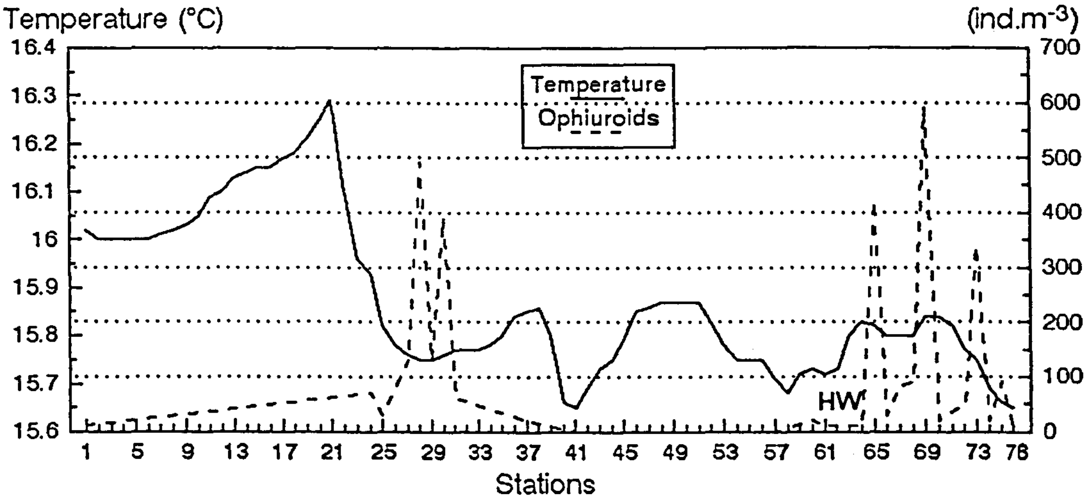


Fig. 29. (A) Distribution of the ophiuroids larvae with temperature for the 5 June; (B) distribution of the ophiuroids larvae with temperature for the 11 June, showing two distinct peaks. H.W. indicates the time of occurence of high water. H.W. indicates the time of occurence of high water.

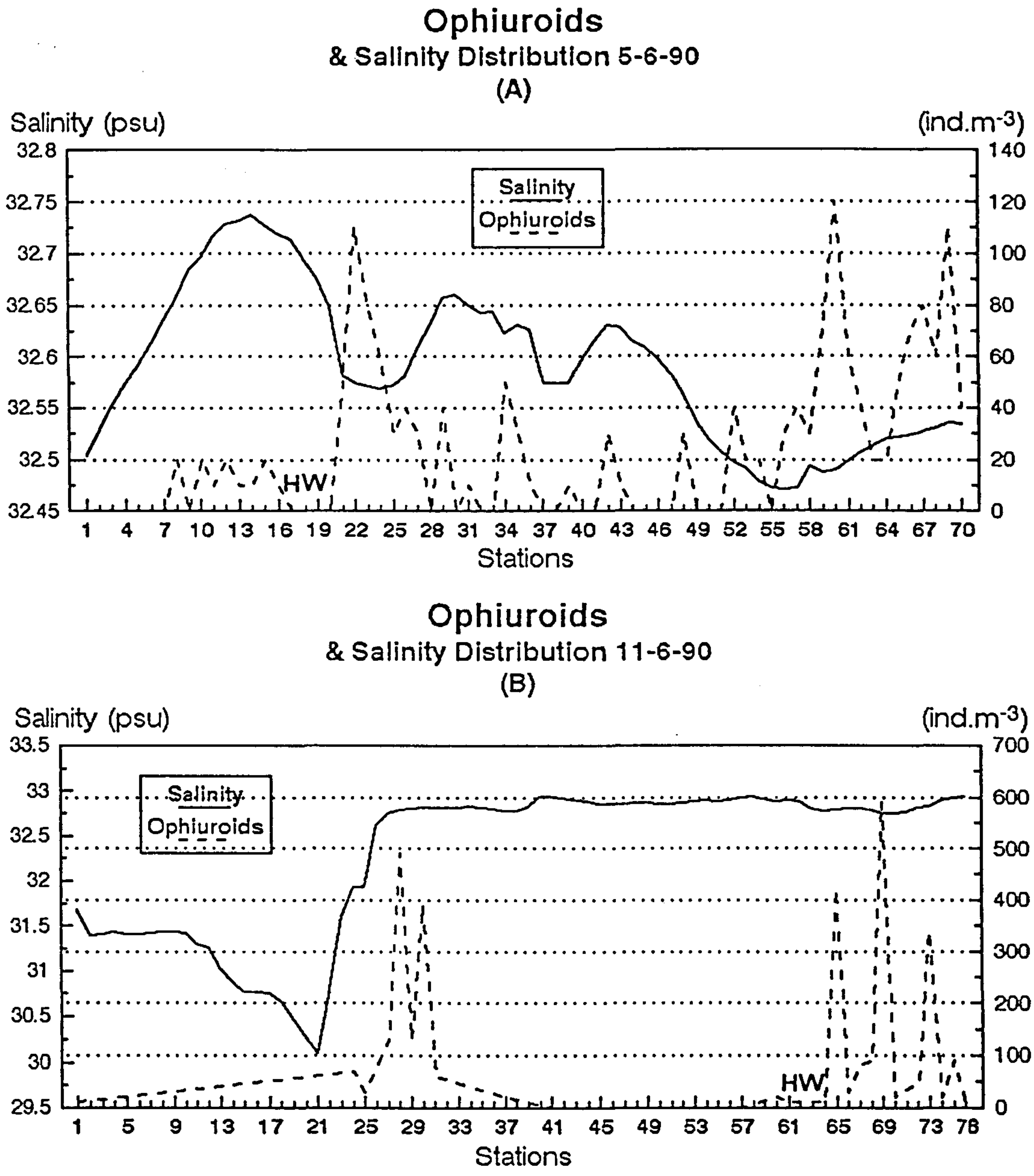


Fig. 30. A) Distribution of the ophiuroids larvae with salinity for the 5 June; (B) distribution of the ophiuroids larvae with salinity for the 11 June, showing two distinct peaks. H.W. indicates the time of occurence of high water.

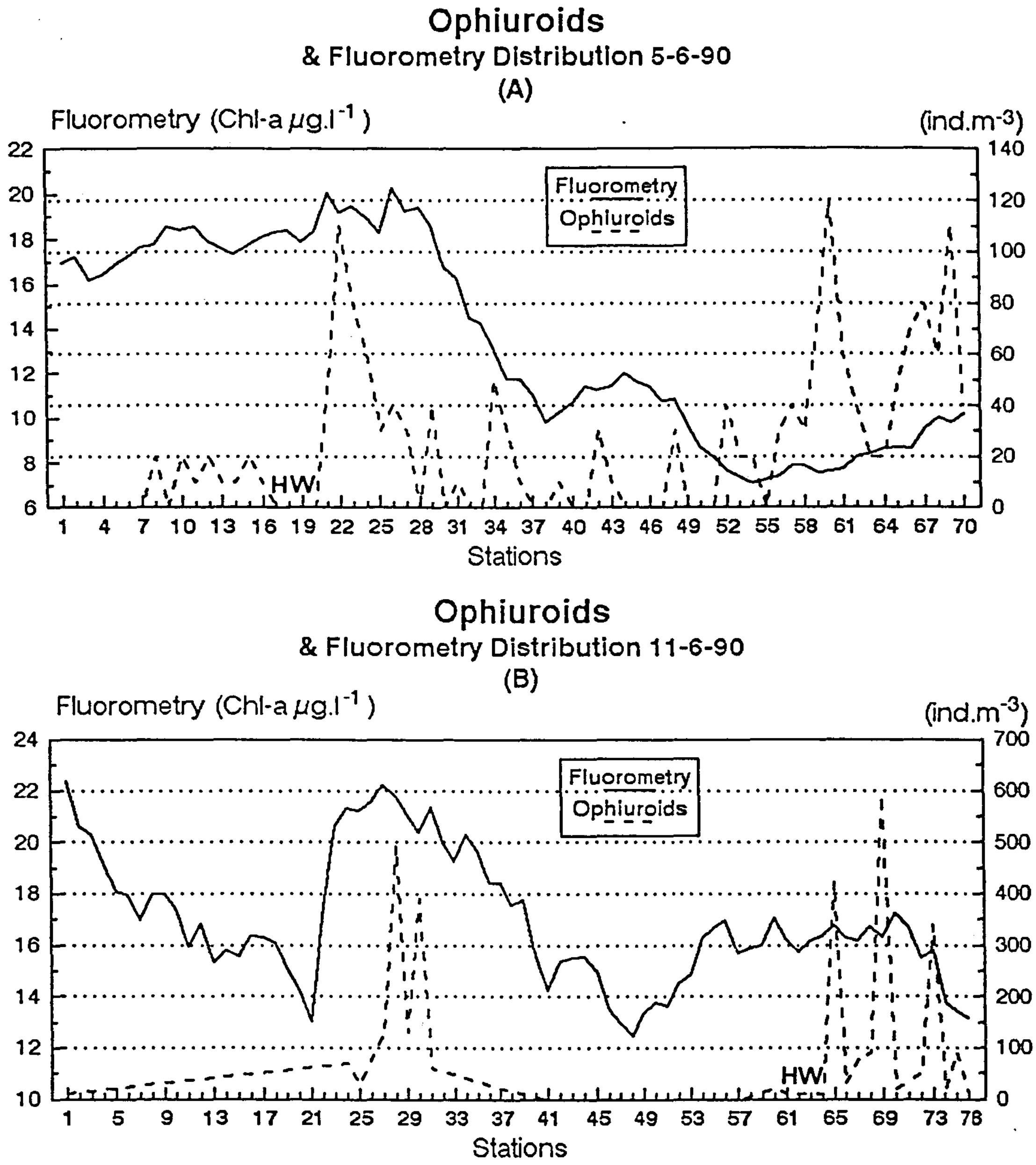


Fig. 31. (A) Distribution of the ophiuroids larvae with fluorometry for the 5 June; (B) distribution of the ophiuroids larvae with fluorometry for the 11 June, showing the two distinct peaks concomitant with the nutrient-rich waters coming from the Westerschelde and Oosterschelde. H.W. indicates the time of occurence of high water.

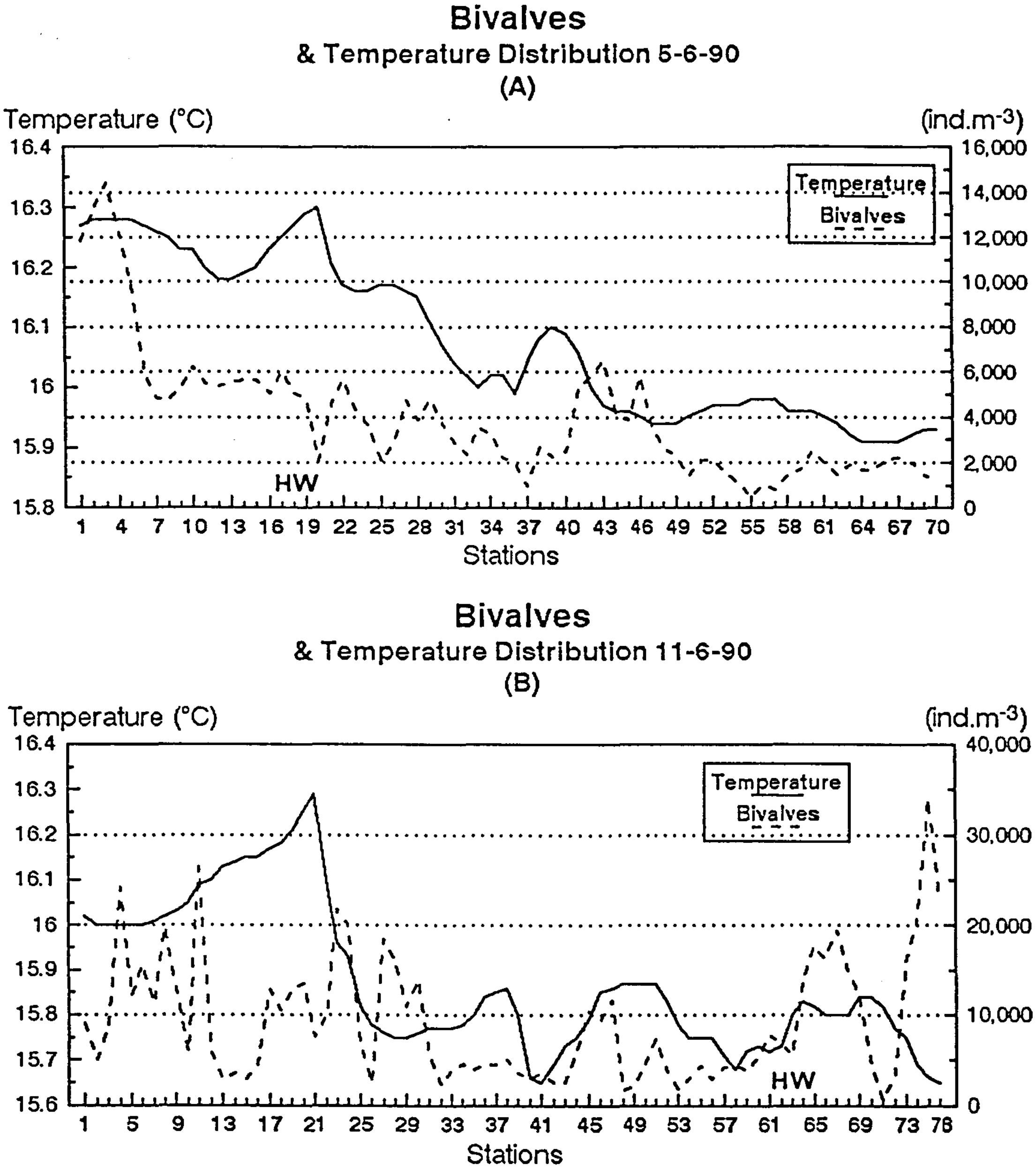


Fig. 32. (A) Distribution of the bivalves larvae and temperature for the 5 June. (B) Distribution of the bivalves larvae and temperature for the 11 June. H.W. indicates the time of occurence of high water.

Ophiuroids assoiciated with a fluorometry of 18 Chl-a $\mu g.l^{-1}$ (station 22), at the Westerschelde, and at station 60 along the Dutch coast with a lower fluorometry value of 7.9 Chl-a $\mu g.l^{-1}$. For the 11 June (Fig. 31 B), the highest densities were found at station 28 along the flood-tide channel of the Westerschelde in the proximity of Vlissingen, at a fluorometry value of 19.9 Chl-a $\mu g.l^{-1}$, and at station 69 at the Oosterschelde at a lower fluorometry value of 7.9 Chl-a $\mu g.l^{-1}$.

The spatial distribution of the Ophiuroids larvae suggest the existence of two distinct input points respectively at the two branches of the Schelde estuary. During the first cruise the effect of the South-West wind enhanced more Ophiuroids larvae to be transported Northward , and to be dispersed over a larger area. During the second cruise the lower wind velocity and the inverse direction limited the larval dispersion to more confined geographical locations.

The bivalves distribution with temperature shows for the first transects (Fig. 32 A) the highest density value of 14,100 $ind.m^{-3}$ was found at station 4 on the northern part of the Belgian coast concomitant with a temperature value of 16.28 °C, and the lowest density value of 510 ind/m3 at station 55 with a temperature reading of 16.03 °C. For the second transect (Fig. 32 B) the highest density value of 34,000 $ind.m^{-3}$ was found at station 74 at the Oosterschelde concomitant with a temperature value of 15.65 °C.

The bivalves distribution with salinity for both transect are presented respectively in Figs. 33 A & 33 B. During the first cruise the larvae were dispersed more uniformly over a large area due to the South-West wind action. For the second cruise it is possible to identify two areas of possible larval input, one located at the mouth of the Westerschelde estuary between station 17 to station 25 concomitant with the low salinity value, and a second input located at the Oosterschelde between station 72 to station 76 at a salinity value of 32.75 (psu). During the second cruise the salinity gradient between the Westerschelde and the Oosterschelde and the bivalves larvae were less uniformly distributed.

The distribution of the bivalves larvae in respect to fluorometry shows for the first cruise (Fig. 34 A) that apart from the first peak that was found at station 4 concomitant with a fluorometry value of 16.4 Chl-a $\mu g.l^{-1}$ the larvae distribution do not follow the one of fluorometry. For the second cruise (Fig. 34 B) the fluorometry distribution shows the nutrient rich waters of the Westerschelde in the flood-tide channel running parallel to the Dutch coast at Vlissingen between station 23 to 28 concomitant with the larval density increase. In the Oosterschelde region the fluorometry value decreases to a value of 13.5 Chl-a $\mu g.l^{-1}$ concomitant with the second larval peak. The bivalves density at the Oosterschelde region was two times higher than during the first cruise. This result was a good indication of

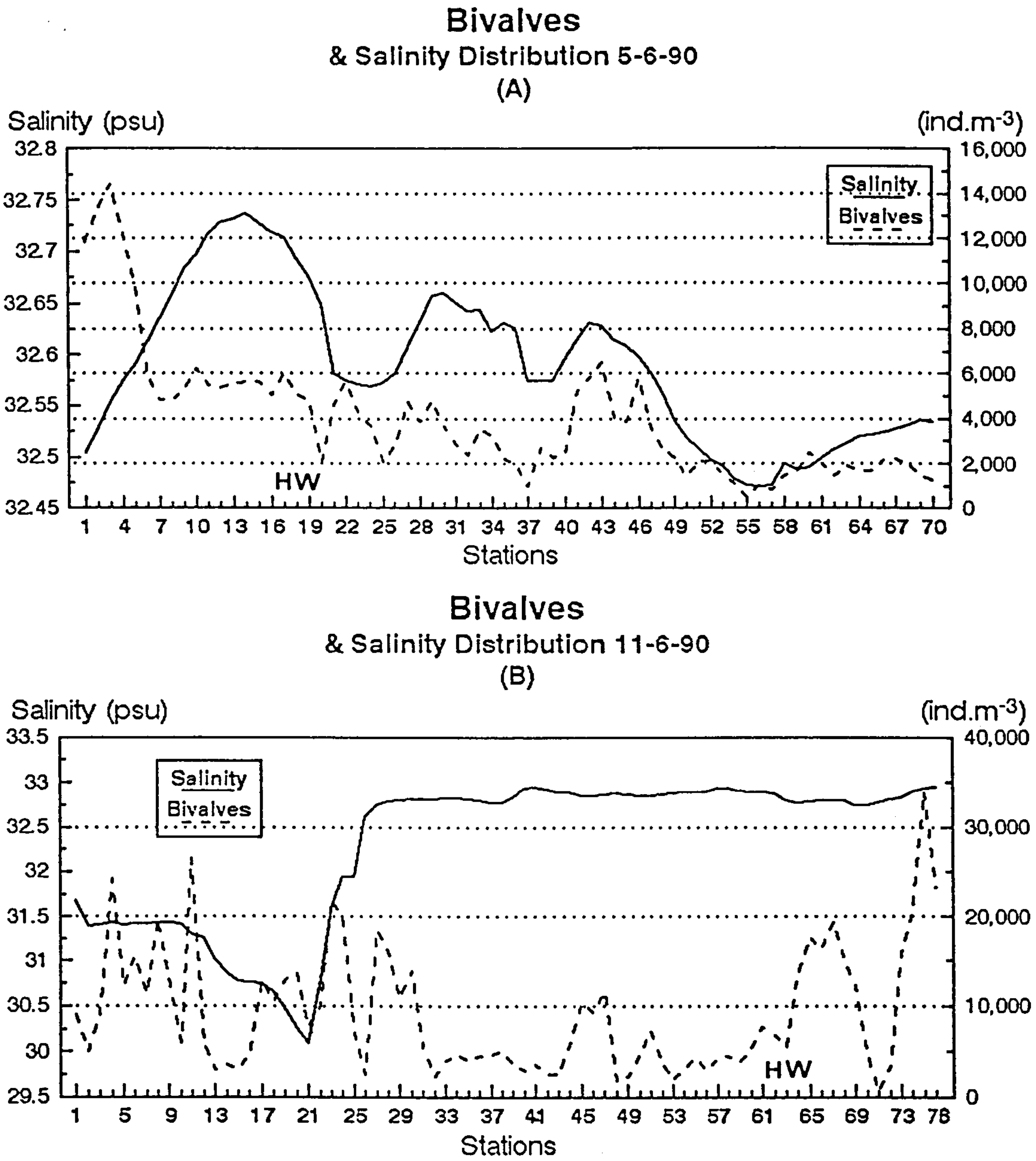
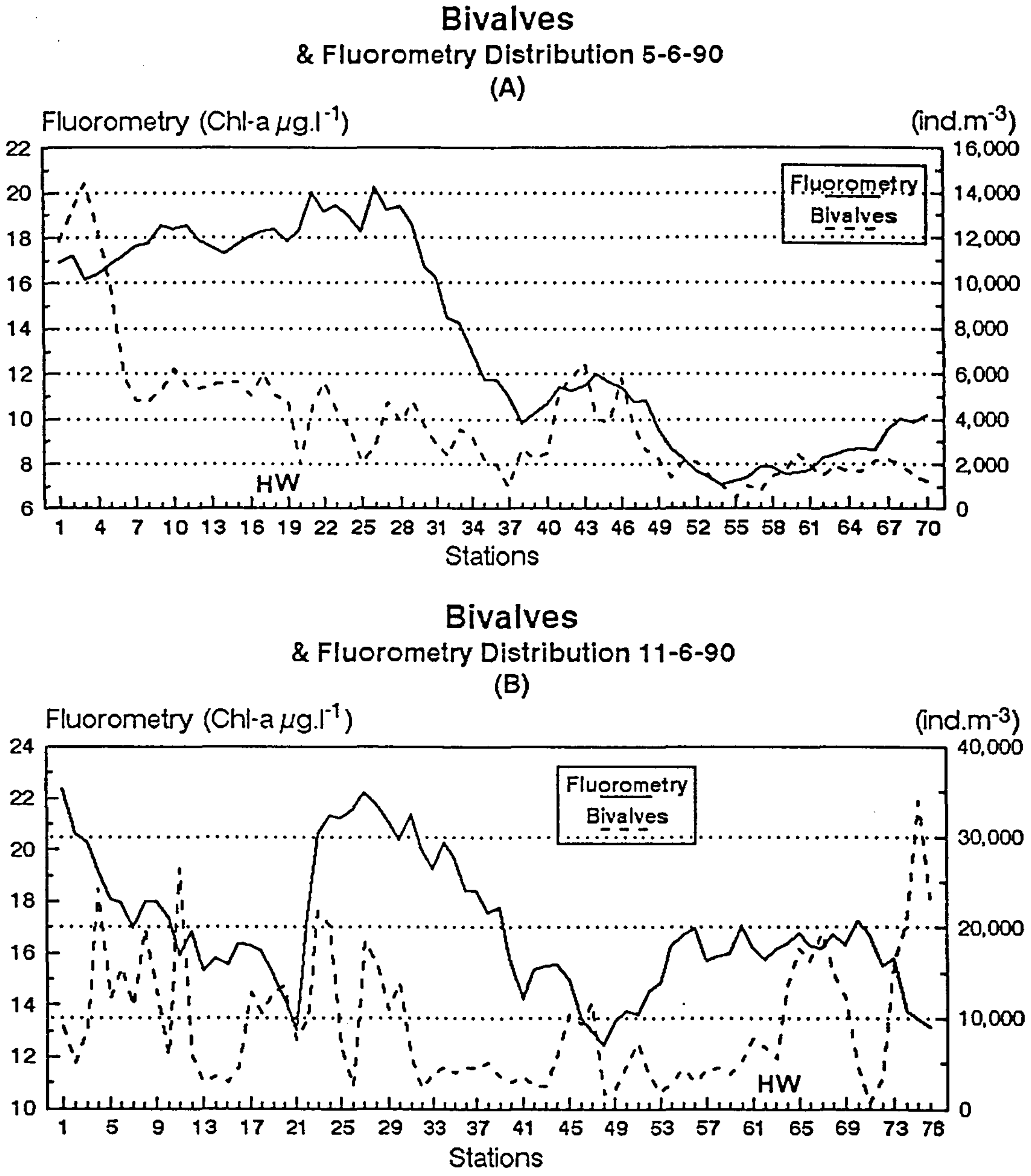


Fig. 33. (A) Bivalves density distribution and salinity for the 5 June. (B) Bivalves density distribution and salinity for the 11 June. H.W. indicates the time of occurence of high water.



Bivalves & Fluorometry Distribution 5-6-90 (A)

Bivalves & Fluorometry Distribution 11-6-90 (B)

Fig. 34. (A) Bivalves density distribution and fluorometry for the 5 June. (B) Bivalves density distribution and fluorometry for the 11 June. H.W. indicates the time of occurence of high water.

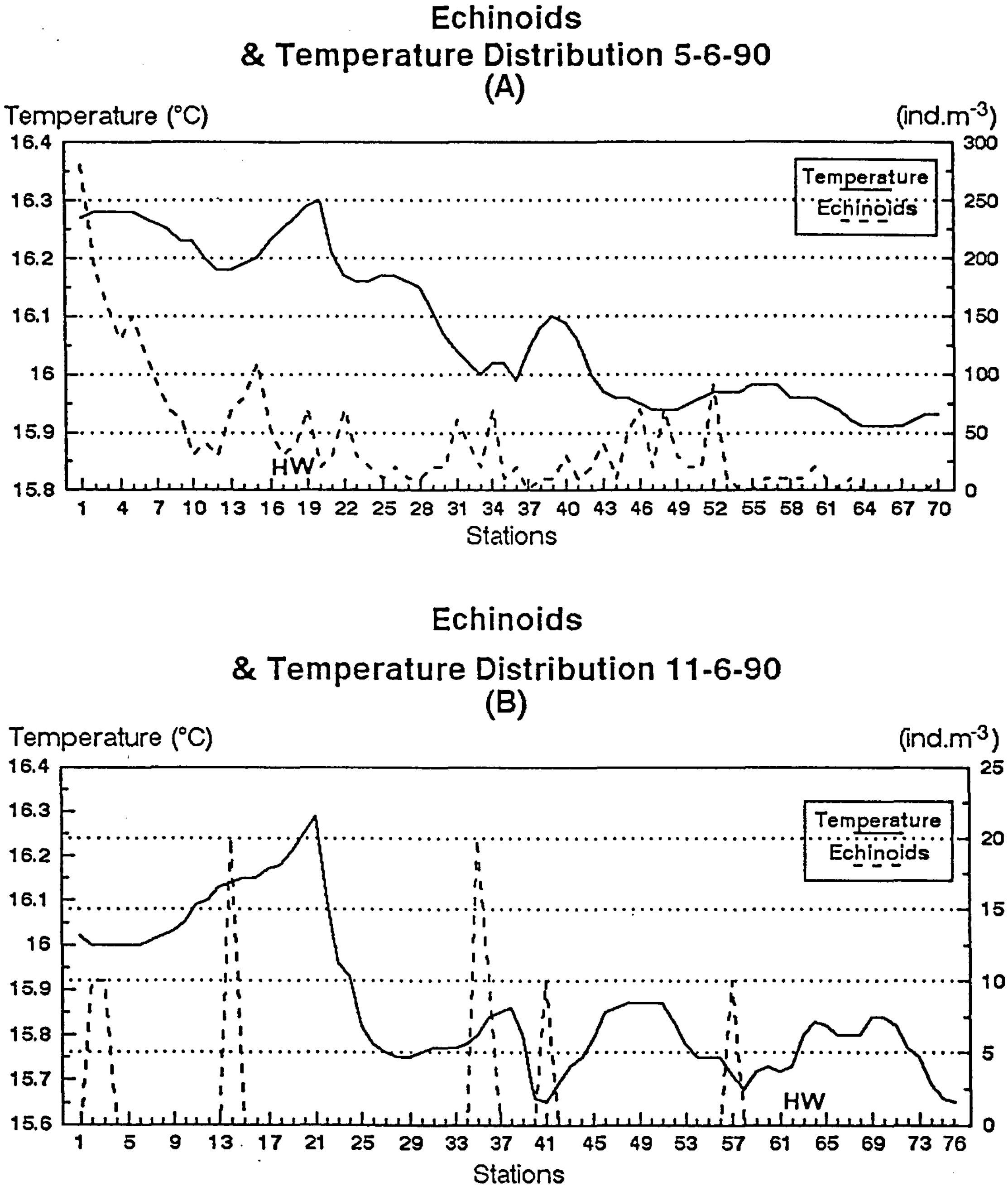
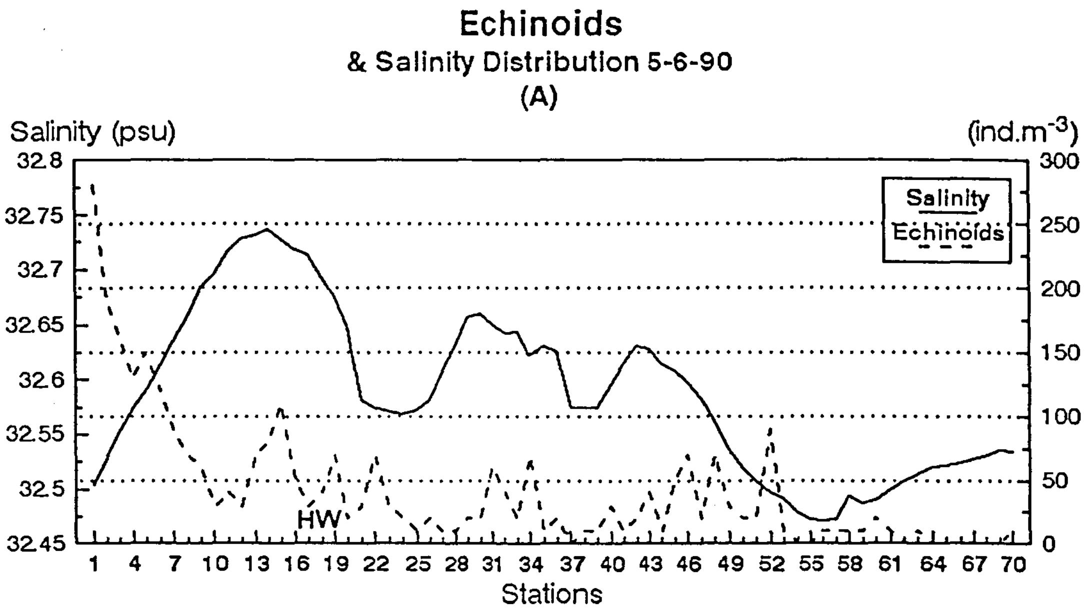


Fig. 35. (A) Echinoids density distribution and temperature for the 5 June. (B) Echinoids density distribution and temperature for the 11 June. H.W. indicates the time of occurence of high water.



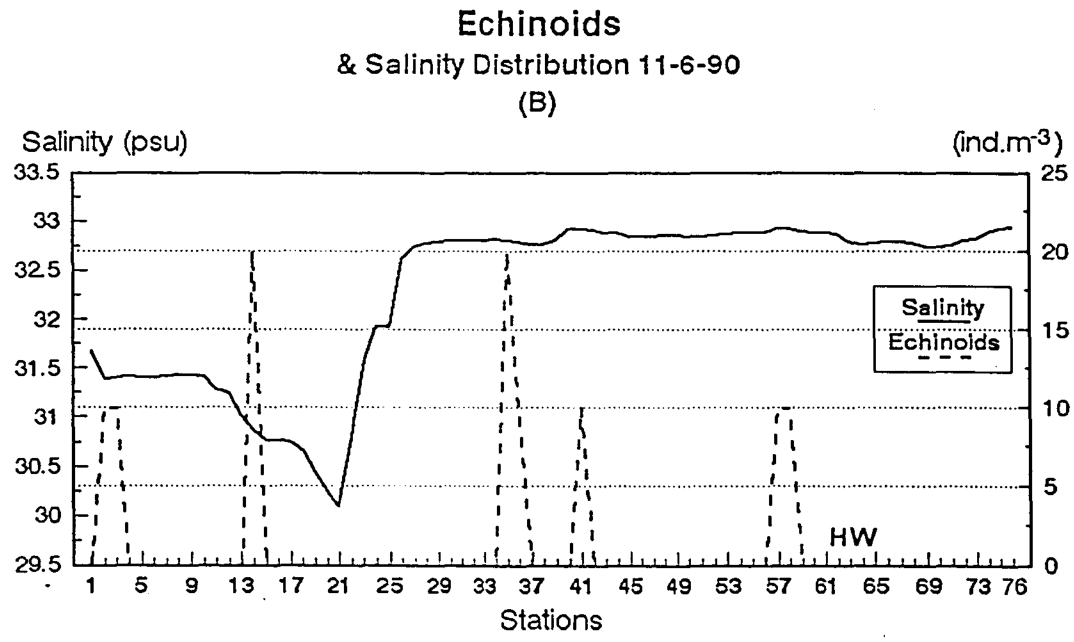
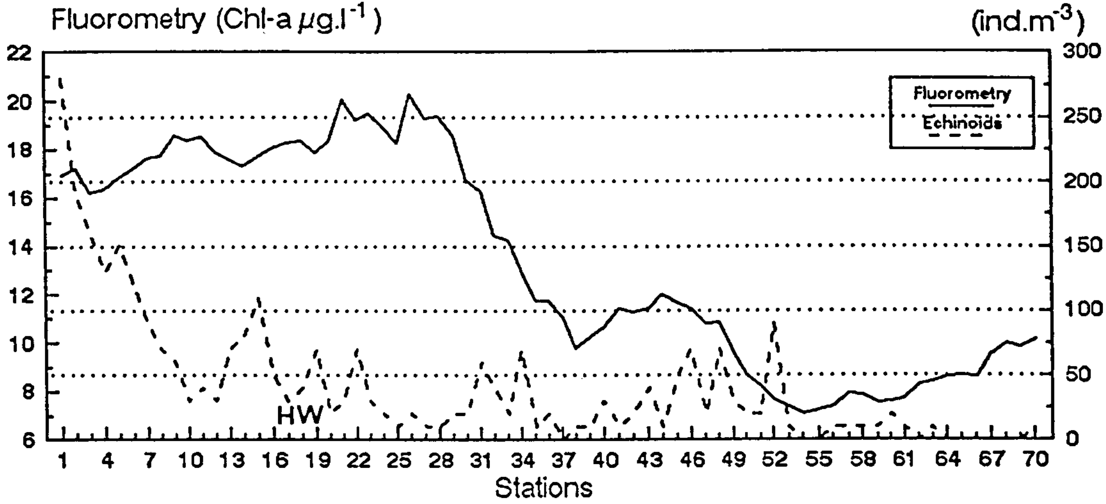


Fig. 36. (A) Echinoids density distribution and salinity for the 5 June. (B) Echinoids density distribution and salinity for the 11 June. H.W. indicates the time of occurence of high water.

Echinoids

& Fluorometry Distribution 5-6-90

(A)



Echinoids

& Fluorometry Distribution 11-6-90

(B)

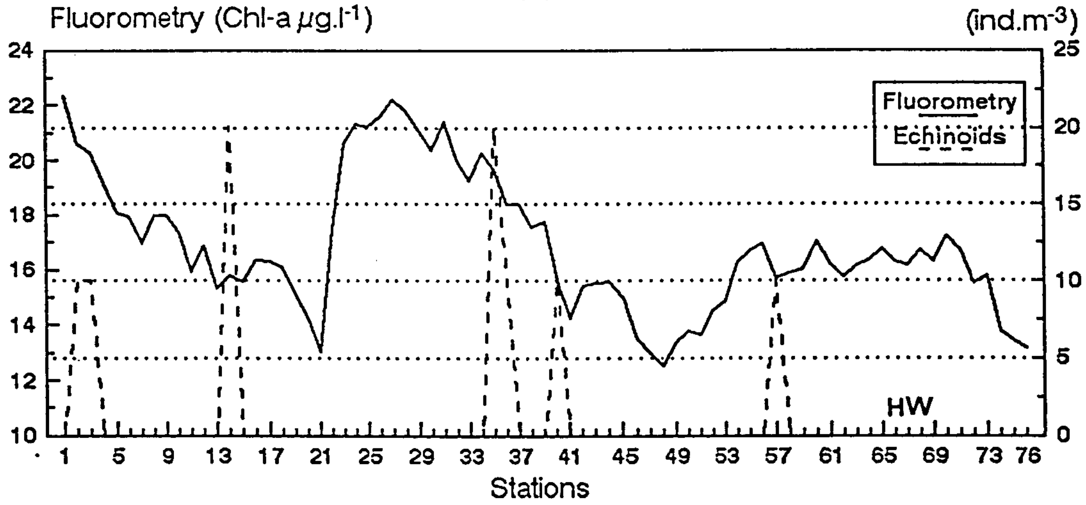


Fig. 37. (A) Echinoids density distribution and fluorometry for the 5 June. (B) Echinoids density distribution and fluorometry for the 11 June. H.W. indicates the time of occurence of high water.

the variability in the period of larval release by the adult population and showed the difficulty in timing the sampling with the presence of the larvae in the water column.

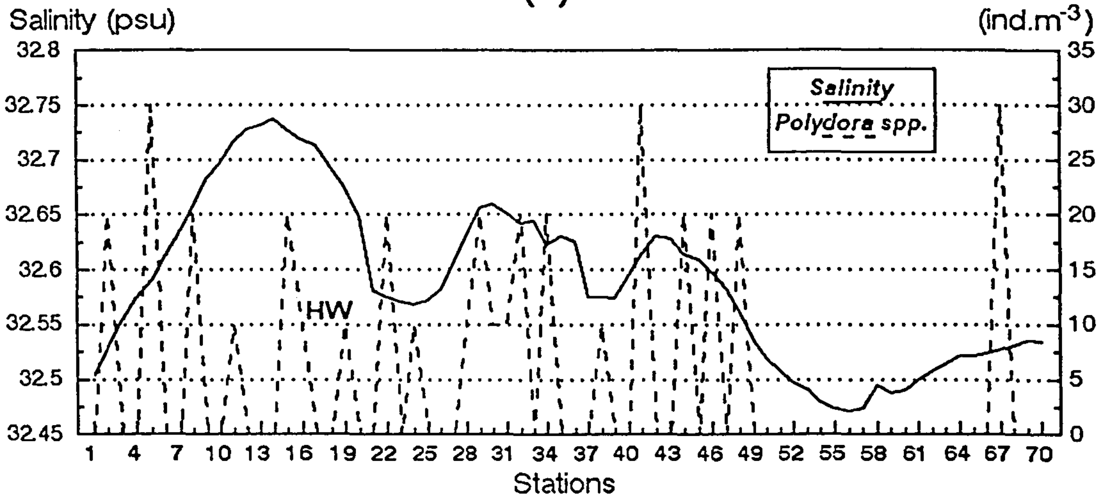
The echinoids distribution is reported concomitant with temperature (Figs. 35 A & 35 B), salinity (Figs. 36 A & 36 B) and fluorometry (Figs. 37 A & 37 B) for both cruise. The echinoids larvae are regarded as biological marker of waters coming from the Calais-Dover strait (Davoult *et al.*, 1988). The presence of the echinoids larvae during the second cruise was very poor in comparison with the first cruise during which the South-West wind might have been the cause of the transport of the echinoids larvae from the French coast to the Belgian-Dutch coast. For the second cruise, with inverse wind conditions (North-East) the echinoids density distribution shows isolated peaks spatially well defined along the transect, as an indication of possible input from local adult population present in the Westerschelde and Oosterschelde region. The results also indicated that there was not any large density larval patch transported from northern locations southward.

The larvae of *Polydora spp.* were present not in very high density and only the distribution during the first cruise is presented in Fig. 38 A togheter with the salinity distribution. The larvae were dispersed over a large area due to the South-West wind action, and only an isolated peak value was present in the Oosterschelde region at station 67.

The larvae of *Nephtys spp.* were also not present in very high density and only their spatial distribution during the second cruise is presented in Fig. 38 B toghether with salinity. This result shows the presence of two clear peaks. The first is limited to the northern part of the Belgian coast and the Westerschelde estuary mouth between station 9 to station 25, and a second one confined to the Oosterschelde area. This distribution pattern can be regarded as an indication that the population of *Nephtys spp.* present in Westerschelde and Oosterschelde estuary were spatially separated.

The PCA results from the correlation matrix among stations based on the $\sqrt{\sqrt{}}$ transformed species density (representing the taxonomic group in Table. 8.) shows in Figs. 39 A & 39 B the scaling of the 70 and 76 observations on the first principal plane (axes 1 and 2) respectively for the first and second cruise on the 5 and 11June 1990. For the 5 June the first axis accounts for 31% of the total variance and the second for 24% (together 55%), for the 11 June the first axis accounts for 36% of the total variance and the second for 17% (together 53%).

Polydora spp.
& Salinity Distribution 5-6-90
(A)



Nephtys spp.
& Salinity Distribution 11-6-90
(B)

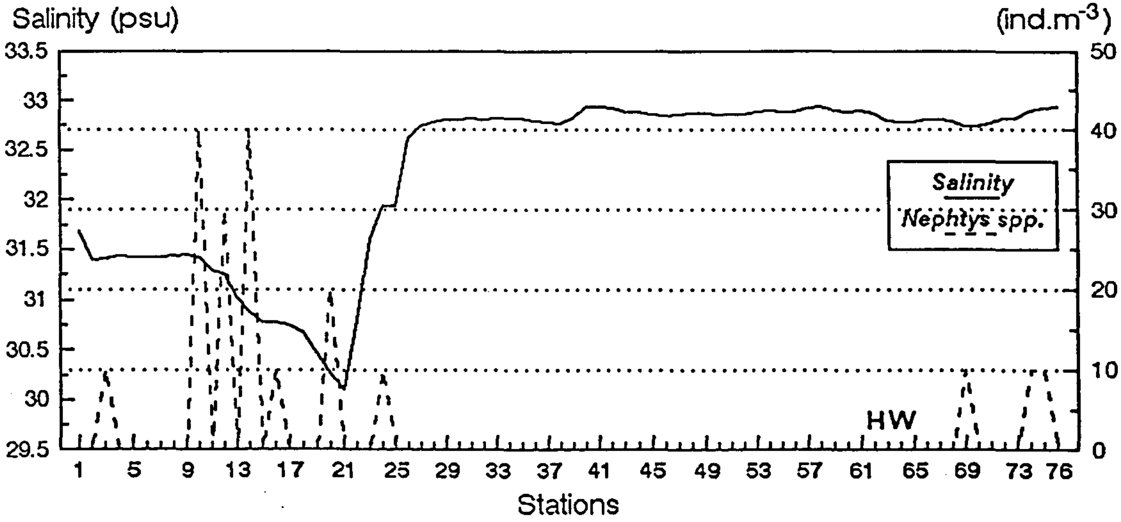


Fig. 38. (A) *Polydora* spp. density distribution with salinity for the 5 June. (B) *Nephtys* spp. density distribution with salinity for the 11 June. H.W. indicates the time of occurence of high water.

The results allowed to identify four major groups of stations: one representing the stations located on the northern part of the Belgian coast in the proximity of the ebb-tide channel of the Westerschelde (NW), one representing the totality of the coastal stations (CS), one representing the off-shore sations (OFF) and a fourth group coded as (OST) representing the Oosterschelde stations. These results showed the presence of a spatial structure in the data sets and suggested the presence of two possible gradients: one in the South-North-East direction between the Westerschelde and the Oosterschelde, and one between the coastal and off-shore stations along the transect. The PCA analyses did not sufficiently describe the discontinuities occuring in the two multispecies time series of biological samples collected along the two transect and thereforethis justified the need to further the analysis of the data-set with the use of chronological clustering.

2.3. 2. *Abiotic and biotic boundaries through Chronological Clustering Analysis*

The chronological clustering results are reported for the species matrix and the environmental matrix. For the 5 June the station-species matrix results in Fig. 40 A show that in terms of species composition the transect was divided into three major groups and the division occured at station 15 in the proximity of the Westerschelde mouth, and at station 57 at the Voordelta-Oosterschelde. The polychaetes were the key taxa characterising the Belgian coast and the Echinoids at the Westerschelde and along the Dutch coast, the Ophiuroids at the Voordelta-Oosterschelde area.

For the station-environmental matrix Fig. 40 B shows that the stations were divided into four groups: the first group from station 1 to 19 including the stations located on the Belgian coast and at Wielingen in the ebb-tide channel of the Westerschelde; the second grouping the Westerschelde stations from station 19 to 28; the third group representing the Dutch coastal stations from Vlissingen to the proximity of the Voordelta-Oosterschlde region; and finally the fourth group representing the stations at the Voordelta-Oosterschelde area. The break points in the data series correspond to the major spatial differences found in the environmental descriptors suggesting that each geographical location can be defined spatially.

For the 11 June the station-species matrix results in Fig. 41 A show that in terms of species composition the transect was divided in two groups and the

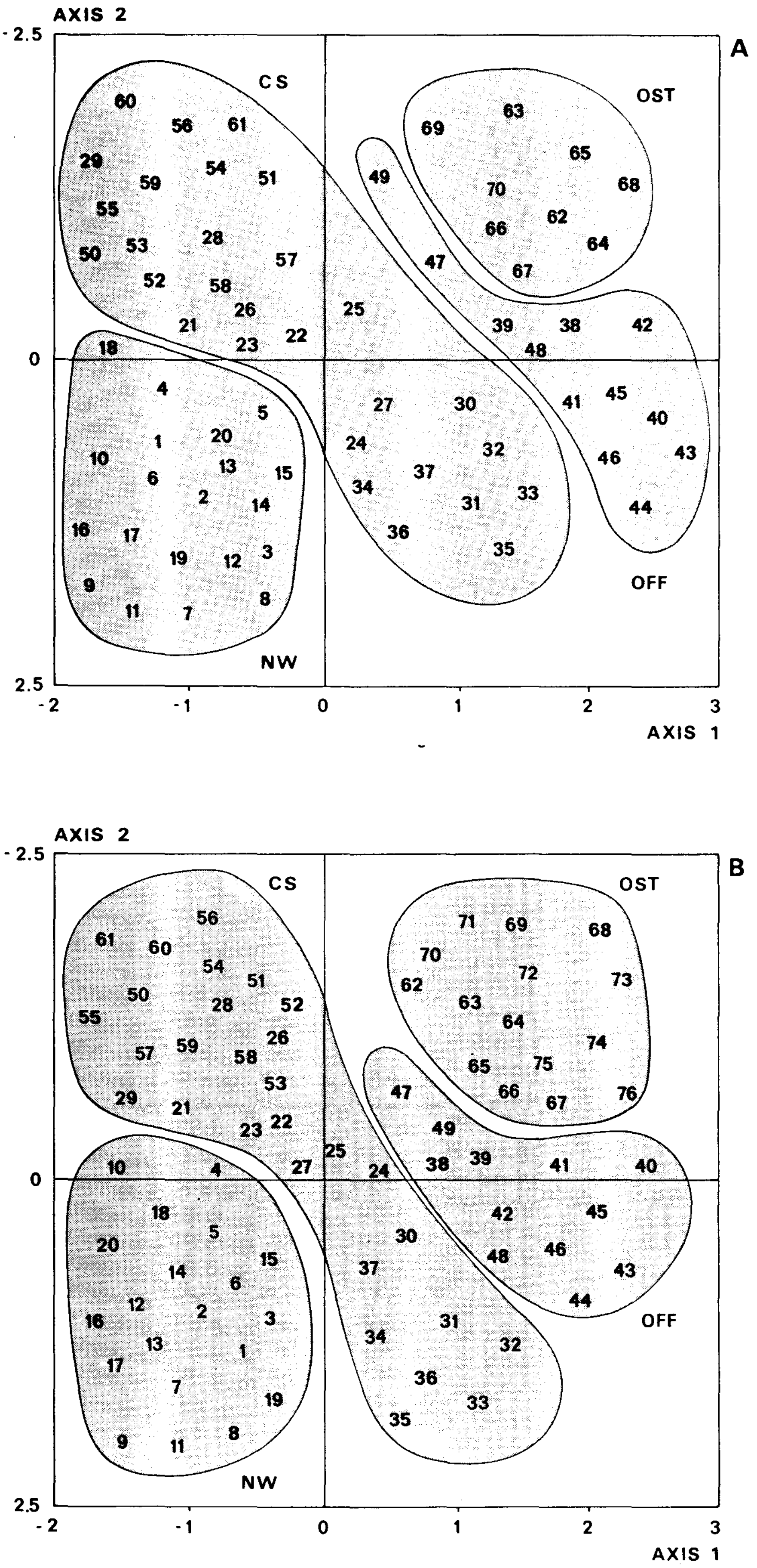


Fig. 39. (A) PCA for the 5/6/90: scaling of the 70 observations, (B) PCA for the 11/6/90: scaling of the 76 observations. Classification results are represented by envelopes. Stations located on the northern Belgian coast & ebb-tide channel of the Westerschelde are indicated by (NW), coastal stations (CS), off-shore stations (OFF) and Oosterschelde stations (OST).

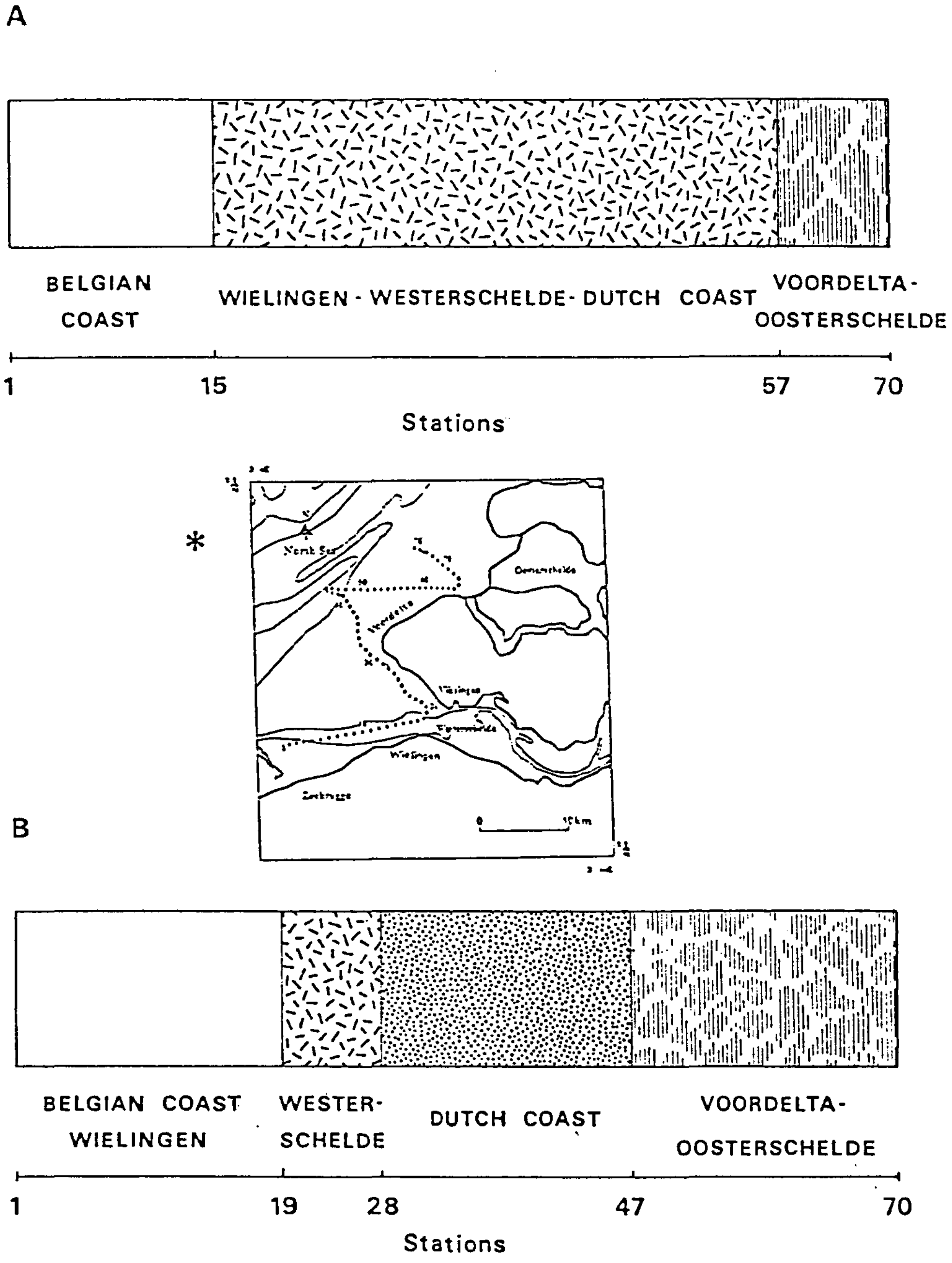


Fig. 40. Schematic representation of the chronological clustering for the 5/6/90. (A) Species matrix chronological clustering. (B) Environmental matrix chronological clustering. Connectedness level Co is 50% and the group expansion test are shown for a significance level $\alpha = 0.20$. (*) Map indicating the location of the stations along the transect.

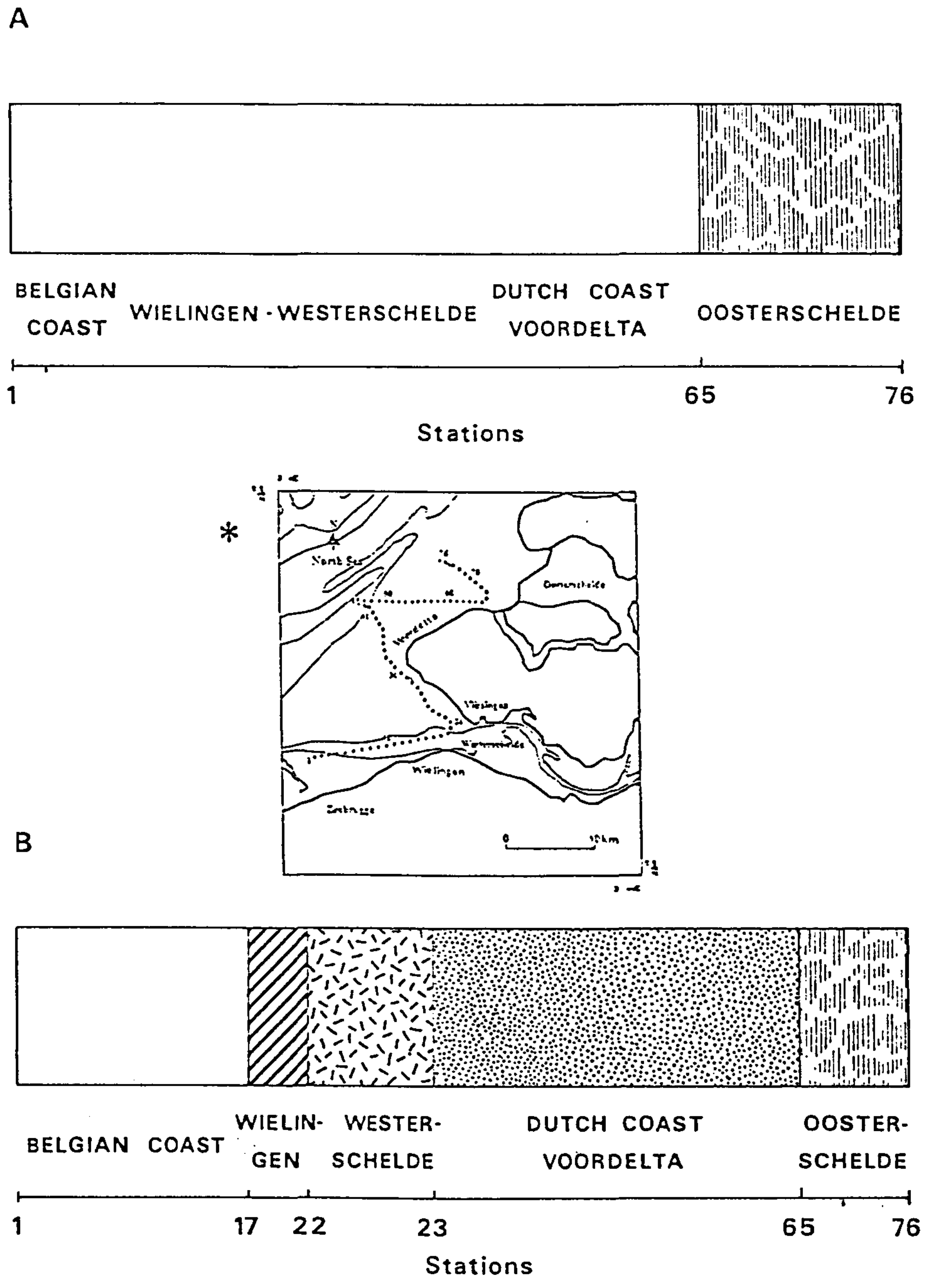


Fig. 41. Schematic representation of the chronological clustering for the 11/6/90. (A) Species matrix chronological clustering. (B) Environmental matrix chronological clustering. Connectedness level Co is 50% and the group expansion test are shown for a a significance level $\alpha = 0.20$. (*) Map indicating the location of the stations along the transect.

division occured at station 65 at the Oosterschelde. The *Nephtys spp.* and the bivalves were the key-species for the first group of station, while the ophiuroid larvae were associated with the stations at the Oosterschelde. During the second cruise less mixing occured due to the faible wind condition and the chronological clustering analysis defined well the meroplankton community belonging to the Oosterschelde.

For the station-environmental matrix Fig. 41 B shows that the stations were also divided into more groups according to the environmental descriptors used in the analysis. The first group of stations are located on the Belgian coast, the second characterised the ebb-tide channel of the Westerschelde at Wielingen, the third group represents the water proper of the Westerschelde, the fourth group is located along the Dutch coast and in the Voordelta region, and the final cluster defines the Oosterschelde station.

The ANOVA on the taxonomic clusters in terms of the environmental variables showed that for both transects the differences in salinity and tide height and fluorometry between the different clusters were significant ($p<0.001$), the differences in density and depth were significant with ($p<0.005$). Temperature was not significant. The ANOVA on the environmental clusters in terms of the meroplankton composition showed for both transects the differences between the different zone were significant for the Ophiuroids ($p<0.001$) and for *Nepthys spp.*, Echinoids and Bivalves ($p<0.005$).

These results show that the transect crossed different geographical areas with well-defined environmental characteristics. Changes in the wind conditions between the first and the second cruise modified the environmental descriptors which in turn modified the grouping of the stations.

2.3.3. Relations with the environment

The results of the Kruskal-Wallis H test (Table 9) show that temperature changes were not significant over the whole area studied.

Density, fluorometry and depth were significant ($p<0.005$) as an indication of the abiotic differences between the Westerschelde and Oosterschelde especially in terms of fluorometry as a possible reflection of larger nutirent input from the Westerschelde. Salinity and the tide height resulted highly significant ($p<0.001$).

The water ciculation in the Westerschelde is dominated by tides, and the tidal currents can reach values of $1 \mathrm{m.sec}^{-1}$ or more. The order of magnitude of the residual currents defined as the mean currents over one or several tidal periods varies typically from 1 $cm.sec^{-1}$ to 3 $cm.sec^{-1}$ at the mouth of the estuary.

Abiotic variables	5 June 90	11 June 90
Salinity	$p<0.001$	$p<0.001$
Temperature	NS	NS
Density	$p<0.005$	$p<0.005$
Fluorometry	$p<0.005$	$p<0.005$
Depth	$p<0.005$	$p<0.005$
Tide height	$p<0.001$	$p<0.001$

Table 9. List of the environmental variables tested for differences between the groups defined by the chronological clustering . The significance level of the Kruskal-Wallis H test are reported for each cruise.

This tidally-induced variability and the biotic conditions in the estuaries are very variable both in time and space and this is likely to be reflected in the species composition changes, at a community level, in the macrobenthos and in the meroplankton distribution. The tide height significance level indicated that the horizontal displacement of meroplanktonic larvae can be fairly large, and in areas of strong tidal currents like the one under study, this displacement could reach several tens of kilometres affecting the spatial distribution of meroplankton over large areas.

2.3.4. Scaling of the observations through non-metric Multidimensional Scaling (MDS)

2.3.4.1. Similarity between geographical locations through the Bray-Curtis dissimilarity measure

The results obtained from the Bray-Curtis dissimilarity measure are presented in the form of dendrograms. For the first transect in Fig. 42 A the Belgian coast and the location at Wielingen in the proximity of the mouth of the Westerschelde resemble each other in terms of species composition. The Westerschelde is separated from this group but the level of similarity with the first cluster still high. As we moved along the transect the Dutch coastal area and the Voordelta-Oosterschelde representing the next two clusters, are both separated from the Westerschelde. This could be an indication that the South-West wind caused more mixing in the surface waters and the geographical locations in term of species composition were not well difined as for the second transect in Fig. 42 B. In this case the Oosterschelde was well separated from the Westerschelde and from the Dutch coast-Voordelta region indicating a clear separation between the two branches of the Schelde estuary. These results showed the importance to relate species distribution with geographical locations and the need to consider space as functional in ecological studies.

The cluster divisions obtained from this analysis at a pelagic level, can be informative for the recruitment of macrobenthos and give more idea about how to relate planktonic larval appearance and availability to the adult macrofaunal community present at each location. The composition of the meroplankton communities in the different areas is changing quite considerably both in time and space. Planktonic organisms are affected by hydrodynamical processes and their distribution is subjected to a great variability. To measure ecologically meaningful changes between tightly coupled planktonic and benthic phases within the same water mass it remains a very complex aspect in benthic studies.

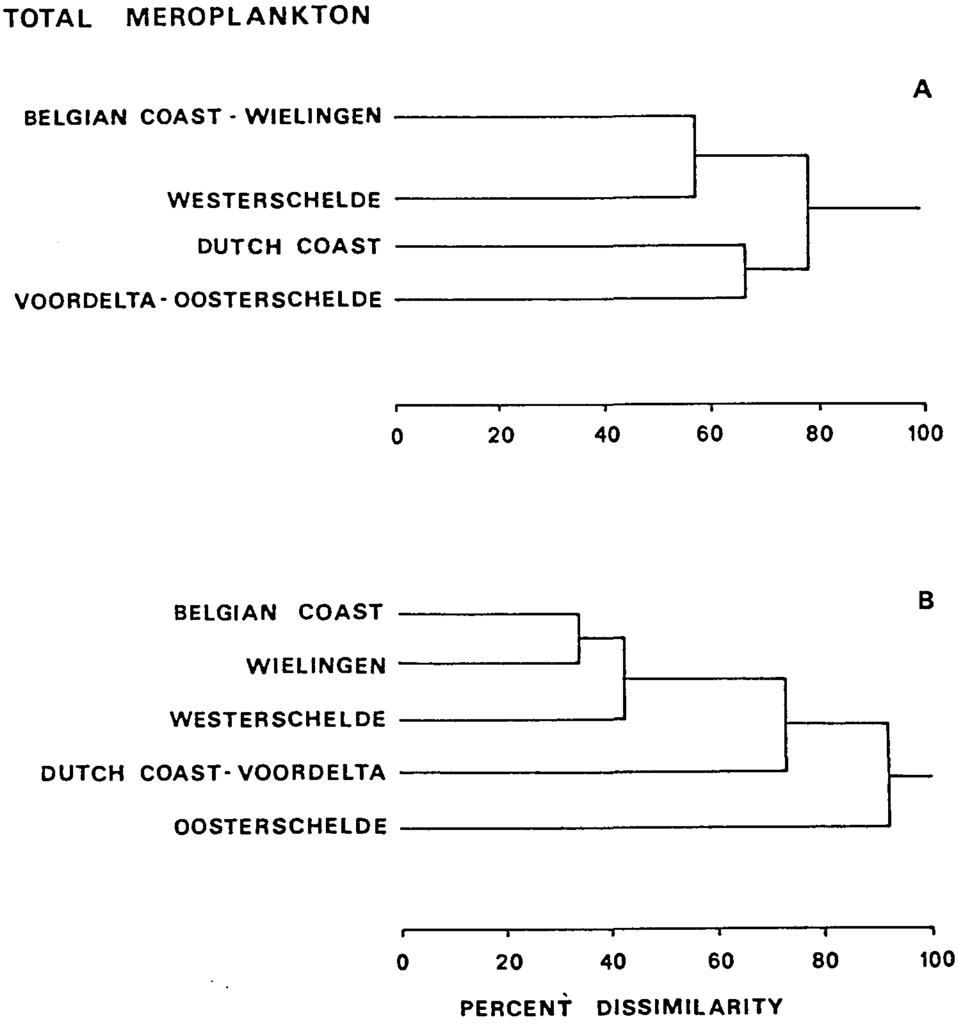


Fig. 42. Dendrogram based on the Bray-Curtis coefficient expressed as a percent of dissimilarity. (A) results for the 5/6/90; (B) results for the 11/6/90.

2.3.4.2. Non-metric Multidimensional Scaling (MDS)

The results from the non-metric multi-dimensional scaling (MDS) show a very similar pattern to the one obtained with the chronological clustering and the Bray-Curtis dissimilarity measure. The final stress values of the MDS are low, between 0.03 and 0.04, indicating a good fit. The results for both transects in Figs. 43 A & 43 B show the succession of the stations along the transect from South to North-East indicating clearly the different geographical locations.

For the first cruise in Fig. 43 A it was possible to identify four clusters representing the Belgian coast and Wielingen (B-W), the Westerchelde stations (WS), the Dutch coast stations (DC), and the Voordelta-Oosterschelde station (V-OST). These results showed the presence of a spatial gradient from South to North indicating the Westerschelde as a possible transition area for meroplankton larvae between the northern Belgian coast and the Dutch coast.

For the second cruise in Fig. 43 B, the analysis allowed to divide the stations into five clusters: one representing the Belgianc coast (B), one the stations at Wielingen (W), one the Westerschelde stations (WS), one the Dutch coast and Voordelta stations (DC-V), and a final cluster grouping togheter the Oosterschelde staions (OST).

This result obtained for the second cruise showed the possible effect of the North-East wind on the surface waters in reversing the drift transport from a South-North-East direction to a North-East-South direction.
For both transects the Oosterschelde region was always well apart from the other geographical locations. This result confirmed the early observation during RENORA 1988 and further pointed out the retention characteristic of this area due to little exchange with the North Sea. These results however did not give any direct indication on the species-environment relationships.

Therefore was important to understand further if the spatial structure present in the species data always comes from a spatial structuring of the environmental variables or if some spatial stucture is actually present in the species data, that is not generated by the spatial structure in the environmental data.

To try to answer these question a direct gradient analysis using CCA was performed, because it allowed the computation of unconstrained residual axes summarizing the species variation that remains after the effect of the environmental variables has been taken out.

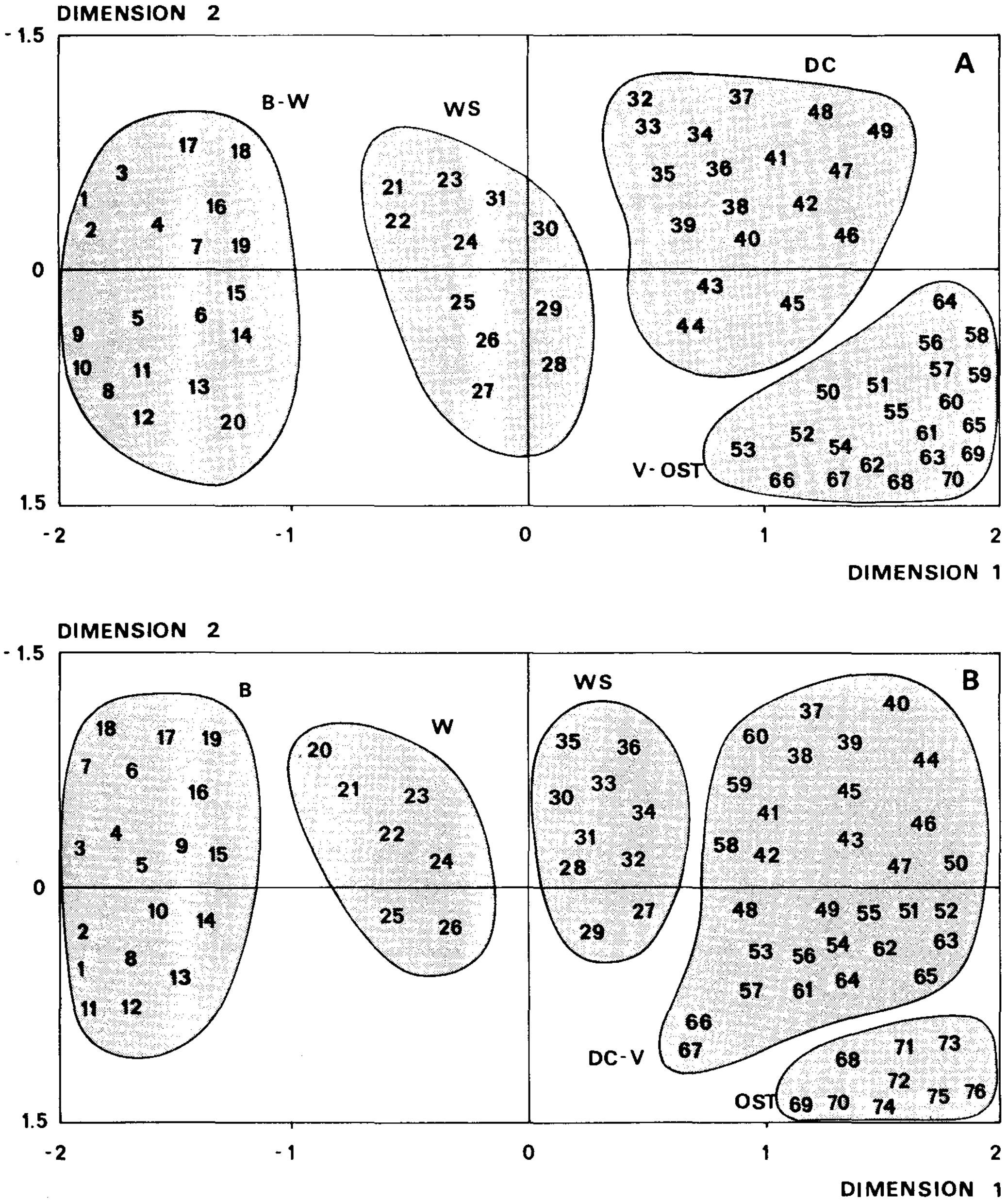


Fig. 43. Non-metric multi-dimensional scaling (MDS) plot in 2 dimensions for meroplankton data. (A) results for the 5/6/90 (B) results for the 11/6/90. Species abundances were √√-transformed and between-sample similarities calculated with the Bray-Curtis coefficient. Stress for the MDS is low, between 0.04 and 0.06. Classification results are represented by envelopes. (B) Belgian coast, (B-W) Belgian coast & Wielingen, (W) Wielingen, (WS) Westerschelde, (DC) Dutch coast, (DC-V) Dutch coast & Voordelta, (V) Voordelta, (V-OST) Voordelta & Oosterschelde and (OST) Oosterschelde, are abbreviations denoting the different groups in the MDS.

2.3.5. Species-environment relationships through Canonical Correspondence Analysis (CCA)

The CCA results are presented respectively for the 5 and 11 June 1990 in Figs. 44 A & 44 B. Here only the first two canonical axes (axes 1 and 2) are represented and commented upon.

The results shows the presence of the salinity-density gradient opposite to the tide, and a fluorometry-temperature gradient opposite to depth. For the first transect on the 5 June the first axis accounted for 39% of the total variance and the second axis for 19% (together 58%). For the second cruise of the 11 June the first axis accounted for 41% of the total variance and the second axis for 22% (together 63%).

For both transects the polychaetes *Lanice conchilega* (LAN), *Pectinaria koreni* (PECT), *Magelona mirabilis* (MAG), *Ampharetidae* (AMPH) and the echinoids larvae are associated with the salinity-density gradient. The bivalves larvae (BIV), and the polychaetes *Polydora spp.* (POLY) and *Nephtys spp.* (NEPH) are associated with the tide. The ophiuroids larvae (OPHI) were correlated with the fluorometry-temperature gradient opposite to depth indicating waters coming from the Westerschelde estuary.

The first axis can be interpreted as an indicator of the general trend in the meroplankton succession indicated by the direction of the arrows. Axis 2 differentiates species whose distribution is influenced or favour by the presence of nutrient-rich waters.

The largest axis, explaining most of the variance, represents the salinity gradient, which is strongly positively correlated with density. Almost perpendicular to the salinity gradient, and correlated factors, the temperature and fluorometry gradient indicates the lack of correlation between these two gradients. In fact the salinity-density gradient reflects more the spatial structure in the environment, while temperature and fluorometry gradient reflect more a temporal variation. Less important in explaining the meroplankton community structure was depth, and this result was found also for the RENORA 1989 campaigns.

In ecological terms the Westerschelde area can be considered as a transition zone between the northern part of the Belgian coast and the Voordelta-Oosterschelde region along the Dutch coast in the north-east direction, and between the Belgian coast and the French coast in a southward direction. The 'ecological-environmental' boundaries found can shift according to

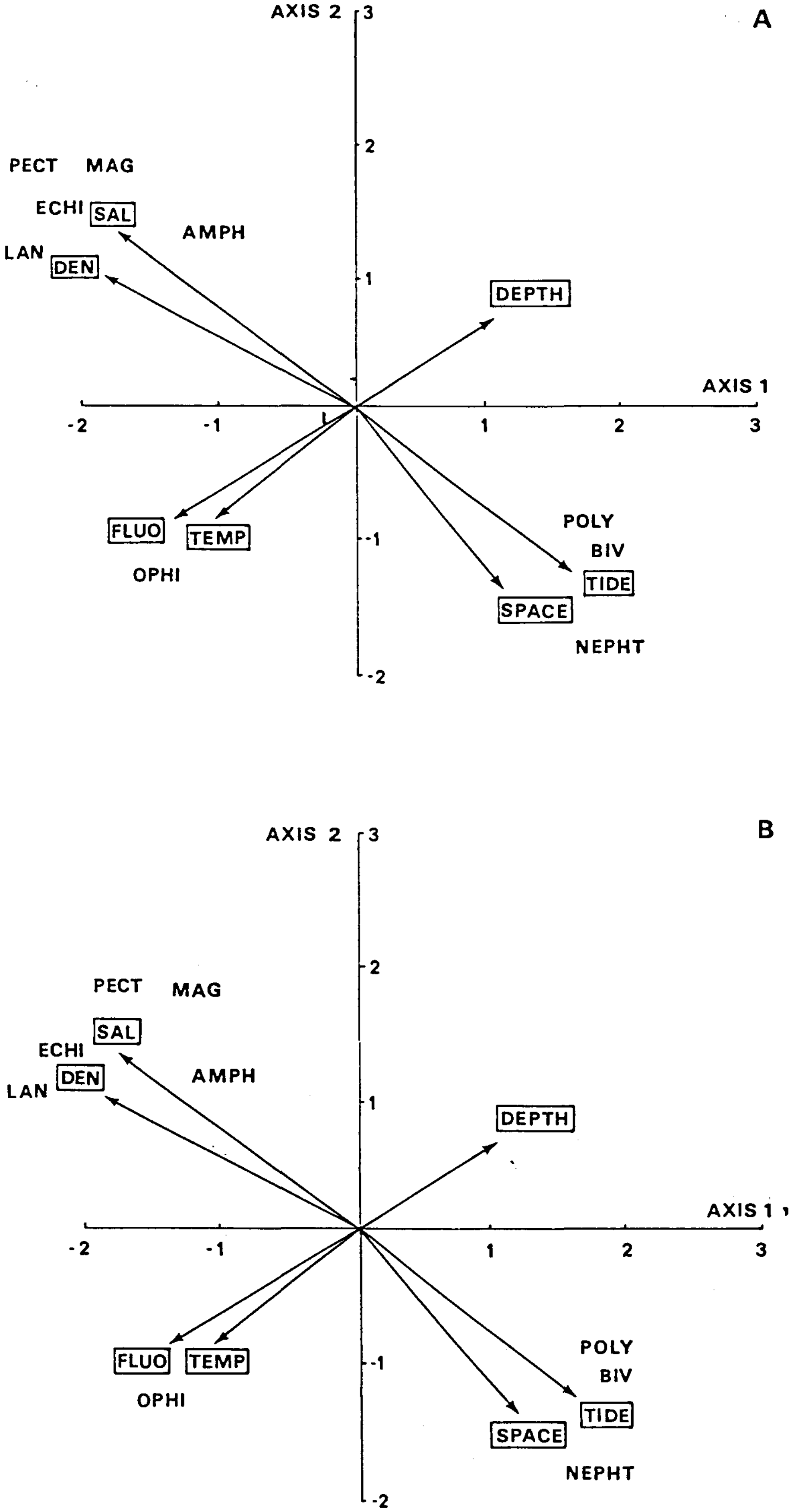


Fig. 44. Biplot based on canonical correspondence analysis (CCA) of meroplankton with respect to 6 environmental variable and space. (A) results for the 5/6/90 (B) results for the 11/6/90. The first two axes in the CCA ordination are presented. The salinity-density gradient (mainly spatial) explained most of the variance.

meteorological forcing thus playing a major role in structuring the macrobenthos.

The CCA results showed that the meroplankton spatial variation can be partly explained by the set of environmental variable but still remains difficult to quantify the percentage of the variation due to the environment alone.

2.3.6. Partitioning the species variation through Partial Canonical Correspondence Analysis (partial CCA)

The partial constrained CCA analyses for each cruise are presented in Table. 10. The percentage of the total variation of the species matrix was divided into four fractions. For the first cruise of the 5 June (Fig. 45 A) the whole variation of the species matrix explained by fractions (a), (b) and (c) was 66.3% and the overall variation including the unexplained fraction (d) was divided as follows:

- fraction (a) 9.5% the nonspatial environmental variation
- fraction (b) 43.1% the spatially structured environmental variation
- fraction (c) 13.7% the spatial species variation not shared by the environmental variables
- fraction (d) 33.7% the expression of the unexplained variation.

For the second cruise of the 21 June the whole variation of the species matrix was 69.5% and was explained by the same four fractions:

- fraction (a) 10.5%
- fraction (b) 50.3%
- fraction (c) 8.7%
- fraction (d) 30.5%

The Monte Carlo permutation test on the trace statistics for both set of analyses were significant at a Bonferroni-corrected level of 0.05/4 = 0.0125.

Data	SE	SS	SE/S	SS/E	Total inertia
5-6-90	0.149	0.161	0.027	0.039	0.283
11-6-80	0.621	0.602	0.105	0.089	1.02

PERCENTAGE OF VARIATION

CCA **5-6-90**	**CCA** **11-6-90**
Step (1) : 0.149 . 100/0.283 = 52.6%	Step (1) : 0.621 . 100/1.02 = 60.8%
Step (2) : 0.161 . 100/0.283 = 56.8%	Step (2) : 0.602 . 100/1.02 = 59%
Step (3) : 0.027 . 100/0.283 = 9.5%	Step (3) : 0.105 . 100/1.02 = 10.5%
Step (4) : 0.039 . 100/0.283 = 13.7%	Step (4) : 0.089 . 100/1.02 = 8.7%
Total explained variation = 66.3%	Total explained variation = 69.5%

Table. 10. The results of the constrained CCA analyses are reported as the amount of canonical inertia explained by the SE (species-environment matrices), SS (species-space matrices), SE/S (species-environment matrices constrained by the space matrix), SS/E (species-space matrices constrained by the environment matrix). Total inertia indicates the sum of all unconstrained eigenvalues. The overall amount of explained variation as a percentage of the total variation of the species-matrix expressed by fractions (a,b,c) for the 5-6-90 was 66.3% obtained by summing step (1) and step (4), or step (2) and step (3), and partitioned as : (a) nonspatial environmental variation (step 3) : 9.5%; (b) spatially structured environmental variation (step 1 - step 3, or step 2 - step 4) : 43.1%; (c) spatial species variation that is not shared by the environmental variables (step 4) : 13.7%; (d) unexplained variation and stochastic fluctuations : 100 - 66.3 = 33.7%. For the 11-6-90 the total explained variation was 69.5% and partitioned as : (a) 10.5%, (b) 50.3%, (c) 8.7%, (d) 30.5%.

(c) - The effect of the South-West wind during the first cruise enhanced more mixing with the nutrient-rich waters coming from the Westerschelde. Fraction (c) representing the purely spatial variation showed the importance of space as an explanatory variable.

(d) - The unexplained variation, fraction (d), would have been larger if the spatial structure was not included in the model. The use of more environmental variables is not necessarily a solution to explain this fraction of the variability. The unexplained variation can represent partly the large amount of stochastic variation, or unmeasured factors and biotic processes such as behavioural responses whose spatial structure is still difficult to model (Birks, 1994).

(b) - For the second cruise fraction (b) was higher, suggesting that under fable wind condition the spatial structure inbedded in the environment could explain even further the species variation.

(a) - The occurence of macrobenthic larvae in the coastal location crossed by the transect is again like for the 1989 transects correlated to a large extent with the spatial gradient present in the environmental variables, and changes in the spatial structure of the environmental variables do influence the meroplankton community structure.

In order to quantify the different fractions that explain the species variation and allows to understand better the variation between the spatial and environmental component and also to derive a general framework for the causal modelling of the various fractions partitioned (Figs. 45 A & 45 B). (Borcard & Legendre, 1994). The different fractions exctracted from the constrained CCA analysis can be used to list the various cause-to-effect relations that can be contained in each fractions from (a) to (d) as pointed out by (Borcard & Legendre, 1994).

2.3.7. Causal modelling and spatial autocorrelation through Path analysis Mantel and partial Mantel tests

The Mantel test among the three matrices considered (1: geographic distance matrix; 2: environmental variables matrix; 3: species matrix) for the two sampling dates gave the following correlations :

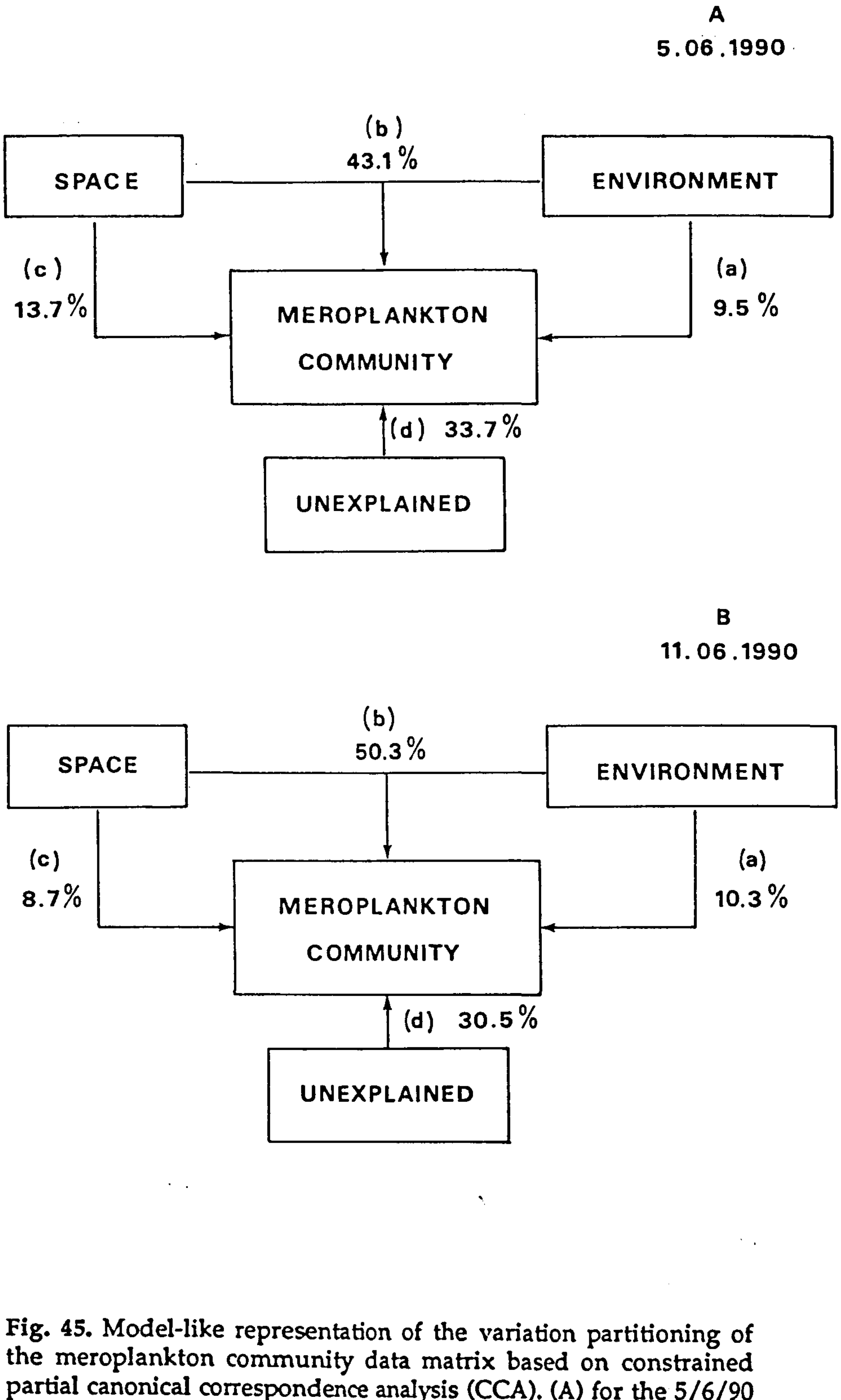


Fig. 45. Model-like representation of the variation partitioning of the meroplankton community data matrix based on constrained partial canonical correspondence analysis (CCA). (A) for the 5/6/90 (B) for the 11/6/90.

(5-6-90)

$R_{1,2}$ = 0.398 ($p<0.001$)
$R_{1,3}$ = 0.158 ($p<0.001$)
$R_{2,3}$ = 0.412 ($p<0.001$)

(11-6-90)

$R_{1,2}$ = 0.425 ($p<0.001$)
$R_{1,3}$ = 0.181($p<0.001$)
$R_{2,3}$ = 0.449 ($p<0.001$)

For both sets of calculations the null hypothesis (H_0) that the multivariate data are not autocorrelated as a gradient was rejected at the 1% significance level according to the test of significance of the Mantel statistics (Mantel 1967).

The partial Mantel tests for the two campaigns gave the following correlations :

(5-6-90)

$R_{1,2}$ = 0.370 ($p = 0.00001$)*
$R_{1,3}$ = -0.007($p = 0.65692$) N. S.
$R_{2,3}$ = 0.385 ($p = 0.00000$)*

(11-6-90)

$R_{1,2}$ =0.391($p = 0.00000$)*
$R_{1,3}$ = -0.012($p = 0.87456$) N. S.
$R_{2,3}$ = 0.417 ($p = 0.00001$)*

The partial Mantel tests for the two transects shows that the computed partial correlation between the geography (space) matrix and the species (meroplankton) matrix were ($R_{1,3}$) non-significant.

The correlation between geography (space) matrix and the environment ($R_{1,2}$); and between the environment and the species (meroplankton, $R_{2,3}$) were highly significant (*) at a Bonferroni-corrected probability level of 0.05/4 = 0.0125.

This result shows that the structure in the meroplankton distribution comes from the structuring of the environmental variable.

The Mantel statistics describing the influence of the environment on the meroplankton community structure for the 5 June, is reduced from 0.412 to 0.385 when controlling for the effect of space.

The specific influence of the environment is therefore 0.385 while the difference 0.163 (0.398 · 0.412 = 0.163), can be regarded as the influence of the spatial structure inbedded in the environment on the species distribution.

For the 11 June the Mantel statistics describing the influence of the environment on the meroplankton was reduced from 0.449 to 0.417 when controlling for the effect of space. The influence of the environment is 0.417, and the difference 0.190 (0.425 · 0.449 = 0.190), corresponds to the influence on the species distribution exerted by the spatial structure present in the environment. The simple Mantel test statistic values where used to compute a path analysis for each case. The results of the path analyses are reported in Table 11.

5 June 1990	**Environment**	**Taxonomic groups**
Geography	0.398* $p < 0.0001$	–0.007 $p = 0.6569$ N. S.
Environment	-----	0.414* $p < 0.0001$
11 June 1990	**Environment**	**Taxonomic groups**
Geography	0.425* $p < 0.0001$	–0.011 $p = 0.8746$ N.S.
Environment	-----	0.454* $p < 0.0001$

Table 11. Transect 2, campaigns of 1990. Path coefficients (i.e., standard partial regression coefficients), computed from simple Mantel correlations, represent direct causal covariance. Significance is assessed using partial Mantel tests: (*) significant, (N. S.) non significant at the Bonferroni-corrected probability level of 0.05/3 = 0.01667

The paths between *Geography* and *Environment* are about 0.3 to 0.4 and all very significant. The paths between *Geography* and *Species* are near 0 for both transects (actually -0.007 and -0.011). The paths analysis between *Environment* and *Species* are between 0.4 to 0.5 and all very highly significant.

This means that the spatial structure in the species data always comes from a spatial structuring of the environmental variables. The Mantel tests and the partial Mantel tests are in accordance with the results of the CCA analyses.

The spatial gradient present in the environment can explain quite considerably the variation we observed in the distribution patterns of meroplankton in this coastal locations influenced by the presence on the two branches of the Schelde estuary. Following the causal modelling framework proposed by Legendre & Troussellier (1988) some causal link for the observed structures in the meroplankton distribution were hypothesized in a form of an explanatory model. The only causal model compatible with these observation are reported in Table 12.

Model	**Predictions of the model if the model is true**	**Computed results (all 2 transects)**
Space	$R_{1,2}$ signif. $\neq 0$	yes
⇓	$R_{2,3}$ signif. $\neq 0$	yes
	$\lvert R_{1,2} \rvert \geq \lvert R_{1,3} \rvert$	yes
Environment	$\lvert R_{2,3} \rvert \geq \lvert R_{1,3} \rvert$	yes
⇓	$R_{1,2} \cdot 3$ signif. $\neq 0$	yes
	$R_{2,3} \cdot 1$ signif. $\neq 0$	yes
Meroplankton	$R_{1,3} \cdot 2$ not signif.	yes
	$\lvert R_{1,2} \cdot 3 \rvert \leq \lvert R_{1,2} \rvert$	yes
	$\lvert R_{2,3} \cdot 1 \rvert \leq \lvert R_{2,3} \rvert$	yes
	$R_{1,2} \times R_{2,3} \approx R_{1,3}$	yes

Table 12. Predictions of the model of causal relationship supported by the results in Tables 1 and 2. Matrix 1 = "Geography", matrix 2 = "Environment", matrix 3 = "Meroplankton". $R_{1,2}$ is the Mantel correlation between matrices 1 and 2, etc. ; $\lvert R_{1,2} \rvert$ is the absolute value of a correlation coefficient. '$R_{1,2}$ signif. $\neq 0$' means that the correlation is significantly different from zero; '$R_{1,3} \cdot 2$ not signif.' means that the correlation is not significantly different from zero at the pre-selectected significance level.

The proposed model shows that for both sampling dates with the community composition changes because of changes in the ecological descriptors with reference to the environmental control model (ECM).

This information is based on causal analysis which makes prediction involving the values of the simple correlations (Mantel test) and of partial correlation (Partial Mantel test).

The results of actual computations indicate which predictions are realized. If we consider that the data represent samples taken from a stretch of geographic space, as always in ecological studies, the analysis of the spatial structure itself can be regarded as a good way to test for the validity of the correlations, since it can be the cause of false relation due to the autocorrelated nature of most environmental variables.

The results obtained from the simple and partial Mantel statistics and the path analysis reinforced the validity of the departure hypothesis predicting that the structure present in the species data was generated by the shift in the structure of the environmental variables and not by spurious correlations induced by a common spatial or temporal structure.

The partial Mantel tests appeared to be quite powerful in bringing out dependence patterns between linked biological communities and their environment. These results offered a much clearer picture of complex interactions among the meroplankton and the environment than previous studies. The environmental variables that seem to have affected more directly the meroplankton structure were descriptors of the physical and chemical properties of the sea, therefore this stressed further the importance to link physical-biological processes.

2.3.8. Discussion and Conclusion

The first objective of RENORA 1990 was to understand the mechanisms regulating meroplankton dispersal in relation to ecohydrodynamical and recruitment processes in the coastal area in front of the two branches of the Schelde estuary, which can be regarded as a transition zone between the French coast in the Southern Bigth of the North Sea, and the Dutch coast and German Bight in the North Sea.

The second objective was to further validate the member/vagrant hypothesis (Sinclair, 1988) in determining population variability and life-cycle continuity, by considering the changes in the physical environment as an important regional and geographical features acting on species life-cycle closure and on biodiversity.

The spatial distribution of the abiotic variables suggested that the contact between the water masses coming from the Westerschelde and the off-shore waters resulted in establishing a strong salinity gradient in the South-West - North-East direction and vice versa according to the wind direction and other meteorological events. The fluorometry measurements confirmed further the hypothesis that nutrient-rich water masses coming from the Westerschelde can influence, under favourable North-East wind condition, the French coast as far as Calais.

This showed the importance of the spatial structure of the environment descriptors, and indicated that the spatially distinct peaks in the meroplankton could be defined by these spatial-temporal shifting boudaries within the spatially structured environment.

The major differences in the taxonomic composition and environmental characteristics were found between the Westerschelde and the Oosterschelde. The results of the PCA confirmed that these two geographical locations were well apart and that, although the same species such as the ophiuroids, *Polydora spp.*, and *Nephtys spp.* were found in both areas, the larvae were possibly coming from distinct adult populations. Concerning the echinoids larvae it was clear from the 1989 results that this larvae were transported by advection from the south coastal region of the Southern Bight of the North Sea and reached the northern part of the Belgian coast and the Westerschelde.

The bivalves larvae were found in the water masses converging on the salinity front system at the Westerschelde mouth, and these larvae were passively transported through the frontal system, in agreement with the observation by Mann (1988) on the distribution of bivalves larvae at a frontal system in the James River in Virginia.

Similar results were obtained in a study based on the spatial distribution of zooplankton in the Westerschelde estuary by Soetaert & Van Rijswijk (1993), but the authors did not further their analysis by finding the possible causal relationships underlying the observed ecological processes.

It is however more difficult to estimate the part of the variability induced by global environmental changes against local environmental conditions. The spatio-temporal evolutions of natural ecosystems do not result from a simple addition of different processes but from their interaction (Frontier & Pichod-Viale, 1995).

Ecological boundaries were defined through chronological clustering, Bray-Curtis dissimilarity and the MDS. The polychaetes were the key taxa along the Belgian coast at Wielingen; echinoids characterize the Westerschelde and the Dutch coast; and ophiuroids were distinctive of the Westerschelde-Dutch coast and Voordelta-Oosterschelde area.

These results showed that changes in the wind conditions between the first and the second cruise modified the spatial structure of the environmental descriptors, which in turn modified the grouping of the stations. The Westerschelde area can be defined as a transition zone between the northern part of the Belgian coast and the Voordelta-Oosterschelde region along the Dutch coast in the north-east direction, and between the belgian coast and the French coast in a southward direction.

The meroplankton composition along this gradient can change according to the changes in the spatial structure of the environmental variables. An interchange at a species compositional level can therefore occur between northern-southern locations enhanced by meteorological forcing. Monitoring these changes taking place at a pelagic level can give important information concerning the expected changes in the macrobenthos community, both in terms of species recruitment succes and bionomical changes of the adults.

The direct species-environment relationship expressed by the CCA biplot showed more clearly the species-environmental relationships.

The ophiuroids were associated with fluorometry, suggesting their preference to nutrient-rich waters. Due to a lack of previous study on this subject, it was not possible to formulate any specific ecological hypothesis on this association. One possibility may be the fact that since echinoderms larvae may obtain a greater portion of their nutrition from uptake of DOM (Pedrotti & Fenaux, 1992), the ophiuroid larvae were found concomitant with the fluorometry peaks value at the Westerschelde and Oosterschelde.

The other species were associated to the same environmental variables as for the transect 1989, confirming that the salinity-density gradient opposite to the tide-space explained most of species-environment relationships.

The whole species variation explained through the partial constrained CCA showed for the first cruise on the 5 June 1990 that fraction (c) representing the percentage of the variation in the species matrix due to the 'purely spatial' structure, was slightly higher than in the second cruise a week later on the 11 June 1990. This result suggested that in the coastal locations considered, the effect of strong South-West wind induced changes in the surface waters distribution. Therefore the spatial structure of the geographic locations played an important role as a functional factor in the system, maybe by limiting the off-shore transport of the larvae, thus increasing the maintenance of a larval flux close to the adult sub-tidal macrobenthos community.

During the second cruise on the 11 June the wind direction was inversed from South-West to a North-East, with a decrease of the wind velocity and wind stress on the surface waters. Under these circumstances, the environmetal structure was more evident, showed the presence of the Westerchelde and Oosterschelde clearly defined by the spatial distribution of the abiotic variables.

Fraction (b), representing the percentage of variation in the species matrix due to environment and space, was higher than in the first cruise, suggesting that with less wind forcing on the surface water and less mixing, the spatial changes in the environmental variables explained more the variation observed at the species level.

These results were important informations to be included in the causal modelling approach to test the strenght of the possible causal link between species and environmental variables.

The spatial gradient present in the environmental variables resulted then to be the major force explaining the variation observed in the spatial distribution of the meroplankton. The model indicated that changes in the spatial structure of the environmental variables do influence the meroplankton community structure. This was, as in the 1989 campaigns, in agreement with the environmental control model (ECM).

Ecological conclusion

The discontinuities occurring in two multispecies time series of biological samples collected along the transect in the Belgian-Dutch coastal region were described by chronological clustering. These results showed that the Westerschelde mouth area can be considered as a transition zone between the northern part of the Belgian coast and the French-belgian coast southward, and between the Dutch coastal area northward.

The major differences were found both in terms of environmental descriptors and taxonomic composition between the Westerschelde and the Oosterschelde. Significant differences between clusters were found in terms of salinity, fluorometry ($p<0.001$) and for ophiuroids ($p<0.001$) and echinoids, bivalves, and Nephtys spp.*($p<0.005$).*

The species-environment relationships explained by the CCA analyses indicated that most of the species variability was explained by the salinity-density gradient opposite to the tide-space gradient as an indication that the spatial differences in the salinity distribution do clearly have an effect on the meroplankton distribution. The fluorometry indicated that the ophiuroids larvae were related to chlorophyll-rich water, maybe due to their ability to extract DOM from the water column. This result could be an indication that the time of release of ophiuroids larvae into the water column coincide with high availability of phytoplankton.

The results of causal modelling produced a synthetic model of causal relationships, which confirmed the same observation as for RENORA 1989. The *observed relationships (correlations) between species and environmenta variables were causal and in all four cases (transects 1989 & 1990) the spatia pattern of the species can be fully attributed to the spatial pattern of th environmental variables. These observations were compatible with the followin causal model: Space* $\Rightarrow$ *Environment* $\Rightarrow$ *Meroplankton.*

This model suggested that the pelagic phase of the recruitment o planktotrophic marine invertebrates larvae is regulated to a larger extend b spatially structured physico-chemical environmental processes which allows life-cycle closure and the maintenace of a biological continuum in the coastal are studied. However the ecological-environmental boudaries found can shif according to meteorological forcing thus playing a major role in structuring th macrobenthos.

Chapter III.
General Discussion - Ecological Conclusion

CHAPTER III. GENERAL DISCUSSION and ECOLOGICAL CONCLUSION

Spatial structures in ecology

Spatial variability can be regarded as a fundamental characteristic structuring the community and the environment which the organisms inhabit. As stated by Gould (1970), 'all our efforts to understand spatial pattern, structure, and process have indicated that it is precisely the lack of independence, the interdependence of spatial phenomena that allows us to substitute pattern, and therefore predictability and order, for the chaos and apparent lack of interdependence of things in time and space'.

When considering ecosytems as geographical entities, this concept of spatial structure allows the inclusion of both biotic and abiotic components as interacting descriptors. As argued by Grimm (1995) this spatially based perspective links species interactions in a way that their effects on ecosystem processes can be assessed.

In the analysis of ecological processes it is necessary to use methods that can integrate directly the spatial information of the data, and as argued by Legendre (1990), 'organisms are not distributed evenly or at random in nature, for the good reason that spatial stuctures are functional in ecosystems, and not the result of some random process; a spatially homogeneous ecosystem simply could not function'.

This departure point made it possible to obtain a better spatial description of the ecological processes for the Southern Bight of the North Sea, and to detect different structures in the data, such as environmental gradients. A better knowledge of the spatial organization of ecological processes resulted in a better understanding of the spatial behaviour of the environmental descriptors used in any ecological studies.

The form and scale dependence of spatial autocorrelation was important for identifying and interpreting the mechanisms controlling species pattern formation. Ecological processes involving the spatial structure of interactions between the taxa making up the community were best studied by examining the pattern of multivariate data.

In the case of pelagic-benthic systems, such as the one studied, it appeared that species were strongly linked to specific regional physical-environmental processes during the pelagic phase of their life-cycle and that this linkage was directly related to recruitment processes. An understanding of the different linking levels of ecological organization at the interface between the pelagic phase/benthic phase were particularly important in addressing new questions concerning the dispersal and recruitment of macrobenthos.

The difficulties in quantitatively assessing coupling between different life-history phases of the pelagic-benthic invertebrate transition were still very large (Feller *et al.*, 1992; Kenny *et al.*, 1990; Butman, 1994). In aquatic environments the spatial heterogeneity of the physical environment generates a diversity in communities as well as in the biological and ecological processes that can be observed at various points in space (May, 1984; Legendre & Fortin, 1989).

The contribution of the present study to a better understanding of the meroplankton spatial structure in the Southern Bight of the North Sea

Recalling the departure point of this research: **does the coupling of spatial physical-biological processes affects the dispersal of meroplankton?** The answer to this question for many geographical areas is affirmative (Sinclair, 1988).

The need to pose again this question in the context of this study was justified by the fact that no previous work had been reported on the dispersal of meroplankton in relation to the macrobenthos communities in the Southern Bight of the North Sea, although the interest to study recruitment processes in this location was pointed out by previous studies on the macrobenthos community structure on the French coast by Dewarumez (1979) and Souplet & Dewarumez (1980), and on the Belgian-Dutch coast by Govaere *et al.*, (1980), Vermeulen & Govaere (1983) and more recently by Craeymeersch *et al.*, (1990).

The study area is characterized by the presence of a benthic continuum dominated by the bivalve *Abra alba*, and is subjected to yearly fluctuation (Fromentin & Ibanez, 1994) and taxonomic changes (Luczak et al., 1993) influenced by meteorological events and hydrodynamical processes. The mechanisms regulating the meroplankton dispersal were not clearly understood and for this reason the first phase (1988-1990) of the RENORA project (pelagic study) tried to further understand the major causes responsible for the interchange at a taxonomic level along a South-West-North-East gradient from Gravelines (France) to the Dutch delta region (The Netherlands) and *vice versa*.

The results obtained by Belgrano *et al.*, (1990) demonstrated the existence of a larval flux between sandbanks running parallel to the French coastline following the major circulation patterns. These patterns were inversed by the specific residual tidal currents regimes acting at a local regional scale, allowing larvae coming from the North-Eastern regions to settle in the southern coastal locations as far as Calais.

These earlier results suggested the need to set up more specific sampling campaigns to answer the following specific questions concerning recruitment from a more causal and functional point of view:

1 - *Is tidal-induced variability a regulating process for meroplankton distribution?*

2 - *Are there differences in meroplankton densities in the various water masses characterized by environmental descriptors and frontal system? Do changes in the spatial structure of the environmental descriptors influence the meroplankton community structure and recruitment processes?*

3 - *Are the relationships (correlations) between species and environmental descriptors causal, or simply a result from the presence of a common spatial gradient in both sets of variables?*

4 - *Are spatially structured physico-chemical environmental processes responsible for life-cycle closure and the maintenance of the biological continum of the sub-tidal macrobenthos communities present in the coastal area studied?*

We have now to consider to what extent the present study answered the above questions

1 - The results obtained in 1988 clearly showed that tidal currents were the major force determining the changes in the density distribution of meroplankton larvae at Oostende and at the Oosterschelde in the Southern Bight of the North Sea. Path analysis showed that the larvae were strongly correlated with the tide and with tide-coupled environmental factors. The hydrodynamic processes and physical advective factors exert a strong control over meroplankton patterns distribution at different scales. The field observations confirmed that tidal processes were positively correlated with larval dispersal, and extended the validity of the member/vagrant hypothesis (Sinclair, 1988) to the geographical area studied.

The size and diversity of the larval supply to the macrobenthos could well be a function of the variation of the hydrodynamics. The mixing of larvae seems to be more effective in the coastal waters of the two sampling locations, where the speed and direction of residual tidal currents were more variable than those of the general current system in the Southern Bight of the North Sea.

2- The hydrodynamic processes in the coastal areas studied seem to play an important role in maintaining a low larval cross-shelf transport due to the strong along-coast currents regime. This resulted in a retention of larvae close to the coastal regions, and a possible low mortality rate due to a limited off-shore transport.

The results obtained during the RENORA campaigns in 1989 & 1990 confirmed that the coastal system studied with respect to the meroplankton community could be regarded as a complex biological fluxes system governed by the wind conditions that might alter the transport and dispersion of the larvae in a South-West-North-East direction or the reverse.

The observed distributional pattern of meroplankton showed, that echinoids larvae were associated with water masses coming from the southern part of the French coast, and that their dispersal was strongly dependent on the South-West wind regime. The ophiuroids larvae were related to nutrient-rich water, maybe as argued above, due to their ability to extract DOM from the water column. These results suggested that the release time of ophiuroids larvae into the water column coincided with high availability of phytoplankton. The polychaetes larvae were found in areas of water masses convergence and at the frontal system formation. The bivalves larval dispersal can be regarded as strongly dependent on tidal current regimes and flushing rates of estuaries, and this confirmed the earlier observation by Mann (1988) and Andrews (1988) concerning their dispersal.

These observations were also in agreement with the early study on the distribution of echinoderms and other larvae in the North Sea by Rees (1954). A five-years data-set analysis showed that higher density of *Echinocardium cordatum*, *Ophiura albida*, and of polychaetes larvae were characteristic of the Southern Bight of the North Sea. Furthermore the work of Rees (1954) showed, by comparing the percentage composition of the macrobenthos and that of the larvae for the above taxa, that the existence of a pelagic-benthic coupling could have been one of the reasons for the retention processes.

The RENORA results suggested that wind effects were not linearly correlated with the meroplankton densities as argued by Armonies (1992), but i was rather the hydrographic regime that most effectively changed the structure of the environmental variables, which in turn determined meroplankton variability and retention rates.

The discontinuities occurring in the four multispecies time series sampled showed the existence of ecological boundaries, defined both by their taxonomic contents and environmental variables. The formation of salinity fronts, mainly due to the water masses displacement from the Westerschelde and the Rheine-Meuse delta region southward, determined a shift back in the scaling of the stations based on the taxonomic composition. This showed that changes in the spatial structure of the environmental variables directly affected the spatial distribution of meroplankton.

The CCA analyses indicated that most of the species variability was explained by the salinity-density gradient opposite to the tide-space gradient, and for the 1990 transects by the fluorometry distribution which was positively correlated with the ophiuroids. These results confirmed the importance of the environmental variables in determining meroplankton variability and gave a better indication of the species-environment correlations.

3 - The response was achieved in two steps: first the use of covariables in the partial constrained ordination (CCA) showed the possibility of partialling out the environmental and spatial variation to test to what extent these fractions accounted for the observed meroplankton successional patterns. In a second step causal modelling (path analysis and Mantel tests) showed the significance of the correlations between space, environment, and meroplankton, and suggested a partition into direct and indirect causal relationships.
In the partial CCA, the purely environmental fraction (a) largely reflected site-scale ecological patterns determined by local environmental factors. The spatially covarying environment component fraction (b) reflected more the regional-scale ecological processes influenced by environmental variables that covaried geographically when the space component was regarded as a cubic or trend-surface regression. These results were complementary with the MDS and showed that processes at a local scale, such as the formations of salinity fronts, affected the meroplankton distribution, which in turn was reflected in the scaling of the stations.

What appeared to be less clear was what the purely spatial fraction (c) reflected ecologically in the meroplankton variation. As pointed out in this study and by Borcard & Legendre (1994) and Legendre (1993), fraction (c) might have reflected spatial population or community based processes, unmeasured abiotic environmental factors, or some past events (historical dynamic) that are reflected today in the spatial structure of fraction (c).

Considering the unexplained variation fraction (d), it will be interesting as suggested by Birks (1994), to map this fraction as the site ordination score, based in this case on the meroplankton residual variation unexplained by the available spatial and environmental variables.

The use of the spatial terms in the data analysis permitted the explanation of the spatial variation of the species composition and the segregation of the deterministic components of the unexplained variation, fraction (d) to local area within the sampling locations. The observed relationships (correlations) between species and environmental variables were causal, and in all four cases (transects 1989 & 1990) the spatial pattern of the species was fully attributed to the spatial pattern of the environmental variables. These observations were compatible with the following causal model:

$$\text{Space} \Rightarrow \text{Environment} \Rightarrow \text{Meroplankton.}$$

4 - This model gave a positive answer to the question posed earlier, and suggested that the pelagic phase of the recruitment of planktotrophic marine invertebrates larvae was regulated, to a larger extent, by spatially structured physico-chemical environmental processes which allow life-cycle closure and the maintenace of a biological continuum in the coastal area studied. However the ecological-environmental boundaries found could shift according to meteorological forcing; thus the latter factor plays a major role in structuring the macrobenthos.

The changing structure of the environmental descriptors had a clear effect on the larval pool, both in size and diversity. This variation could be regarded as a function of the variability of different spatial processes specific to well defined hydrodynamic regions such as the Oosterschelde.

In the Southern Bight of the North Sea, the coupling of physico-chemical processes and their spatial structure, as described in this study, can be regarded as the major cause in determining an ecological constraint, which in turn limited the spatial range of a species, and also its distribution within that range.

The spatial processes described do have an effect on the diversity of a larval patch. For example a patch of larvae can spend weeks or months in the plankton and therefore is likely to be more mixed than a patch of larvae that are pelagic for only few hours or days. Thus, if species are established in relation to their proportion present in the patch, this may represent a stochastic source for recruitment variability. These final considerations are closely related to the second phase of the RENORA project, dealing with the larval settling, survival rate, and the interaction with meiofauna.

The pelagic phase of the RENORA project showed the importance to consider spatial processes as functional processes in recruitment studies. The ecological boundaries established by the spatially structured physico-chemical environmental processes could shift according to the meteorological forcing, thus allowing changes in the taxonomic composition along a South-West-North-East gradient.

The overall results pointed out the need of understanding recruitment processes occuring at a spatial scale of 1 to 10 m, and at a temporal scale of days and weeks, to describe what is known as micro patches (Levin, 1995). This implies a clear understanding of the larval settlement rate and the interaction between the newly settled larvae as temporary meiofauna, and the permanent meiobenthos.

This research work is part of the second phase of the RENORA project in progress, where Mr. C. Luczak is currently studying that aspect of recruitment of benthic invertebrates closely related to population/community dynamic at different spatial and temporal scales.

Ecological conclusion

The spatial distributional patterns of meroplankton were generated by the physical geographic regional structure that allowed life-cycle closure. Meroplankton larvae were found within the distributional limits of the adult macrobenthic community. Different species can share during the time of recruitment a common distributional area. Physical processes such as residual tidally-generated circulation and wind conditions maintained the larvae within favourable settling benthic habitat.

The observed population patterns in the Southern Bight of the North Sea can be regarded as species-specific life cycles closure in relation to an appropriate geographical location.

Changes in the physical environment can provide either new infrastructure for the settling of new species, such as the case on Ensis directus *on* *the French coast of the North Sea (Luczak* et al., *1993), or unfavourable habitat causing the collapse of species life-cycle-closure.*

The spatial scale and coherence of the planktonic phase of macrobenthic species in relation to physical processes determined the species richness. The persitence of larvae distribution in a favourable settling area such as the Oosterschelde at a time scales up to one month can be regarded as the key-factor for life-cycle continuity and species richness.

The discontinuities occurring in the multispecies time series of biological samples collected along the four transects showed that the Westerschelde mouth area can be considered as a transition zone between the Northern part of the Belgian coast and the French-belgian coast southward, and between the Dutch coastal area Northward. The major differences were found both in terms of environmental descriptors and taxonomic composition of the communities between the Westerschelde and the Oosterschelde.

The species-environment relationships indicated that most of the species variability was explained by the salinity-density gradient opposite to the tide-space gradient and by fluorometry.

The relationship correlations between species and environmental descriptors were explained by a model of causal relationships:

$$\textit{Space} \Rightarrow \textit{Environment} \Rightarrow \textit{Meroplankton}$$

The above model was valid for all four cases and demonstrated that the structural forces intrinsic to a community, as well as community composition, change because of modifications in the environmental variables; this paradigm is known as the environmental control model (ECM).

The spatial pattern of the species was fully attributed to the spatial pattern of the environmental variables, and was completely 'explained away' by them; no significant spatial pattern remains in the species data after controlling for the effect of the environmental variables.

This research showed the importance of studying the spatial structure of ecological processes in more detail to quantitatively assess the coupling between different life-history phases of pelagic-benthic invertebrates.

Limitation of the RENORA project

The overall results obtained during the different RENORA campaigns showed the limitations of the sampling strategy and, as a consequence, the lack of important informations on residual tidal currents displacement and wind direction and velocity. These informations are needed to study in more detail the spatial structure of the data and attempt to produce maps of the observed abiotic and biotic variations as suggested by Borcard & Legendre, (1994).

A new sampling campaign should not only consider an horizontal transect like in the RENORA campaigns of 1989 & 1990 but also a grid of point defined over the study area covering at least between 10-100 km and located 1 km apart since these are the space-time scales that will allow major oceanographic features such as fronts and eddies, to be coupled with biological processes (Steele, 1995).

This sampling strategy will allow firstly the samples to be spread over a larger area and to be weighted in proportion to site heterogeneity, and secondly to analyse the spatial distribution of the data at different scales of observation.

In this way it could be possible to understand further the existence of a biological continuum in the spatial organisation of ecological processes, or on the contrary the existence of breaking points in the spatial structure, corresponding to different organisational levels.

The changes at a spatial organisational level could than be detected by *structure functions* such as variogram, two-dimensional correlogram, spatial autocorrelograms, and kriging (Legendre & Fortin, 1989) and by the study of the changes at a fractal dimension (Mandelbrot, 1977; Bradbury & Reichelt, 1983; Frontier 1986; Logan & Wilkinson, 1990).

One of the major pitfalls in the planning of the RENORA campaign was that the sampling strategy was not related to any specific data analysis, and therefore the way most of the data gathered were not sufficient for more specific spatial analysis, such as the use of geostatistical methods or the applications of geographical information systems (GIS).

A more efficient oceanographic vessel than the one used is of paramount importance to test further the influence of climatic changes on the distribution of meroplanktonic larvae and to allow to take samples regardless of severe weather conditions at sea.

We can conclude from this research work that the spatial structure of the physical and biological environment is important in determining the range and temporal rate of change of environmental conditions experienced by organisms living in and moving through that environment. Ecologists who sample spatial distribution of organisms have now to consider *a priori* that their data are structured in space.

The various physical and biological processes that contributed to the observed biological pattern differ in the range of spatial scales over which they were effective. The partitioning of the variation of the meroplankton community structure reinforced the preconceived models on larval dispersion and most importantly suggested the need to return to sampling with better models in mind. The methods described can be a useful approach to the interpretation of the dynamics of marine ecosystems.

Perspectives for future research

Species-environment relationships, current state-of-the-art. There is an increasing concern about impacts of global environmental change on biological systems in connection with, for example, the rates of change of biological diversity and the subsequent effects on community structure and ecosystem processes. There is, however, a shortage of information on species-environment relationships in many biological systems. Recent developments in applied statistics, in particular in the field of multivariate analysis, randomisation and permutation tests, and calibration, have provided biologists with new tools allowing to explore, establish, and quantify species-environment and community-environment relationships.

Future research. There is a need to study in more detail the spatial and temporal heterogeneity of the marine pelagic environment in the Southern Bigth of the North Sea in order to describe further faunal associations and their interrelationships, and to determine what factor or combination of factors underly the observed distribution. Furthermore it will be very important to learn more about the horizontal and vertical distribution of individual species and from detailed on-site studies of particular coastal locations, describe the zoogeographic scale of correlation, to investigate distributional patterns in multispecies assemblages, and their relation to broad features of the coastal hydrodynamic.

The developments of Geographic Information System (GIS) will allow the examination of ecological pattern at spatial scales larger than was previously possible. At the same time, more importance has to be given to the study of abiotic and biotic processes at small scales (1m-1km) to further understand the role played by these structuring forces as regulating factor in populations dynamic and communities composition.

There is a need of long-term ecological studies and the development of new techniques to reconstruct past communities and environments and to extend the temporal scale of ecological studies, and the need of frequent sampling to highlight the importance of small-scale temporal variation. Furthermore experimental and observational studies should match the temporal and spatial scale interaction to consider the effects of rare events on spatial patterns.

The increasing availability of large data sets across temporal and spatial scales, and the urgent need to solve large-scale environmental problems, should stimulate a joint effort from theoretical and empirical studies to attempt to integrate patterns and processes across scales, for a better understanding of how patterns and processes at one spatial or temporal scale affect those at other scales. For this it is necessary to address important ecological questions according to different level of organization as proposed by Lubchenco *et al.*, (1991) as reported in Table 13.

Ecological research in the Southern Bight of the North Sea and elsewhere should be directed more to the analysis of biodiversity as a key factor in maintaining species and habitat diversity, and to developing management strategies for maintaining natural and human-dominated ecological systems. Biodiversity is an important key factor in future environmental policies; it is essential that there be further research in this area to plan for the management of sustainable ecological systems and to ensure that the special expertise of ecological related sciences is available to environmental-decision-makers in all sectors of society. (Lubchenco *et al.*, 1991).

Level of organisation Ecological topics	Questions
Communities	
Community Structure	How does community structure affect individual species embedded within the community? To what degree are some species interchangeable without affecting community processes?
Biotic Diversity	What are the patterns, causes, and consequences of spatial and temporal variation in species diversity? What processes account for the patterns in biological diversity across a geographic range? Do speciation patterns serve as clues to those process? What are the rates of loss of biological diversity across different locations and taxonomic groups?
Succession	What processes retard or accelerate the succession rate in ecological communities?
Community Stability	How well do communities resist environmenta forces that may perturb them? What properties of communities lead to resilience in the face of environmental change? How rapidly do communities return to their initial state, and what factors determine the recovery rate? How resistant are communities to invasion by new species? How might we predict the ability of a new specie to become stablished in a given community?

Table 13. Ecological problems at different levels of organization (after Lubchenco et al., 1991).

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Fig. 14. (A) *Polydora* spp. density distribution and temperature for the 10 June shows two distinct populations one from station 1 to 23 (French coast), and one from station 39 to 64 (French-Belgian coast). (B) *Polydora* spp. density distribution and temperature for the 21 June, due to the North-East wind effect more larvae are transported southward. H.W. and L.W. indicates the time of occurence of high water and low water.

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Fig. 17. (A) *Pectinaria koreni* density distribution and salinity for the 21 June shows that high density of larvae are located within the salinity front between station 38 to 40. (B) Echinoids density distribution and salinity for the 21 June. Higher densities of larvae are found before the area of the salinity front on the French coast. H. W. indicates the time of occurence of high water.

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Fig. 19. (A) PCA for the 10/6/89: scaling of the 64 observations. (B) PCA for the 21/6/89: scaling of the 67 observations. Classification results are represented by envelopes. Salinity front stations (SF), coastal station (CS) and off-shore station (OFF).

Fig. 20. Schematic representation of the chronological clustering for the 10/6/89. (A) Species matrix chronological clustering. (B) Environmental matrix chronological clustering. Connectedness level Co is 50% and the group expansion test are shown for a alpha significance level = 0.20.

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Fig. 22. Non-metric multi-dimensional scaling (MDS) plot in 2 dimensions for meroplankton data. (a) results for the 10/6/89 (b) results for the 21/6/89. Species abundances were √√-transformed and between-sample similarities calculated with the Bray-Curtis coefficient. Stress for the MDS is low, between 0.03 and 0.05. Classification results are represented by envelopes. (FC) French coast and (F-BC) French-Belgian coast are abbreviations denoting the different groups in the MDS.

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Fig. 40. Schematic representation of the chronological clustering for the 5/6/90. (A) Species matrix chronological clustering. (B) Environmental matrix chronological clustering. Connectedness level Co is 50% and the group expansion test are shown for a alpha significance level = 0.20.

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Fig. 44. Biplot based on canonical correspondence analysis (CCA) of meroplankton with respect to 6 environmental variable and space. (a) results for the 5/6/90 (b) results for the 11/6/90. The first two axes in the CCA ordination are presented. The salinity-density gradient (mainly spatial) explained most of the variance.

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13.7%; (d) unexplained variation and stochastic fluctuations : 100 - 66.3 = 33.7%. For the 11-6-90 the total explained variation was 69.5% and partitioned as : (a) 10.5%, (b) 50.3%, (c) 8.7%, (d) 30.5%.

Table. 11. The path analysis from the simple Mantel test are reported as direct causal covariance regression values.

Table. 12. Possible model of causal relationship supported by the data and partially by the computed results. R1 is the geographic distance matrix (space), R2 is the environmental variables matrix (environment), and R3 is the species matrix (meroplankton).

Table 13. Ecological problems at different levels of organization (after Lubchenco et al., 1991).

List of Abbreviations

List of Abbreviations

Biotic variables

(AMPH) Ampharetidae
(BIV) Bivalves
(ECHI) Echinoids
(LAN) *Lanice conchilega*
(MAG) *Magelona mirabilis*
(NEPHT) *Nephtys* spp.
(OPHI) Ophiuroids
(PECT) *Pectinaria koreni*
(POLY) *Polydora* spp.

Abiotic variables

(H.W.) High water
(L.W.) Low water
(DEN) Density
(FLUO) Fluorometry
(SAL) Salinity
(TEMP) Temperature

Clusters

(B) Belgian coast
(B-W) Belgian coast & Wielingen
(CS) Coastal stations
(DC) Dutch coast
(DC-V) Dutch coast & Voordelta
(F-BC) French coast & Belgian coast
(FC) French coast
(OFF) Off-shore stations
(OST) Oosterschelde
(V-OST) Voordelta & Oosterschelde
(W) Wielingen
(WS) Westerschelde

Appendix

Appendix

List of pubblication in relation to the present study

* **Belgrano A. and J.-M. Dewarumez** (1995). The influence of tidal-induced variability on the distribution of meroplankton larvae in the Southern Bight of the North Sea. *Oceanologica Acta* (in press Vol. 18/N° 4).

* **Belgrano A., Legendre P., Dewarumez J.-M. and Frontier S.** (1995). Spatial structure and ecological variation of meroplankton - a. The Southern Bight of the North Sea (French-Belgian coast). *Mar. Ecol. Prog. Ser.* vol. 128: 43-50

* **Belgrano A., Legendre P., Dewarumez J.-M. and Frontier S.** (1995). Spatial structure and ecological variation of meroplankton - b. The Southern Bight of the North Sea (Belgian-Dutch coast). *Mar. Ecol. Prog. Ser.* 128: 51-59

Belgrano A., Legendre P. (1995). Spatial structure and ecological variation of meroplankton in the Southern Bight of the North Sea: a causal modelling approach. (submitted to *Journal of Plankton Research,* August 1995).

* full proof included

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The influence of tidal-induced variability on the distribution of meroplankton larvae in the Southern Bight of the North Sea

North Sea
Tide
Meroplanktonic larvae
Path analysis
Causal relationships

Mer du Nord
Marée
Larves méroplanctoniques
Analyse des coefficients de direction
Relations causales

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ABSTRACT

Tidal currents proved to be the major force determining the changes in the density distribution of meroplankton larvae in the Southern Bight of the North Sea. Path analysis showed that the larvae are strongly correlated with the tide and with tide-coupled environmental factors. Hydrodynamic processes and physical advective factors exert a strong control over meroplankton pattern distribution at different scales.

RÉSUMÉ

Influence de la variabilité induite par la marée sur la distribution des larves méroplanctoniques dans la baie sud de la Mer du Nord.

Les variations des distributions de densités des larves méroplanctoniques dans la baie sud de la Mer du Nord sont principalement conditionnées par les courants de marée. L'analyse des coefficients de direction montre que la présence des larves est fortement corrélée avec la marée et les facteurs environnementaux qui lui sont liés. Les processus hydrodynamiques contrôlent ainsi les distributions du méroplancton à différentes échelles.

Oceanologica Acta, 1995, **18**, 5, 523-530

INTRODUCTION

The hydrodynamic regime of the Southern Bight of the North Sea is characterized by strong mesoscale currents produced by tides and winds (Nihoul and Ronday, 1975; Nihoul and Runfala, 1981). The Westerschelde estuary ebb-tide channel and flood-tide channel are responsible for the dilution of the Westerschelde estuary waters with the North Sea (Nihoul *et al.*, 1989). The Oosterchelde estuary is characterized by strong tidal currents (Dronkers and Zimmerman, 1982). The presence of two storm surge barriers (Wetsteyn *et al.*, 1990) reduced the water exchange with the North Sea by approximately 28 % (Leewis and Waardenburg, 1990). The retention hypothesis (Iles and Sinclair, 1982) and the member/vagrant hypothesis (Sinclair, 1988), attempted to account for population variability and life-cycle continuity by considering the effectiveness of retention and the spatial constraints exerted upon marine organisms by physical environmental processes such as advection-diffusion transport. The larvae of benthic marine invertebrates are dispersed at a variety of spatial and temporal scales (Scheltema, 1986). Previous studies on larvae dispersion considered extensively the benthic boundary layer (Butman, 1987; Butman *et al.*,

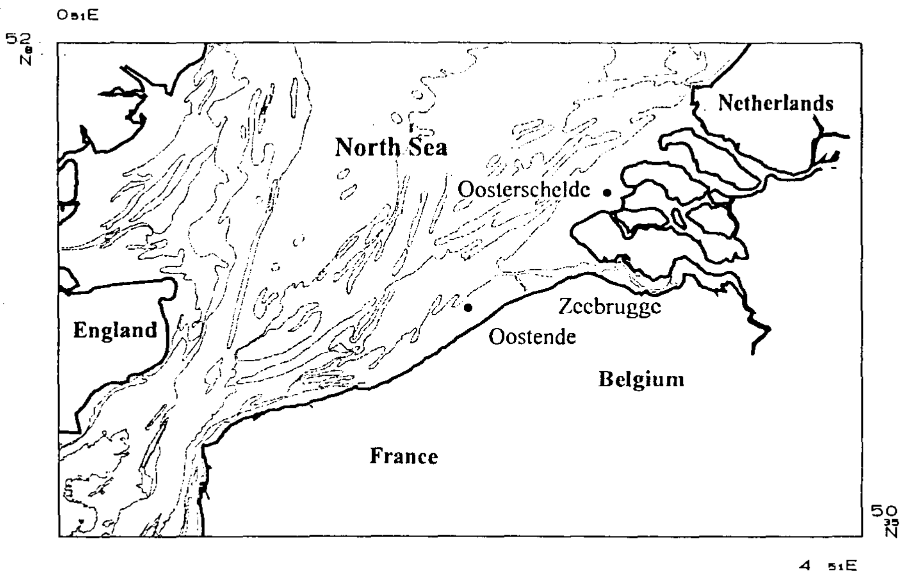


Figure 1

Locations of the sampling stations (black point) in the Southern Bight of the North Sea.

1988), but only few studies of dispersal considered the processes that might influence the density distribution of larvae in the upper water column (Levin, 1990). The studies on passive transport and behaviour of larvae in estuarine conditions (Wolf, 1974) and in a marine bay (Banse, 1986) suggested that hydrodynamic and physico-chemical processes are responsible for the retention of the larvae within a distinct water mass. The early observations by Levin (1983; 1986) showed the importance of relating the density distribution of pelagic larvae to the time of occurrence of high and low water. Epifanio (1988) and Mann (1988) stressed the importance of relating hydrographic measurements and larval distribution to salinity discontinuities. The aim of this study is to show how meroplanktonic larvae are dispersed over a tidal cycle at two coastal locations characterized by strong tidal current, and to estimate by path analysis the relative strengths of direct and indirect interactions among variables (Wootton, 1994). Path analysis can be used to test several alternative hypotheses concerning the causal relationships among variables (Sokal and Rohlf, 1981; Tukey, 1954) and to measure the strengths of the predicted causal links within the ecosystems considered (Turner and Stevens, 1959; Turner and Mittleback, 1990).

MATERIAL AND METHODS

Data

The two sampling stations were located in the Southern Bight of the North Sea (Fig. 1; Cadiou, 1993). Meroplankton samples were taken every hour from a stationary boat, at 3 m depth, during one tidal cycle (12 hours at Oostende and 13 hours at the Oosterschelde), using a 80 µm mesh size plankton net model WP2 (UNESCO, 1968). The filtered volume was controlled by a TSK (Tsurimi-Seiki-Kosakusho, Japan) flowmeter. The tide excursion was monitored by the use of an AANDERAA currentmeter. Temperature, salinity, dissolved oxygen, were measured using a CTD probe (SEABIRD), the turbidity NTU (Nephelometric Turbidity Unit) was recorded with a nephelometer with a Tyndall effect (DRT 1000, HF Instrument). The meroplankton samples were preserved in 10 % per volume of formalin (4 % formaldehyde). The larvae present in each sample were sorted according to the method proposed by Frontier (1969; 1972) and Lagadeuc (1992).

Statistical analysis

Non-parametric procedures (Ardisson *et al.*, 1990) were used since the meroplankton mean densities departed significantly from a normal distribution (Kolmogorov-Smirnov test, $P < 0.001$). All the density data were first transformed to their natural logarithm to approximate normality and achieve homogeneity of the variances. Homogeneity was tested by the use of the Barlett test (Sokal and Rohlf, 1981). The Spearman's test (Castonguay *et al.*, 1992) was used to determine the existence of any correlations between species data and environmental descriptors. The cumulated function method proposed by Ibanez *et al.* (1993) was used to detect the general trend of the meroplankton density distribution in relation to the tide excursion. This method can be applied to any chronological series and the reference value k could be, as in this case, the mean of the series. After subtracting k from all the data we added these residuals to obtain the cumulated function. Path analysis was carried out on three correlation matrices based on Pearson correlation coefficients corresponding to the physical forcing (tide height and tidal current velocity), environment (abiotic factors), biology (meroplankton density) using the Piste program (Vaudor, 1992). Path analysis can be regarded as a sequence of multiple regression and correlations according to an *a priori* hypothesis (Wootton, 1994). In this particular case the causal links to be tested were the direct

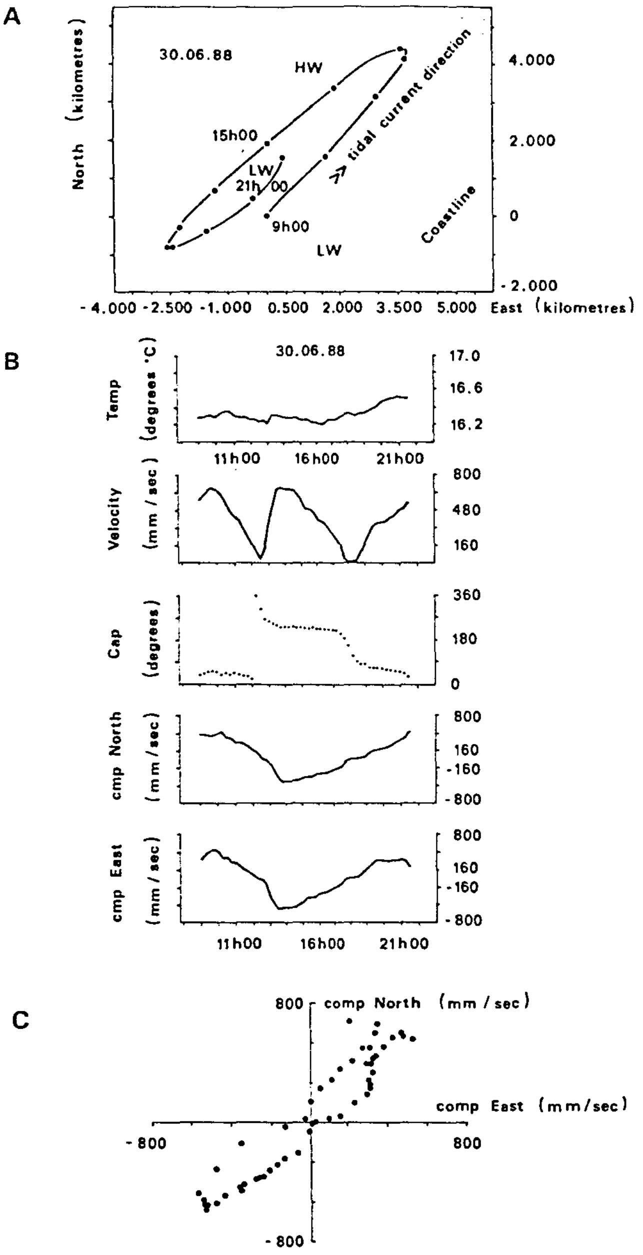


Figure 2

(A) AANDERAA currentmeter trajectory at Oostende, showing the movement of the tide, and the occurrence of low water (LW) and high water (HW). (B) From top to bottom are reported the AANDERAA readings of temperature (°C), current velocity (mm s^{-1}), current direction (degrees), and the tidal component North and East. (C) The plot result of the tidal component North and East.

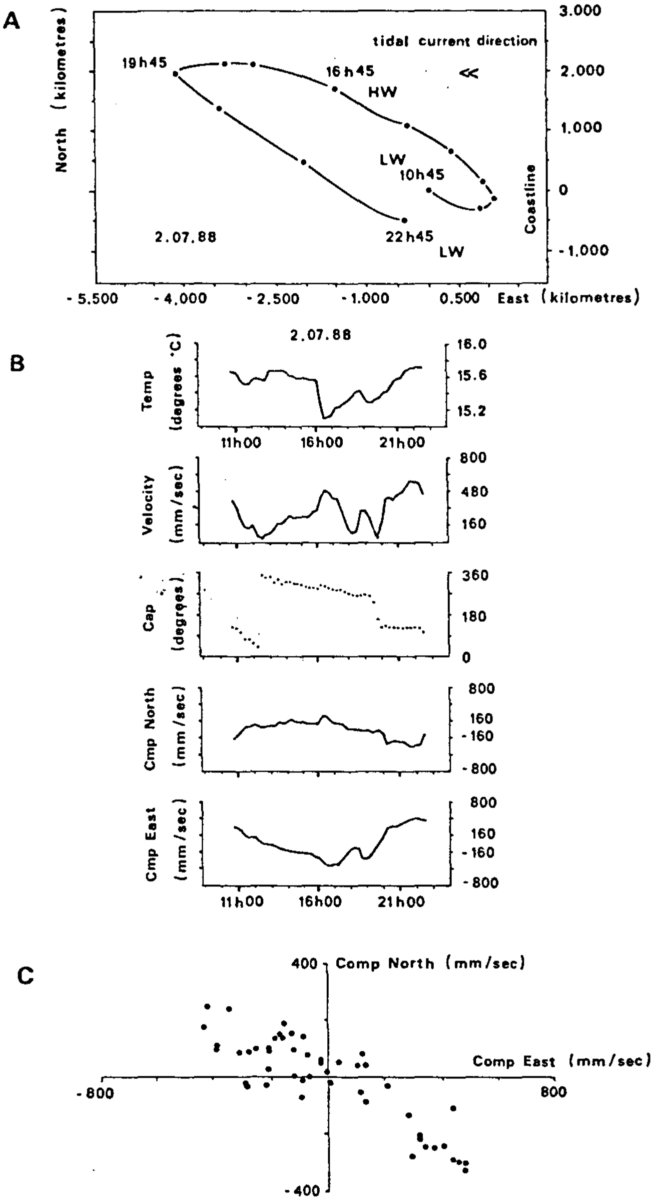


Figure 3

(A) AANDERAA currentmeter trajectory at the Oosterschelde, showing the movement of the tide, and the occurrence of low water (LW) and high water (HW). (B) From top to bottom are reported the AANDERAA readings of temperature (°C), current velocity (mm s^{-1}), current direction (degrees), and the tidal component North and East. (C) The plot result of the tidal component North and East.

and indirect effect of the tide and the environment on the meroplankton density distribution. The tests of significance in the Piste program are based on the usual tests of significance of multiple regression, and assume that the coefficients used for the data input are Pearson coefficients and that the relations are linear. The computed results are reported as direct causal covariance regression values with the corresponding levels of probabilities, since the path analysis used was standard and not based on Mantel statistics, the significance tests of path coefficients were used for interpretation (Nantel and Neumann, 1992).

RESULTS

Hydrographic parameters

The results of the AANDERAA currentmeter for Oostende (Fig. 2*A*) shows the excursion of the tide from 9h00 to 22h00 running parallel to the coastline. At low water, which occurs at 9h06, the tide moves northward turning at 12h30 and approaching the high water time at 14h10 eastward and turning at 10h00 northward, reaching the second low water time at 21h36. The tidal components are reported in Figure 2*B*. The highest tidal current velocity at

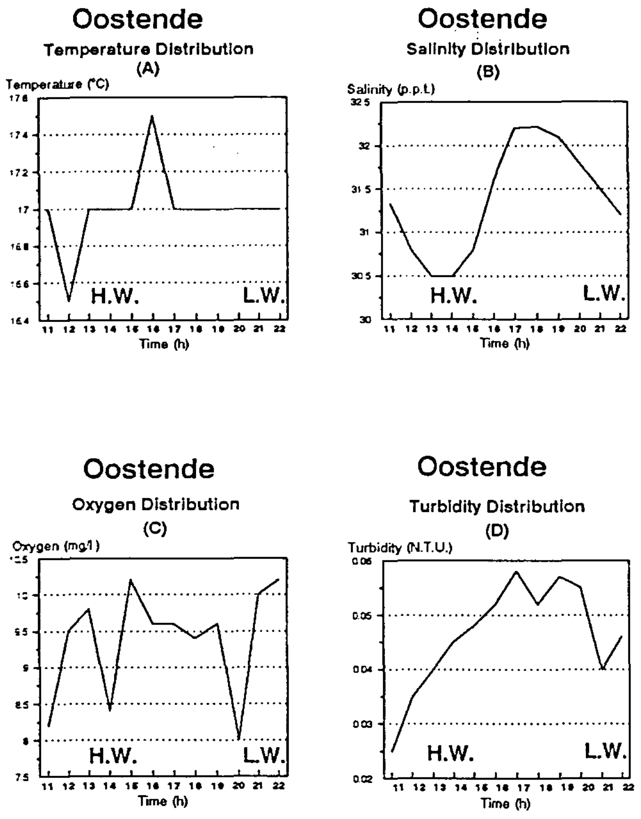


Figure 4

Abiotic variables at Oostende: (A) Temperature; (B) Salinity; (C) Oxygen; and (D) Turbidity. H. W. and L. W. indicate the time of occurrence of high and low water.

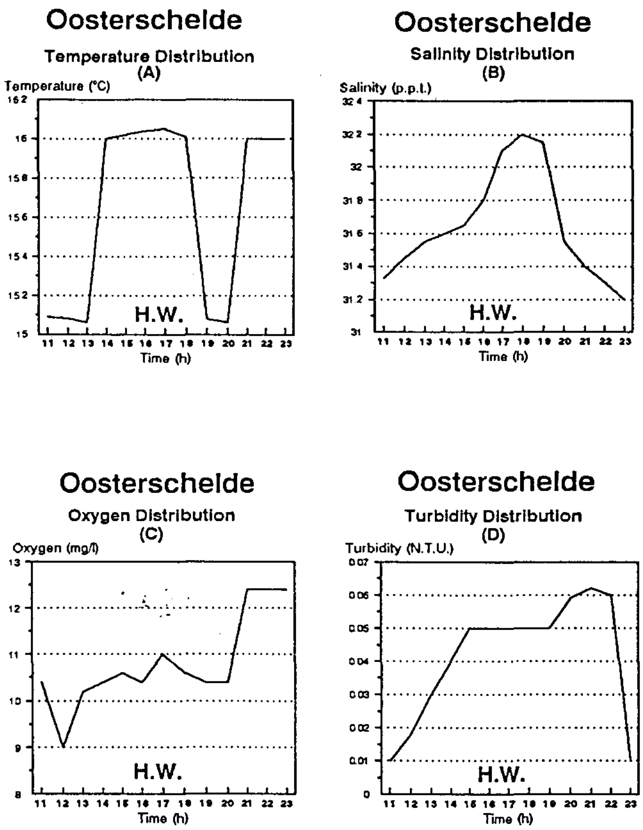


Figure 5

Abiotic variables at Oostende: (A) Temperature; (B) Salinity; (C) Oxygen; and (D) Turbidity. H. W. indicates the time of occurrence of high water.

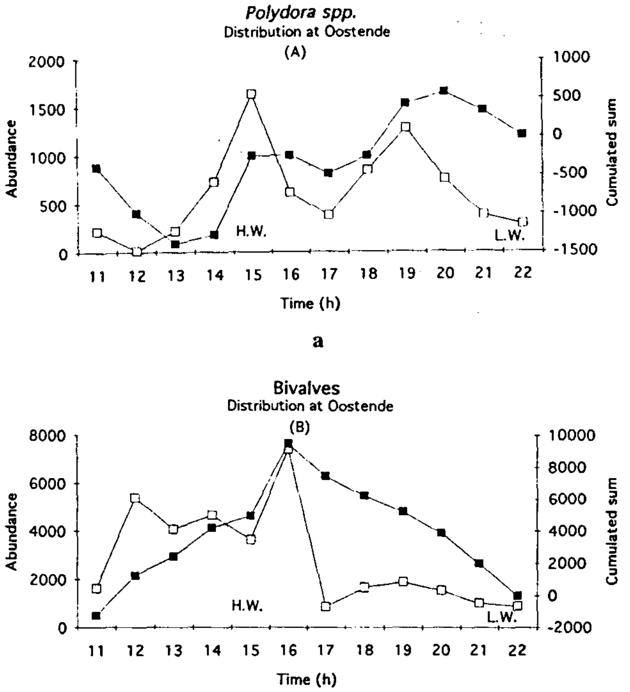
650 mm s^{-1} was found at high water running at 225° E. The tidal components (North-East) are plotted in greater detail in Figure 2*C*. The AANDERAA readings obtained for the Oosterschelde station shows the excursion of the tide (Fig. 3*A*). At low water, at 10h15, the tide turns northward in the direction of the North Sea, leaving the Oosterschelde estuary and reaching high water at 16h25. The tide turns again at 19h45, approaching the second low-water time at 23h05, entering the Oosterschelde estuary at 90°. The tidal component measurements (Fig. 3*B*) show that the highest current velocity at 580 mm s^{-1} was found at the ebbing of the tide approaching the second low water margin at 90°. The tidal components (North and East) are plotted in Figure 3*C*, showing the looping circulation pattern in front of the storm surge barrier at the Oosterschelde.

Abiotic descriptors

The temperature distribution at Oostende (Fig. 4*A*) shows an increase from 17 °C to 17.5 °C after high water at 14h10, the lowest temperature value 16.5 °C being found at 12h00 just after the first low water margin at 11h00. The salinity distribution (Fig. 4*B*) shows more or less the same pattern with the lowest value 30.5 between 13h00–14h00 and the highest value 32.25 between 18h00–19h00. The oxygen distribution (Fig. 4*C*) follows the tide, the highest values of 10.25 mg l^{-1} being found at 15h00 and 22h00. The lowest oxygen value 8 mg l^{-1} was found at 20h00. The turbidity distribution (Fig. 4*D*) shows a clear increase after low water at 11h00 through the high water time until 17h00, with values ranging from 0.02 to 0.058 NTU. The temperature distribution at the Oosterschelde (Fig. 5*A*) shows a bimodal pattern following the tide with the highest values at 17h00 (16.1 °C), and at 23h00 (16.0 °C). The lowest values (15.1 °C) were found at 13h00 and 20h00. The salinity distribution (Fig. 5*B*) reaches its highest value at 18h00 with 32.2 after the high water time at 16h25. The oxygen distribution (Fig. 5*C*) shows an increase in the oxygen concentration concomitant with the ebbing of the tide at 21h00 at a value of 12.5 mg l^{-1}. The lowest value of 9 mg l^{-1}. was found at 12h00. The turbidity distribution (Fig. 5*D*) shows a clear increase from the ebbing of the tide at 12.00 with 0.01 NTU until 15h00 with 0.05 NTU; the highest value was however found at 21h00 with 0.062 NTU concomitant with the second ebbing of the tide approaching the low water margin at 23h05.

Biotic descriptors

The meroplankton taxa present at Oostende were polychaeta larvae of *Polydora* spp. and the larvae of bivalves. The

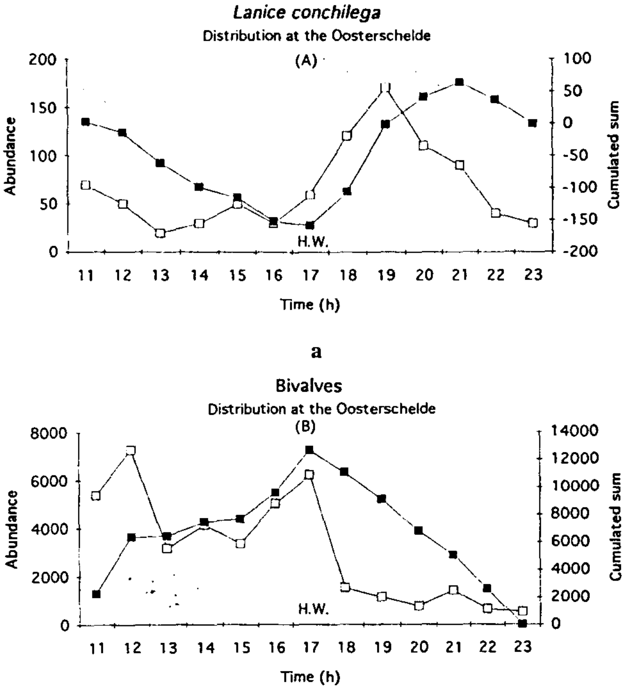


a

b

Figure 6

(a) Polydora *spp. and (b) bivalve larvae distribution at Oostende; white square line showing the density values not transformed, black square line showing the transformed density values to cumulated sum. H. W. and L. W. indicate the time of occurrence of high and low water.*



a

b

Figure 7

(a) Lanice conchilega *and (b) bivalve larvae distribution at the Oosterschelde; white square line showing the density values not transformed, black square line showing the transformed density values to cumulated sum. H. W. indicates the time of occurrence of high water.*

cumulated sum distribution was calculated and plotted respectively in Figures 6 *a* and 6 *b*. *Polydora* spp. reaches the highest density value at 15h00 after the high water at 14h10, with 1,650 ind. m^{-3}. The cumulated sum curve (black square line) shows more clearly the differences in density values between the two flooding periods with the two density peaks at 15h00 and 20h00. The bivalve distribution shows a clear density peak at 16h00 after the high water time at 14h10, with a density value of 9,500 ind. m^{-3}. The cumulated sum curve (black square line) shows better the decreasing density value following the tidal excursion. The results obtained were subjected to Sperman's correlation test. Both *Polydora* spp. and the bivalves were strongly correlated with the tide (Spearman's r_s, $P < 0.01$) with turbidity (Spearman's r_s, $P < 0.05$), and salinity (Spearman's r_s, $P < 0.01$). For the station at the Oosterschelde, the meroplankton taxa present were polychaeta larvae of *Lanice conchilega* and the bivalves larvae. The results show for *Lanice conchilega* (Fig. 7 *a*) a density peak at 19h00 with 155 ind. m^{-3}, during the ebbing of the tide. The cumulated sum (black square line) estimated much better the increase of bivalve larvae density concomitant with the ebbing of the tide. The bivalves larvae (Fig. 7 *b*) show a unimodal pattern with a distinct peak at 17h00 and a density value of 12,500 ind. m^{-3}. For both taxa, the cumulated sum shows that highest density value was found after high-water at 17h00. Both taxa were strongly correlated with the tide (Spearman's r_s, $P < 0.01$). The larvae were positively correlated with salinity (Spearman's r_s, $P < 0.01$); and with turbidity (Spearman's r_s, $P < 0.05$).

Path analysis

The results of the path analysis are represented in the form of path diagrams (Fig. 8). For Oostende, the direct path coefficient from (Tide) towards (Species) and the indirect path coefficient from (Environment) towards (Species) are highly significant statistically, at a level of ($0.05 \geq p > 0.01$). The direct path coefficient from (Tide) towards

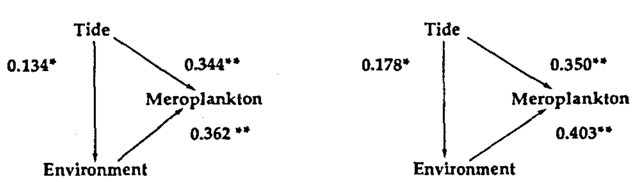


Figure 8

*Path diagrams for Oostende and the Oosterschelde. Arrows designate the direction of the causal links, number next to arrows represent the estimated path coefficients. The probabilities level of the regression coefficients is indicated by ** for $0.05 \geq p > 0.01$ and * for $0.01 \geq p > 0.005$.*

(Environment) is also statistically significant at a level of $(0.01 \geq p > 0.005)$. For the Oosterschelde, the results are similar, although the path coefficient representing the indirect effect of (Environment) towards (Species) proved to be higher. The expected correlation between tide and meroplankton for Oostende in Figure 8 is the direct path between tide and environment added to the indirect path from the environment to meroplankton and the path from tide to meroplankton $(0.134 + (0.344 \times 0.362) = 0.258)$. The expected correlation between environment and meroplankton is the path from environment to meroplankton plus the paths from tide to environment and tide to meroplankton $(0.362 + (0.134 \times 0.344) = 0.408)$. For the Oosterschelde, the expected correlation between tide and environment is 0.319 and the expected correlation between environment and meroplankton is 0.465. The use of path analysis furnished additional information about the system studied. The path coefficients provided further insights concerning the strengths of association supported by the causal links between the variables.

DISCUSSION

Advection and suspension by tidal currents as postulated by Uncles and Joint (1983), seem to be among the major forces determining concentration of planktonic organisms in turbid coastal areas. The bimodal pattern in the observed meroplankton density distribution confirmed the early observation by Levin (1986). Carriker (1951) found that younger stages of larvae ebb and flow in a passive manner with the tide. Wood and Hargis (1971) found that the density maxima of bivalves larvae coincided with an increase in salinity concomitant with the flood of the tide. Our results confirmed the importance of considering tide-coupled environmental factors as processes regulating the dispersion and retention of the early stages of invertebrate larvae in estuaries and coastal locations. Provenzano *et al.* (1983) found that the majority of early stages of zoeae larvae were sychronized with the night-time slack tides in order to assure the transport of the larvae to the mouth of the estuary concomitant with the salinity values required for the development of the zoeae. The correlations found with the salinities and turbidity can be regarded as a consequence of the tidally-induced variability. From these observations we can confirm that the studied larvae acted as either passive particle or neutrally buoyant objects. The results supported the early hypothesis by Levin (1986) and Banse (1986), concerning the spatial and temporal distribution of larvae as moving patches in response to tidal currents (Wyatt, 1973), and as related to water masses defined by the T-S diagram. The tidal excursion pattern confirmed the observation reported by Nihoul (1975), and the tidal component (North and East) at the Oosterschelde confirmed the looping circulation pattern described by Kohsiek *et al.* (1989). The selective or passive use of tidal currents by pelagic stages of benthic invertebrates can allow the animals to remain close to the adult population or, on the other hand, to serve as a larval supply to neighbouring benthic communities (Roughgarden *et al.*, 1987). Though pelagic larvae of benthic invertebrates are capable of selectivity in the use of currents (Butman, 1987), the results suggested that hydrodynamic processes controlled to some considerable extent the distribution of the larvae near the surface, causing aggregation of passive larvae patches at different scales (Barry and Dayton, 1991). The distribution of *Polydora* spp. and bivalves larvae at Oostende and of *Lanice conchilega* and bivalves larvae at the Oosterschelde further supported the hypothesis that larval dispersal can be regarded as a passive process controlled by oceanic circulation (Levin, 1983). The different tidal regime of the two locations studied suggested that the observed difference in the local density distribution of the larvae may be the result of active or passive redistribution of larvae in near-bottom water (Butman, 1989) and of hydrodynamic events occurring at the benthic boudary layer (BBL), as reported by Fréchette *et al.* (1993). At the Oosterschelde, due to the effect of the storm-surge barrier in reducing the water exchange with the North Sea, the distribution of the larvae can be regarded to some extent as being controlled by the looping circulation system of the tide. These results further reinforce the hypothesis that at the Oosterschelde the adult benthic population can be regarded as self-sustaining (Scholten *et al.*, 1990), their reproductive effort being favoured by the hydrodynamic processes which characterise this location. The use of path analysis demonstrated the importance of assessing the various direct and indirect paths between variables and gave an indication of the strength of the causal links between the tide, environment and meroplankton. Since the data used represented a portion of the geographic space sampled, the correlations found by path analysis are likely to have been generated by variables which are autocorrelated, as in most environmental studies (Legendre and Troussellier, 1988). The spatial structure of the data suggested the need to collect further information and to use partial Canonical Correspondence Analysis (ter Braak, 1988; Borcard *et al.*, 1992), and the partial Mantel statistics (Smouse *et al.*, 1986; Legendre and Fortin, 1989) in order to determine whether the causal relations between variables are spurious or real and to propose a possible model of causal relationships. However, in order further to understand the meroplankton distribution in coastal and estuarine locations in relation to tidal-induced variability and its effect on meroplankton, it is necessary to achive a detailed knowledge of both hydrography and the seasonal changes in the rate and direction of advection related to wind forcing (Hill, 1995, 1994).

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Spatial structure and ecological variation of meroplankton on the French-Belgian coast of the North Sea

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ABSTRACT: The spatial pattern of specific populations or communities plays an important role in ecological theories such as species diversity, community succession and stability. A method based on canonical correspondence ordination (CCA) and constrained ordination was used to partition the variation observed in the species abundance data matrix into 4 independent components: spatial, environmental, spatial + environmental, undetermined. Mantel and partial Mantel test results were in accordance with CCA results.

KEY WORDS: North Sea · Meroplankton · Community structure · Canonical correspondence analysis (CCA) · Constrained ordination · Monte Carlo permutation test · Mantel statistics

INTRODUCTION

Meroplankton species and hydrological monitoring data were collected along a transect in the Southern Bight of the North Sea. The coastal locations studied are characterized by the presence of a benthic community continuum dominated by the bivalve *Abra alba*, which is subjected to seasonal and yearly fluctuations (Dewarumez et al. 1991). Most of the benthic species have a pelagic phase during their life cycle, with the meroplanktonic larvae dispersed over a period of time which varies from 1 wk to 1 mo. The complexities involved in the interpretation of the effects of localised wind-driven advection transport on the intensity of water mass movements in relation to the changes in the distribution and abundance of meroplankton and zooplankton in this area have been discussed by many authors (Colebrook 1978, Colebrook & Taylor 1984, Belgrano et al. 1990, Dewarumez et al. 1991). The aim of this study was to assess the spatial hetereogeneity of the meroplankton community structure in relation to hydrodynamic and environmental processes, in order to understand the mechanisms involved in the larval dispersion and the complex biological fluxes existing in the coastal waters between the English Channel and the Southern Bight of the North Sea (Luczak et al. 1993).

Multivariate analysis techniques such as classification, clustering and ordination are commonly used to describe marine ecological data. Classification can be regarded as a hierarchical assignment of objects into groups and is either agglomerative or divisive. Clustering permits combination into groups of species, times, and locations. The results are presented in the forms of dendrograms for hierarchical methods and by partition for non-hierarchical methods. Ordination techniques reduce the dimensionality of the data sets and the variance is expressed by few component axes. The majority of the ordination techniques are based on 2 types of response models: a linear or monotonous and a unimodal Gaussian. Unfortunately, no specific techniques are available when the response curve is bimodal and for this reason new approaches and new methods for analysing ecological data are necessary. An awareness of these limitations is therefore important in choosing and correctly using the most appropiate statistical methods to test hypotheses and explore field results.

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The development of multivariate statistical techniques (ter Braak 1988a) allows the application of partially constrained ordinations, where by means of multiple linear regression it is possible to remove the signal and effects of covariables such as environmental parameters or spatial constraints. The method proposed by Borcard et al. (1992) was based on canonical correspondence analysis (CCA). This technique allows measurement of the amount of variation as a sum of canonical eigenvalues for the species matrix which can be explained by environmental variables. In most cases environmental variables alone are not able to fully explain the amount of variation observed in the species community structure. The need to compare sets of biotic and abiotic data with spatial coordinates or distance between the samples as suggested by ter Braak (1987) is extremely important for further understanding the concept of spatial hetereogeneity, which can be regarded as functional in ecosystems.

The spatial component of the community structure can be isolated from the species-environment component to detect if the environmental control model can explain the variation observed (May 1984). The application of this method to marine ecological data sets is presented here by considering the associated statistical problem of spatial autocorrelation across geographic space. The spatial autocorrelation of plankton communities can be used to quantify community dissimilarities (Mackas 1984). In this case space was used as an explanatory variable (Legendre & Fortin 1989). The results obtained by applying CCA and the Mantel and partial Mantel tests are reported here. These methods are suitable for extracting the relationship of species with the environment, taking into account the spatial component present in the data (Borcard & Legendre 1994).

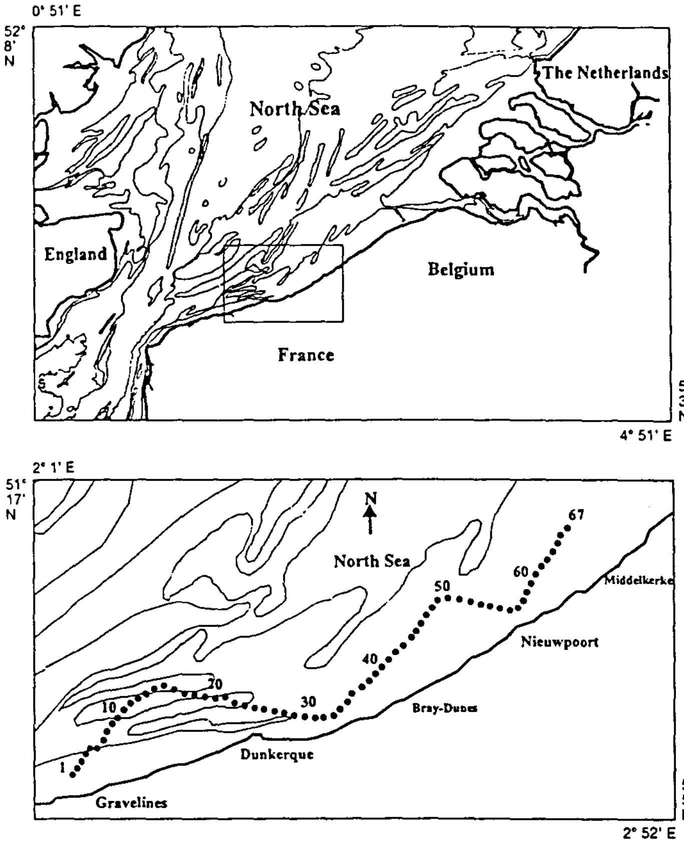

Fig. 1. Schematic map of the study area. Sampling transect along the coastline is presented by a dotted line

METHODS

Data. The sampling cruises were conducted on 10 and 21 June 1989 along a transect from Gravelines (France) to Middelkerke (Belgium), 35 nautical miles into the Southern Bight of the North Sea (Fig. 1) in connection with the research program RENORA founded by the PNDR (Programme National sur le Déterminisme du Recrutement, France). Temperature, salinity and water density were measured at 20 s intervals by a hydrological probe. Depth and corrected depth were measured on board by the Color Echo Sounder system (model Raytheon V800). For meroplankton, 64 and 67 samples, respectively, were collected during the 2 cruises at 3 m depth by a volumetric pump (PCM Moineau, 200 l min^{-1}). Each sample corresponded to 5 min continuous pumping. Samples were filtered on board using a 80 µm mesh size plankton net attached to the pumping system. Meroplankton samples were counted according to the method proposed by Frontier (1969, 1972). A list of environmental variables and names of taxonomic groups are reported in Table 1. The wind direction and velocity data were obtained from the meteorological station at Dunkerque (France).

Table 1. Taxonomic groups and environmental variables

Taxonomic group	Environmental variables
Lanice conchilega	Salinity (ppt)
Pectinaria koreni	Temperature (°C)
Magelona mirabilis	Density (kg m^{-3})
Polydora spp.	Corrected depth (m)
Nephtys spp.	Tidal height (m)
Ampharetidae	
Bivalves	
Echinoids	

Table 2. Each step of the 4 canonical correspondence analyses (CCA); • indicates the data matrix input, – indicates no input. Covariables were used in Steps (3) & (4)

CCA input	Species matrix	Covariables matrix	Environmental matrix	Spatial matrix
Step (1)	•	–	•	–
Step (2)	•	–	–	•
Step (3)	•	Spatial matrix	•	–
Step (4)	•	Environmental matrix	–	•

Numerical analysis. The data for the CCA were divided into 3 matrices: (1) species densities, (2) environmental variables and (3) geographic locations of the samples (spatial component). Following Legendre (1990), and Borcard et al. (1992), the geographic coordinates of the sampling locations were used to perform a cubic trend surface regression to ensure the extraction of more complex structures, such as patches, and not only the linear gradient pattern in the species matrix. The 3 data sets were analysed using CCA, with the spatial and the environmental matrices as covariables, alternatively (Table 2). Running 2 canonical ordinations constrained by a set of explanatory variables (covariables) allowed us to measure the impact on the species data of the effects of environmental conditions and of the spatial structure. With the awareness that in some cases the species and the environmental variables share the same spatial structure, the degree of variation in the species data owing to the spatial structure was partialled out by the use of covariables. The 4 steps in Table 2 represent the 4 fractions of the variations as suggested by Borcard et al. (1992). The p-values for each analysis were determined by a Monte Carlo permutation test. A Mantel test as proposed by Mantel (1967) and partial Mantel tests (Smouse et al. 1986) were computed to correlate and link the ecological structure with the spatial gradient present in the environment (Legendre & Troussellier 1988, Legendre & Fortin 1989). The 3 data matrices were transformed into distance matrices prior to these tests; euclidean distances among sampling locations were used to form the spatial distance matrix. The CANOCO program of ter Braak (1988b) was used for the CCA in conjunction with the Monte Carlo permutation test. The Mantel and partial Mantel tests were performed with the programs of the the R Package for Multivariate Data Analysis by Legendre & Vaudor (1991).

RESULTS

Spatial variation of the physical and biological data

The transport of water masses coming from the English Channel and entering the North Sea at Calais is greatly influenced by meteorological factors; the mean transport velocity can change from an estimate of 1 km d^{-1} for the English Channel to 5 km d^{-1} for the Dover-Calais strait (Pingree et al. 1975, Pingree & Maddock 1977, Prandle 1978). The general circulation pattern tends to be in the northeast direction, but the wind can change and reverse this general trend (Djenidi et al. 1986, Dewarumez et al. 1991). The first cruise on 10 June was characterized by a southwest wind with a mean wind velocity of 3.9 m s^{-1}. Wind conditions were reversed during the second cruise on 21 June with a northeast wind of mean velocity 5.3 m s^{-1}. The temperature distribution in Fig. 2A shows a clear input of warm water for the first cruise (18.70°C) at Stn 4, concomitant with Gravelines Power Station. The mean temperature value was 15.20°C. Under the influence of the southwest wind the colder water masses coming from the Dover-Calais strait can reach the Belgian coast as far as Middelkerke. The second

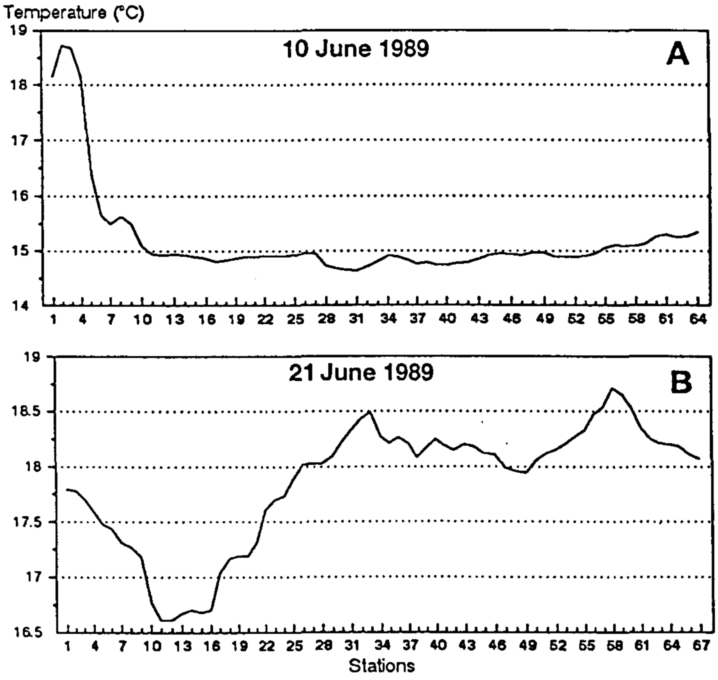

Fig. 2. (A) Temperature distribution for the first cruise shows an increase in temperature at Stn 4 (Gravelines Power Station), and the general lower temperature values coming from the Calais-Dover strait under the influence of the southwest wind. (B) Temperature distribution for the second cruise shows warmer water coming from the Belgian coast (Stn 67) reaching the coastal location (Stn 16) along the French coast under the influence of the northeast wind

cruise on 21 June (Fig. 2B) showed the effect of the northeast wind on temperature distribution; warmer water from the Belgian coast was transported southward, thus reaching the French coast. The mean temperature value was 17.85°C, decreasing to a minimum value of 16.65°C at Stn 11. The salinity distribution in Fig. 3A shows for the 10 June cruise the presence of 3 salinity fronts: one between Stns 2 & 7 of 0.6 ppt, which can be regarded as an anomaly due to the presence of the Gravelines Power Station; one between Stns 30 & 40 of 1.2 ppt; and one between Stns 52 & 60 of 1.4 ppt. The mean salinity value was 32.85 ppt. For the second cruise on 21 June (Fig. 3B), the salinity distribution showed the presence of 2 fronts: one from Stns 34 to 40 of 0.8 ppt, and one from Stns 48 to 52 of 0.5 ppt. The mean salinity value was 32.69 ppt. As an example of the spatial distribution of one of the meroplankton taxa, the density values of *Polydora* spp. are presented together with the temperature and salinity distribution. The adults of *Polydora* spp. were present in the macrobenthos as a distinct population, one characterizing the French coast (Souplet & Dewarumez 1980, Souplet et al. 1980), and one the Belgian coast (Daro & Polk 1973). The larval dispersion of these polychaetes under different wind conditions can bring changes in the spatial distibution and spatial structure of the population. The highest density values of *Polydora* spp. were found on 10 June (Fig. 4A) at Stn 4, with 160 ind. m^{-3}, concomitant with the highest temperature value of 18.7°C, and also at Stn 55, with 110 ind. m^{-3}. The larvae distribution in relation to salinity (Fig. 5A) showed that higher densities were located before and after the salinity front (Stns 3, 4, 43, 55). For 21 June (Figs. 4B & 5B), the highest density value was found at Stn 58 with 2080 ind. m^{-3}, concomitant with high temperature values (18.6°C), and located after the salinity front. During this cruise the effect of the wind was apparent in that more larvae of *Polydora* spp. were transported south along the Belgian coast (Stns 67 to 50), reaching the French coast as far as Stn 25.

Canonical correspondence analyses

The results of the 4 CCAs for each cruise are presented in Table 3. The percentage of the total variation of the species matrix accounted

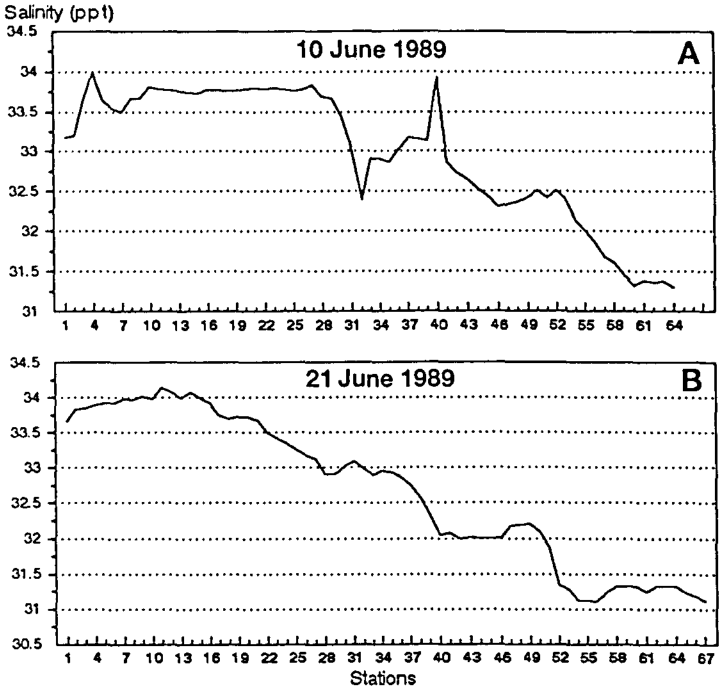

Fig. 3. (A) Salinity distribution for the first cruise shows the presence of salinity fronts between Stns 2 & 7 (Gravelines Power Station), 30 & 40, 52 & 60. (B) Salinity distribution for the second cruise shows the presence of 2 salinity fronts between Stns 34 & 40, 48 & 52; the effect of the northeast wind enhances the transport of less saline water coming from the Scheldt estuary and reaching the French coast

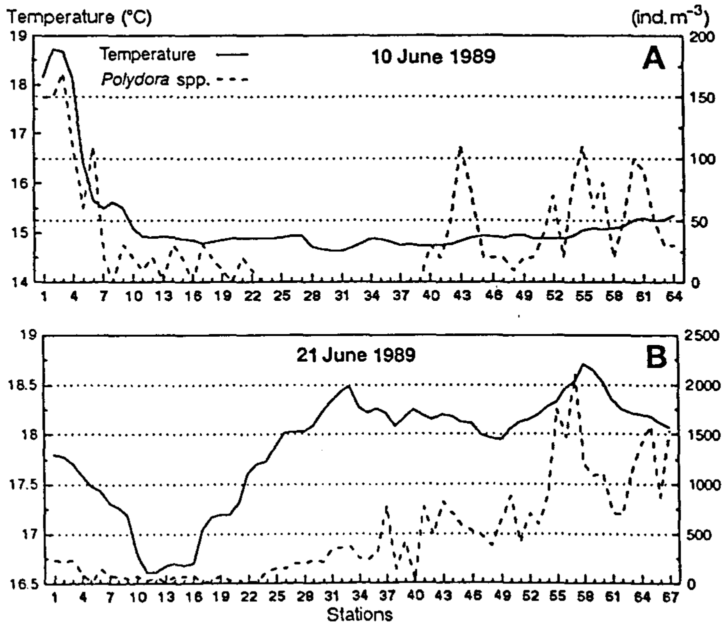

Fig. 4. *Polydora* spp. density distribution and temperature for (A) the first cruise shows 2 distinct populations, one from Stns 1 to 23 (French coast) and one from Stns 39 to 64 (French-Belgian coast), (B) the second cruise; due to the northeast wind more larvae are transported southward

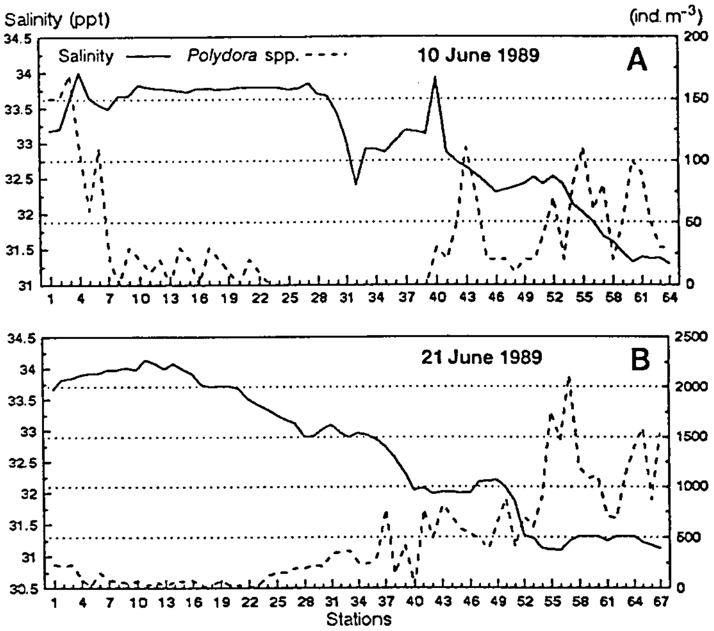

Fig. 5. *Polydora* spp. density distribution and salinity for (A) the first cruise, (B) the second cruise. Higher densities of larvae are found before or after a salinity front

for by each step of the analysis was obtained as suggested by Borcard et al. (1992) and Borcard & Legendre (1994). For the 10 June cruise (Fig. 6A), the whole variation of the species matrix was 67.3% and was explained in the following fractions: Fraction (a) representing the nonspatial environmental variation, accounted for 9.6% of the total variation; Fraction (b), which can be regarded as the spatially structured environmental variation, accounted for 42.6%; Fraction (c), representing the spatial species variation not shared by the environmental variables, accounted for 15.1% of the total variation, and Fraction (d), which can be regarded as the expression of the unexplained variation and the possible stochastic fluctuations, was equal to 32.7% of the total variation. Results for 21 June are presented in Fig. 6B.

The Monte Carlo permutation tests on the trace statistics for both sets of analyses were significant at a Bonferroni-corrected α' probability level of 0.05/4 = 0.0125. During the first cruise, the effect of the southwest wind maintained the general water circulation pattern along the coastal locations sampled, and mixing with water masses coming from the Scheldt estuary did not occur. During the second cruise, northeast wind conditions reversed the general trend of the water circulation pattern, inducing more mixing with the water masses coming from the Scheldt estuary. The change in environmental conditions resulted in an increase of Fractions (a) and (b) on 21 June. The variation in the species matrix due to the influence of the environment was 1.5% higher, and the influence of the environment together with the spatial component was 5.5% higher. The amount of the strictly spatial variation in Fraction (c) that remains unexplained by environmental variables was higher during the first cruise, suggesting that under the southwest wind condition the space component is stronger. In the reversed wind condition, Fraction (c) was reduced from 15.1% to 8.5%, showing the greater importance of changes in the environmental conditions rather than the purely spatial. The undetermined variation, Fraction (d), was very similar for both cruises, suggesting that this amount of variation can be regarded as the effect of local effects, such as short-term tidally induced variability and mesoscale changes in the residual current pattern. It is however very important that the results identify and quantify this information.

Table 3. Results of the canonical correspondence analyses (CCA) are reported as the amount of canonical inertia explained by the SE (species-environment matrices), SS (species-space matrices), SE/S (species-environment matrices constrained by the space matrix) and SS/E (species-space matrices constrained by the environment matrix). Total inertia indicates the sum of all unconstrained eigenvalues. The overall amount of explained variation as a percentage of the total variation of the species matrix for 10 June 1989 was 67.3%, obtained by summing Steps (1) & (4), or Steps (2) & (3), and partitioned as: (a) nonspatial environmental variation (Step 3): 9.6%; (b) spatially structured environmental variation (Steps 1 to 3 or Steps 2 to 4): 42.6%; (c) spatial species variation not shared by the environmental variables (Step 4): 15.1%; (d) unexplained variation and stochastic fluctuations: 100 – 67.3 = 32.7%. For 21 June 1989 the total explained variation was 67.7% and partitioned as: (a) 11.1%, (b) 48.1%, (c) 8.5%, (d) 32.3%

Date	SE	SS	SE/S	SS/E	Total inertia
10 June 1989	0.152	0.168	0.028	0.044	0.291
21 June 1989	0.634	0.607	0.119	0.091	1.07

Percentage of the variation

CCA 10 June 1989	CCA 21 June 1989
Step (1): 0.152 × 100/0.291 = 52.2%	Step (1): 0.634 × 100/1.07 = 59.2%
Step (2): 0.168 × 100/0.291 = 57.7%	Step (2): 0.607 × 100/1.07 = 56.7%
Step (3): 0.028 × 100/0.291 = 9.6%	Step (3): 0.119 × 100/1.07 = 11.1%
Step (4): 0.044 × 100/0.291 = 15.1%	Step (4): 0.091 × 100/1.07 = 8.5%
Total explained variation = 67.3%	Total explained variation = 67.7%

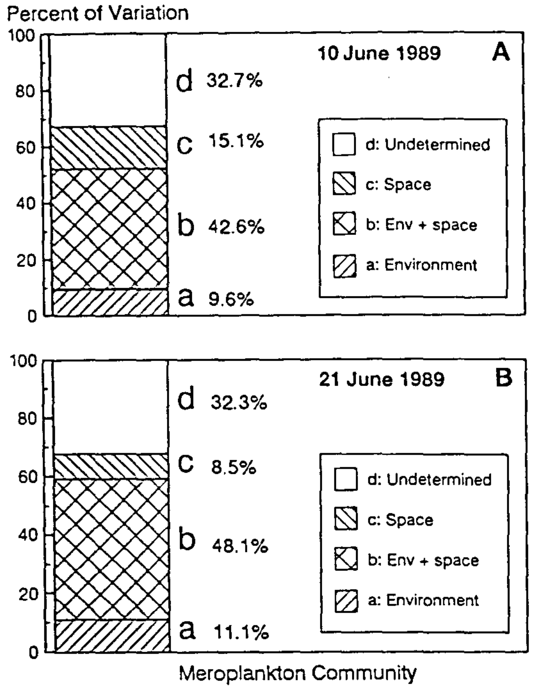

Fig. 6. (A) Variation partitioning of the meroplankton community data matrix for the first cruise. The whole variation of the species matrix is partitioned into 4 fractions: (a) nonspatial environmental, (b) spatially structured environmental variation, (c) spatial species variation not shared by the environmental variable, (d) undetermined variation and stochastic fluctuations. (B) Variation partitioning of the meroplankton community data matrix for the second cruise

Mantel and partial Mantel tests

The Mantel test among the 3 matrices considered (1) geographic distance, (2) environmental variables and (3) species for the 2 sampling dates, with the following correlations:

10 June 1989: $R_{1,2} = 0.498$ $(p < 0.001)$
$R_{1,3} = 0.389$ $(p < 0.001)$
$R_{2,3} = 0.512$ $(p < 0.001)$

21 June 1989: $R_{1,2} = 0.560$ $(p < 0.001)$
$R_{1,3} = 0.315$ $(p < 0.001)$
$R_{2,3} = 0.589$ $(p < 0.001)$

For both sets of calculations the null hypothesis (H_0) that the multivariate data are not autocorrelated as a gradient was rejected at the 1% significance level according to the test of significance in Mantel statistics (Mantel 1967, Legendre & Fortin 1989).

The partial Mantel tests for the 2 cruises gave the following correlations:

10 June 1989: $R_{1,2} = 0.377$ $(p < 0.001)^*$
$R_{1,3} = 0.179$ $(p = 0.04592)$ ns
$R_{2,3} = 0.398$ $(p < 0.001)^*$

21 June 1989: $R_{1,2} = 0.488$ $(p < 0.001)^*$
$R_{1,3} = -0.022$ $(p = 0.05612)$ ns
$R_{2,3} = 0.524$ $(p < 0.001)^*$

The partial Mantel tests for the 2 transects show that the computed partial correlation between the geography (space) matrix and the species (meroplankton) matrix ($R_{1,3}$) was non-significant (ns). The correlations between the geography (space) matrix and the environment ($R_{1,2}$), and between the environment and the species (meroplankton, $R_{2,3}$) were highly significant (*) at a Bonferroni-corrected α' probability level of 0.05/4 = 0.0125. This result shows that the structure in the meroplankton distribution comes from the structuring of the environmental variable. If we compare the 2 sampling cruises, the Mantel statistic describing the influence of the environment on the meroplankton community structure for the 10 June cruise is reduced from 0.512 to 0.398 when controlling for the effect of space, but remains very highly significant. The specific influence of the environment is therefore 0.398, while the difference of 0.254 (0.498 × 0.512 = 0.254) can be regarded as the influence of the spatial structure imbedded in the environment on the species distribution. For 21 June, the Mantel statistic describing the influence of the environment on meroplankton was reduced from 0.589 to 0.524 when controlling for the effect of space. The influence of the environment of 0.524, and the difference of 0.329 (0.589 × 0.560 = 0.329), correspond to the influence on the species distribution exerted by the spatial structure present in the environment. The Mantel and partial Mantel tests were in accordance with the results of the CCAs. The spatial gradient present in the environment can partly explain the variation we observed in the distribution patterns of *Polydora* spp. This shows that changes in the spatial structure of the environment do influence the meroplankton community structure. A more important point as proposed by Legendre & Troussellier (1988) is to interpret Mantel and partial Mantel tests in a causal framework. Following their models, the results above indicate that the environmental matrix has a significant effect on the species matrix, but there remains some significant yet unexplained spatial variation in the species data.

DISCUSSION AND CONCLUSION

The meroplankton community composition changes because of changes in ecological descriptors with reference to the environmental control model. Hudon & Lamarche (1989) suggested the importance of considering the physiographic characteristics of the study area in order to test the effects of climatic and hydrographic factors on the advection and survival of planktonic crustacean larvae. The effects of wind-driven water mass exchange on the distribution of pelagic organisms was tested by Christopher et al. (1987).

The results presented in this paper suggest the importance of considering *a priori* the presence of spatial autocorrelation in the data and to regard this as a departure point for any ecological research. As suggested by Mackas (1984), it is important to determine to what extent samples in different locations are dependent on their separation. The use of CCA offered the possibility to factor out the covariables, in this case environmental variables and the geographic distance between samples, in a partial ordination (ter Braak 1987), and to test the variation occurring between samples along a successional pattern (Palmer 1993). The inclusion of space in the form of a spatial distance matrix allowed quantification of the amount of variability associated with a precise spatial structure. This variability, expressed by the Fraction (c), can either be explained or not explained by the environmental variables considered, and can also suggest the importance of using other environmental variables to explain spatial variability. Species variability is not always related and controlled directly by the set of environmental variables chosen, but by other effects such as meteorological events or top-down ecological processes (Legendre 1990). The CCA associated with the Monte Carlo permutation test and the method proposed by Borcard et al. (1992) were found to be adequate for representing species environmental relationships, taking into account the spatial component, and for testing the significance on the environmental variables. In this canonical ordination technique the linear combination of the environmental variables that can account for the dispersion of the species score is more strongly expressed by the first axis. This method also performs well in the presence of skewed species distributions (Palmer 1993), and the arch effect present in other multivariate techniques is generally avoided (Økland 1986, Michin 1987).

The utility of CCA in respect to other ordination methods have been extensively discussed by several authors (ter Braak & Prentice 1988, Palmer 1993). In this study the use of the covariables and associated significance tests further extends the validity of this ordination technique. The concept of homogeneity in ecological communities on the basis of locations sampled can be explored by using CCA and the selected set of environmental variables as covariables. The use of Mantel and partial Mantel tests provided further useful information on the significance of spatial autocorrelation. The Mantel test for matrix correlation measured to what extent the variation in distance matrix A corresponded to the variation in distance matrix B. The partial Mantel test measured the level of correlation between matrices A and B, while controlling for the effects exerted by matrix C. The partial Mantel statistic can be regarded as causal modelling (Smouse et al. 1986, Legendre & Troussellier 1988), and used to predict, as in the present work, the possible effects of the environmental variables on the meroplankton community structure compared to the effect of space.

The presence of a spatial structure shared by the species community and the environment may, as suggested by Legendre & Troussellier (1988), overestimate the interaction occurring at different degrees of intensity between the species and the set of environmental variables measured. The method used, however, allowed us to quantify this kind of association and to give useful information in a more classical modelling approach. The Mantel and partial Mantel tests were used to remove the influence of environmental variables from classification in biological space, and to point out the importance of spatial and environmental structures within the system studied. The changes in wind conditions explained the possible transport of meroplankton in the opposite direction to the prevailing northeasterly residual tidal current (Belgrano et al. 1990), allowing for a southwesterly dispersal (Luczack et al. 1993). Monitoring the dispersal of meroplankton species at a pelagic level can be extremely useful as a biological tracer of water masses and as a quantifier of the availability of larvae to the adult benthic community in relation to recruitment processes.

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Spatial structure and ecological variation of meroplankton on the Belgian-Dutch coast of the North Sea

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ABSTRACT: Spatial structure and the spatial autocorrelation of meroplankton compositional patterns were investigated by canonical correspondence analysis (CCA) and complementary Mantel statistics to contribute to the understanding of the complex biological fluxes in the coastal waters between the Belgian coast and the Scheldt estuary region. The use of covariables in a partial ordination method allows the partitioning of environmental and spatial variation in order to test meroplankton successional patterns. The direction and intensity of wind was responsible for a northeasterly transport of larvae. Reverse wind conditions allowed for a southwesterly larval dispersal. The spatial pattern of the species comes from the spatial pattern of the environmental variables, and is completely explained by them, so that no significant spatial pattern remains in the species data after controlling for the effect of the environmental variables. The spatial structure therefore can be regarded as an explanatory variable in ecological studies.

KEY WORDS: North Sea · Meroplankton · Spatial heterogeneity · Canonical correspondence analysis (CCA) · Constrained ordination · Mantel statistics · Environmental control model

INTRODUCTION

The aim of this study was to quantify the spatial heterogeneity of the meroplankton community structure in a coastal location situated within an estuarine system, and to identify the factors responsible for it. Studying spatial structure in ecosystems is important for understanding ecological stability (May 1984), and should be considered in ecological research programs (Legendre et al. 1989). The development of new statistical methods (ter Braak 1987, 1988b, Borcard et al. 1992) allows detailed study of the spatial structuring of the environment related to biological processes and further understanding of community-based spatial processes. The hydrodynamic regime of the Southern Bight of the North Sea is characterized by strong mesoscale currents produced by tides and winds, concomitant with residual currents generated by the flow through the North Sea of the 2 branches of the North Atlantic current (Nihoul 1975, 1980, Nihoul & Runfala 1981, Nihoul & Ronday 1975), and by the presence of a residual gyre along the Belgian coastal zone off Zeebrugge. The Westerschelde estuary ebb-tide channel, running parallel to the northern Belgian coast reaching Oostende, and the flood-tide channel running parallel to the Dutch coast at Vlissingen are responsible for the dilution of the Westerschelde estuary waters with the open sea (Nihoul et al. 1989). The Oosterschelde estuary is characterized by strong tidal currents and can be regarded as a well-mixed zone (Dronkers & Zimmerman 1982). The closure of 2 storm surge barriers in 1986 and 1987 (Wetsteyn et al. 1990) resulted in the reduction of the amount of water exchange with the North Sea by approximately 28% (Leewis & Waardenburg 1990).

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METHODS

Data. The sampling campaigns were conducted on 5 and 11 June 1990 along a transect from Zeebrugge (Belgium) to the eastern Scheldt estuary (The Netherlands), 40 nautical miles into the Southern Bight of the North Sea (Fig. 1), in connection with the research program RENORA founded by the PNDR (Programme National sur le Déterminisme du Recrutement, France). The NOAA-AVHRR satellite images for the period of the RENORA campaign (May to June 1990) and the wind direction and velocity were obtained from KNMI (Royal Netherlands Meteorological Institute). Fluorometry, temperature, salinity and water density were measured at 20 s intervals by a hydrological probe. Depth and corrected depth were measured on board by the Color Echo Sounder system (model Raytheon V800). For meroplankton, 70 and 76 samples were collected during the 2 cruises at 3 m depth by a volumetric pump (PCM Moineau, 200 l min^{-1}), and sorted according to Frontier (1969, 1972). Environmental variables measured and taxonomic groupings used are listed in Table 1.

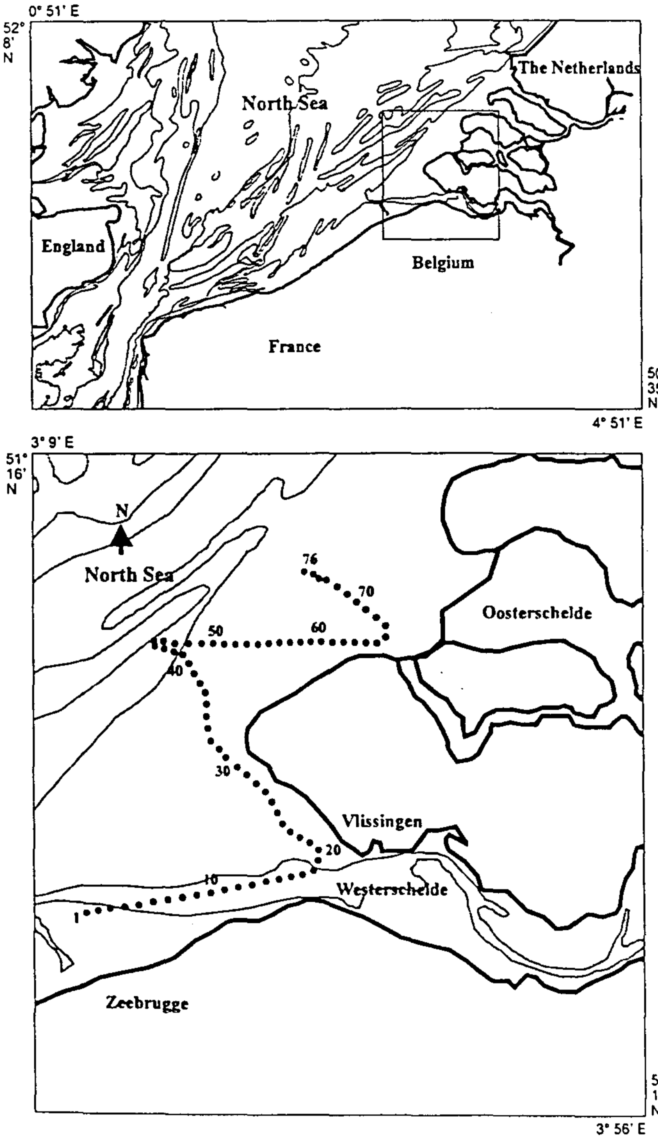

Fig. 1. Schematic map of the study area. The sampling transect along the coastline is represented by a dotted line

Table 1. Taxonomic groups and environmental variables

Taxonomic groups	Environmental variables
Lanice conchilega	Salinity (ppt)
Pectinaria koreni	Temperature (°C)
Magelona mirabilis	Density (kg m^{-3})
Polydora spp.	Corrected depth (m)
Nephtys spp.	Tidal height (m)
Ampharetidae	Fluorometry (chl *a* µg l^{-1})
Bivalves	
Echinoids	
Ophiuroids	

Numerical analysis. The 3 matrix data sets were tested with a canonical correspondence analysis (CCA). The CCAs were performed following ter Braak (1988a), and the method proposed by Borcard et al. (1992). The p-values for each analysis were determined by a Monte Carlo permutation test. The spatial distance matrix was produced by a cubic trend surface regression based on the geographic coordinates of the sampling stations along the path of the boat (Borcard et al. 1992). The Mantel and partial Mantel tests were performed following the methods proposed by Mantel (1967), Smouse et al. (1986), Legendre & Troussellier (1988) and Legendre & Fortin (1989). The CANOCO program (ter Braak 1988b), and the R Package for Multivariate Data Analysis (Legendre & Vaudor 1991) were also used in this study.

RESULTS

Abiotic and biotic spatial variation

The composite NOAA-AVHRR images from the end of May to mid June 1990 clearly show the major spatial differences in sea surface temperatures (Fig. 2A) and suspended matter distribution (Fig. 2B). Temperature values range from 15°C close to the coast to 13°C in the waters surrounding the Schelde estuarine system. The suspended matter distribution showed that the major inputs of nutrient-rich waters came from the Westerschelde. The first cruise on 5 June was carried out after a week of strong southwest winds with gusts up to 30 m s^{-1}; during sampling the southwest wind velocity decreased to 7 m s^{-1}. The second cruise on 11 June was

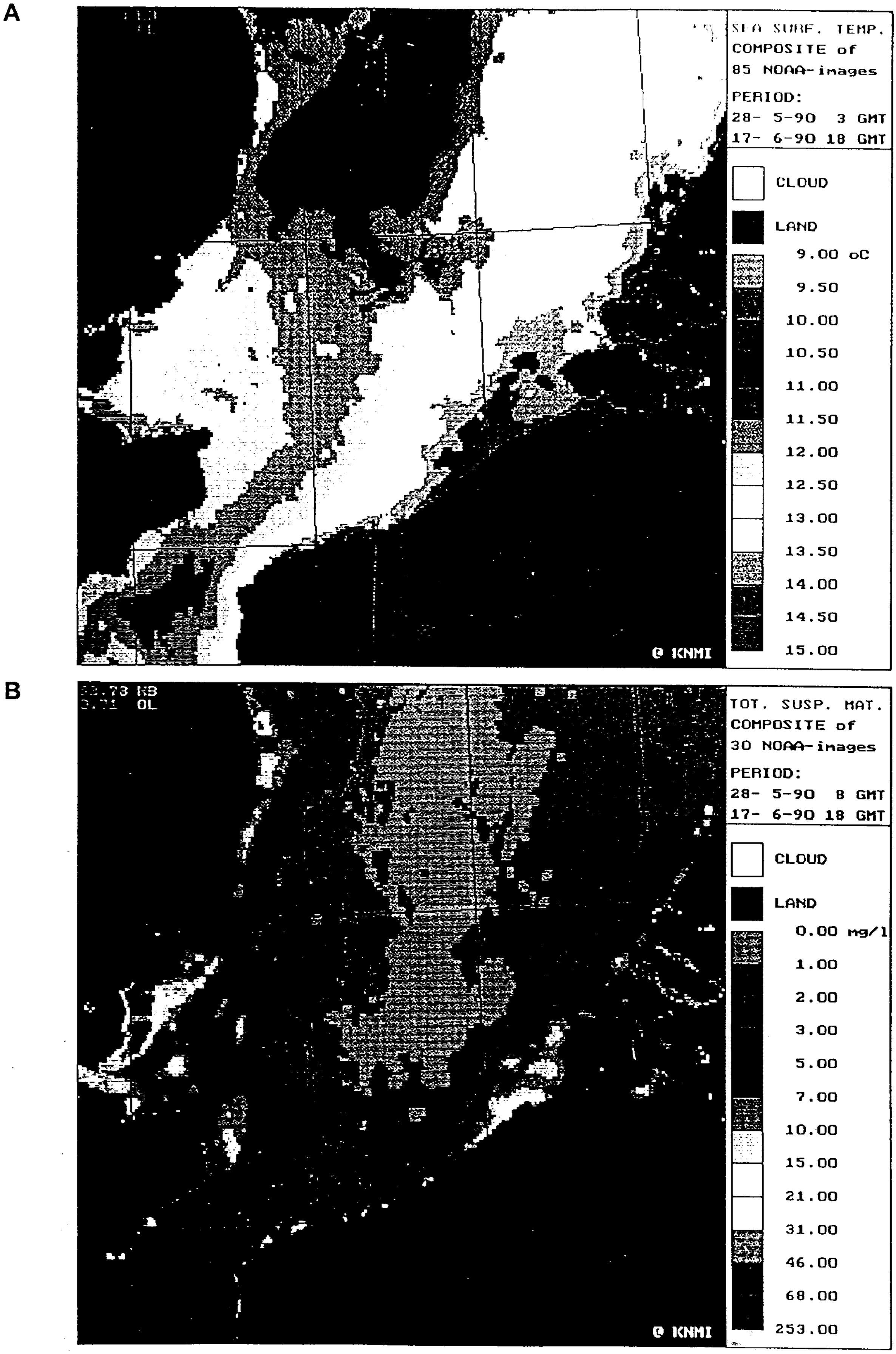

Fig. 2. NOOAA-AVHRR satellite composite images (KNMI 1990), showing (A) the sea surface temperature distribution and (B) the total suspended matter distribution for 28 May to 17 June

subjected to a northeast wind with an estimated wind velocity of 5.5 m s^{-1}. The temperature distribution for 5 June (Fig. 3A) showed the highest value of 16.3°C at Stn 20 at the mouth of the Westerschelde, decreased towards the Oosterschelde, and reached the lowest value of 15.91°C at Stn 64. During the second cruise the temperature distribution (Fig. 3B) clearly showed the input of warmer water coming from the Westerschelde, with the highest value of 16.29°C at Stn 21. The salinity distribution for 5 June (Fig. 4A) showed that the highest salinity value of 32.73 ppt was found at Stn 15 on the northern Belgian coast, and decreased towards the Westerschelde (Stn 20) and along the Dutch coast (Stns 30 to 40); the lowest salinity value of 32.47 ppt was found in proximity to the Oosterschelde at Stn 55. For 11 June the salinity distribution (Fig. 4B) clearly showed the presence of the Westerschelde with the lowest value of 30.10 ppt at Stn 21. The highest salinity was found at Stn 41 along the Dutch coast, with a value of 32.95 ppt. The total suspended matter distribution, as a measure of chlorophyll *a* (chl *a*), showed on 5 June (Fig. 5A) the highest value of 20 chl *a* µg l^{-1} at Stns 22 and 28 at the mouth of the Westerschelde.

The fluorometry distribution decreased as we moved along the Dutch coast, reaching the lowest value of 7.0 chl *a* µg l^{-1} at Stn 54. During the second cruise, the fluorometry distribution (Fig. 4B) showed the input of nutrient-rich waters (22.05 chl *a* µg l^{-1}) coming from the Westerschelde along the flood-tide channel running parallel to the Dutch coast from Stns 21 to 30. At the Oosterschelde (Stn 70), the fluorometry value was 17.2 chl *a* µg l^{-1}. The distribution of the 3 environmental variables described here was subjected to a southwest wind during the first cruise, which enhanced mixing. During the second cruise, a light northeast wind condition caused less mixing to occur.

As an example of the spatial distribution of the taxonomic group, we present the distribution of the ophiuroid brittle star larvae along with temperature, salinity, and fluorometry distribution. The ophiuroid density distribution with temperature (Fig. 6A) showed the highest density value of 120 ind. m^{-3} at Stn 60 for the first cruise, concomitant with a temperature value of 16°C. On 11 June (Fig. 6B), the ophiuroid density distribution showed 2 distinct input points between Stns 26 and 31 (500 ind. m^{-3}) at the mouth of the western Scheldt, and

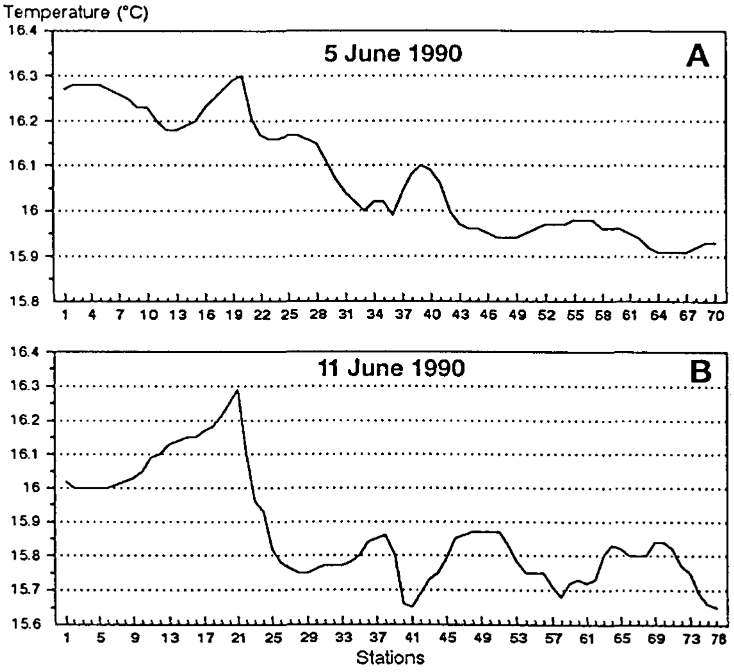

Fig. 3. (A) Temperature distribution for the first cruise, influenced by the southwest wind; (B) temperature distribution for the second cruise, influenced by a light northeast wind

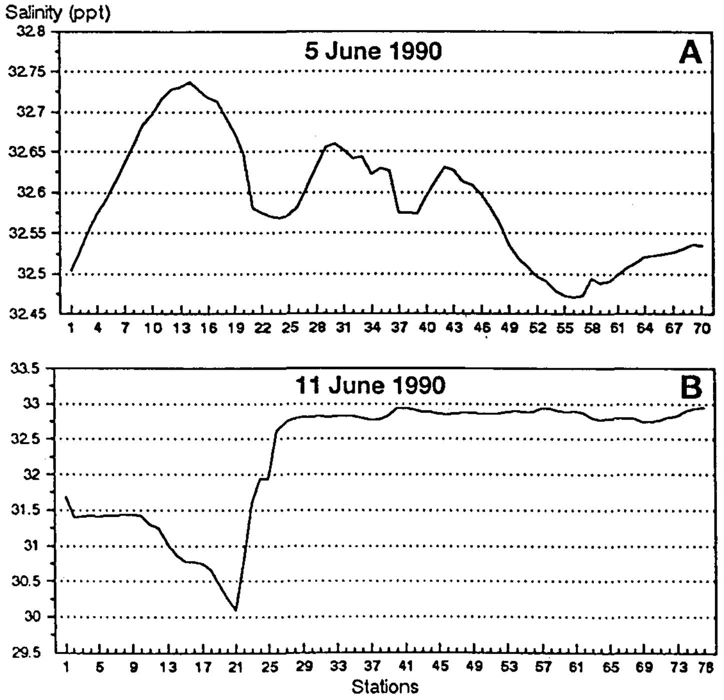

Fig. 4. (A) Salinity distribution for the first cruise, (B) salinity distribution for the second cruise showing the presence of Westerschelde water at Stn 21

between Stns 64 and 76 (590 ind. m^{-3}), at the eastern Scheldt. For the first transect the highest density of ophiuroid was associated with a salinity value of 32.51 ppt (Fig. 7A) at Stn 60; for the second cruise (Fig. 7B), the highest density was found at Stn 69 at a salinity value of 32.92 ppt. When considering the ophiuroid distribution in respect to fluorometry, we found that for 5 June (Fig. 8A), the highest density values of ophiuroid were associated with a fluorometry of 18 chl *a* µg l^{-1} (Stn 22), at the western Scheldt, and at Stn 60 along the Dutch coast with a lower fluorometry value of 7.9 chl *a* µg l^{-1}. For 11 June (Fig. 8B), the highest densities were found at Stn 28 along the flood-tide channel of the western Scheldt in proximity to Vlissingen, at a fluorometry value of 19.9 chl *a* µg l^{-1}, and at Stn 69 at the eastern Scheldt at a lower fluorometry value of 7.9 chl *a* µg l^{-1}. The spatial distribution of the ophiuroid larvae suggested the existence of 2 distinct input points, at the 2 branches of the Scheldt estuary. During the first cruise the effect of the southwest wind enhanced northward transport of ophiuroid larvae and their dispersal over a larger area. During the second cruise, the lower wind velocity and the reversed direction limited the larval dispersion to more confined locations.

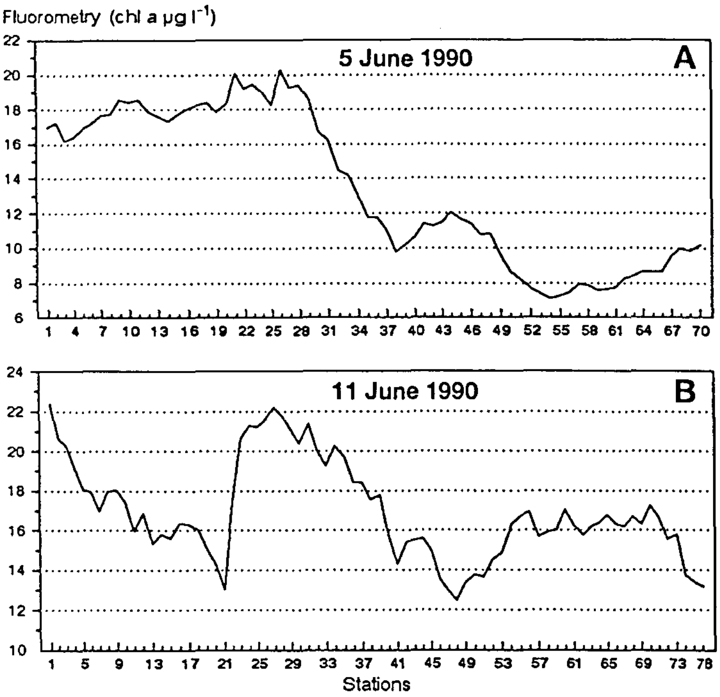

Fig. 5. (A) Fluorometry distribution for the first cruise, showing more mixing occurring due to the effects of the southwest wind; (B) fluorometry distribution for the second cruise, with light northeast wind conditions and the presence of nutrient-rich waters coming from the Westerschelde (Stns 22 to 33). Input from the Oosterschelde (Stns 61 to 76) is clearly detectable

Canonical correspondence analyses

The CCAs for each cruise are presented in Table 2. The percentage of the total variation of the species matrix was divided into 4 fractions. For the first cruise on 5 June (Fig. 9A), the whole variation of the species matrix was 66.3%, and was explained by Fractions (a) 9.5%, the nonspatial environmental variation: (b) 43.1%, the spatially structured environmental variation, (c) 13.7%, the spatial species variation not shared by the environmental variables; and (d) 33.7%, the expression of the unexplained variation. For the second cruise on 21 June the results are reported in Fig. 9B. The Monte Carlo permutation test on the trace statistics for both sets of analyses was significant at a Bonferroni-corrected α' probability level of 0.05/4 = 0.0125. The effect of the southwest wind during the first cruise enhanced more mixing with the nutrient-rich waters coming from the Westerschelde. Fraction (c), representing the purely spatial variation, showed the im-

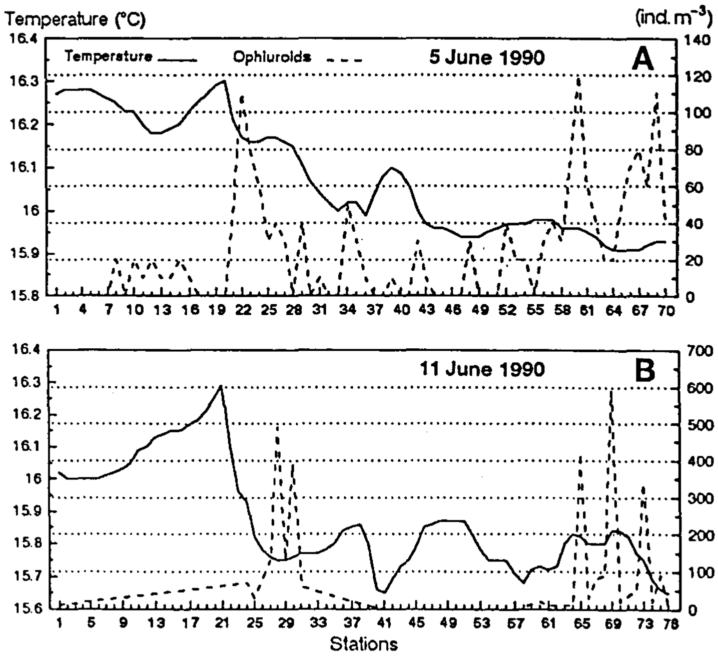

Fig. 6. Distribution of ophiuroid larvae with temperatures for (A) the first cruise, (B) the second cruise, showing 2 distinct populations

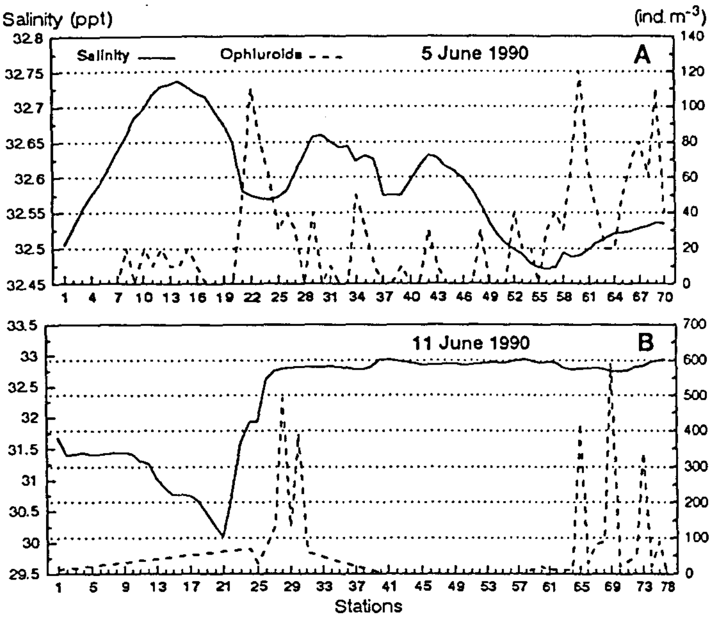

Fig. 7. Distribution of ophiuroid larvae with salinity for (A) the first cruise, (B) the second cruise

portance of space as an explanatory variable. The unexplained variation, Fraction (d), would have been larger if the spatial structure was not included in the model. The use of more environmental variables is not necessarily a solution for explaining this fraction of the variability. The unexplained variation can partly represent the large amount of stochastic variation, and partially unmeasured factors and biotic processes, such as behavioural responses, whose spatial structures are still difficult to model (H. J. B. Birks pers. comm.). For the second cruise Fraction (b) was higher, confirming that the structure in the meroplankton distribution comes from the structuring of environmental variables. To be able to quantify the different fractions that explain the species variation and allow a better understanding of the variation between the spatial and environmental component and also to derive a general framework for the causal modelling of the various fractions partitioned it was necessary to perform the complimentary Mantel statistics (Borcard & Legendre 1994).

Mantel and partial Mantel tests

The Mantel test among the 3 matrices considered (1) geographic distance, (2) environmental variables, and (3) species for the 2 sampling dates, with the following correlations:

5 June 1990: $R_{1,2} = 0.398$ ($p < 0.001$)
$R_{1,3} = 0.158$ ($p < 0.001$)
$R_{2,3} = 0.412$ ($p < 0.001$)

11 June 1990: $R_{1,2} = 0.425$ ($p < 0.001$)
$R_{1,3} = 0.181$ ($p < 0.001$)
$R_{2,3} = 0.449$ ($p < 0.001$)

For both sets of calculations the null hypothesis (H_0) that the multivariate data are not autocorrelated as a gradient was rejected at the 1 % significance level according to the test of significance in Mantel statistics (Mantel 1967). The partial Mantel tests for the 2 campaigns gave the following correlations:

5 June 1990: $R_{1,2} = 0.370$ ($p < 0.001$)*
$R_{1,3} = -0.007$ ($p = 0.65692$) ns
$R_{2,3} = 0.385$ ($p < 0.001$)*

11 June 1990: $R_{1,2} = 0.391$ ($p < 0.001$)*
$R_{1,3} = -0.012$ ($p = 0.87456$) ns
$R_{2,3} = 0.417$ ($p < 0.001$)*

The partial Mantel tests for the 2 transects show that the computed partial correlation between the geography (space) matrix and the species (meroplankton) matrix ($R_{1,3}$) was non-significant (ns). The correlations between the geography (space) matrix and the environment ($R_{1,2}$); and between the environment and the species (meroplankton, $R_{2,3}$) were highly significant (*) at a Bonferroni-corrected α' probability level of 0.05/4 = 0.0125. This result shows that the structure in the meroplankton distribution

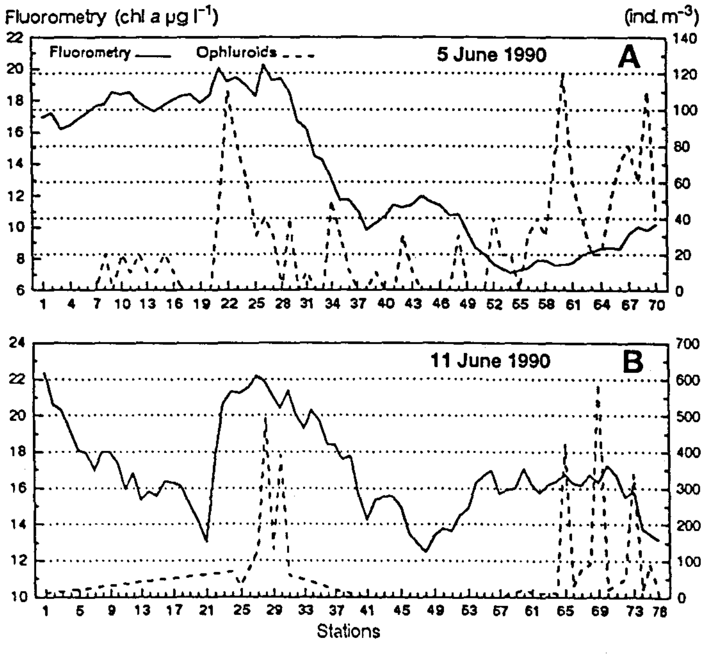

Fig. 8. Distribution of ophiuroid larvae with fluorometry for (A) the first cruise, (B) the second cruise

Table 2. Results of the canonical correspondence analyses (CCA) are reported as the amount of canonical inertia explained by the SE (species-environment matrices), SS (species-space matrices), SE/S (species-environment matrices constrained by the space matrix), and SS/E (species-space matrices constrained by the environment matrix). Total inertia indicates the sum of all unconstrained eigenvalues. The overall amount of explained variation as a percentage of the total variation of the species-matrix for the 5 June 1990 was 66.3%, obtained by summing Steps (1) & (4), or Steps (2) & (3), and partitioned as: (a) nonspatial environmental variation (Step 3): 9.5%; (b) spatially structured environmental variation (Steps 1 to 3, or Steps 2 to 4): 43.1%; (c) spatial species variation not shared by environmental variables (Step 4): 13.7%; (d) unexplained variation and stochastic fluctuations: 100 − 66.3 = 33.7%. For 11 June 1990 the total explained variation was 69.5% and partitioned as: (a) 10.5%, (b) 50.3%, (c) 8.7%, (d) 30.5%

Date	SE	SS	SE/S	SS/E	Total inertia
5 June 1990	0.149	0.161	0.027	0.039	0.283
11 June 1990	0.621	0.602	0.105	0.089	1.02

Percentage of variation

CCA 5 June 1990	CCA 11 June 1990
Step (1): 0.149 × 100/0.283 = 52.6%	Step (1): 0.621 × 100/1.02 = 60.8%
Step (2): 0.161 × 100/0.283 = 56.8%	Step (2): 0.602 × 100/1.02 = 59%
Step (3): 0.027 × 100/0.283 = 9.5%	Step (3): 0.105 × 100/1.02 = 10.5%
Step (4): 0.039 × 100/0.283 = 13.7%	Step (4): 0.089 × 100/1.02 = 8.7%
Total explained variation = 66.3%	Total explained variation = 69.5%

comes from the structuring of the environmental variables. The Mantel statistic describing the influence of the environment on the meroplankton community structure for 5 June is reduced from 0.412 to 0.385 when controlling for the effect of space. The specific influence of the environment is therefore 0.385, while the difference of 0.163 (0.398 × 0.412 = 0.163) can be regarded as the influence of the spatial structure imbedded in the environment on the species distribution. For 11 June, the Mantel statistic describing the influence of the environment on meroplankton was reduced from 0.449 to 0.417 when controlling for the effect of space. The influence of the environment of 0.417, and the difference of 0.190 (0.425 × 0.449 = 0.190), correspond to the influence on the species distribution exerted by the spatial structure present in the environment.

DISCUSSION AND CONCLUSION

As stated by Gould (1970), 'all our efforts to understand spatial pattern, structure, and process have indicated that it is precisely the lack of independence, the interdependence of spatial phenomena that allows us to substitute pattern, and therefore predictability and order, for the chaos and apparent lack of interdependence of things in time and space'. The results obtained in this study show the importance of considering the spatial component to describe the distribution of pelagic organisms. The innovative method of Borcard et al. (1992) quantified the percentage of the variation in the species matrix accounted for by the different fractions considered.

During the first cruise on 5 June, Fraction (c), representing the percentage of the variation in the species matrix due to the 'purely spatial' structure, was slightly higher than in the second cruise. This result suggested that in the coastal locations considered, the effect of strong southwest winds induces changes in the surface water distribution, and therefore, spatial structure plays an important role as a functional factor in the ecosystem. During the 11 June cruise the wind conditions were reversed, with a northeast wind and a very weak velocity. Under these circumstances the environmental structure was more evident, showing the presence of the 2 branches of the

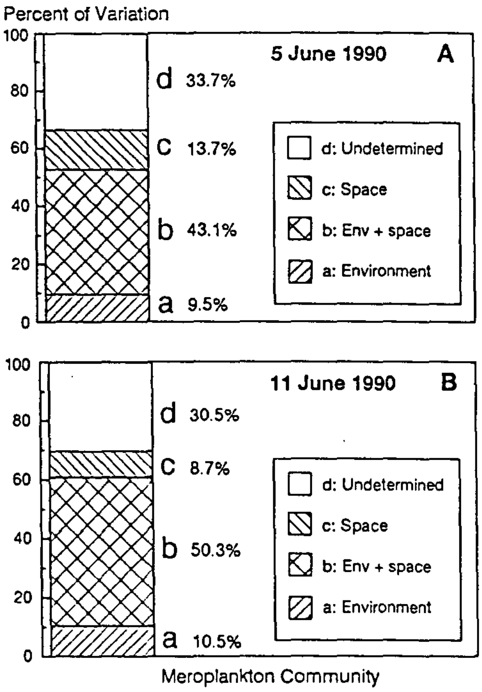

Fig. 9. (A) Variation partitioning of the meroplankton community data matrix for the first cruise. The whole variation of the species matrix is partitioned into 4 fractions: (a) nonspatial environmental, (b) spatially structured environmental variation, (c) spatial species variation not shared by the environmental variable, (d) undetermined variation and stochastic fluctuations. (B) Variation partitioning of the meroplankton community data matrix for the second cruise

Schelde clearly defined by the spatial distribution of abiotic variables. Fraction (b), representing the percentage of variation in the species matrix due to environment and space, was higher than in the first cruise, suggesting that with less wind forcing the surface water and less mixing, the spatial changes in the environmental variables more clearly explained the variation observed at the species level. The use of more environmental variables in the CCA allowed for the performance of a multiple linear least-squares regression with the weighted averages of the species as dependent variables and the environmental variables as independent variables (Palmer 1993). The use of covariables as suggested by ter Braak (1988a) as partial ordination allowed the partialling of the environmental and spatial variations, and the linkage of these factors to the species data (Legendre 1990).

The results obtained from the Mantel tests clarified, as suggested by Legendre & Troussellier (1988), the relations between the factors influencing the environmental variables and the influence of the environment on species distribution. The spatial fraction of the variation can be used as an explanatory variable when the environmental factors considered are not sufficient to explain the remaining spatial variation. The use of spatial terms in the data analysis allowed us to explain the spatial variation of the species composition and to segregate the deterministic components of the unexplained variation, Fraction (d), to a local area within the sampling locations (Borcard et al. 1992). CCA and the complementary Mantel statistics can be used as exploratory techniques to investigate homogeneous ecological communities. The partial Mantel tests appeared to be quite powerful in bringing out dependence patterns between linked biological communities and their environments.

The spatial structure in the species data considered in this work came from a spatial structuring of the environmental variables with reference to the environmental control model (ECM) (Whittaker 1956, Borcard & Legendre 1994). The partial ordination technique allowed selection of the environmental and spatial factors that can explain variations in species composition. The use of covariables in CCA and tests for statistical significance such as the Monte Carlo permutation test further extended the validity of using this method in direct gradient analysis (ter Braak & Prentice 1988, Birks & Austin 1992).

It is important to include spatial structure in ecological studies because it highlights the importance of the spatial variation, Fraction (c), in the species composition and can therefore be considered as a predictive variable. Legendre & Troussellier (1993) showed that spatial structuring played an important role in a water circulation model to predict the spatial variations of the abundance of phytoplankton and heterotrophic bacteria in a brackish lagoon and to reduce the amount of unexplained variation. As stated by Mackas (1984), 'closely spaced or continuous samples are needed to resolve the detailed pattern of spatial variability; significant fractions of the total variance would be unresolved by conventional point sampling and would contribute to an inflated estimate of the residual statistical noise'. The coastal system studied in respect to the meroplankton community can be regarded as a complex biological flux system governed by wind conditions that can alter the transport and dispersion of larvae in a southwest-northeast gradient (Luczack et al. 1993). The meroplankton distribution pattern may correspond partly to the structuring of measured environmental variables, which in turn are themselves spatially structured, or to the fact that the stretch of coastline studied is itself a structuring factor. Turning the discussion to the ecologist, we may conclude from this work that partitioning the variation of the meroplankton community structure gives support to preconceived models of larval dispersion. Most importantly it suggests the need to go back to sampling with better models in mind. The method described can be a useful approach to the interpretation of the dynamics of marine ecosystems.

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