

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.

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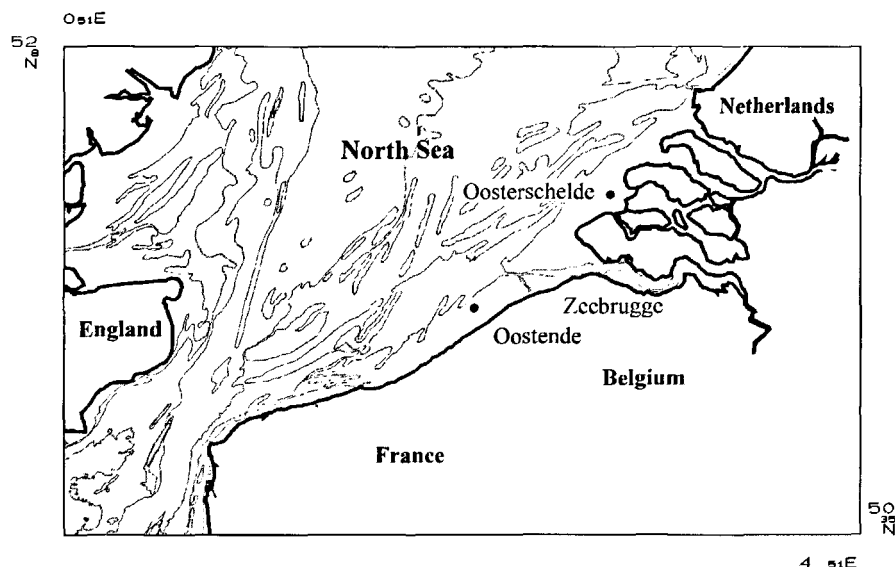
INTRODUCTION

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 μ m 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 (Ardissou *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

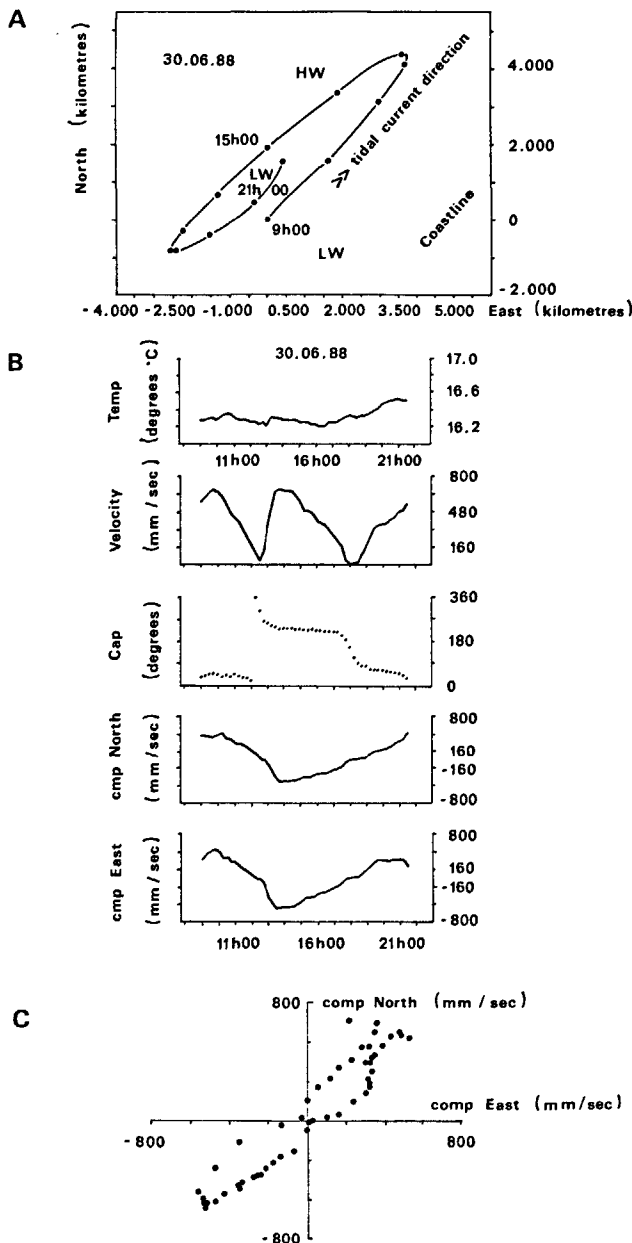


Figure 2

(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 ($^{\circ}\text{C}$), 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).

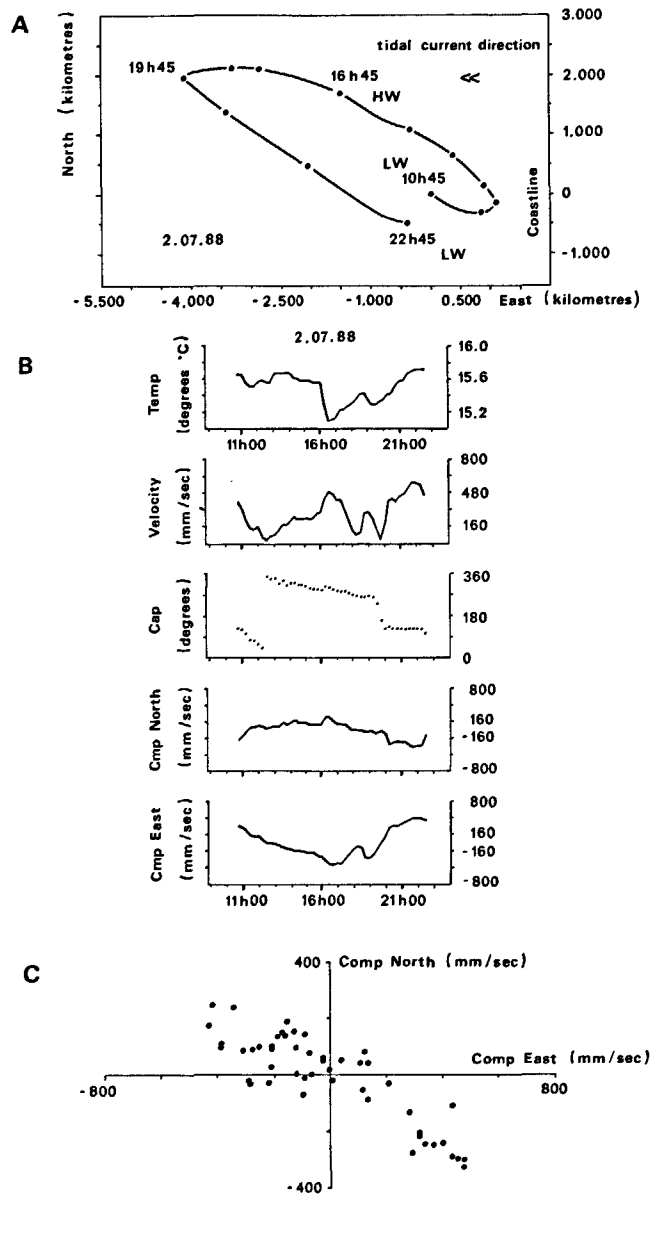


Figure 3

(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 ($^{\circ}\text{C}$), 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.

RESULTS

Hydrographic parameters

The results of the AANDERAA currentmeter for Oostende (Fig. 2A) 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 2B. The highest tidal current velocity at

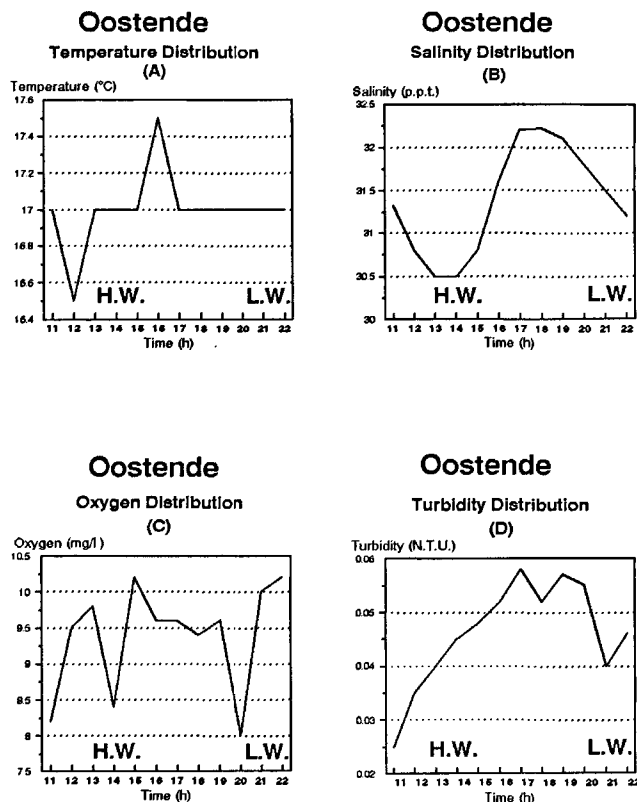


Figure 4

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.

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 2C. The AANDERAA readings obtained for the Oosterschelde station shows the excursion of the tide (Fig. 3A). 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. 3B) 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 3C, showing the looping circulation pattern in front of the storm surge barrier at the Oosterschelde.

Abiotic descriptors

The temperature distribution at Oostende (Fig. 4A) 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. 4B) 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

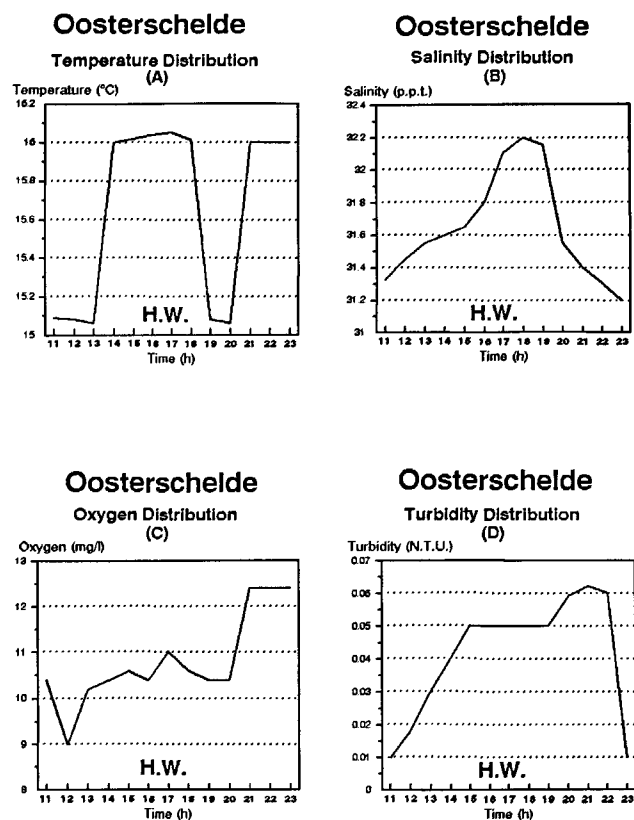


Figure 5

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

oxygen distribution (Fig. 4C) 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. 4D) 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. 5A) 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. 5B) reaches its highest value at 18h00 with 32.2 after the high water time at 16h25. The oxygen distribution (Fig. 5C) 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. 5D) 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

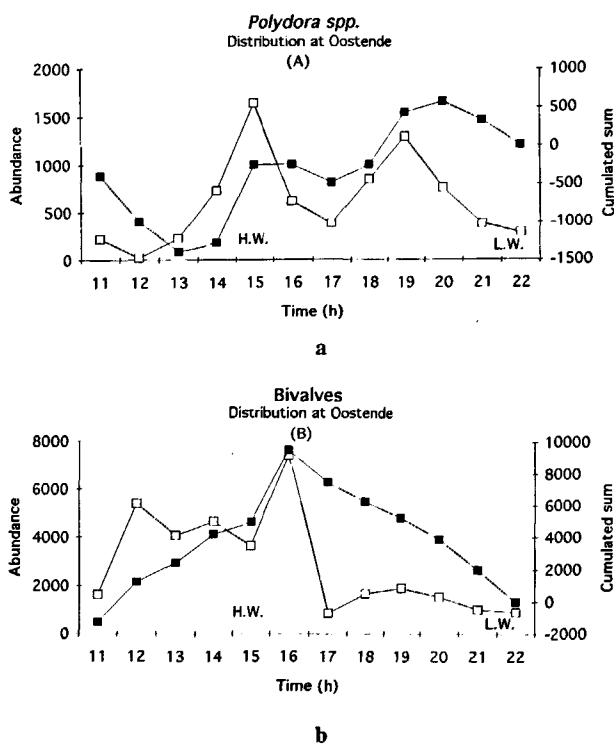


Figure 6

(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.

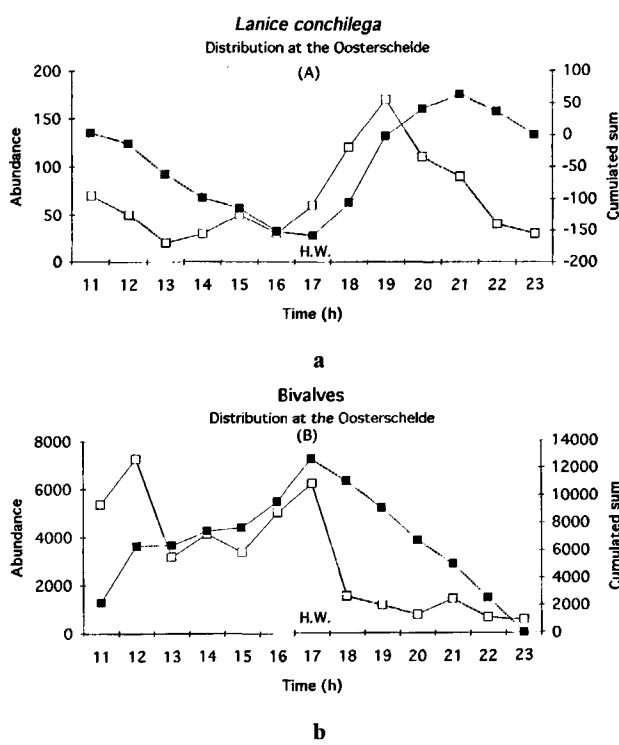


Figure 7

(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 Spearman'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

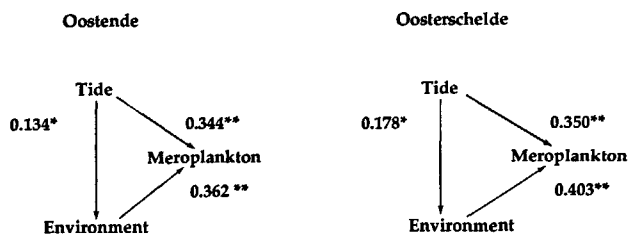


Figure 8

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 synchronized 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 boundary 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 achieve 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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