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Ecology of zooplankton in European estuaries

Proceedings of the Workshop held in Arcachon
May, 19-21, 1992

PREFACE

In this special volume of the *Cahiers de Biologie Marine* are collected articles presented during the Workshop "Ecology of Zooplankton in European estuaries" held at the Centre for Biological Oceanography in Arcachon (19-21 May 1992). The meeting gathered most of the planktonologists participating to the CEC MAST JEEP 92 project : "Major Biological Processes in European tidal Estuaries", chaired by Professor Carlo Heip. It was also the final meeting of the participants to the European network of laboratories EPEE : "Écologie du Plancton dans les Estuaires Européens" supported by the French Ministry of Research and Space.

Estuarine zooplankton deserves particular interest at least for two reasons :

- Estuaries are essential as breeding grounds or nursery areas for fish of commercial interest. Zooplankton organisms are obligate food source for juvenile fish.
- Estuarine pelagic ecosystems have come under increasing pressure from the discharge of domestic and industrial effluents. Zooplankton can be used as an indicator of anthropogenic stress.

The importance of organic matter in estuarine ecosystems is widely recognized. Zooplankton organisms consume and utilize a part of the organic matter introduced or produced in the estuary. However, the exact role of zooplankton in the transformation of organic matter is an open question. Few estimates of biomass of zooplankton have been undertaken in estuaries, consequently, production estimates remain uncommon. Furthermore, the origin and fate of this production are far from being fully understood. Some simple questions have no clear general answers :

- Grazing zooplankters feed on both living and non-living particles. What is the proportion of phytoplankton necessary to sustain the planktonic secondary production ? Is there a selection for phytoplankton ? What is the nutritional importance of detritus to estuarine zooplankton ?
- Zooplankters produce new living organic matter. What is the part of the planktonic production used by higher trophic levels ? What is the fate of the remaining production ? Is it recycled within the estuary or expelled to the sea ?

The participants to the workshop did not intend to answer all these questions but to compare their own experience from different estuaries and to present up-to-date results around three main topics : (1) distribution of zooplankton and its relation with hydrological factors, (2) population dynamics and production, including modelling, (3) grazing activity and organic matter. The papers published in the present volume illustrate these different aspects. They also reflect the will of cooperation between European specialists of estuarine zooplankton.

The workshop was sponsored by the MAST R & D programme JEEP 92 from the CEC, the French Ministry of Research and Space, and IFREMER.

Finally, I would like to express my gratitude to Professeur Pierre Lasserre, editor-in-chief of the *Cahiers de Biologie Marine* for accepting to publish the proceedings and Mrs Bernadette Lasserre, secretary of redaction, for her careful attention in preparing this volume.

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The CEC-MAST JEEP 92 Project
Major Biological Processes in European tidal Estuaries

Tidal estuaries in Europe serve important economic functions including transport, industry and tourism but also drainage of waste from domestic, industrial and agricultural activities. Estuaries are under heavy and increasing pressure from human activities in very large areas since they drain water carrying nutrients, organic matter and toxic materials from the terrestrial environment and the river system to the sea. For example, in the Dutch delta area the water of more than 300 000 km^2 of land surface from seven European countries is concentrated.

Whereas estuaries serve an important role for economic activities they have important natural values as well. Tidal estuaries are characterized by high secundary production rates reflected in important biomass values for benthic and zooplankton populations and the larvae and juvenile stages of fish. They serve as overwintering or passage stations for large populations of palaearctic birds. Estuarine plants and animals are adapted to high environmental variability and possess potentially valuable genetic characteristics. Salt marshes may serve as a natural defence against the rising sea level.

The major biological processes in estuaries may be linked to the production and mineralisation of organic matter. The mineralisation of the organic waste originating from human activities and the subsequent increase of nutrients and primary production is a matter of great concern. There is evidence that increased primary production is absorbed at least partially by increased benthic metabolism and that the biomass of benthos in estuarine and coastal systems is now increasing on the long term. The eutrophication of coastal marine areas originates from land-based human activities and the effect of measures such as the reduction of phosphate and nitrate concentrations in effluents largely depends on how these substances are transferred through the estuary, which is a non-linear system and therefore not easily predictable.

Another matter for concern is the introduction of toxic material in estuarine and coastal environments which may severely change the functioning of the estuarine filter system. Although the toxic effects of single and even mixed pollutants in laboratory condition have been studied intensively, the fate of many pollutants in the natural estuary remains unclear. Current efforts of modelling the transfer of pollutants in the food web or measuring the accumulated toxicity in higher food web levels will be more valuable if they are based on knowledge of the important structural and functional characteristics of the estuary.

The Joint European Estuarine research Programme JEEP 92 is aimed at a better understanding of effects of organic matter import and production on the ecology of the European estuaries. By integrating results from existing European research efforts and by specific research on certain topics it is hoped to achieve a better understanding of the responses within the estuarine system. In the first programme (1991-1993) the major research effort was devoted to selected biological processes (primary and secundary production, bacterial production, effects of organic loading on meio- and macrofauna) as they relate to nutrients and organic matter. A second important goal was the comparison of structures and processes between different estuaries. As a part of this objective, the zooplankton of several European estuaries is studied in a group of scientists chaired by Dr J. Castel from Arcachon. The main zooplankton species are the same or very similar in many estuaries and meaningful comparison and generalisations are therefore possible. The group organised a workshop in Arcachon in May 1992. In this workshop much attention was devoted to studies on the ubiquist *Eurytemora affinis*, but several new and interesting results from studies on hyperbenthos are presented as well. The quality of the research has allowed publication in this special volume of *Cahiers de Biologie Marine*. It will serve as an excellent basis for future pan-European studies on zooplankton in tidal estuaries.

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Summer zonation and development of zooplankton populations within a shallow mesotidal system : the estuary of Mundaka.

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Abstract : Two sampling series carried out in the estuary of Mundaka in July and August 1990 allowed us to obtain detailed information on the summer zonation and development of zooplankton populations under particular environmental conditions, i.e. very low river discharge throughout the study period.

Copepods (largely dominated by *Acartia bifilosa)* and gastropod larvae were not only the dominant taxa, but also the main cause of the spatial and temporal patterns observed in the micro and mesozooplankton assemblages. Both showed maxima around 30 ‰ salinity, but higher densities of microzooplankton were usually found at higher salinities than those corresponding to mesozooplankton, due mainly to the seaward skewed distribution of copepod nauplii. Large ciliates and rotifers distributed upstream than former taxa, dominating in salinities below 25 ‰, but their contribution to total zooplankton was relatively low. Temporal variations in the copepod abundance reflected the development of successive cohorts of A. *bifilosa,* with an estimated generation time of about 25 days. The observed synchrony between the abundance of gastropod larvae and tidal amplitude supports the hypothesis that larval release took place around the spring tides, following a semilunar rhythmicity. As a result of these periodical fluctuations in the abundance of gastropod larvae, the compositional structure of the zooplankton community showed noticeable short-time changes in synchrony with the neap-spring tidal cycle.

Résumé : Deux séries d'échantillonnages pratiquées dans l'estuaire de Mundaka en juillet et août 1990 ont permis d'obtenir des informations détaillées sur la zonation estivale et le développement des populations zooplanctoniques soumises à des conditions environnementales particulières, c'est-à-dire un très faible débit fluvial pendant la période d'étude. Les Copépodes (largement dominés par *Acartia bifilosa)* et les larves de Gastéropodes sont non seulement les taxons dominants mais aussi les principaux responsables des variations spatiales et temporelles observées sur le micro et mesozooplancton. Ces deux catégories dimensionnelles présentent un maximum autour d'une salinité de 30 ‰, mais les densités les plus élevées en microzooplancton sont généralement trouvées à des salinités plus fortes que celles correspondant au maximum d'abondance du mesozooplancton, surtout à cause 'une distribution asymétrique, déportée vers la mer, des nauplii de Copépodes. Les grands Ciliés et les Rotifères sont distribués plus en amont que les taxons précédents et sont dominants à des salinités inférieures à 25 ‰, mais leur contribution au zooplancton total est assez faible. Les variations temporelles de l'abondance des Copépodes reglète le développement de cohortes successives de l'espèce *A. bifilosa,* avec un temps de génération estimé à 25 joures. Le synchronisme observé entre l'abondance des larves de Gastéropodes et l'amplitude de marée appuie l'hypothèse d'une émission de larves autour des marées de vives-eaux, suivant une périodicité semi-lunaire. En conséquence de ces fluctuations périodiques de l'abondance des larves de Gastéropodes, la composition et la structure de la communauté zooplanctonique présente des modifications sensibles à court terme et synchronisées au cycle morte eau-vive eau.

INTRODUCTION

River discharge and tidal currents have a major effect on estuarine zooplankton dynamics. Currents displace zooplankton populations and thereby reduce standing crops in the main body of the estuary, especially in small systems characterized by strong river inflows (Kennish, 1990).

The estuary of Mundaka is a small mesotidal system (13 km in length and a mean depth of 2-3 m) with an estimated mean ratio of tidal prism volume : estuarine water volume greater than 1, and a relatively low average river inflow in relation to the volume of the estuarine basin (Villate *et al.*, 1989), although strong increases in freshwater inputs are frequent due to the torrential regime of tributary streams.

The study of an annual cycle showed that true estuarine holoplankters such as *Eurytemora* species cannot develop in this estuary, while estuarine-marine species (mainly *Acartia bifilosa*) reach maxima in summer, during the period of greater hydrological stability (Villate, 1991). Phytoplankton biomass and productivity also peak in summer because of the higher insolation and temperature coupled with low river discharge (Madariaga & Orive, 1989). The increase of river runoff results in an abrupt transition from low to high salinities within the estuary, and under these conditions neritic zooplankton and semiplanktonic organisms dominate in waters of higher and lower salinity respectively, while estuarine-marine populations maintain low or negligible densities (Villate, 1991 ; Madariaga *et al.*, 1992).

Therefore, summer time seems to be an appropriate period to analyse, in detail, the population dynamics of inhabitant zooplankton in the estuary. During the summer 1990, two sampling series were made in July and August for data on hydrography and plankton, including zooplankton samples for studies on abundance and composition. The last freshet preceding the sampling period occurred in late June but had low intensity and short endurance, and during the study period the river flow fell into values below the average. Thus, the aim of the present study is to analyse the zooplankton zonation and short time variability over a period of very low river discharge in an attempt to know the factors which regulate zooplankton dynamics within the estuary when river runoff disturbances are minimal.

METHODS

Sampling was performed in July and August 1990. Longitudinal gradients of salinity were obtained at 12 permanent stations (Fig. 1) over 21 days periods each month (from 7 until 28 July and from 6 until 27 August) at 3 daily intervals. Salinity was measured from surface to bottom at 0.5 m deep intervals. These surveys were carried out over less than two hours around the high tide slack. The collection of zooplankton samples was made 7 times per month from 9 until 27 July and from 8 until 26 August at 3 daily intervals. Samples were obtained from the surface and 0.5 m above the bottom at 3 stations previously selected according to salinity distributions.

Salinity was measured *in situ* using a WTW field conductivimeter accurate to ± 0.1 ‰. A water pump was used to take zooplankton samples. The zooplankton was fractioned by filtering sequentialy known volumes of the pumped water through meshes of 200 and 20 μm. Samples were fixed with 4 % buffered formalin. Identification and enumeration of individuals were made under a stereoscopic microscope. In the fraction removed by the 20 μm mesh, neither the smaller protozoans, which could not be distinguished, nor the copepod

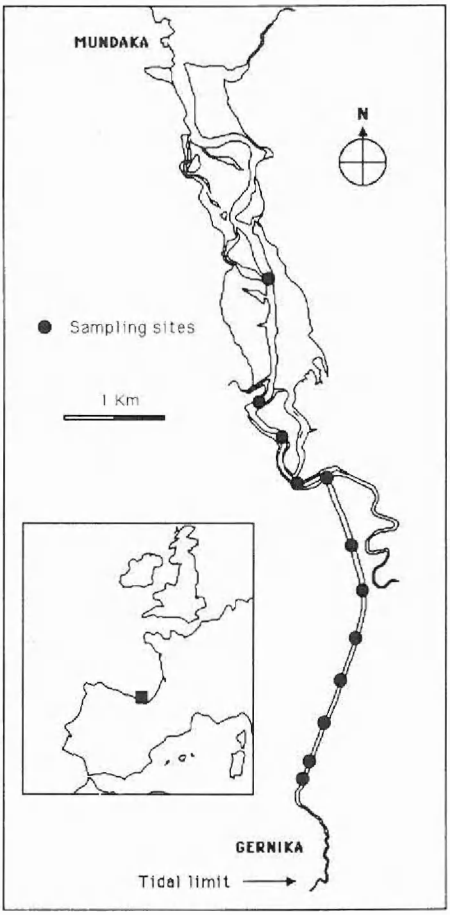

Fig. 1 : Study area showing station positions.

eggs were counted. To calculate densities and to eliminate zero values zooplankton data were expressed as the number of individuals per l for organisms collected in the 20 to 200 μm fraction (microzooplankton), and per m^3 for organisms collected in the > 200 μm fraction (mesozooplankton), after converting to $\log_{10}(x + 1)$. Tidal amplitudes shown in this paper correspond to the port of Bilbao, nearby the estuary of Mundaka. They are only useful to describe spring-neap tidal cycles, since values of tidal range within the estuary of Mundaka are smaller (unpublished data).

RESULTS

At high tide the outer half of the estuary was mostly filled by waters around 35 ‰, while mixed waters of less than 30 ‰ were always found in the inner half, with increasing stratification upstream (Fig. 2). Salinity distribution showed temporal variations depending on tidal amplitude, but in general, salinity increased upstream from July to August.

Abundances of micro and mesozooplankton showed a similar distribution pattern in relation to salinity (Fig. 3), with absolute maxima of more than 10^3 individuals.l^{-1} and 10^5 individuals.lm^{-3} respectively in waters around 30 ‰. The highest densities of microzooplankton, however, were usually found in waters of higher salinity than those corresponding to the mesozooplankton.

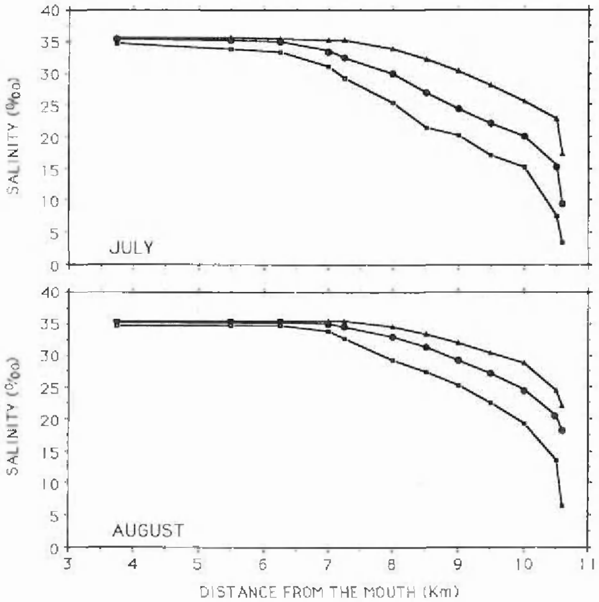

Fig. 2 : The spatial distribution of salinity in July and August at high tide, showing mean (filled circles), greatest and lowest values for each sampling site.

Copepods and gastropod larvae were the main constituents in both zooplankton fractions, but in the microzooplankton assemblage copepods (mainly naupliar stages) largely dominated in terms of number. In this fraction, copepod nauplii comprised, on average, 48.2 % of the total (range : 74.7-12.5 %), gastropod larvae 19.5 % (58.1-0.3 %), and polychaete larvae 19.4 % (49.0-2.8 %). Ciliates and rotifers, which dominated in some microzooplankton samples, only accounted for 2.8 % and 1.3 % respectively. Among mesozooplankton constituents postnaupliar stages of *Acartia bifilosa* contributed 42.5 % to the total (88.7-0.4 %), gastropod larvae 38.5 % (98.6-1.3 %), and barnacle larvae 8.5 % (30.2-0.3 %). The relative abundance of copepod species in the mesozooplankton fraction was 91 % for *A. bifilosa*, 2 % for *Acartia grani*, and 6 % for the grouped neritic species (mainly *Oithona nana, Paracalanus parvus* and *Oncaea media*). *Calanipeda aquaedulcis, Canuella furcigera* and other species of meiobenthic harpacticoids accounted for the rest.

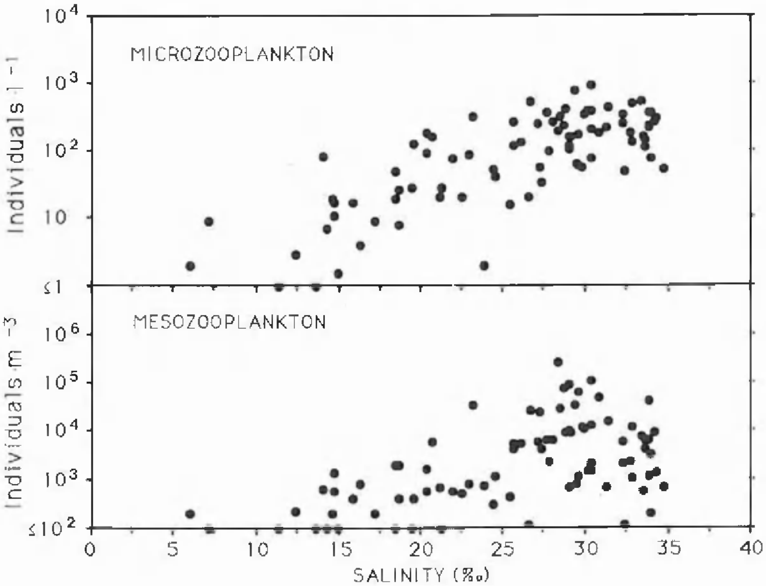

Fig. 3 : Distribution of total microzooplankton and mesozooplankton densities in relation to salinity.

The distribution of main taxa in relation to salinity is shown in Figures 4 and 5. Among constituents of the microzooplankton assemblage, ciliates and rotifers peaked in waters of less than 25 ‰, although rotifers skewed toward waters of higher salinity than ciliates. Gastropod and polychaete larvae peaked in waters around 30 ‰, and copepod nauplii in waters above 30 ‰. Postnaupliar stages of copepods (mainly copepodites of *A. bifilosa*) collected in the microzooplankton fraction were more abundant in waters around 30 ‰. In the mesozooplankton, most of the main taxa also reached the highest densities in waters around 30 ‰, while neritic species showed highest densities in waters above 32 ‰.

Figure 6 shows temporal variations in tidal amplitude, micro and mesozooplankton abundance, and relative abundance of main taxa. Temporal variations in the mean abundance differed between micro and mesozooplankton assemblages, while copepods and gastropod larvae alternated in dominance but not at the same time in both fractions. The dominance of gastropod larvae in the microzooplankton assemblage occurred around the spring tides, whereas in the mesozooplankton assemblage it occurred mainly towards the neap tides. Polychaete larvae also dominated occasionally in the microzooplankton assemblage in July.

Temporal variations in the average density of the main zooplankton taxa are presented in Figure 7. Gastropod larvae showed remarkable fluctuations in time. They peaked at approximately 12-15 days intervals, and the greatest number of larger forms (fraction > 200 µm) were usually found some days later than the smaller forms (fraction < 200 µm), which peaked around the spring tides (see also figure 6). Polychaete and barnacle larvae abun-

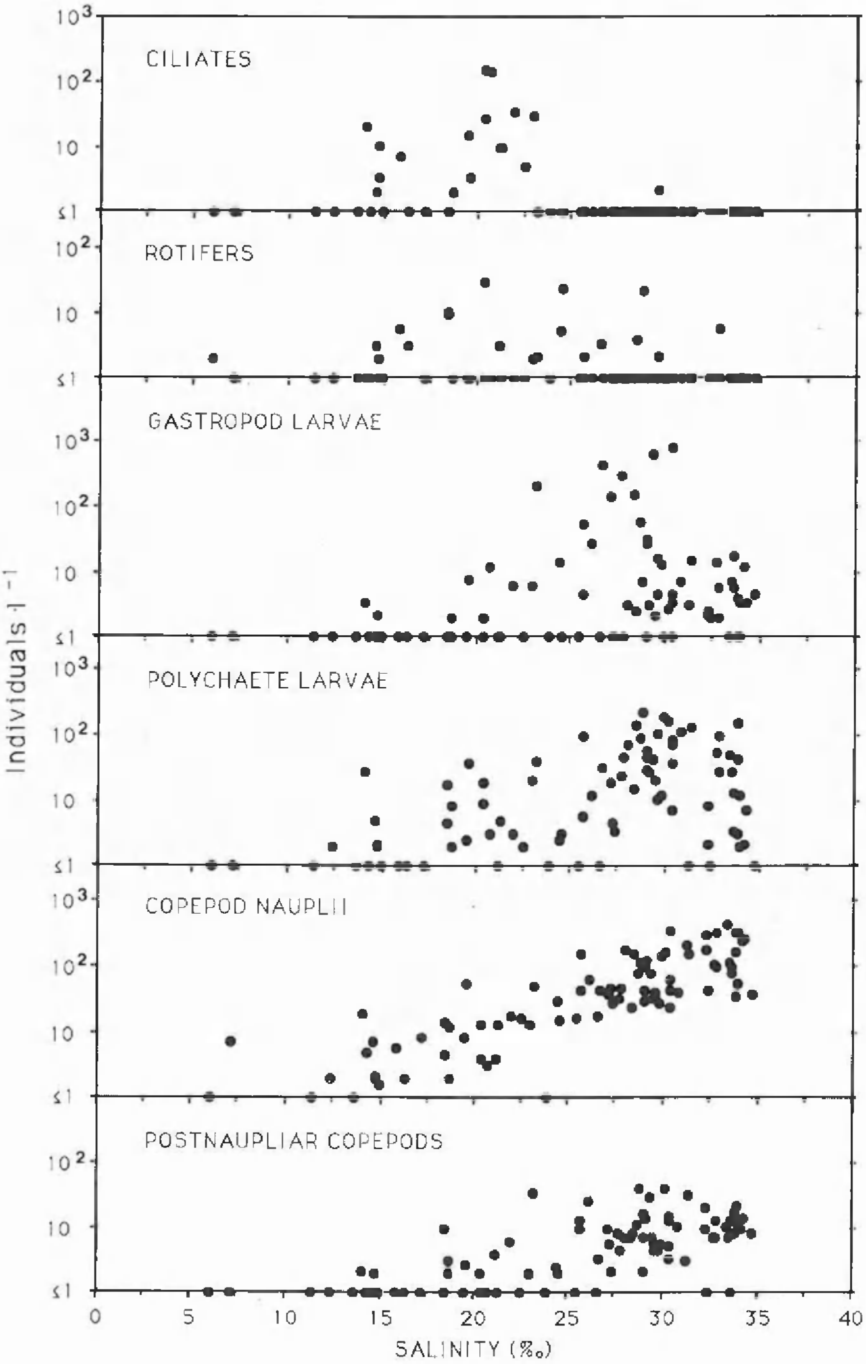

Fig. 4 : Distribution of the main microzooplanktonic taxa in relation to salinity.

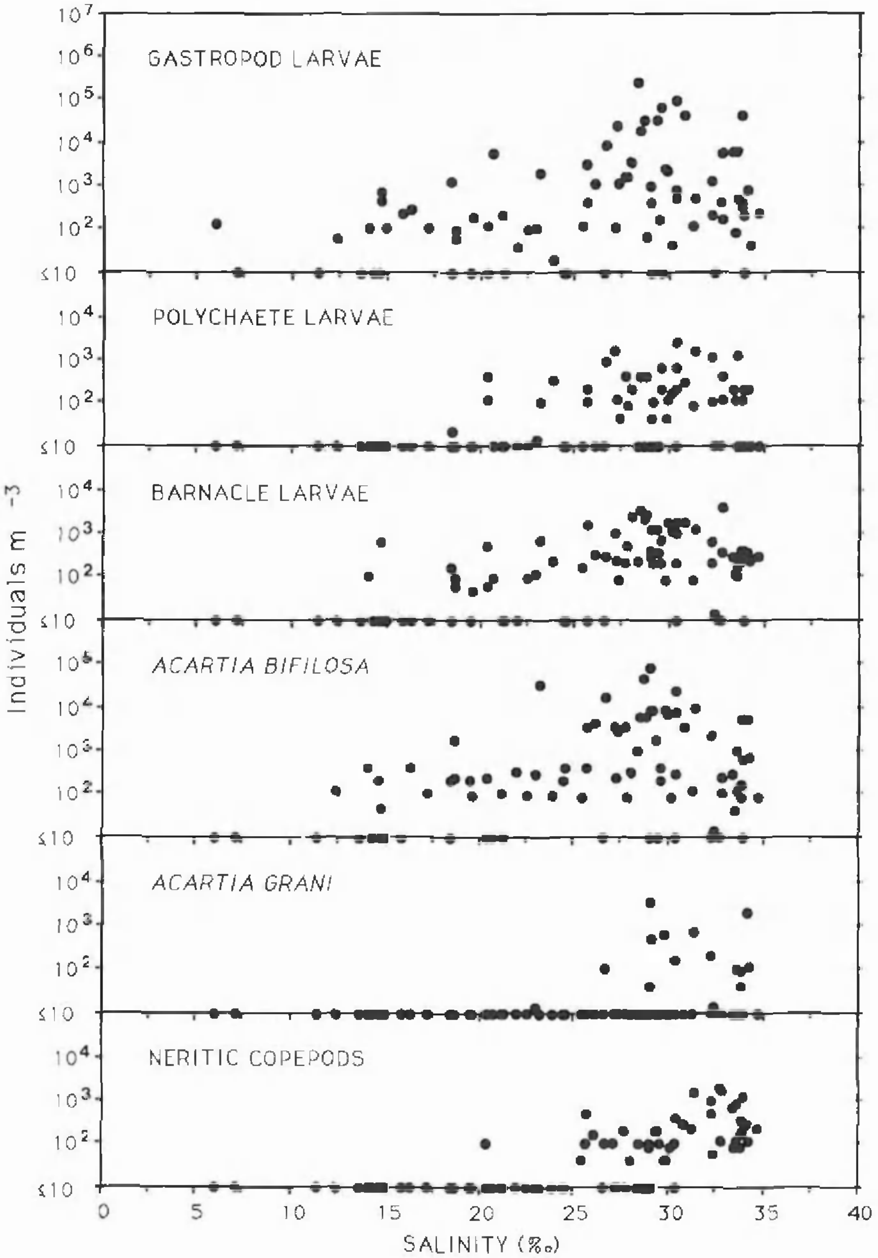

Fig. 5 : Distribution of the main mesozooplanktonic taxa in relation to salinity.

dances fluctuated slower than those of gastropod larvae, and did not show clear temporal trends. Among copepods, larger individuals of *A. bifilosa* peaked three times during the study period, nauplii maxima occurred following the adult peaks of this species, and smaller postnaupliar stages were more abundant before or at the same time as when larger stages peaked.

DISCUSSION

The maintenance of very low river discharge throughout the study period resulted in a clear predominance of euhaline waters within the estuary, while mixed waters of less than 30 ‰ comprised a small percentage of the total volume at high tide.

The great variability in the occurrence and abundance of zooplankton taxa in collected samples reflected patchy distributions and noticeable temporal fluctuations in most of them. However, regular variations in relation to salinity, and clear trends in the temporal evolution of average abundances, were observed for the dominant taxa, indicating an established spatio-temporal structure of populations rather than random fluctuations.

Although most of the main taxa, and consequently the total zooplankton, reached maxima in waters around 30 ‰, the highest densities of microzooplankton skewed towards waters of more salinity that those of macrozooplankton. Ciliates and rotifers dominated in most of the microzooplankton samples collected below 25 ‰, peaking further up the mesozooplankton maxima, but their densities were lower than those of copepod nauplii which usually peaked in waters of more than 30 ‰. Rotifers have also been reported to be dominant in the metazoan zooplankton in the meso-polyhaline region of other estuaries, but their temporal occurrence seem to be highly variable (e.g. Ambler *et al.*, 1985 ; Dolan & Gallegos, 1991), as occurred in our samples. Among protozoans, as only large ciliates were counted, the observed densities most probably underestimated the real importance of this group in the microzooplankton assemblage. For instance, Dolan (1991) reported that larger ciliates were numerically a minor component of total ciliate numbers in the mesohaline region in the Chesapeake Bay. Mesozooplankton distribution in relation to salinity mainly reflected the distributions of *A. bifilosa* and gastropod larvae, which were almost coincident with maxima around the 30 ‰. The highest densities of polychaete and barnacle larvae also occurred in waters of around 30 ‰. As these waters were located in the inner half of the estuary at high tide, and watermasses confined to the inner half of the estuary at high tide do not reach the mouth of the estuary at low tide (Anonymous, 1986 ; Villate *et al.*, 1989), this indicates that the three dominant meroplanktonic groups together with *A. bifilosa* maintained their population maxima within the estuary, moving around of the middle part.

The distribution shown by *A. bifilosa* in relation to salinity agrees with that observed in the Severn estuary (Collins & Williams, 1981), but in other estuarine systems its summer maxima are found in waters of less salinity (e.g. D'Elbee, 1984 ; Castel, 1985 ; Taylor, 1987). Probably not only salinity but also other factors control the horizontal distribution

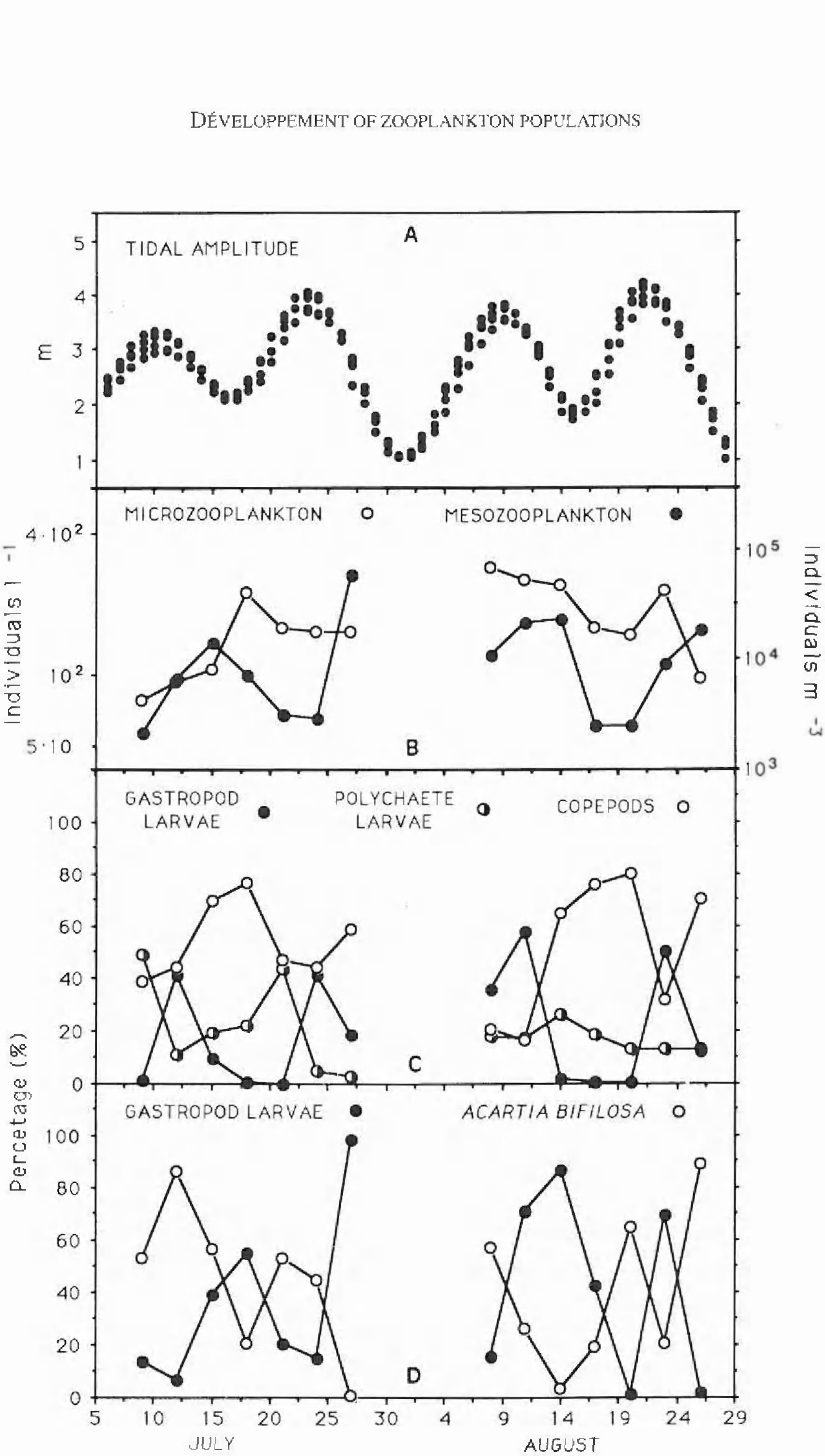

Fig. 6 : Temporal variations of the tidal amplitude (A), the mean abundance of microzooplankton (ind.l^{-1}) and mesozooplankton (ind.m^{-3}) (B), and the relative contribution of dominant taxa to the total microzooplankton (C) and macrozooplankton abundance (D).

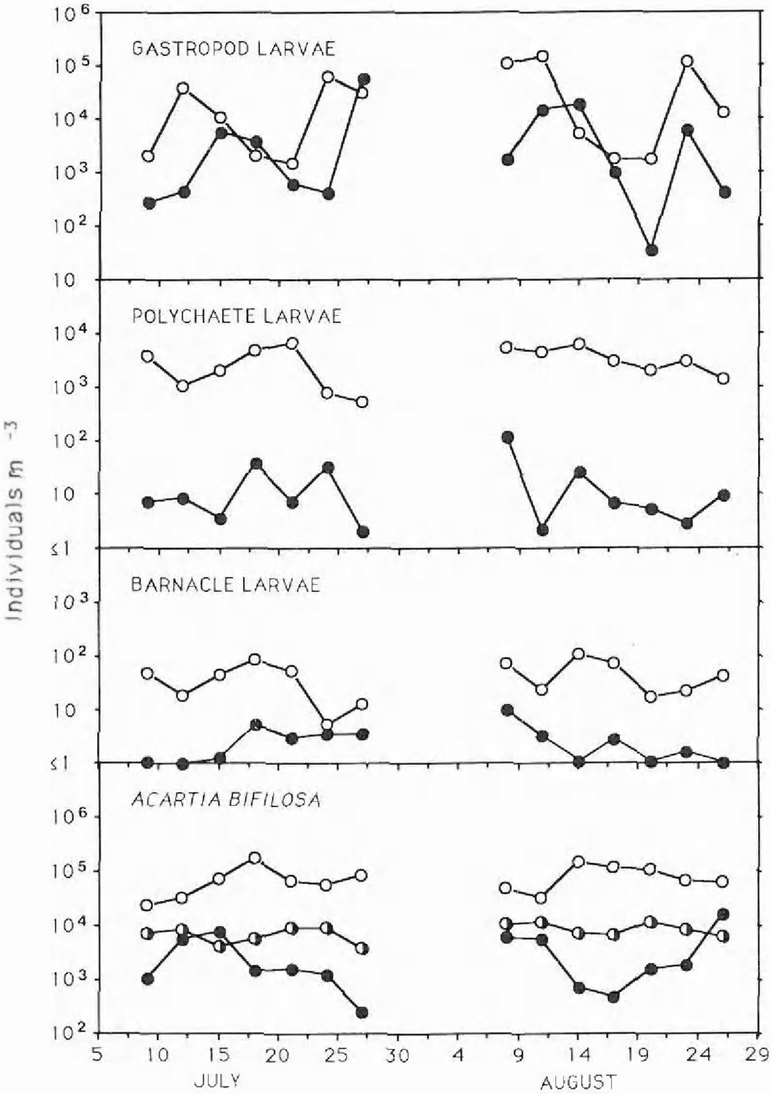

Fig. 7 : Temporal variations of the mean abundance of gastropod larvae (open circles for the microzooplankton and filled circles for the macrozooplankton), polychaete larvae (ibidem), barnacle larvae (open circles for naupliar stages and filled circles for cypris), and postnaupliar stages of *A. bifilosa* in the mesozooplankton (filled circles), postnaupliar stages in the microzooplankton (half-filled circles) and nauplii (open circles).

patterns of estuarine copepods. In a tidal system where the estuarine species *A. tonsa* was dominant, Jacobs (1968) reported that this species had a marked density maximum in a specific region although there were not appreciable gradients of salinity, temperature or food ; and Taylor (1987) also pointed out that one of the most interesting phenomena encountered in the Forth estuary was the ability of the dominant copepod species to congregate and attain their maxima in the middle estuary.

The observed periodicity in abundance fluctuations of gastropod larvae, and the delay in the occurrence of larger forms peaks in relation to those of smaller forms, suggest that four distinct cohorts of veligers had developed during the study period. The synchrony between abundance fluctuations and tidal amplitudes allows us to suppose that these gastropods followed a semilunar rhythmicity, with larval release around the time of spring tides. With regard to the gastropod *Littorina littorea*, Thorson (1946) already pointed out that it could hardly be doubted that the spawnig of this species takes place rhythmically, but the relation to the lunar phases was not considered. Semilunar rhythms with larval release around the time of spring tides seem to be widely distributed among other meroplanktonic groups such as littoral and supralittoral decapods, which is likely because they involve shared functional advantages (Forward, 1987). The abundance pulses of gastropod larvae had a noticeable effect on the compositional structure of the zooplankton community, resulting in a temporal alternance in the dominance of gastropods or copepods in synchrony with the neap-spring tidal cycle.

Polychaete larvae, almost exclusively composed of spionids, did not show regular variations easily assignable to distint cohorts. In estuarine polychaetes, most species have relatively short planktonic life, extending not more than 2-3 weeks (Cazaux, 1970, 1984), but continuous reproduction and recruitment seem to be common among estuarine oportunistic spionids (e.g. Zajac, 1991).

In Barnacle larvae, a clear synchrony between larval stages had not been established. Cypris larvae were more abundant in the second half of July and early August, while the abundance of naupliar stages fluctuated without a defined tendency. Barnacle larvae of some species have development times in the plankton of 5-6 or even 8 weeks (Bousfied, 1953, in Minchinton & Scheibling, 1991 ; Salman, 1982), but in most of them the planktonic life does not expand more than 5 weeks, and cypris larvae peak approximately 1 month later than nauplii (Lang & Ackenhusen-Johns, 1981). Therefore, the greater number of cypris in the latter half of July and early August could be related, if at all, to a nauplii pulse occurring before the study period.

Although copepod nauplii were not identified to species level, it can be supposed that the collected nauplii were primarily those of the species *A. bifilosa*, since species composition of nauplii are generally in agreement with those of adult copepods (Barlow, 1955 ; Conley & Turner, 1991). Moreover, nauplii peaked just after *A. bifilosa* adults, denoting reproductive sets of this species, since a hatching success of eggs within 2 days can be expected according to Daan (1989). When periods of increased egg production are short and the number of emerging nauplii has a gaussian distribution, copepod cohorts may remain distinct (Fransz *et al.*, 1991). In our case, 3 distinct cohorts of *A. bifilosa* had been distinguished over the study period. The time between successive peaks was approximately 25 days, and the estimated time of development from hatching to adults, infered from sequential peaks of nauplii and *A. bifilosa* adults, was around 20 days. This agrees with what has been observed in other copepod species of similar size. Thus, a development time from hatching to adult of 18-21 days, and a generation time of around 25-26 days have been reported for *Paracalanus parvus* (Landry, 1983 ; Davis, 1984). A duration from egg to the point in time when 50 % of the female are fertilized of approximately 20 days (Stφttrup *et al.*, 1986), and a generation time of 4 weeks in the favourable season has been estimated for *Acartia tonsa* (Sabatini, 1989).

The seaward skewed distribution of nauplii with regard to that of larger individuals of *A. bifilosa* could be explained by a size-dependent differential transport or retention of individuals. Tidal exchange plays a major role in the transport of planktonic copepods in estuaries (Lewis & Thomas, 1986), but the mechanisms implied in the retention of estuarine species seem to be complex. For instance, the distribution and retention of the estuarine copepod *Eurytemora* have been explained by hydrodynamic processes, in the same manner as the suspended particles (Castel & Veiga, 1990), and by the ability of individuals to change their position by differential tidal swimming (Hough & Naylor, 1991). Anyway, given that weight and swimming capability increase with developmental stage, both passive and active transport could account for the differential distribution of stages along the estuary.

It is interesting to point out that on 12 and 15 July, most of the larger copepodites and adults of *A. bifilosa* were found covered by colonial ciliates. However, a clear relationship between the occurrence of these ciliates and the population development of *A. bifilosa* had not been established. According to Fenchel (1987), colonial peritrichs which appear attached to copepods could have a significant ecological impact, but this has never been studied.

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Roscoff

Long-term distribution of zooplankton in the Gironde estuary and its relation with river flow and suspended matter.

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Abstract : Mesozooplankton changes taking place in the Gironde estuary (South West France) were investigated during 14 years (1978-1991). The dominant autochthonous species, i.e. the Copepods *Eurytemora affinis*, *Acartia bifilosa* and the Mysids *Neomysis integer* and *Mesopodopsis slabberi* were taken into account and their long-term distribution was related to river flow, salinity, current velocity and suspended matter.

There was a great decrease of the river flow during the period of investigation, due to a general deficit in pluviosity. On the contrary, the general trend for salinity was an increase from 1978 to 1991. For the suspended matter, a general increase was observed between 1978 and 1981-1982, then a very sharp decrease occurred from 1984 onwards. The same trend was observed for the current velocity and was related to modifications of the morphology of the channels in the study area.

E. affinis was inversely correlated with salinity and positively correlated with the river flow. An inverse correlation between *A. bifilosa* trend of abundance and river flow was observed mainly during the first ten years. Despite high salinities during the last three years, the average abundance of *A. bifilosa* was not regularly increased probably because of the poor exchanges of water during this period (decrease of the current velocity). The distribution of *N. integer* was slightly correlated with environmental factors, probably because the species is capable of displacement in the water and has benthic affinities. On the contrary, *M. slabberi* which is more pelagic, displayed the same distributional trend as *Acartia*.

It is concluded that in the Gironde estuary, the degree of human alteration is weak and that the long-term distribution of the zooplankton can be explained by the natural environmental variability. The dominant factor is the river flow which governs the movements of the populations along the estuary. Emphasis is given to the fact that, in zooplankton research, time series must be long enough (> 10 years) to allow any convincing interpretation of long term changes.

Résumé : La distribution à long terme du mésozooplancton a été étudiée dans l'estuaire de la Gironde (sud-ouest de la France) au cours d'une période de 14 années (1978-1991). Seules les espèces autochtones dominantes ont été prises en considération : les Copépodes *Eurytemora affinis*, *Acartia bifilosa* et les Mysidacés *Neomysis integer*, *Mesopodopsis slabberi* et leur distribution temporelle a été reliée au débit fluvial, à la salinité, à la vitesse du courant et à la quantité de matières en suspension.

On constate une décroissance générale des débits au cours de la période d'étude, à cause d'un déficit pluviométrique. Au contraire, la tendance générale pour la salinité est une augmentation de 1978 à 1991. En ce qui concerne les matières en suspension, on observe une augmentation entre 1978 et 1981-1982, puis une diminution très prononcée à partir de 1984. La même évolution est notée pour la vitesse de courant dont la diminution semble liée aux modifications de la morphologie des chenaux dans la zone d'étude.

E. affinis est inversement corrélé avec la salinité et positivement avec le débit fluvial. L'évolution des effectifs suit assez bien celle des matières en suspension ; la corrélation n'est pas significative car il existe un léger décalage temporel entre les deux variables. Une corrélation inverse entre l'abondance d'A. *bifilosa* et le débit fluvial est observée, surtout pendant les dix premières années. Malgré de fortes salinités, l'abondance moyenne en *A. bifilosa* n'est pas régulièrement augmentée au cours des trois dernières années probablement à cause de la faiblesse des échanges d'eaux pendant cette période (décroissance des vitesses moyennes de courant). La distribution de *N. integer* est peu corrélée avec les facteurs de l'environnement probablement parce que cette espèce est capable de mouvements autonomes dans la masse d'eau et parce qu'elle a des affinités benthiques. Au contraire, *M. slabberi*, qui est plus pélagique, montre une distribution ayant la même tendance que celle d'*A. bifilosa*.

Il semble bien que l'estuaire de la Gironde soit peu affecté par les activités humaines et que l'évolution à long terme du zooplancton puisse être expliquée par la variabilité naturelle de l'environnement. Le facteur dominant est le débit fluvial qui gouverne le mouvement des populations le long de l'estuaire. L'étude met en évidence que dans le domaine de la recherche en planctón, les séries temporelles doivent être suffisamment longues (> 10 ans) pour permettre des interprétations convaincantes sur les modifications à long terme.

INTRODUCTION

Although estuaries are intensively studied in the perspective of management, long-term series are not so numerous, especially for zooplankton. Continuous zooplankton data for a period of greater than 3-4 years are limited in number.

Haertel *et al.* (1969) reported on a 5 years study from the Columbia River estuary (Oregon, USA). Their study was related to the possibility of reduction of the water flow due to the construction of dams, as well as to the increase of human population and industrial growth in the drainage basin. They found *Eurytemora affinis* to be the major zooplankter. Regression analysis indicated a close correlation between phosphate levels and *Eurytemora* abundance. They also showed that high temperature may be responsible for the late summer-early autumn depression in *Eurytemora* abundance. However, their work was not made in the perspective of studying long-term evolution of zooplankton and the authors did not conclude about the long-term trend of zooplankton populations.

A study of year-to-year variation of abundance and seasonal cycle over 7 years was made by Frolander *et al.* (1973) in the lower Yaquina Bay (Oregon). They showed that the annual cycle of coastal currents controls the annual cycle of zooplankton species composition but there were no persistent trends in zooplankton abundance over the sampling period.

In the Sacramento-San Joaquin Delta (California), Orsi & Mecum (1986) observed a long-term decline of all freshwater zooplankton groups over a 7 year period. In the cases of Rotifers and Copepods the decline was significantly correlated with a decline in chlorophyll *a*. A reduction in the organic waste loading to the delta as a result of improved waste treatment was mentioned as a possible cause of the phytoplankton decline. The brackishwater Copepod *Eurytemora affinis* was excluded from the analysis.

In Europe, long-term (9 years) dynamics of mesozooplankton densities was studied at Seili (Northern Baltic) by Vuorinen & Ranta (1987). Zooplankton was dominated by Rotifers and the Copepods *Acartia* spp. and *Eurytemora affinis hirundoides*. There was a considerable year-to-year variation in the relative abundance of zooplankton species. The mesozooplankton responded to salinity changes due to changing hydrography occurring in the Baltic Sea ; 1/3 of the taxa increased in numbers, while most of the taxa (2/3) decreased in numbers. However, in most cases these changes were not distinguishable from random fluctuations.

At the same sampling site, and during 9 subsequent years, Viitasalo *et al.* (1990) monitored the abundance of crustacean mesozooplankton in relation to changes in salinity (decrease) and eutrophication. The most important species, *Acartia bifilosa*, increased with time while the other dominant species, *Eurytemora affinis*, showed no obvious trend. These unexpected results could not be attributed to any single environmental factor.

In general the conclusions from these long-term series are rather disappointing. Several hypotheses can explain this lack of consistent conclusion.

- In the above examples, sampling was made once at each sampling date (except in the Columbia River where samples were taken at low and high tide). Thus the shifting of the populations upstream and downstream with the tide was not considered. It is clear that this shifting is the principal source of short-term variability in the abundance estimates, increasing the variance associated with each data point. However this does not apply to the Baltic where the tidal amplitude is very low.
- The other possibility is that the time-series may be too short to detect any long-term change in zooplankton populations.
- Finally, the natural variability of the estuarine populations may be too large to allow the detection of any long-term change.

This paper report on the mesozooplankton changes taking place in the Gironde estuary (South West France) in 1978-1991. Only the dominant autochthonous species, i.e. the Copepods *Eurytemora affinis* (Poppe), *Acartia bifilosa* (Giesbrecht) and the Mysids *Neomysis integer* (Leach), *Mesopodopsis slabberi* (Van Beneden) are taken into account. As compared with other studies, the representativeness of the data is improved by i/ sampling during a whole tidal cycle at each sampling date, ii/ providing a longer time-series (14 years). The main explicative factors considered here are river flow, salinity, current velocity and suspended matter concentration which are thought to represent the general hydrology of the estuary.

STUDY AREA

The Gironde estuary (Lat. 45°20'N, Long. 0°45'W) is the largest French estuary and covers an area of 625 km^2 at high water (Fig. 1). The freshwater inflow to the estuary is brought by the rivers Garonne and Dordogne, the total drainage of which covers approximately 71 000 km^2. The two rivers join 70 km from the inlet. In the middle and lower estuary, two main channel systems are separated by a network of bars, shoals, islands and secondary channels. The mean yearly combined discharge of the Garonne and the Dordogne varies between 800 and 1 000 m^3 s^{-1}. The discharge varies seasonally, usually reaching a maximum in January-February (mean 1 500 m^3 s^{-1}) and a minimum in August-September (mean 250 m^3 s^{-1}). During average tidal conditions, the period of freshwater flushing is 20 days at flood tide, 86 days at low water. Tidal current velocities vary considerably and can reach 2 m s^{-1}. According to the terminology of Pritchard (1955), the Gironde is a "Type B" estuary (intrusion of a salt wedge with tides) during high river flow and a "Type C" (partially mixed) during low river flow.

The mean upstream limit of the saline intrusion (0.5 ppt) is located about 75 km from the inlet during low river flow and 40 km from the inlet during high river flow. The density gradient, i.e. the salinity gradients, result in a residual circulation system. The higher the fluvial discharge in the main channel of the lower estuary, the stronger the upstream residual circulation on the bottom.

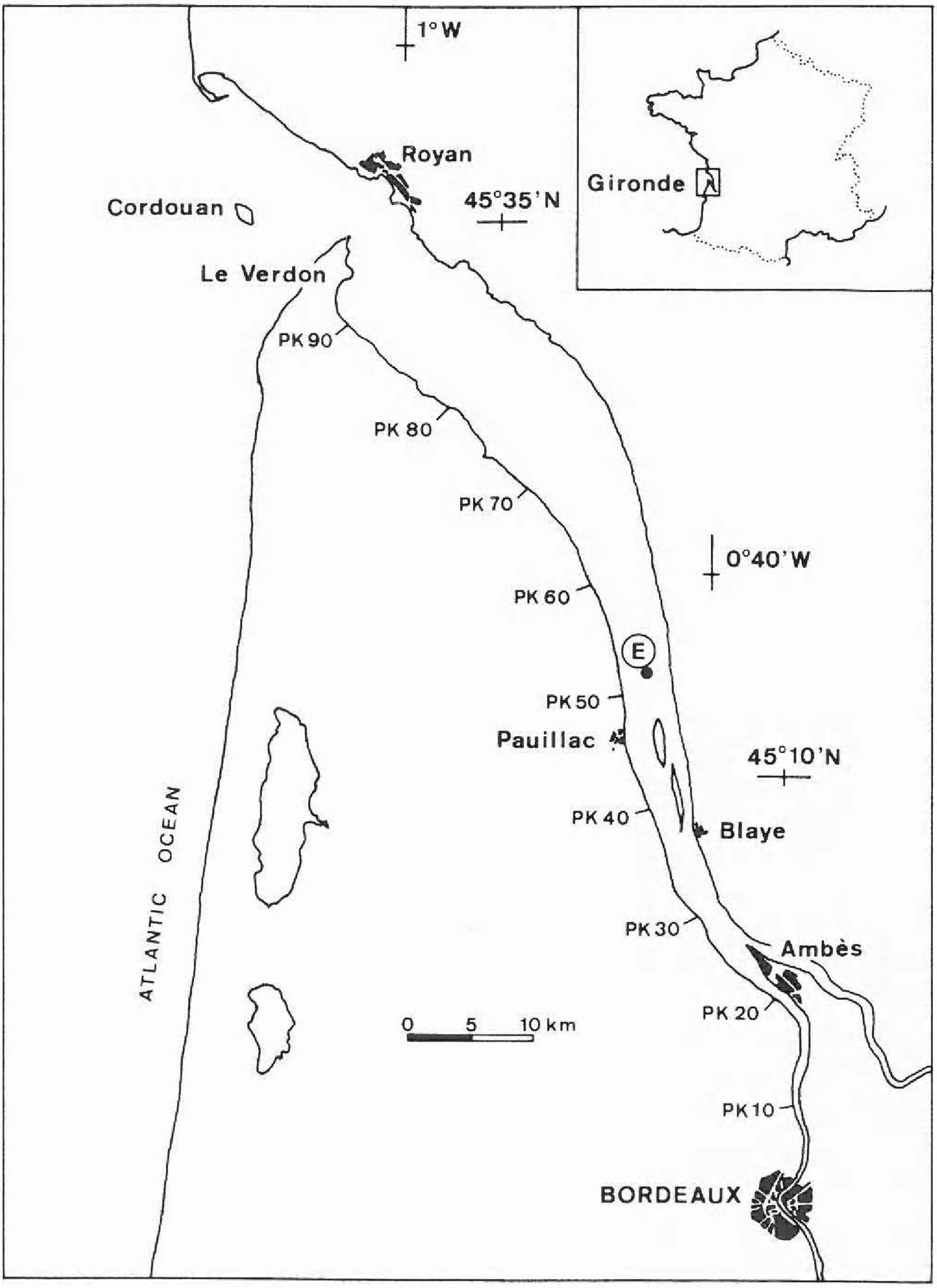

Fig. 1 : Map of the Gironde estuary showing the sampling station E (52 km downstream the city of Bordeaux).

One of the main feature of the Gironde estuary is the high turbidity of the water, with particulate concentrations that may exceed 1 g l^{-1} in a large part of the estuary. All the silt and clay in suspension in the Gironde estuary originates from the Garonne and Dordogne rivers. These two river systems supply between 1.5 and 3 10^6 t of suspended sediment annually, with a mean of about 2.2 10^6 t. A well developed turbidity maximum forms at the upstream limit of the salinity intrusion, in the zone of convergence of bottom residual currents. This maximum migrates to the lower estuary during the winter and spring high river flow, and to the upper estuary during summer and fall low river flow. During low river flow, the mass of turbid water stretches downstream at ebb and upstream at flood, thus covering a zone of more than 70 km in length. Conversely, during high river discharge, the turbidity maximum zone is much more restricted in space, leading to very high suspended matter concentrations (several g/l). The accumulation and migration of the turbidity maximum seems to be a purely dynamic phenomenon, with little relationship to variations in salinity (Jouanneau & Latouche, 1981). Because of the circulation and transportation patterns, a particle entering the estuary may remain in the maximum turbidity zone for one year or more before being expelled to the sea.

MATERIAL & METHODS

One sampling station (Station E, 52 km from the city of Bordeaux) was selected in the oligo-mesohaline zone of the estuary (Fig. 1). This station is considered as representative of the autochthonous zooplankton community (Castel & Feurtet, 1992).

The zooplankton data were collected from May 1978 to November 1991. Samples were taken monthly in winter and fortnightly in summer. Sampling was generally done from February to November during the years 1978-1984. From 1985 onwards, sampling was performed between March and November and duplicate campaigns were made only in July (Tabl. I). The sampling ranged over 163 months and the number of samples totalled 1 484. Zooplankton was collected with a standard WP2 net. One tow was made just below the surface and another near the bottom. Each tow was 1 to 2 min long. Samples were obtained at appox 2 h intervals during a tidal cycle and were made against the current. The volume of water filtered through the net was monitored with a TSK mechanical flowmeter or with a Hydrobios digital flowmeter. During the first 2 year the filtration coefficient was calculated by comparison with the values recorded by a flowmeter placed outside the net's mouth. The volumes filtered and the filtration coefficients were usually 4 to 25 m^3 and 75 to 95 % respectively. The catch was preserved in 4 % seawater/formalin.

At the same time and with the same periodicity the following variables were measured : temperature, salinity, current velocity, suspended matter concentration (dry weight after filtration on GF/C).

For the numerical analyses surface and bottom samples and measurements were averaged. When two sampling campaigns were made during the same month, the values obtained were averaged. Missing values were interpolated by computing the mean between the preceding value and the following one. Two subsequent missing values were not interpolated and the file was compressed.

The first step in the analysis was to graph the original data against time. To investigate long-term trends in the zooplankton numbers, the abundance estimates were adjusted by removing the seasonal effect. In order to remove the seasonal variation in plankton abundances and environmental parameters, residuals were calculated by substracting the corresponding monthly average of the forteen-year period from each observation (Chatfield, 1984). The residuals were log-transformed except for temperature and salinity. Linear correlation was used to evaluate the covariance of changes in zooplankton abundances and environmental factors ; Pearson correlations were calculated between time and zooplankton abundance residuals and environmental residuals.

TABLE I

Number of sampling campaigns undertaken in the Gironde estuary according to months during the study period (1978-1991). N° SI. : number of zooplankton samples taken each year. * Refers to campaigns during which only environmental variables could be measured.

	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	Sum
J	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
F	*1	1	1	1	1	*1	0	0	0	0	0	0	0	0	6
M	0	1	1	1	1	1	1	1	1	0	1	1	1	1	12
A	0	1	1	1	1	1	1	1	1	1	1	1	1	1	13
M	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
J	2	2	2	2	2	2	1	1	1	1	1	1	1	1	20
J	2	2	2	2	2	2	2	2	2	2	2	2	2	2	28
A	2	2	2	2	2	2	1	1	1	1	1	0	0	0	17
S	0	1	0	0	0	1	1	1	1	1	0	1	1	1	9
O	1	0	1	1	1	0	0	0	0	1	1	1	1	1	9
N	1	1	0	0	0	1	1	1	1	1	1	1	1	1	11
D	0	0	1	1	1	0	0	0	0	0	0	0	0	0	3
Sum	10	12	12	12	12	12	10	9	9	9	9	9	9	9	143
N° SI	108	144	126	140	138	126	80	90	90	90	90	90	90	82	1 484

RESULTS

Hydrography

Water temperature correlated positively with time ($r = 0.493$, $p<0.01$). This trend is illustrated by the evolution of the maximum temperatures. For instance a maximum value of 22 °C was recorded on 29 August 1978 and a value as high as 26.5 °C was noted on 23 July 1991. However, the temperature data show that the year 1984, winter 1985 and winter-spring 1986 have been colder than the long-term average for the whole period (Fig. 2).

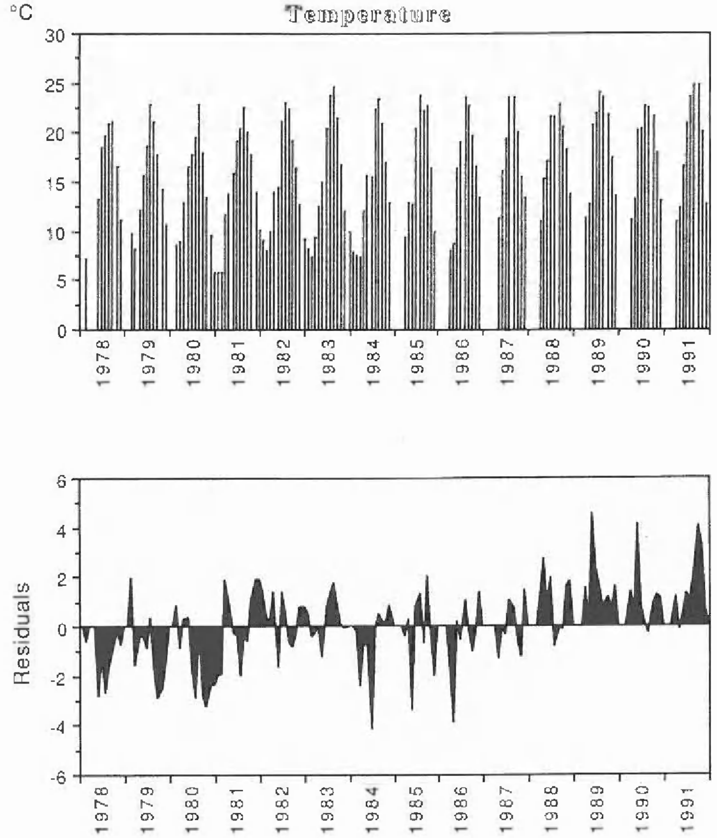

Fig. 2 : Averaged surface and bottom water temperatures in the Gironde estuary. The upper panel gives the original data (n = 138) and the lower graph displays deviations from the long-term monthly averages.

On average, the river flow is the lowest in August-September and the highest in February (Tabl. II). There was a general decrease of the river flow during the period of investigation, except in 1988 when a significant increase was observed (Fig. 3). The observation of the residuals clearly shows the general decrease trend of the river flow with the exception of 1988. The overal correlation with time was - 0.417 ($p<0.01$). The general decrease of the river flow was mainly due to a deficit in pluviosity occurring in 1986, 1987 and from 1989 onwards. The most striking feature is a protraction of the low water period.

The salinity regime at the sampling station falls in the oligo-mesohaline range. Contrary to the river flow, the general trend for salinity was an increase from 1978 to 1991 (correlation with time, $r = 0.541$, $p<0.01$). The same exception was found in 1988 (Fig. 4). Salinity is normally inversely correlated to the river flow. The general trend of the salinity evolution is inverted compared with that of the river flow but the correlation is not absolute (Tabl. III). This is especially clear when comparing the amplitude of the variations which

TABLE II

Average monthly values (1978-1991) of environmental variables and zooplankton densities in the middle Gironde estuary.

	F	M	A	M	J	J	A	S	O	N
Temperature (°C)	7.77	9.76	12.63	16.17	19.62	22.45	22.84	20.70	16.73	12.02
Salinity (ppt)	1.24	1.74	2.09	2.14	2.65	4.78	7.41	8.71	7.60	4.83
River flow (m^3/s)	1 593	1 379	1 406	1 250	758	447	304	312	509	740
SPM conc. (mg/l)	1 353	1 463	1 315	1 199	1 090	865	749	867	1 167	1 624
E. affinis (N/m^3)	5 232	11 386	11 430	15 108	7 129	3 777	1 678	1 103	1 377	2 671
A. bifilosa (N/m^3)	0	6	53	144	67	689	695	304	209	39
N. integer (N/m^3)	0	3	17	58	81	104	52	23	14	6
M. slabberi (N/m^3)	0	2	17	46	132	476	485	273	145	31

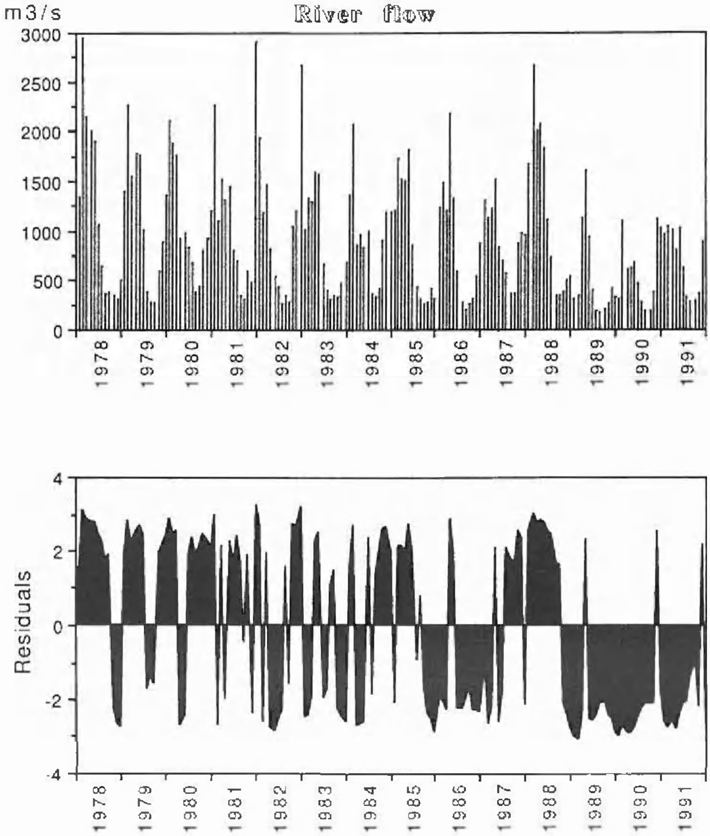

Fig. 3 : River flow (Garonne + Dordogne) in the Gironde estuary. The upper panel gives the original data (n = 168) and the lower graph displays deviations from the long-term monthly averages.

TABLE III

Correlation coefficients between environmental variables and between factors and zooplankton population densities (the seasonal effect removed from all data sets).
The level of significance is indicated by * $p<0.05$, ** $p<0.01$.

	Temperature	Salinity	River flow	SPM conc.
Temperature (°C)		0.417**	- 0.293**	No meaning
Salinity (ppt)			- 0.619**	- 0.207*
River flow (m^3/s)				0.063
E. affinis (N/m^3)	- 0.241*	- 0.333**	0.311**	0.032
A. bifilosa (N/m^3)	0.063	0.274**	- 0.288**	0.130
N. *integer* (N/m^3)	0.061	0.001	- 0.071	0.105
M. *slabberi* (N/m^3)	0.062	0.292**	- 0.346**	0.152

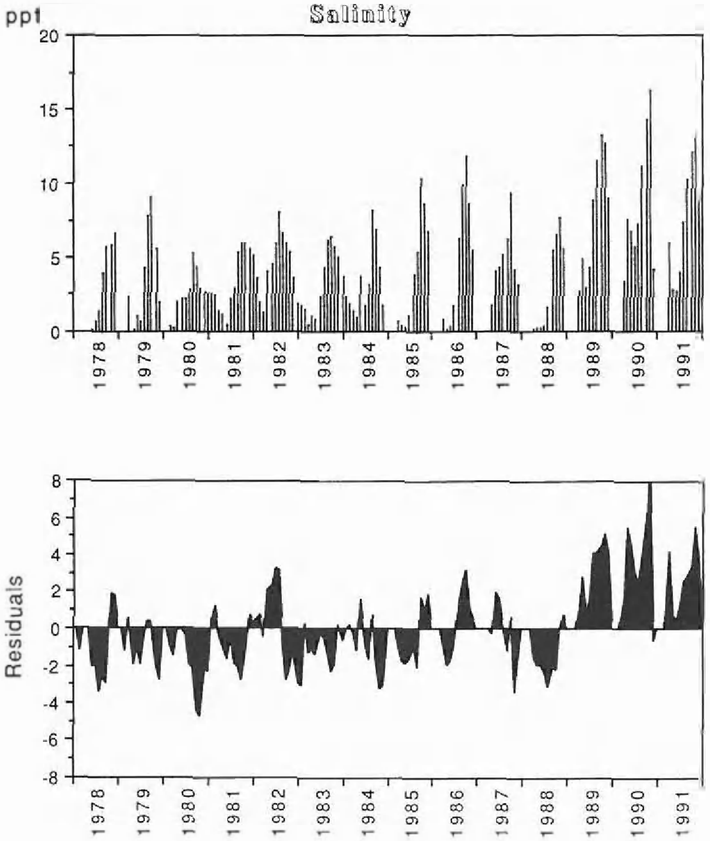

Fig. 4 : Averaged surface and bottom salinities in the Gironde estuary. The upper panel gives the original data ($n = 138$) and the lower graph displays deviations from the long-term monthly averages.

are not the same for both variables. Besides these long-term changes there were the normal annual fluctuations in salinity (the highest values in late summer-early spring and lowest values in winter ; Tabl. II). There was a good correlation between salinity and temperatures (seasonally adjusted).

On average net velocity was negatively correlated with time ($r = -0.255$, $p<0.05$). However, two distinct phases could be distinguished : a phase of increase from 1978 to 1982 and a decreasing phase from 1983 onwards (Fig. 5).

For the suspended matter, the trend was slightly different, although the general tendency was a decrease with time ($r = -0.341$, $p<0.01$). In a first phase a general increase was observed between 1978 and 1981-1982. Values were higher than the mean in 1982-1984, and then from 1984 onwards, a very sharp decrease occurred (Fig. 6).

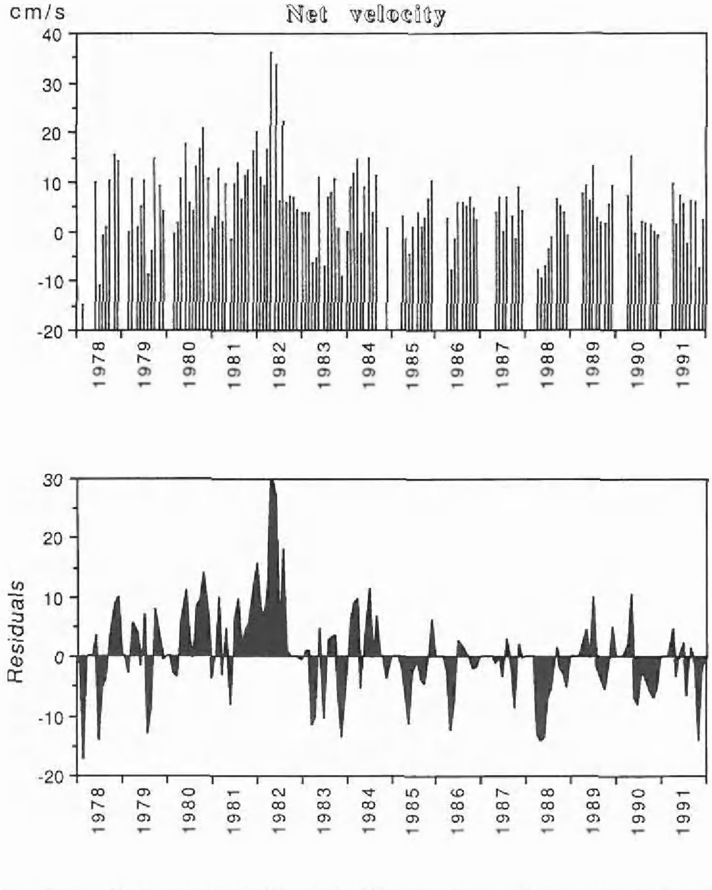

Fig. 5 : Averaged surface and bottom net velocities in the Gironde estuary. The upper panel gives the original data (n = 136) and the lower graph displays deviations from the long-term monthly averages. Positive values indicate an upstream direction of the net velocity, negative values indicate downstream net velocities.

The suspended matter concentration depends on the river flow and resuspension. In the present study, the correlation between SPM and river flow was non significant. Conversely, a good correlation ($r = 0.543$, $p<0.01$) was found between SPM concentration (in mg/l) and net velocity (m/s) computed from the current velocity measurements made during each tidal cycle.

Zooplankton populations

The autochthonous zooplankton community is dominated by two copepod species : *Eurytemora affinis* (Poppe) and *Acartia bifilosa* (Giesbrecht). High numbers of *Acartia tonsa* Dana can be recorded in summer but during a short period of time, thus the species is not included in the analysis. The Mysids *Neomysis integer* (Leach) and *Mesopodopsis slabberi* (Van Beneden) are not true planktonic forms but young individuals are found in significant number in most samples. They are taken into account in the present study.

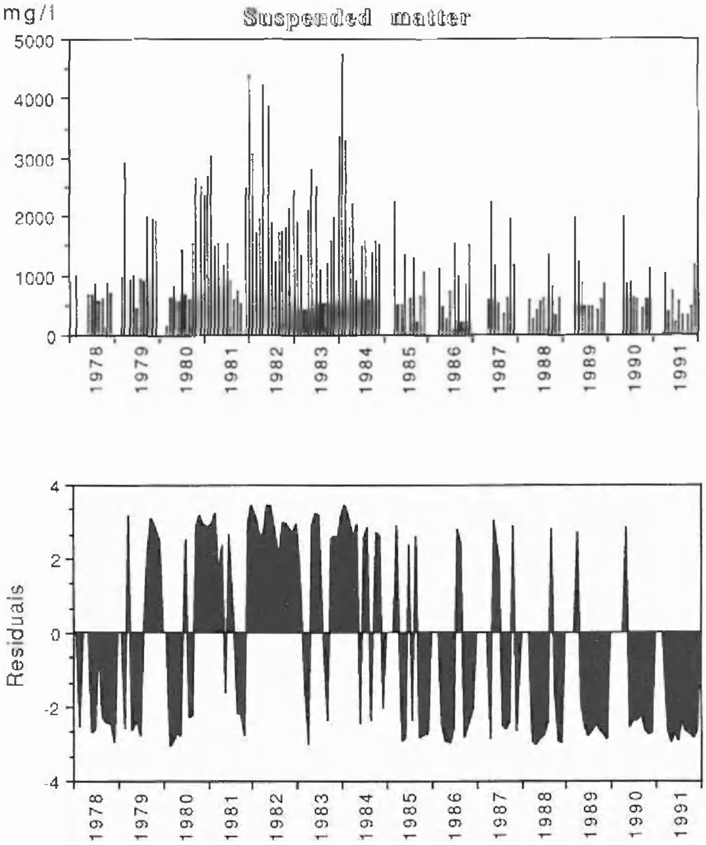

Fig. 6 : Averaged surface and bottom suspended matter concentrations in the Gironde estuary. The upper panel gives the original data ($n = 137$) and the lower graph displays deviations from the long-term monthly averages.

Eurytemora affinis is clearly the most dominant species in the oligo-haline zone of the Gironde estuary (Castel & Veiga, 1990), as it is the case in most estuaries. It is mostly abundant in spring, with a maximum in May (Tabl. II). Lowest densities are observed in September when temperature and salinity are high. During the study period *Eurytemora* showed an oscillatory behaviour, especially when considering the peaks of abundance, with a maximum in 1984 and in 1991 (Fig. 7). However, the trend for the mean abundance (residuals) was not the same as the trend for maximum abundance. During the first part of the study, the trend for *Eurytemora* was inversely related to that of the suspended matter (compare Fig. 7 and 6). However, the correlation was non existent over the whole sampling period.

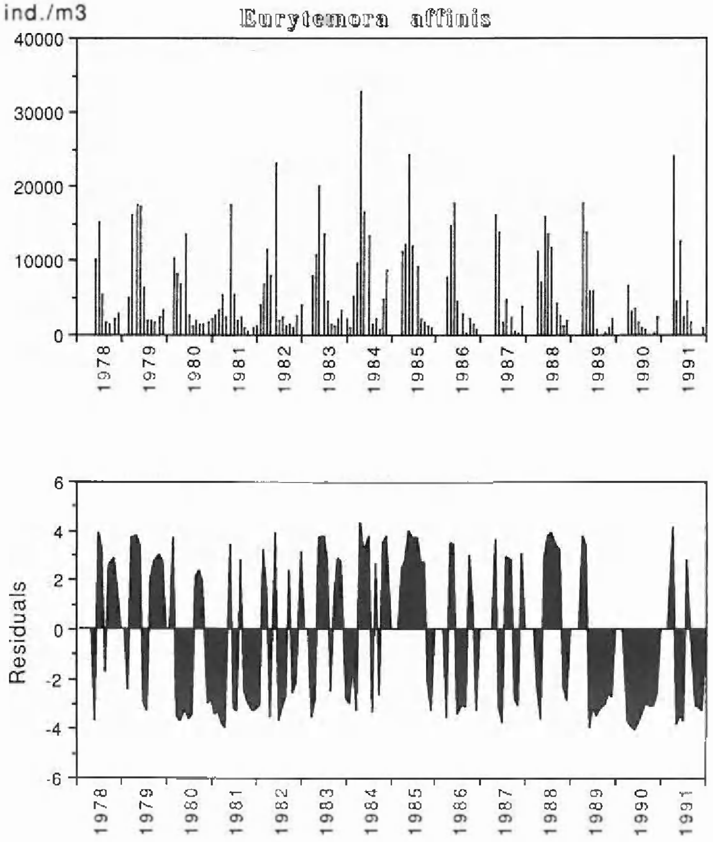

Fig. 7 : Averaged surface and bottom densities of the Copepod *Eurytemora affinis* in the Gironde estuary. The upper panel gives the original data (n = 135) and the lower graph displays deviations from the long-term monthly averages.

During the second phase (1984 onwards), *Eurytemora* abundances followed the general trend observed for the river flow. During this period, the river flow decreased significantly. Furthermore, the current velocity decreased, especially the flood current. This can explain that, during this period, *Eurytemora* became more sensitive to the river flow variation in the study area. Consequently, the population was also affected by high salinity. Over the whole sampling period, *Eurytemora* was inversely correlated with temperature and salinity and positively correlated with the river flow (Tabl. III).

Acartia bifilosa is much less abundant than *Eurytemora*. Its maximum abundance is observed in late July-August (Tabl. II). *Acartia* lives more seaward than *Eurytemora* and prefers higher salinity (Castel, 1981). The general trend of increase observed for the salinity was found in *Acartia* population but the correlation was not very high (r = 0.274). *Acartia* was mainly correlated to salinity till 1988. Similarly, an inverse correlation between *Acartia* trend of abundance and the river flow was observed mainly during this first period

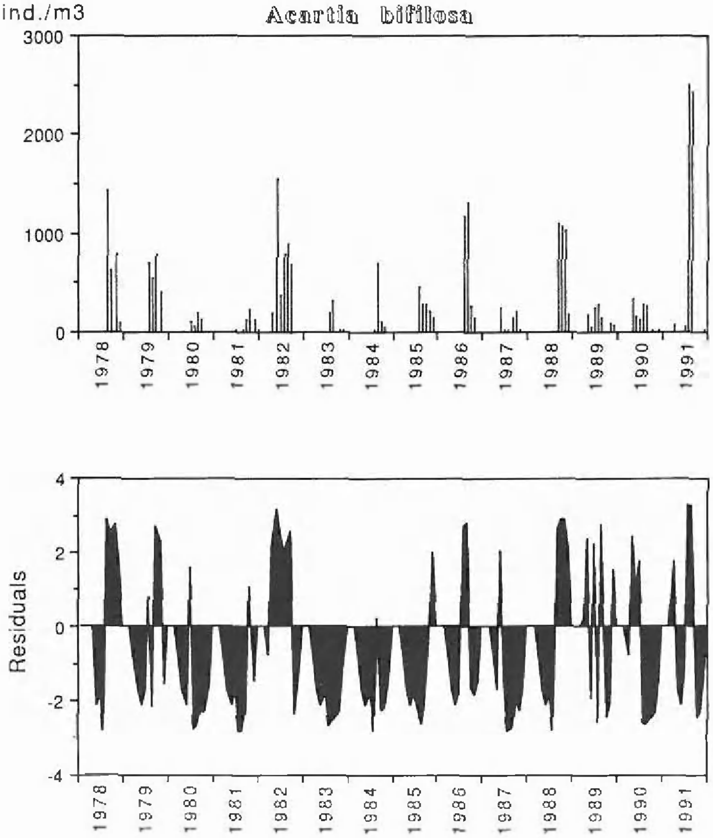

Fig. 8 : Averaged surface and bottom densities of the Copepod *Acartia bifilosa* in the Gironde estuary. The upper panel gives the original data (n = 135) and the lower graph displays deviations from the long-term monthly averages.

of ten years. Thereafter, the correlation was quite nonexistent. Despite high salinities during the last three years, the average abundance of *Acartia* was not regularly increased (Fig. 8).

Neomysis integer is a typical inhabitant of the oligo-mesohaline zone of the estuary. It is most abundant in July (Tabl. II). The peaks of abundance tended to increase from 1978 to 1987 (Fig. 9). However, after extraction of the seasonal effect, no trend was evidenced (correlation with time, r = - 0.110), except low values from 1989 to early 1991 probably due to the high salinities. *N. integer* lives preferentially near the bottom (pers. obs., Sorbe, pers. comm.). This together with its capacity of swimming make it more independent of the water mass displacement, which can explain the lack of correlation between *N. integer* and the environmental variables.

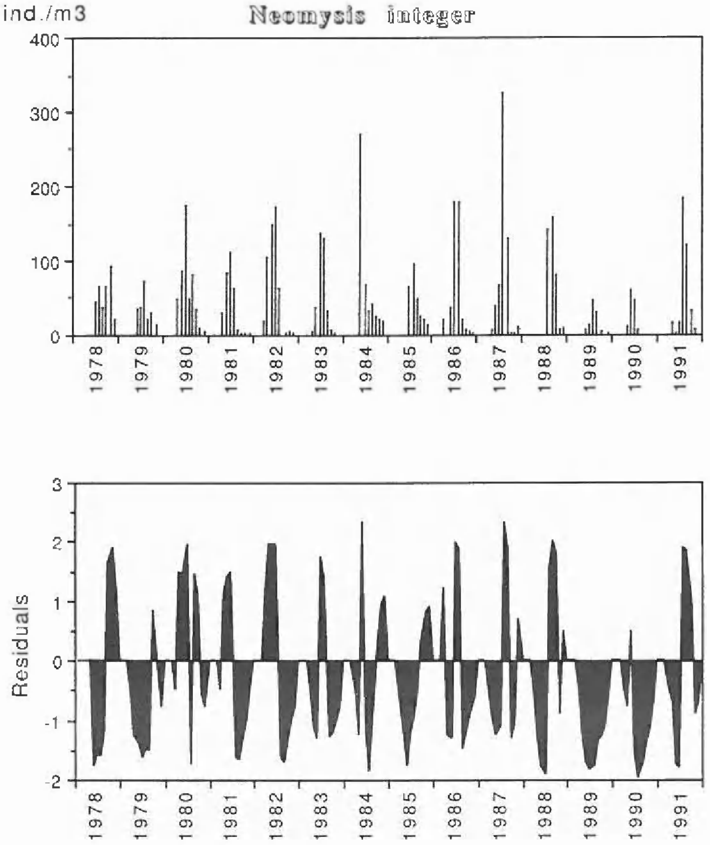

Fig. 9 : Averaged surface and bottom densities of the Mysid *Neomysis integer* in the Gironde estuary. The upper panel gives the original data (n = 135) and the lower graph displays deviations from the long-term monthly averages.

Mesopodopsis slabberi lives more downstream than *N. integer*. It colonizes the polyhaline zone. At the sampling station, maximum abundance is recorded in late July-August (Tabl. II). Like *A. bifilosa, M. slabberi* did not show a clear trend of abundance during the study period (Fig. 10). Both species had a very similar trend of evolution (correlation between residual, r = 0.718, p<0.01). Contrary to *N. integer, M. slabberi* is more pelagic and colonizes the whole water mass (pers. obs., Sorbe, pers. comm.). This can explain the better correlation found between *M. slabberi* and environmental factors (i.e. salinity). Although *Mesopodopsis* was correlated with salinity and inversely correlated with river flow, the increase in salinity during the years 1989-1991 was not followed by a clear increase in the abundance.

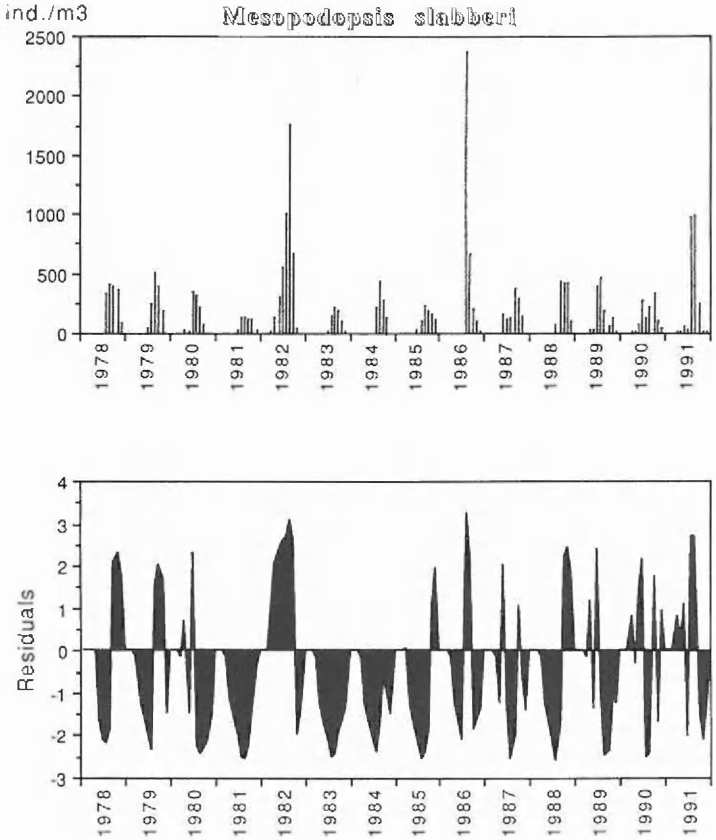

Fig. 10 : Averaged surface and bottom densities of the Mysid *Mesopodopsis slabberi* in the Gironde estuary. The upper panel gives the original data (n = 135) and the lower graph displays deviations from the long-term monthly averages.

DISCUSSION

Two main factors can explain the long-term trend of zooplankton population densities in the Gironde estuary during the period 1978-1991. There was a clear decrease of the river flow (except in 1988) probably caused by the general evolution of the climatological conditions (deficit in pluviosity). The impact of the construction of dams on the rivers of the drainage basin cannot be neglected but information is lacking. The second factor is the modification of the morpho-sedimentology of the study area due to the natural migrations of the banks (maps provided by P. Castaing, pers. comm.). To this hydro-morphological modification is associated a decrease of the current velocity (Fig. 11).

The decreasing trend of evolution of river flow and current velocity has consequences on ecological factors such as salinity and suspended matter concentration. The mean salinity normally increased in correlation with the reduction of river flow. The suspended matter

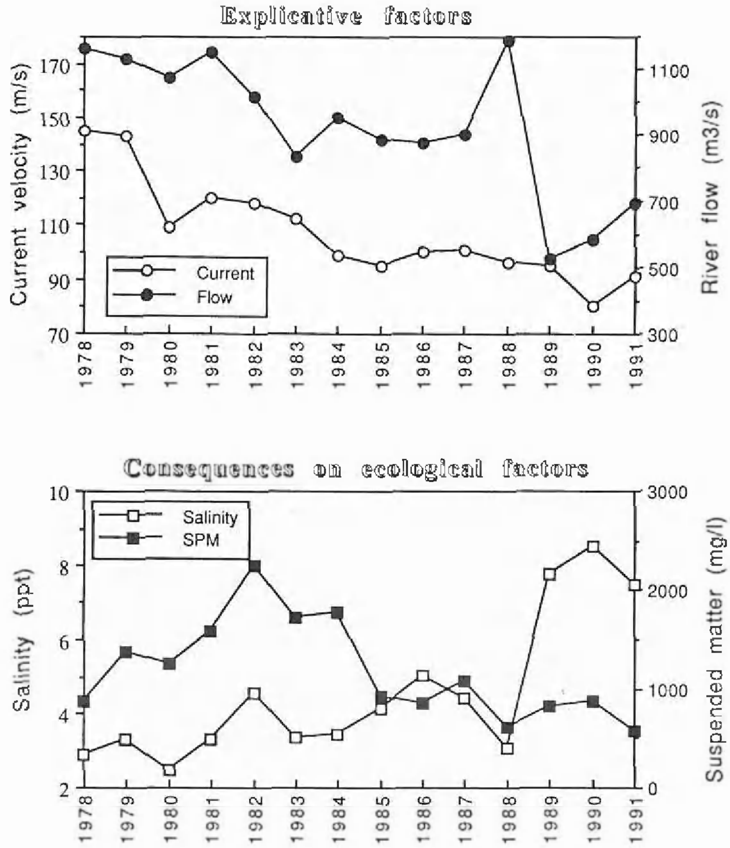

Fig. 11 : Summary of the long-term trend of the most important environmental factors influencing zooplankton populations in the Gironde estuary. Current velocity is the mean maximum velocity.

concentration depends on the river flow and the resuspension. During the first phase of the study (1978-1981), the river flow was extremely high. The turbidity maximum was pushed downstream the study area. Maximum SPM concentrations were recorded 15 km downstream the sampling area (P. Castaing & J.-M. Jouanneau, pers. comm.). Then, with the decrease of the river flow, the turbidity zone moved upstream and was situated exactly at the sampling station in 1982-1984. This is corroborated by the fact that, during this period, the net velocity increased and was oriented upstream. The last phase, with very low SPM concentrations, can be explained by two hypotheses :

- As the river flow continued to decrease, the turbidity zone continued to move upstream. In fact, the turbidity zone was often observed near Bordeaux.
- The second explanation is that due to the decrease of the current velocity, the resuspension was low. It is probably why the increase in river flow observed in 1988 was not followed by an increase in suspensed matter concentration.

All these trends in the hydrodynamics probably explain the evolution of the zooplankton populations. *Eurytemora affinis* lives preferentially in the upper part of the estuary. Its downstream distribution is limited by both salinity and the maximum turbidity zone. The maximum of the population is found just upstream the maximum of SPM concentration or in the turbidity cloud if the SPM concentration is not too high (Castel, 1984 ; Castel & Feurtet, 1989). This distribution is the result of transport processes (Castel & Veiga, 1990) leading to a kind of "amassment" in the zone of high turbidity (Soltanpour-Gargari & Wellershaus, 1984). Thus the long-term trend of evolution of *E. affinis* can be explained by the relative position of the population and of the turbidity maximum. At the beginning of the study, high abundance of *Eurytemora* was recorded, as the turbidity maximum was situated downstream the sampling station. With the upstream migration of the turbidity maximum, the abundance of *Eurytemora* decreased at the sampling point, the population being pushed upstream. Samples taken in 1989-1991 showed that the abundance was significantly higher 20 km upstream the station E (unpublished data). Furthermore, the decrease in abundance was probably accentuated by the high salinities occurring at the end of the sampling period.

Acartia bifilosa, which is a polyhaline species, has a maximum abundance downstream the sampling station. Its abundance in the middle estuary is greatly influenced by the salinity and by the river flow. This influence has been demonstrated recently (Ibanez *et al.*, in press). However, the strong increase in salinity observed in 1989-1991 did not result to such an extent to an increase of *Acartia* abundance. A possible explanation is that the colonisation of the sampling area was restricted due to the reduction of water circulation : it is likely that the decrease of the flood current velocity has reduced the flux of water in the study area. The same occurred for the Mysid *Mesopodopsis slabberi*, a species with the same spatial and temporal distribution as *Acartia*.

In summary, during the period 1978-1991, the hydrology of the middle estuary was characterized by two phases corresponding to i/ a fluvial dominated estuarine system (1978-1984) and ii/ to a mixed system with low water exchanges (1984-1991). During the first phase, *Eurytemora* was favoured by low salinity but was affected by high SPM concentrations, and *Acartia* did not colonize very well the area due to low salinity. During the second phase, *Eurytemora* was transported upstream and was affected by high salinities at the sampling point ; *Acartia* was theoretically favoured by high salinity but was affected by low exchanges of water.

From all the data, it seems clear that the long-term evolution of zooplankton in the Gironde estuary can be explained in great part by the general hydrology. The dominant factor is the river flow which governs the movements of the populations along the estuary. The SPM concentrations also affect the populations (Sellner & Bundy, 1987 ; Castel & Feurtet, 1987) but the variations of SPM concentration depend on both the river flow and the morphology of the bottom.

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Distribution and abundance of shallow-water hyperbenthic mysids (Crustacea, Mysidacea) and euphausiids (Crustacea, Euphausiacea) in the Voordelta and the Westerschelde, southwest Netherlands.

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Abstract : The hyperbenthic mysids and euphausiids of the subtidal shallow coastal waters (the Voordelta) and the Westerschelde estuary in the Delta area (SW Netherlands) were regularly sampled between 1988 and 1991. Two salt marshes in the brackish part of the estuary were studied in the same period. Eight mysid species and one euphausiid species were identified. The spatial and seasonal distribution patterns of all species are described. The most abundant species in the coastal area is *Schistomysis spiritus*, followed by *Mesopodopsis slabberi*, *Schistomysis kervillei*, and *Gastrosaccus spinifer*. In the marine part of the Westerschelde the same four species are dominant but densities are generally higher than in the coastal area. Only *Siriella armata* and the euphausiid *Nyctiphanes couchi* never enter the estuary. Highest mysid densities, mainly *M. slabberi* and the estuarine endemic *Neomysis integer*, are found in the brackish part of the Westerschelde. *Praunus flexuosus* is a euryhaline species with a preference for the intertidal areas. The estuarine populations of *N. integer*, *M. slabberi*, *P. flexuosus*, and - to a lesser extent - *S. spiritus* seem to utilise the salt marshes during periods of reproduction.

Résumé : Les mysidacés et euphausiacés suprabenthiques d'une zone côtière sous-tidale peu profonde (le *Voordelta) et l'estuaire* de l'Escaut occidental, dans la région du Delta (SW des Pays-Bas) ont été échantillonnés à partir à intervalles réguliers entre 1988 et 1991. Deux marais maritimes situés dans la partie saumâtre de l'estuaire ont été étudiés pendant la même période. Huit espèces de mysidacés et une espèce d'euphausiacé ont été identifiées. La distribution spatiale et temporelle de toutes les espèces est décrite. L'espèce la plus abondante dans la zone côtière est *Schistomysis spiritus*, suivie par *Mesopodopsis slabberi*. *Schistomysis kervillei* et *Gastrosaccus spinifer. Dans la partie marine* de l'Escaut les *quatre mêmes* espèces sont dominantes mais leur densité sont généralement plus élevées que dans la zone côtière. Seuls *Siriella armata* et l'euphausiacé *Nyctiphanes couchi* n'entrent jamais dans l'estuaire. Les plus fortes densités en mysidacés, surtout *M. slabberi* et l'espèce estuarienne endémique *Neomysis integer*, sont observés dans la partie saumâtre de l'Escaut. *Praunus flexuosus* est une espèce euryhaline, avec une préférence pour les zones intertidales. Les populations estuariennes de *N. integer, M. slabberi, P. flexuosus* et, *dans une moindre mesure, S. spiritus* semblent utiliser les marais maritimes pendant les périodes de reproduction.

INTRODUCTION

In comparison to other groups of marine invertebrates, e.g. zooplankton (De Pauw, 1975 ; Soetaert & Van Rijswijk, in press), macrobenthic animals (Wolff, 1973, Craeymeersch *et al.*, 1990 ; Meire *et al.*, 1991) and meiobenthic animals (Heip *et al.*, 1990 ; Vanreusel, 1990, 1991), the mysids and euphausiids of the Delta area in the southwest Netherlands (and in Dutch waters in general) have hardly been studied. This is probably mainly due to the problems involved in sampling the lower part of the watercolumn (the hyperbenthal), where most shallow water mysids concentrate during the day (review in Mauchline, 1980). This lack of studies contrasts with the recognized importance of mysids in coastal and estuarine food webs : they are reported to be omnivorous feeders and they constitute an important part of the diet of fish and shrimps (review in Mauchline, 1980).

Information on the mysid fauna of the area is scattered in rather dated and often 'grey' literature. Hoek (1887) gives a list of the mysids of Dutch waters including the Delta area and Tesch (1910) covers the mysids and euphausiids of the surface waters of the Southern Bight of the North Sea. Van Beneden (1860), Kramp (1913) and Zimmer (1932) provide some information on the mysid fauna of the Belgian coast. Occasional records of mysids can be found in the extensive studies of the macrozoobenthos of the Delta area (Wolff, 1973) and in a study of the zooplankton of the Westerschelde estuary (De Pauw, 1975). Data are available on the distribution and population biology of *Praunus flexuosus* and *Neomysis integer* in the saline Lake Grevelingen (Borghouts, 1978 ; Fortuin, 1980 ; Platenkamp, 1983). In studies of the hyperbenthos of the Voordelta (Hamerlynck & Mees, 1991) and the Westerschelde (Mees & Hamerlynck, 1992 ; Mees *et al.*, in press) mysids are the dominant component. Data also exist on the neritic mysid and euphausiid fauna in the surface plankton near the Texel lightship, situated some 200 km north of the area under consideration (Van der Baan & Holthuis, 1969, 1971).

This study focuses on the distribution and abundance of the mysids of the shallow coastal area in front of the mouth of the rivers Rhine, Meuse and Schelde (the Voordelta) and of the Westerschelde. In order to assess horizontal seasonal migrations the temporal variability in the distributional patterns is also investigated. Studies on the population biology and the trophodynamics of the different species will be published elsewhere.

MATERIAL AND METHODS

The Voordelta stretches from the Dutch-Belgian border in the south to the Hoek van Holland in the north. Offshore, the area is arbitrarily defined by the Mean Tidal Level (MTL) - 15 m depth contour. The study covers only the central part of the Voordelta (Fig. 1) at the mouth of the former Grevelingen and Oosterschelde estuaries. The abiotic environment is discussed in Louters *et al.* (1991). Between August 1988 and July 1989 ten surveys were conducted at approximately monthly intervals in 12 localities : stations 1-4 in the ebb-tidal delta of the Grevelingen, stations 8-12 in the ebb-tidal delta of the Oosterschelde and stations 5-7 in the more seaward Banjaard area between both ebb-tidal deltas. In each station 2 samples were taken : one in the gully at a depth of about MTL - 10 m and one on the sandbank slope at a depth of about MTL - 5 m. As no consistent differences were found between these two depth strata, the number of individuals caught in both samples were pooled and divided by 2 for the purpose of this paper.

The Westerschelde estuary (Fig. 2) is the lower part of the river Schelde. The maritime zone of the tidal system is about 70 km long from the North Sea (Vlissingen) to the Dutch-Belgian border near Bath. The Westerschelde is the last remaining true estuary of the Delta area and is characterised by a marked salinity gradient. The abiotic environment is discus-

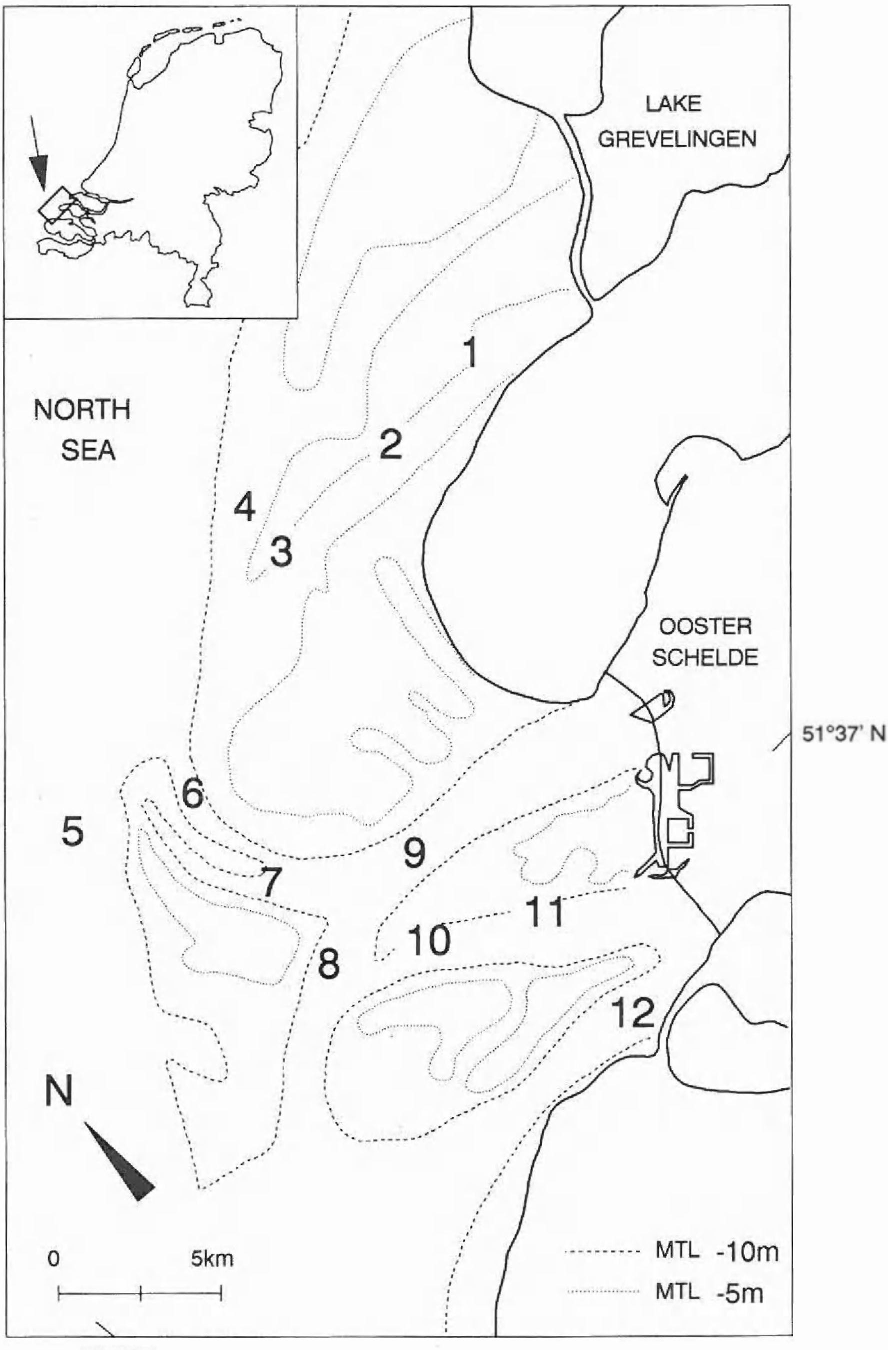


Fig. 1 : Map of the Voordelta with the sampling localities.

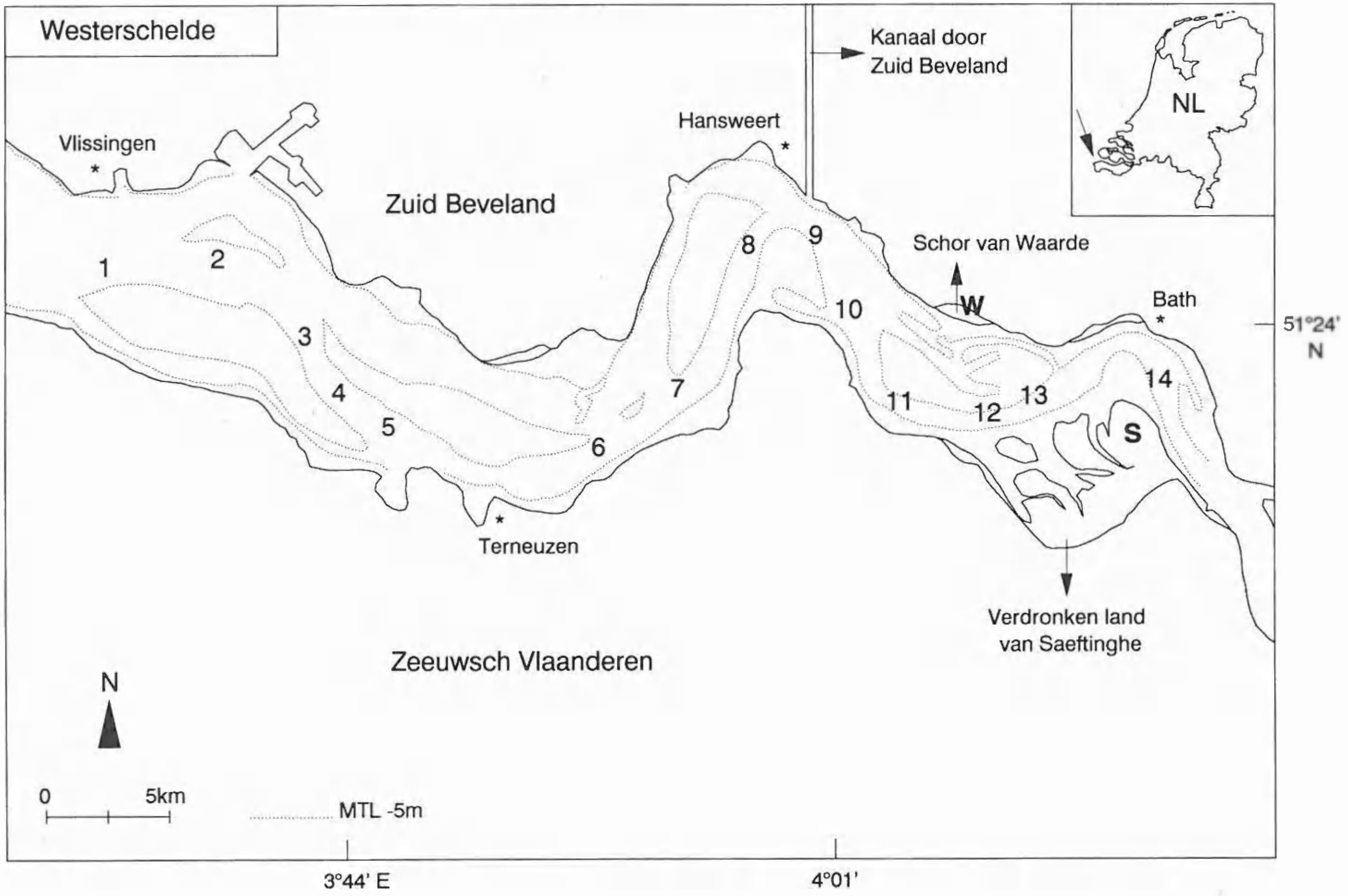


Fig. 2 : Map of the Weserschelde with the subtidal (1 to 14) and intertidal (W and S) sampling localities.

sed in Van Eck *et al.* (1991) and Heip (1988, 1989). Between April 1990 to April 1991 thirteen surveys were conducted. Each survey comprised 14 stations along the salinity gradient. On 3 occasions (March, April and May 1991) 5 additional samples were taken upstream from Bath to the city of Antwerp. All samples were taken in the subtidal channels. Where possible, the MTL - 10 m isobath was followed. Besides the subtidal surveys, monthly samples were taken at two intertidal stations in the salt marshes of Saeftinghe and Waarde (S and W in Fig. 2) from March 1990 to November 1990. The salt marsh of Waarde (107 ha) is a long-drawn marsh situated on the right bank of the estuary. It is drained by one major creek which runs parallel to the main channel of the estuary. The salt marsh of Saeftinghe (2 760 ha), situated on the left bank north of the harbour of Antwerp, is one of the largest of western Europe. It is drained by several large creeks which run perpendicular to the main estuarine channel. An overview of all sampling dates is presented in Table I.

TABLE I

Sampling dates for the different subareas (S is the salt marsh of Saeftinghe, W the salt marsh of Waarde).

Voordelta	Westerschelde	Salt marshes
10-08-1988	24-04-1990	15-03-1990 S
20-09-1988	21-05-1990	23-03-1990 W
15-11-1988	20-06-1990	05-04-1990 W
01-12-1988	26-07-1990	11-04-1990 S
16-01-1989	23-08-1990	22-04-1990 W
13-02-1989	29-09-1990	10-05-1990 S
17-03-1989	24-10-1990	11-06-1990 S
11-04-1989	27-11-1990	20-06-1990 W
10-05-1989	12-12-1990	03-07-1990 W
08-06-1989	21-01-1991	09-07-1990 S
26-06-1989	22-02-1991	08-08-1990 S
	18-03-1991	17-08-1990 W
	24-04-1991	10-10-1990 S
		15-10-1990 W
		05-11-1990 S
		30-11-1990 W

All subtidal samples were taken during daytime when hyperbenthic mysids are known to concentrate near the bottom. The samples were collected with a hyperbenthic sledge (Hamerlynck & Mees, 1991) which consists of a heavy metal frame equipped with two nets one above the other. The sledge is one meter wide. Both nets are 4 m long and have a mesh size of 2*2 mm in the first 3 m and 1*1 mm in the last 1 m. The contents of both nets were pooled for this study. The total area of the nets' mouth is 0.8 m^2 and it samples the hyperbenthal from 20 to 100 cm above the bottom. The sampler was towed for approximately 1 000 m (radar readings from fixed points) at an average ship speed of 4.5 knots relative to the bottom. The total area sampled was 1 000 m^2. Trawling was always done with the tide. Thus, the maximal amount of water filtered in one trawl was 800 m^3.

The salt-marsh samples were taken passively with a fyke net modified after McIvor & Odum (1986). The net is 5 m long with a 1*1 mm mesh and has a weir at the end. The mouth area of the net is 1*1 m. It was mounted on an iron frame and two heavy weights were attached at the lower end in order to keep the frame on the bottom of the creek. Ropes attached to the frame prevented lateral movement of the gear. The net was installed in the creek at low water, its mouth facing the current. Sampling covered a whole tidal cycle, the orientation of the gear evidently being changed at high tide. The net was emptied every 1 hour. Simultaneous measurements (every 15') of water height and current velocity in the creek allowed calculation of the volume of water filtered by the net.

During sampling temperature, salinity and dissolved oxygen content of the water were measured near the bottom.

The samples were preserved in a buffered formaldehyde solution, 7 % final concentration. In the laboratory all mysids and euphausiids were sorted out, identified to species level and counted. Special attention was payed to the presence of juvenile animals in the samples. These are defined as animals with no distinguishable secondary sexual characteristics. In female mysids a marsupium (or at least the oostegites) are visible and males are characterized by elongated fourth pleopods and a lobus masculinus between the flagellae of the antennal peduncle. The identification keys of Tattersall & Tattersall (1951) and Mauchline (1984) were used for mysids and euphausiids, respectively.

The reported densities in each station are the mean number of individuals per sample taken in that station (N/1 000 m^2), averaged over the whole study period. Densities of the intertidal samples are numbers per 1 000 m^3 of water filtered through the net.

The temporal patterns in the densities of the mysid and euphausiid populations are presented as the variation of average densities over all stations per subarea (Voordelta, Westerschelde) per sampling campaign. In order to describe the migrations and seasonal patterns in the Westerschelde, the main channel of the estuary is divided into a western and eastern part on the basis of community analyses in previous work (Mees & Hamerlynck, 1992 ; Mees *et al.*, in press). The marine part of the estuary (west) comprises the 8 downstream stations and the brackish part (east) comprises stations 10 to 14. Station 9 represents a transitional situation between the two communities and was eliminated for the purpose of this analysis. The seasonal variations in abundance in the salt marshes of Waarde and Saeftinghe are also presented separately.

Other faunal components of the hyperbenthos included amphipods, larval decapods, fish eggs, larval and postlarval fish, isopods, cumaceans, chaetognaths and a variety of other, less abundant groups. For full species lists we refer to Hamerlynck & Mees (1991) and Mees *et al.* (in press).

RESULTS

In total only eight species of mysid and one euphausiid were recorded (Tabl. II). Total mysid densities often exceeded 5 000 and 50 000 individuals per sample in the Voordelta and the Westerschelde, respectively. The Euphausiid *Nyctiphanes couchi* was only recorded in the Voordelta and always in low numbers with a maximum of 12 individuals per sample.

Most mysid species occur in both subareas, though not necessarily throughout the year. *Siriella armata* is restricted to the Voordelta. *Neomysis integer* and *Acanthomysis longicornis* were only recorded in the estuary, though for the latter species this concerns a single record (twelve specimens) in the mouth of the estuary.

TABLE II

Mysid and euphausiid species found in the Voordelta (V) and in the brackish (WB) and marine (WM) parts of the Westerschelde estuary and in the tidal creeks of the salt marshes (S). Capital letters indicate main distribution subarea.

Mysidacea	
Siriella armata (Milne-Edwards, 1837)	V
Gastrosaccus spinifer (Göes, 1864)	V, WM (wb)
Schistomysis spiritus (Norman, 1860)	V, WM (wb, s)
Schistomysis kervillei (Sars, 1885)	V, WM (wb, s)
Praunus flexuosus (Müller, 1776)	WB, S (v, wm)
Mesopodopsis slabberi (van Beneden, 1861)	V, WM,WB, S
Neomysis integer (Leach, 1814)	WB, S
Acanthomysis longicornis (Milne-Edwards, 1837)	WM
Euphausiacea	
Nyctiphanes couchi Bell, 1853	V

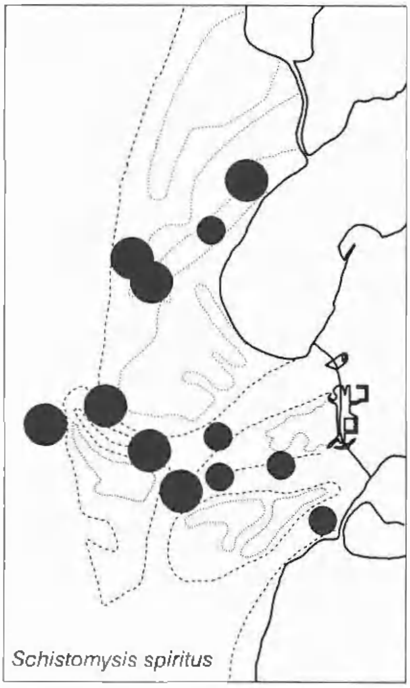
Spatial distribution

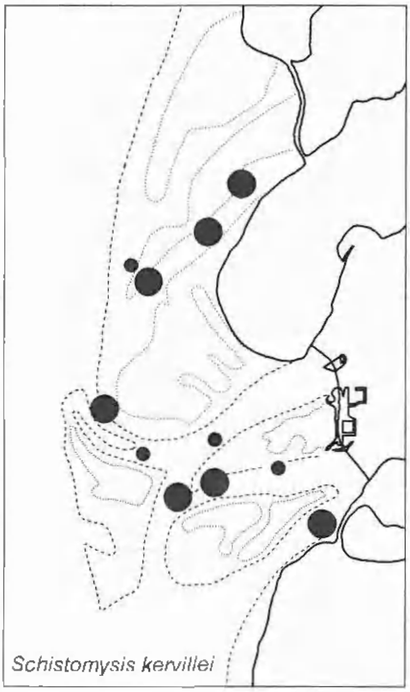
The geographical distribution and abundance of all mysid species and the single euphausiid are presented separately for the Voordelta and the Westerschelde (Figs. 3 & 4).

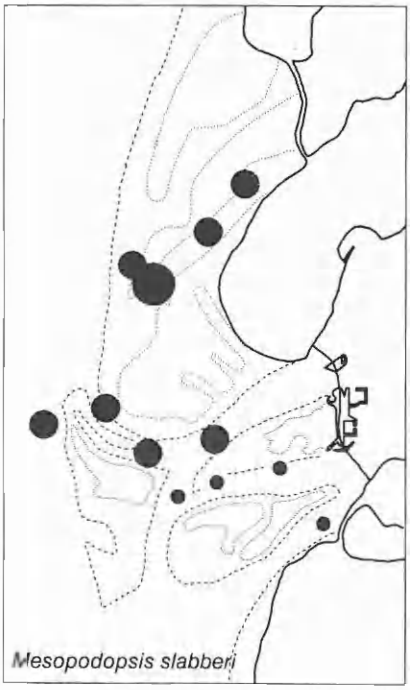
Voordelta

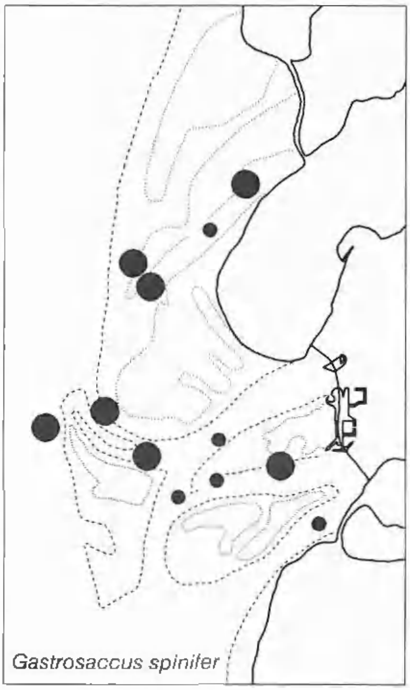
In the Voordelta (Fig. 3), average densities are never higher than 1 000 individuals. *Schistomysis spiritus* is the most abundant species in the area, followed by *Schistomysis kervillei, Mesopodopsis slabberi* and *Gastrosaccus spinifer*. The four species have overlapping geographical distributions. Densities are on average higher in the more sheltered area (see Louters *et al.*, 1991) of the ebb-tidal delta of the Grevelingen, and lower in the more dynamic ebb tidal delta of the Oosterschelde. The Banjaard stations are characterized by intermediate densities and are dominated by *S. spiritus. S. kervillei* is never found in the most seaward Banjaard stations.

Siriella armata and *Praunus flexuosus* are both large, shallow water species (Tattersall & Tattersall, 1951). They occur in low densities in the more inshore stations of the Voordelta, never in the Banjaard area. *Nyctiphanes couchi*, the euphausiid, is restricted to the marine waters of the Voordelta and is most common in the more seaward Banjaard stations.


Schistomysis spiritus


Schistomysis kervillei


Mesopodopsis slabberi


Gastrosaccus spinifer

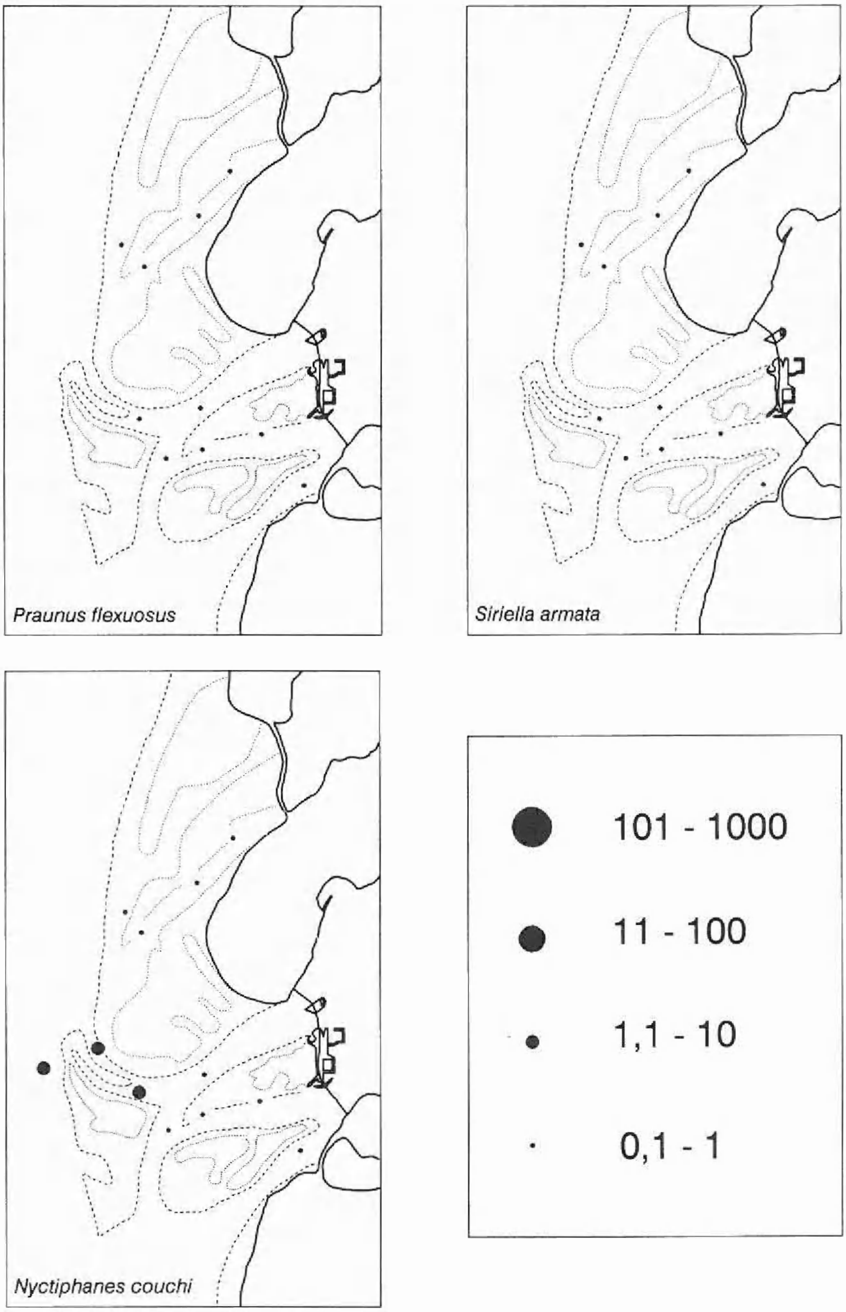


Fig. 3 : Distribution of all species caught in the Voordelta. Densities are yearly averages of the numbers of individuals caught per trawl (N/1 000 m^2).

Westerschelde

In the Westerschelde, the two most abundant mysid species are *Neomysis integer* and *Mesopodopsis slabberi*. Both species reach average densities of more than 1 000 individuals in the upstream stations (Fig. 4). *Neomysis integer* is confined to the brackish zone of the estuary. The species is recorded in salinities ranging from 25 to 8 g/l and is very abundant in the main channel as well as in both salt marshes. It was never caught downstream from station 6, nor in the Voordelta. The lacustrine limit of the population lies a few kilometres upstream of station 14 as exemplified by the results of the campaign from April 1991 (Fig. 5). This result is typical for all three surveys conducted upstream of the Dutch-Belgian border : a very rapid decline in abundance where oxygen saturation becomes less than 40 %.

Mesopodopsis slabberi is common throughout the estuary.

As for *N. integer*, densities are highest in the brackish part, with the upstream limit defined by the oxygen depletion zone. In the western, marine part of the estuary the species is generally more abundant than in the Voordelta.

Both *Schistomysis* species also penetrate into the estuary but they were never found at the innermost stations. In the marine part of the estuary densities of *S. kervillei* are comparable to those in the Voordelta. It is the only common mysid of the estuary which was never found in the salt marshes. *S. spiritus* is far less abundant in the Westerschelde than in the Voordelta and seems to be the more marine species of the two. It enters the saltmarshes only occasionally.

Gastrosaccus spinifer occurs in higher densities in the downstream stations of the Westerschelde than in the Voordelta. Densities decrease towards the upstream part. This species has only rarely been caught in the salt marsh of Saeftinghe, never in the salt marsh of Waarde.

Praunus flexuosus is a shore species which is common in brackish waters and in tidal zones around the coasts (Tattersall & Tattersall, 1951). It has a clear preference for the salt marsh areas (especially the salt marsh of Waarde). In the main channel of the estuary, it is only abundant in the 6 most brackish stations.

Acanthomysis longicornis is a rare occurrence in the area. The only record is a single catch of twelve individuals at station 2 in October 1990.

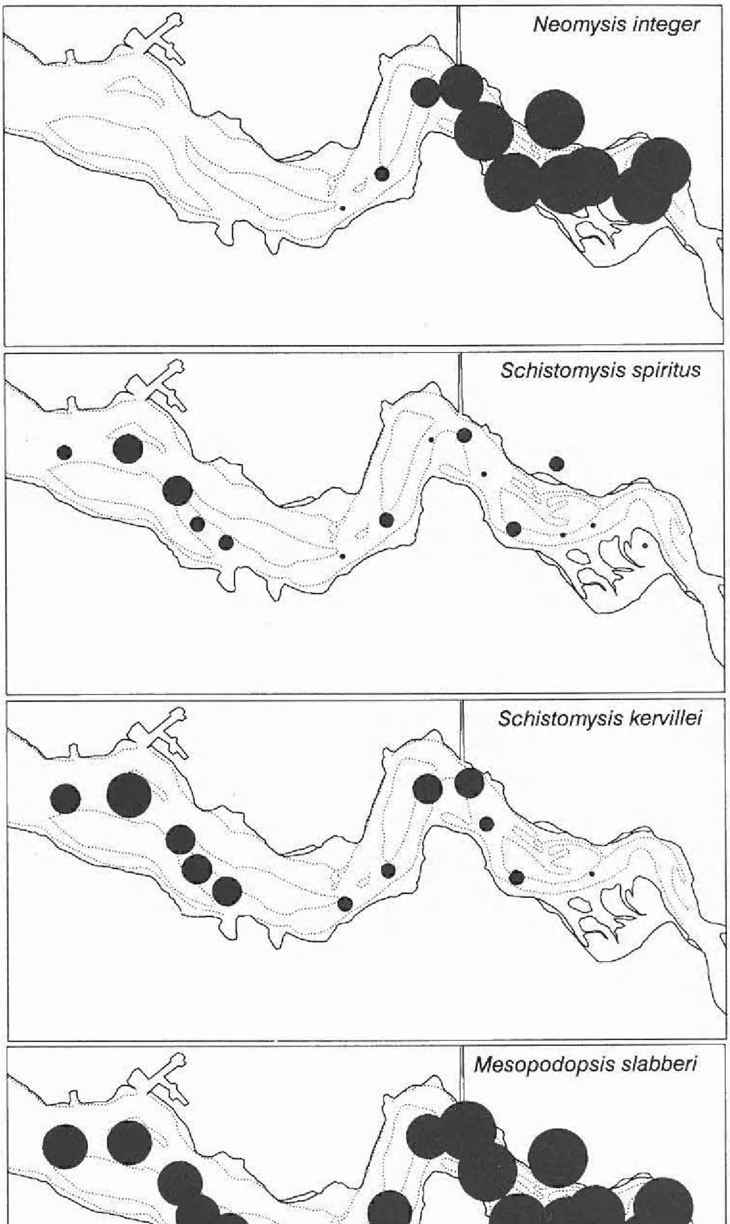
Temporal patterns

Marked seasonal variations are noted in the catches of the regularly occurring species.

Voordelta

In the Voordelta (Fig. 6), *Schistomysis spiritus, Mesopodopsis slabberi* and *Schistomysis kervillei* have two clear peaks in abundance : one in autumn and one in spring. These maxima coincide with periods of higher reproductive activity, with a lot of juveniles recruiting into the catch.

In the two former species there is a strong peak in abundance during spring (March-April) and a smaller one in autumn (September-November). For *S. kervillei* the autumn



Neomysis integer

Schistomysis spiritus

Schistomysis kervillei

Mesopodopsis slabberi

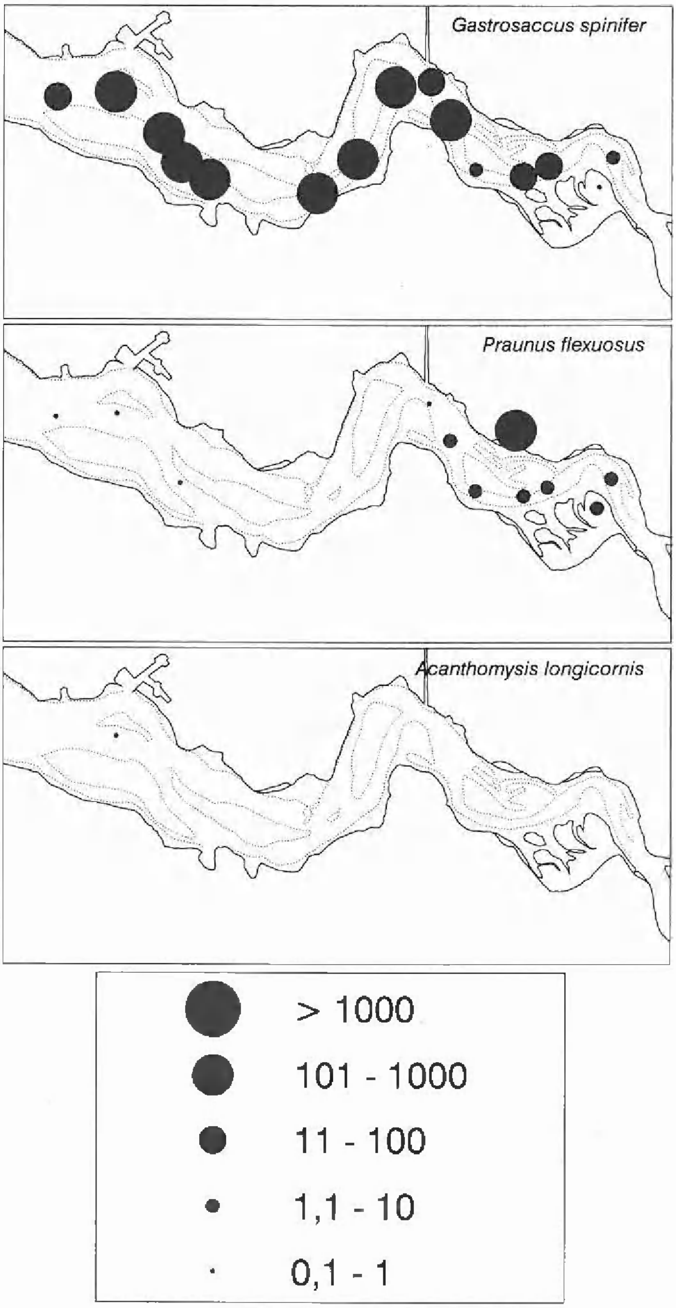


Fig. 4 : Distribution of all species caught in the Westerschelde and the salt marshes. Densities are yearly averages of the numbers of individuals caught per trawl (N/1 000 m²) for the sledge samples and N/1 000 m³ for the salt marsh samples.

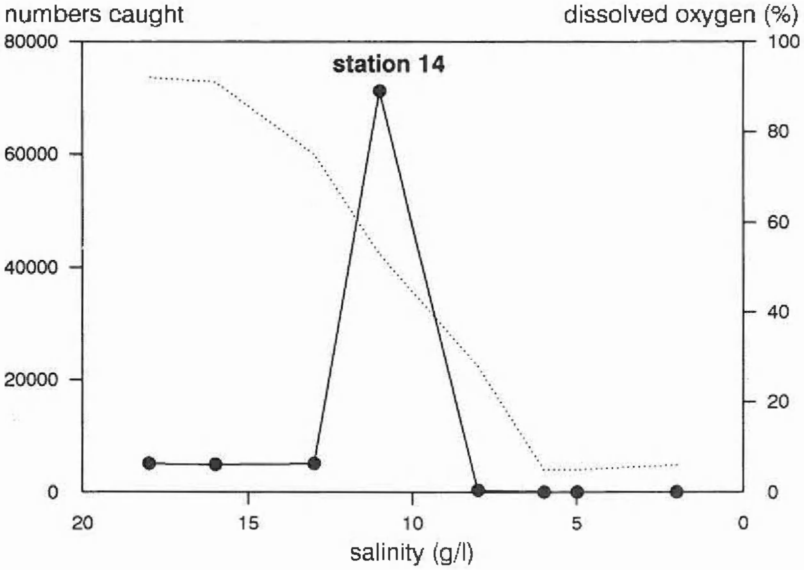


Fig. 5 : Densities of *Neomysis integer* along the salinity gradient from station 11 upto Antwerp in April 1991. Dissolved oxygen concentration is presented by the dotted line.

peak is observed somewhat later (November) and it is more pronounced than the spring peak. For all three species lowest numbers were found in winter (January-February) and in summer (June-August).

Gastrosaccus spinifer shows a more erratic seasonal pattern. This is a burrowing species (Mauchline, 1980) and catches are probably influenced by many factors such as wind, wave action, sediment characteristics, etc. Still, spring and autumn reproduction periods were observed and the same winter and summer minima as for the other species were evident.

Siriella armata also shows a bimodal abundance pattern. A small autumn maximum is observed in September. Densities are low in November and December, but increase again from January onwards to reach a spring maximum in March. The species was not recorded in the area from June through August. Neither of the two small abundance peaks were linked to recruitment of juveniles. Throughout the study period catches consisted solely of adults.

Praunus flexuosus (Fig. 6) and *Nyctiphanes couchi* (Fig. 7) are the only species which have maximal abundances during the winter months : *P. flexuosus* is only caught in late autumn and winter, *N. couchi* is present in the area from January to early June with peak densities from February to April.

Westerschelde

Schistomysis spiritus (Fig. 8) seems to be a typically marine species. It is absent from the estuary from late spring (June) until autumn (September). It enters the marine part of the

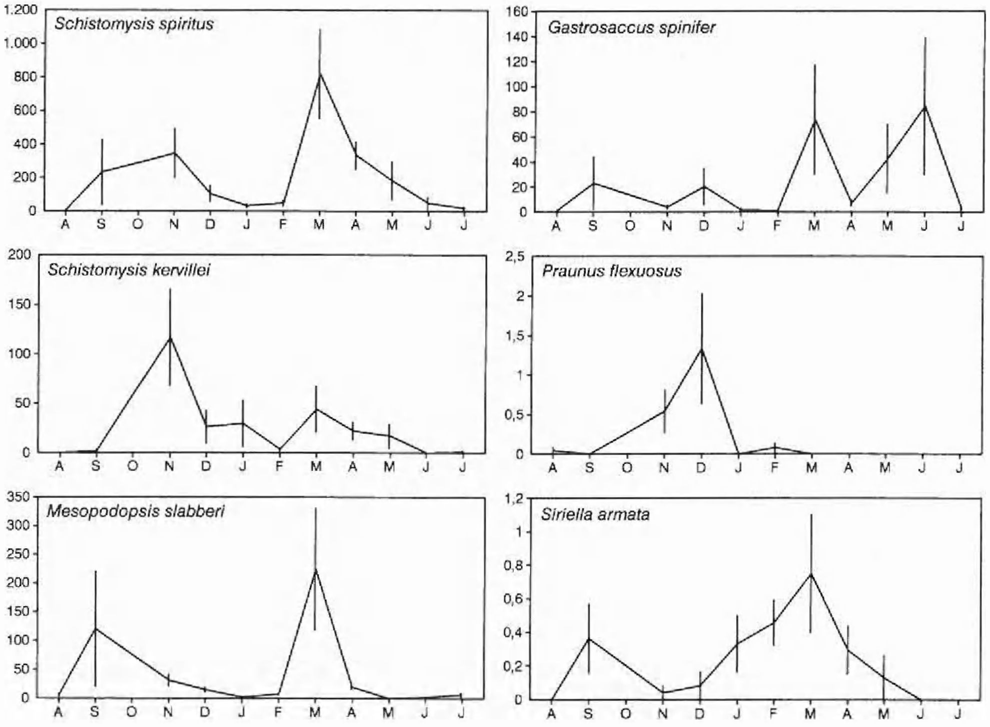


Fig. 6 : Seasonal variation of the number of individuals for the mysid species in the Voordelta (with standard errors). Densities are numbers caught per trawl averaged over all stations per sampling date (N/1 000 m²).

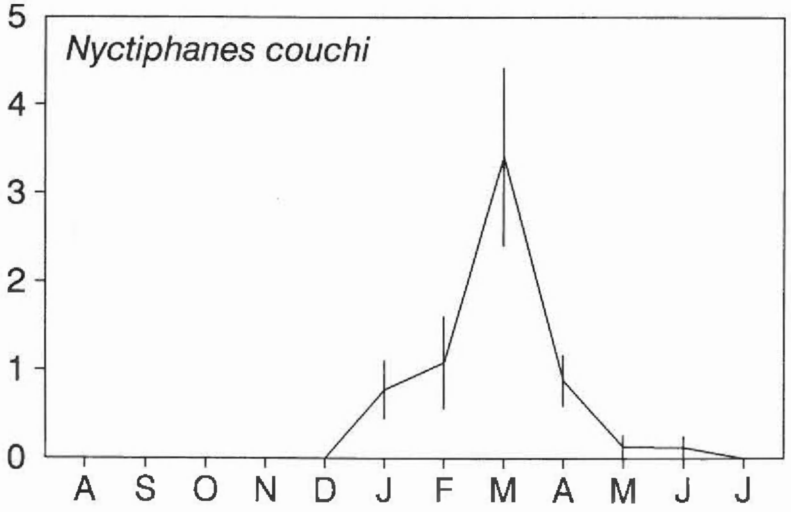


Fig. 7 : Seasonal variation of the number of individuals of *Nyctiphanes couchi* in the Voordelta, with standard errors.

estuary in low numbers in late autumn and winter. Here, the species reaches maximal abundance in spring (March to May, with a peak in April). At the time of this spring peak a small number of *S. spiritus* penetrate into the brackish part of the estuary and even enter the salt marshes. In the salt marsh of Waarde a small reproductive peak was recorded : all animals caught in April were juveniles.

Schistomysis kervillei and *Gastrosaccus spinifer* (not figured) are present in the western part of the estuary throughout the year. Average numbers are generally lower than 100 individuals per 1 000 m^2. *S. kervillei* is most abundant from November through April, with peak abundances of 650 individuals per 1 000 m^2 in January and early March. The *G. spinifer* population shows reproductive peaks in the marine part of the estuary in March and April (maximum of 100 individuals per 1 000 m^2 in April) and again from July through September (maximum of 450 individuals per 1 000 m^2 in August). At the time of peak abundance a small part of both populations also migrates to the brackish stations (densities never higher than 10 and 50 individuals per 1 000 m^2 for *S. kervillei* and *G. spinifer*, respectively).

Praunus flexuosus (Fig. 8) is only observed in the marine part of the estuary (and in the Voordelta) in late autumn, winter and early spring (October through March). During winter (January to early March) it seemed to be absent from the eastern part of the estuary. Its occurrence in the salt marshes is restricted to certain periods of the year : in spring (April to June), an important reproductive peak is observed in the saltmarsh of Waarde, followed by a less intense peak in the larger saltmarsh of Saeftinghe during the summer months (June to August). After reproduction the adults seem to migrate to the main channel of the estuary where the species is most abundant during autumn. Juveniles were only rarely observed in the upstream subtidal stations.

Mesopodopsis slabberi (Fig. 8) is virtually absent from the estuary in winter : from November through February it is only present in low numbers in the downstream stations. It enters the marine part of the estuary in important numbers in early spring where it remains abundant throughout summer and autumn. The abundance of *M. slabberi* resembles the two-peaked pattern observed in the Voordelta : a spring maximum (March) and an extended summer-autumn maximum (June-October). In late spring, the bulk of the population moves into the eastern part of the estuary. Migration into the eastern part is completed by August when very high densities are observed in the subtidal stations of the main channel. *M. slabberi* makes extensive use of the saltmarshes only in autumn : maximal densities recorded were of 176 individuals per m^3 (mainly juveniles) in October in Saeftinghe. By November the species has left the brackish waters.

Neomysis integer (Fig. 9) is confined to the brackish part of the estuary. Numbers are high throughout the year. Three maxima in abundance are observed, all of which correspond to reproductive peaks : one in spring (March-April), a large one in summer (July-August) and one in autumn (October-November). Details on the population biology of this species will be published elsewhere (Mees *et al.*, submitted). The species also utilises the salt marshes (mainly the salt marsh of Waarde in spring and the salt marsh of Saeftinghe in

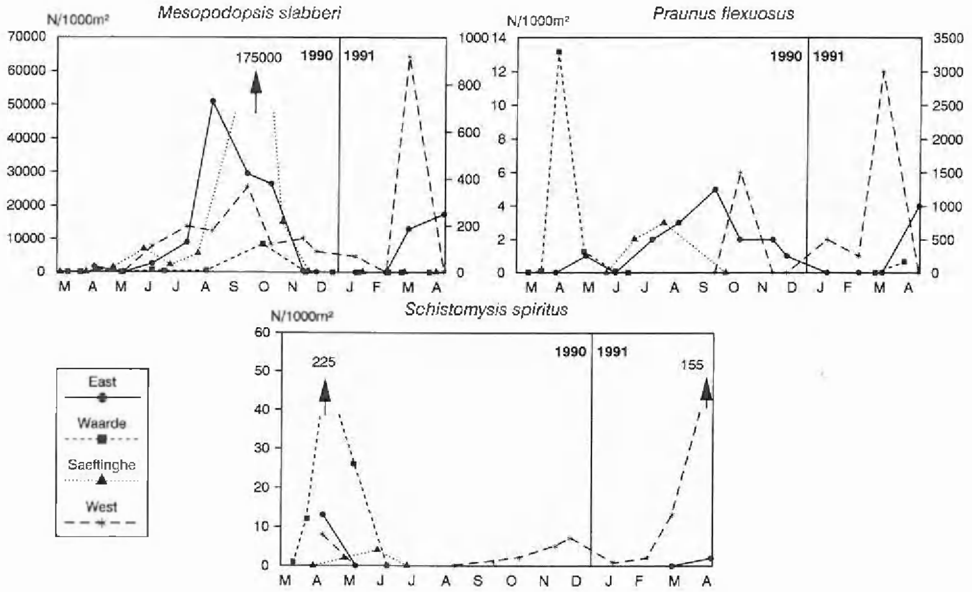


Fig. 8 : Seasonal variation of the number of individuals for the mysid species in the Westerschelde. Densities are numbers caught per trawl averaged over all stations per sampling date (N/1 000 m² for the subtidal samples and N/1 000 m³ for the salt marshes). Note *Mesopodopsis slabberi* West and *Praunus flexuosus* Waarde follow the right Y-axis.

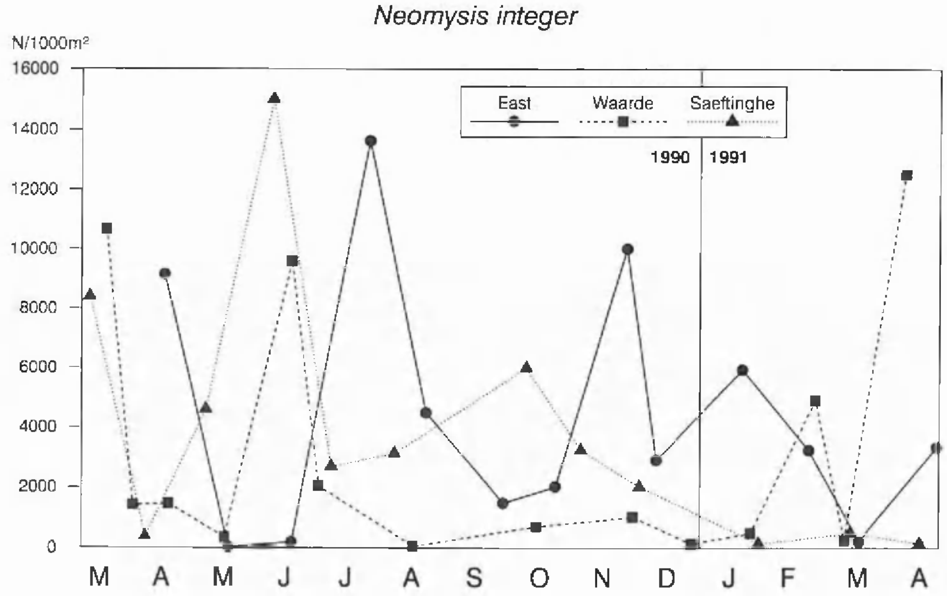


Fig. 9 : Seasonal variation of the number of individuals of *Neomysis integer* in the different subareas of the Westerschelde.

summer and autumn), where the density maxima are always earlier than in the main estuary. The data suggest that the animals enter the shallow, sheltered marshes for reproduction, as the young are found earlier here than in the main estuarine channels.

DISCUSSION

Most of the information available on the mysid fauna of the Delta area comes from the bycatch in zooplankton studies (e.g. De Pauw, 1975) or from macrobenthos samples taken with grabs (e.g. Wolff, 1973). It is therefore not surprising that new species are found and that densities of the common species were previously underestimated. The mysid *Acanthomysis longicornis* and the euphausiid *Nyctiphanes couchi* are new to the Delta region. The former species is new to the Dutch fauna. All other species are found to be far more abundant and widespread in the area than previously reported.

Euphausiids

Nyctiphanes couchi is the only euphausiid species encountered in the study area. It is the only euphausiid common in the southern North Sea. The species is restricted to temperate latitudes of the northeastern Atlantic. It is present in the North Sea, around Britain, southwards to the Bay of Biscay and northwest Africa and in the Mediterranean (Mauchline, 1984). It is thought to be indicative for the inflow of Atlantic water through the Channel (Van der Baan & Holthuis, 1969). All euphausiids are strictly marine organisms which do not occur in brackish or fresh waters (Mauchline, 1984). They do not occur commonly in regions shallower than about 100 m. Consequently, they live at some distance from the shore. Euphausiids are not restricted to the hyperbenthal. They have a pelagic way of life, probably colonising the whole water column. They are known to form seasonal breeding aggregations in the late winter to facilitate mating. Those that survive the breeding season disperse. This dispersal often involves shallower regions than were occupied by the breeding aggregations. *N. couchi* is absent from the southern North Sea from May to August (Tesch, 1911 ; Glover, 1952). Our results compare well to these general remarks and to the observations of Van der Baan & Holthuis (1969) in the surface waters near the Texel light ship : numbers are never high and greatest density is recorded in winter and early spring in the most offshore stations.

Mysids

General remarks

As can be seen from Figure 6 the variability in the densities reported for the mysid species in the Voordelta are rather high. This is not the case for the variability in the Westerschelde, and especially in the eastern part. This is probably due to the swarming behaviour of most of these species which seems to be far less pronounced in estuarine habitats.

Spatial patterns of the individual species

Only 12 individuals of *A. longicornis* were caught. These were all taken in one haul, suggesting that this species too forms aggregations. Mauchline (1971c) thought the species to be a possible exception to this widespread social behaviour.

Schistomysis spiritus was already reported by Hoek (1886) from the Voordelta in the mouth of the Oosterschelde estuary. Tesch (1911) reported it from several locations along the Dutch coast. It is a euryhaline, littoral and neritic species (Tattersall & Tattersall, 1951) which occurs from the west coast of Norway to the west coast of France.

Schistomysis kervillei was found by Hoek (1886) in the Oosterschelde and Tesch (1911) reported it from various places in the Delta area. It is also a euryhaline species (Tattersall & Tattersall, 1951) distributed from the British Isles to southern France. It is often recorded from estuaries (e.g. Sorbe, 1981 ; Williams & Collins, 1984). Another species of the same genus, *Schistomysis ornata*, was previously recorded from the Westerschelde by De Pauw (1975). It was not found in the present study. *S. ornata* generally lives in deeper waters from 30 to 100 m and only in fully marine conditions (Mauchline, 1970 ; Fossa & Brattegard, 1990 ; Sorbe, 1991). Since *S. ornata* and *S. kervillei* are morphologically quite similar it is suggested the individuals found by De Pauw belong to the latter species.

Hoek (1886) reports *Praunus flexuosus* as the most common mysid species of the Dutch fauna, being especially abundant in the Westerschelde and Oosterschelde estuaries. Hoek's (1886) observation probably relates to the conspicuousness of the species due to its large size and its habit to aggregate in dense shoals near the low water mark. The same author found only 2 individuals of *Neomysis integer* in the brackish part of the Westerschelde estuary, though the present study reveals it to be much more abundant than *Praunus flexuosus*. Both species are also very abundant in the Delta Area's saline and brackish lakes such as Lake Grevelingen (Platenkamp, 1978 ; Fortuin, 1980) and Lake Veere (Borghouts, 1978).

Mesopodopsis slabberi was reported by Hoek (1886) from the Oosterschelde. Tesch (1910) reports it to be common in the Delta area in salinities ranging from 2.6 to 30 g/l. It occurs from Norway to western Africa. It is also found in the Mediterranean and the Black Sea. Records from southern and western Africa are thought to concern different species (Wittmann, 1992).

The only *Gastrosaccus* species found during the study period was *G. spinifer.* It is common in the whole southern North Sea (Tesch, 1910). It is distributed from the west coast of Norway south to West Africa and the Black Sea. De Pauw (1975) found it in the western part of the Westerschelde. This is the most common mysid species in grab samples from the Delta area and has a preference for sandy sediments (Wolff, 1973). This explains why the species is more variable in its distribution than other species (see also Williams & Collins, 1984). *Gastrosaccus sanctus* was not recorded in this study although it is reported to be common in the Voordelta as well as in the marine part of the westerschelde (Hoek, 1886). This species essentially lives in shallower waters of less than a few metres depth (Tattersall & Tattersall, 1951), a stratum which was not covered in this study.

Neomysis integer was never caught in the Voordelta nor in the marine part of the Westerschelde, suggesting an efficient retention mechanism. Tesch (1911) reports it to be common and characteristic for low salinity waters in the Delta area. Upstream of the Dutch-Belgian border, which nearly coincides with the 10 g/l isohaline, there is a rapid extinction of all hyperbenthic life (Fig. 5). The high input of organic matter in this part of the estuary results in an intense bacterial activity which rapidly exhausts the dissolved oxygen. The location of this zone of oxygen depletion (oxygen saturation values lower than 40 %) is stable in space and time (Mees, unpubl. data ; Van Eck *et al.*, 1991). In normal situations estuarine populations of *Mesopodopsis slabberi* and *Neomysis integer* are present upto the 5 g/l isohaline and nearly freshwater, respectively. Wolff (1973) found *N. integer* elsewhere in the Delta area in nearly fresh water. De Pauw (1975) already pointed to the absence of these species from lower salinity waters (with the same upstream distribution limit at Bath) and suggested a relation to the heavy pollution in the area. It is interesting to note that in the early 1950's both *M. slabberi* and *N. integer* still occurred some 20 km upstream of Bath (Leloup & Konietzko, 1956). The data presented here are the first evidence that dissolved oxygen concentrations can act as primary controlling factors in the distribution and behaviour of a mysid species.

Temporal patterns

The seasonal maxima and minima in the observed population densities can be real or apparent (Mauchline, 1971c). Real maxima are those caused by increases in the size of the population owing to active breeding and production of young. Apparent seasonal maxima can be caused by a disaggregated population aggregating in an area so that they are sampled more effectively than previously or by migration into the area from elsewhere. In the Voordelta, *Schistomysis spiritus*, *Schistomysis kervillei*, *Mesopodopsis slabberi*, and *Gastrosaccus spinifer* have two periods of real population increase which largely explain the spring and autumn maxima. The low numbers in winter and summer can be due to natural mortality and/or to active migration either to deeper or to shallower waters and/or to active migration into the estuaries and marine bays bordering on the area.

The observations of *Praunus flexuosus* in the Voordelta and the marine part of the Westerschelde are probably a 'washout' phenomenon linked to the winter state of the river Schelde. The species' retention mechanisms seem less strong than in *N. integer*.

The lower numbers of mysids found in winter are often attributed to a migration from shallow coastal to deeper offshore waters in winter (e.g. Hesthagen, 1973). Van der Baan & Holthuis (1971) already suggested this behaviour for *Gastrosaccus spinifer*, *Schistomysis kervillei* and *Mesopodopsis slabberi* since these species displayed winter maxima in their offshore sampling station. The same migration pattern probably applies for *Schistomysis spiritus*. Populations of *S. spiritus* tend to occur deeper during winter (Mauchline, 1967) and Van der Baan & Holthuis (1971) also observed a winter peak. For all these species, the winter maximum is probably a combination of natural mortality and migration to deeper waters.

The summer minima in the Voordelta are more difficult to explain, but are possibly also partly real and partly apparent. Predation may be an important factor in determining the seasonal abundance of species. The sudden decrease of nearly all mysid populations in early summer in the Voordelta is preceded by a bloom of the ctenophore *Pleurobrachia pileus* and the cnidarian *Aurelia aurita*. Other potential predators in the hyperbenthal include chaetognaths and demersal fish. In early summer the 0-group gadoids *Merlangius merlangus* and *Trisopterus luscus* are strongly dependent on mysids for their food supply (Hamerlynck & Hostens, 1993). Interestingly in the adjacent Belgian coastal area the goby *Pomatoschistus lozanoi*, which is very abundant in the area (Hamerlynck *et al.*, in press) and which is virtually exclusively dependent on mysids for most of the year (Hamerlynck *et al.*, 1990), switches to feeding on to macrobenthic animals in August. As these fish also make extensive use of intertidal areas this suggests there are truly very few mysids available in the coastal area at that time. Therefore the summer minimum of most species is unlikely to be explained by a mass migration into shallower areas. An exception may be *Mesopodopsis slabberi* whose summer decline in the Voordelta is accompanied by a great increase of the population in the Westerschelde estuary.

The seasonal patterns of population maxima and minima in the marine part of the Westerschelde are analogous to those observed for the Voordelta, though the autumn peak tends to occur earlier. This is conform to the findings of Mauchline (1984) who observed that estuarine and littoral species tend to occur maximally during the warmer months of the year but if they occur in offshore environments the seasonal maxima of occurrence tend to occur in the autumn and winter.

The highly seasonal pattern of *N. integer* in the brackish part of the estuary parallels that of other European populations (e.g. Mauchline, 1971a). *P. flexuosus* is a shallow water, littoral species (Tattersall & Tattersall, 1951 ; Mauchline, 1971b) which agrees with the higher densities found in the intertidal samples. Its apparent absence from the brackish waters in the coldest months may reflect the lack of salt marsh samples from that period. It is well possible that the population overwinters in the salt marshes. The summer-autumn maximum of *Mesopodopsis slabberi* in the eastern part of the estuary is a combined effect of active migration and reproduction. A population decrease caused by a combination of natural mortality and active migration out of the brackish waters probably explains the winter minimum.

The estuarine populations of *Neomysis integer*, *Mesopodopsis slabberi*, *Praunus flexuosus*, and - to a lesser extent - *Schistomysis spiritus* (only in the salt marsh of Waarde) seem to utilise the salt marshes during periods of reproduction. Peak densities of the juveniles of these species are first observed in the intertidal samples. Only later do they migrate into the main channel.

ACKNOWLEDGEMENTS

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The hyperbenthic Amphipoda and Isopoda of the Voordelta and the Westerschelde estuary.

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Abstract : Data are reported on the amphipods and isopods taken in a sledge-type hyperbenthos sampler in the subtidal of the Voordelta, a shallow coastal area and the Westerschelde, the last true estuary of the delta area (SW Netherlands). More than 300 samples were collected between 1988 and 1991. Two salt marshes in the brackish part of the estuary were sampled monthly with a flume net in 1990 and 1991.

A total of 46 amphipod species (42 gammarideans, 3 caprellids and 1 hyperiid), 19 of which are new for the area were recorded. The dominant amphipod species in the Voordelta and the marine part of the Westerschelde estuary are *Atylus swammerdami* and *Gammarus crinicornis*. Estimated densities of both species are high comparison to these estimated from macrobenthos samples taken in the same area. This suggests that an important part of the population swims above the bottom and is subsequently overlooked in benthos surveys using only grabs or corers. Some amphipod species that had not been previously recorded from the area were found to be quite common inhabitants of the hyperbenthal.The dominant species in the brackish part of the estuary are *Corophium volutator, Gammarus salinus, Pleusymtes glaber* and *Bathyporeia* species. In the salt marshes the same species are dominant but densities are much higher than in the main estuarine channel. *Gammarus zaddachi* is only present in the salt marshes.

The only abundant Isopoda are *Idotea linearis* in the Voordelta and *Paragnathia formica, Eurydice pulchra* and *Lekanesphaera rugicauda* in the salt marshes. From a total of 8 species, there were no new records for the study area.

Résumé : Ce travail présente des données sur les amphipodes et les isopodes échantillonnés avec un traineau suprabenthique dans la partie sous tidale du Voordelta, une zone côtière peu profonde, et dans l'Escaut occidental, le dernier véritable estuaire de la région du delta (SW des Pays Bas). Plus de 300 échantillons ont été récoltés entre 1988 et 1991. Deux marais maritimes situés dans la partie saumâtre de l'estuaire ont également été échantillonnés en 1990 et 1991 grâce à un filet à cadre placé dans les chenaux de marée.

Un total de 46 espèces d'amphipodes (42 gammaridés, 3 caprellidés et 1 hyperiidé), dont 19 nouveaux pour la région, ont été recensés. Les espèces dominantes d'amphipodes dans le Voordelta et la partie marine de l'estuaire de l'Escaut sont *Atylus swammerdami* et *Gammarus crinicornis*. Les densités de ces deux espèces sont fortes comparées à celles estimées pour le macrobenthos dans la même région. Ceci suggère qu'une part importante de la population nage au-dessus du fond et est donc sous-estimée lors des prélèvements de benthos utilisant uniquement des bennes ou des carottiers. Quelques espèces d'amphipodes qui n'avaient pas encore été récoltées dans la région se sont révélées être tout-à-fait commun dans le suprabenthos. Les espèces dominantes dans la partie saumâtre de l'estuaire sont *Corophium volutator, Gammarus salinus, Pleusymtes glaber* et *Bathyporeia* sp. Dans les marais maritimes les mêmes espèces sont dominantes mais en densités bien plus élevées que danss le chenal principal de l'estuaire. *Gammarus zaddachi* est présent uniquement dans le marais maritime.

Les seuls isopodes abondants sont *Idotea linearis* dans le Voordelta et *Paragnathia formica, Erydice pulchra* et *Lekanesphaera rugicauda* dans les marais maritimes. Sur un total de 8 espèces recensées, aucune n'est nouvelle pour la région.

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INTRODUCTION

Three main European rivers, the Rhine, the Meuse and the Scheldt, enter the North Sea in the so-called Dutch Delta in the southwest of the Netherlands (Fig. 1).

Information on the amphipod species present in the area is rather scarce. Hartog (1963, 1964) discussed the presence of the Tallitridae and Gammaridae. Amphipods are also included in the list of the crustaceans of the Dutch Delta in Wolff (1973).

Since these studies were completed major engineering works have altered most of the estuarine branches of the Delta (Heip, 1989). The Westerschelde remains a true estuary, the Oosterschelde has become a marine bay, the Grevelingen is now a saline Lake and the Haringvliet is a freshwater basin.

More recent data on the amphipods of some subareas can be found in macrobenthic studies (Buijs *et al.*, 1989 on the Voordelta ; Meire *et al.*, 1991 on Oosterschelde and Westerschelde ; Craeymeersch *et al.*, 1992 on the Westerschelde).

Some data on the isopods can be found in the synopses of Holthuis (1956), Huwae (1977) and Pinkster & Platvoet (1986) and the study of Wolff (1973).

All studies mentioned used Van Veen grabs or boxcorers as sampling gear. In contrast, the data in this study were obtained with a hyperbenthic sledge and a flume net. Besides providing information on the presence and the abundance of amphipods and isopods in part of the Dutch Delta, a comparison with the densities obtained with grabs and corers is given.

MATERIALS AND METHODS

The Voordelta stretches from the Dutch-Belgian border in the south to the Hoek van Holland in the north. Offshore, the area is arbitrarily defined by the Mean Tidal Level (MTL) -15 m depth contour. The study covers only the central part of the Voordelta (Fig. 1) at the mouth of the former Grevelingen and Oosterschelde estuaries. The abiotic environment is discussed in Louters *et al.* (1991). Between August 1988 and July 1989 ten surveys were conducted at approximately monthly intervals in 12 localities : station 1-4 in the ebb-tidal delta of the Grevelingen, stations 8-12 in the ebb-tidal delta of the Oosterschelde and stations 5-7 in the more seaward Banjaard area between both ebb-tidal deltas. In each station 2 samples were taken : one in the gully at a depth of about MTL-10 m and one on the sandbank slope at a depth of about MTL -5 m. As no consistent differences were found between these two depth strata, the number of individuals caught in both samples were pooled and divided by 2 for the purpose of this paper.

The Westerschelde estuary (Fig. 1) is the lower part of the river Schelde. The maritime zone of the tidal system is about 70 km long from the North Sea (Vlissingen) to the Dutch-Belgian border near Bath. The Westerschelde is characterised by a marked-salinity gradient. The abiotic environment is discussed in Heip (1988) and Van Eck *et al.* (1991). Between April 1990 to April 1991 thirteen surveys were conducted. Each survey comprised 14 stations along the salinity gradient. On 3 occasions (March, April and May 1991) 5 additional samples were taken upstream from Bath up to the city of Antwerp. All samples were taken in the subtidal channels. Where possible, the MTL - 10 m isobath was followed. Besides the subtidal surveys, monthly samples were taken at two intertidal stations in the salt marshes of Saeftinghe and Waarde (S and W in Fig. 1) from March 1990 to March 1991. The salt marsh of Waarde (107 ha) is a long-drawn marsh situated on the right bank of the estuary. It is drained by one major creek which runs parallel to the main channel of the estuary. The salt marsh of Saeftinghe (2 760 ha), situated on the left bank north of the harbour of Antwerp, is one of the largest of western Europe. It is drained by several large creeks which run perpendicular to the main estuarine channel.

All samples were taken during daytime. The samples were collected with a hyperbenthic sledge (Hamerlynck & Mees, 1991) which consists of a heavy metal frame equipped with two nets one above the other. The sledge is one metre wide. Both nets are 4 m long and have a mesh size of 2*2 mm in the first 3 m and 1*1 mm in the last 1 m. The contents of both nets were pooled for this study. The total area of the nets' mouth is 0.8 m^2 and it samples the hyperbenthal from 20 to 100 cm above the bottom. The sampler was towed for approximately 1 000 m (radar readings from fixed points) at an average ship speed of 4.5 knots relative to the bottom. The total area sampled was 1 000 m^2. Trawling was always done with the tide. Thus, the maximal amount of water filtered in one trawl was 800 m^3.

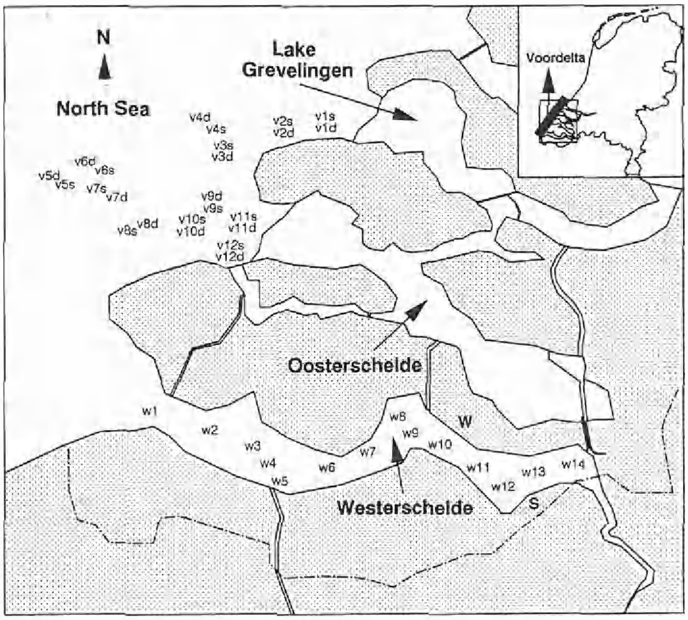

Fig. 1 : Map of the study area, showing subareas and sampling stations. The salt marsh sites are denoted with W (salt marsh of Waarde) and S (Salt marsh of Saeftinghe).

The salt-marsh samples were taken passively with a fyke net modified after McIvor & Odum (1986). The net is 5 m long with a 1*1 mm mesh and has a weir at the end. The mouth area of the net is 1*1 m. It was mounted on an iron frame and two heavy weights were attached at the lower end in order to keep the frame on the bottom of the creek. Ropes attached to the frame prevented lateral movement of the gear. The net was installed in the creek at low water, its mouth facing the current. Sampling covered a whole tidal cycle, the orientation of the gear evidently being changed at high tide. The net was emptied every 1 hour. Simultaneous measurements (every 15') of water height and current velocity in the creek allowed calculation of the volume of water filtered by the net.

During sampling temperature, salinity and dissolved oxygen content of the water were measured near the bottom.

The samples were preserved in a buffered formaldehyde solution, 7 % final concentration. In the laboratory all amphipods and isopods were sorted out, identified to species level (except for the *Bathyporeia* species) and counted. The identification key of Lincoln (1979) was used for the amphipods, the key of Naylor (1972) for the isopods.

The reported densities in each station are the mean number of individuals per sample taken in that station expressed as individuals per 1 000 m^3 filtered.

The temporal patterns in the densities of the amphipod and isopod populations are presented as the variation of average densities over all stations per subarea (Voordelta, Westerschelde, both salt marshes) per sampling campaign. In order to describe the migrations and seasonal patterns in the Westerschelde, the main channel of the estuary is divided into a western (marine) and eastern (brackish) part on the basis of community analyses in previous work (Mees & Hamerlynck, 1992 ; Mees *et al.*, in press). The marine part of the estuary comprises the 8 downstream stations and the brackish part comprises stations 10 to 14. Station 9 is a transitional situation between the two communities and was eliminated for the purpose of this analysis. The seasonal variations in abundance in the salt marshes of Waarde and Saeftinghe are also presented separately.

Other faunal components of the hyperbenthos included mysids, euphausiids, larval decapods, fish eggs, larval and postlarval fish, cumaceans, chaetognaths and a variety of other, less abundant groups. For full species lists we refer to Hamerlynck & Mees (1991) and Mees *et al.* (in press). Data on the mysids and euphausiids were reported separately (Mees *et al.* 1993).

RESULTS AND DISCUSSION

All amphipod and isopod species recorded during the study are listed in Table 1. The symbols used give a rough indication of the abundance.

TABLE I

List of the Amphipoda and Isopoda species caught.

	VOORDELTA	WESTERSCHELDE		WAARDE	SAEFTINGHE
		Marine	Brackish		
AMPHIPODA					
Gammaridea					
Orchomene nana	oo				
Amphilochus neapolitanus	o				
Ampelisca brevicornis	oo				
Metopa alderi	o				
Metopa pusilla	o				
Stenothoe marina	oo	o			
Stenothoe valida	o				
Orchestia gammarellus				●●	●
Chaetogammarus marinus				oo	
Gammarus crinicornis	●●●	●●●		o	
Gammarus duebeni				o	
Gammarus salinus	oo		●●	●●	●●
Gammarus locusta	●				
Gammarus oceanicus	oo				
Gammarus zaddachi				●●	●●
Maera grossimana	o				
Melita hergensis	oo				
Melita obtusata	oo				
Melita palmata	oo			o	
Bathyporeia Species	●●	oo	●●	●●●	●●
Haustorius arenarius	oo			o	o
Urothoe brevicornis	o				
Urothoe poseidonis	oo				
Monoculodes carinatus	o				
Pontocrates altamarinus	oo	oo			
Pontocrates arenarius	oo				
Megaluropus agilis	o				
Apherusa ovalipes	o				
Pleusymtes glaber		o	●●	●●	●●
Atylus falcatus	●●				
Atylus swammerdami	●●●	●●	oo		o
Gammaropsis nitida	o				
Microprotopus maculatus	o				
Corophium arenarium		o	oo		o
Corophium lacustre				o	●
Corophium volutator		●	●●●	●●●●	●●●●
Ischyrocerus anguipes		o			
Jassa falcata	●●	o			
Jassa marmorata	oo	oo			
Jassa pusilla	o				
Parajassa pelagica	o				
Dyopedos porrectus	o				

	VOORDELTA	WESTERSCHELDE Marine	 Brackish	WAARDE	SAEFTINGHE
Caprellidea					
Phtisica marina	oo				
Pariambus typicus	●●				
Caprella linearis	oo	oo			
Hyperiidea					
Hyperia galba	oo	oo			
ISOPODA					
Paragnathia formica				●●	●●
Eurydice pulchra	oo	oo	oo	●●●●	●●●
Lekanesphaera rugicauda		oo	●	●	●●
Idotea baltica	oo				
Idotea chelipes				o	
Idotea emarginata	●				
Idotea linearis	●●	oo			
Jaera albifrons				oo	

Legend

o	caugth only once
oo	density < 0.5 ind./1 000 m^3
●	density > 0.5 ind./1 000 m^3 < 1 ind./1 000 m^3
●●	density > 1 < 10 ind./1 000 m^3
●●●	density > 10 < 100 ind./1 000 m^3
●●●●	density > 100 100 ind./1 000 m^3

One clear feature is the high number (33) of gammaridean amphipod species recorded in the Voordelta and the low number (6) recorded in the eastern part of the Westerschelde. The western part of the estuary has an intermediate number of species (12). Taking the caprellid and the (only) hyperiid amphipods into account this difference becomes even more pronounced. The saltmarshes have about the same number of species as the western part of the estuary. This is due to the presence of intertidal species, which also reach high abundances. Typically, low species diversity coincides with high abundances in the brackish part of estuaries (Remane, 1958).

The opposite picture emerges for the isopods for which equal numbers were recorded in the different subareas. It are again the intertidal isopods which reach the highest densities.

AMPHIPODA

New records for the Voordelta are *Orchomene nana, Amphilochus neapolitanus, Metopa alderi, M. pusilla, Stenothoe valida, Gammarus oceanicus, Maera grossimana, Melita hergensis, Monoculodes carinatus, Apherusa ovalipes, Gammaropsis nitida, Jassa marmorata, Parajassa pelagica* and *Dyopedos porrectus* for the gammarideans, *Caprella linearis* for the caprellids and *Hyperia galba* for the hyperiids. Most of these are rare species in the hyperbenthos samples except for *O. nana* which occurs regularly, though always in low numbers, in the Voordelta stations furthest from the shore. The species is a widely recorded marine species and it may locally be very common (Lincoln, 1979). Possibly this species spends a substantial proportion of its time in the hyperbenthal.

The marine amphipods *Cheirocratus sundevalli* and *Leptocheirus pilosus* were recorded by Wolff (1973) but were not found in this study. Hartog (1964) mentions *C. sundevalli* as a rare amphipod of Lake Veere and the Oosterschelde. *L. pilosus* was found a few times in the intertidal by Wolff (1973). *Microprotopus maculatus*, which was caught only once in this study, was recorded in low numbers in the Voordelta by Buijs *et al.* (1989). Again, Wolff (1973) found it to be a scarce representative of the benthic fauna. This species was also found in the stomachs of gobies (*Pomatoschistus minutus* and *P. lozanoi*, collected in the Voordelta (Hamerlynck, unpubl.). In the Belgian coastal area *M. maculatus* is very abundant in goby stomachs especially in association with the caprellid *Pariambus typicus* and the radiole crowns of *Lanice conchilega* (Hamerlynck *et al.*, 1986, Hamerlynck *et al.*, 1990). The absence of the species from the hyperbenthos samples suggests the species does not often leave the cover of the *Lanice* beds, at least not during the daytime.

Wolff (1973) also recorded a number of strictly intertidal species and some species of very low salinity waters, e.g. *G. pulex*, not found in this study. Hartog (1964) recorded *Chaetogammarus stoerensis*, *C. obtusatus* and *Gammarellus angulosus* but these were not found in the present study. In the Voordelta Buijs *et al.* (1989) recorded three relatively rare amphipod species (average density below 0.1 ind./m^2) that were not found in the present study, namely : *Ampelisca gibba*, *A. spinipes* and *Perioculodes longimanus*. On the other hand seventeen amphipod species found in the Voordelta in the present study were not recorded by Buijs *et al.* (1989). The commonest of these : *Gammarus locusta*, *Melita palmata* and *O. nana* may be truely hyperbenthic. Still, the studies of Buijs *et al.* (1989) were restricted to autumn and as *M. palmata* and *G. locusta* were recorded by Hartog (1964) this may be a seasonal rather than a distributional effect.

New records for the Westerschelde estuary are *Corophium lacustre*, *Ischyrocerus anguipes* (single record) and, more importantly, *Pleusymtes glaber*. Though *P. glaber* was recently also recorded in Van Veen grab samples in the Westerschelde (Ysebaert, T. pers. comm.), it seems to spend a substantial proportion of its time in the hyperbenthal. According to Lincoln (1979) *P. glaber* is a rocky shore species. In contrast, the species was quite abundant in the eastern part of the Westerschelde and in the salt marshes of Waarde and Saeftinghe (densities of 8, 2 and 7 ind./1 000 m^3, respectively).

The Voordelta

Dominant species in the hyperbenthos of the Voordelta are : *Atylus swammerdami*, *A. falcatus*, *Gammarus crinicornis*, *G. locusta*, *Jassa falcata* and *Bathyporeia* spec. The temporal pattern in the recorded densities of four of the most abundant species is shown in Fig. 2.

Atylus swammerdami is the most important amphipod in the hyperbenthos of the shallow coastal area. Locally it reached peak densities of almost 1 500 ind./1 000 m^3. Average densities in the Voordelta and western part of the estuary were 47 and 2 ind./1 000 m^3, respectively. The species was also recorded occasionally in the brackish part of the estuary and there was a single record in Saeftinghe. There is a clearly bimodal abundance pattern

(Fig. 2) with a peak in June (160 ind./1 000 m^3) and one in September (145 ind./1 000 m^3). These two peaks may represent two cohorts.

Buijs *et al.* (1989) recorded densities of 4 ind./m^2 in the Voordelta in autumn. This means that in September at least 3 % (assuming 100 % efficiency of the hyperbenthic sledge) of the population is present in the hyperbenthal.

Gammarus crinicornis is the second most abundant amphipod in the coastal area of the Dutch Delta, with a mean density of 8 ind./1 000 m^3 in the Voordelta and 15 ind./1 000 m^3 in the western part of the estuary. Peak density in the Voordelta is recorded in April (40 ind./11 000 m^3). Buijs *et al.* (1989) recorded densities of 1 ind./m^2 in autumn. In this study the autumn (sept.-nov.) density was 5 ind./1 000 m^3, meaning that about four times as much animals were sampled with the sledge than with a bottomsampler. In beam trawl samples of epibenthic animals in the Voordelta (Hamerlynck *et al.*, submitted) the species is often found in high numbers among colonies of hydrozoans and bryozoans, together with *A. swammerdami* (Mees, unpubl. data). *G. crinicornis* is an important component of the hyperbenthos in the marine part of the Gironde estuary (Sorbe, 1981). The species is probably mostly epibenthic but commonly swims about in the hyperbenthal. Lincoln (1979) characterizes the species as intertidal on exposed sandy beaches, but this study shows the species also occurs abundantly in the shallow subtidal.

Both *A. swammerdami* and *G. crinicornis* are important in the food web of this coastal ecosystem as they are both frequently eaten by fish (Hamerlynck, unpubl. data). In the stomachs of *Pomatoschistus* species, the most abundant fish in the area (Hamerlynck *et al.*, submitted), several dozens of individuals of *A. swammerdami* were found per stomach (Hamerlynck, unpubl. data).

Atylus falcatus is the next most abundant species in the Voordelta (1 ind./1 000 m^3). This species is only present in the hyperbenthos from April till June. In the Van Veen grab and boxcore samples (Buijs *et al.*, 1989) the species is more abundant than *A. swammerdami*, which suggests it is more endobenthic. *A. falcatus* seems to have a preference for the ebb tidal delta of the former Grevelingen estuary where the sediment is fine sand with 5 to 20 % mud (Hamerlynck *et al.*, 1992). The species also figures prominently in the food of gobies in the area (Hamerlynck, unpubl.).

Jassa falcata is a typical fouling organism that builds tubes. It occurred regularly in the hyperbenthic samples (0.7 ind./1 000 m^3). Highest abundances were recorded in May and June. In contrast to the former species it has a preference for the more dynamic areas of the Voordelta.

Bathyporeia species are burrowing amphipods which pose considerable identification difficulties. Mean abundance for the genus is 0.8 ind./1 000 m^3 in the Voordelta and 0.2 ind./1 000 m^3 in the marine part of the Westerschelde. Two species were identified with certainty : *B. elegans*, which is the most abundant species by far, and *B. guilliamsoniana*, whose adults can easily be identified by their large size. Other occurrences in the Voordelta are most probably *B. pelagica* and *B. sarsi*. Highest abundances were recorded in April and May (3.2 ind./1 000 m^3). *Bathyporeia* species reach densities of over 100 ind./m^2 in the Van Veen grab samples on the sandbanks which are exposed to the strongest wave impact (Buijs

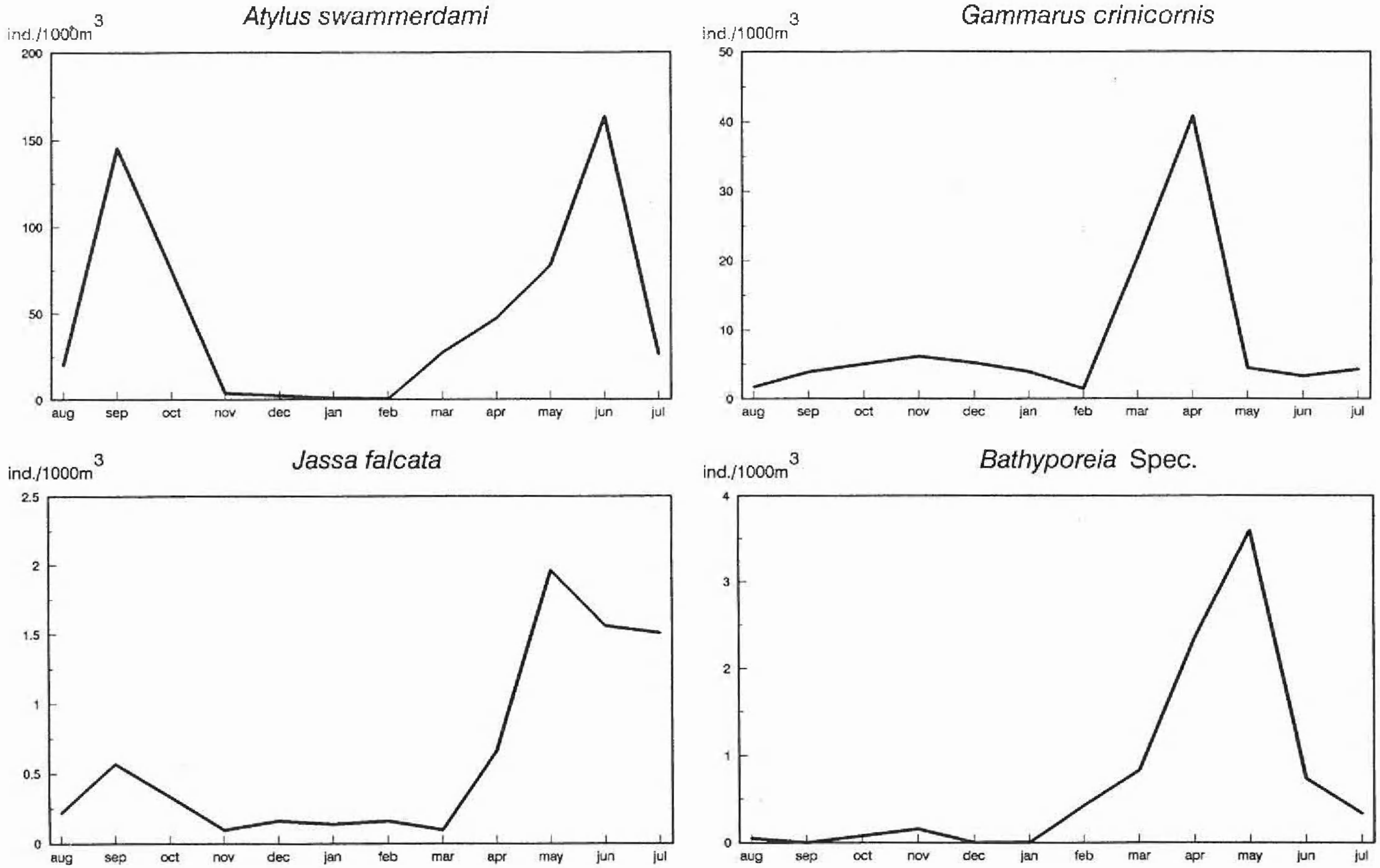

Fig. 2 : Seasonal variation in density of the *Atylus swammerdami*, *Gammarus crinicornis*, *Jassa falcata* and *Bathyporeia* species in the Voordelta.

et al., 1989). Another burrowing amphipod *Haustorius arenarius* was rarely found in Voordelta though, according to Buijs *et al.* (1989) it is quite abundant (2 ind./m^2). The species is also a common inhabitant of the sandbanks in the brackish part of the Westerschelde (14 ind./m^2) (Mees, unpubl. data). The single records from the saltmarshes may refer to animals washed in from the estuary.

Gammarus locusta is the last species to reach relatively high densities in the hyperbenthos of the Voordelta (0.54 ind./1 000 m^3). Peak abundance is in September (9 ind./1 000 m^3). According to Lincoln (1979) the species is restricted to fully marine habitats. Still a single individual was caught in the Salt Marsh of Waarde and Hartog (1964) recorded it in mid estuary. Buijs *et al.* (1989) did not record this species, so it may be epibenthic or hyperbenthic.

Hartog (1964) and Pinkster & Platvoet (1986) doubted the occurrence of *Gammarus oceanicus* in the Dutch Delta, and stated it is restricted to the Eems-Dollard estuary in the north of The Netherlands. However, two individuals were caught at 5 m depth in the ebb-tidal delta of the former Grevelingen estuary.

Caprellids and hyperiids were only caught in the marine part of the study area (Voordelta and marine part of the Westerschelde). Caprellids are typically 'Aufwuchs' species attached to colonies of hydrozoans or bryozoans, except for *Pariambus typicus* which also occurs on sandy or muddy bottoms. Mean density in the hyperbenthal was 0.34 ind./1 000 m^3. The same value was found for the other regularly caught caprellid *Caprella linearis*. In contrast, Buijs *et al.*, (1991) found very high densities of *P. typicus* (13 ind./m^2) in the Voordelta but did not record the other two caprellids, which accords with their life-styles : epibenthic Aufwuchs for *Caprella* species with regular swimming bouts in the hyperbenthal, mainly endobenthic for *P. typicus*, also with frequent ventures into the hyperbenthal. *P. typicus* is also one of the preferred prey species of *Pomatoschistus* species ; both in the Belgian coastal area (Hamerlynck *et al.*, 1986, 1990) and in the Voordelta (Hamerlynck, unpubl.). Wolff (1973) recorded only *Phtisica marina* which was rare in this study.

The records of the commensal hyperiid *Hyperia galba* coincided with the "bloom" of its host *Aurelia aurita* in May and in September-October.

Westerschelde and salt marshes

In the marine part of the Westerschelde, only the two dominant species from the Voordelta, *G. crinicornis* and *A. swammerdami* remained important. *Corophium volutator* was relatively important in the hyperbenthal (0.8 ind./1 000 m^3). These may be animals flushed out from the rich populations in the brackish part and the saltmarshes. The marine part of the estuary contained low abundances of some typical representatives of both the marine and the brackish environment.

In the brackish part of the estuary quite a different amphipod community was found. *Corophium volutator* is the dominant species, becoming very abundant in the salt marshes. It is a tube building amphipod that can occur in densities of over 20 000 ind./m^2 in benthic core samples taken in the tidal creeks of the marshes (Cattrijsse, unpubl. data) or on the intertidal areas of the estuary (Ysebaert, T., pers. comm.). It was found in the hyperbenthal in high densities (estuary 15 ind./1 000 m^3, Waarde 245 ind./1 000 m^3, Saeftinghe 229 ind./

1 000 m^3) for a large part of the year (Fig. 3). Its high abundance may reflect active dispersal or less likely passive flushing out.

The other Corophium species (*C. arenarium, C. lacustre, C. acherusicum*) are rare occurrences in the hyperbenthal of the brackish part of the estuary and the marshes. *C. arenarium*, is a typical estuarine inhabitant, regularly recorded in intertidal core samples by Meire *et al.* (1989). It occurs in the hyperbenthal only occasionally. According to Lincoln (1979) *C. lacustre* is a typical inhabitant of marshes and ditches but has been recorded only a few times. *C. acherusicum* was only caught on two occasions, once in the seaward part and once in Saeftinghe. Wolff (1973) also listed *C. insidiosum* and *C. multisetosum* for the Dutch Delta.

In the brackish part of the estuary *Bathyporeia* species reaches average densities of 3 ind./1 000 m^3, 37 ind./1 000 m^3 in Waarde en 2 ind./1 000 m^3 in Saeftinghe. As in the-Voordelta only a small part of the population of these burrowers is present in the hyperbenthal. Benthic grab samples in this part of the estuary recorded about 100 ind./m^2 on the sandbanks in August (Mees unpubl. data). Craeymeersch *et al.* (1992) report densities of about 120 ind./m^2 in the eastern part of the estuary.

Gammarus salinus is a very common gammarid, mostly caught in the salt marshes (45 and 53 ind./1 000 m^3 in Waarde and Saeftinghe respectively) and in the eastern part of the estuary (9 ind./1 000 m^3). The species was also observed, be it at relatively low densities (0.44 ind./1 000 m^3), at some localities in the ebb tidal delta of the former Grevelingen estuary. Hartog (1964) recorded it also in the coastal waters and stated that *G. salinus* expands its range of occurrence to seaward at times of high precipitation. As most of the records of *G. salinus* in the Voordelta were in summer it seems unlikely that the animals were washed out to sea. At that time the sluices connecting Lake Grevelingen to the sea are closed and fresh water inputs to the Voordelta from the Rhine are generally minimal. Hartog (1964) also states the species is rare in the Westerschelde. As with *G. crinicornis* and *A. swammerdami* it is therefore thought that *G. salinus* is mainly epibenthic. Seasonal density fluctuations were generally similar in both salt marshes (Fig. 3) with maxima in late autumn and during spring.

Gammarus zaddachi was recorded by Hartog (1964) exclusively in the very low salinity reaches of the estuary near Antwerp. In this part of the estuary nowadays all hyperbenthic life has disappeared because of hypoxia (Mees *et al.*, 1993). In the present study *G. zaddachi* was only found in the salt marshes (7 ind./1 000 m^3 in Waarde, 2 ind./1 000 m^3 in Saeftinghe). The absence of the species from the estuarine samples may either be due to the anoxia in the primary habitat or due to the fact that it is an intertidal species.

Within the Tallitridae, in contrast with Hartog (1963) and Wolff (1973), only *Orchestia gammarellus* was recorded in the present study. *O. gammarellus* lives near the high-water mark and was only caught when large amounts of plant material were washed out of the marshes (Waarde 3 ind./1 000 m^3, Saeftinghe 1 ind./1 000 m^3). Although *O. gammarellus* occurs in relatively low densities in the marsh samples it is frequently found in the stomachs of fishes leaving the marshes during ebb (Cattrijsse, unpubl. data).

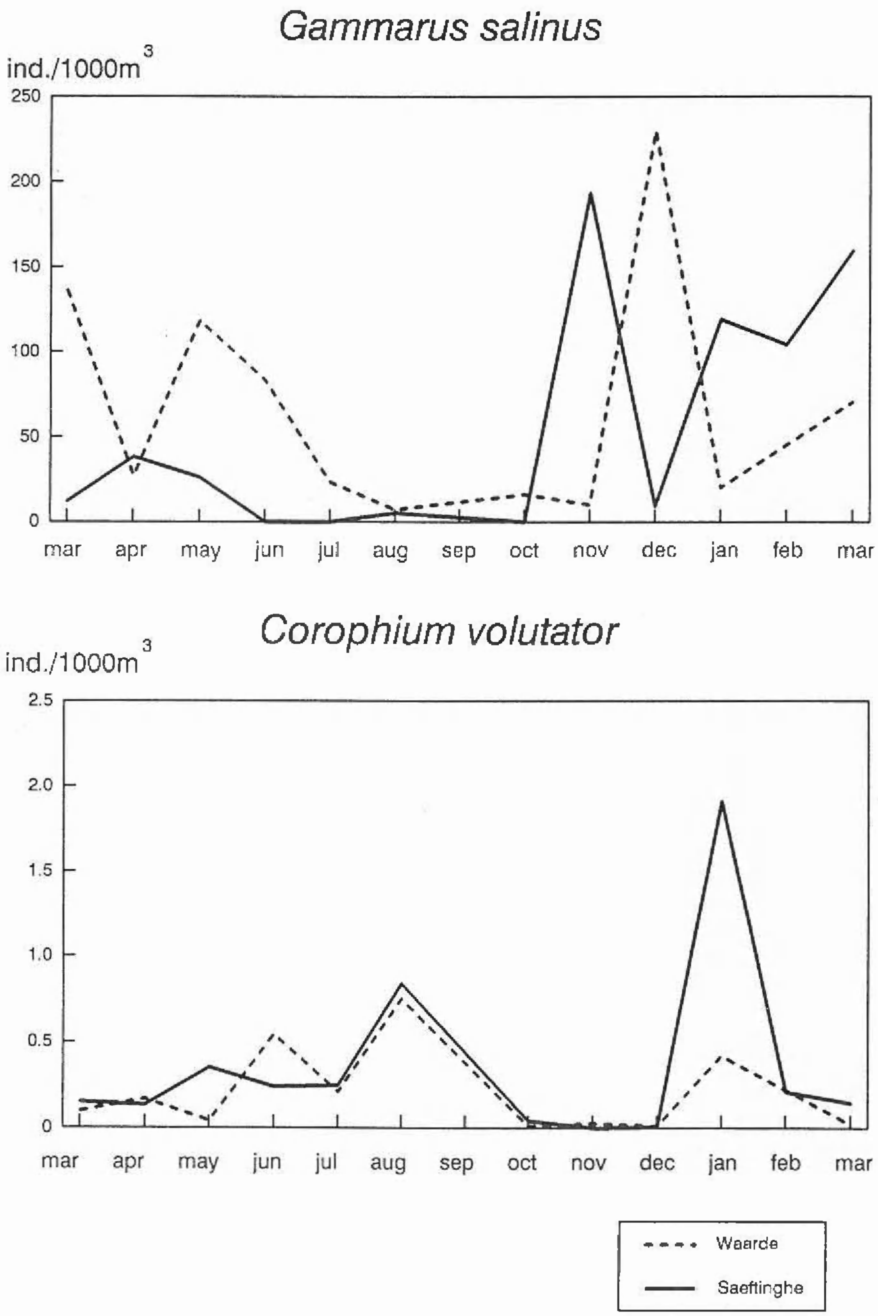

Fig. 3 : Seasonal variation in density of the *Corophium volutator* and *Gammarus salinus* species in both salt marshes.

Chaetogammarus marinus was only recorded in the salt marsh of Waarde. It was observed mostly in spring (0.001 ind./1 000 m^3). The absence of the species from Saeftinghe is in accordance with the findings of Hartog (1964). Still, the sampling techniques used in the present study are less than adequate for intertidal amphipods.

ISOPODA

The number of species of Isopoda recorded in the present study is very low compared with the studies of Holthuis (1950, 1956), Huwae (1977) and Wolff (1973). A lot of these isopods are intertidal and were therefore less than adequately sampled. For example *Jaera albifrons*, the most common littoral isopod in the Netherlands (Huwae, 1977), was only caught a few times in the salt marsh of Waarde. Other intertidal species make extensive use of the hyperbenthal, e.g. the semi-parasitic *Paragnathia formica, Lekanespheara rugicauda* and *Eurydice pulchra*. These species were recorded as common by Holthuis (1950, 1956), Huwae (1977) and Wolff (1973) and were also found abundantly in the present study.

Eurydice pulchra was the only isopod recorded in all subareas. It is was only recorded a few times in the Voordelta (0.01ind./1 000 m^3), but reaches very high densities in the saltmarshes (Waarde 151 ind./1 000 m^3, Saeftinghe 64 ind./1 000 m^3). *E. affinis* was reported from the Oosterschelde by Wolff (1973) and Huwae (1977) classifies it as a common marine species but it was not recorded in the present study.

Lekanesphaera rugicauda (formerly *Sphaeroma*) is recorded regularly in the brackish part of the estuary. It is more abundant in the salt marshes (Waarde 5 ind./1 000 m^3, Saeftinghe 30 ind./1 000 m^3). Holthuis (1956) is unsure about the distribution because of possible confusion With *L. hookeri*, a brackish water species which occurs in non-tidal waters behind the dykes (Huwae, 1977). Using the identification key of Naylor (1972) the species can easily be distinguished.

In the Voordelta only *Idotea linearis* has been caught in substantial numbers (1.14 ind./1 000 m^3). According to Huwae (1977) it is a very common isopod in coastal waters. *I. emarginata* was regularly caught in the Voordelta but in low densities (0.46 ind./1 000 m^3, with a peak of 32 ind./1 000 m^3 in one of the stations most distant from the shore). *I. baltica* was only caught a few times. This is in contrast to the findings of Huwae (1977) who states *I. emarginata* is rare while *I. baltica* is a common sublittoral species. *I. chelipes* was only caught once in the salt marsh of Waarde, although it is a common isopod in brackish water pools.

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Estimating secondary production for the brackish Westerschelde copepod population *Eurytemora affinis* (Poppe) combining experimental data and field observations.

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Abstract : *Eurytemora affinis* (Poppe) (Copepoda : Calanoida) development is studied through cultures supplied with naturally occurring particulate matter (Western Schelde estuary) and kept at six constant temperatures in the range 2-20 °C. At 2 °C the copepods do not reach the copepodite stages and at 5 °C, do not develop further than the fourth copepodite stage.

A field production estimate is given combining the biomass present in the field and weight specific growth rates derived from the culture experiment. The P/B obtained are very close with those measured for the same species in other estuaries.

Résumé : Le développement du Copépode *Eurytemora affinis* (Poppe) a été étudié grâce à des cultures dans lesquelles la nourriture fournie était constituée de particules provenant du milieu naturel (estuaire de l'Escaut occidental) et maintenues à six températures constantes dans la gamme 2-20 °C. À 2 °C les Copépodes n'atteignent pas le stade copépodite 1 et à 5 ° C les individus ne dépassent pas le 4e stade copépodite.

Une estimation de la production naturelle a été faite en combinant la biomasse mesurée dans le milieu et les taux spécifiques de croissance pondérale calculés à partir des élevages expérimentaux. Les valeurs de P/B obtenues sont très proches de celles mesurées pour la même espèces dans d'autres estuaires.

INTRODUCTION

Calanoids copepods constitute a dominant group in estuarine planktonic communities. Among them, the species *Eurytemora affinis* (Poppe) is distributed world wide and particularly abundant in the brackish areas of the North Atlantic zone where it alone may represent more than 90 % of the planktonic copepods. With densities up to 100,000 individuals per m^3 (Bakker *et al.*, 1977), this species plays a significant role in the estuarine trophic food web such as a link to higher exploitable levels (Mauchline, 1970 ; Burkill & Kendall, 1982).

Such high densities make any quantitative approach of the estuarine productivity strongly relying on precise knowledge about the *in situ* dynamics of these populations. Unfortunately the existence of mixed cohorts resulting from a continuous reproduction makes it hard to elucidate the demographic dynamics of these populations, even through a high frequency field sampling. Thus, one has to turn to laboratory cultures.

The two main variables controlling population dynamics in the field are bemperature and food availability (quantity and quality) (Nassogne, 1970 ; Klein-Breteler & Gonzalez, 1988). In cultures devoted to a description of field processes, one has to keep a high similarity between experimental and field conditions concerning temperature and food availability. If such conditions are reproduced within the cultures, one may expect the copepods to express a similar metabolism as in the field.

Most of the published data concerning the development rate of this species used cultures supplied with artificial food (Heinle, 1970 ; Katona, 1970 ; Heinle & Flemer, 1975 ; Burkill & Kendall, 1982 ; Vuorinen, 1982). However many papers dealing with zooplankton grazing gave evidence of the importance of suspended and sedimentary inert particles in the diet of many calanoid copepods including *E. affinis* (Heinle & Flemer, 1975 ; Heinle *et al.*, 1977 ; Lenz, 1977 ; Chervin, 1978 ; Boak & Goulder, 1983 ; Roddie, 1988 ; Powell & Berry, 1990). As far, only Poli (1982) and Poli & Castel (1983) produced results about the duration of *E. affinis* development in cultures supplied with naturally occurring particulate matter (Gironde estuary, France). However, according to the specificity of the estuarine particles in term of their nutritive potential, such experiments can not be generalized and have to be done for each estuary.

Firstly, cultures of *E. affinis* (Western Schelde estuary) have been performed in so called 'field simulated' conditions of temperature and food availability in order to obtain growth rates matching natural rates. These growth rates were then applied to the abundances measured in the field population over a year cycle to provide an estimate of the *in situ* secondary production.

This study is a part of a multi-disciplinary research of the Westerschelde, aiming at an ecosystem model of the entire estuary, and part of the Joint European Estuarine Program (Jeep I, MAST Program) of the Commission of the European Community.

METHODS

Sampling of the natural populations

Field sampling and samples processing have been performed by K. Soetaert and P. van Rijswijk ; the field data used here are part of Soetaert & Rijswijk (submitted). The sampling area was in the lower estuarine part of the Schelde, called the Westerschelde. Zooplankton and auxiliary environmental data were collected from October 1989 to October 1990 on thirty surveys with a mean time interval of twelve days between each. During each survey twelve stations were sampled along a longitudinal transect from the mouth of the Westerschelde (Vlissingen) to Antwerp (limit of the saline intrusion). At each sampling point hundred liters of water were collected (pump Pleuger type, n#64) beneath the surface, above the bottom and at mid depth. These samples were poured over a 55 µm mesh size net, pooled and fixed in buffered 4 % formaldehyde. The present study concerns only with the depth averaged results of the stations situated in the 10 ‰ salinity area (central part from the estuary). All development stages from the copepod *Eurytemora affinis* were enumerated and their biomass were directly measured or calculated by length-weight regression. Cephalothorax of copepods was measured using a digitizing tablet connected to a microscop, weights measured using a CAHN electronic balance (precision 0.1 µg) after a 24 hours drying process at 60 °C.

Copepods culturing

The copepods used in the cultures (*Eurytemora affinis*) were isolated from the brackish part of the Western Schelde estuary (the Netherlands) in April 1990, June 1990 and March 1991 with a high speed sampler ("Nackthai" Hydrobios, towed at ≃ 3 knots) with a mesh size of 300 µm. Salinity was always around 10 ‰. The temperature ranges used in the cultures were chosen according to the corresponding field temperature (Table I).

TABLE I

Temperatures in the field at the sampling dates and corresponding ranges used in the cultures.

Date	April 1990	June 1990	March 1991
Temperature in the field (°C)	10	17	5
Temperature(s) in cultures (°C)	10	14 17 20	2 5 8

Culture medium characteristics

Each week about 40 l of water were collected from the same water mass as the copepods. This water was used as a culture medium stock after being filtered on a 55 µm mesh size sieve and maintained at field temperature. Settlement of particles was prevented by continuous pumping with an ordinary aquarium pump. The size spetrum of suspended particles, total particulate content (Coulter Counter) and chlorophyll pigment concentration (fluorimetry) were measured every two days in the culture medium stock to check the variations of these potential trophic indicators. In April 1990, these measurements have only been performed during the second half of the culture experiment.

Eggs incubation time

Paired copepods were incubated in 100 ml glass beakers filled with 40 ml culture medium and held at 2, 5, 8 and 14 °C (30 replicas per temperature). The beakers were checked twice a day in order to measure the incubation time counted between the egg sac appearance and the hatching of at least 50 % of the eggs.

Development rate

Copepods were cultured from adult to adult in 100 ml glass beakers filled with 40 ml of culture medium and held at the experienced temperatures (at least 30 copepods for each temperature). The density in these culture units was 10 and 2 individuals for nauplii and copepodites respectively. The culture medium was renewed every two days in the beakers from the main stock. The copepods were checked every two days and their state of development was then noted.

Weight specific growth rates measurements

The molts released by copepods when accessing to a new stage were systematically collected, identified and measured. The molts lengths were converted into dry weights following a Log/Log weight length regression estimated in the course of this experiment. The mean development stage durations and dry weights being known, the weight specific growth rate was estimated following the 'instantaneous growth rate method' given in Rigler & Downing (1984) and modified by Polishchuk (1990). This method assumes the weight specific growth rate to be constant within a stage, i.e. :

$$g_i = \frac{1}{W_i}\,\frac{dW}{dt} = dLn(W_i)\,dt$$

approximated by :

$$g_i = \frac{Ln(W_i(t_2)) - Ln(Wi(t_1))}{(t_2 - t_1)}$$

When $(t_2\text{-}t_1)$ equals the duration of stage i, the stage and weight specific instantaneous growth rate g_i can be calculated using for $W_i(t_1)$, the weight when entering stage i (W_i) and for $W_i\ (t_2)$, the weight when leaving stage i (W_{i+1}). The stage duration being expressed in days, g_i is then a daily rate instead of a real instantaneous rate.

Adults reproductive effort

When reaching adulthood copepods almost stop to grow, most of their metabolism is then involved in the reproductive effort, this output as to be known for an estimate of the whole population production. At 8, 14, 17 and 20 °C, twenty couples have been followed from maturation to death and their reproductive products (eggs for the females, spermatophores for the males) have been counted and weighed.

Assuming these growth and fecundity rates representative for the field conditions (cultures supplied with naturally occurring particules) one can combine it to the biomasses measured in the field to give an estimate of the *in situ* secondary production integrated over the sampling time interval following the formula given by Polishchuk (1990) :

$$IP = \sum_i gi\,\frac{B_i(t_2) - B_i(t_1)}{Ln[B_i(t_2)\,/\,B_i(t_1)]}\,(t_2 - t_1)$$

RESULTS

Culture medium characteristics

Salinity in the culture medium was maintained between 10 and 13 ‰ corresponding to the range observed in the sampling area. The particulate spectrum measured every two days showed no particular trend during the one week storage (Fig. 1). This rather constancy points out the efficiency of the continuous pumping in maintaining particles in suspension without affecting their size spectrum. Some microscopical examinations done on this water (C. Bakker & M. Vinck, pers. comm.) revealed a predominance of plant detritus and small phytoplanktonic cells (<10 µm ; mainly microflagellates). Throughout all this experiment, the same kind of spectrum has been observed. Moreover, the total particulate and pigment contents did not change significantly (particles : $t = 2.911$, $p<0.005$; pigments : $t = 1.204$, $p<0.25$) during and among the culture experiments (Fig. 2).

Eggs Incubation time

The eggs incubation time showed a pronounced inverse relationship with temperature with mean values of 10.3 days at 2 °C, 6.5 days at 5 °C, 4.3 days at 8 °C and 2.4 days at 14 °C. These values showed a good agreement with the formula of Corkett & Mc Laren (1970) ($D = 1640 (T + 10.4)^{-2.05}$) defined for the same species (from Halifax waters, N.S). This formula was used in what follows to calculate the egg incubation times.

Development rate

At the lower temperatures, 2 and 5 °C, the copepods did not achieved a complete development. At 2 °C, it was impossible to obtain a transition to the copepodite stage, even for

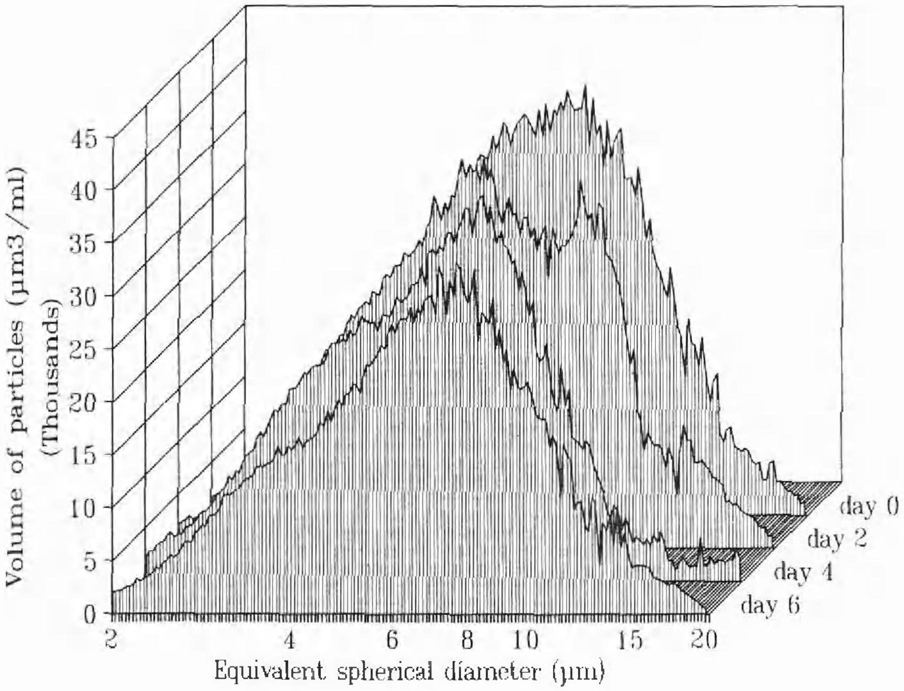

Fig. 1 : particulate spectra (Equivalent spherical diameter) of the culture medium measured during a one week storage (Coulter-Counter particles counter fitted with a 100 µm orifice tube).

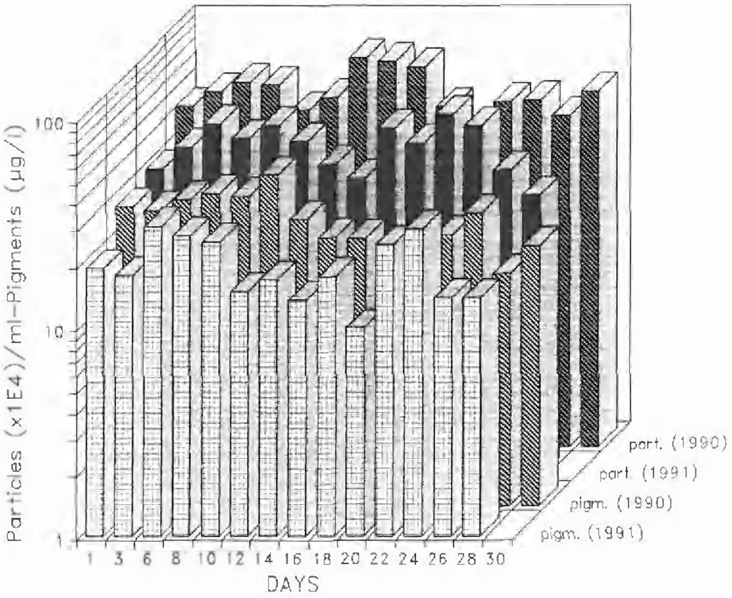

Fig. 2 : Total particulate content (2 to 60 µm E.S.D.) and pigments content in the culture medium in June 1990 and March 1991.

nauplii older than 5 weeks. Whereas at 5 °C no copepod succeeded to molt to the fifth copepodite stage even after 60 days counted from hatching. This mechanism has been inspected for nauplii by transferring a group of 36 days old nauplii raised at 2 °C in a water-bath set to 5 °C. After two days at 5 °C some of them began to molt and this molting process went on during 20 days when the last nauplii did finally molt. In a second group of nauplii kept at 2 °C and used as control, no molting was recorded. Moreover, almost 30 % of these nauplii were dead after 80 days at 2 °C. These copepods perhaps reached a physiological limit beyond which it is no more possible to survive as nauplii.

A complete developement was obtained for the temperatures over 5 °C (Tabl. II). The development rate increased with temperature from 8 to 17 °C whereas this trend was far less pronunced between 17 and 20 °C. Heip (1974) suggested the use of the following equation : $D = a \times T^b$ (D : development time, T : temperature, a and b : parameters) to modelize such temperature dependent development rate for many copepods species. The calculation of a and b resumes to a regression analysis performed after a Log-Log transformation ($Log(D) = Log(a) + bLog(T)$). The temperature dependent development functions provided mean residence times (D_i) in each development stages (i) within a continuous thermic range. A better adjustment of the a and b values has been obtained by a calibration procedure run with the Seneca modelling package (Scholten *et al.*, 1990) as described in Escaravage (submitted) (a and b calibrated values are given in Tabl. III).

TABLE II

Development stages mean durations (n : number of cultured copepods, d : mean stage duration, C.I. : *confidence interval at 95 %)*

	Temperature (°C)	n	$\bar{d}$ (days)	C.I. (95 %)
naupliar stages	8	75	15.4	0.50
	10	97	7.9	0.14
	14	81	6.0	0.31
	17	95	4.9	0.14
	20	96	4.0	0.26
Copepodite I	8	37	3.5	0.50
	10	53	3.0	0.23
	14	34	2.6	0.21
	17	32	1.8	0.18
	20	32	1.9	0.11
Copepodite II	8	37	3.9	0.50
	10	53	2.2	0.25
	14	34	1.8	0.06
	17	32	1.6	0.10
	20	32	1.6	0.19
Copepodite III	8	37	5.2	0.70
	10	53	3.0	1.01
	14	34	1.7	0.08
	17	32	1.5	0.11
	20	32	1.8	0.20
Copepodite IV	8	37	11.3	1.70
	10	53	5.1	1.51
	14	34	1.9	0.12
	17	32	1.5	0.09
	20	32	1.9	0.22
Copepodite V	8	37	14.1	1.30
	10	53	5.8	1.60
	14	34	3.5	1.19
	17	32	2.3	0.42
	20	32	2.6	0.46
egg laying to adult	8	37	57.6	5.25
	10	53	26.8	3.50
	14	34	17.4	1.94
	17	32	14.2	0.94
	20	32	13.5	1.90

Stage specific growth rates estimate

A Log/Log weight length regression was calculated from individuals sacrificed in the course of the culture experiments. No significative difference was found among the cultures (different temperatures) or between the cultures and the field. Following, all these data were pooled to establish a common weight length regression for the field and the culture

TABLE III

a and b paramerers charachterizing the stage specific temperature dependent development rate (Development time = $a_i\ xT^{b_i}$).

Development stages i	b_i	a_i
Nauplii	- 1.60	448.781
Copepodite I	- 1.30	62.429
Copepodite II	- 1.30	64.832
Copepodite III	- 1.30	74.992
Copepodite IV	- 1.96	530.682
Copepodite V	- 1.96	791.096

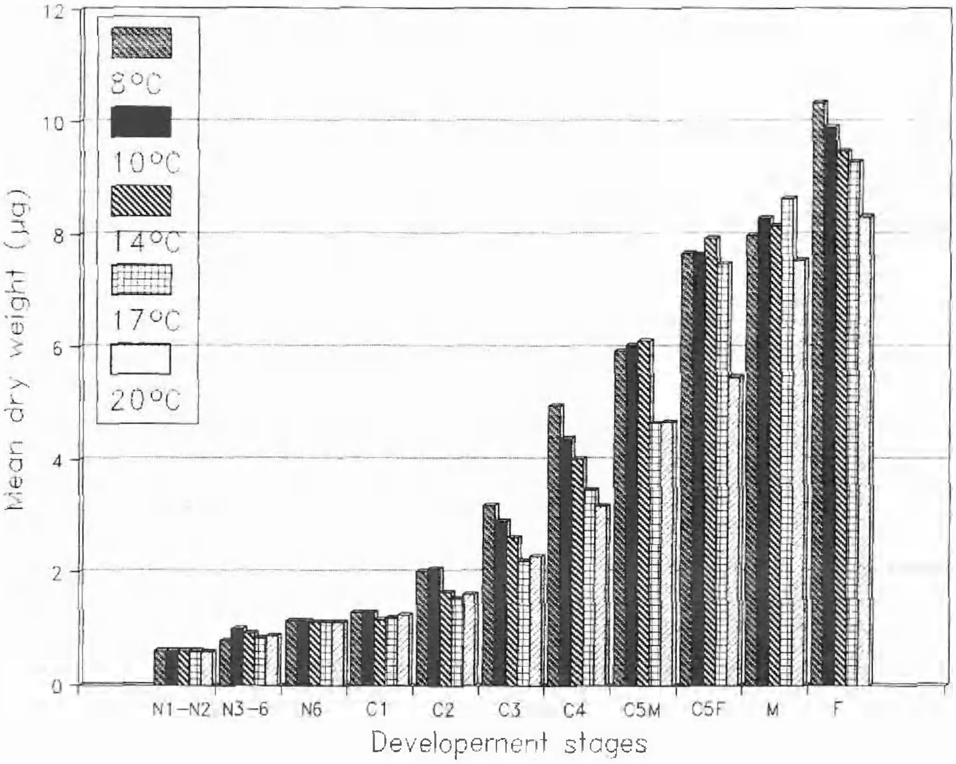

Fig. 3 : Stage specific dry weight obtained for different culture temperatures.

(Log(W) = 2.441 x Log(L) - 6.095, $r^2 = 0.97$, $p<0.05$). This relation was used to convert the molt lengths into the corresponding individual body dry weights from which were calculated the mean stage specific individual dry weights (Fig. 3).

From the mean stage development times (Tabl. II) and the mean stage individual weights were calculated weight specific instantaneous growth rates (see Methods for formulae).

The whole adult production was obtained by summing the reproductive production with the slight weight increase measured between the maturation and the death. These results were expressed in µg D.W./mg D.W./day and compared with the mean daily somatic production measured from N2 to C5 (Fig. 4). The ratio between the reproductive and the somatic productions was not constant, it varied from 50 to 150 % for the females but only from 40 to 60 % for the males. The male production reached 40 to 90 % of the female production.

Estimate of the in situ production

The *in situ* biomass evolution (Fig. 5) is characteristic for this species and can be divided in three phases : Winter emergence, Spring peak, Summer disappearance. Such pattern is supposed originated from a composition of internal dynamics (temperature controlled) and external control (predation, competition) (Bradley, 1975).

Combining this data set with the culture results (temperature controlled stage specific growth rates) one is able to estimate the production realized by the natural production (for-

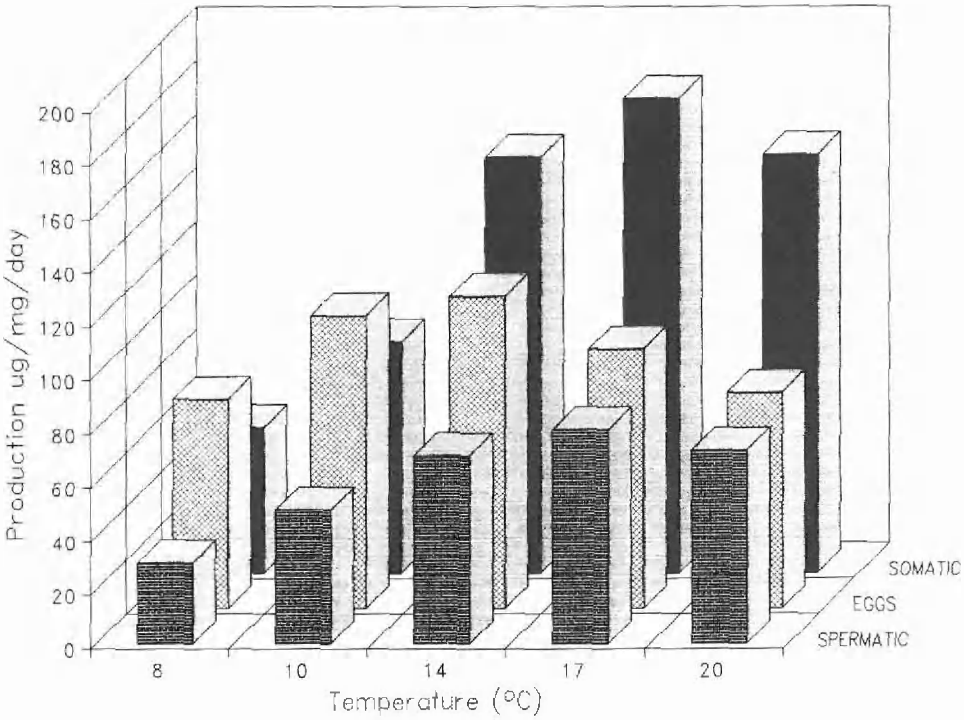

Fig. 4 : Eggs, spermatophores and somatic production expressed as weight specific daily productions.

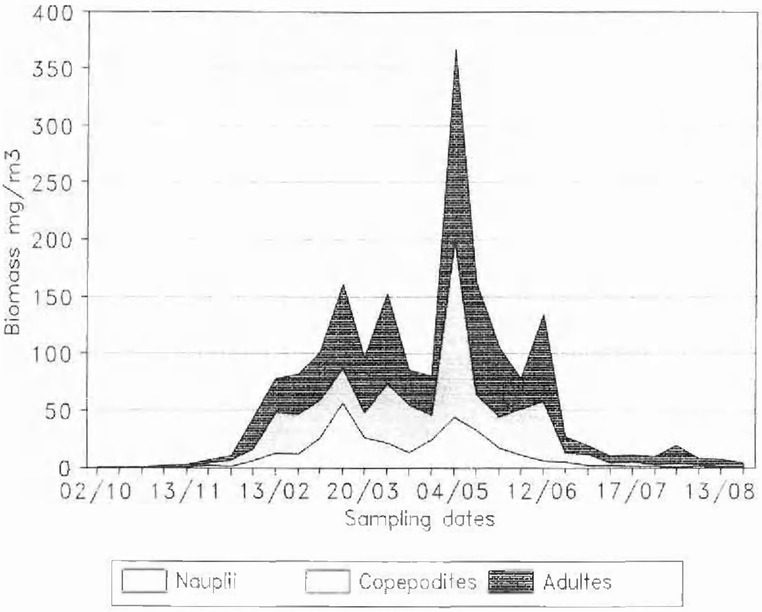

Fig. 5 : Biomass of *E. affinis* measured in the Western Schelde from October 1989 to October 1990.

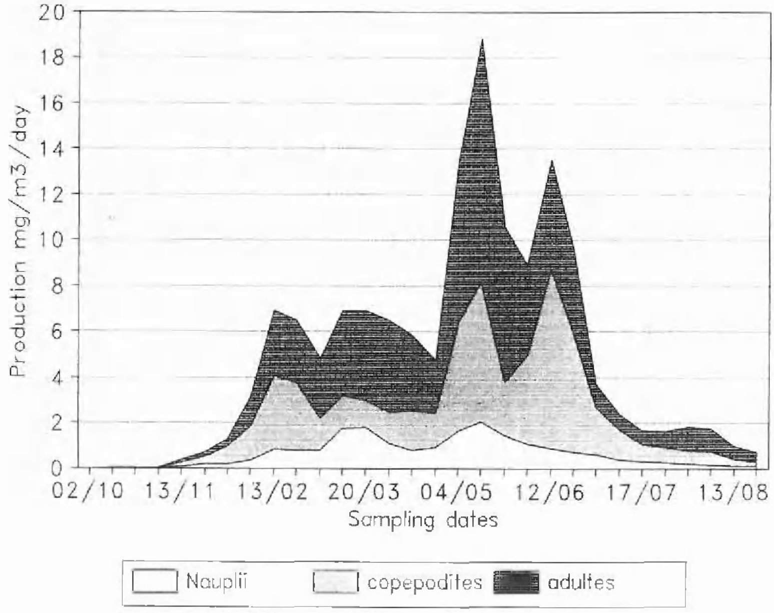

Fig. 6 : Production estimates obtained using the biomass showed in Figure 5 and the Polishchuk (1990) formula.

mulae in Methods) (Fig. 6). The production realized by the adults (including the reproductive effort) represented 50 % of the total production. The daily production was estimated by 5 mg/m^3/day and the annual integrated production by 1.6 g/m^3. A global P/B of 33 year $^{-1}$ was found for the whole population.

DISCUSSION

Culture conditions

One of the main problem arising in the course of these culture experiments was the quality of the culture medium in term of food availability. As soon as the medium was introduced in the beakers, particles began to settle, leading to an impoverishment of the water column. However observations made on *E. affinis* feeding behavior suggested this copepod able to overcome this impoverishment of the water column by switching from a typical pelagic grazing to a more benthic like foraging activity. Thus it was very common after the two days of incubation in the culture medium to see copepods, apparently in search of food, foraging among the settled particles whereas the water column was almost clear of any suspension. The following comparisons made with copepods cultures in optimal food conditions argue in favor of the efficiency of this feeding behavior plasticity.

Comparisons with other culture conditions

In previous studies *E. affinis* was cultured in an excess of algal food (Heinle & Flemer, 1975 ; Vuorinen, 1982), or as in our case with natural food directly collected in the field (Poli & Castel, 1983) (Tabl. IV, Fig. 7). The models corresponding to cultures supplied with algal food are quite similar which can lead both experiments reproduced true standardized

TABLE IV

Development times obtained for *E. affinis* in laboratory cultures,
Dn : Naupliar development (hatch to CI), Dc : Copepodite development (CI to CV),
Dt : total development = Dn + Dc (* : model adjusted on data provided by the authors).

Authorities	Locality	T°C	S ‰	Fitted Model
Heinle-Flemer 1975 (*)	Patuxent River	5.5-25	0-13.6	$Dt = 557.25 \times T^{-1.272}$
Vuorinen 1982	Archipelago Sea	7-20	5.5±0.1	$Dn = 278 \times T^{-1.289}$ $Dc = 272 \times T^{-1.249}$
Poli-Castel 1983	Gironde Estuary	10-25	0.5-5	$Dn\ 590 \times T^{-1.57}$ $Dc = 41 \times T^{-0.43}$
Present study	Western Schelde	8-20	10-13	$Dt = 1146 \times T^{-1.542}$

optimal food conditions. The present experiment diverge from the food standardized cultures by the longer development times observed for lower temperatures whereas for Poli & Castel (1983) the main divergence relies on an longer development time for higher temperatures. Burkill & Kendall (1982) comparing their natural food supplied cultures of *E. affinis* with the algal supplied cultures of Heinle & Flemer (1975) found also an increase in the development time, far more pronounced at low temperature (twice as long at 5 °C but only + 15 % at 15 °C). These differences between standardized and natural experiments and even among this last group result obviously from the various quantity and quality of food used in these experiments. However it must be noticed that the development rate can in certain concitions (e.g. low temperatures in Gironde and high temperatures in Westerschelde) be similar in food saturation and in natural food supplied cultures.

The control of copepods development rate by the food availability has also been described by Vidal (1980) who concluded that the food concentration required for maximum growth was related to the temperature.

It becomes then obvious that the food quality not only controls the body size and weight of the copepods as stated by Klein-Breteler & Gonzalez (1988) but also the development rate. For this reason, Burkill & Kendall (1982) advice against the use of food optimal cultures for field extrapolations for it yields production overestimates from 10 to 80 %.

The cultures run at the lower temperatures showed an overstress of the exponential relation between temperature and development rate ressembling a development delaying for the later naupliar (N3-6) and copepodite (C4-5) stages at 2 and 5 °C. This has also been described by Poli (1982) for *E. affinis* (Gironde estuary, France) fed with naturally occurring par-

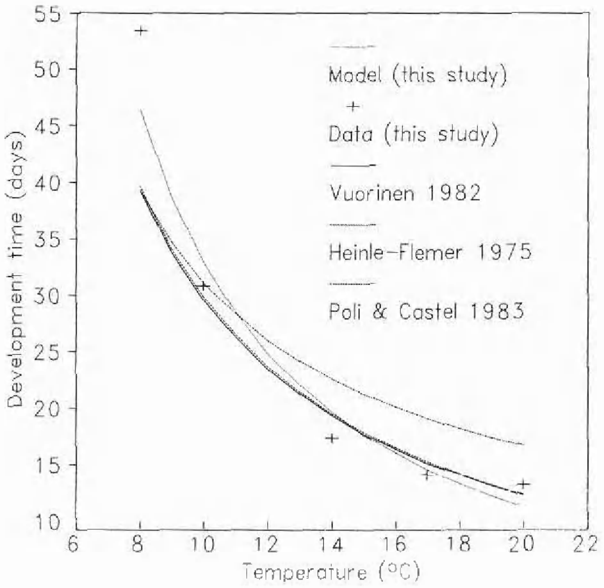

Fig. 7 : Comparison with other models found for *E. affinis* from hatching to adulthood.

ticulate matter as it was impossible to raise the copepod until adulthood at 10 °C for nauplii did not succeed to molt into first copepodite and finally died.

Production of *Eurytemora affinis*

One original result of this study is the significative production represented by the male reproductive effort, a compartment usually neglected in field production estimates. Moreover the male production seemed undergoing a similar temperature control than the juvenile growth rate (Fig. 4). Such relationship, still needing additional data to be parametrized, could be a mean to get estimate of the juvenile growth rate through short term experiments measuring the male production. Such an approach converges with the findings of Corkett & Mc Laren (1970) who established correspondances between the egg production and the juveniles growth rates for many pelagic copepods species.

Comparisons can be made between the present estimate of production and others obtained for the same species in comparable environments (Tabl. V). Whereas the biomass differed in the different areas, the P/B values showed remarkably close values. This converged with the similarities observed for the development rates obtained in cultures supplied either with natural particulate matter or with algal cultures. Both these observations underlined the ethophysiologic plasticity of the estuarine species.

TABLE V

Biomass, Production and P/B ratios measured for *Eurytemora affinis* in other estuarine locations compared with the present study.

Authorities	Locality	Biomass (mg/m$^{3)}$)	Production (mg/m^3/day)	P/B ratio (an^{-1})
Heinle (1969)	Patuxent River	75	6.25	30.4
Allan *et al.* (1976)	Rhode River	47	3.83	29.4
Burkill & Kendall (1982)	Bristol Channel	8 x 10^{-3}	0.24 x 10^{-3}	33
Castel & Feurtet (1989)	Gironde Estuary	86	7.70	32.8
This study	Western Schelde Estuary	67.49	5	33

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Roscoff

Difficulties in estimating mortality rates of *Eurytemora affinis* in the brackish water region of the Elbe estuary.

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Abstract : Mortality rates of the copepod *Eurytemora affinis* from the Elbe estuary were estimated. From April to September 1989 six samples were taken twice a week during the flood phase at an anchor station (km 695) in the oligohaline section of the Elbe estuary.

Maxima of different instars were found at different times during the flood phase. The peaks of abundance were shifted from low to high water as the organisms grew older : it seems that the population would be slowly driven out of the estuary.

To obtain a representative value of the population density for the calculation of mortality rates a weighted average of the abundance of each sampling day was used. With these data cohort analysis was carried out. Highest daily mortality rates occurred between naupliar stages V and VI. Mean mortality rates of nauplii were 0,15-0,26 d^{-1}. For copopodids low daily mortality rates of 0,05 d^{-1} were estimated. Mortality in estuaries not only consists of predation and physiologically death. In addition the transport of animals from upstream and losses of animals to the downstream part of the estuary that the spatial separated maxima of different instats of *Eurytemora affinis* during a tidal phase affected the estimation of mortality rates.

Résumé : Les taux de mortalité du Copépode *Eurytemora affinis* ont été estimés dans l'estuaire de l'Elbe. D'avril à septembre 1989, six échantillons ont été prélevés deux fois par semaine à marée montante dans une station fixe (km 695) située dans la zone oligohaline de l'estuaire de l'Elbe. Les maximums des différents stades de développement sont observés à différents moments au cours du flot. Les pics d'abondance sont décalés de la basse mer vers la haute mer au fur et à mesure que les organismes deviennent plus âgés.
Il semble bien que la population soit déportée lentement hors de l'estuaire. De manière à obtenir une valeur de densité représentative de la population pour le calcul des taux de mortalité, une moyenne pondérée de l'abondance obtenue à chaque date d'échantillonnage a été utilisée. A partir de ces données, une analyse de cohorte a été pratiquée. Les plus forts taux journaliers de mortalité se produisent entre les stades naupliens V et VI. Les taux moyens de mortalité des nauplii se situent entre 0,15 et 0,26 j^{-1}. Pour les copépodites, les taux de mortalité sont plus faibles, de l'ordre de 0,05 j^{-1}. En milieu estuarien, la mortalité ne résulte pas uniquement de la prédation et du stress physiologique. Le transport des individus depuis l'amont et les pertes vers la partie aval influencent également les taux de mortalité. Il a pu être montré pour l'estuaire de l'Elbe que la séparation spatiale des différents stades de développement de *Eurytemora affinis* pendant le cycle de marée pouvait affecter l'estimation des taux de mortalité.

INTRODUCTION

Population dynamics of zooplankton are mainly regulated by natality and mortality rates. The precision of a mortality rate depends on the estimation of the number of individuals belonging to a population and the time interval between sampling dates. The difficulty in estuaries is to obtain a representative value of population density. Advective processes caused by tidal action are responsible for high variability within zooplankton samples. So the distribution of the population during a tidal cycle has to be well-known to develop an adequate sampling strategy. The problem of sampling strategies is discussed by Gagnon &

Lacroix (1982) and Sameoto (1975). For the Elbe estuary an investigation in 1986/1987 showed that the distribution of the different instars of *Eurytemora affinis* during a tidal cycle was not uniform (Peitsch & Kausch, accept.). So the strategy was to sample at least half a tidal cycle because maxima of different instars were found at different times during a tidal phase.

Investigation of population dynamics of *Eurytemora affinis* in the Elbe estuary were carried out in spring and summer 1989.

There are only a few investigations of population dynamics of zooplankton in european estuaries (Arndt, 1985 ; Castel & Feurtet, 1989 ; Christiansen, 1988 ; Formsma, 1978).

METHODS

Sampling

Zooplankton samples were collected from April to September 1989. Sampling was carried out at an anchor station near the city of Brunsbüttel (km 695) in the oligohaline region. It started at low water and samples were taken every hour until high water. Samples were taken every three or four days.

Zooplankton samples were collected using an electric driven pump with a capacity of 40 l/min. Integrated samples were taken from the river bottom to water surface. 10 l water thus obtained were poured through a 55 µm mesh and preserved in 4 % buffered formaldehyde. Abundance of the different instars of *Eurytemora affinis* was recorded as numbers per liter.

Calculating

To get a representative value of population density the individuals of the population were regarded as a load and therefore the total numbers (L) of an instar passing through the cross section during a flood phase were estimated. The flow of water (Q) through the cross section at km 695 for the time interval from the middle of the time distance between two samplings (S_0, S_1) to the middle of the time distance between the following samples (S_1, S_2) was calculated and multiplied with the number (N) of individuals. This was repeated for all six samples. By using this method samples taken at high current velocities become more important, because more water passes the cross section during the same time interval.

1. Calculation of water flow through the cross section :

$Q = A * v * t$

v = mean current velocity at cross section km 695 during time interval t

A = area of cross section at km 695

$$t = \frac{t1-t0}{2} + \frac{t2-t1}{2}$$

2. Total numbers of an instar passing the cross section during flood tide :

$L = Q_1 * N_1 + Q_{12} * N_2 + \dots\dots\dots\dots Q_6 * N_6$

N = numbers of instar i in the samples

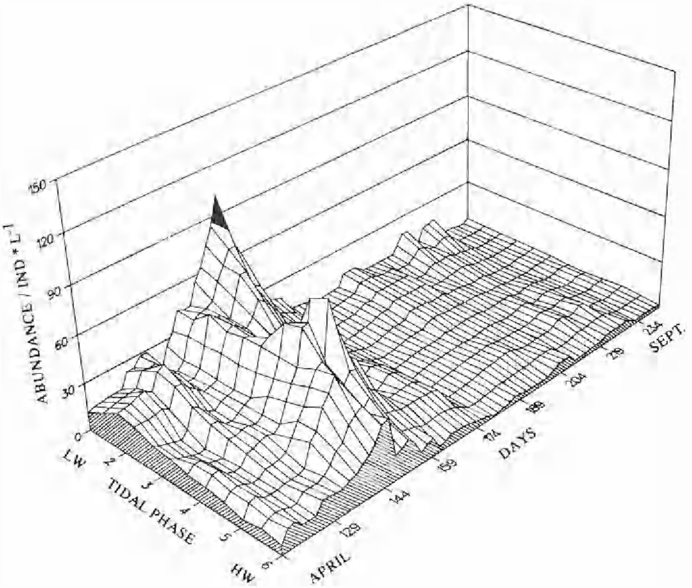

Fig. 1 : *Eurytemora affinis*. Seasonal and tidal dependent distribution of the abundance of naupliar II.

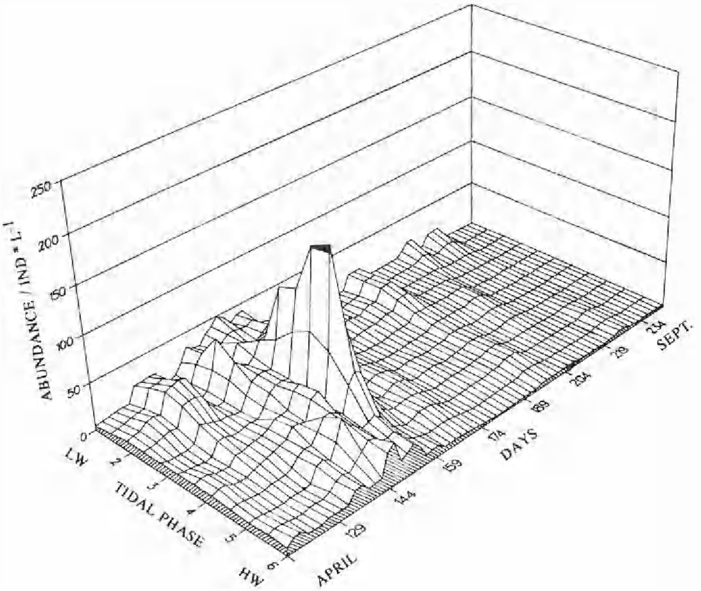

Fig. 2 : *Eurytemora affinis*. Seasonal and tidal dependent distribution of the abundance of naupliar III.

For further calculations of population dynamics it was necessary to get *one* representative value of N for each sampling day. Therefore a weighted average was calculated :

$$Na = \frac{L}{Vf}$$

Na = weighted numbers of instar i

Vf = flood volume $(Q_1 + Q_2 ..... + Q_6)$

Now a two-dimensional distribution of seasonal development of every instar could be plottet. Based on this data cohort analysis of Rigler & Cooley (1974) were used to investigate population dynamics.

The number of an instar in a cohort (Ni) was calculated from the area under the curve of a cohort divided by instar duration time.

For calculation of mortality rates the formula of Landry (1978) was used.

$$m = \frac{-\ln\left(\frac{Ni + 1}{Ni}\right)}{t}$$

m = mortality rate
Ni = numbers of instar i
Ni + 1 = numbers of instar i + 1
t = time interval

RESULTS

Distribution

The abundance in every sample (six samples) during the flood phase and the seasonal development of the different instars of *Eurytemora affinis* is shown (Fig. 1 to 4). At the end of May and beginning of June the population maximum occurred. Maximum of the naupliar II (Fig. 1, maximum marked black) was found at low water. The maximum of the naupliar stage III (Fig. 2) is located at the beginning of the flood phase. Copepodid I (Fig. 3) showed highest abundance in the middle of the flood phase and the corresponding maximum of the adults (Fig. 5) appeared at high water.

The maxima of the different instars during the flood phase were found at different times during the flood phase. As the organisms grew older in spring time the abundance maximum was shifted from low to high water and it seems that the population is slowly driven out of the estuary.

Separation of cohorts

Fig. 6 shows seasonal development of the population based on the calculated abundances (Na) of each instar. Three cohorts could be separated by the method of Rigler & Cooley (1974). The first cohort started in at the beginning of May and the third cohort ended at the end of August.

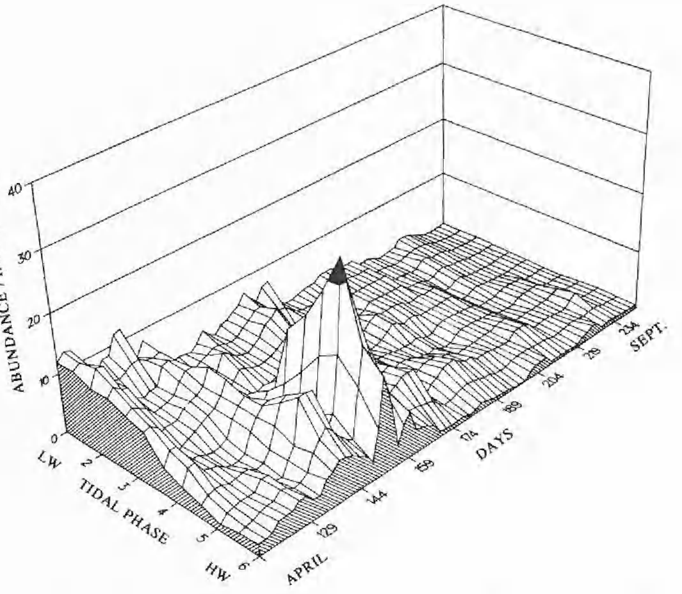

Fig. 3 : *Eurytemora affinis*. Seasonal and tidal dependent distribution of the abundance of copepodid I.

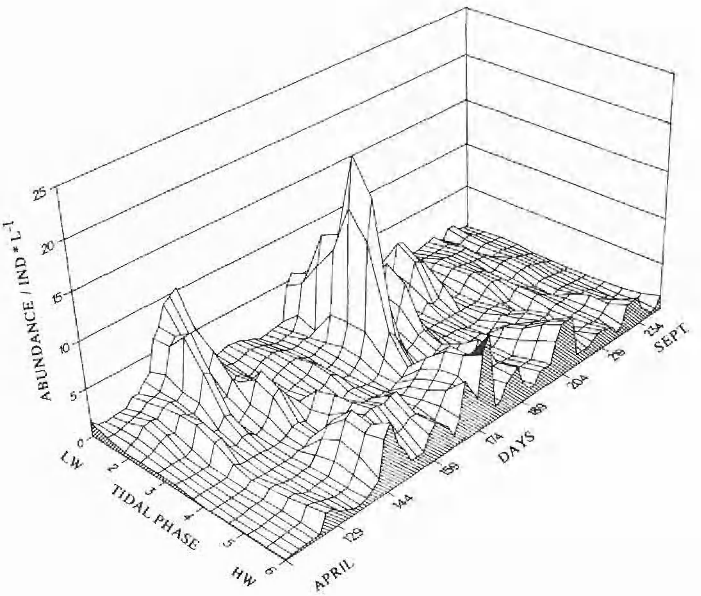

Fig. 4 : *Eurytemora affinis*. Seasonal and tidal dependent distribution of the abundance of copepodid IV.

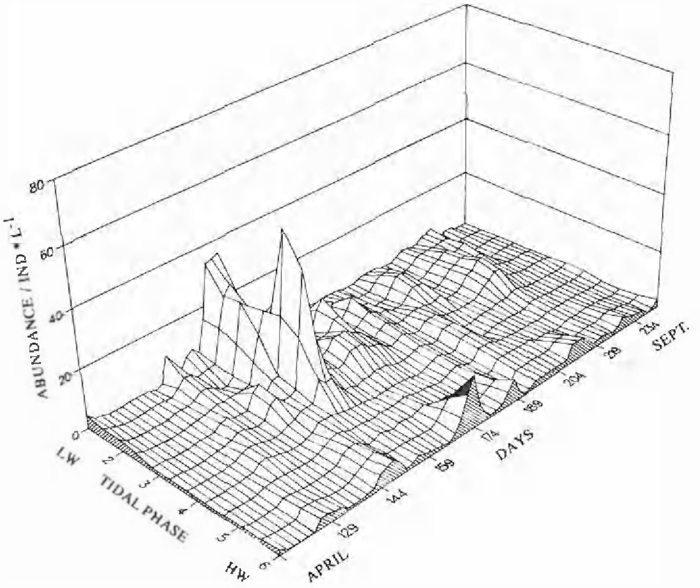

Fig. 5 : *Eurytemora affinis*. Seasonal and tidal dependent distribution of the abundance of adults.

Mortality rates

Instantaneous daily mortalitry rates are shown in Fig. 7-9 for the different instars of the three cohorts. In all cohorts highest daily mortality rates occurred between naupliar stages V and VI and lowest between the first and second copepodid stage. The mean mortality rates of naupliar and copepodids are compared in Tab. I. The mortality rates of the copepodid stages were equal in all three cohorts. Changes of the mortality rate of the naupliar have great influence on the survival rate, which was highest in cohort 2 where lowest mortality of naupliar occurred.

TABLE I

Mean mortality rates (d^{-1}) of naupliar and copepodid stages of *Eurytemora affinis*.

	naupliar	copepodid
cohort 1	0.26	0.05
cohort 2	0.15	0.05
cohort 3	0.25	0.05

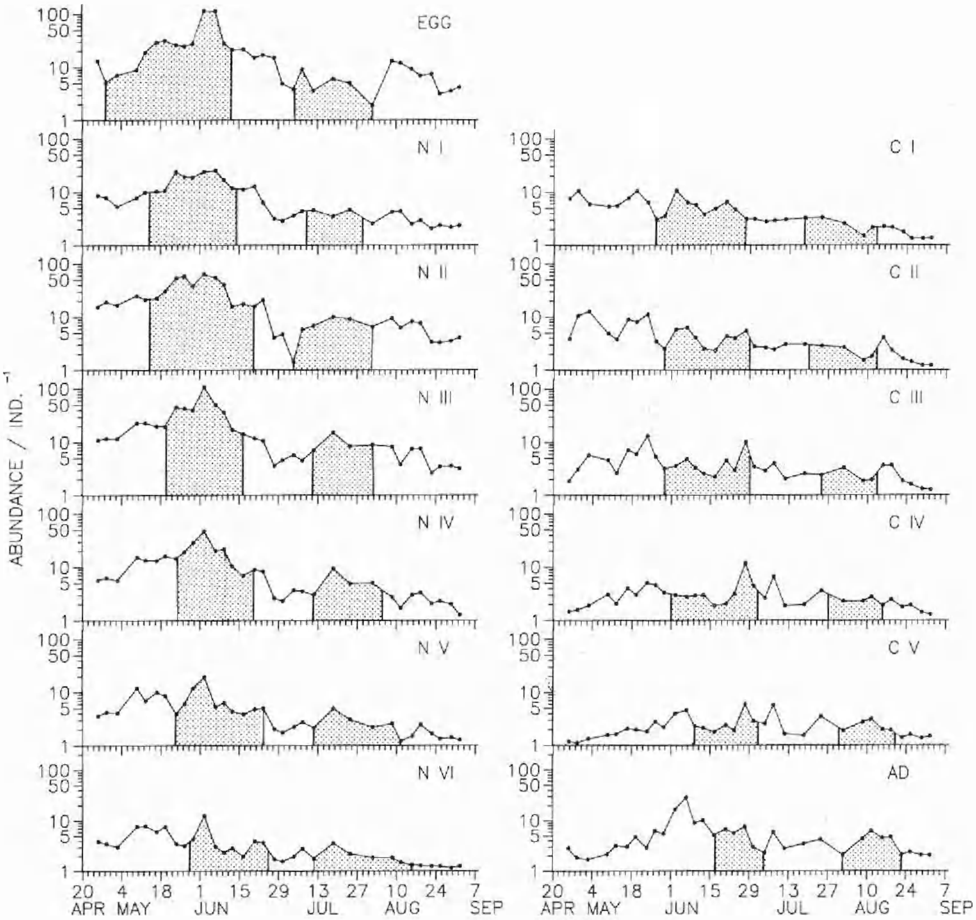

Fig. 6 : Cohorts of different instars of *Eurytemora affinis*.

DISCUSSION

It is an important result that in the Elbe estuary the distribution of the different instars of *Eurytemora affinis* is not uniform during flood phase. As it could already be shown by (Peitsch & Kausch, accept.) for a tidal cycle in 1987 maxima of the instars occur at different times during the tidal phase. So sampling has to include more than one or two samples during a half tidal cycle to catch maxima of all instars. Sampling at hourly intervals are regarded as sufficient because it could be shown that regular tidal dependant change in the instar density occurs (Peitsch & Kauch, accept.).

A representative value of the number of each instar is obtained by calculating a weighted average, which takes into account the different current velocities. A numerical average could lead to an overestimation of the numbers of an instar if the maximum is found during low current velocities or to an underestimation if maximum abundance occurs at high flow.

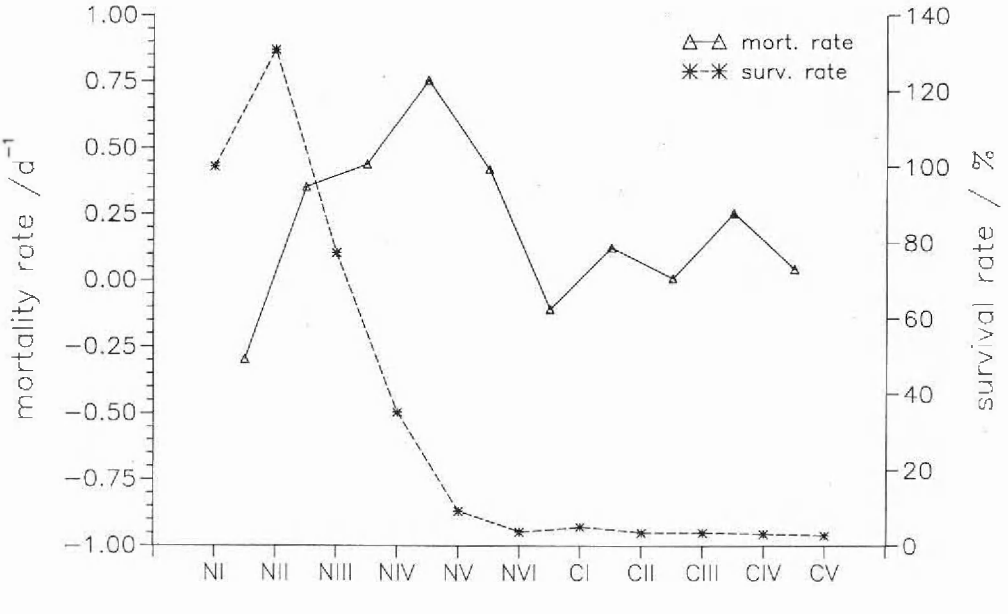

Fig. 7 : Daily mortality rates and survival rates of different instars of *Eurytemora affinis* in cohort 1.

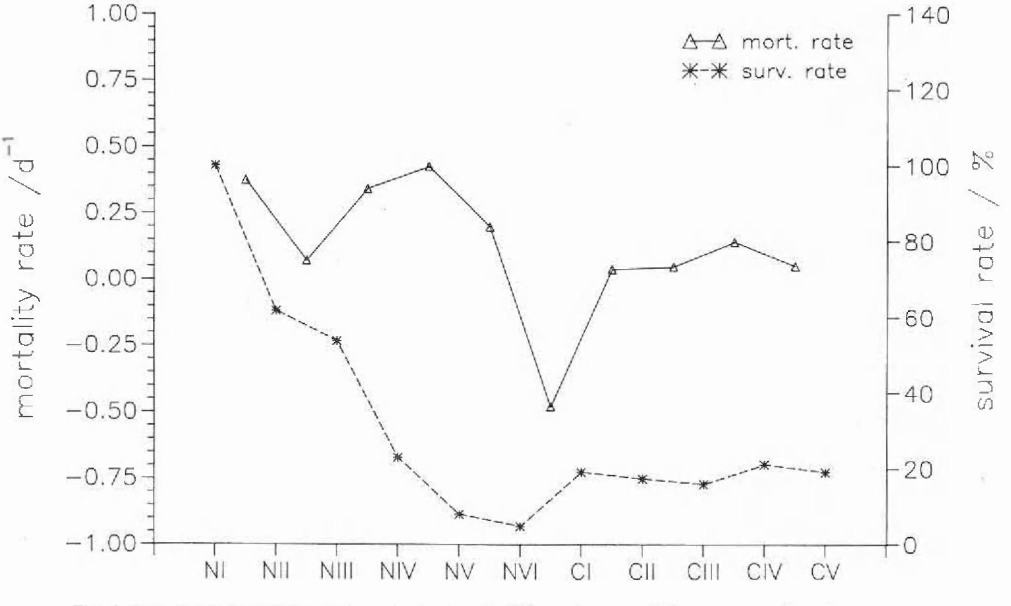

Fig. 8 : Daily mortality rates and survival rates of different instars of *Eurytemora affinis* in cohort 2.

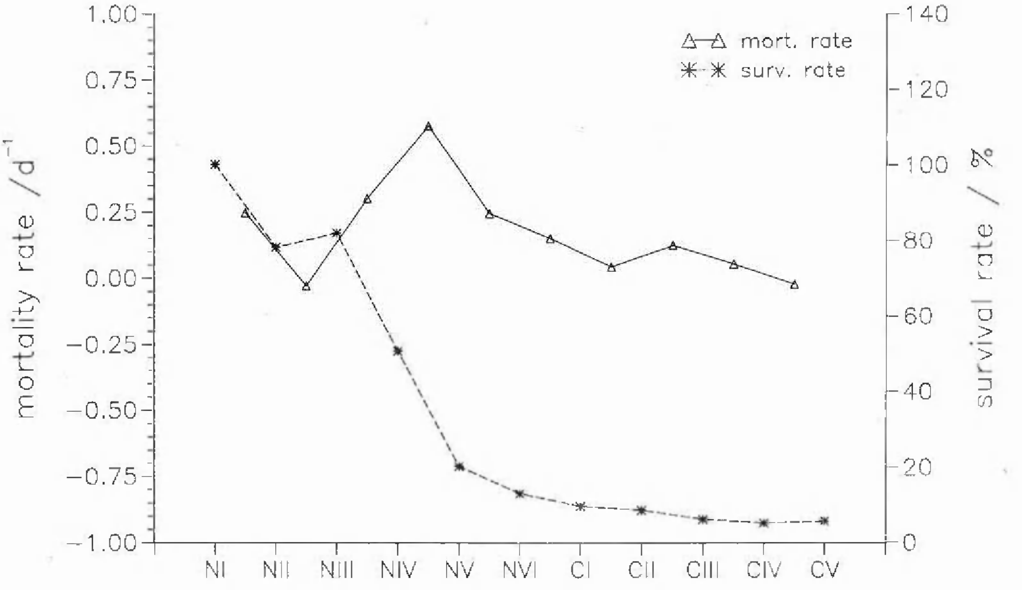

Fig. 9 : Daily mortality rates and survival rates of different instars of *Eurytemora affinis* in cohort 3

Over- or underestimation in fact will cause too low or high mortality rates. So treating the instars as a load and taking samples in sufficient short time intervals, will minimize the error, which is caused by the unequal distribution of the population and the special hydrographic conditions of estuaries.

Even calculating a representative number of individuals of each instar this way, a wrong estimation could be possible. Only a distinct section of the estuary is recorded by sampling during flood phase. At every tide individuals from upstream were added to the population and at the downstream boundary animals get lost from this section. For example the older copepodids i.e. C IV (Fig. 4), show more than one maximum during flood phase of one sampling day. This "additional" maximum at low water could be the reason for an overestimation of numbers of these stages and therefore to low values for the mortality rate are calculated. In addition it has to be taken into account that the development of the population is not uniform in different regions of the estuary. Lower flushing rates in flat water regions or branches of the river may support population development there. Especially, in the Elbe estuary these regions are assumed to be important breeding areas for the *Eurytemora affinis* population. In other estuaries salt marshes are supposed to be breeding places for *Eurytemora affinis* and *Acartia tonsa* (De Pauw, 1973 ; Trinast, 1975).

To solve this problem one needs good models of real flushing and exchange rates of water masses to calculate more realistic mortality rates.

Of course mortality rates in estuaries are also composed of predation rates and physiological death.

An explanation of the high mortality rates of the naupliar stages could be an age dependent mortality like Fager (1973) postulated it for zooplankton. High naupliar mortality for *Eurytemora affinis* was also found by Allan *et al.*, (1976). Mortality rates in the Elbe estuary in spring time were only a little bit higher than estimated by Heinle & Flemer (1975) for the Patuxent river estuary. In the Elbe estuary in spring invertebrate predators and fish larvae feed on naupliar, especially *Osmerus eperlanus* is an important predator of *Eurytemora affinis* (Ladiges, 1935). A regulation of populations at the level of early instars is often found for populations which produce a lot of descendants. Daan (1989) regards food limitation as a reason of high naupliar mortality in the north sea.

In summer fish larvae had grown up and naupliar mortality decreased in the Elbe estuary.

Until now the different components of the mortality rates could not be separated. The contribution of predators and food limitation to mortality rates has to be investigated in particular to get an idea of the special part of "mortality" caused by estuarine conditions.

For the Elbe estuary the importance of the distribution dependent error in estimating mortality rates could be shown.

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In situ grazing activity of planktonic copepods in the Gironde estuary.

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Abstract : Gut contents of *Acartia bifilosa* and *Eurytemora affinis*, temperature, salinity, chlorophyll pigments and suspended particulate matter concentration (SPM), have been measured during tidal cycles, in different seasons, in a highly turbid estuary, (Gironde, SW France).

SPM concentration and chlorophyll pigments varied as a fonction of tide. There was a good correlation between chlorophyll pigments and SPM concentration.

Phytoplankton ingestion, estimated between 165 and 569 ng C. cop^{-1}. d^{-1} for *E. affinis*, and 133-545 ng C. cop^{-1}. d^{-1} for *A. bifilosa* did not seem sufficient to sustain copepods metabolism. An exception was found for *A. bifilosa* during a phytoplankton bloom period, with a daily ingestion from 1 256 to 1 654 ng C. cop^{-1}. d^{-1}. In this case *Acartia*'s nutritional requirements were probably completely covered by phytoplankton ingestion. *Acartia*'s gut contents were related to chl *a* / SPM ratio, and were seriously affected by high SPM concentration.

Résumé : Le contenu intestinal de *Acartia bifilosa* et *Eurytemora affinis*, la température, salinité, pigments chlorophylliens et concentration de matière en suspension (MES), ont été mesurés pendant des cycles de marée, en différentes saisons, dans un estuaire très turbide (Gironde, SW de la France).

Les concentrations de MES et pigments chlorophylliens varient en fonction de la marée. Il existe une bonne corrélation entre les pigments chlorophylliens et la concentration en MES.

L'ingestion de phytoplancton, comprise entre 165 et 569 ng C. cop^{-1}. j^{-1} pour *E. affinis*, et de 133 à 545 ng C. cop^{-1}. j^{-1} pour *A. bifilosa*, ne paraît pas suffisante pour maintenir le métabolisme des copépodes. Une exception est notée pour *A. bifilosa* pendant une période de bloom phytoplanctonique, pendant laquelle l'ingestion journalière se situe entre 1 256 et 1 654 ng C. cop^{-1}. j^{-1}. Dans ce cas, les besoins nutritionnels d'*Acartia* sont probablement complètement couverts par l'ingestion de phytoplancton. Les contenus intestinaux de *A. bifilosa* sont liés à l'indice chl *a* / MES, et sont sérieusement affectés par les fortes concentrations en MES.

INTRODUCTION

The importance of terrestrial inert particles in estuaries and coastal areas makes difficult to understand the relationship between phytoplankton and copepods. In some estuaries the primary production is not sufficient to sustain the secondary production (Heinle & Flemer, 1975). Detrital particles, enriched with bacteria and ciliates have been proposed as complementary source of carbon (Heinle *et al.*, 1977 ; Berk *et al.*, 1977 ; Boak & Goulder, 1983 ; Gyllenberg, 1984 ; Poulet, 1976).

On the other hand, if copepods can swallow inert particles (Wilson, 1973 ; Sautour, 1991), the active choice of phytoplanktonic cells by copepods has been shown by high speed cinematography (Price *et al.*, 1983 ; Paffenhofer *et al.*, 1982).

The quality of food can be determinant in the development of these species. Generally it is accepted that phytoplankton is the more nutritive food source for copepods, but mortality rate can decrease with a mixed regime, phytoplankton and detritus (Heinle *et al.*, 1977 ; Poli, 1982 ; Roman, 1984).

The Gironde is a higly turbid estuary, with particulate concentrations that are tidally resuspended and that may exceed 1 g. l^{-1} in the oligohaline area (maximum during the study 7 g. l^{-1}). A well developed turbidity maximum forms at the upstream limit of the salinity intrusion, in the zone of convergence of bottom residual currents. A more thorough description of the estuary is given by Latouche & Jouanneau (1981), and Castel, this volume.

The two dominant planktonic copepods of the Gironde estuary, *Acartia bifilosa* (Giesbrecht) and *Eurytemora affinis* (Poppe) are spatially separated. The abundance of *E. affinis* is positively correlated with the suspended particulate matter concentration, and hydrodynamical processes are sufficient to explain the distribution of *E. affinis* in the estuary (Castel & Veiga, 1990). *A. bifilosa* develops downstream the turbidity maximum area ; highest densities are found in spring (Castel, 1985). In late summer, *Acartia tonsa* Dana is also present. In the Gironde estuary the light penetration is strongly limited by turbidity, and primary production may be not sufficient to sustain the zooplanktonic production. The average production of *E. affinis* in the oligohaline area is between 5 and 12 mg.m^{-3}. d^{-1} (Castel & Feurtet, 1989). In the same area, primary production measured by C^{14} incorporation in samples incubated at a depth of 50 cm, is practically zero (CNEXO, 1977). Most of the phytoplankton which is present in the turbidity maximum originates from the resuspension of phytobenthos or from the river and from the marine part of the estuary (Irigoien & Castel, 1992). On the other hand, the stock of particulate organic carbon in the estuary is very important, reaching approximately 66.10^{3} t (Lin, 1988). Thus, the phytoplanktonic cells present in the water column appear "diluted" in a huge quantities of non-living particles.

In order to understand the role of zooplankton in the transformation of organic matter, in such estuarine ecosystems, it is necessary to know which of the various potential food items (detritus, phytoplankton, microzooplankton) are eaten, and to what extent, under which circumstances. Since phytoplankton is supposed to be the principal source of food for copepods, the purpose of this work was to quantify the "in situ" phytoplanktonic ingestion of the two dominant planktonic copepods of the Gironde estuary, *Eurytemora affinis* and *Acartia bifilosa*, in relation with environmental parameters.

MATERIAL AND METHODS

Six field campaigns were completed in May and October 1990, and in March, April, July and October 1991. Sampling were made at two sites of the estuary. One in the oligohaline area of the estuary (station J), highly influenced by the turbidity maximum and dominated by *E. affinis*, and another in the polyhaline area (station A), more influenced by the salinity intrusion, and dominated by *A. bifilosa* (see fig. 1). In each case , samples were collected every 2 hour during a period ranging from 14 to 48 hours. Additionally in August and October 1991 two longitudinal transects of the estuary were performed. Some other preliminary measurements were made in March and April 1990.

The following variables were measured : salinity, temperature, suspended particulate matter and chlorophyll concentrations, together with the gut fluorescence analysis of the copepods. Samples were taken at two depths : 1 m below the water surface and 1 m above the bottom.

Temperature and salinity were measured with a Kent Eil 5005 probe. Pigments in the water were measured by fluorometry (Turner 112), on 90 % acetone extracts, before and after acidification, according to Neveux (1983). Pigments concentrations were calculated

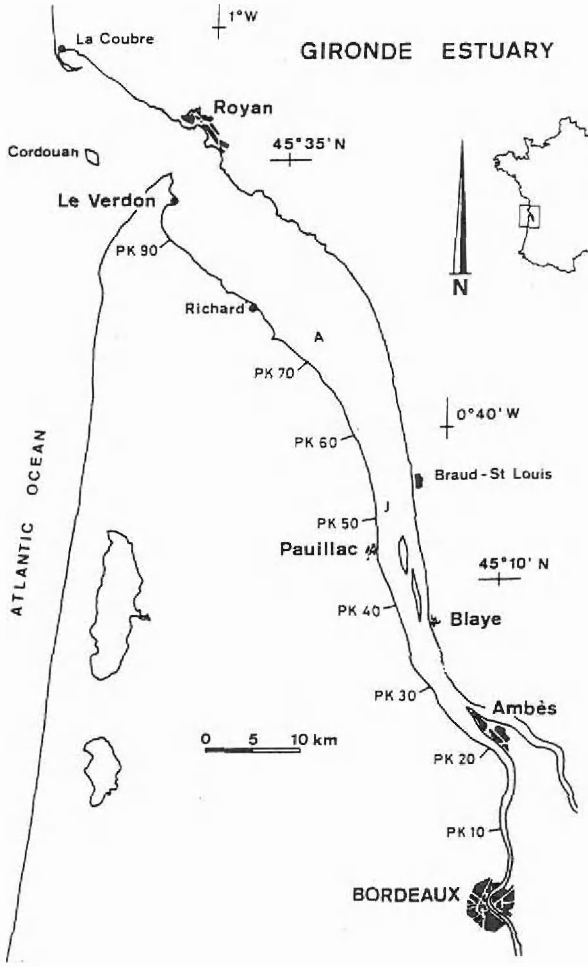

Fig. 1 : Map of the Gironde estuary showing the sampling stations. Pk refers to the distance, in Km, from the city of Bordeaux. May 90 : 24 h cycle at station A and 24 h cycle at station J. October 90 : 48 h cycle at station J. March 91 : 48 h cycle at station J. April 91 : 48 h at station A. July 91 : 14 h cycle at station A and 14 h cycle at station J. October 91 : 14 h cycle at station A and 14 h cycle at station J.

using the equations given by Lorenzen (1967). Results are given in chlorophyll a (µg. l^{-1}) and pheopigments (µg. l^{-1}). Suspended particulate matter concentration (SPM) was estimated as dry weight (60 °C, 24 h) after filtration on Whatman GF/C. For SPM and chlorophyll pigments three replicates were performed by point.

Copepods gut contents fluorescence was measured by the method of Mackas & Bohrer (1976). Copepods were collected with a WP2 net (200 µm mesh size), and immediately frozen in liquid nitrogen. In the laboratory each sample was placed under dissecting microscope with a minimum light and copepods were placed into 5 ml 90 % acetone tubes. Three subsamples containing between 10 and 40 individuals (adults and copepodids 5) were measured by point. Pigments were extracted for 24 hours at 4 °C. Fluorescence was measured as were the pigments in the water and results are given in equivalents chl *a* (µg chl *a* + 1.51 µg pheopigments), (Bautista *et al.*, 1988).

Ingestion (I) was calculated multiplying the gut content (G) by the gut passage time (r) : I = r.G (Mackas & Bohrer, 1976). Daily ingestion was obtained multiplying instantaneous ingestion (I) and sampling interval (120 min). Gut passage times were previously determined in laboratory conditions for different temperatures (unpublished data).

Results are expressed in carbon, using the ratio C : chl *a* equivalents = 50 : 1 (Dagg & Grill, 1980).

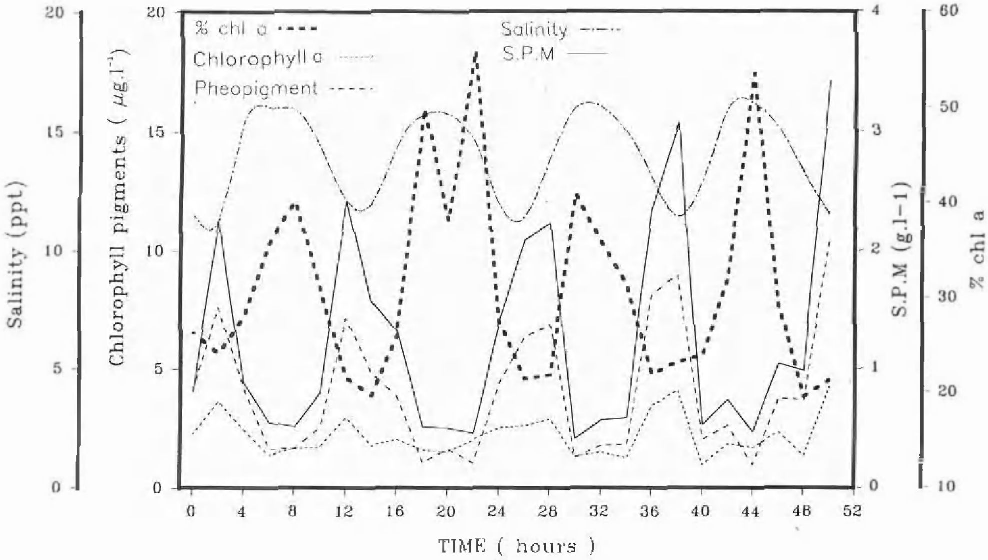

Fig. 2 : Gironde estuary. Changes in chl *a* (µg.l^{-1}), pheopigments (µg.l^{-1}), % chl *a* (chl *a* / chl *a* + pheopigments), SPM (g.l^{-1}) and salinity (ppt) during 4 tidal cycles. Station J, in the oligohaline area, October 1990.

RESULTS

ENVIRONMENTAL CONDITIONS

Short term variations in the tidal estuaries are essentially a consequence of tidal cycles. A signifiant example is given in fig 2. Maximum SPM concentrations were found at low tide. Chlorophyll *a* and pheopigments concentration were strongly linked to SPM, showing maxima at low tide. Conversely the percentage of chl *a* [chl a/(chl *a* + 1.51 pheopigments)) was low at low tide and increased significantly at high tide as a function of SPM concentration. Some exceptions were noted in July and August 1991, at the polyhaline station (A), where huge quantities of diatoms (probably *Pleurosira laevis*) were observed. In those cases the chl *a* concentration showed maxima at high tide, but pheopigments concentration was always linked to SPM. This bloom did not appear in the oligohaline area, more influenced by SPM concentration (Fig. 3 for August 1991). The summary of these results is presented in table I. Chlorophyll *a* was significantly correlated with SPM concentration ($p < 0.01$), except in July and August. Pheopigments were always significantly correlated with SPM concentration, without exception.

To take into account this relation between chlorophyll pigments and SPM we have used the chl *a*/SPM ratio proposed by Castel & Feurtet (1986) as an index of food availability for zooplankton. In general this ratio increases at high tide and decreases from downstream to upstream as a function of SPM (Fig. 3, fig. 4).

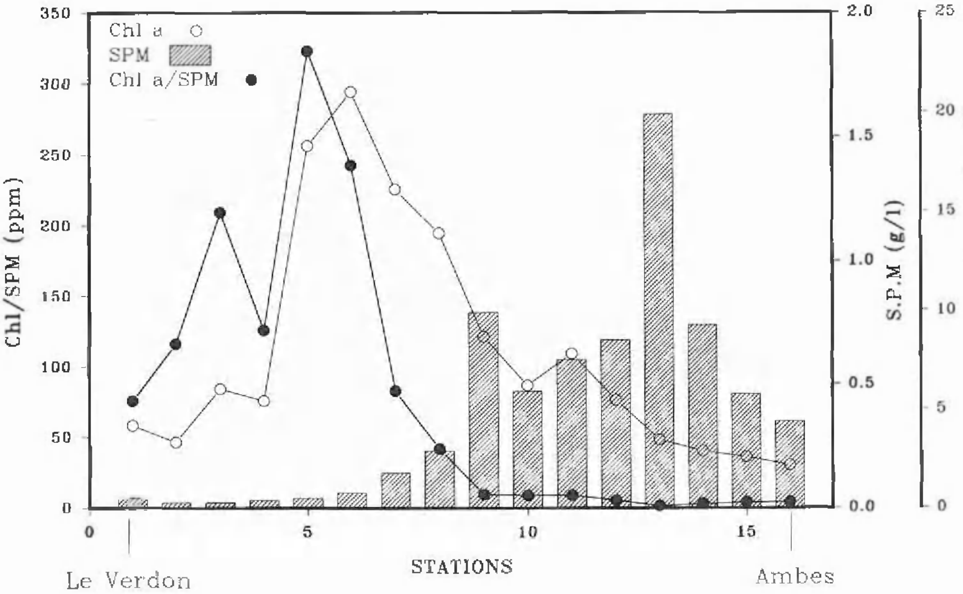

Fig. 3 : Changes in chl *a* concentration (µg.l^{-1}), SPM concentration (g.l^{-1}), and chl *a* / SPM ratio (ppm) along the Gironde estuary during a phytoplanktonic bloom period. August 1991. Samples were taken every 2 nautic miles.

TABLE I

Correlation between chlorophyll *a* and SPM concentration, and between pheopigments and SPM concentration in the Gironde estuary. Stations A and J are indicated in fig 1. Transect = stations covering the whole salinity gradient. ** $p < 0.01$.

DATE	Station	chl *a*-SPM	r	phe-SPM	r
May 90	A	$y = 1.87 X + 2.51$	0.84**	$y = 2.21 X - 0.61$	0.96**
May 90	J	$y = 2.25 X + 1.19$	0.96**	$y = 2.23 X - 0.16$	0.96**
October 90	J	$y = 0.98 X + 1.01$	0.93**	$y = 2.99 X + 0.22$	0.98**
March 91	J	$y = 0.77 X + 0.23$	0,89**	$y = 4.09 X + 1.31$	0.95**
April 91	A	$y = 1.41 X + 0.3$	0.79**	$y = 3.53 X + 0.1$	0.90**
July 91	A	$y = 3.56 X + 3.33$	- 0,33	$y = 3.98 X - 0.08$	0.94**
July 91	J	$y = 1.48 X + 0.75$	0.92**	$y = 4.1 X - 0.05$	0.97**
August 91	Transect	$y = 3,63 X + 6.9$	- 0.37	$y = 4.1 X + 0.58$	0.90**
October 91	J	$y = 0.76 X + 1.79$	0.74**	$y = 2.33 X + 0.28$	0.95**
October 91	A	$y = 3.36 X + 0.91$	0.92**	$y = 2.31 X + 0.35$	0.85**
October 91	Transect	$y = 1.39 X + 1.07$	0.73**	$y = 3.53 X - 0.33$	0.97**

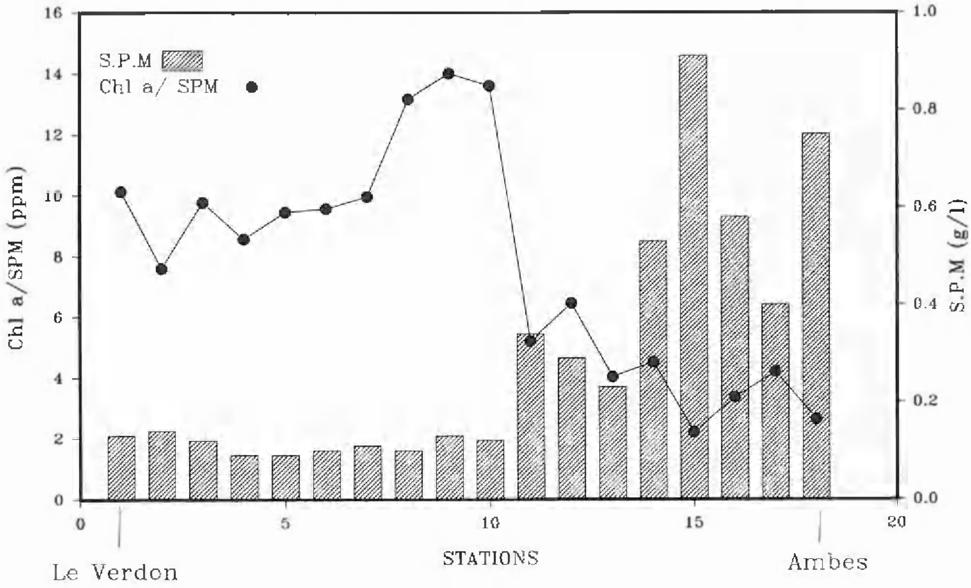

Fig. 4 : Changes in chl *a* / SPM ratio (ppm), and SPM concentration ($g.l^{-1}$), along the Gironde estuary. October 1991. Samples were taken every 2 nautic miles. See difference in chl *a* / SPM ratio compared to the phytoplanktonic bloom period (Fig. 3).

COPEPOD INGESTION

No significant differences were found between day and night samples (Fig. 5). A good correlation was found between the gut contents of *A.bifilosa* and chl *a*/SPM ratio (Fig. 6) ($\log y = 0.78 \log x - 1.65$ $r = 0.62$ $p < 0.01$ $n = 138$). There was also an inverse relation ship between *A. bifilosa* gut contents and SPM concentration, (Fig. 7) ($\log y = -0.52 \log x - 1.33$ $r = -0.50$ $p < 0.01$ $n = 138$). Direct observations under dissecting microscope showed that the *Acartia*'s guts in high turbid samples were practically empty. Conversely there was no relationship between *Acartia*'s gut contents and chl *a* concentration ($r = 0.017$). No relationships were found between measured parameters and *E. affinis* gut contents (chl *a* $r = 0.027$, chl *a*/SPM $r = 0.19$, SPM $r = -0.12$, log-log transformed data $n = 189$).

Table II shows the daily ingestion of phytoplanktonic carbon and the range of gut contents of *A. bifilosa* and *E. affinis*. The phytoplanktonic carbon ingestion presented a seasonal variation, increasing in summer and decreasing in spring when the temperature was low. Highest ingestion rate was found for *A. bifilosa* during the phytoplankton bloom.

DISCUSSION

In highly turbid estuaries, with a complicated hydrology, as the Gironde, the use of index like chl *a*/SPM ratio seems more appropriate than the single chl *a* concentration so as to understand seasonal and spatial distribution of phytoplankton.

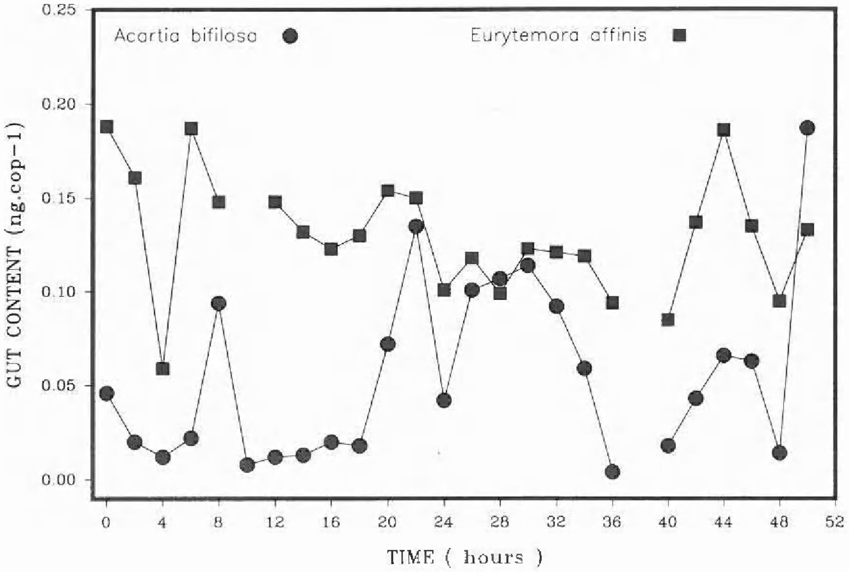

Fig. 5 : Gironde estuary. Changes in *A. bifilosa* and *E. affinis*' gut contents (ng chl *a* equivalents. cop^{-1}) during 4 tidal cycles. Station J, in the oligohaline area, October 1990.

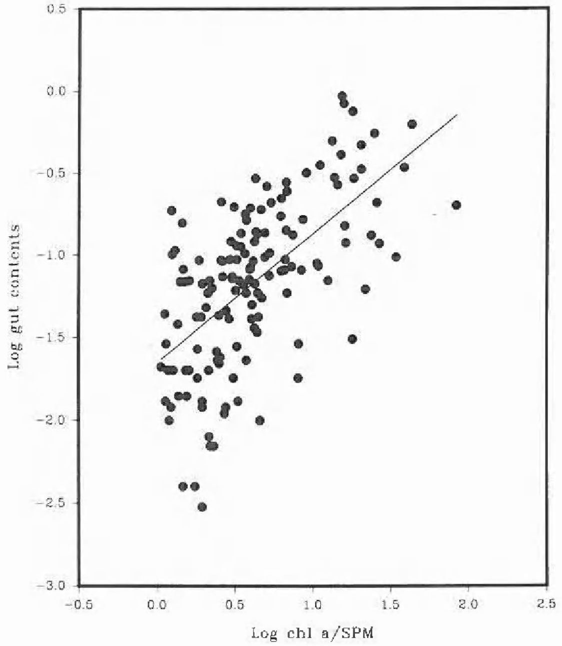

Fig 6. : Log gut contents of *Acartia* sp. in relation to log chl *a* / SPM ratio. Data from all campaigns. Fitted curve : $Y = 0.78\ X - 1.65$, $r = 0.62$, $p < 0.01$, $n = 138$.

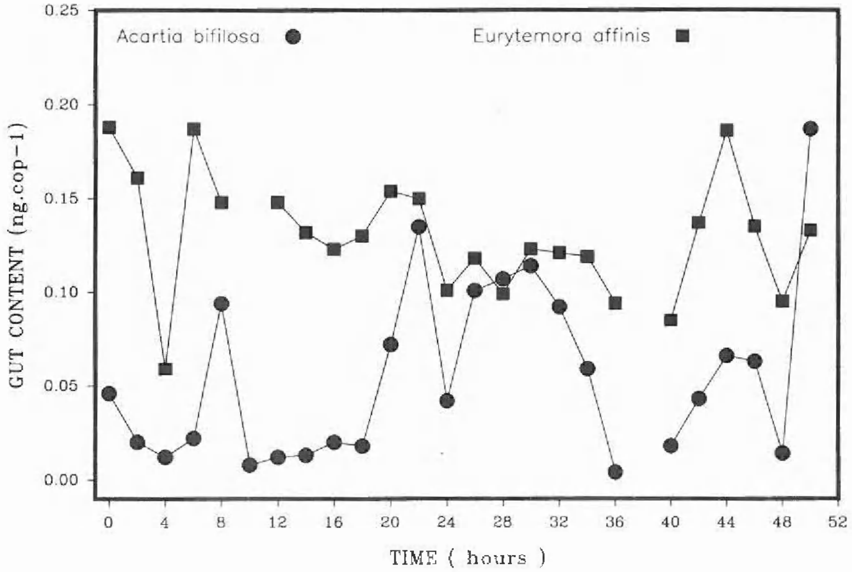

Fig. 5 : Gironde estuary. Changes in *A. bifilosa* and *E. affinis*' gut contents (ng chl *a* equivalents. cop^{-1}) during 4 tidal cycles. Station J, in the oligohaline area, October 1990.

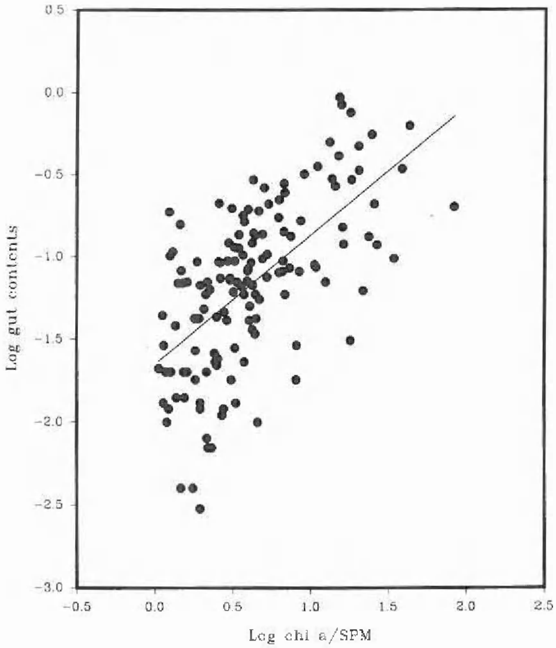

Fig 6. : Log gut contents of *Acartia* sp. in relation to log chl *a* / SPM ratio. Data from all campaigns. Fitted curve : $Y = 0.78 X - 1.65$, $r = 0.62$, $p < 0.01$, $n = 138$.

TABLE II

Estimated daily ingestion of phytoplankton carbon (surface and bottom average), employed gut passage times and measured maximum and minimum gut contents (equivalents chl *a*), at each campaign for the copepods *Eurytemora affinis* and *Acartia bifilosa* in the Gironde estuary. * measurements on *A. tonsa*.

DATE	T(°C)	*Eurytemora*			*Acartia*		
		Daily Ingestion ng.C cop.1.d-1	r min-1	Gut contents ng.cop-1 ng. C.cop-1.d-1	Daily Ingestion	r min-1	Gut contents ng.cop-1
May 90	18 °C	390	0.038	0.485-0.053	481	0.043	0.354-0.031
October 90	18 °C	379	0.038	0.224-0.059	181*	0.043	0.294-0.01*
March 91	10 °C	182	0.018	0.217-0.046		0.027	
April 91	10 °C	340	0.018	0.592-0.163	163	0.027	0.211-0.012
July 91	22 °C	561	0.043	0.220-0.112	1 455	0.05	0.932-0.08
October 91	20 °C	328	0.041	0.137-0.067	191	0.047	0.163-0.013

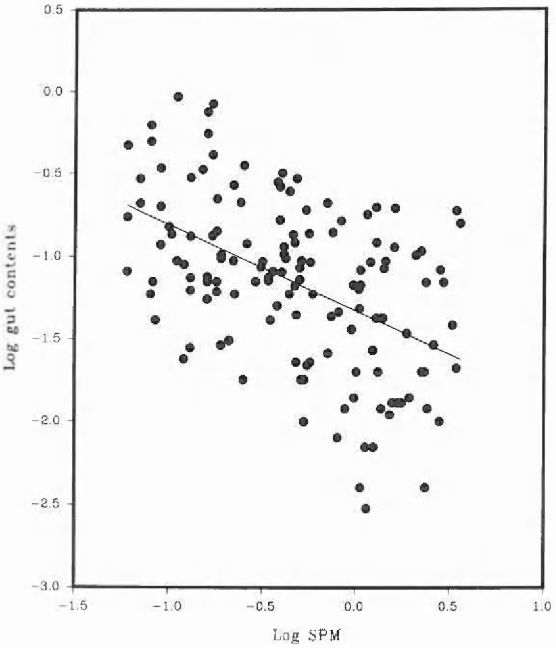

Fig 7. : Log gut contents of *Acartia* sp. in relation to log SPM concentration. Data from all campaigns. Fitted curve : $Y = -0.52 X - 1.33$, $r = -0.5$, $p < 0.01$, $n = 138$.

This ratio seems to give a good idea of the "accessibility" of phytoplankton for copepods, which is illustrated by the good relationships between chl *a*/SPM ratio and *Acartia*'s gut contents. This "accessibility" may be very important for the biology of the species. For example, if phytoplankton carbon is accompanied by large amount of detritus, *A. tonsa*'s reproduction rate should decrease strongly (Paffenhofer, 1991). Such a relationship is not found for *E. affinis* which lives in the most turbid part of the estuary. The phytoplanktonic carbon ingested per day by *E. affinis* in this study is generally lower than the one estimated by other authors in laboratory conditions. The phytoplankton ingestion of *E. affinis* in the Gironde estuary represents from 5 to 20 % of those calculated by Barthel (1983) with *E. affinis* fed *Nannochloris* sp. The ingestion of *E. affinis* can be also estimated by the egg production, using the equation $I = [(E).(Ce)] / [Ki]$ (Peterson *et al.*, 1990), where E = egg production rate (eggs. female^{-1}.d^{-1}), Ce = carbon contents of an egg and Ki = gross efficiency of egg production. The carbon contents was estimated applying a carbon to volume conversion factor of $0.14.10^{-6}$ g C. m^{-3} (Kiorboe *et al.*, 1985). The egg volume was estimated by Feurtet (1989) (egg diameter = 91.5 µm). Egg production rate was estimated by Castel *et al.* (1983), (E = 6.2 eggs. fem^{-1}. d^{-1}). Ki is variable, between 0.33 (Peterson *et al.*, 1988) for *Calanoides carinatus* feeding *Thalassiosira weissflogii* and 0.09 - 0.18 for *E. affinis* with different levels of algal food (Heinle *et al.*, 1977). The ingestion estimated in that way is between 1 100 (Ki = 0.33) and 3 868 (Ki = 0.09) ngC.cop^{-1}. d^{-1}. The 1 100 ngC.

cop^{-1} l. d^{-1} value represents 56 % of females' carbon weight. Conversely, the ingestion calculated measuring gut contents is only 20 % of copepods' carbon weight. It seems that the phytoplankton ingestion is not enough for *E. affinis*.

Studies about *A. bifilosa* are scarce, but we can compare our results with those obtained with *A. tonsa*. This species is also present in the Gironde during the summer and has been frequently studied in other estuaries. Gut contents measured in the present study are generally lower than the one reported by Stearns *et al.* (1987) in the Newport estuary, (0.498 to 1.46 ng. cop^{-1}), except for values found during the bloom period, (0.118 to 0.932 $ng.cop^{-1}$). This may be explained by two factors : the gut contents given by Stearns *et al.* (1987) corresponds to the females only, which are bigger and eat more material than males. On the other hand, the values of chl *a* found in the Gironde are sensibly lower than those of the Newport estuary. In spring in the polyhaline area of the Gironde, the concentration of chl *a* varies in a range of 1 to 7 $\mu g.l^{-1}$ (7 to 17 $\mu g.l^{-1}$ in the Newport estuary). Only during the bloom situation, with a limited spatial and temporal distribution, similar values have been found, with a maximum of 21 $\mu g.l^{-1}$.

Daily phytoplanktonic carbon ingestions found in the present study are generally in the lower limits of those reported by Roman (1977) in laboratory experiments, with *A. tonsa* feeding *Nitzchia closterium* (312-1 812 ng $C.cop^{-1}.d^{-1}$) or detritus of *Fucus vesiculosus* (375-5 060 ngC. $cop^{-1}.d^{-1}$). Our results at similar temperatures are between 133 and 545 ng C. $cop^{-1}.d^{-1}$, and between 1 256 and 1 654 ng C. $cop^{-1}.d^{-1}$ during the bloom period. These ingestions represent about 7 to 27 % of *Acartia*'s carbon weight, and about 63 to 83 % during bloom period.

This variability of the results is probably due to the capacity of *Acartia* to ingest other particles than phytoplankton cells, eg. detritus (Roman, 1977, 1984), plastic beads (Wilson, 1973), nauplii (Anraku & Omori, 1963 ; Londsdale *et al.*, 1979). In other sense a carnivorous behaviour could be more productive energetically (Conover & Corner, 1968 ; Corner *et al.*, 1976).

The apparent contradiction between a low phytoplankton carbon ingestion (except during bloom period) and the selection of large phytoplankton cells (Tackx & Daro this volume), could be explained by an opportunist behaviour of *Acartia* (Turner, 1984), which would prefer large particles, either phytoplankton cells or nauplii.

Contrary to *E. affinis* it is likely that the nutritional capacities of *A. bifilosa* are seriously affected by high SPM concentrations. This could be explained by the low chl *a*/SPM ratio, found in the turbidity maximum, leading to a "dilution" of phytoplanktonic cells. Another explanation could be the difficulty to find large particles in the turbidity maximum, mainly formed by small particles (mean diameter : 4-11 µm, maximum frequency : 1.5-2.5 µm) (Weber *et al.*, 1991 ; Irigoien, 1990). *Acartia* cannot feed efficiently on small cells, because it does no create low-amplitude mandible 2 motions (Price *et al.*, 1983). In both cases, low chl *a*/SPM ratio and small particles, the energetic cost to find large particles, phytoplankton cells or others, may be excessive. This difficulty could, somehow, determine the spatio temporal distribution of *A. bifilosa* in the Gironde.

On the contrary the phytoplankton ingestion by *E. affinis*, seems to be not affected by SPM concentration. The shape of its mandible does not allow it to catch so large particles as *Acartia* does (Castel, 1981 ; Richman *et al.*, 1977). As it lives in the most turbid area of the estuary it probably has to complete its nutrition with other detrital particles.

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Feeding behaviour of the coastal copepod *Euterpina acutifrons* on small particles.

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Résumé : Dans les zones estuariennes les Copépodes planctoniques constituent un maillon important de la chaîne alimentaire : proies ou éventuellement compétiteurs de nombreuses espèces commercialisables (Bivalves par exemple). La nutrition des Copépodes dans ces milieux riches en particules en suspension (algues et particules inertes) de petite taille est donc une question de premier intérêt. Le comportement alimentaire de *Euterpina acutifrons*, un des Copépodes dominant en zone côtière, a été étudié expérimentalement. Plusieurs espèces d'algues ont été offertes : *Isochrysis galbana*, *Chaetoceros calcitrans*, *Skeletonema costatum*. Lorsque le diamètre des cellules algales offertes est faible, l'ingestion des Copépodes croît linéairement avec la concentration. Le taux de filtration apparent n'est pas corrélé à la concentration algale et reste pratiquement constant pour une même algue. L'ingestion et la filtration augmentent avec le diamètre de l'algue proposée. De plus, *Euterpina acutifrons* ingère des particules inertes de petite taille (billes de 5 µm) sans aucune valeur nutritive. Ces sphères sont détectées mécaniquement. Ce résultat indique que les Copépodes peuvent ingérer des particules détritiques inertes qui peuvent éventuellement compléter l'apport nutritionnel dû aux algues.

Abstract : Planktonic Copepods constitute an important group of the food chain in estuaries. They are preys or eventually competitors of a lot of species with economic interest (e. g. Bivalves). The nutrition behaviour of Copepods in these ecosystems, where small particulate suspended matter (algae and inert particles) is abundant, is of a great interest. The feeding behaviour of *Euterpina acutifrons*, a dominant Copepod in coastal areas, was studied experimentally. Several algal species were offered : *Isochrysis galbana*, *Chaetoceros calcitrans*, *Skeletonema costatum*. The ingestion rate of Copepods fed with small algae increases linearly with the concentration of cells. The clearance rate is not correlated to the algal concentration and remains quite constant. In addition, ingestion and filtration rates increase with the cells diameter when different species are proposed. *Euterpina acutifrons* ingests small inert particles (5 µm beads) with no nutritional value. These particles are detected mechanically. This suggests that Copepods can complement their algal diet in the ecosystem with detritic particles.

INTRODUCTION

A lot of species among Copepods are usually classified as herbivorous filter feeders. Filter feeders can ingest different kind of particles especially in estuaries where algae are mixed with inert particles. Small algae and small inert particles can constitute an important part of the "food" available for filter feeders in these ecosystems. The utilization of this stock by Copepods is of a great interest because they constitute the preys for a lot of young instars of economic interest (fish or shrimp). On the other hand they can compete for food with adults or young instars of some species. The benthic invertebrates (Oysters, Mussels) constitute a good example in the neritic zone. Indeed the larvae of these species are herbivorous and adults can ingest too a quite important amount of old settled planktonic algae. Zooplanktonic filter feeders essentially feed on phytoplanktonic stock. Among them, herbivorous Copepods seem to exert a great pressure on algal stock due to their high biomass. In fact, these ones can be sometimes in competition with Bivalves. Bivalves larvae feed on nano-plankton (Lucas, 1982, 1983) ; on the contrary, herbivorous Copepods tend to graze large-sized algae (Cowles, 1979 ; Schnack, 1979 ; Price & Paffenhofer, 1984). However, Copepods can also ingest the most abundant algae (Poulet & Chanut, 1975 ; Runge, 1980) whatever their size. They can also switch their feeding activity from one size class to another. This is the case when the energy gain is more important (Poulet, 1974 ; Daro, 1985 ; Tackx *et al.*, 1989). These observations suggest that Bivalves (larvae and adults) and Copepods can feed on the same algae (e. g. during algal spring bloom).

Detritus forms a major part of particulate suspended matter in estuarine ecosystems. The particles caught by zooplankton are not essentially algal cells as it is the case in open areas where algae are dominant. The great quantity of these inorganic suspended particles in the water masses forces organisms to a great adaptability. Planktonic Copepods were considered as herbivorous for a long time. Since a few years, studies are carried out in order to determine the feeding behaviour of Copepods on detritus (Lenz, 1977 ; Roman, 1977, 1984 ; Gaddy & Parker, 1986). These inorganic particles play an important role in the feeding behaviour of planktonic Copepods and this aspect is generally not taken into account in the laboratory experiments. Therefore investigations of ingestion and filtration rates of Copepods determined in the laboratory must consider these inorganic particles.

The ingestion of inorganic particles by planktonic Copepods can be studied throughout their "nutrition" on plastic beads whose size is similar to those of usually ingested algae. This kind of study was done in different ways. Richman *et al.* (1977) proposing a mixt nutrition to Copepods, have shown that they ingest essentially the largest beads. On the other hand, very small beads are ingested as well when proposed in great quantities. The Copepods studied by Donaghay & Small (1979) and Huntley *et al.* (1983) particularly ingested algal cells when they were fed on a mixture of algal cells and polystyrene beads. Selective feeding of marine Calanoid Copepods was shown by Poulet & Marsot (1978) : the Copepods essentially ingested semi-permeable beads (variable sizes) containing algal flavors. Demott (1988) showed a great preference of the Copepod *Eudiaptomus* for treated spheres when algae are scarce. This selectivity disappeared when algae are abundant, the untreated and the flavored beads were equally ingested. This author also noticed that the capacity to select particles is less important for *Temora longicornis* and *Pseudocalanus* sp (marine Calanoid Copepods) than for *Eudiaptomus*.

The Copepod used in the present work is the planktonic Harpacticoid *Euterpina acutifrons*. This species can be very abundant during some periods of the year (i. e. algal spring bloom) in littoral ecosystem used for Bivalves farming (Castel & Courties, 1982 ; Sautour, 1991).

First, the variations of grazing activity was studied according to the concentration and the quality of the algae. Several algae were used : *Isochrysis galbana* (5 µm) and *Chaetoceros calcitrans* (8 µm) usually utilized for the nutrition of Bivalves larvae, and *Skeletonema costatum* (chains of cells : 18 µm) used for older larvae.

Euterpina acutifrons lives in ecosystems with high particulate suspended matter concentration. Therefore, it is necessary to know its feeding behaviour on inert particles whose size is similar to those of ingested algae. This ingestion was studied with plastic beads whose diameter is the same as *Isochrysis galbana*.

MATERIAL AND METHODS

Zooplankton samples were collected in Arcachon Bay using a WP2 net (200 µm meshsize). The animals were carried to the laboratory immediately after sampling in order to minimize the variations of temperature. The samples were diluted to avoid high mortality (due to a decrease of dissolved oxygen or due to excretion products). The animals were anesthetized in seawater containing magnesium chloride and samples were sorted using a binocular microscope. Adult *Euterpina acutifrons* were transferred in large containers and kept in an air-conditioned room. The temperature was fixed to 19 °C for all the experiments.

Feeding behaviour was investigated in a classical way (Frost, 1972) : Copepods were placed in experimental beakers containing different algal species (different concentrations) or beads ; control jars were used for algae. Ingestion and filtration rates were calculated by measuring the decrease of particles in experimental beakers after 24 hours. Copepods were starved for 2 hours before each experiment, in order to start the experiments with the same nutritional conditions.

Ingestion and filtration of small-algae

The choice of the containers and the determination of the number of Copepods by jars is the result of a compromise (Sautour, 1991) : 500 ml glass containers and 7 Copepods in each one. Copepods placed in the beakers produced dissolved organic products (nitrogen and phosphorus) which create an enrichment in the algal production (Roman & Rublee, 1980 ; Sautour, 1991). A known amount of nitrogen and phosphorus was added to the control containers in order to obtain the same algal production. Experimental jars were then placed in the dark, at 19 °C, for 24 hours. Algae used in the experiments were 1 month old as recommended by Mullin (1963).

The ingestion rate (I_a) was calculated by measuring the difference of algal concentration (in terms of chl *a* equivalent) at time t, in the control (C_c) and in the experimental beakers (C_e). For one hour and for one Copepod : $I_a = (C_c - C_e) .v/(n.t)$, where v represents the volume of the containers, t the duration of the experiment and n the number of Copepods per jar.

The filtration rate is the ratio between the ingestion rate (I_a) and the initial algal concentration in the beakers (C_o) : $F = I_a/C_o$.

Ingestion and filtration of small inert particles

The diameter of the beads used for the experiments was 5 µm. This size was chosen in order to allow comparisons with ingestion and filtration rates determined with *Isochrysis galbana* (diameter around 5 µm). A range of beads concentrations was realized. The higher value was determined according to the concentration of *Isochrysis galbana* during a spring bloom (Sautour (1991) : 34 mg of chl *a* equivalent per cubic meter = 21 000 particles per ml). Thirteen concentrations of beads from 640 to 28 000 particles.ml^{-1} were prepared in twenty-six 250 ml beakers (two replicates for each concentration). In addition, four (2 + 2) beakers were used containing a greater amount of beads (49 000 and 75 000 beads.ml^{-1}) ; these two concentrations were chosen to consider the very important quantity of particulate suspended matter sometimes observed in littoral ecosystems. Copepods died in two flasks during the experiment, so the results are presented for only 28 beakers.

At time 0, five animals were added in the containers (after starvation) and placed in the dark, at 19 °C. Jars were permanently shaked in order to prevent beads settling. After 24 hours the beads were counted using a binocular microscope.

The difference of particles number in the beakers between time t (N_t) and time 0 (N_0), divided by the number of Copepods (n) and the duration of the investigation (t) gives the ingestion rate (I_b) : $I_b = (N_t\text{-}N_0)/(n.t)$. The calculation of the filtration rate is the same as for the algae : $F = I_b/N_0$.

RESULTS

Ingestion and filtration of small algae

The ability of Copepod ingestion is variable according to the algae proposed. In all cases, the ingestion rate is strongly linked to algal concentration (Fig. 1). The global aspect of the curve of ingestion is the same for the 3 algae : ingestion rate linearly increases with algal concentration. The regression line calculated for these experimental values derives from the model : I = a.C+b, where I is the ingestion rate (ng chl *a*.Cop^{-1}.h^{-1}) and C the algal concentration in the experimental beakers (ng chl *a*.ml^{-1}).

Isochrysis galbana : $I_a = 0.4925C\text{-}1.1046$ ($r = 0.88$ for $n = 30$; $p < 0.005$).

Skeletonema costatum : $I_a = 0.5284C\text{-}0.3264$ ($r = 0.62$ for $n = 60$; $p < 0.005$).

Chaetoceros calcitrans : $I_a = 0.1941C\text{-}0.5050$ ($r = 0.79$ for $n = 30$; $p < 0.005$).

No relationships are found between filtration rate and algal concentration for the three algae (Fig. 2). The observation of residuals obtained from the model indicates an identical variability for the low and the high concentrations. This allows to reject the hypothesis of the influence of measurement sensitivity on low values (greater variance).

Thus, filtration rates are not influenced by cell concentration although the mean values show important variations according to the proposed algae : 0.41 ml.h^{-1} for *Isochrysis galbana*, 0.45 ml.h^{-1} for *Skeletonema costatum* and 0.12 ml.h^{-1} for *Chaetoceros calcitrans*.

Ingestion and filtration of small inert beads

Ingestion rates are comprised between 2 700 and 26 300 particles per Copepod and per hour. These values increase according to the concentration of beads (Fig. 3). From the data, two models seem adapted to represent ingestion rate (Ib, in number of beads per Copepod and per hour) according to the initial concentration of particles (C_0) : a linear one and a cur-

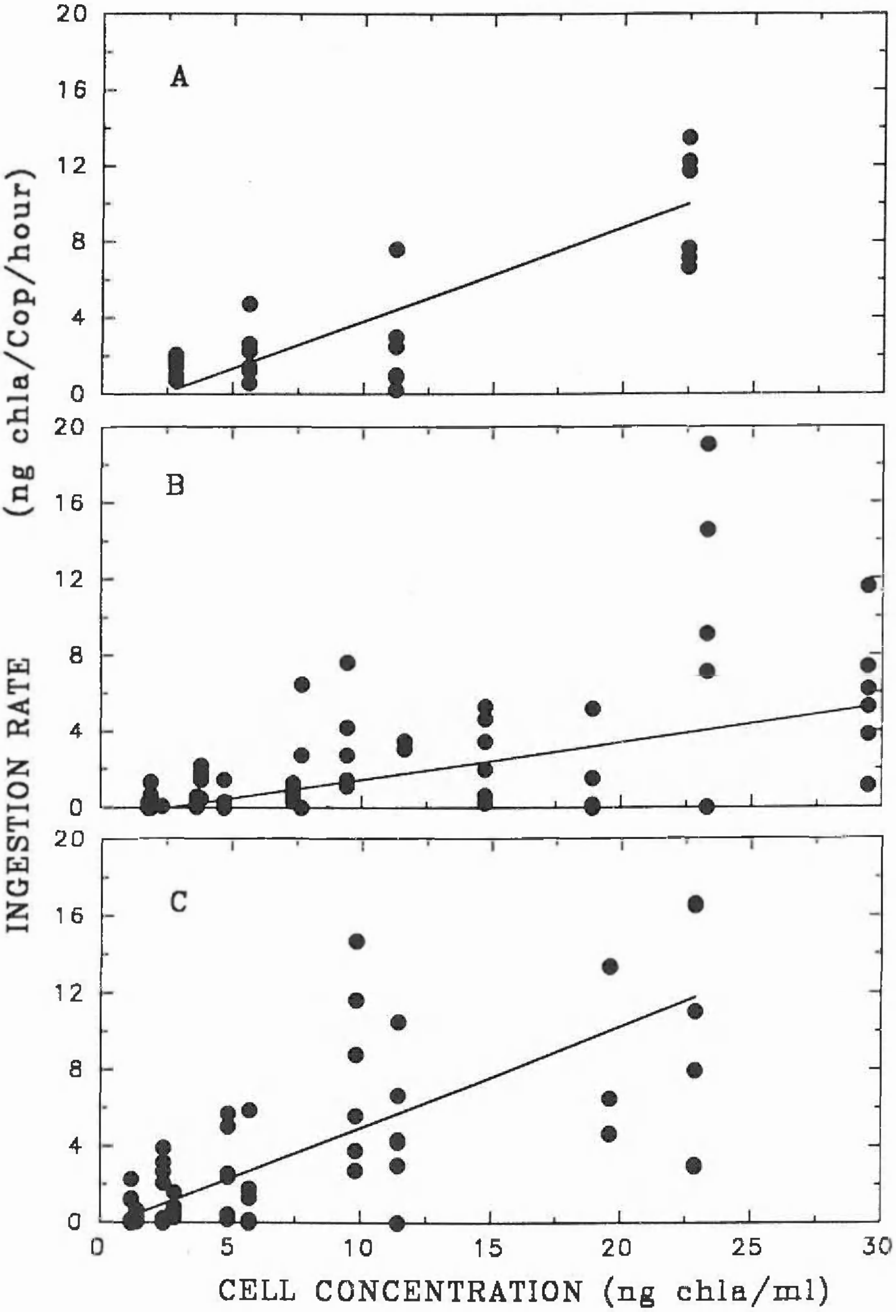

Fig. 1 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Ingestion rate (ng chl *a*.Cop^{-1}.h^{-1}) of Copepods fed with (A) *Isochrysis galbana*, (B) *Chaetoceros calcitrans*, (C) *Skeletonema costatum*.

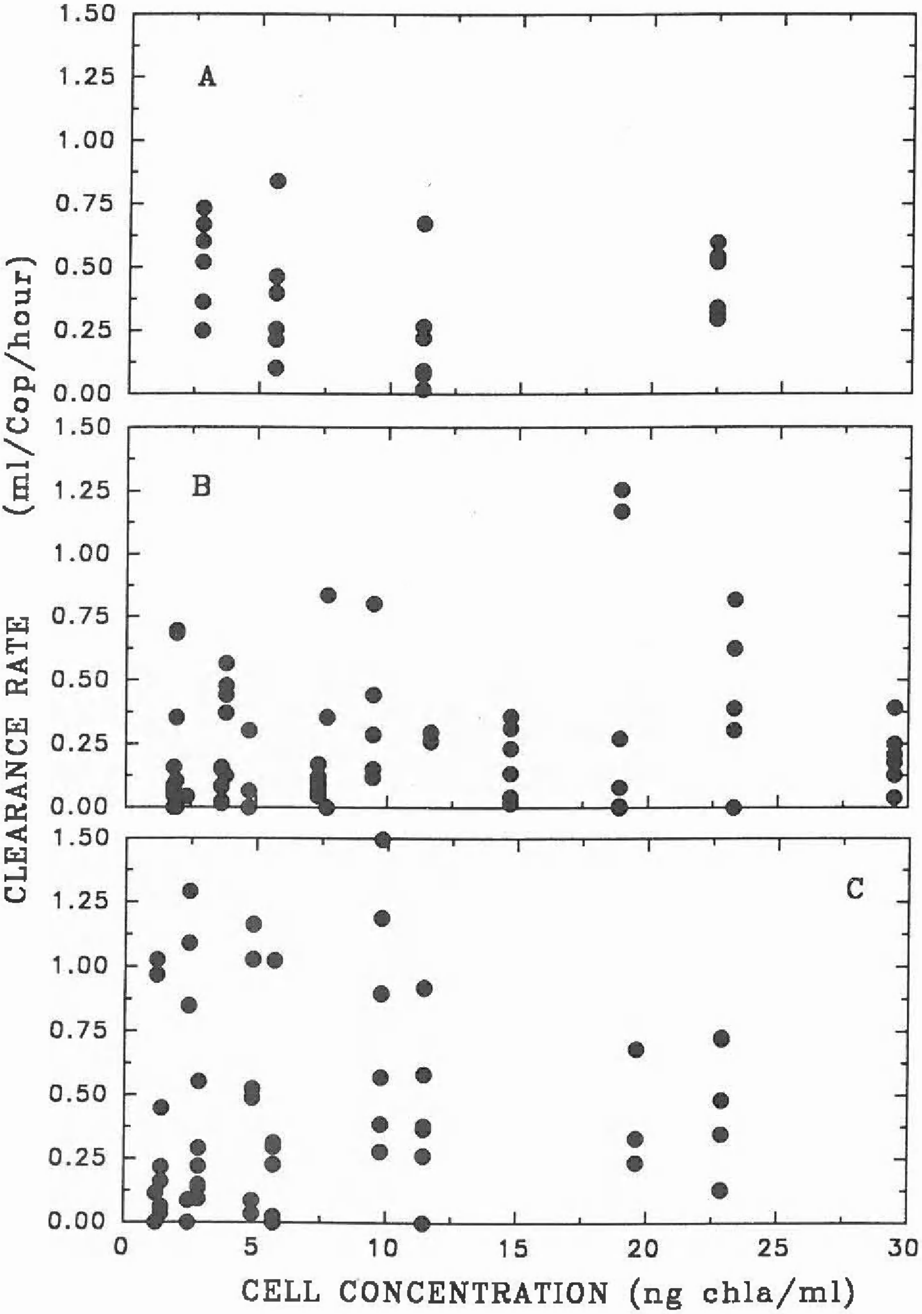

Fig. 2 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Clearance rate (ml.Cop^{-1}.h^{-1}) of Copepods fed with (A) *Isochrysis galbana*, (B) *Chaetoceros calcitrans*, (C) *Skeletonema costatum*.

vilinear one. In our case, the linear model : $I_b = 0.321C_o + 2059.01$ ($r = 0.93$ for $n = 28$, $p < 0.005$) does not reflect the real ingestion of Copepods. Ingestion rate would be greater than 0 for an initial concentration of 0 ($p < 0.005$). Our results show that both models should be used (Fig. 3). For low beads concentrations, the ingestion rate rapidly increases according to a polynomial model : $I_b = 398.86 - 0.87702C_o + 5.0714C_o^2 10^{-4}$ ($r = 0.98$; $n = 11$; $p < 0.005$). The second part of the curve is a line which equation is $I_b = 0.28192C_o + 3856.2$ ($r = 0.91$ for $n = 19$; $p < 0.005$).

The values of filtration rates (F_b) fluctuate between 0.091 and 1.46 ml per Copepod and per hour (Fig. 4). The best correlation is found for the model : $Fb = - 0.036 + 6.0356C_o 10^{-5} + 6.5140C_o^2 10^{-8}$ ($r = 0.96$ for $n = 11$; $p < 0.005$) for the low concentrations. Then the values decrease according to the model $F_b = 48.526C_o^{-0.4626}$ ($r = 0.73$; $n = 19$; $p < 0.005$).

In addition, the models used to explain ingestion and filtration rates for the low values of concentration of beads suggest that ingestion and filtration begin for a concentration of approximatively 500-1 000 beads.ml^{-1} (Fig. 3 and 4).

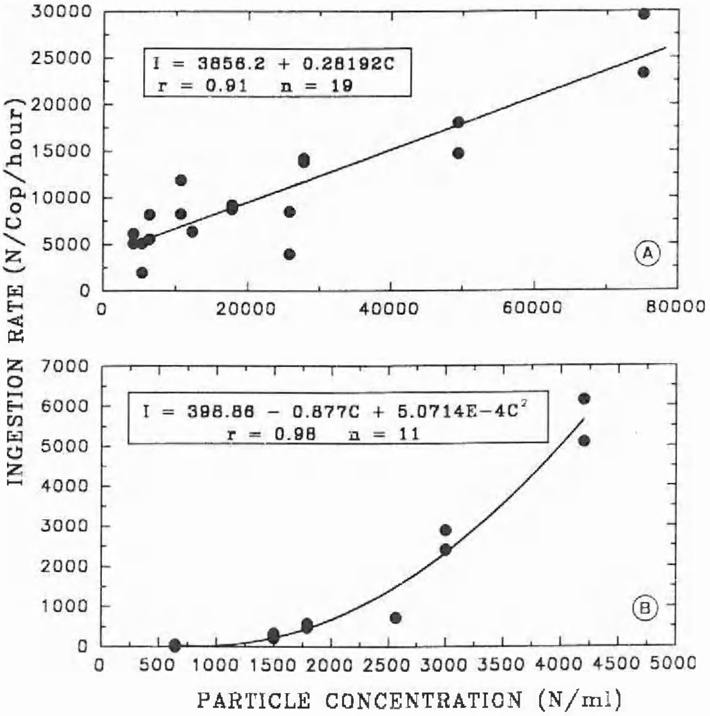

Fig. 3 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Ingestion rate (beads.Cop^{-1}.h^{-1}) when small spheres are offered (5 µm). (A) high concentrations. (B) low concentrations.

DISCUSSION

General aspect of the model of ingestion of small algal cells

In laboratory condition, herbivorous Copepods usually show a pattern indicating an increase of ingestion rates with cell concentration up to a maximal rate which remains unchanged with further increase of algal concentration. These results are shown by numerous authors for different species : *Calanus helgolandicus* (Corner *et al.*, 1972), *Calanus pacificus* (Frost, 1972), *Temora longicornis* (O'Connors *et al.*, 1980 ; Daro, 1985), *Paracalanus* sp (Ambler, 1986), *Centropages hamatus* (Kiorboe *et al.*, 1982), *Neocalanus* sp (Dagg & Walser, 1987), *Eurytemora affinis* (Barthel, 1983). On the contrary, the thresholds are not always observed under natural conditions (Huntley, 1981) and in the laboratory (Deason, 1980).

In the present study, the ingestion rates determined for *Euterpina acutifrons* increase with algal concentration without reaching a plateau. As described by Frost (1972), the plateau is obtained for algal concentrations which increase when the diameter of the cells decreases. Algae used in the present study are small compared to those habitually used in studies or usually ingested by Copepods (Frost, 1972, worked with *Coscinodiscus* sp for

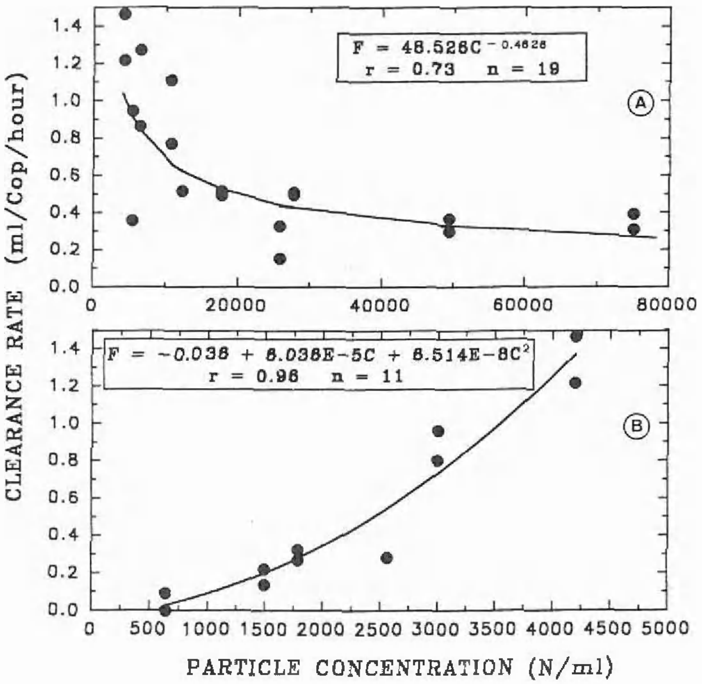

Fig. 4 : *Euterpina acutifrons*. Laboratory experiment (19 °C). Filtration rate ($ml.Cop^{-1}.h^{-1}$) when small spheres are offered (5 µm). (A) high concentrations. (B) low concentrations.

instance). The maximum ingestion rate could have been observed if higher cell concentrations had been used. The increase of ingestion rate according to the cell concentration can be describe with a linear model (Dagg & Walser, 1987) or with a curvilinear model (exponential : O'Connors, 1980). The linear model is the most appropriate to explain the variations of ingestion rates of *Euterpina acutifrons* fed with small algal cells (correlation coefficient always significant : $p < 0.005$).

This direct proportionality between ingestion and cell concentration, can be explained by the feeding behaviour of the Copepods. The feeding activity of planktonic grazers depends on the size of the particles ingested. Every species, and among them every instar, preferentially eats in one range of algal size spectrum (Paffenhofer, 1971 ; Allan *et al.*, 1977 ; Daro, 1985). The Copepods are unselective feeders and filter water when the sizes of the particles are under the threshold bounding these size classes. The linear model is observed for animals searching their food at random and independently of algal concentration. The results obtained in the present work for *Euterpina acutifrons* fit to an unselective feeding (Copepod) on small algal cells.

Filtration of small algal cells

In the present study, the calculation of the filtering rate is based on the measurement of the decrease of the amount of particles during time. This quantity divided by the initial concentration, the duration of the experiment and the number of animals used, gives a volume of water swept clear per animal and per hour. The volume swept clear corresponds to the volume really filtered when Copepods have a filtration efficiency of 100 %.

The concept of filtration efficiency depends on : (i) the morphological characteristics of the Copepods, (ii) the physical characteristics of the fluid, (iii) the movements of the filtering appendages (Hargrave & Geen, 1970 ; Nival & Nival, 1973 ; Rubenstein & Koehl, 1977).

In the case of *Euterpina acutifrons*, the filtration efficiency increases with the size of the algae. For the same algal concentration the amount of algae ingested is higher when animals are fed with *Skeletonema costatum* instead of *Isochrysis galbana*. *Chaetoceros calcitrans* is a particular case. This alga is weakly ingested by *Euterpina acutifrons*, even when its size is intermediate compared to the 2 others algae used in this work. This can be explain by (i) the presence of spines at the surface of the algae which can disturb the ingestion of cells, (ii) a low nutritive quality of the algae (Urry, 1965 ; Poulet & Marsot, 1978 ; Price *et al.*, 1983), which can be rejected by Copepods Huntley *et al.*, 1983. These results are similar to those found by Hargrave & Geen (1970) who demonstrated that *Chaetoceros calcitrans* rejected by Copepods was not ingested by zooplankton.

Thus, the volume swept clear is an underestimation of the volume really prospected by the grazers. It is therefore necessary to keep in mind that the filtration activity of Copepods is greater than the filtration measured with small algal cells. The volume filtered is only an apparent volume which increases, for a same algal concentration, with the diameter of the algae up to the volume really filtered (Nival & Nival, 1973). Thus, the notion of apparent filtering rate (or clearance rate) is more adapted than the one of filtering rate.

In addition, the clearance rate of *Euterpina acutifrons* does not vary with the algal concentration. These results were soon described by numerous authors (e. g. : Schnack, 1979 ; Huntley, 1981). The clearance rate is lower for *Isochrysis galbana* than for *Skeletonema costatum* (larger cells). An increase of filtration efficiency is noticed when the size of the particles offered increases. The very low clearance rate calculated for *Chaetoceros calcitrans* can be explained in the same way as for ingestion rates.

Ingestion and filtration of small inert beads

The very low concentration used in this study allows to investigate the feeding activity of Copepods at low particles concentrations (the lowest concentration of beads utilized correspond to a chlorophyll concentration of 1.04 mg.m^{-3}). The mixed model obtained is made of a polynomial one and a linear one. These results are clearly displayed : (i) Copepods ingest inert particles with no nutritional quality (soon described by Richman *et al.*, 1977 ; Huntley *et al.*, 1983), (ii) in the case of *Euterpina acutifrons*, this ingestion of inert small beads starts over a certain concentration of particles, (iii) these ingestion rates increase proportionally according to the initial beads concentration in the beakers.

In summary, *Euterpina acutifrons* mechanically ingests small size particles (5 µm in this investigation) because ingestion linearly increases with beads concentration ; this result was described earlier by numerous authors (Conover, 1966 ; Cowles, 1979 ; Price *et al.*, 1983). However, this ingestion begins only when beads concentration is higher than 500-1 000 beads.ml^{-1}.

If the nutritional activity of *Euterpina acutifrons* was only a passive phenomenon, we would observe an ingestion even for the very low concentrations and the ingestion would always linearly increase with the concentration of beads. This is not the case : *Euterpina acutifrons* ceases feeding at low concentrations. Therefore Copepod grazing is stimulated by high enough concentrations of beads. This implies only mechanical stimuli and consequently mechanical receptors (Fig. 5). The presence of mechanoreceptors does not preclude the existence of chemoreceptors : they may be here inoperative because beads are not flavored. The stimuli can be detected in 2 ways (Cowles & Strickler, 1983) : (i) Copepods can assess food concentration by moving their feeding appendages (including the mechanoreceptors) so as to propel themselves through the water, (ii) Copepods can cease appendages movements and use the sinking behaviour as a mechanism for scanning the water column.

\- CONCENTRATION OF PARTICLES +

Number of stimuli induces ingestion and filtration		Number of stimuli induces constant filtration
Low number of stimuli Ingestion = 0 Filtration = 0	Ingestion increases : polynomial + linear models Filtration decreases : polynomial model	Ingestion : linearly increases Filtration = constant

Fig. 5 : *Euterpina acutifrons*. Recapitulative table of the feeding behaviour when small beads are offered.

The hypothesis of a break of feeding activity (induced by a high metabolic expense due to a low concentration of particles) requires here the presence of mechanical stimuli : the filtration activity would stop before a critical frequency of stimuli.

The filtration rates decrease very rapidly with the increase of the concentration of beads in the second part of the curve (Fig. 4). They reach a minimum value and remain quite constant. The decrease and the stabilization are probably due to an adjustment of the feeding behaviour. This adjustment can be induced by mechanoreceptors : Copepods scan a large volume of fluid when the concentration of particles is low (but over the threshold described above). When the concentration of beads increases, the quantity of spheres found by Copepods increases and the Copepods filter less and less water until a critical value. This minimum volume of filtered water is determined by a certain concentration of beads in the water. This suggests the existence of a second threshold detected mechanically. This would permit the stabilization of the scanned volume of water when particles are abundant.

As described by Mullin *et al.* (1975), the ingestion increases with concentration to a maximal rate when particles concentration is higher. This is probably due to a saturation of the filtering appendages or to the filling of the gut. This result was not confirmed for the concentrations of particles used in the present work.

CONCLUSION

The results of the present work suggest several answers concerning the feeding behaviour of the Copepod *Euterpina acutifrons.*

. *Euterpina acutifrons* is a passive filter feeder when small algae are proposed. Ingestion linearly increases with algal concentration and does not reach any maximal value for the algal concentrations used in this study.

. The clearance rates are not correlated to algal concentration and remain quite constant.

. The filtration efficiency of the Copepod *Euterpina acutifrons* is greater for *Skeletonema costatum* (size 18 µm) than for *Isochrysis galbana* (diameter : 5 µm).

. The ingestion and clearance rates of *Chaetoceros calcitrans* are very low according to those found for the 2 others algae. This is probably due to a low nutritional value or to the presence of spines on the cells.

. *Euterpina acutifrons* ingests small-size inert particles without any nutritional value. The ingestion increases with beads concentration.

. The ingestion ceases before a minimum threshold of particles in the water. The ingestion increases first according to a polynomial model, then linearly increases. The existence of this threshold implies mechanoreceptors. They stimulate the beginning of the feeding activity.

. The clearance rate decreases according to a polynomial model with concentration of beads until a minimal volume.

. The ingestion threshold suggests 2 hypothesis : (i) Copepods cease their feeding activity when the energy gain is too low, (ii) the break of ingestion constitute a refuge for phytoplankton.

In summary, *Euterpina acutifrons* ingests small algal cells and can be, for instance, a trophic competitor for Bivalve larvae when there are small algae in the water. This Copepod ingests, too, small inert particles which are detected mechanically. These ones can supplement algal diet in the ecosystem, especially in areas where particulate suspended matter is abundant (Sautour, 1991). In addition, the threshold of ingestion (induced by a high metabolic expense due to a low concentration of particles) suggest the existence of a "refuge" for phytoplanktonic species (Mullin *et al.*, 1975). This hypothesis prevents the extinction of phytoplanktonic algal species by grazing.

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Influence of size dependant ^{14}C uptake rates by phytoplankton cells in zooplankton grazing measurements.

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Abstract : C^{14} is currently used to label natural phytoplankton food in zooplankton grazing experiments. Carbon content per unit volume and rate of carbon uptake both decrease with cell size, following different regressions. When working with multi species phytoplankton assemblages, this physiological property results in a disproportional distribution of tracer to phytoplankton carbon biomass. Because most zooplankton organisms select certain sizes of cells, this disproportionate distribution of tracer results in bias of clearance rates determined on the total phytoplankton population with the ^{14}C method.

This paper combines experimentally determined clearance rates of the copepods *A. tonsa* and *T. longicornis* measured on natural particulate matter distributions in combination with theoretical calculations of the ^{14}C clearance rates. It is shown that in these examples, clearance rates measured by the ^{14}C method would underestimate the grazing pressure on the phytoplankton carbon stock by 7 to 24 %.

Résumé : Le C^{14} est couramment utilisé pour marquer le phytoplancton dans les expériences de broutage par le zooplancton. Le contenu en carbone, ainsi que le taux d'assimilation décroissent en fonction de la taille de la cellule suivant différentes régressions. Lorsque le phytoplancton est constitué de plusieurs espèces, cette propriété physiologique résulte en une distribution disproportionnée du marqueur dans la biomasse phytoplanctonique. Comme la plupart des organismes zooplanctoniques sélectionnent certaines tailles de cellules, cette distribution disproportionnée résulte en une estimation biaisée des taux de filtration déterminés sur le phytoplancton total par la méthode au ^{14}C.

Cet article combine des résultats expérimentaux de taux de filtration sur de la matière particulaire totale par les copépodes *Acartia tonsa* et *Temora longicornis* et des calculs théoriques de ces mêmes taux obtenus par la méthode au ^{14}C. Il a pu être montré, dans ces exemples, que les taux de filtration estimés par la méthode au ^{14}C sous-estiment de 7 à 24 % la pression de broutage exercée sur le phytoplancton.

INTRODUCTION

In general, zooplankton grazing studies aim at quantifying the grazing pressure on a phytoplankton population. This flux is usually quantified in carbon, in order to be intergratable in carbon-flow models of the ecosystems studied.

Daro (1978) introduced a version of the ^{14}C method (Nauwerck, 1959) which allows measurement of zooplankton grazing activity on the totality of a natural phytoplankton population. By introducing a high concentration of ^{14}C to the natural water, ^{14}C uptake by the natural phytoplankton population is sufficiently high to allow its quantification in the phytoplankton and the zooplankton feeding on it after one hour already. Since its introduction, the method has been widely applied. Alternations mainly concerned introduction of a prelabelling period for the natural phytoplankton population prior to the introduction of the zooplankton (Roman & Rublee, 1981 ; Baars & Fransz, 1984).

In order for the ^{14}C method to result in a correct measurement of the grazing pressure on the phytoplankton standing stock, it is necessary that the ^{14}C taken up and the phytoplankton biomass (in terms of carbon) are proportionally distributed over the entire size range in which the phytoplankton population occurs. In other words, if one uses the method to determine the grazing pressure of a zooplankton species on a natural phytoplankton population, one assumes that the ^{14}C taken up by the various phytoplankton species is proportional to the contribution of each species to the total phytoplankton biomass. This condition is essential, because most zooplankton organisms are known to feed size - selectively. Especially adult calanoid copepods are known to graze selectively on phytoplankton volume peaks. These volume peaks are generally caused by large - sized phytoplankton species (Poulet, 1973, 1974, 1978 ; Richman *et al.*, 1977 ; Gamble, 1978 ; Cowles, 1979, Tackx *et al.*, 1989).

If the growth rate (= ^{14}C uptake) and carbon content of the cells follow disproportional regressions with cell size, the above conditions are not fulfilled, and a discrepancy will arise between the grazing pressure measured by ^{14}C incorporation and the actual grazing pressure on the stock of phytoplankton carbon.

Banse (1976) has established the relationship between growth and respiration rate of various species of phytoplankton from literature data on measurements performed with cultures grown under identical conditions. His results show that growth rate, expressed per carbon weight of the cel, declines with cell size. An overview of the regressions reported by Banse, 1976 is given in table Ia.

TABLE I

Overview of regressions between a) growth rate and cell carbon and b) cell carbon and cell volume for planktonic phytoplankton species as found in literature with g : growth rate (pgC $cell^{-1}$ hr^{-1}) ; C : cell carbon content (pgC $cell^{-1}$) ; V : cell volume (μm^3 $cell^{-1}$).

a) growth rate : $\log g = b \log C + a$

regr.	b	log a	specification	source
1.	0.94	- 1.25		Banse, 1976
2.	0.87	- 1.08		Banse, 1976
3.	0.94	- 1.19		Banse, 1976

b) cell carbon : $\log C = b \log V + a$

regr.	b	log a	specification	source
4.	0.760	- 0.290		Mullin *et al.* 1966
5.	0.758	- 0.422	diatoms	Strathmann, 1967
6.	0.806	- 0.460	non diatoms	Strathmann, 1967
7.	0.760	- 0.352	diatoms	Eppley, 1974
8.	0.940	- 0.600	non diatoms	Eppley, 1974

The carbon content of unicellular algae has been quantified as a function of cell volume by several authors : Mullin *et al.* 1966 ; Strathmann, 1967 ; Eppley, 1974. An overview of the regressions found is given in table Ib. This paper evaluates to what extent possible disproportional labelling of various cell sizes can result in bias in ^{14}C measurements of zooplankton grazing pressure on natural phytoplankton populations.

MATERIAL AND METHODS

Experimental grazing data obtained from Tackx *et al.* (1989) were used as a basis for the evaluation of potential bias in ^{14}C experiments. These authors performed grazing experiments using the Coulter counter to quantify the grazing activity of adult calanoid copepods *Acartia tonsa* and *Temora longicornis* on natural particulate matter from the Oosterschelde, a tidal inlet in the South - West Netherlands. Besides the Coulter analysis of the total particulate matter in 20 size classes ranging from 3 to 100 µm Spheric Equivalent Diameter (S.E.D.), the phytoplankton in the samples on which grazing was measured, was counted and sized microscopically, allowing to situate the phytoplankton volume distribution within the particulate matter distribution measured by Coulter. This also allowed to quantify the number of phytoplankton cells eaten in each size class (assuming no discrimination between phytoplankton and non-phytoplankton particles within each size class). For details on experimental procedures and calculations, the reader is referred to Tackx *et al.*, 1989.

Because the degree of bias in ^{14}C results will depend on the combination of the size distribution of available phytoplankton and the pattern of selectivity performed by the zooplankton on this phytoplankton distribution, three different situations of natural phytoplankton distributions were chosen : a) a situation where the phytoplankton is concentrated in a narrow peak around 40 µm S.E.D., b) a situation where the phytoplankton occurs in a major peak around 60 µm and a smaller peak around 20 µm S.E.D. and c) a situation with a low concentration of phytoplankton, in which the phytoplankton is distributed more homogeneously among the 5- 100 µm size range, with a peak around 8 µm and one around 30 µm S.E.D. (fig. 1, a, b, c ; after Tackx *et al.*, 1989).

It was shown by Tackx *et al.*, 1989 that on phytoplankton distributions of the type shown in a and b, both *A. tonsa* and *T. longicornis* select the volume peak of the distribution. On phytoplankton distributions of the type shown in c, both copepod species select the peak of larger particles, but at the same time they also feed on the smaller size range. For *A. tonsa*, this feeding on smaller particles is more pronounced than for *T. longicornis*.

The results of a hypothetical ^{14}C experiment carried out on these three samples were simulated and compared with the results obtained in terms of carbon (calculated from the Coulter results) by the following calculations.

$$\mathrm{Ci} = 0.760 \log \mathrm{V} - 0.290$$

$$\mathrm{CT} = \sum_{I=1}^{20} \mathrm{Ci.\,ni}$$

$$^{14}\mathrm{Ci} = 0.87 \log \quad \mathrm{Vi} - 1.08$$

$$^{14}\mathrm{CT} = \sum_{I=1}^{20} {}^{14}\mathrm{Ci.\,ni}$$

$$\mathrm{ICi} = \mathrm{Ii\ Ci}$$

$$\mathrm{ICT} = \sum_{I=1}^{20} \mathrm{ICi}$$

$$\mathrm{I}^{14}\mathrm{Ci} = \mathrm{Ii}\ ^{14}\mathrm{Ci}$$

$$\mathrm{I}^{14}\mathrm{CT} = \sum_{I=1}^{20} \mathrm{I}^{14}\mathrm{Ci}$$

$$\mathrm{Fc} = \mathrm{ITC/CT}$$

$$\mathrm{F}^{14}\mathrm{C} = \mathrm{I}^{14}\,\mathrm{CT}/^{14}\mathrm{CT}$$

with :

Ci : carbon content per cell in size class i (pg ; calculated following regression 5. in table Ib).

CT : total phytoplankton carbon concentration in the sample (pg C ml^{-1}).

^{14}Ci : ^{14}C concentration per cell in size class i after one hour of labelling (pg ^{14}C cell $^{-1}$; calculated following regression 2. in table Ia).

^{14}CT : total ^{14}C concentration in the sample after one hour of labelling (pg ^{14}C ml^{-1}).

Ii : ingestion rate measured in size class i calculated from the Coulter data following Frost, 1972 (nr ind^{-1} hr^{-1}). The assumption was made that all particles consumed are phytoplankton cells. Negative ingestion rates were counted as zero.

ICi : ingestion rate in carbon obtained from size class i (pg C ind^{-1} hr^{-1}).

ICT : total ingestion rate in carbon (pg ind^{-1} hr^{-1}).

$I^{14}Ci$: ingestion rate of ^{14}C obtained from size class i (pg^{14}C ind^{-1} hr^{-1}).

FC : clearance rate on the total phytoplankton biomass on a carbon basis (mlind^{-1} hr^{-1}).

$F^{14}C$: clearance rate on the total phytoplankton biomass calculated on a ^{14}C basis (ml ind^{-1} hr^{-1}).

It was assumed that all cells eaten are entirely consumed, i.e. no sloppy feeding or cell breakage take place, so that all the radioactivity present in consumed cells is measured in the zooplankton.

RESULTS

Fig. 1 d, e, f show the calculated carbon distribution, and the distribution of ^{14}C after 1 hour in experiment a, b and c respectively. These graphs demonstrate the discrepancy between the distribution of the tracer food and the actual stock of phytoplankton.

Table II shows the FC and the $F^{14}C$ values calculated for *A. tonsa* and *T. longicornis* in each experiment.

The $F^{14}C$ values are lower than the FC values in all cases. Expressed as percent of FC values, $F^{14}C$ values vary from maximally 93 to minimally 76 %. In experiments a and b, the percentages calculated for *A. tonsa* and *T. longicornis* are quite comparable, in experiment c, $F^{14}C$ for *T. longicornis* is a considerably greater underestimation of FC (76 %) than $F^{14}C$ for *A. tonsa* (87 %).

TABLE II

FC (ml ind^{-1} hr^{-1}) and $F^{14}C$ (ml ind^{-1} hr^{-1}) calculated for *A. tonsa* and *T. longicornis*.

experiment/species	FC	$F^{14}C$	$F^{14}C$ as % of FC
a) *A. tonsa*	1.18	1.09	92
T. longicornis	1.25	1.16	93
b) *A. tonsa*	0.73	0.62	85
T. longicornis	1.12	0.93	83
c) *A. tonsa*	0.75	0.65	87
T. longicornis	0.76	0.58	76

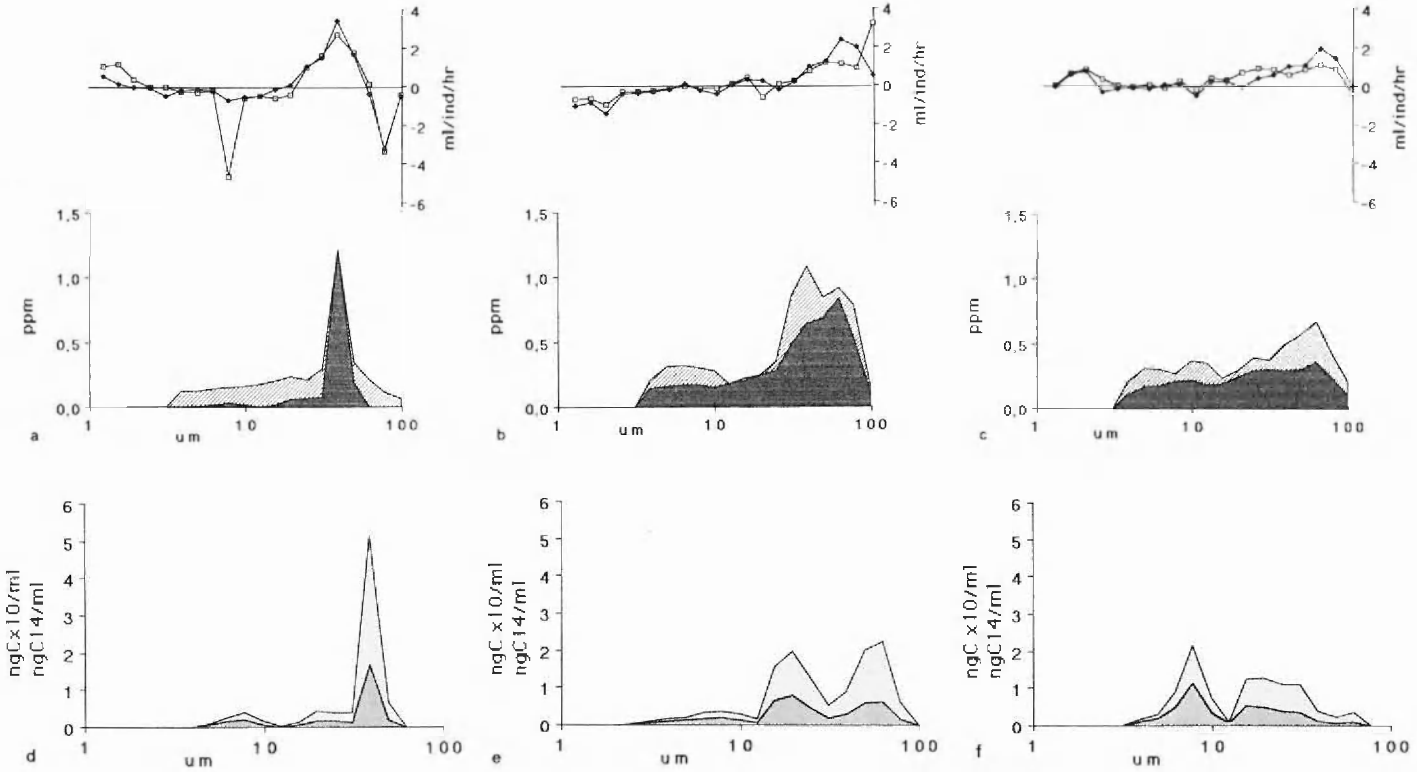

Fig. 1 a, b, c : Size distribution of 3 natural water samples from the Oosterschelde expressed in volume. Total particulate matter (striped, left axis) : phytoplankton distribution (shaded, left axis). Clearance rates measured for *A. tonsa* (open squares, right axis) and *T. longicornis* (black diamonds, right axis) on theses samples (after Tackx *et al.*, 1989). X axis is in logaritmic scale.

d, e, f : Size distribution of phytoplankton carbon (lightly shaded) and ^{14}C taken up after one hour (darkly shaded) in the samples shown in a, b and c respectively. Note that the ^{14}C concentrations are one order of magnitude smaller than the C concentrations.

DISCUSSION

The use of Coulter obtained results in this paper is not meant to suggest that these results are in any aspect a more reliable measurement of copepod grazing activity than those obtained from other methods. The Coulter and microscopical results were merely used as basic data sets on which to evaluate the performance of the ^{14}C method in quantifying grazing pressure on phytoplankton carbon stocks under natural conditions. Theoretical limits to the degree of variation in phytoplankton biomass distribution and selectivity of zooplankton feeding behavior are hard to define within realistic circumstances. Therefore, we have prefered to use experimentally obtained data as a basis to evaluate the possible degree of bias occuring in ^{14}C measurements. The types of distributions used correspond to other (mainly total particulate matter distributions) reported in zooplankton grazing experiments with natural samples (Allan *et al.*, 1977 ; Gamble, 1978 ; Poulet, 1973, 1974, 1976, 1978). The assumption that all particles eaten are phytoplankton has been argumented extensively in Tackx *et al.*, 1989. Even if this assumption is not completely fulfilled, the agreement between clearance rate pattern, and phytoplankton distribution strongly suggests that the amount of phytoplankton cells eaten in each size class is proportional to the concentration of phytoplankton in this size class (Fig. 1 a, b, c). Consequently, the factors of importance to this evaluation would remain within the same proportion and the same type of bias (see below) would occur in ^{14}C measurements.

Regression (2) was chosen from Banses (1976) table 1 because it covers the broadest range of planktonic cell sizes. The formula of Mullin *et al.* (1966) was chosen in accordance to the use of this formula in the paper of Banse (1976).

The results shown in table II demonstrate the dependance of the bias in $F^{14}C$ values on the phytoplankton distribution and the selectivity pattern exerted by the animals feeding on it. The lowest underestimation in comparison with FC occurs in experiment a (7 and 8 % for *A. tonsa* and *T. longicornis* respectively). In this situation, the narrow peak of phytoplankton around 40 µm size, and low concentration of phytoplankton in other size classes necessitates feeding on this one peak. Thus, the disproportionality between the ^{14}C and the carbon distribution is of little consequence, as both *A. tonsa* and *T. longicornis* are feeding in the limited size range where also the bulk of the phytoplankton biomass is situated.

In situation b, the $F^{14}C$ values underestimate FC by 15 and 17 % for *A. tonsa* and *T. longicornis* respectively. In this case both species feed selectively on the peak around 60 µm. Clearance rates (as measured by Coulter) on the second peak of smaller phytoplankton species (around 25 µm S.E.D.) are considerably lower. This second peak has a higher ratio of ^{14}C per unit cell carbon, so that the total amount of ^{14}C taken up by the animals, which is mainly contributed to by the low - labelled big cells, underestimates the proportion of the phytoplankton carbon eaten by 15 and 17 % for *A. tonsa* and *T. longicornis* respectively. In situation c, both *A. tonsa* and *T. longicornis* select cells with a S.E.D. > 40 µm, although the bulk of the phytoplankton volume is situated between 15-40 µm S.E.D. At the same time, both species also feed to a considerable extent on particles in the 10-40 µm size range. In this case the tendency of *A. tonsa* to feed more on smaller particles than *T. longicornis* results in a considerably less important underestimation of the F value (13 as compared to 24 %).

The data presented here show an underestimation of F^{14}C values in relation to FC values in all cases. Theoretically, the inverse could also be found, in case small particles would be preferably eaten (e.g. by young copepod development stages). Allan *et al.*, 1977 have investigated the selectivity of feeding of juvenile *Eurytemora affinis* and *Acartia tonsa* on natural Chesapeake Bay water. They report that selectivity (i.e. the tracking of biomass peaks measured by Coulter counter) starts with the metamorphosis from Nauplius VI to copepodite I. Poulet (1977) also reports peak tracking by copepodite stages CI-CIII of *Pseudocalanus minutus*, although they obtain the bulk of their food from small sized particles (< 20 µm S.E.D.). Feeding of young juvenile stages being little studied, it seems problable that most ^{14}C measurements with copepods tend towards underestimation rather than overestimation of the real grazing pressure exerted on the phytoplankton stock under study. Even in monospecies cultures, a decline of the ^{14}C/C ratio will occur with cell size. As most copepods, including copepodite stages,tend to select the right side of the volume peak (Gamble, 1978 ; Richman *et al.*, 1977 ; Poulet, 1973; 1977; 1978) ; this will result in an (limited) underestimation F^{14}C values.

It should be stressed that this underestimation is inherent to the method, because it results from basic physiological properties of algal communities. It occurs in addition to any other, experimentally induced underestimations which can occur in the ^{14}C method, such as loss of radio activity through cell breakage and egestion (Zhang *et al.*, in press).

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