# 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 $\pm 0.1$ ‰. 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
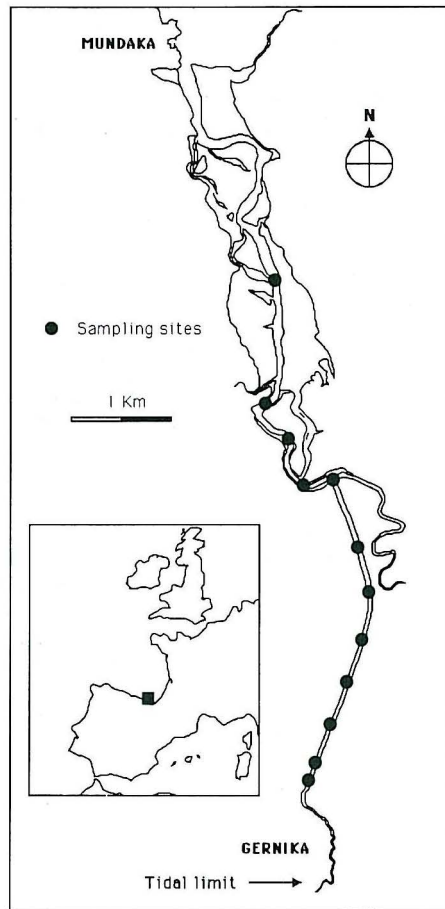
Fig. 1 : Study area showing station positions.

eggs were counted. To calculate densities and to eliminate zero values zooplankton data were expressed as the number of individuals per 1 for organisms collected in the 20 to 200 µm fraction (microzooplankton), and per m³ 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 strati-

fication 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 rela-
tion to salinity (Fig. 3), with absolute maxima of more than $10^3$ individuals.$l^{-1}$ and $10^5$ indi-
viduals.$lm^{-3}$ respectively in waters around 30 ‰. The highest densities of microzooplank-
ton, however, were usually found in waters of higher salinity than those corresponding to
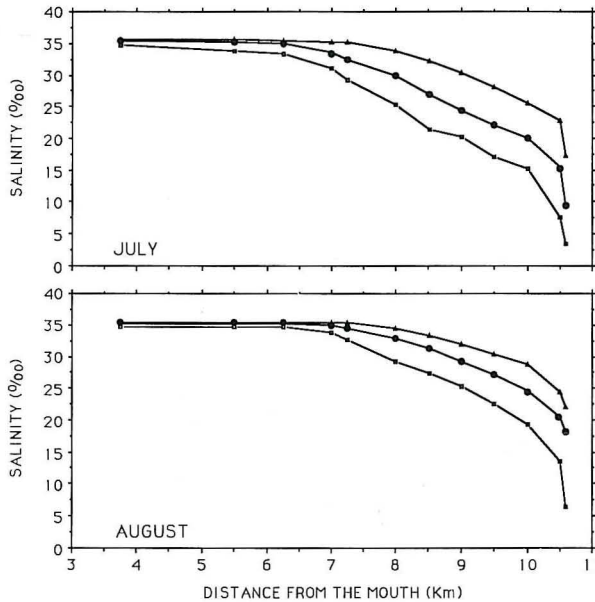the mesozooplankton.



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 frac-
tions, 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 poly-
chaete larvae 19.4 % (49.0-2.8 %). Ciliates and rotifers, which dominated in some micro-
zooplankton samples, only accounted for 2.8 % and 1.3 % respectively. Among mesozoo-
plankton 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*
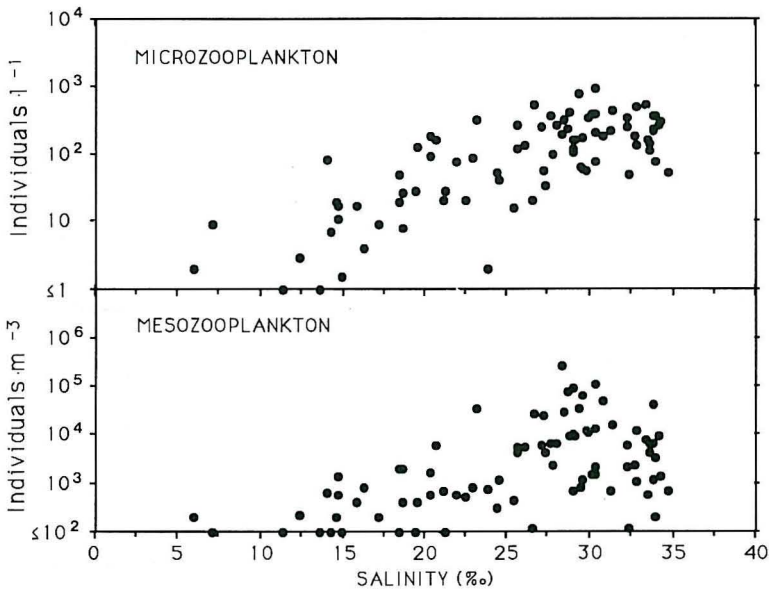and other species of meiobenthic harpacticoids accounted for the rest.

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-
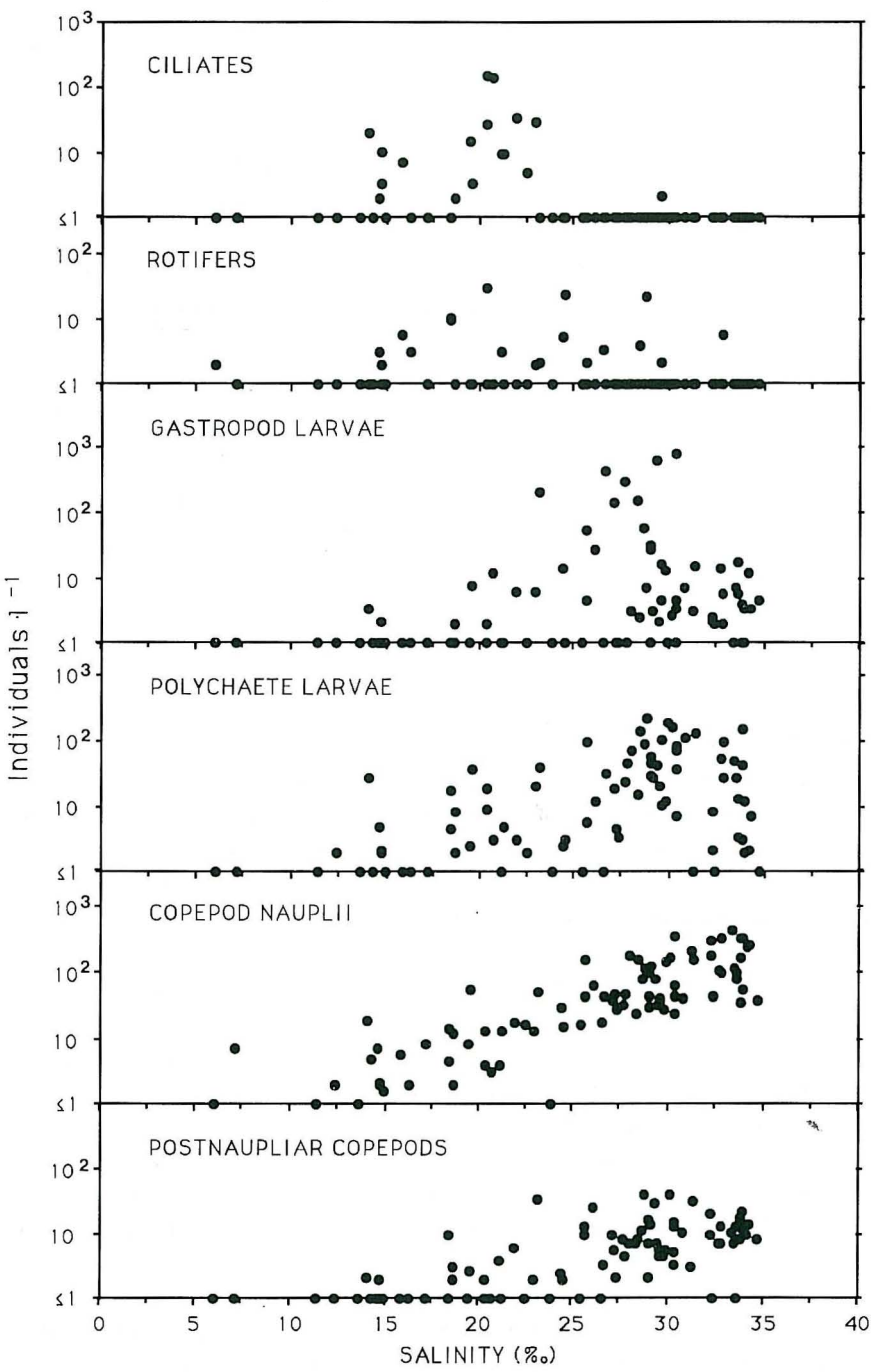
Fig. 4 : Distribution of the main microzooplanktonic taxa in relation to salinity.
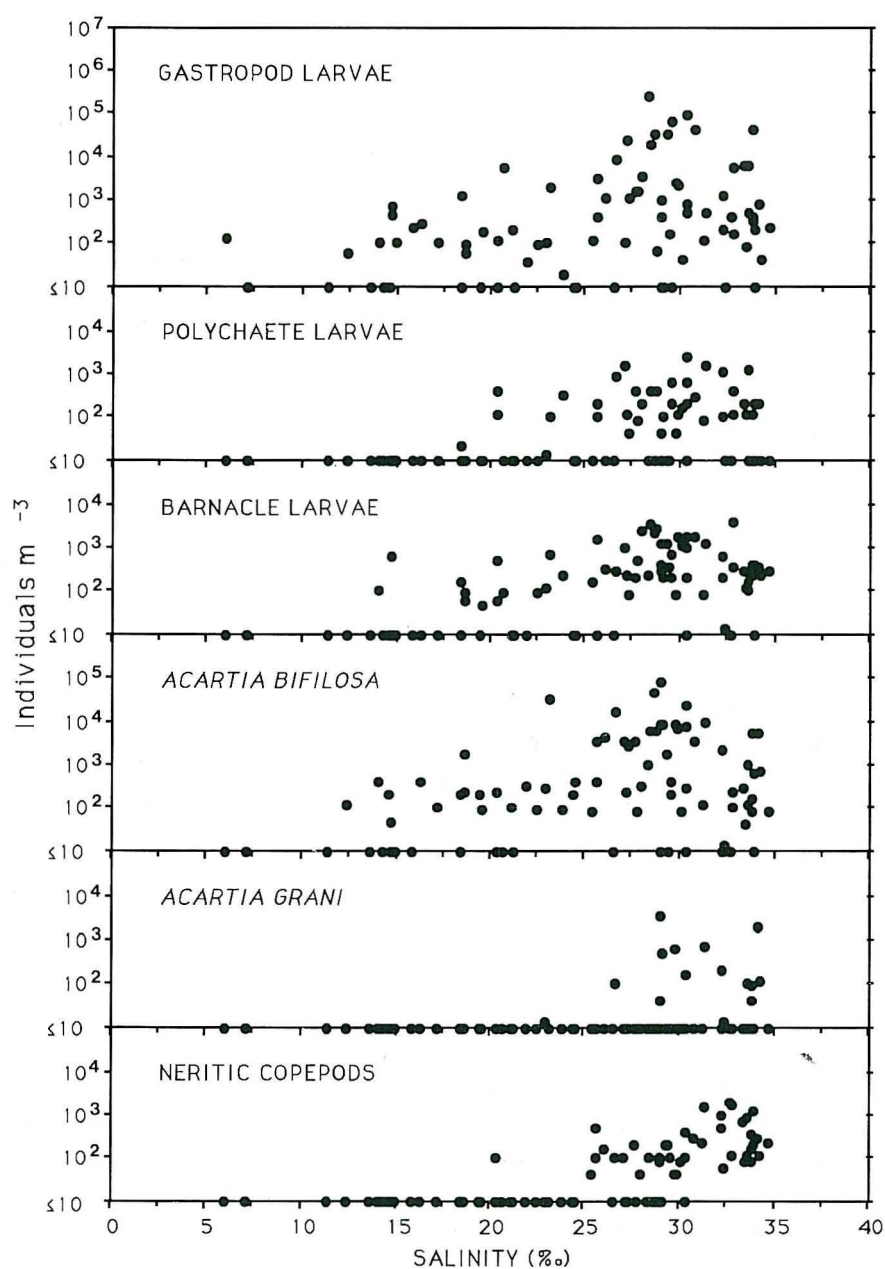
Fig. 5 : Distribution of the main mesozooplanktonic taxa in relation to salinity.

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
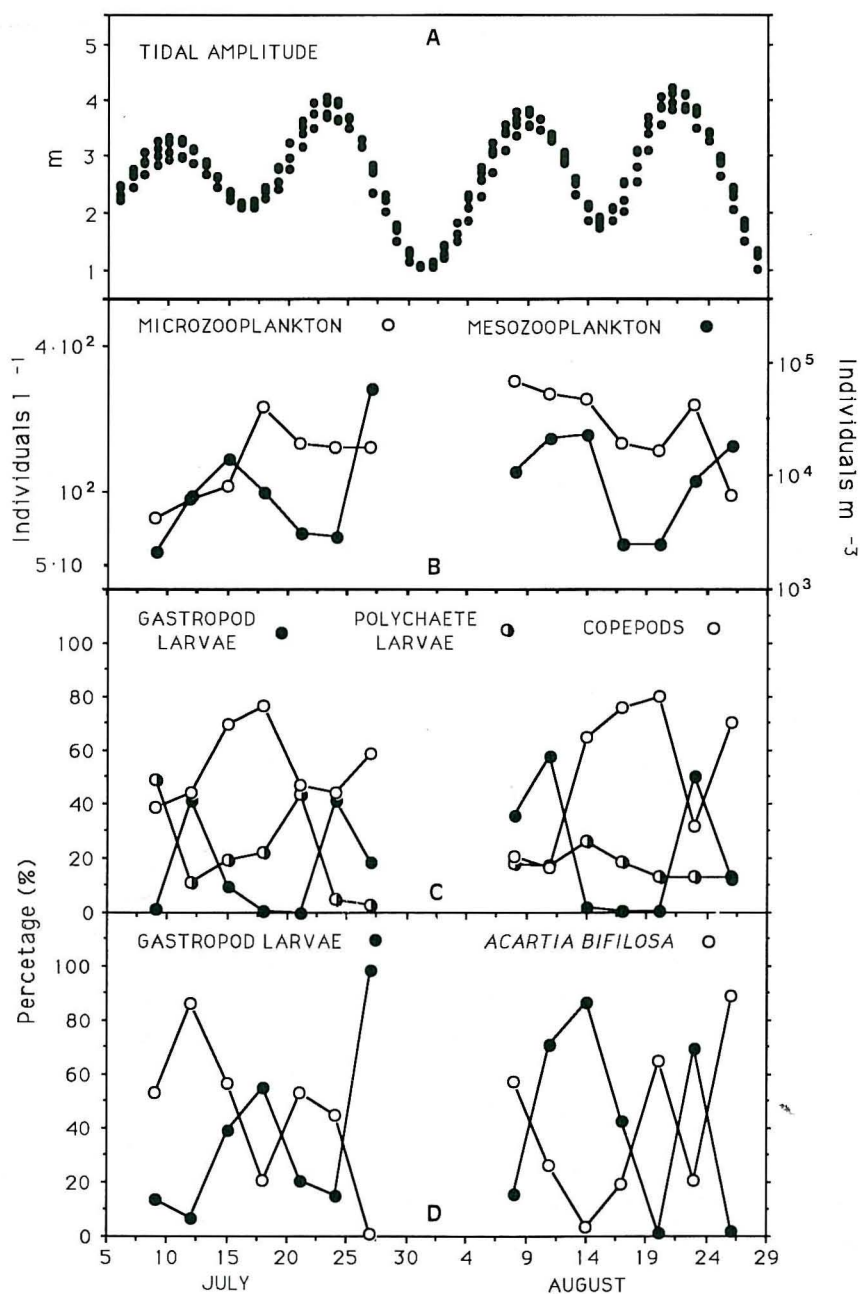
Fig. 6 : Temporal variations of the tidal amplitude (A), the mean abundance of microzooplankton (ind.l⁻¹) and mesozooplankton (ind.m⁻³) (B), and the relative contribution of dominant taxa to the total microzooplankton (C) and macrozooplankton abundance (D).
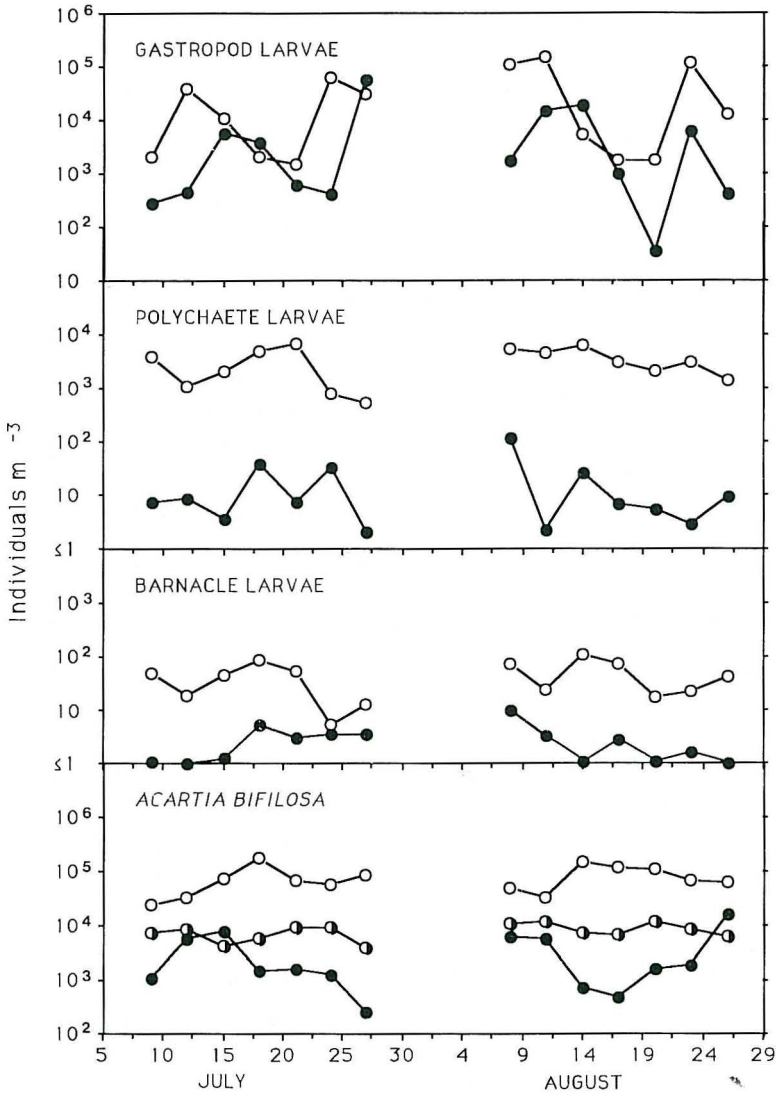
Fig. 7 : Temporal variations of the mean abundance of gastropod larvae (open circles for the microzooplankton and filled circles for the macrozooplankton), polychaete larvae (ibidem), barnacle larvae (open circles for naupliar stages and filled circles for cypris), and postnaupliar stages of *A. bifilosa* 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 (Støttrup *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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