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Zooplankton assemblages in the shallow tidal estuary of Mundaka (Bay of Biscay).

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Abstract : Spatial and temporal variability of zooplankton assemblages were studied in the tidal estuary of Mundaka, from May 1981 to July 1982, in relation to factors controlling estuarine hydrodynamics. Salinity range and maintenance of mixed waters were related to the tidal amplitude and rainfall, which drives river discharge. At high tide, the study zone appeared mainly as a polyhaline system, in which *Acartia bifilosa* was the only perennial component of the estuarine-marine assemblage, and true estuarine copepods (genus *Eurytemora)* were absent. Among neritic holoplankters, *Paracalanus parvus* and *Acartia clausi* dominated and no seasonally stable euryhaline and stenohaline assemblages were found. Among meroplankton groups, larvae of Polychaete Spionids was predominant toward the upper estuary, while Bivalve veligers had the lowest penetration in the estuary from the neritic zone. Some nectobenthic organisms associated with muddy benthic habitats, such as Praniza larvae of *Paragnathia formica* and ostracod Cytherids, characterized the plankton community of the upper estuary during periods of low abundance of estuarine holoplankton. According to the hierarchical clustering of samples from zooplankton data, summer-autumn, winter and spring periods were separated as seasonal units, which also differed with regard to hydrological features. The mixed water persistency and the development of estuarine species were higher in summer, when low freshwater inflows and neap tides coincided. By contrast, high-salinity waters and neritic zooplankton filled the estuary in spring by the effect of spring tides coupled with low freshwater inflows.

Résumé : La variabilité spatio-temporelle du zooplancton a été étudiée dans l'estuaire de Mundaka pendant 14 mois (mai 1981 - juillet 1982 en fonction des facteurs qui règlent l'hydrodynamisme. Les variations de la salinité et la persistance des masses d'eau saumâtres ont été mises en rapport avec l'amplitude de la marée et les précipitations, qui gouvernent le débit fluvial. A pleine mer, la zone étudiée apparaît comme un milieu surtout polyhalin, dans lequel *Acartia bifilosa* est la seu le espèce pérennante de l'ensemble estuarien-marin et les copépodes vraiment estuariens (genre *Eurytemora*) sont absents. Parmi l'holoplancton nérétique *Paracalanus parvus* et *Acartia clausi* sont les espèces dominantes et on n'a pas observé d'ensembles euryhalins ou stenohalins temporellement stables. Parmi le méroplancton, les larves de polychètes spionidés prédominent vers l'intérieur de l'estuaire, tandis que les véligères de lamellibranches ont la plus faible pénétration dans l'estuaire. Quelques organismes nectoenthiques provenant des fonds vaseux, principalement des larves pranizes de *Paragnathia formica* et des ostracodes, sont les composants les plus caractéristiques de la communauté planctonique de l'intérieur de l'estuaire pendant les périodes de faible abondance de l'holoplancton estuarien. Suivant le regroupement hiérarchique des échantillons selon les données de zooplancton, les périodes été-automne, hiver et printemps ont été séparées comme unités saisonnières, lesquelles se différencièrent aussi par les aspects hydrologiques. La persistance des eaux mixohalines et le développement des espèces estuariennes atteint son maximum en été, quand le débit fluvial est faible et pendant les marées de morte-eau. Par contre, les eaux marines et le zooplancton néritique envahissent tout l'estuaire au printemps à la faveur des marées de vive-eau et de faibles apports fluviaux.

INTRODUCTION

Among environmental factors influencing the composition and dynamics of zooplankton communities in estuaries, the volume of fresh water inflow, the tidal exchange and the salinity distribution pattern play a predominant role. Given the wide variety of estuaries with regard to the above mentioned hydrological characteristics ; the recognition of different estuary types and the study of zooplankton in relation to its particular environmental properties seem to be useful to the transfer of knowledge on zooplankton dynamics between estuaries of the same type. In this sense, zooplankton composition, zonation and seasonal variations are better documented for large estuaries, while less information is available for small tidal estuaries.

Along the Basque coast there are several estuaries of this type, which are being studied during the last decade. Nevertheless, few works have been focused on brackish water zooplankton : Villate & Orive (1981a, 1981b) reported on the spatio-temporal distribution of copepod and cladocera populations during an annual cycle within the Plencia estuary. D'Elbée & Castel (1982) dealt with total zooplankton composition and distribution from fresh waters to euhaline waters four times in the year in the Adour estuary. San Vicente *et al.* (1988) described midsummer zooplankton composition and distribution in the Orio estuary.

In the Mundaka estuary, a preliminary study of zooplankton community was made as part of a multi-disciplinary ecological study on the valley and estuary of Gernika-Mundaka. Data on species composition, distribution and seasonal variations are shown in a recent paper (Villate, in press). In the present contribution, seasonal and spatial zooplankton assemblages in the Mundaka estuary are differentiated by multivariate analysis techniques and related to environmental conditions throughout an annual cycle. The effect of river discharge -stated from rainfall- and tidal rhythms on the zonation and development of populations will be analysed in an attempt to predict zooplankton dynamics within the estuary.

Study area

The Mundaka estuary (43° 20' N, 3° W) is a mesotidal system about 13 km long, in which intertidal areas form the larger percentage of the total estuarine area. Tidal amplitude ranges from around 4 m at spring tides, to around 1 m at neap tides, and the estimated ratio of tidal prism volume and estuarine water volume fluctuates from 1.89 to 0.90 (Villate *et al.*, 1989). It is barely navigable during low tide but at high tide the average depth ranges from 2 to 5 m depending on tidal amplitude. It remains navigable up to the Gernika channel, a narrow channel through which the study area receives fresh water inputs from Oka stream. The river discharge can be considered low, since mean values of 0.048 $m^3 s^{-1}$ at low-flow periods and 4.8 $m^3 s^{-1}$ at high-flow periods have been recorded.

According to salinity gradients at high tide, five sampling sites were located between the channel and the coastal line (Fig. 1). Three stations were in the inner salt marshes zone and the other two in the outer estuary.

MATERIAL AND METHODS

Sampling was performed from May 1981 to July 1982. Over this period 17 surveys were carried out monthly or at 15 day intervals. Sampling started one hour before high tide at station 1 and finished two hours later at station 5. In February and March 1982, at neap tides, station 1 was not used due to the shallow depth of the water column.

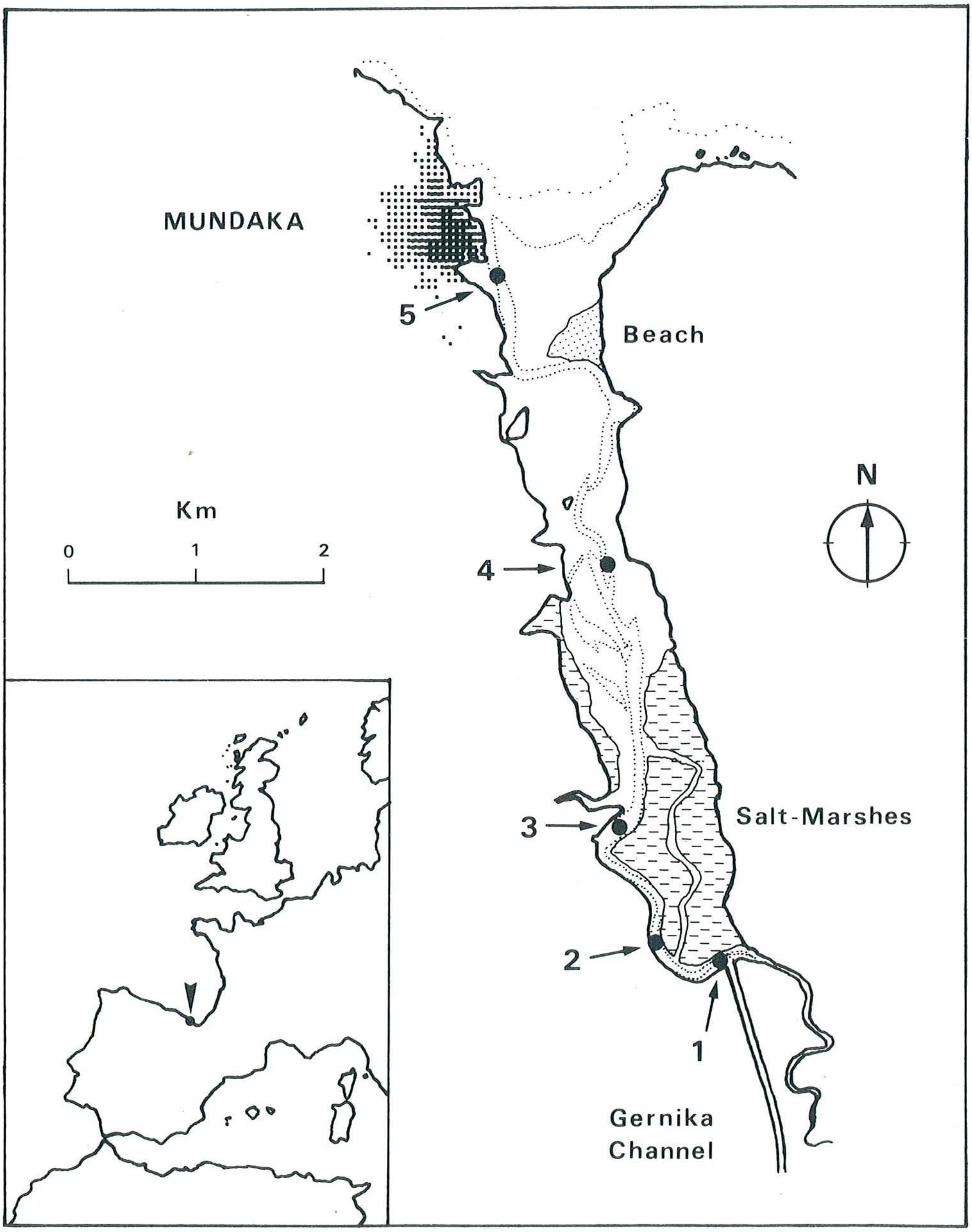


Fig. 1 : Maps of the Bay of Biscay and the study area in the estuary of Mundaka, showing depth contours in meters at low tide and the location of five sampling sites.

To determine salinity, water samples were obtained at the surface and near the bottom with a Van Dorn 6 l bottle. Daily rainfall values were provided by the Meteorological Service of Sondika Airport.

Zooplankton was collected using a mouth-reducing cone net with 35 cm diameter mouth, 1.2 m long and 1.13 m^2 of 250 μm aperture filtering mesh. Two horizontal hauls were carried out at each station, one near the water surface and the other near the bottom. When depth was less than 2 m, only one haul was taken. The net was towed for 5 minutes at a speed of 0.4 $m \cdot sec^{-1}$. Samples were preserved immediately in 5 % borax buffered formaldehyde. The filtered volume of water was estimated from the net mouth area and the haul length. Filtration efficiency was considered to be 100 %. The identification and counting of organisms was done under a stereoscopic microscope. The majority of the holoplankton forms were identified to species level. Among the meroplankton, medusae were identified to species, but the other groups were categorized as class or families.

To relate spatial and temporal variations of zooplankton species and groups to environmental parameters, surface and bottom data were averaged for the water column. Statistical analysis of zooplankton data were performed using the SPAD multivariate analysis package (Lebart & Morineau, 1982). The grouping of samples from zooplankton composition and abundance was made by means of the nearest-neighbor clustering method (Benzécri, 1982). Correspondence analysis was used to associate zooplankton assemblages with sampling sites.

RESULTS

The seasonal pattern of salinity in the estuary is shown in figure 2 in relation to rainfall and tidal amplitude. The highest salinity was found in early spring (April), coinciding with a period of spring tides and little rainfall. The lowest salinity was found in winter, coinciding with neap tides and high rainfall values. In these periods mean values of salinity ranged from 27 to 34 ‰ and from 18 to 23 ‰, respectively. In the summer and autumn periods the salinity range within the estuary were similar (between 21 and 26 ‰). The differences were the summer rainfall and tidal amplitude were low or moderate, while the autumn rainfall remained high and tidal amplitudes were high or moderate.

According to the Venice System for the classification of brackish waters (anonymous, 1959), the study area appeared as a mainly polyhaline system for most of the year.

The cluster of samples in five classes, obtained by means of the similarity analysis (Fig. 3), illustrates seasonal variations rather than spatial ones for the zooplankton community. The similarity between successive cruises was great in winter, from January to March. As can be seen in figure 4, spring cruises (grouped into classes 4 and 5) also show a similarity higher than that observed between summer-autumn cruises (mainly grouped into classes 1 and 2). In general, the analysis leads to the differentiation of three periods throughout the annual cycle : winter, spring and summer-autumn. However, in the latter, the zooplankton community showed less spatial and temporal homogeneity.

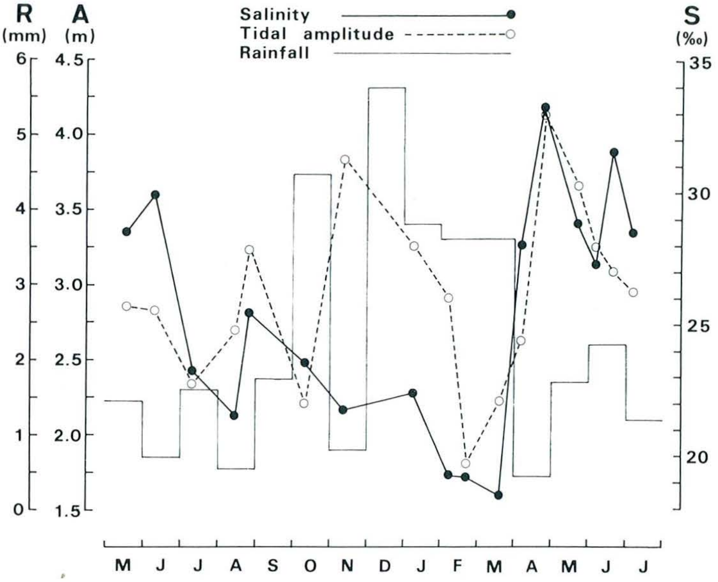
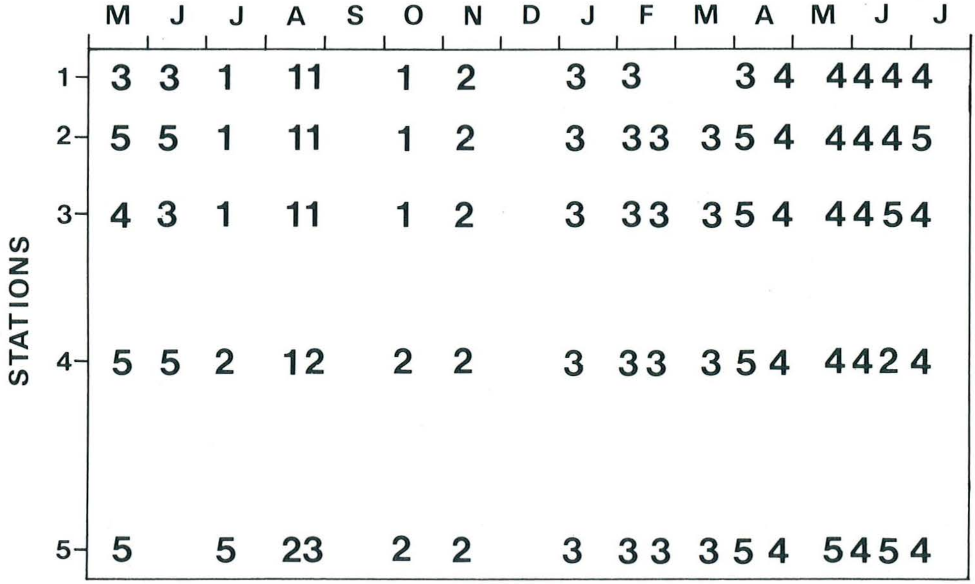


Fig. 2 : Seasonal variations of the average salinity (S ‰), monthly rainfall mean (R) and the average tide amplitude of 4 days before the cruise (A).



STATIONS	M J J A S O N D J F M A M J J
1	3 3 1 11 1 2 3 3 3 4 4444
2	5 5 1 11 1 2 3 33 354 4445
3	4 3 1 11 1 2 3 33 354 4454
4	5 5 2 12 2 2 3 33 354 4424
5	5 5 23 2 2 3 33 354 5454

Fig. 3 : Clustering of samples in 5 classes, according to the hierarchical classification of samples by means of the zooplankton composition.

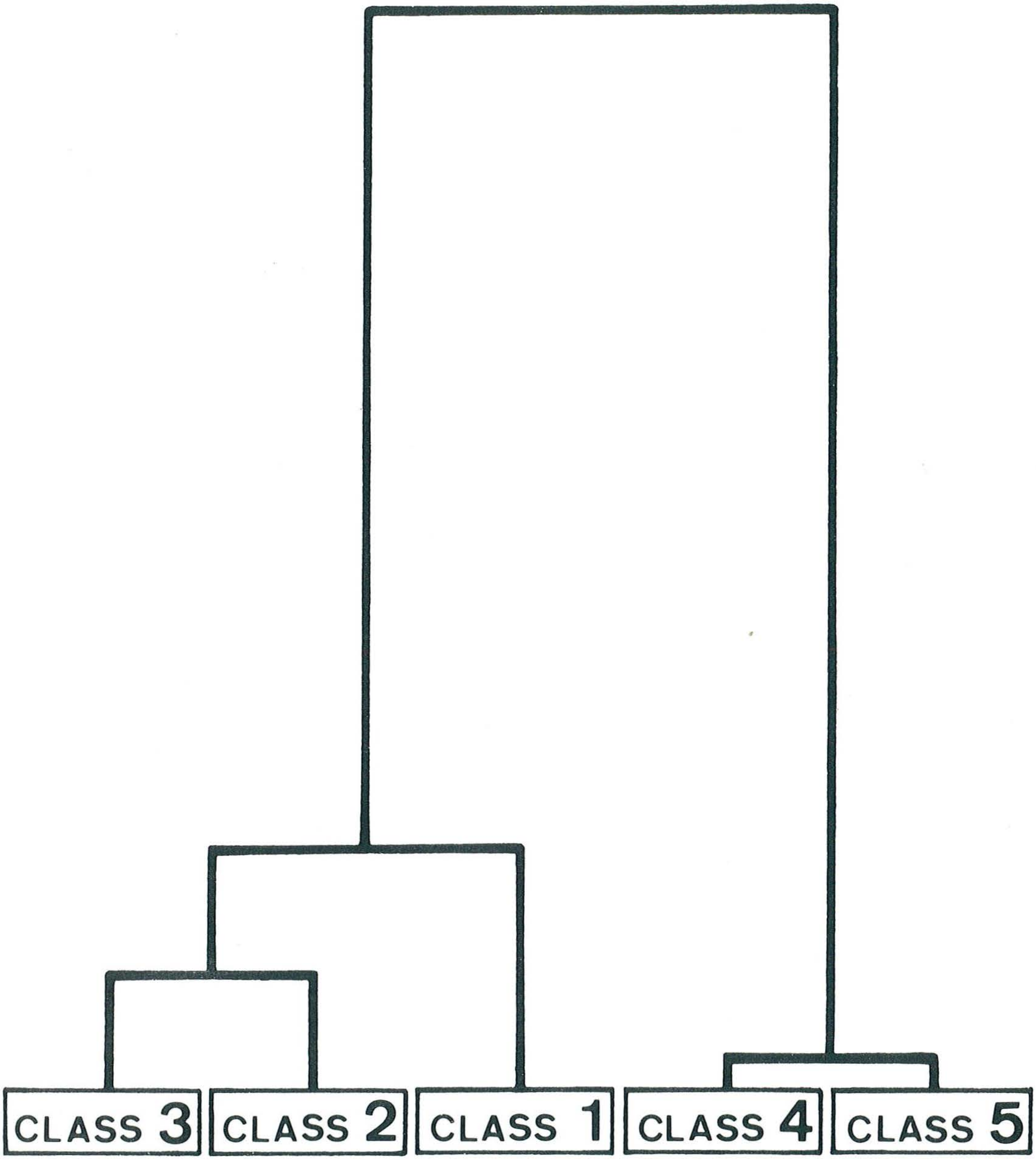


Fig. 4 : Dendrogram of similarity of 5 classes, according to the hierarchical classification of samples by means of the zooplankton composition.

After separating the cruises of the three periods above mentioned to minimize variability due to seasonal changes in the community structure, correspondence analysis was applied to the zooplankton data. The first axis of analysis accounted always for spatial differences along the estuary, while the second and third axis accounted mainly for differences among cruises (Fig. 5-7).

The analysis of summer-autumn cruises (Fig. 5) included 21 zooplankton taxa. In this period the upper estuary was characterized by the copepods *Acartia bifilosa* and *Acartia grani*, while the outer zone was characterized by a varied assemblage mainly consisting of the copepods *Acartia clausi, Centropages typicus, Temora longicornis, Corycaeus anglicus* and *Oithona helgolandica*, the cladoceran *Evadne spinifera*, the chaetognatha *Sagitta* sp (juveniles) and the siphonophora *Muggiaea* sp (mainly *M. atlantica*). Other neritic holoplankters, such as the copepod *Paracalanus parvus* and the appendicularian *Oikopleura* sp (mainly *O. dioica*), did not show as clearly an outward trend as the preceding species. Some meroplankters and nectobenthic organisms such as Praniza larvae of the isopod *Paragnathia formica*, ostracod Cytherids, Barnacle nauplii, Gobid fish larvae and the hydromedusae *Obelia* sp showed an inward trend. Seasonal changes are illustrated along the second axis, with the neritic assemblage of the low estuary characterized by *Sagitta* sp and *A. clausi* in the early summer and mainly characterized by *E. spinifera* in the late summer and autumn. In the innermost zone the estuarine holoplankters (*A. bifilosa* and *A. grani*) were the most representative constituents of the zooplankton community of the early and middle summer and the nectobenthic organisms (Praniza larvae of *P. formica* and ostracod Cytherids) were the most representative constituents of the community of the late summer and autumn.

The analysis of winter cruises (Fig. 6) included 15 taxa. In this period *A. bifilosa* and ostracod Cytherids were the only constituents of the inner assemblage. *A. bifilosa* appeared to be mainly associated with late winter and ostracods with early winter. In the neritic assemblage, Spionid larvae and the copepods *Ctenocalanus vanus* and *Clausocalanos* sp were characteristic of the community of early winter and Foraminifera, Barnacle larvae, *Pseudocalanus elongatus* and *Oikopleura* sp in late winter.

The analysis of spring cruises (Fig. 7) included 28 taxa. In this period *A. bifilosa* was the only constituent of the estuarine zooplankton. Some meroplankters and nectobenthic organisms (mainly Spionid larvae, Praniza larvae of *P. formica* and the hydromedusae *Obelia* sp) showed a clear inward trend in contrast to the majority of the other neritic holoplankters. Among them, the seaward trend was more evident in Foraminifera, *Sagitta* sp, *C. anglicus, T. longicornis, C. typicus, Calanus* sp (copepodids) and *P. elongatus*. The arrangement of samples on the axis of the analysis indicates that during the cruises of April and May 1982 the zooplankton community was very homogeneous within the estuary. This was similar to the community occurring in the low estuary in the other cruises. Temporal variability shown in the second axis was mainly due to meroplankters such as Cyphonaute larvae, Echinoplutei larvae of echinoid Diadematoidea and Spionid larvae, which characterized the April community, and Praniza larvae of *P. formica, Obelia* sp, *Sagitta* sp, *Oncaea media, C. anglicus* and *Euterpina acutifrons*, which characterized the May community.

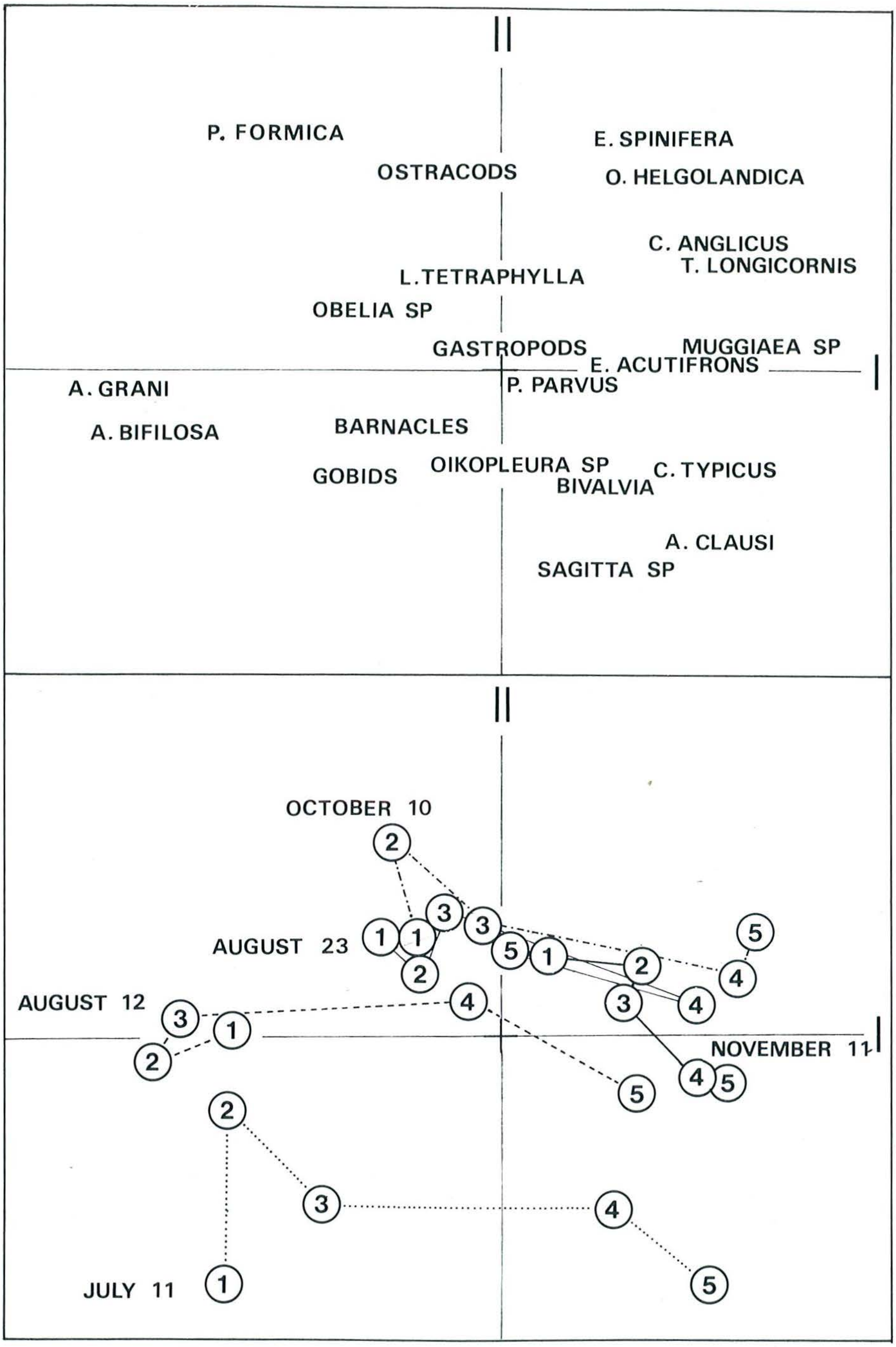


Fig. 5 : Arrangement of zooplankton taxa and samples on the plane of axes I and II on the correspondence analysis for the surveys from July 81 to November 82.

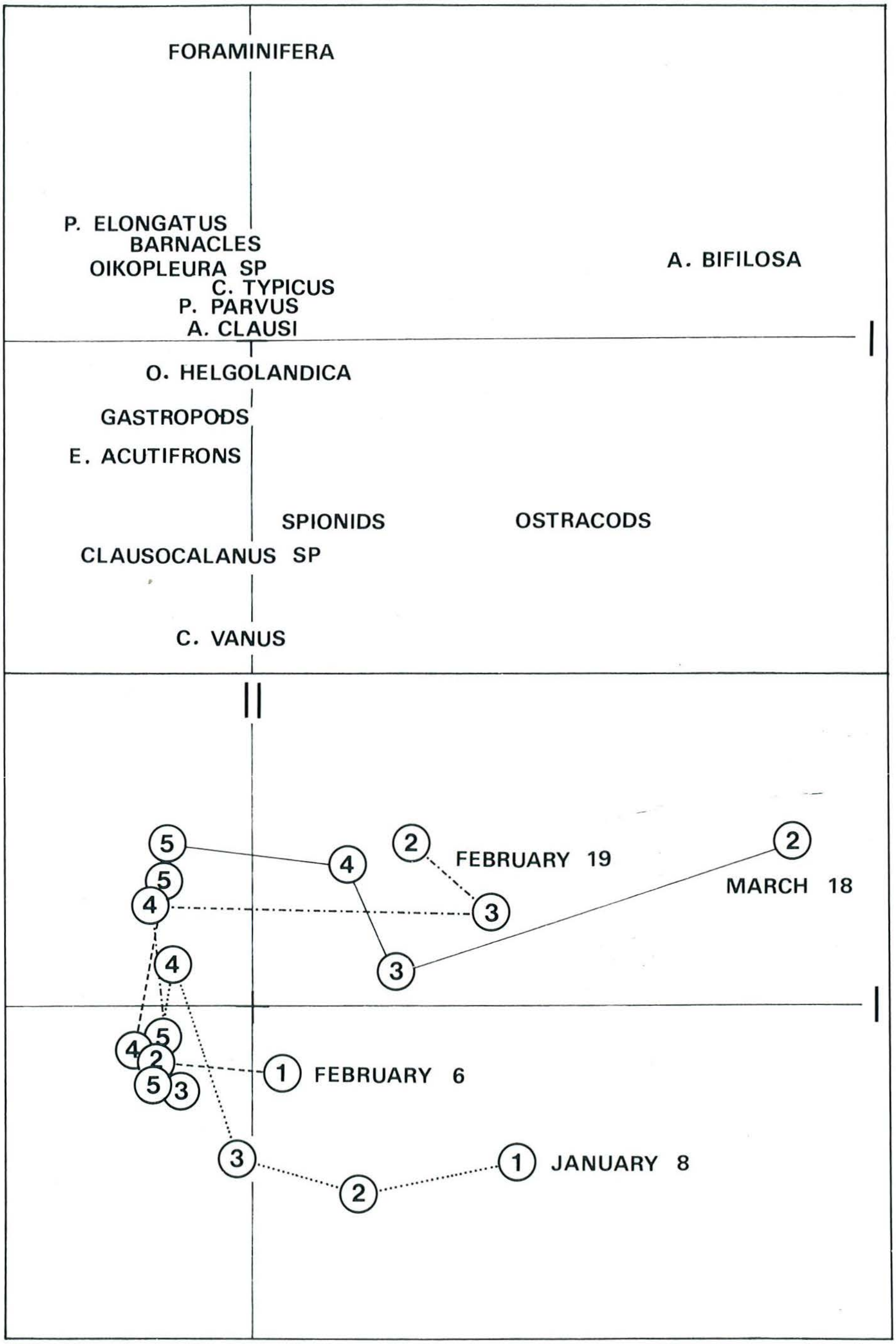


Fig. 6 : Arrangement of zooplankton taxa and samples on the plane of axes I and II on the correspondence analysis for the surveys from January 82 to March 82.

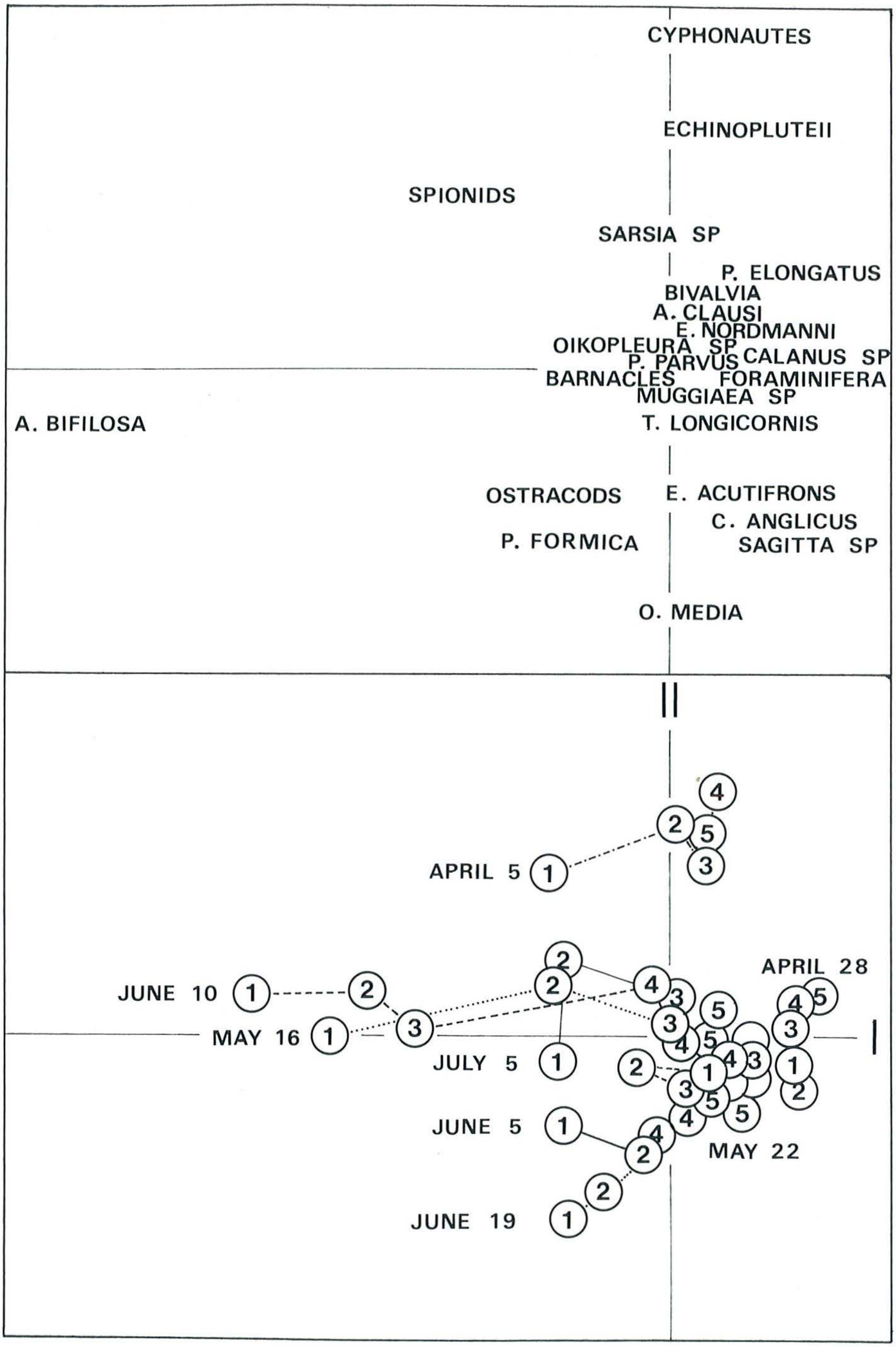


Fig. 7 : Arrangement of zooplankton taxa and samples on the plane of axes I and II on the correspondence analysis for the surveys from May 81 to June 81 and from March 82 to July 82.

The spatial and temporal variations in the abundance of taxa which made a major contribution for the variability of zooplankton community, are shown in figure 8. The species of the inner assemblage *A. bifilosa* and *A. grani* showed maximum densities in summer, *A. bifilosa* in the upper estuary in July and *A. grani* downstream (station 3) in August. The presence of both species were rare in the low estuary. During the annual cycle, *A. bifilosa* remained in the water column while *A. grani* occurred only from late spring to early autumn. Praniza larvae of *P. formica* and ostracod Cytherids were common taxa in the upper estuary. Praniza larvae did not show a well defined seasonal maxima, while Ostracods were clearly more abundant during the summer-autumn period. Spionid larvae occurred in higher numbers in late spring and early summer, and spatially their maxima were found in the middle estuary. The greatest abundance of Barnacle nauplii occurred in the spring and its maxima within the estuary were variable. *P. parvus* and *A. clausi* were the dominant species of copepods in the estuary and both showed maxima in the spring. However, less abundance of *A. clausi* and *P. parvus* were found in the summer-autumn and winter respectively. Although both were usually more abundant in the low estuary, sometimes they appeared in larger numbers upstream from the estuary mouth (station 5). Foraminifera showed maxima in the spring and, spatially its abundance was higher at the estuary mouth. *Muggiaea* sp peaked in the spring and disappeared in the winter. Its abundance decreased considerably in the summer and increased in the autumn. Although *Muggiaea* sp was usually more abundant seaward, in the spring maximum it showed a regular distribution along the whole study area.

DISCUSSION

The seasonal pattern of zooplankton variability explained by the cluster analysis was found to be strongly related to the seasonal pattern of salinity, which appeared mainly as a consequence of rainfall coupled with tidal amplitude variations. Thus, the lower salinities occurring during winter cruises are easily explained by high discharges of fresh water (high rainfall) and relatively low penetration of sea-water (neap tides). The effect of the high river runoff on the salinity within the estuary seemed to be somewhat neutralized by the greater volume of sea water introduced during flood tides (spring tides) in autumn cruises. Although less fresh water (low rainfall) came into the estuary in the summer period, salinity ranges and zooplankton community showed greater similarity with the autumn period than with spring and winter. The relatively low salinity found in summer could be explained by the greater retention time of waters within the estuary, which is favoured by the decrease of river discharge (Bakker & De Pauw, 1975), and the low tidal exchange (neap tides). Moderate or low river discharges coupled with high or moderate sea-water penetration were found to be responsible for the high salinities and great abundance of neritic zooplankton during spring cruises.

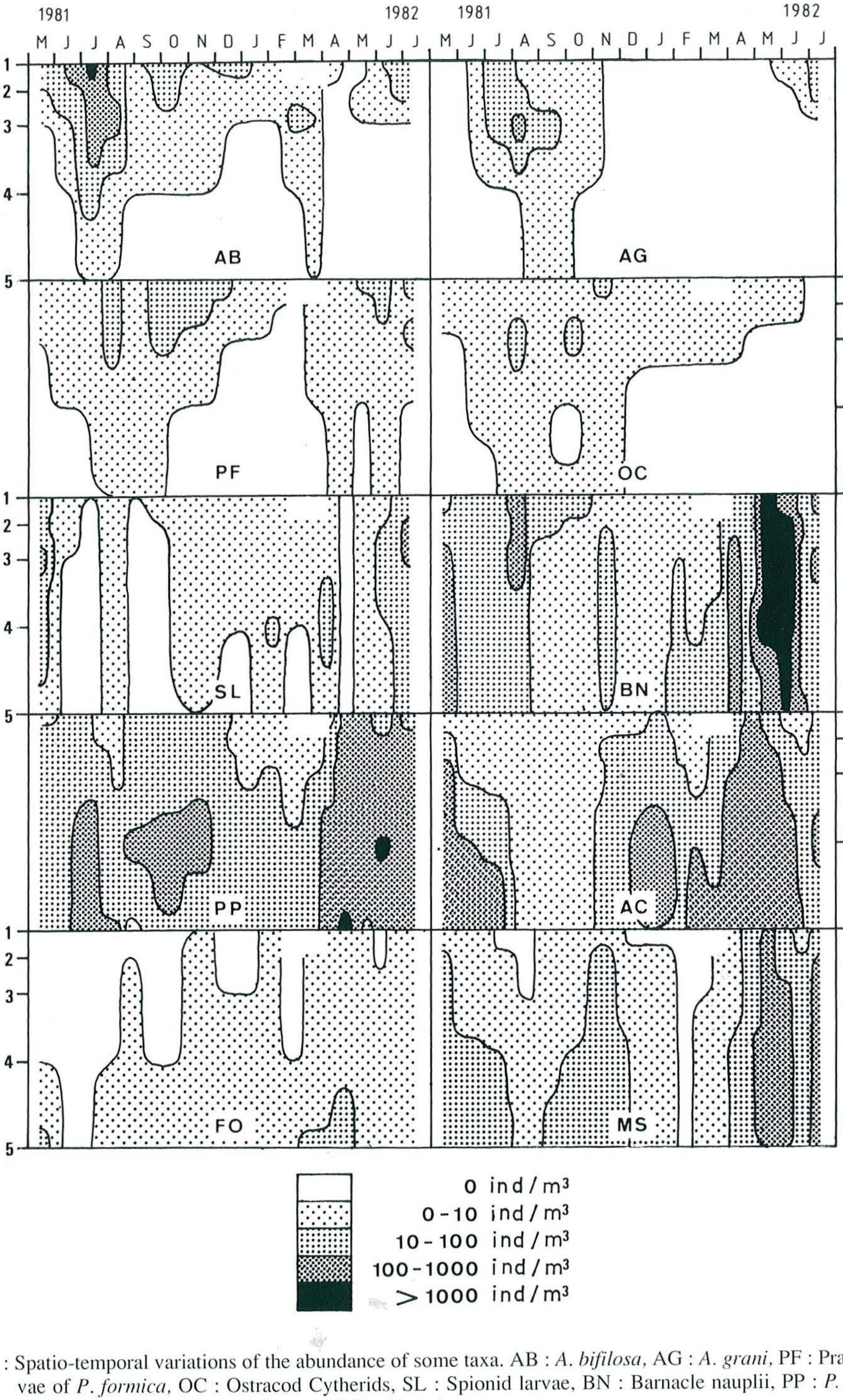


Fig. 8 : Spatio-temporal variations of the abundance of some taxa. AB : *A. bifilosa*, AG : *A. grani*, PF : Praniza larvae of *P. formica*, OC : Ostracod Cytherids, SL : Spionid larvae, BN : Barnacle nauplii, PP : *P. parvus*, AC : *A. clausi*, FO : Foraminifera and MS : *Muggiaea* spp.

Variability of zooplankton along the estuary was mainly accounted for by the spatial segregation of neritic species from *A. bifilosa*, which showed the innermost distribution. This species is included in the estuarine and marine category (Collins & Williams, 1981, 1982) and its distribution in estuaries of northern latitudes is upstream from neritic species and downstream from true estuarine species of the genus *Eurytemora*. *Eurytemora* is a dominant zooplankter in large estuaries such as the Gironde (Castel, 1981). However, *Eurytemora* was not found in the Mundaka estuary, and neither has it been found in the nearby estuary of Plencia (Villate & Orive, 1981 a). The optimum development of *Eurytemora* seems to be in the oligohaline range of salinity, from 0.5 to 5 ‰ (Soltanpour-Gargari & Wellershaus, 1984, 1985, 1986). Also, the maintenance of its populations depends on the estuarine area size occupied by water of the optimal salinity (Jeffries, 1962). Thus, the lack of a wide and permanent body of oligohaline waters could account for the absence of this genus species in small tidal estuaries such as Mundaka.

The seasonal pattern shown by *A. bifilosa* in the Mundaka estuary did not match what was observed in a previous annual cycle in the nearby estuary of Plencia (Villate & Orive, 1981 a). Also, it was for the a different seasonal pattern of salinity found. The annual cycle of *A. bifilosa* described northern European estuary of Ems (Baretta, 1980 ; Baretta & Malschaert, 1988) is just the opposite to the one observed in the Mundaka estuary. In the Ems estuary a seasonal succession of copepods species, mainly caused by temperature, is observed, with *A. bifilosa* appearing as a cold period species. By contrast, in the Mundaka estuary the temporal pattern of this species seems to depend on hydrodynamics within the estuary rather than seasonal variations. Thus, the greatest development of the *A. bifilosa* population was observed in summer, when river discharge and tidal exchange are supposedly low (low rainfall and neap tides). The increase of freshwater inflows (high rainfall) seems to be mainly reponsible for the decrease of this species in autumn and winter. This is an assumption from the fact that optimum development of planktonic organisms in estuaries is only to be expected during periods of small river discharge (Bakker & De Pauw, 1975).

A. grani also appeared, together with *A. bifilosa*, clearly segregated from neritic species, but only occurring during the warm period. The disappearance of *A. grani* in autumn could mean less tolerance by this species of hydrological stress, since it has been considered an indicator species of hydrological stability (Rodriguez, 1979).

According to the spatial segretation of taxa illustrated by the analysis, some non-planktonic organisms such as Praniza larvae of *P. formica* and ostracod Cytherids formed a different group from the estuarine and the marine assemblages. The presence of these benthic or hyperbenthic organisms in water column involves resuspension processes, which may be due to the effects of tides, river flux, meteorological factors (Settlemyre & Gardner, 1977 ; Ward, 1981), and swimming vertical displacements (Alldredge & King, 1985). Thus, their spatial distribution in the estuary seems to depend mainly on the zonation of their benthic habitats, as proven by species of meiobenthic harpacticoids which frequently occurred in plankton samples taken in the Mundaka estuary (Villate, 1984).

Among meroplankton groups, the larvae of polychaete spionids showed the greatest inward distribution, while bivalve veligers constantly showed the clearest outward trend.

This agrees with the segregation pattern for meroplankton groups observed in other estuarine systems (Bakker & De Pauw, 1975 ; Castel & Courties, 1982). Barnacle larvae appeared in major numbers in the inner zone during the summer-autumn period and in the low estuary in winter. As an identification to species level was not made, it has not been possible to determine if the variations are associated with changes of specific composition. Nevertheless, the presence of at least three species of barnacles on the shore-line of the Basque coast (Borja *et al.*, 1982) and the well-defined spawning times, as shown by most of the Barnacle species (Lang & Ackenhusen-Johns, 1981), suggests seasonal variations in the specific composition of the Barnacle larvae.

According to the spatial segregation of neritic holoplankton species shown by correspondence analysis ; the inward trend was mainly represented by *P. parvus* and *Oikopleura* sp in the summer-autumn period, by *A. clausi, P. parvus* and *C. typicus* in winter, and by *Oikopleura* sp, *Muggiaea* sp and *P. parvus* in spring. By contrast, the main taxa of the outward trend were *Muggiaea* sp and *T. longicornis* in summer-autumn, *P. elongatus* and *Oikopleura* sp in winter, and Foraminifera and *Sagitta* sp in spring. Therefore, euryhaline or stenohaline assemblages with a stable specific composition did not appear. Only holoplankton assemblages with great ecological differences maintain an unchangeable and specific composition in the estuary, as which occurred with the assemblages being permanently characterized by *A. bifilosa* and by neritic species.

Seasonal patterns of the dominant holoplankters *P. parvus* and *A. clausi* are well documented in neritic and coastal waters of Basque Country in the years 1976, 1979-1980 and 1981-1982 by Vives (1980), Casamitjana & Urrutia (1982), Villate & Orive (1981a) and Villate (1986). In this area *P. parvus* always shows an annual maximum in the summer or early autumn and *A. clausi* in early spring. However, in the Mundaka estuary both showed maxima in spring, during which the highest salinity waters filled the study area by the effect of spring tides coupled with low river discharges. The lower abundance of *P. parvus* in the summer and autumm seems to be a consequence of the low salinity of the estuary rather than a consequence of the seasonal development pattern of this species.

In conclusion, the Mundaka estuary is mainly a polyhaline system in which true estuarine zooplankton cannot develop. River flows driven by rainfall and tides were found to be the main factors controlling the seasonal development of estuarine-marine populations, and the spatial distribution of estuarine-marine and neritic species within the estuary. This in turn controls the variations of community structure throughout the annual cycle. Given that important fluctuations caused by the variability of river flows from year to year can be expected in estuaries (Carter & Dadswell, 1983), the observed seasonal pattern should not be extrapolated to further annual cycles. However, the spatio-temporal evolution of zooplankton populations within the estuary seems to be predictable with a certain degree of accuracy from rainfall variations and tidal regime.

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