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Comparative spring distribution of zooplankton in three macrotidal European estuaries

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Abstract

The zooplankton of three european estuaries (Ems, Gironde and Westerschelde) was investigated during spring 1992 by means of samples taken along the salinity gradient. The three estuaries are comparable in terms of total area, flushing time and salinity gradient but differ by their level of eutrophication (highest in the Westerschelde), suspended matter concentration (highest in the Gironde) and potential phytoplankton production (highest in the Ems). Copepods and meroplankton dominated the zooplankton in the three estuaries. The dominant copepod species were *Eurytemora affinis* and *Acartia bifilosa.* The distribution of *E. affinis* along the salinity gradient differed between the estuaries. Peaks of abundance were observed at 0 PSU in the Gironde, 6 PSU in the Ems and 9 PSU in the Westerschelde. The downstream shift of the population in the Westerschelde was likely due to anoxic conditions occurring in the oligohaline zone. In the Gironde the downstream distribution of *E. affinis* was limited by the very high suspended matter concentration found in the maximum turbidity zone. Whatever the estuary, the parameters of the population of *E. affinis* and maximum abundance values were similar. However, the influence of the better quality of the available food was suggested in the Ems where individual dry weights and egg production were higher than in the two other estuaries. The influence of a good quality of food in the Ems was confirmed by the development of a large population of *Acartia bifilosa* (as abundant as *E. affinis*) and highest values of adult individual weights.

The meroplankton (essentially Polychaete and cirripede larvae) was much more developed in the Ems than in the Westerschelde and Gironde. This was likely due to the large extent of mudflats and hard substrates in the Ems favouring adult settlement and hence the number of larvae locally produced.

Introduction

In estuaries, the zooplankton community is largely dominated by Calanoid Copepods. Copepod production may be very high (up to 56.2 mg DW m^{-3} d^{-1}, Heinle, 1969) and phytoplankton primary production has been shown to be sometimes too low to support growth of herbivorous copepods (Heinle & Flemer, 1975). In such a case they have to complete their diet with detritus (Heinle & Flemer, 1975; Heinle *et al.*, 1977; Boak & Goulder, 1983).

The distribution of zooplankon taxa in estuaries is classically known to depend on physical constraints: e.g. temperature (Castel *et al.*, 1983), salinity (Gunter, 1961; Jeffries, 1962; Bakker & De Pauw, 1975), flushing and mixing (Soltanpour Gargari & Wellershaus, 1985; Castel & Veiga, 1990). However, the dominant copepod species (*Eurytemora affinis* and *Acartia bifilosa* in the northern hemisphere) are euryhaline and eurythermic (3–30 °C and 2–35 PSU, Castel, 1981) and their distribution could also be affected by biotic factors such as food availability, competition and predation (Bradley, 1975; Burkill & Kendall, 1982; Baretta & Malschaert, 1988).

Meroplanktonic larvae also contribute significantly to the estuarine zooplankton. They often show a marked seasonality related to the breeding activity of the adults living in the benthos (Williams & Collins, 1986). The abundance of the meroplankton moreover depends on the surface of intertidal areas and hard substrates which are colonized by benthic organisms.

The aim of the present study was to compare the distribution of zooplankton in three tidal estuaries: the Ems, Westerschelde and Gironde, showing a clear salinity gradient but differing by their primary production and by the load of suspended particulate matter.

The Ems estuary has relatively low turbidity (100 mg l^{-1}), allowing considerable values of primary production (100 gC m^{-2} y^{-1} de Jonge, 1993). The Westerschelde estuary is less turbid (<100 mg l^{-1}) but supports high amounts of organic pollution which induce an important decrease in dissolved oxygen in the oligohaline zone near Antwerp (Heip, 1989). The average primary production is 50 gC m^{-2} y^{-1} (Soetaert & Herman, 1995). The Gironde estuary is a highly turbid estuary (>500 mg l^{-1}) with a reduced primary production (10 gC m^{-2} y^{-1}, Etcheber, 1986; Lin, 1988).

The spatial and temporal patterns of the zooplankton in the three estuaries are well-known (Baretta & Malschaert, 1988; Soetaert & van Rijkswijk, 1993; Castel, 1981). As expected, the distribution of species is conditioned by the salinity gradient but the abundances of the species are difficult to compare since the authors have used different sampling techniques. In these studies, the importance of chlorophyll content of the water and suspended matter concentration in explaining zooplankton community structure has been assessed but the conclusions are mainly valid for within-site observations.

In the present study samples were taken quasi-simultaneously in the three estuaries during the spring period, i.e. the period of maximum abundance, using the same plankton net. The distribution pattern of the species is related to the salinity gradient and some hypotheses are proposed to explain the general role of feeding conditions on the abundance and biomass of the dominant species.

Methods

Study areas (Fig. 1, Table 1)

The Ems-Dollard estuary (north of the Netherlands) covers an area of about 500 km^2. Freshwater enters the estuary by different sources of which the most important is the river Ems with a mean annual discharge of 125 m^3 s^{-1}. A second freshwater source is the Westerwoldsche Aa river. The water discharge is roughly 10% of that of the river Ems (De Jonge, 1988). The maximal current velocity is 1.5 m s^{-1}. This estuary is well mixed except in the Dollard where a stratification can occasionally be detected. The zone of maximum turbidity (100–400 mg l^{-1}) is observed in the oligohaline region (De Jonge, 1988). Intertidal flats constitute about 36% of the total area of the estuary; in the Dollard they comprise 85% of the surface. The mean water depth in the middle part of the estuary is about 3.5 m; it is much lower (1.2 m) in the Dollard.

The Westerschelde estuary (S. W. of the Netherlands) can be divided into 3 parts: a marine zone (70 km long from Vlissingen to Walsoorden), a central zone (50 km long, from Walsoorden to the river Rupel) and a fluvial zone where the tidal influence is still observed (Peters & Sterling, 1976). The total surface area is about 600 km^2. In the first zone, mixing of the water is intense, while it is only partial in the central zone. The water depth in the navigation channel is 15–20 m. A zone of maximum turbidity (100 mg l^{-1}) is observed close to Antwerpen. The freshwater input due to the river Schelde is about 105 m^3 s^{-1} (Heip, 1989). The maximum current velocity in the brackish zone is 1.65 m s^{-1} (Bakker & De Pauw, 1975). The tidal flats and the salt marshes occupy a surface of 110 km^2 (Oenema *et al.*, 1988).

The Gironde estuary, (S.W. of France) covers an area of 625 km^2 at high water. Freshwater inflow to the estuary is brought by the rivers Dordogne and the Garonne. The mean yearly freshwater discharge is 900 m^3 s^{-1} (Castel, 1993). Maximum current velocity can reach 2 m s^{-1}. The mean water depth is 5–19 m. The waters are partially mixed during low river flow and slightly stratified during high water discharge (Jouanneau & Latouche, 1981). The extent of the intertidal flats are very low (50 km^2) except at the mouth of the estuary. One of the main characteristics of the Gironde is the high turbidity of the water: particulate concentrations of 1 g l^{-1} at the surface and 10 g l^{-1} near the bottom are common values in the oligohaline zone (Jouanneau & Latouche, 1981).

Sampling

As it is difficult to describe zooplankton composition and distribution in terms of geographical location because of the continuous movement of the estuarine water masses, we chose to use salinity as a descriptor of spatial distribution pattern because of its conservative properties (Baretta & Malschaert, 1988). Thus, samples were taken throughout the estuaries along the salinity gradient from 0 to 30 PSU (interval: 3 PSU).

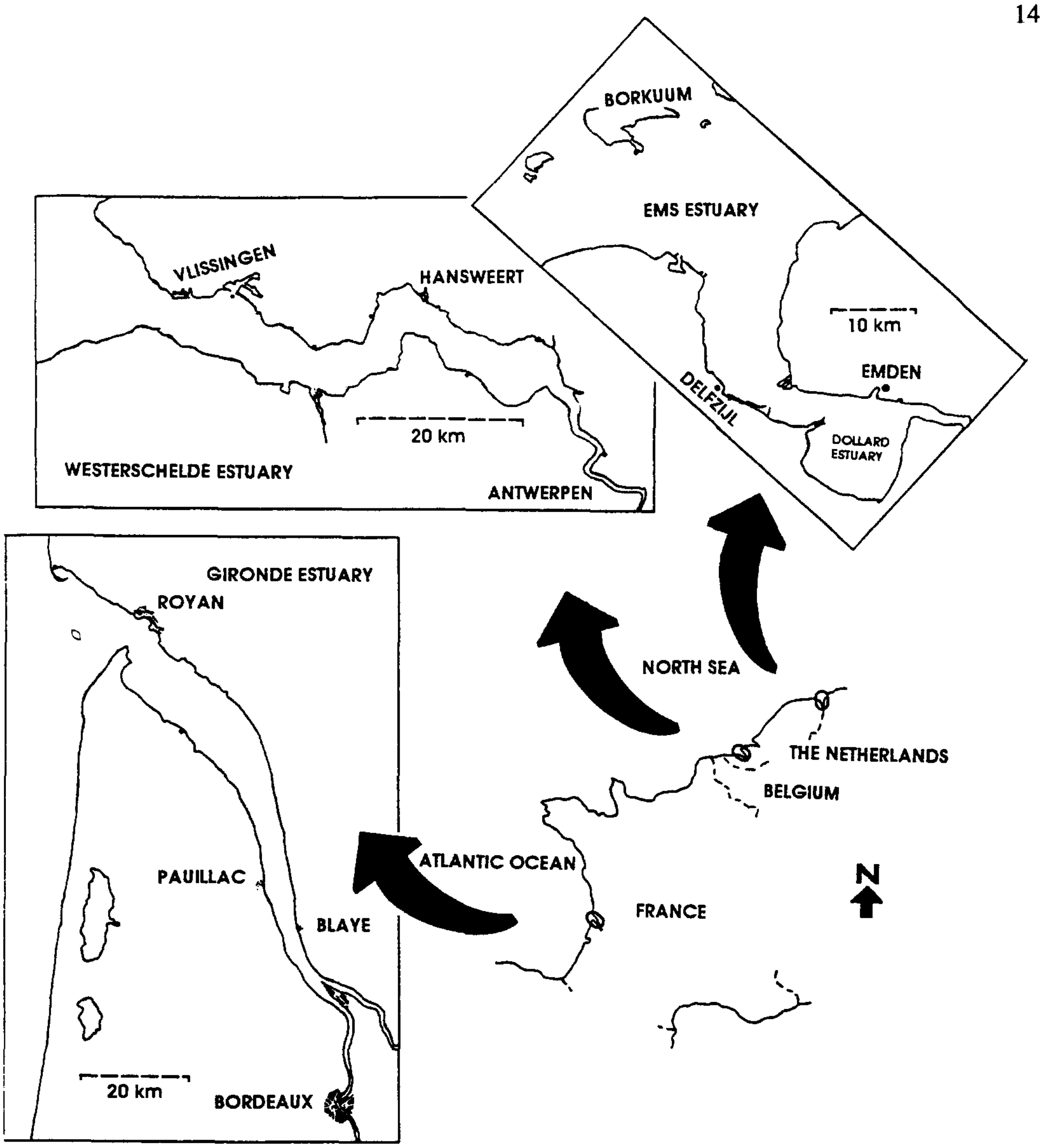

Fig. 1. Geographical location of the sampling areas.

In the Gironde, monthly samples were obtained from March to June 1992. Due to local constraints, sampling was made in March, April and June in the Westerschelde (30 PSU were never sampled), and only in March and May in the Ems. In the Ems and Westerschelde, oblique zooplankton hauls were carried out whereas in the Gironde, surface and bottom samples were taken.

Zooplankton was collected with a standard WP2 net (200 μm mesh size; Fraser, 1966). This mesh size was selected to avoid rapid clogging of the net in these highly turbid zones. Thus, this study only concerns the mesozooplankton. The volume filtered ranged from 4 to 20 m^3 per haul (Hydrodata digital flowmeter, model 438110). Samples were rinsed with filtered estuarine water, concentrated and immediately stored in buffered 4% formalin.

Data analysis

In the laboratory, the different taxa were sorted under a binocular microscope and the developmental stages of the different copepod species were identified and counted. For *Acartia* spp: adults were identified at the species level but the developmental stages were identified at the genus level only. Abundances obtained

Table 1. Average values of the environmental factors suspected to act on the distribution and abundance of estuarine zooplankton. SPM and POC values are given for the maximum turbidity zone. All data from the literature, except temperature. (1) De Jonge (1988,1993), (2) Laane *et al.* (1987), (3) Burdloff (1993), (4) Oenema *et al.* (1988), (5) Heip (1989); (6) Soetaert & Van Rijswijk (1993), (7) Soetaert & Herman (**this volume**), (8) Jouanneau & Latouche (1981), (9) Etcheber (1986), (10) Irigoien & Castel (submitted), (11) Lin (1988).

	Ems	Westerschelde	Gironde
Tidal flat area (km^2)	240(1)	110(4)	50(8)
Tidal flat (% area of the estuary)	51	18	8
Water residence time (days)	38 (1)	75(5)	20–70(8)
SPM conc. (mg l^{-1})	100–400(1)	60–400(3, 6)	500–1000(9, 10)
POC (%)	3.00–4.00(2, 3)	3.50(3, 7)	1.45(3, 9)
Chlorophyll *a* (μg l^{-1})	2–10(1)	4–7(6)	1–8(10)
Production (gC m^{-3} y^{-1})	48(1)	9(7)	<5(11)
Sampling temperature (°C)	6.5–11.8	8.2–19.0	11.0–18.6

from surface and bottom samples in the Gironde were averaged in order to make comparisons with the integrated samples taken in the Ems and in the Westerschelde. Monthly abundances were averaged per salinity zones.

For *Eurytemora affinis* the number of eggs per egg-sac were counted from pools of 30 ovigerous females taken at random in samples representing the maximum peak abundance of the population. Copepodid instars (copepodids CII to CVI) of the two dominating taxa, *Eurytemora affinis* and *Acartia* spp, were counted and weighed. Weight measurements were made on material preserved for at least one month since a storage period <30 d causes variable weight changes (Kulhman *et al.*, 1982). Samples corresponding to the peak abundance of both taxa were chosen for this analysis (*E. affinis*: in April, at 6 and 9 PSU respectively in the Gironde and in the Westerschelde and at 6 PSU in the Ems in May; *Acartia* spp in May, at 9 and 15 PSU respectively in the Gironde and in the Ems and at 18 PSU in the Westerschelde in April). These samples were supposed to be representative of populations having optimal developmental conditions. Copepods were rinsed with distilled water and dried at 60 °C for 24 hours. Three aliquots of 20 individuals of each instar were weighed on a Mettler ME22 microbalance (sensitivity: 0.1 μg). Body carbon weights were obtained by multiplying individual dry weights by a factor 0.4 (Parsons *et al.*, 1977). Total biomass of each instar was calculated by multiplying its individual carbon weight by its abundance. Results are given in carbon weight per cubic meter.

Comparisons between sex ratios, individual dry weights and total biomass were made either with t-test or with non parametric tests (*Wilcoxon-Mann-Whitney test* or *Kruskal-Wallis test,* when the data were not normally distributed or when the homogeneity of variances was not verified).

Results

Gross taxonomic composition and distribution

The zooplankton of the 3 estuaries was divided into the following 3 groups: copepods, meroplankton and other organisms (Figs 2 and 3).

Copepods dominated the zooplankton in the 3 estuaries, particularly in the oligohaline zone (0.5 to 5 PSU, Venice system of classification of saline waters) and mesohaline (5 to 18 PSU) zones. At the limit of the limnetic zone in the Ems and in the Westerschelde freshwater copepods (*Cyclops* spp and *Eudiaptomus gracilis*) were found. Furthermore freshwater cladocerans and the rotifer *Brachionus plicatilis* were observed in the Westerschelde. In the Gironde, the oligohaline zone was only characterized by *E. affinis*, while the species was quite absent in the Westerschelde at lowest salinities.

E. affinis developed in the mesohaline zone of the Ems and Westerschelde, when its abundances decreased drastically in the Gironde. In the Ems, *A. bifilosa* and meroplankton (polychaetes) were also abundant in this zone. Some neritic taxa appeared spo-

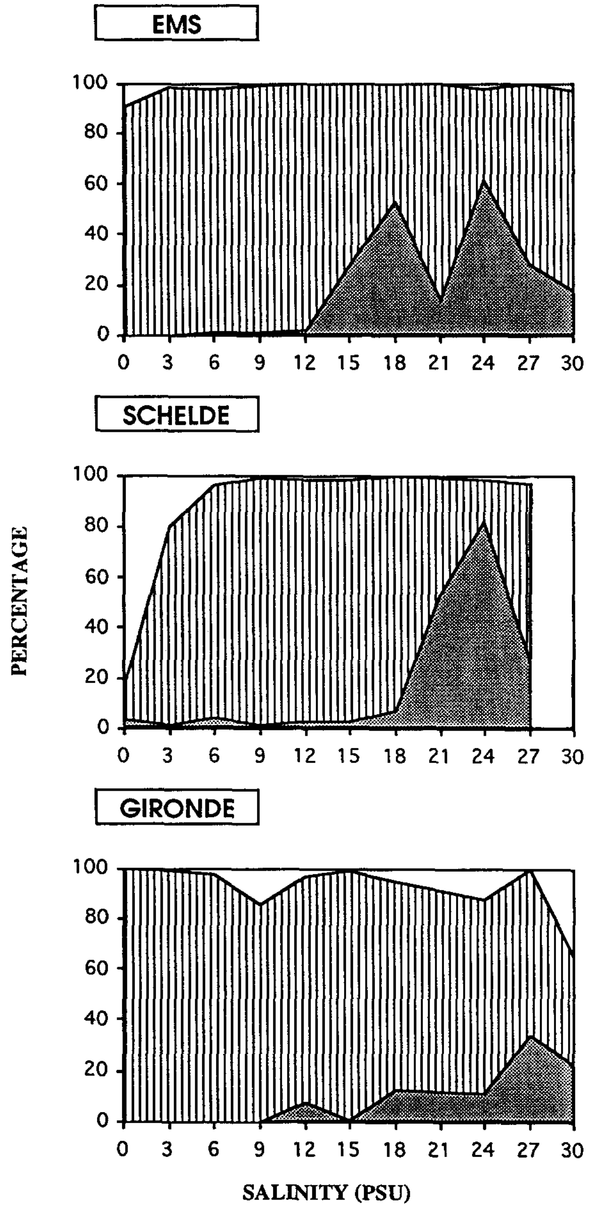

Fig. 2. Relative abundance of copepod (hatched) and meroplankton (grey) communities as a function of salinity in the 3 estuaries during spring 1992.

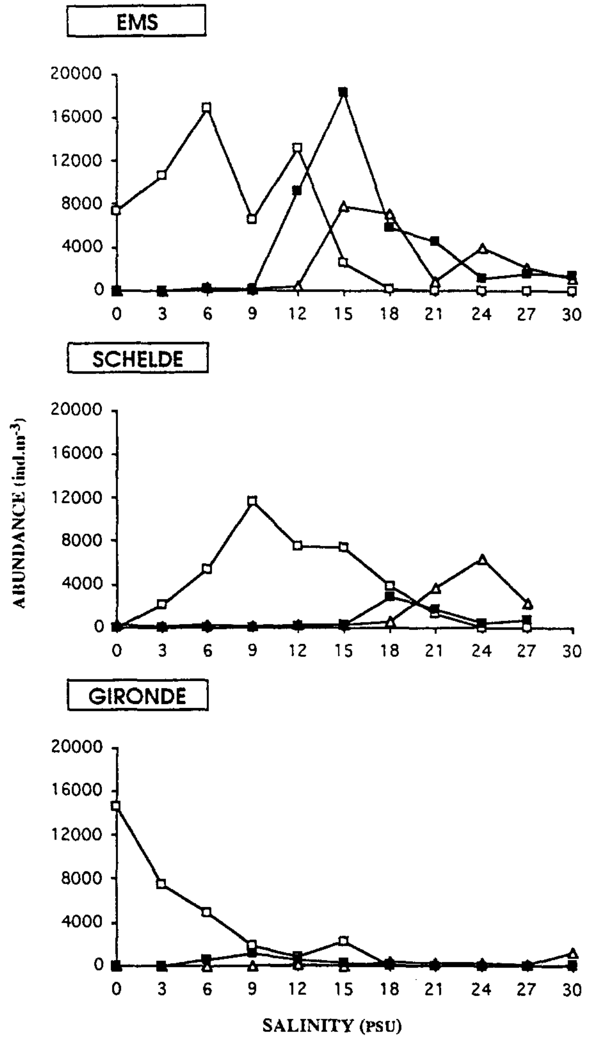

Fig. 3. Eurytemora affinis (-□-), *Acartia* spp (-■-) and meroplankton (-△-) abundances as a function of salinity in the 3 estuaries during spring 1992.

radically in the mesohaline zone of the three estuaries: cnidaria, ctenophora (over 12 PSU in Westerschelde and 15 PSU in the 2 other estuaries) and the cladoceran *Podon* sp (over 12 PSU in Ems and Gironde).

The polyhaline zone (18 to 30 PSU) was further characterized by neritic copepods and meroplankton. Copepod abundance was variable (maximum values: 3800 ind m^{-3} in the Ems, 2300 ind. m^{-3} in the Gironde and 5100 ind m^{-3} in the Westerschelde) and their penetration into the estuaries differed from one estuary to the other. These allochtonous species could be divided into 2 groups. The first one was composed of euryhaline copepods (*Centropages hamatus*, *Temora longicornis*, *Paracalanus parvus*, *Pseudocalanus elongatus*, *Euterpina acutifrons*) and the second one was composed of more oceanic copepods (*Oithona helgolandica*, *Calanus helgolandicus*, *Oncaea* spp, *Corycaeus* spp). This second group, plus *E. acutifrons*, did not penetrate in the Westerschelde during spring. The dominating species of the neritic community in the 3 estuaries were always *C. hamatus* and *T. longicor-*

nis. The meroplankton was dominated by polychaete and cirripede larvae and its importance varied between estuaries (Figs 2, 3). The cirripedes were characteristic from 24 to 30 PSU in the Ems and from 21 to 27 PSU in the Westerschelde. At the highest salinities, the Gironde estuary was also characterized by the cladocerans (*Podon* sp) and the Ems also by Gastropod and bivalve larvae.

On average, the most important zooplankton assemblage was constituted by copepods: essentially *Eurytemora affinis* and *Acartia* dominated (*Acartia bifilosa* dominated below 18 PSU and was accompanied by *A. discaudata* and *A. clausi* at higher salinities). Peak abundances of *E. affinis* were in the same order of magnitude in the 3 estuaries: 16800 ind. m^{-3} in the Ems, 14500 ind m^{-3} in the Gironde and 11500 ind m^{-3} in the Westerschelde. Contrarily, the maximum abundance of *A. bifilosa* was much higher in the Ems (18200 ind m^{-3}) than in the 2 other estuaries (1100 ind m^{-3} in the Gironde and 2800 ind m^{-3} in the Westerschelde).

Eurytemora affinis

The peaks of abundance were not observed at the same salinities in the 3 estuaries: 0 PSU in the Gironde, 6 PSU in the Ems and 9 PSU in the Westerschelde. In addition, this species occurred in a wider range of salinity in the Ems and in the Westerschelde than in the Gironde (Fig. 4). The abundance peaks (Fig. 5) were mainly due to the young instars (copepodids CII and CIII), particularly in the Ems. Downstream and upstream the abundance peaks, aged instars (copepodids CIV to CVI) dominated. In the 3 estuaries, the average sex ratio (males/females) calculated for copepodids V was lower than the one determined for adults ($p = 0.05$ *t*-test, in the Ems and Westerschelde, n.s. in the Gironde). The global values (CV + CVI) calculated for the Ems (0.79, SD = 0.60) and the Westerschelde (1.06, SD = 0.65) were not significantly different (*t*-test). The sex ratio determined in the Gironde (1.52, SD = 0.44) was significantly higher ($p = 0.05$) than that determined in the Ems. The highest abundance of ovigerous females were observed downstream the peak of the population in the Gironde and in the Westerschelde; in the Ems their distribution was wider. The highest values of fecundity were found in the Ems estuary (37 eggs $female^{-1}$ SD = 13) and lowest in the Gironde estuary (14 eggs $female^{-1}$ SD = 8); values obtained in the Westerschelde were intermediate (27 eggs $female^{-1}$ SD = 5).

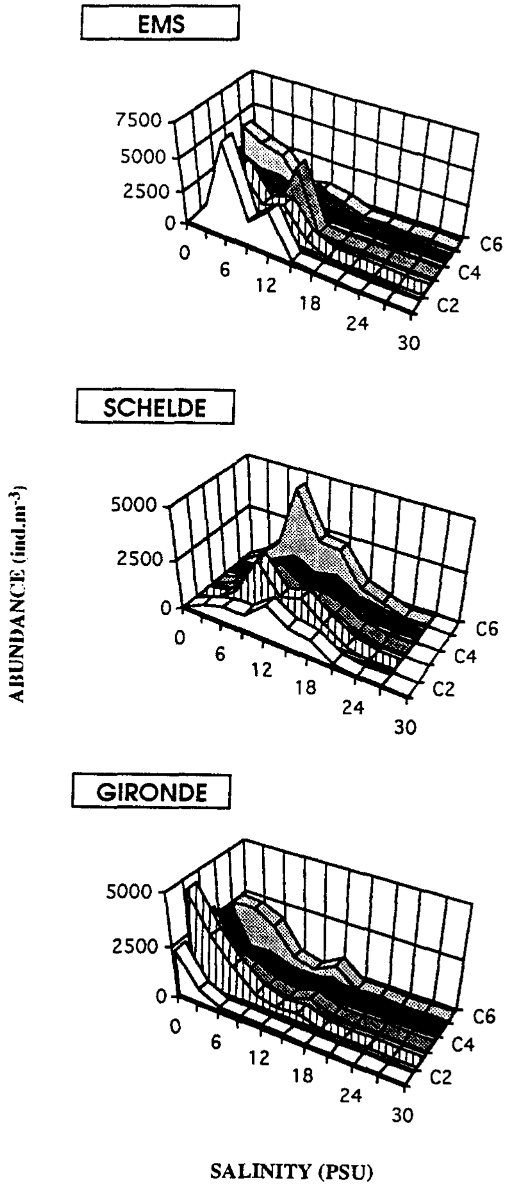

Fig. 4. Copepodid (II to VI) abundances of *Eurytemora affinis* as a function of salinity in the 3 estuaries during spring 1992.

Acartia spp

As for *Eurytemora affinis*, abundance peaks of *A. bifilosa* were not situated at the same salinity in the 3 estuaries: 9 PSU in the Gironde, 15 PSU in the Ems and 18 PSU in the Westerschelde. Although *Acartia* copepodids were not determined at the species level, it is likely that most individuals found in the mesohaline zone belong to *A. bifilosa*. Adults (CVI) dominated in the 3 estuaries (Figs 6 and 7) and were relatively

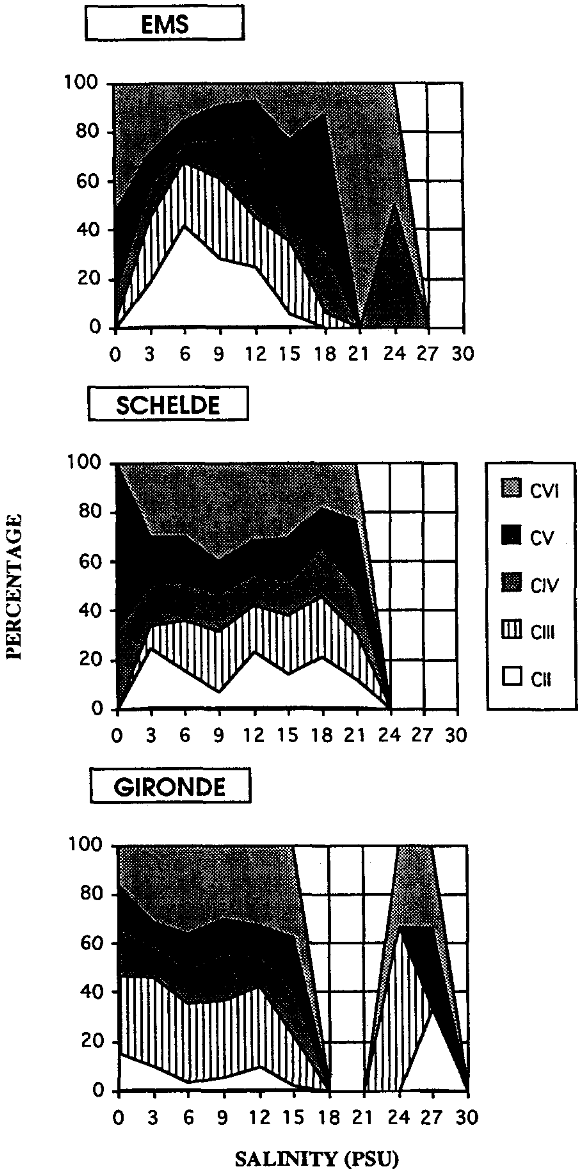

Fig. 5. Relative abundances of copepodids (II to VI) of *Eurytemora affinis* as a function of salinity in the 3 estuaries during spring 1992.

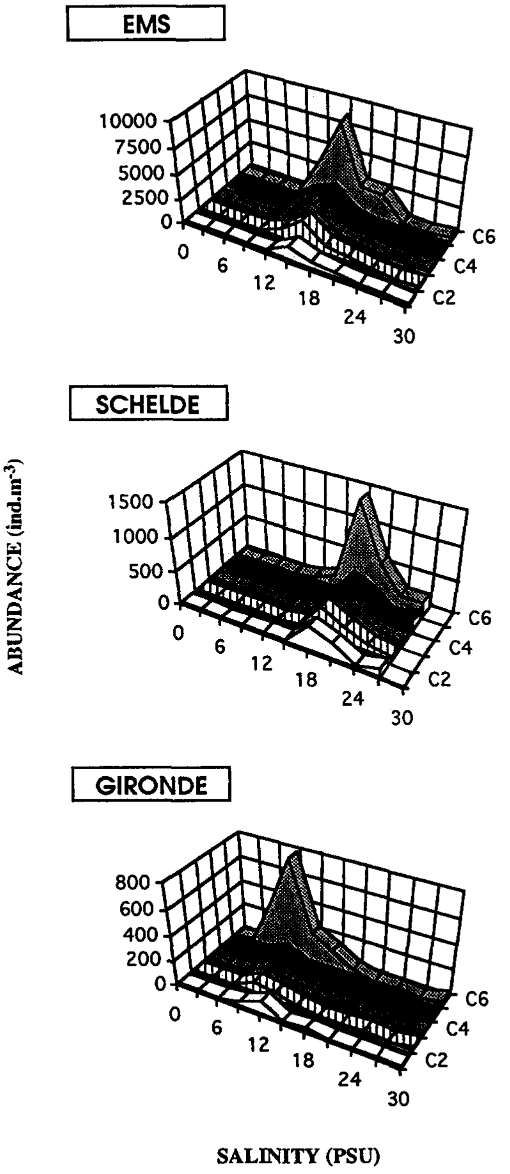

Fig. 6. Copepodid (II to VI) abundances of *Acartia* spp as a function of salinity in the 3 estuaries during spring 1992.

more abundant just upstream the abundance peak of the population. In the bulk of the adult population, males dominated in the Ems and females dominated in the Gironde. The situation was intermediate in the Westerschelde. The global sex ratio (CV + CVI) was not significantly different from one estuary to the other (0.97, SD = 0.33 in the Ems; 0.83, SD = 0.32 in the Gironde; 0.74, SD = 0.59 in the Westerschelde) nor between copepodids V and VI.

The small peaks of copepodids II observed at salinities above 21 PSU were probably produced by the 2 neritic species of this genus: *A. discaudata* and *A. clausi*, since adults were recorded in the estuaries at these salinities.

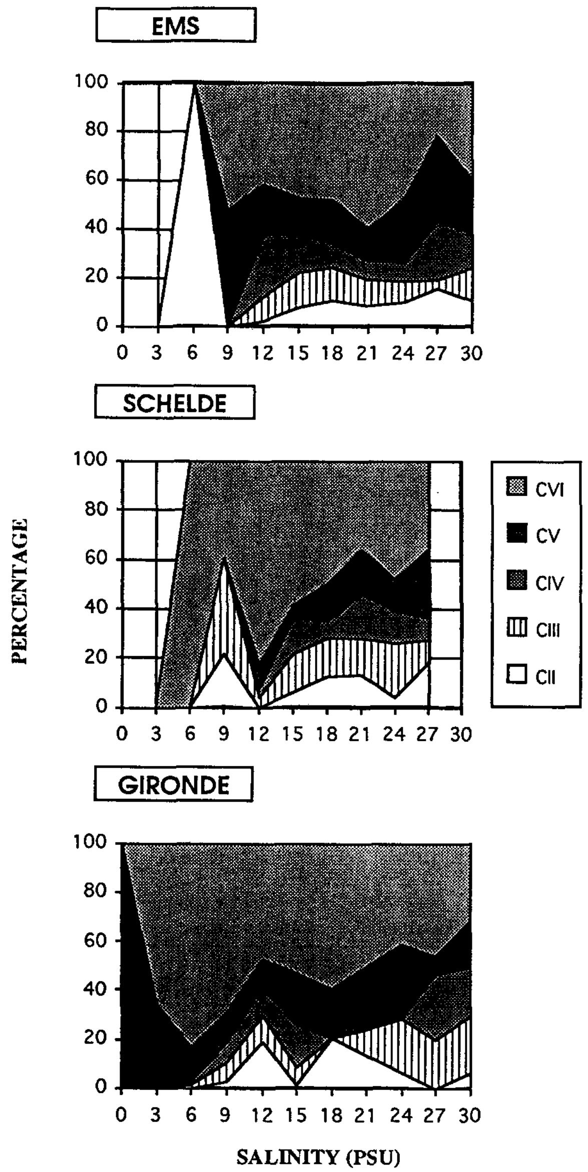

Fig. 7. Relative abundances of copepodids (II to VI) of *Acartia* spp as a function of salinity in the 3 estuaries during spring 1992.

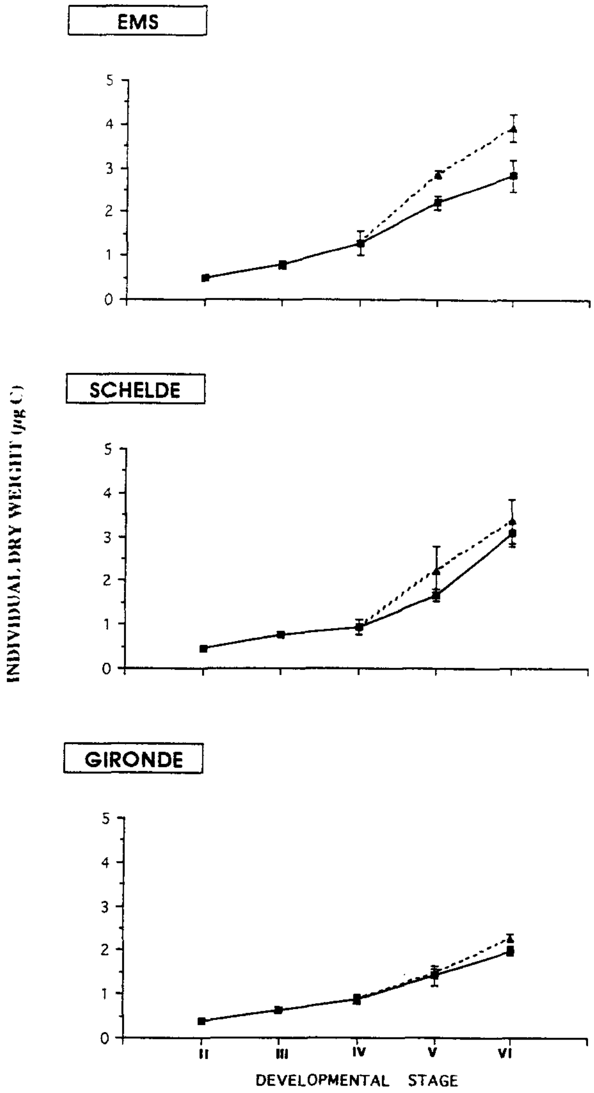

Fig. 8. Individual carbon weight (±standard deviation) of the different stages of *Eurytemora affinis* in the 3 estuaries during spring 1992. (Dotted line = females).

Individual dry weight of the 2 dominant copepod species

For each instar, individual weights of *E. affinis* were lower in the Gironde than in the Ems (Fig. 8, Wilcoxon-Mann-Whitney test, $p = 0.025$). Individual weights in the Westerschelde were intermediate but close to the Ems' (significant difference was only observed between Ems and Westerschelde for CV and between Gironde and Westerschelde for CIII, CV females and CVI, $p = 0.025$). Whatever the estuary, individual weights of females were higher than those of males ($p = 0.025$: stages CV and CVI in the Ems and CVI in the Gironde); however, the difference was not significant in the Westerschelde.

For the young stages (CII to CV) of *A. bifilosa* no difference in weight was found between the Ems and the Gironde, these weights were slightly lower than in the Westerschelde (Wilcoxon-Mann-Whitney test, $p = 0.025$, Fig. 9). Females were heavier in the Ems than in the Westerschelde and males and females were heavier in the Westerschelde than in the Gironde

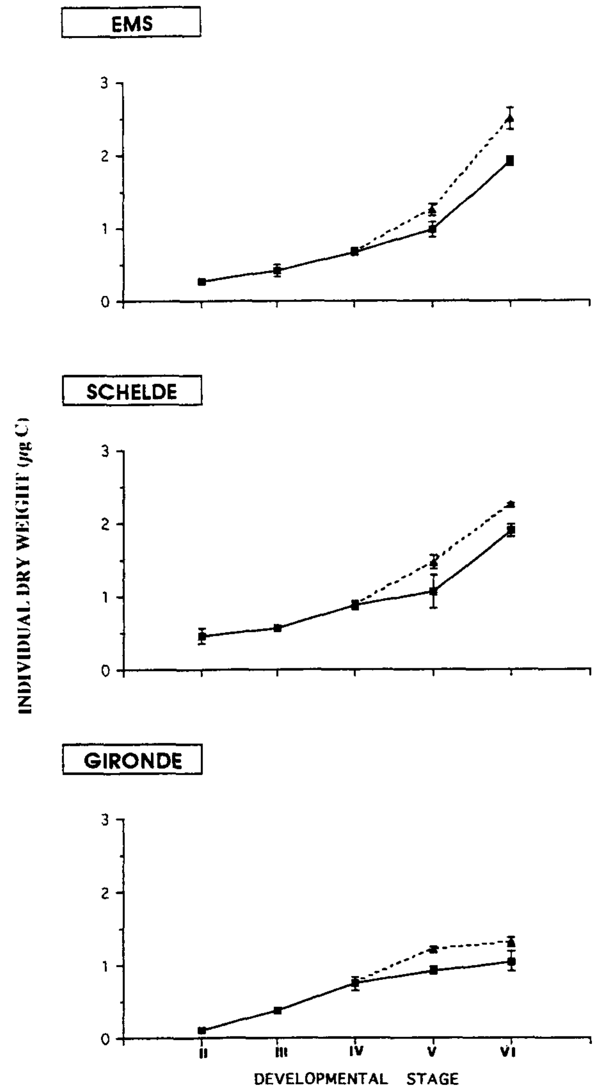

Fig. 9. Individual carbon weight (±standard deviation) of the different stages of *Acartia* spp in the 3 estuaries during spring 1992. (Dotted line = females).

($p = 0.025$). In all cases females had higher weight than males ($p = 0.025$).

Copepod biomass in the oligohaline and mesohaline zones

Copepods being strongly dominant (Fig. 2) in the oligohaline and mesohaline zones, copepod biomass (= *E. affinis* + *A. bifilosa*) was a good approximation of the zooplanktonic biomass. Copepod biomass was significantly different between the 3 estuaries ($p = 0.025$, Kruskal-Wallis test). Highest copepod biomass was found in the Ems (Fig. 10) where the contribution of the dominant species *E. affinis* and *A. bifilosa* was quite similar: 20.54 mgC m^{-3} and 24.53 mgC m^{-3} respectively. In the Westerschelde, biomass was lower than in the Ems (17.68 mgC m^{-3} for *E. affinis* and 4.05 mgC m^{-3} for *A. bifilosa*). The situation was different in the Gironde where the biomass of *A. bifilosa* was very low (1.21 mgC m^{-3}) and the biomass of *E. affinis* was only important in the oligohaline zone (maximum at 0 PSU: 12.84 mgC m^{-3}). In this estuary, the copepod biomass in the mesohaline zone was lower than 7 mgC m^{-3}).

Discussion

The present study was aimed to compare the composition and distribution of the zooplankton in 3 european tidal estuaries showing similarities in terms of total area, flushing time and salinity gradient but differing by their level of eutrophication, SPM concentration and potential phytoplankton production (Table 1). The Ems is not very turbid and is well aerated which allows for the highest primary production. The Westerschelde is subject to anoxia (due to anthropic activities) in its oligohaline zone. The Gironde is a highly turbid estuary with very low primary production, especially in the maximum turbidity zone.

Sampling was concentrated during the spring period which corresponds to the maximum abundance of the dominant species *Eurytemora affinis*: April in the Ems (Baretta & Malschaert, 1988), March–May in the Westerschelde (Soetaert & Van Rijswijk, 1993), April–May in the Gironde (Castel, 1993). The second dominant species, *Acartia bifilosa*, shows a less constant temporal pattern, being most abundant in March–July in the Ems (Baretta & Malschaert, 1988), in late winter in the Westerschelde (Soetaert & Van Rijswijk, 1993), in July–August in the Gironde (Castel, 1993). The reasons of these different seasonal patterns are unknown but this can explain why *A. bifilosa* was much more abundant in the Ems than in the two other estuaries. The third taxon considered in this study, the meroplankton, is always most abundant in spring (Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993; Castel, 1981).

The population of the copepod *Eurytemora affinis* was well developed in the three estuaries. It dominated the zooplankton in the oligohaline zone in the Ems and the Gironde thus confirming previous findings (Baretta & Malschaert, 1988; Castel & Veiga, 1990). In

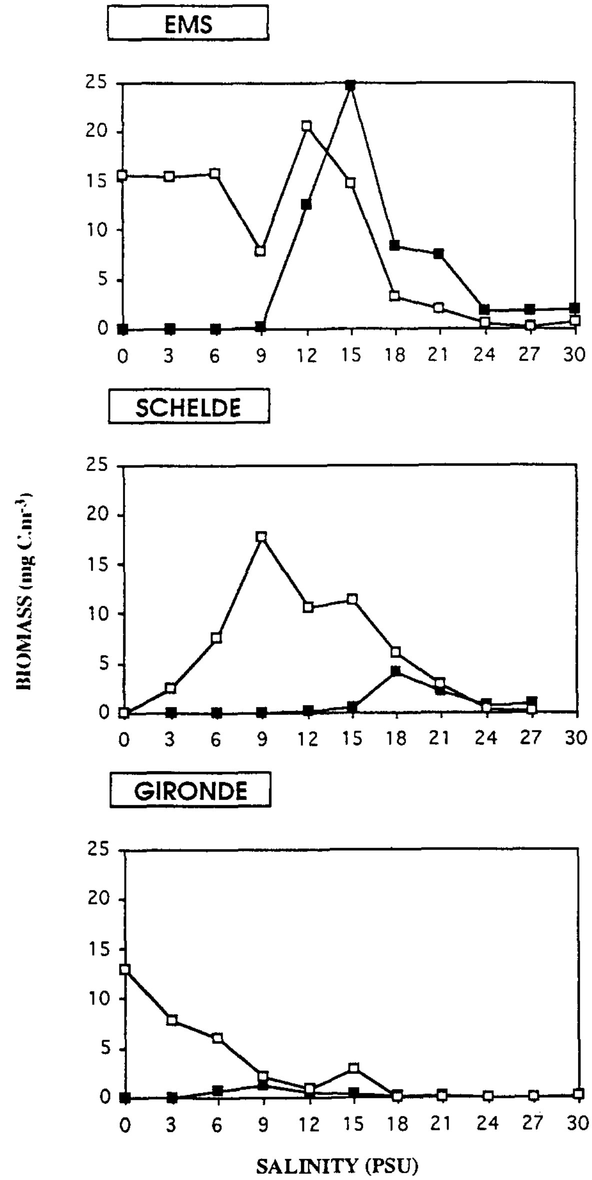

Fig. 10. Biomass (mgC m^{-3}) of *Eurytemora affinis* (□) and *Acartia* spp (-■-) in the 3 estuaries during spring 1992.

the Westerschelde *E. affinis* was most prominent more downstream, at higher salinities. The same observation was made by Soetaert & Van Rijswijk (1993). The downstream shift of the population is likely due to anoxic conditions occurring in the low salinity zone of the Westerschelde. Rotifers and the copepods *Cyclops* spp and *Eudiaptomus gracilis* were the only zooplankters resisting the harsh conditions in the oligohaline zone in the Westerschelde but they were found in low numbers.

E. affinis occurred in a very limited zone (0–15 PSU) in the Gironde. The peak of the population was always found just upstream the turbidity maximum which occurred at 3–6 PSU (data not shown but see Castel, (1995)). It has been shown by Castel & Veiga (1990) that the copepods behave as passive particles and are trapped in the turbidity zone. Castel & Feurtet (1992) also found high mortality rates during periods of high turbidity, confirming the results obtained by Sellner & Bundy (1987) showing that SPM concentrations over 350 mg l^{-1} affect the survival of *E. affinis*. These observations suggest that, in the Gironde, *E. affinis* is limited downstream by the maximum turbidity zone. The broader distribution of *E. affinis* was observed in the Ems estuary, where it appeared from 0 to 27 PSU. The abundance peak of *E. affinis* in the Ems was observed near its salinity optimum (12 PSU in laboratory conditions; Heinle, 1969). However, as shown for the 2 other estuaries, this optimum is not clear in the field. Remarkably enough the abundance peak of *E. affinis* was nearly the same in the three estuaries whatever its location along the salinity gradient. Thus, salinity is unlikely the only variable influencing the distribution of *E. affinis* (Bradley, 1975; Castel & Veiga, 1990). Organic loading has certainly to be taken into account.

Whatever the estuary, common features were observed for the parameters of the populations of *E. affinis*. As usual for copepods, young instars dominated. Adults were more tolerant to lower and higher salinities than copepodids. This is confirmed by studies made on the variations of tolerance to salinity (Von Vaupel-Klein & Weber, 1975). Ovigerous females were generally found downstream the abundance peaks of the populations (this was not clear in the Ems). In addition, the sex ratio calculated for copepodids CV was lower than the sex ratio of the adults indicating a higher male mortality. This could reflect differential mortalities in stage CV during the final molt (as observed for Acartia by Lee & Mc Alice, 1979), or a shorter life span of the males at maturity (Corkett & Mc Laren, 1978). A preferential predation on males (CVI) is unlikely (Sandström, 1980; Vuorinen *et al.*, 1983).

The similar maximum abundance observed in the three estuaries suggests that the nutritive requirements of *E. affinis* are met in the field, even when primary production is low. In this latter case *E. affinis* has to feed on detritus (Heinle & Flemer, 1975: Burkill & Kendall, 1982) which is generally considered of lower nutritive value.

Differences were observed between the individual dry weight measured in the three estuaries. The lightest individuals of *E. affinis* were found in the Gironde, where primary production is generally low. Heaviest individual weights were determined in the Ems where highest values of primary production are to be found. The variations in body weight are unlikely correlated to temperature (temperature during sampling for biomasses: 12.0 °C, 9.0 °C and 14.9 °C for the Ems, Westerschelde and Gironde respectively). Neither suspended matter concentration nor chlorophyll *a* were measured during the present study, but previous observations made in the Gironde indicate a strong influence of the nutritional quality of the particles on the individual weight of *E. affinis*. Feurtet & Castel (1988) showed that adult body weight drops significantly in the maximum turbidity zone where the ratio chlorohyll *a*/SPM, taken as an index of food availability, is the lowest. Furthermore, the condition factor (weight/length^3) is inversely related to SPM concentration (Castel & Feurtet, 1987) both on a spatial and a temporal scale.

The influence of the quality of the available food was also suggested for the production of eggs (highest clutch-size in the Ems, lowest in the Gironde). Presence of phytoplankton is known to favour eggs production (Heinle *et al.*, 1977, Chervin, 1978). Comparing samples taken in spring 1992 in the Elbe, Shannon, Ems and Gironde, and using principal component analysis, Burdloff (1993) showed a good correlation between number of eggs and proteins + carbohydrates + lipids/SPM ratio. Using a stepwise multiple regression analysis, Castel & Feurtet (1992) showed that the ratio chlorophyll *a*/SPM was the most effective variable explaining clutch-size variations in the Gironde estuary. Number of eggs per sac was also correlated (negatively) with temperature. Together, the two variables explained 62% of the variance. In the present study clutch-size was not correlated with temperature (mean temperature during sampling for egg counts: 12.8 °C, 8.7 °C and 14.2 °C for the Ems, Westerschelde and Gironde, respectively) suggesting a strong influence of the nutritional conditions.

The trend found for the number of eggs per egg sac is supported by the trend observed for the sex-ratio. Highest values of the sex-ratio (males/females) was found in the Ems and the lowest in the Gironde. Females *Eurytemora* require repeated fertilization for continued reproduction (Heinle, 1970; Katona, 1975). Thus, for copepods, a predominance of males over females is considered to promote fertilization of the females (Green *et al.*, 1993).

The copepod *Acartia bifilosa* was the second dominant species. It was as abundant as *E. affinis* in the Ems whereas it was collected in much lower number in the Westerschelde and Gironde. The bulk of the population was situated in the mesohaline zone in the Ems and Gironde and at the limit of the polyhaline zone in the Westerschelde. *A. bifilosa* is strongly euryhaline. In the Ems, *A. bifilosa* is a typical winter-spring species occurring at all salinities between 0 and 35 PSU during this period. In summer its occurrence is restricted to salinities between 15 and 30 PSU (Baretta & Malschaert, 1988). In the Westerschelde, maximum abundance of *A. bifilosa* are recorded in late winter between 18 and 30 PSU (Soetaert & Van Rijswijk, 1993). In the Gironde, *A. bifilosa* is generally found between 5 and 22 PSU with a maximum peak around 15 PSU in July (Castel, 1981; Irigoien & Castel, (1995)). Thus the present observations on *A. bifilosa* distribution along the salinity gradient are in accordance with the previous studies. The difference in the maximum abundance reached in the three estuaries could be attributed to a specific influence of temperature as well as differences in nutritional conditions.

The relative abundances of adults *A. bifilosa* were high upstream the density peaks of the populations; Lance (1964) has shown that they are more resistant to high salinity than young instars. The distribution of males was restricted to narrow zones (males are less resistant to dilution than females, Lance, 1964). Males of *A. bifilosa* were highly dominant in the Ems, less in the Westerschelde and females dominated in the Gironde. As for *E. affinis*, high densities of males are probably an adaptive characteristic involving a better fertilization of females. This is consistent with our observations showing the highest population abundance in the Ems and the lowest in the Gironde.

The lowest individual weights were found in the Gironde. Weights of copepodids CII to CIV were significantly higher in the Westerschelde than in the Ems. The weight of copepodids CV were not significantly different and adults were heavier in the Ems than in the Westerschelde. This indicated a faster growth of *A. bifilosa* in the Ems, leading to higher adult biomass. This reinforces the hypothesis that *A. bifilosa* was under the best conditions for developing in the Ems and that nutritional conditions are likely to influence its growth. In the Gironde estuary, Irigoien & Castel

(1995) showed that the productivity (P/B ratio) is positively correlated with the chlorophyll *a*/SPM ratio.

The meroplanktonic community was much more developed in the Ems than in the Westerschelde and the Gironde. In the Gironde, the very low abundance of meroplankton was likely due to the reduced intertidal zones. In the Ems, on the contrary, a very abundant autochthonous meroplankton community (polychaetes and cirripedes) was observed in the mesohaline and polyhaline zones. In accordance with the previous observations of Baretta & Malschaert (1988) we found Polychaet larvae being dominant in the salinities between 15 and 21 PSU and the cirripede larvae being most abundant at 24–30 PSU. This was likely due to the large extent of mud flats in the Dollard estuary, which provide a habitat for polychaetes and to the presence of hard substrates downstream providing settlement areas for cirripedes.

In conclusion, our observations suggest that salinity is not the only factor determining the distribution of species in estuaries. This was especially clear for *E. affinis* which showed abundance peak of the same value at different salinities. It is likely that other factors such as organic loading and eutrophication processes (Westerschelde) or high concentration of suspended particulate matter (Gironde) partly determine the species distribution. However, the difference in individual weights, observed for *E. affinis* and *A. bifilosa*, and of clutch-size for *E. affinis*, suggest that the nutritional conditions were not the same in the three estuaries. This hypothesis is supported by the fact that zooplankton developed best in the Ems where highest primary production is to be found.

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