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Environmental control of mesozooplankton community structure in the Seine estuary (English Channel)

Influence des paramètres environnementaux sur la répartition spatio-temporelle du mésozooplancton de l'estuaire de la Seine

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Abstract

This paper is the first to describe the spatio-temporal changes of mesozooplankton in the Seine estuary. Monthly samples were collected along the estuary in 1996 in order to analyse the seasonal changes of the mesozooplankton community and to identify the major environmental parameters that may influence the spatial distribution of zooplankton in this megatidal estuary. Statistical analysis (canonical correspondence analysis) showed that salinity was the main factor correlated with the longitudinal distribution of zooplankton. Marine species (*Temora longicornis*, barnacle larvae…) were located in the outer part of the estuary, while more oligohaline species (*Eurytemora affinis*) were recorded in the inner part of the estuary. A mixed zone was characterised by the presence of the neritic copepods *Acartia* spp. and *Eurytemora affinis*. The marine species (e.g. *T. longicornis*, *Oikopleura dioica*, Barnacle larvae) showed maximum abundance at the end of spring (June) while the most abundant estuarine species, *E. affinis*, peaked in late winter-spring and declined with the onset of summer. This copepod dominated the estuarine zooplankton throughout the year, and found in the Seine estuary very high favourable conditions to exhibit ultimate abundances (> 190 000 ind m^{-3}) which is one order of magnitude higher than those found in other European estuaries. It represented the main prey for major planktonivorous species such as suprabenthic and fish species located living in the upstream zone of the Seine estuary. © 2002 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Des prélèvements mensuels ont été réalisés en 1996 afin d'analyser les changements temporels de la communauté mésoplanctonique estuarienne et d'identifier les principaux paramètres responsables de la distribution spatiale du zooplancton dans cet estuaire mégatidal. Des analyses statistiques (analyse canonique des correspondances) ont montré que la salinité est le principal facteur contrôlant la distribution spatiale du zooplancton. Une zone intermédiaire comporte un assemblage faunistique composé d'espèces néritiques comme les copépodes du genre *Acartia* et le copépode oligohalin *Eurytemora affinis*. Les espèces marines (e.g. *T. longicornis, Oikopleura dioica*, larves de cirripèdes) atteignent leur maximum d'abondance à la fin du printemps (juin) alors que le copépode prépondérant dans l'estuaire, *E. affinis*, a un maximum à la fin de l'hiver et au début du printemps. Son abondance commence à décliner dès l'été. Cependant, ce copépode domine la communauté mésozooplanctonique estuarienne toute l'année et trouve, dans l'estuaire de la Seine, des conditions de développement très favorables puisque les densités maximales dépassent 190 000 ind m^{-3}, soit un ordre de grandeur plus élevé que dans les autres grands estuaires européens. Il est la proie favorite de nombreuses espèces planctonophages et suprabenthiques ainsi que des poissons fréquentant cette partie amont de l'estuaire de la Seine. © 2002 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Zooplankton; *Eurytemora affinis*; Annual cycle; Environmental parameters; Seine estuary

Mots clés: Zooplancton; *Eurytemora affinis*; Cycle annuel; Facteurs environnementaux; Estuaire de la Seine

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1. Introduction

Environmental variables parameters and anthropogenic influences may stronger affect the distribution of estuarine zooplankton (Vecchione, 1989). The relationship between distribution of copepods and environmental variables have been studied in several estuaries (Capuzzo, 1980; Castel, 1984; Soetaert and Rijswijk van, 1993) and salinity has been shown to be the most important parameter correlating with the distribution of zooplankton (Collins and Williams, 1981). An estuarine classification has been developed according to the Venice system (Mouny et al., 1996) with polyhaline zone (30.0 > surface salinity > 18.0) with marine copepods, mesohaline zone (18.0 > surface salinity > 5.0) with a dominance of the copepod of the genus *Acartia* (Mallin, 1991), and an oligohaline zone (5.0 > surface salinity) with maximal abundance of *Eurytemora affinis* (Soltampour-Gargari and Wellershaus, 1987; Busch and Brenning, 1992). Nevertheless, Bulger et al. (1993) had proposed later an estuarine biological classification based on estuarine salinity zones derived from principal component analysis.

The present paper presents temporal and spatial variations of the mesozooplankton in the Seine estuary. Although this estuary is the largest megatidal estuary in the English Channel, few studies have been carried out on estuarine communities in this ecosystem (Mouny et al., 1996). The objectives of this study are to describe the temporal changes in relative species abundance and, to correlate environmental factors (salinity, turbidity, dissolved oxygen) with the longitudinal distribution of the main zooplanktonic species.

2. Materials and methods

2.1. Study location

The Seine estuary (Fig. 1) is the largest megatidal estuary along the English Channel, with an area of about 150 km^2 at high tide. It is an important area for the French economy, because a quarter of the French population and a third of the industry and agriculture are concentred along the Seine River. Freshwater input into the estuary is primarily from the Seine River with a drainage area of approximately 78 650 km^2. Discharge varies seasonally, from a maximum of 2000 $m^3\ s^{-1}$ in winter to a minimum of 100-200 $m^3\ s^{-1}$ in summer (Mouny, 1998). The Seine estuary is characterized by a maximal turbidity zone with suspended matter concentrations of 1 g l^{-1} generally located in the upper part of the estuary. The morphology combined with regular dredging and the presence of embankments favour the penetration of marine waters into the upstream portion.

2.2. Sampling

To identify the spatio-temporal changes of the mesozooplankton, samples were collected monthly at six sites along the salinity gradient in 1996 between the downstream (49° 27 N/0° 02 E) and the upstream part (49° 26 N/0° 38 E) of the estuary (Fig. 1). The zooplankton was collected with a standard WP2 net (200 µm mesh size; diameter: 0.6 m) equipped with a TSK flowmeter fixed in the mouth part to measure the volume of water filtered. Two plankton tows were made at each site: oblique from bottom to the surface and surface. Each tow lasted 1 to 2 minutes against the tide and filtered a volume of 8 to 70 m^3. For analysis, the mean of oblique and surface abundances were used due to high mixing of the water column (Table 1), and similar order of magnitude of mezooplanktonic abundances in oblique and surface tows. Environmental parameters were recorded at each site at the surface including salinity, temperature, and suspended matter (turbidity) in mg l^{-1}, and dissolved oxygen (mg l^{-1}). The River flow was also recorded for each sampling date (Table 1). Net collections were fixed with 5% buffered formaldehyde for approximately one week then washed and preserved in 70% alcohol. Planktonic organisms were identified and counted under a dissecting microscope according to Frontier's sub-sampling method. Aliquots were used to count ≃ 100 specimens for each species, this abundance being sufficient to obtain a good estimation of their densities (Frontier, 1972). Results were expressed as number of individuals m^{-3}.

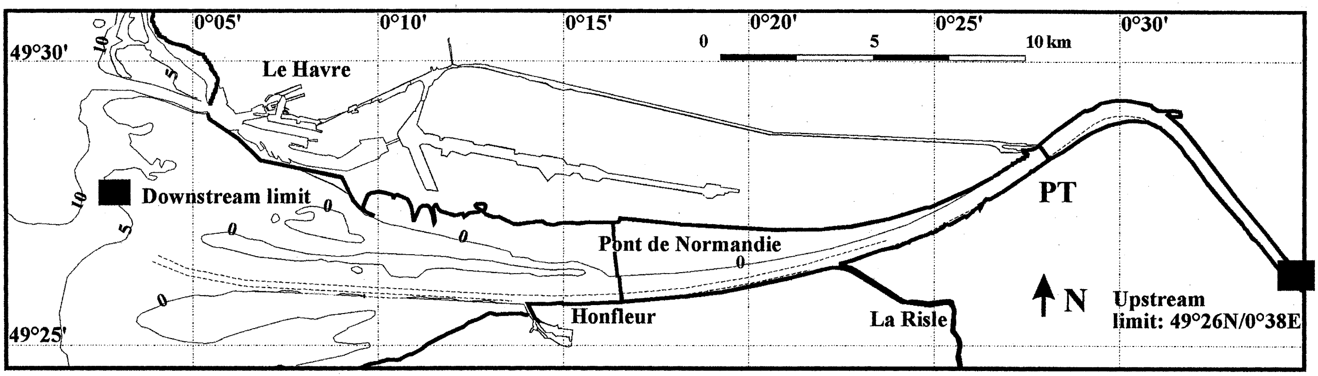

Fig. 1. Map of the Seine estuary (eastern English Channel, France) showing the study site, between downstream (49° 27 N/0° 02 E) and upstream limits (49° 26 N/0° 38 E) in 1996.

Table 1
Number (N) of sites and physical parameters recorded for each longitudinal transect from different month in 1996. Pk: kilometric point (Paris corresponding to 0 km)

Date	N	Distance (pk)	Surface salinity	Bottom salinity	Surface temperature (°C)	Surface turbidity (mg l^{-1})	Bottom turbidity (mg l^{-1})	Freshwater discharge ($m^3 s^{-1}$)
January 28	4	340-368	0.6-18.6	10.0-30.0	6.0-6.3	36.3-51.7	53.9-3881.3	438
February 25	6	340-363	0.4-16.4	0.5-23.9	5.8-7.0	25.3-47.6	54.4-485.0	641
March 27	6	331-362	1.7-12.6	2.4-18.3	9.3-10.0	20.0-35.2	62.2-1764.3	270
April 23	5	327-364	0.4-20.9	0.5-28.1	12.0-13.9	14.8-76.0	56.0-314.4	159
May 28	6	331-366	0.3-19.6	1.0-22.4	14.7-15.8	32.7-114.4	49.3-1758.0	256
June 25	6	323-354	1.0-20.9	1.5-30.6	18.8-21.7	28.8-76.3	52.9-2662.0	140
July 22	6	324-355	1.2-20.4	1.3-21.2	20.8-22.0	56.0-112.2	74.0-537.3	139
August 21	6	334-365	0.4-19.5	0.5-28.7	21.2-22.6	15.3-144.5	320.0-22890.0	224
September 18	6	326-362	0.8-19.5	0.7-19.7	16.6-17.9	101.1-590.0	392.2-63400.0	132
October 20	5	330-362	0.5-12.9	0.5-19.0	15.0-15.5	47.3-69.5	49.2-371.3	191
November 18	5	337-363	0.5-10.5	0.5-25.0	13.2-14.0	99.6-223.1	185.7-1700.0	586
December 16	6	338-372	0.4-18.5	0.4-30.6	6.9-8.2	38.1-109.8	105.5-12400.0	749

2.3. Data analysis

To analyse the spatial distribution of zooplanktonic species, correspondence analysis was performed on the data matrix including all sites from 1996 and species with abundances > 5 ind m^{-3} (70 sites and 22 species). To compare the zooplanktonic distribution with environmental parameters, supplementary statistical analysis were carried out using the Canoco program (ter Braak, 1989) for Canonical community ordination on three different data matrices (total zooplankton, Cladocera and Copepoda matrices). This Canonical correspondence analysis (CCA) was used with species (22 species for total zooplankton, 8 for cladocera and 10 for copepods) and sites where all environmental factors were recorded (57 sites, dissolved oxygen was not recorded in January, February and for one station in August). The CCA constrains the axes in classical Correspondence analysis (CA) (Hill, 1974) to a linear function of measured variables associated with species data (ter Braak, 1986; 1987; Palmer 1993). The inertia associated with CCA compared with the inertia of CA indicates the extent to which the measured variables explain the variability in the species community. Also, CCA classified the different environmental factors associated with their percentage of variance explained. The robustness of this analysis was determined using a Monte Carlo permutation test (ter Braak, 1986). Principal Component Analysis was also performed on three different data matrices (total zooplanktonic, Cladoreca and Copepoda matrix) in order to identify the seasonal changes in the main salinity zones (mesohaline and oligohaline zone); and mean monthly abundance (averaging the oblique and surface densities) of species with an abundance of over 5 ind m^{-3}. The species and codes are listed in Table 2.

3. Results

3.1. Environmental factors and zooplanktonic structure

Except in January (Table 1) when the water column was highly stratified, salinity was relatively homogenous throughout the water column. This was observed in particular in the upstream zone where there was an important mixing of the water column due to the high turbulence in relation with the megatidal regime of the Seine estuary and the relatively low input of freshwater throughout the 1996 year (Table 1). The salinity at each sampling date was

Table 2
List of species and their code used for the different multivariate analysis (correspondence analysis, hierarchical analysis)

Zooplanktonic taxa	Code	Zooplanktonic taxa	Code
Cnidaria		Copepod	
Medusa	medu	*Acantocyclops robustus*	arob
Cladoceran		Other Cyclopoïd	cycl
		Acartia spp.	acar
Alona quadrangularis	aqua	*Centropages* spp.	centrop
Biapertura affinis	baff	*Diaptomus* spp.	diapto
Bosmina spp.	bosm	*Eurytemora affinis*	eaff
Ceriodaphnia spp.	cerio	*Temora longicornis*	tlon
Chydorus spp.	chydo	Other Calanoïd	cala
Daphnia spp.	daph	*Euterpina acutifrons*	eacu
Evadne nordmanni	enor	Other Harpacticoïd	harpa
Evadne spinifera	espi		
Iliocryptus sordidus	isor	Barnacle larvae	barn
		Appendicular	
		Oikopleura dioica	odio

generally included between 0.3-1.0 for the upstream limit to ≈ 20.0 for the downstream limit, except in January, April, August, and December, when the bottom salinity reached ≈ 30.0 (Table 1). The water temperature showed an annual cycle from ≈ 6 °C in winter to ≈ 21 °C in summer (Table 1). The turbidity showed an increase from the downstream to the upstream limits, and a very high vertical gradient with high turbidity near sea bottom (Table 1).

The correspondence analysis and Hierarchical agglomerative classification (HAC) performed on all sampling stations in 1996 (70 sites and 22 species, Table 2), distinguished three assemblages of species-sites (Fig. 2). Group I was characterised by 19 downstream sites dominated by marine species (medusa, *Oikopleura dioica*, *Temora longicornis* and *Evadne* spp.) where the upstream surface salinity limit was 10; group II corresponded to 33 sites located in the middle part of the estuary and characterized by surface salinities of between 15 and 5, influenced by estuarine species essentially copepods *Acartia* spp. and *Eurytemora affinis* (Fig. 2); group III described the 18 upstream sites with surface salinities of between 6 and 0 and was dominated essentially by freshwater cladoceran species (*Bosmina* spp., *Daphnia* spp.) and also by the copepod *Eurytemora affinis*. CCA for the three different zooplanktonic matrices and environmental factors recorded at the sampling sites allowed us to quantify the species-environment relations (Table 3). For the total zooplanktonic community, the four axes explained 93.1% of the variance of the species environment relationship (axis I: 60.7%, axis II: 17.5, axis III: 10.0% and axis IV: 4.9%). The variance explained by the recorded environmental factors was 19%. The P-value computed with the CCA analysis associated with the Monte Carlo test (Table 3) showed that only the surface salinity is statistically significant. For the Cladocera matrix, the axis I-IV explained a cumulative percentage of 98.7% of the variance of species-environment relations (axis I: 73.9, axis II: 19.1, axis III: 3.2 and axis IV: 2.5). The recorded environmental factors explained 50.1% of the variance of the data matrix. Surface salinity and temperature were

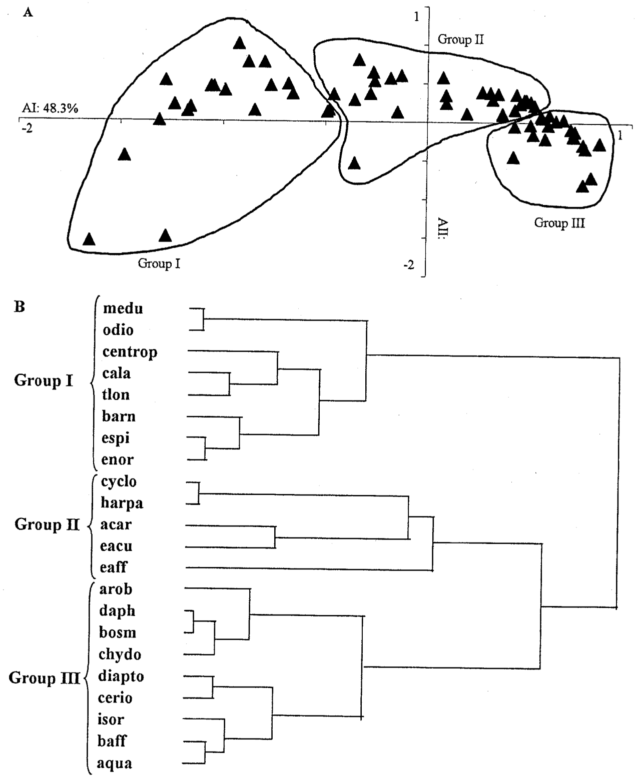

Fig. 2. Zooplankton in the Seine estuary in 1996. A: projection of stations on the first two axes of correspondence analysis; B: Dendrogram of similarity in longitudinal distribution of zooplankton according to hierarchical agglomerative classification.

statistically significant (Table 3). For the Copepoda matrix, the variance explained by the principal axis was 94.6% (axis I: 66.6, axis II: 17.6%, axis III: 6.3 and axis IV: 4.1%) and the environmental parameters recorded for this study explained 21.3% of the variance (Table 3). Surface salinity presented the only statistical significance.

The different analyses showed that hydrological parameters, especially salinity, might have affected the distribution of zooplankton in the Seine estuary. Marine species

Table 3
Summary of the Canonical Correspondence Analysis on three zooplanktonic data matrix and variation of the *P-value* of the different environmental recorded factors for the three data matrix. The P-value is computed with the CCA analysis associated with the Monte Carlo test

	Total zooplanktonic matrix	Cladocera matrix	Copepoda matrix
Cumulative % of variance of species-environment relation (Axis I to IV)	93.1	98.7	94.6
% of Variance explained by recorded environmental factors	19.0	50.1	21.3
Environmental Variable			
Surface salinity	0.01**	0.03*	0.01**
Bottom salinity	0.370^{NS}	0.490^{NS}	0.540^{NS}
Surface dissolved oxygen	0.370^{NS}	0.430^{NS}	0.690^{NS}
Bottom dissolved oxygen	0.870^{NS}	0.250^{NS}	0.150^{NS}
Surface turbidity	0.840^{NS}	0.260^{NS}	0.750^{NS}
Bottom turbidity	0.840^{NS}	0.490^{NS}	0.730^{NS}
Surface Temperature	0.440^{NS}	0.03*	0.280^{NS}
River Flow	0.290^{NS}	0.330^{NS}	0.560^{NS}

* $P \leq 0.05$,
** $P \leq 0.01$,
NS: $P > 0.05$.

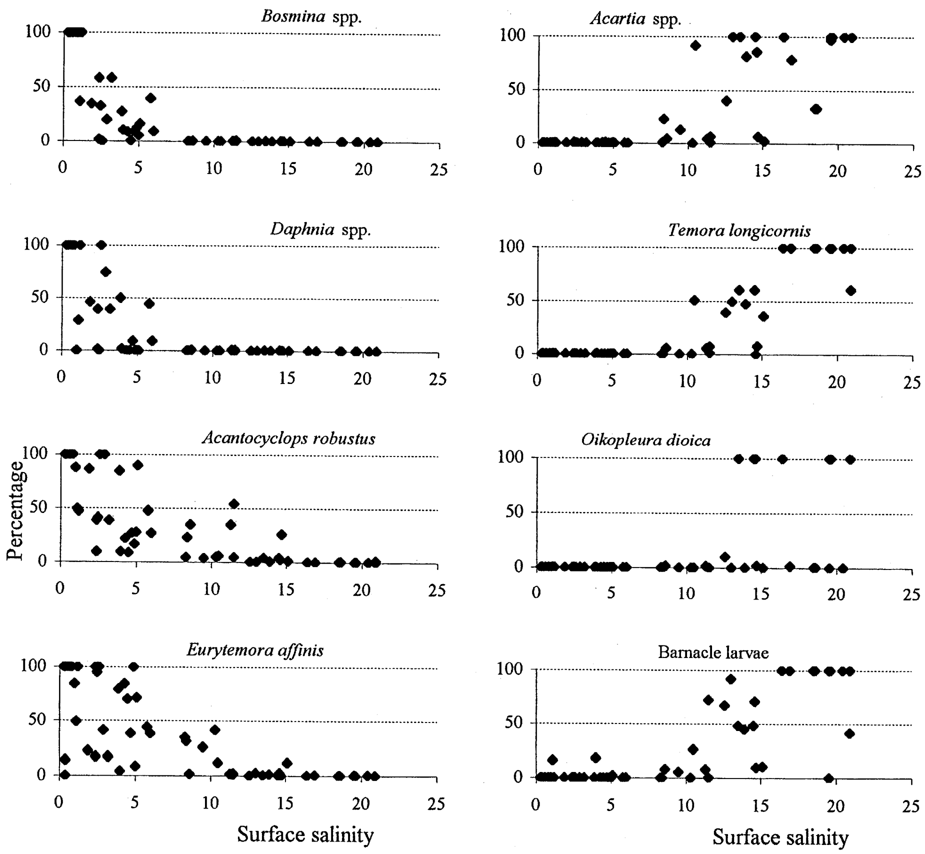

Fig. 3. Plot of relative abundances determined by averaging oblique and surface abundances of main zooplanktonic species along the surface salinity gradient for the 12 sampling dates during 1996 after normalization of abundances from 0 (absence) to 100 (maximum abundance).

(copepod *T. longicornis*, barnacle larvae and appendicular *O. dioica*) reached their greatest abundances in the polyhaline part of the estuary (surface salinities > 15.0-16.0). Freshwater species (cladocera *Bosmina* spp. and *Daphnia* spp., copepod *Acantocyclops robustus*) were more abundant in the upstream part of the estuary where salinity < 3.0 (Fig. 3). Copepods *Acartia* spp. and *Eurytemora affinis* were located in most important surface salinity zone between 0.5 to 22.0 but with highest densities of *Acartia* recorded in surface salinities between 10.0 and 22.0 while greatest abundances of *E. affinis* were observed in surface salinities between 0.5 and 5.0 (Fig. 3). In fact, the maximal abundance of *E. affinis* defined the oligohaline zone with downstream surface salinity of 5.0 and the polyhaline zone was defined by *T. longicornis* with a surface salinity upstream limit of 16.0. The mesohaline zone was defined between 18.0-16.0 and, 5.0, which represented respectively the downstream limit of *Eurytemora affinis* and the upstream limit of *Acartia* spp. (Fig. 3).

3.2. Temporal changes of the mesozooplankton community

Throughout the year, *E. affinis* dominated the zooplankton community of the Seine estuary with 52.0 to 99.9% of the zooplankton at salinities < 18 (Table 4). *Acartia* spp. represented an important part of the zooplankton in the summer period (August and September) in the mesohaline zone with 14 to 45% of the zooplanktonic community. Other species (*Bosmina* spp., *Daphnia* spp., *A. robustus* and *T. longicornis*) represented less than 10% of the zooplankton abundance in both mesohaline and oligohaline zones (Table 4). During the year, the calanoïd copepod *Eurytemora affinis* dominated the mesozooplankton community in the inner part of the estuary including oligohaline and mesohaline zones (Fig. 5). The population increased during the winter and presented maximum densities during spring (between 142 000 and 149 000 ind m^{-3}). The densities declined rapidly in summer reaching low levels in summer and autumn.

Correspondence analysis performed on monthly abundances of main species in the mesohaline zone (nine species) and oligohaline zone (nine species) showed an annual change in the zooplankton community (Fig. 4). HAC, using the factorial coordinates of the first fives axis of the correspondence analysis according to Bruynhooge (1978), described four and three groups respectively for mesohaline and oligohaline zones (Fig. 4). In the mesohaline zone (Fig. 4), the first assemblage corresponded to the end of the summer (August to October), the second group to the March-July period and the third to the winter period (November to February). May was isolated due to the increase in abundances of *Bosmina* spp. (65 ind m^{-3}) and *Daphnia* spp. (25 ind m^{-3}) in relation to a strong discharge

Table 4
Percentage composition of mesozooplanktonic community in reference to main species, in the Seine estuary for main salinity zones (mesohaline and oligohaline zone according to Venice system based on longitudinal surface salinity zonation) in 1996

	J	F	M	A	M	J	J	A	S	O	N	D
Mesohaline zone												
18 < surface saliniy < 5												
Bosmina spp.	0.01	0.02	–	–	0.77	–	–	0.01	–	–	0.12	0.16
Daphnia spp.	0.12	–	–	–	0.36	–	–	–	–	–	0.01	0.18
Acartia spp.	0.09	0.34	0.24	–	0.06	1.79	4.14	45.65	14.36	1.52	0.02	1.33
Eurytemora affinis	96.84	97.66	99.57	99.99	98.65	97.96	95.81	52.20	85.58	98.48	99.76	71.81
Temora longicornis	0.01	0.17	0.01	–	0.06	0.24	0.02	0.03	–	0.01	–	0.12
Oligohaline zone												
5 < surface salinity												
Bosmina spp.	0.77	0.13	0.03	0.01	0.42	0.01	0.04	0.13	0.22	0.02	6.50	0.71
Daphnia spp.	0.85	0.02	0.06	0.01	0.32	–	0.01	0.18	0.01	–	2.74	0.64
Acantocyclops robustus	2.98	0.89	0.29	0.08	0.05	0.03	0.44	1.95	0.06	0.09	16.98	2.24
Acartia spp.	–	–	–	–	–	–	0.01	0.14	0.01	0.01	–	–
Eurytemora affinis	95.40	98.97	99.62	99.90	99.22	99.97	99.51	97.61	99.69	99.88	73.79	96.42

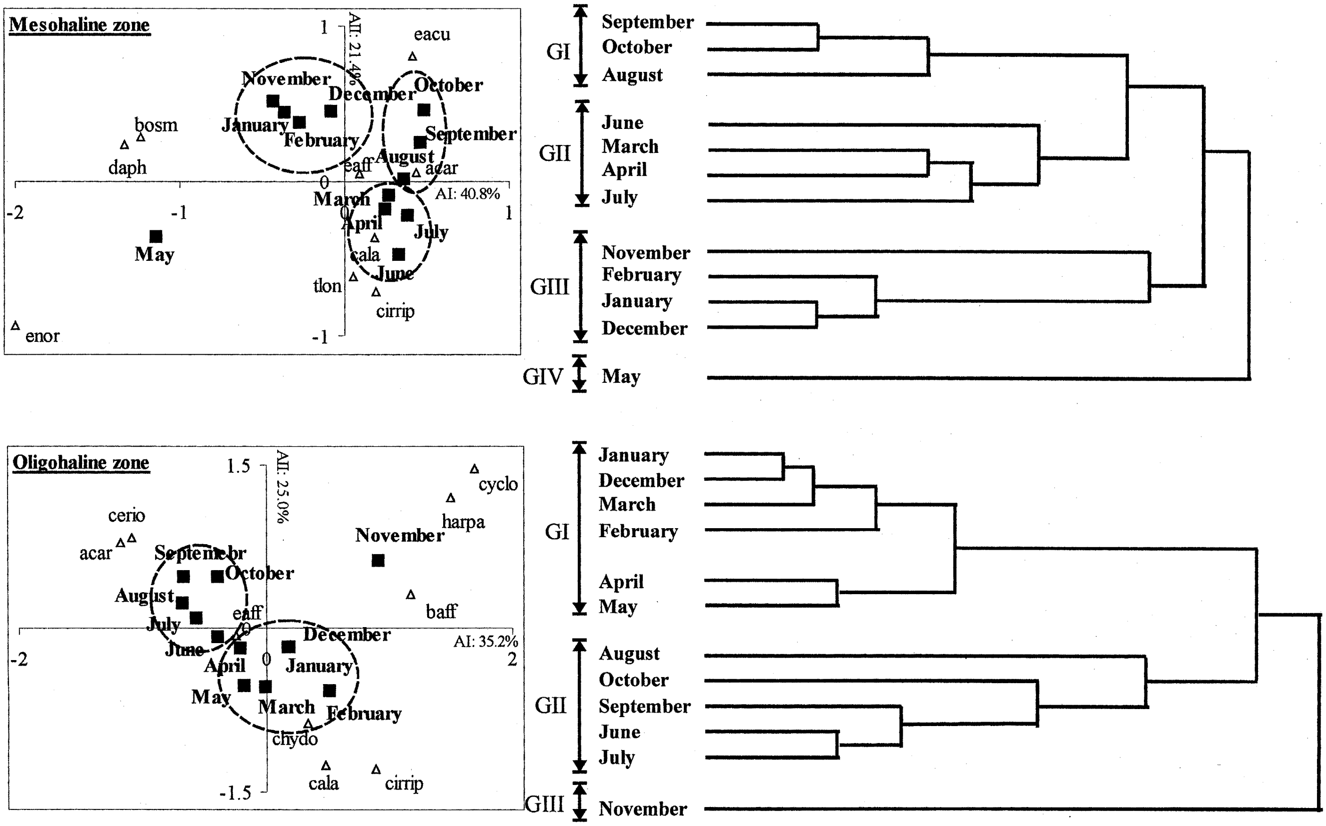

Fig. 4. Projection of stations (assimilated to month) and species on the first two axis of correspondence analysis and associated hierarchical classification for two main salinity zones (mesohaline zone: 18> surface salinity>5; oligohaline zone: 5> surface salinity).

of freshwater during this month. In the oligohaline zone, the first group corresponded to the winter-spring period (December to May) while the second group described the summer-autumn period (June to October). An increase in densities of the cladoceran *Biapertura affinis* (151 ind m^{-3}), and of different benthic harpacticoïd and cyclopoïd (20-25 ind m^{-3}) copepods measured in November was correlated with increased in river flow. The dominant freshwater cladoceran and cyclopoïd also showed a peak in November (Fig. 5).

The highest abundances of typical marine species (*Temora longicornis*, Barnacle larvae and *Oikopleura dioica*) were recorded in the polyhaline zone of the estuary (Fig. 5). The population of these species increased during spring and presented maximal densities in May for barnacle larvae (230 ind m^{-3}) and June for *Temora longicornis* (190 ind m^{-3}) and *Oikopleura dioica* (150 ind m^{-3}). During summer, *Temora longicornis* and Barnacle larvae colonised the inner part of the estuary and presented their maximal abundances in the mesohaline zone as a result of the salinity

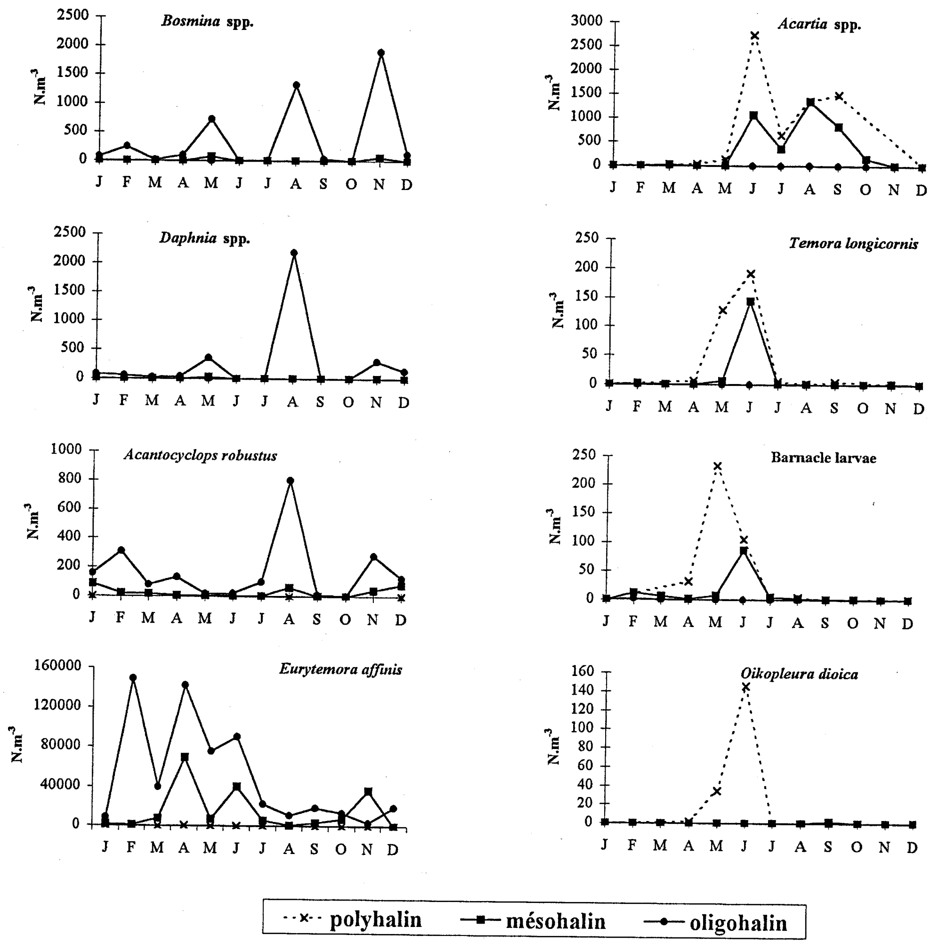

Fig. 5. Seasonal change in abundance (mean of oblique and surface densities) for the main mesozooplanktonic species in the Seine estuary in 1996, in three different surface salinity zones. Polyhaline zone — x —: 30> S> 18; mesohaline zone —■—: 18> S> 5 and oligohaline zone —•—: 5> S.

intrusion. Thereafter, the abundance of these marine species decreased rapidly.

In the polyhaline and mesohaline zones, the neritic copepod *Acartia* spp. increased in abundance during the spring and exhibited two density peaks in June and in September. In the polyhaline zone, the increase was more abrupt and the maximal abundances were higher in this zone (June: 2800 ind m^{-3}, September: 1500 ind m^{-3}) than in the mesohaline zone (June: 1000 ind m^{-3}, September: 850 ind m^{-3}).

The maximal abundances of freshwater species (*Bosmina* spp., *Daphnia* spp. and *Acantocyclops robustus*) were always recorded in the oligohaline zone with generally low abundances in mesohaline and polyhaline zones (Fig. 5). *Bosmina* ssp. presented a regular increases in its abundance and showed successively three main peaks during the year in May, August and November when the abundance reached 1900 ind m^{-3}. *Daphnia* spp. was present with low abundances throughout the year reaching a maximum in August (2200 ind m^{-3}). The cyclopoïd copepod *Acantocyclops robustus* presented three maximum periods with peaks recorded in February, August (maximum abundance: 800 ind m^{-3}) and November.

4. Discussion

4.1. Spatial structure of the mesozooplanktonic community

The results of the CCA, on zooplankton and copepod matrices, show that the salinity gradient described the spatial structure of the mesozooplankton, corroborating observations of other estuaries (Collins and Williams, 1982; Soetaert and Rijswik van, 1993; Laprise and Dodson, 1994; Jassby et al., 1995). Although the maximum turbidity zone is an important environmental phenomenon for biological components in the estuary (Castel, 1984), it seems to play a less important role on zooplanktonic distribution in the Seine River.

In the Seine estuary, three zooplanktonic groups were distinguished in relation to the salinity gradient: (i) polyhaline zone (surface salinity>18.0) characterized by the dominance of copepods *Temora longicornis* and *Centropages* spp. and the cladoceran *Evadne nordmanni*. These marine species penetrate the upstream part of the estuary up to a salinity of 10.0 (Fig. 6); (ii) mesohaline zone (surface salinity = 5.0-18.0) dominated in abundance by the estuarine copepods *Acartia* spp. recorded upstream to a salinity

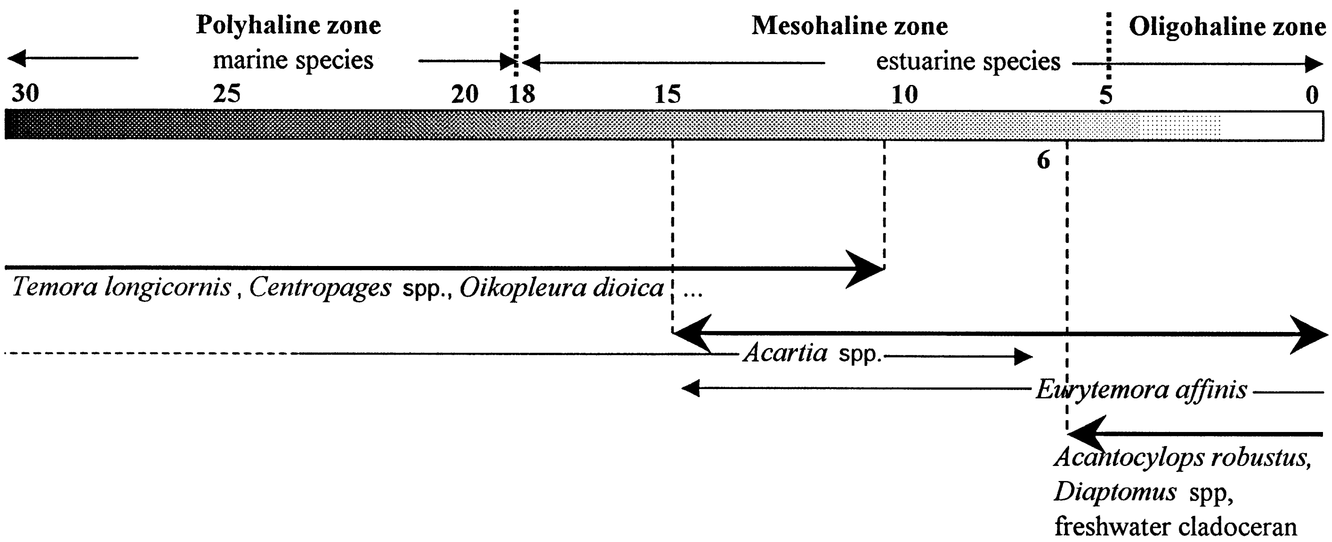

Fig. 6. Synthetic representation of mesozooplankton assemblage along the salinity gradient in the Seine estuary.

of ≃ 5.0 and *Eurytemora affinis* presenting downstream limits of distribution in water salinities of ≃ 16.0-18.0 (Fig. 6). (iii) oligohaline zone (surface salinity <5.0) dominated by the copepod *E. affinis* and the freshwater cladoceran *Bosmina* spp. and *Daphnia* spp. Also, the decrease in euryhaline species abundance and the increase of freshwater species abundances indicated the major role of salinity in the distribution of mesozooplankton in the estuary (Mouny et al., 1996; Mouny, 1998). The presence of euryhaline species in the outer part of the estuary, like *T. longicornis* and barnacle larvae, reflected temporal changes in relation to tidal advection: in fact these species are transported into the estuary during flood and high tide periods (Wang et al., 1994; Schlacher and Wooldridge, 1995). These results confirm the study of Dauvin et al. (1998), who demonstrated that temporal changes in the euryhaline mesozooplankton community, in the Seine region of freshwater influence observed during several tidal cycles reflected the distribution of species along the salinity gradient and periodic tidal longitudinal advection. This phenomenon may represent a large amount of the unexplained variance described by CCA on the spatial mesozooplanktonic community structure. Other parameters may also act on this spatial structure such as predation, which can prevent the distribution of the estuarine copepods in the outer part of the estuary where there is an important marine fish community (Mouny et al., 1996).

4.2. Temporal changes

This is the first year-long study on the mesozooplankton in the Seine estuary. The communities showed in the mesohaline and oligohaline zones an annual cycle in relation to the temporal changes in abundance of zooplanktonic species. The copepods *Acartia* spp. and *Temora longicornis* showed maximal abundances in spring and summer correlated with their reproductive period associated with an increase in water temperature and characterized by an important population of copepodids (Londasle, 1997; Turner, 1982; Castro-Longoria and Williams, 1996; Falkenhaug et al., 1997). This increase in population abundance in the outer part of the estuary is correlated with species recruitment in the euryhaline zone (Bay of Seine) where maximum abundance of *Acartia* spp., *Temora longicornis*, Appendicular and barnacle larvae were recorded, for the same year, in May and June with higher densities in the bay than in the estuary (Mouny et al., 1996). These recruitment periods can explain the transport of these species in the estuary, essentially in the mesohaline zone, by an extension of their spatial distribution area due to the decrease of freshwater runoff of the River Seine during the spring and summer periods. The second peak of abundances of *Acartia* spp. observed at the end of summer in the estuary (polyhaline and mesohaline zones) and in the bay (euryhaline zone) can be related to species succession as recorded in the Gironde estuary by Irigoien and Castel (1995) who demonstrated that two different maximal abundance periods (June and September) were due to the presence of two species complexes *A. bifilosa* and *A. tonsa*, which have different reproducing periods: July for *A. bifilosa* and September for *A. tonsa*. The same species succession along the year is recorded in different estuaries with a mixture of four different *Acartia* species (Baretta and Malschaert 1988). Also, this second abundance peak recorded in the Seine estuary may be due to the presence of several species of the genus *Acartia* (*A. clausi*, *A. discaudata*, *A. bifilosa* and *A. tonsa*) which were not regularly enumerated.

In the Seine estuary, the copepod *Eurytemora affinis* presented a seasonal cycle with a maximal abundance period in spring (presence of juvenile stages) then decreasing after the summer in relation to annual water temperature cycles. This copepod is also the dominant species of the zooplanktonic community in both main salinity zones (mesohaline and oligohaline zones) over the year. The spring

Table 5
Maximum abundance period and maximum densities of *Eurytemora affinis* in four European estuaries [Ems, Shelde and Gironde: Sautour and Castel (1995); Seine: Mouny (1998)]. Sampling method: oblique net (200 µm mesh size).

Estuary	Maximum abundance period	Maximum densities ($N.m^3$)
Ems	April	16 800
Shelde	July	11 500
Gironde	April-May	14 500
Seine	April-May	190 000

period of maximum abundance recorded in the Seine estuary is similar to that observed in the other main megatidal European estuaries (Sautour and Castel 1995, Table 5). But *E. affinis* is about an order of magnitude more abundant in the Seine than other European estuaries (> 190000 ind m^{-3}). The abundance of the mesozooplankon is the Seine estuary is also three times higher than the maximum reported for the US estuaries by Buskey (1993) (61500 ind m^{-3} in the Long Island Sound). This particularity of the Seine estuary may be due to (i) a higher production of this copepod and (ii) a greater concentration of organisms due to the highly canalised nature of the estuary, and (iii) a low consumption of *E. affinis* by the carnivorous organisms living in the estuary. Mouny (1998) and Mouny et al. (1996) showed that *E. affinis* is a link between the phytoplankton and the other components of the pelagic trophic chain, such as suprabenthic species e.g. the decapods *Palaemon longirostris*, the gobiids *Pomatoschistus* spp., and the juveniles of fish occurring in the mesohaline and oligohaline zones of the Seine estuary. Nevertheless, effect of such predation on the *Eurytemora* population should be estimated in the future.

The freshwater species, cladocerans *Bosmina* spp., *Daphnia* spp. and copepod *Acantocyclops robustus* have their maximal abundance periods in summer correlated with the maximum water temperature. The second maximum abundance value recorded for *Bosmina* spp. in November seems to be due to the increase of river flow which carried dominant cladocerans to the downstream part of the estuary.

This study on the spatio-temporal changes of the mesozooplankton in the Seine estuary showed that the most important parameter controlling the zooplankton distribution is the salinity gradient. Species distributions reflected a succession of different zoological assemblages along the salinity gradients in the Seine estuary. These zooplanktonic patterns are less apparent than in other European estuaries due, possibly to the characteristic morphology in the estuary of the Seine. In fact, the estuary's small area (maximum 30 km from estuary mouth to Tancarville), compared to the Gironde estuary (≈ 60 km from mouth to Ambès) and more restrained river mouth, probably explain the juxtaposition of different zooplanktonic communities and the important intrusions of marine and freshwater species, recorded for downstream and upstream parts of the estuary respectively. In addition, the megatidal system observed in the bay of Seine induces more important intrusions of marine water in the Seine estuary than in the Gironde estuary. These morphological and physical constraints may explain the contiguous succession of the zooplanktonic community (marine, estuarine and freshwater community) and the overlap of different zooplanktonic patterns along the salinity gradient. This is consistent with the results of Bulger et al. (1993) who showed for American estuaries from the mid-Atlantic region five overlapping salinity zones for all biological components: freshwater to 4, 2-14, 11-18, 16-27, and 24 to marine. Consequently, the Venice system appears rather arbitrary and not biologically based. In the future, results obtained for the Seine estuary mesozooplankton should be compared with those found in other estuaries and combined with these of other biological compartments (e.g. benthos, and fish) to propose an alternative system of estuarine salinity zones.

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References

Baretta, J.W., Malschaert, J.F.P., 1988. Distribution and abundance of the zooplankton of the Ems estuary (North Sea). Neth. J. Sea Res. 22, 69–81.

Bruynhooge, M., 1978. Classification ascendante hiérarchique de grands ensembles de données: un algorithme rapide fondé sur la construction de voisinages réductibles. Cah. An. Données 3, 7–33.

Bulger, A.J., Hayden, B.P., Monaco, M.E., Nelson, D.M., McCormick-Ray, M.G., 1993. Biologically-based estuarine salinity zones derived from a multivariate analysis. Estuaries 16, 311–322.

Busch, A., Brenning, U., 1992. Studies on the status of *Eurytemora affinis* (Poppe, 1880) (Copepoda, Calanoida). Crustaceana 62, 13–38.

Buskey, E.J., 1993. Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. J. Plank. Res. 15, 907–924.

Capuzzo, J.M., 1980. Impact of power-plant discharges on marine zooplankton: a review of thermal, mechanical and biocidal effects. Helg. Meeresunters. 33, 422–433.

Castel, J., 1984. Dynamique du copépode *Eurytemora affinis* dans l'estuaire de la Gironde: influence du bouchon vaseux. J. Rech. Océanogr. 9, 112–114.

Catro-Longoria, E., Williams, J.A., 1996. First report of the presence of *Acartia margalefi* (Copepoda: Calanoida) in Southampton Water and Horsea Lake, UK. J. Plank. Res. 18, 567–575.

Collins, N.R., Williams, R., 1981. Zooplankton of the Bristol Channel and Severn Estuary. The distribution of four copepods in relation to salinity. Mar. Biol. 64, 273–283.

Collins, N.R., Williams, R., 1982. Zooplankton communities in the Bristol Channel and Severn Estuary. Mar. Ecol. Progr. Ser. 9, 1–11.

Dauvin, J.C., Thiébaut, E., Wang, Z., 1998. Short-term changes in the mesozooplanktonic community in the Seine ROFI (Region of Freshwater Influence) (eastern English Channel). J. Plank. Res. 20, 1145–1167.

Falkenhaug, T., Tande, K., Timonin, A., 1997. Spatio-temporal patterns in the copepod community in Malagen, Northern Norway. J. Plank. Res. 19, 449–468.

Frontier, S., 1972. Calcul de l'erreur sur un comptage de zooplancton. J. Exp. Mar. Biol. Ecol. 10, 121–132.

Hill, M.O., 1974. Correspondence analysis: a neglected multivariate method. Appl. Statist. 23, 340–354.

Irigoien, X., Castel, J., 1995. Feeding rates and productivity of the copepod *Acartia bifilosa* in a highly turbid estuary: the Gironde (SW France). Hydrobiologia 311, 115–125.

Jassby, A.D., Kimmerer, W.J., Monismith, S.G., Cloern, J.E., Powell, T.M., Schubel, J.R., Vendlinski, T.J., 1995. Isohaline position as a habitat indicator for estuarine populations. Ecol. Appl. 5, 272–289.

Laprise, R., Dodson, J.J., 1994. Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St. Lawrence Estuary. Mar. Ecol. Progr. Ser. 107, 67–81.

Lonsdale, D.J., 1977. Composition and seasonality of zooplankton of North Inlet, South Carolina. Chesapeake Sci. 18, 272–283.

Mallin, M.A., 1991. Zooplankton abundance and community structure in a mesohaline North Carolina Estuary. Estuaries 14, 481–488.

Mouny, P., Dauvin, J.C., Bessineton, C., Elkaim, B., Simon, S., 1996. Biological components from the Seine estuary: first results. Hydrobiologia 373/374, 333–347.

Mouny, P., 1998. Structure spatio-temporelle du zooplancton et du suprabenthos de l'estuaire de la Seine. Dynamique et rôle des principales espèces dans la chaîne trophique pélagique. Thèse de Doctorat du Muséum National d'Histoire Naturelle, Paris.

Palmer, M.W., 1993. Putting things in even better order: the advantages of Canonical Correspondence Analysis. Ecology 74, 2215–2230.

Sautour, B., Castel, J., 1995. Comparative spring distribution of zooplankton communities in three megatidal European estuaries. Hydrobiologia 311, 139–151.

Schlacher, T.A., Wooldridge, T.H., 1995. Small-scale distribution and variability of demersal zooplankton in a shallow, temperate estuary: tidal and depth effects on species-specific heterogeneity. Cah. Biol. Mar. 36, 211–227.

Soetaert, K., Rijswijk van, P., 1993. Spatial and temporal patterns of the zooplankton in the Westerschelde estuary. Mar. Ecol. Progr. Ser. 97, 47–59.

Soltampour-Gargari, A., Wellershaus, S., 1987. Very low stretches in estuaries – the main habitat of *Eurytemora affinis*, a plankton copepod. Meeresforschung 31, 199–208.

ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.

ter Braak, C.J.F., 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69, 69–77.

ter Braak, C.J.F., 1989. CANOCO-an extension of DECORANA to analyse species-environment relationships. Hydrobiologia 184, 169–170.

Turner, J.T., 1982. The annual cycle of zooplankton in a Long Island Estuary. Estuaries 5, 261–274.

Vecchione, M., 1989. Zooplankton distribution in three estuarine bayous with different types of anthropogenic influence. Estuaries 12, 169–179.

Wang, Z., Dauvin, J.C., Thiébaut, E., 1994. Preliminary data on the near bottom meso- and macrozooplanktonic fauna from the eastern Bay of Seine: faunistic composition, vertical distribution and density variation. Cah. Biol. Mar. 35, 157–176.