

# Benthic Boundary Layer fauna from the Seine Estuary (eastern English Channel, France): spatial distribution and seasonal changes

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One hundred and three suprabenthic hauls in the Seine Estuary were taken on a marine to fresh water gradient with a modified Macer-GIROQ sledge during 1996 to collect Benthic Boundary Layer fauna. Two main species assemblages were identified along the salinity gradient: (1) a marine assemblage located in the downstream part of the estuary dominated by amphipods and mysids such as *Schistomysis* spp. and *Gastrosaccus* spp.; (2) an estuarine assemblage essentially dominated by the mysid *Neomysis integer*, recorded along the salinity gradient with maximal abundance observed between 15–10 psu. The decapod *Palaemon longirostris* and the goby *Pomatoschistus microps* were located in the upstream part of the estuary where they presented maximal abundances. Some species used the estuary during juvenile development such as the mysid *Mesopodopsis slabberi* (Van Beneden, 1861) and decapod *Crangon crangon*. Although the morphological characteristics of the Seine Estuary (weak estuarine area and important dredging) are different than other major European estuaries such as Gironde, Westerschelde and Ems, the longitudinal distribution of the demersal community presented similar patterns in all sites. Nevertheless, monthly sampling permitted to determine the seasonal location and abundance changes of the demersal assemblages in the Seine estuary. Marine assemblages presented maximal densities during summer and autumn while estuarine species were most abundant during spring and summer. Longitudinal changes of main demersal species during an annual cycle showed an increase of spatial distribution along the salinity gradient for marine and neritic species during spring and summer with a penetration of species in the estuary. The abundances of both assemblages were very high (annual mean  $> 5000 \text{ ind } 100 \text{ m}^{-3}$ ) whereas the biomass of the estuarine assemblage was very important (annual mean  $\cong 38 \text{ g ash-free dry weight } 100 \text{ m}^{-3}$ ).

## INTRODUCTION

The main objective of this study was to document the spatial and temporal variation in community structure of the benthic boundary layer fauna, and especially for suprabenthic fauna, of the Seine estuary. Benthic Boundary Layer macrofauna (BBL macrofauna) can be classified into three groups according to their size and their bottom dependence (Wang & Dauvin, 1994; Wang et al., 1994; Zouhiri & Dauvin, 1996; Vallet & Dauvin, 1998): (1) mesozooplankton such as calanoid copepods and crustacean larvae; (2) macrozooplankton including euphausiids, chaetognaths, fish larvae, polychaetes and cephalopods; and (3) suprabenthos including all swimming bottom-dependent animals which perform seasonal or daily vertical migrations above the bottom (Brunel et al., 1978). The suprabenthos includes amphipods, cumaceans, decapods, isopods, leptostraceans, mysids, pycnogonids and tanaids. This mobile compartment is important in the functioning of coastal and estuarine ecosystems (e.g. Boyson, 1975; Buhl-Jensen & Fossa, 1991; Mees et al., 1993a; Mees & Jones, 1997). In estuaries, density and biomass of the suprabenthic compartment

are much higher than in neighbouring coastal areas. Mysids, such as *Neomysis integer* (Leach, 1814), are presenting very high abundances especially in the highly turbid brackish water zone and are important food for fish (Sorbe, 1981; Hamerlinck et al., 1990; Mouny et al., 1998; Zouhiri et al., 1998) and shrimp (Sitts & Knight, 1979). In estuarine systems, the suprabenthic community seems to be an important component of the food chain (Mees et al., 1993b; Mouny et al., 1998; Dauvin et al., 2000).

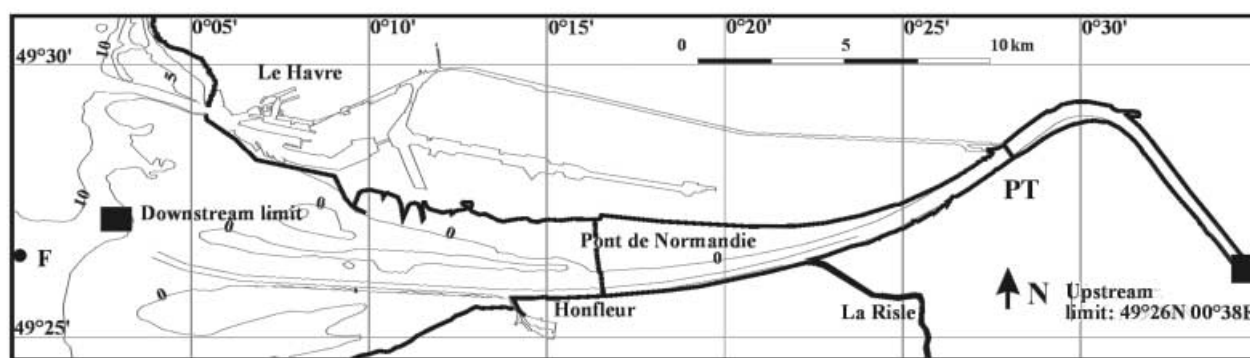
In the Seine Estuary, in contrast to many other northern European estuaries (Gironde, Westerschelde and Ems), few studies have recorded the BBL community. Studies of the suprabenthos have been conducted in the neighbouring coastal zone in the Bay of Seine (Wang & Dauvin, 1994; Vallet & Dauvin, 1998) and also in the estuary (Mouny et al., 1996, 1998). The aims of this study in the Seine Estuary were: (1) to identify the spatial structure and distribution of the BBL community, with an interest for suprabenthic fauna, from the outside part of the estuary (marine zone) to the freshwater part during the year in relation to environmental factors such as salinity, dissolved oxygen and turbidity; and (2) to identify seasonal changes in abundances of the distinct assemblages.

## MATERIALS AND METHODS

*Study site*

Sampling sites were located in the Bay of Seine and the Seine Estuary from the mouth of the estuary to the upstream limit of the salinity intrusion upstream of the Pont de Tancarville (Figure 1). The sites were chosen for their different environmental characteristics. A littoral site (F, 49°26'N–00°01'E, pk 371) with an important marine influence was at 10 m of depth (at low tide) on

muddy fine sand. This site was affected by freshwater discharge from the Seine River and the salinity remained lower than 35 psu throughout the year, the seabed salinity could be lower than 30 psu during Seine swelling (Table 1). Estuarine sites, located between 49°27'N–00°02'E (downstream limit, pk 370) and 49°26'N–00°38'E (upstream limit, pk 323), were affected by tidal intrusion and freshwater discharge which induced high salinity, turbidity and depth (between 5 and 10 m at low tide) changes. In this estuarine zone the Maximal Turbidity Zone (MTZ)



**Figure 1.** Map of the Seine Estuary (eastern English Channel, France) showing site F (49°26'N 00°01'E) and the estuarine sites located between the downstream limit (49°27'N 00°02'E) and the upstream limit (49°26'N 00°38'E) sampled in 1996. PT, Pont de Tancarville.

**Table 1.** Number (*N*) of samples and physical parameters recorded at site F (mean of salinity, temperature and turbidity of three samples) and for each longitudinal transect along the salinity gradient in the estuary from different months in 1996.

Date	N	Distance (pk)	Surface salinity (psu)	Bottom salinity (psu)	Surface temperature (°C)	Surface turbidity (mg l <sup>-1</sup> )	Bottom turbidity (mg l <sup>-1</sup> )	Freshwater discharge (m <sup>3</sup> s <sup>-1</sup> )
<b>Site F (49°26'N 00°01'E)</b>								
28 January	3	371	31.4	33.0	7.1	21.9	9.4	438
27 February	3	371	25.2	32.5	6.0	15.8	22.9	746
28 March	3	371	31.3	32.6	7.6	2.5	15.3	241
24 April	3	371	23.3	31.8	12.2	13.7	10.8	149
30 May	3	371	30.2	32.7	13.7	29.8	40.2	217
24 June	3	371	29.8	33.7	17.0	5.5	7.0	133
23 July	3	371	31.8	32.5	19.5	13.5	22.3	165
22 August	3	371	31.0	32.4	20.6	7.8	19.4	222
19 September	3	371	32.6	33.5	17.0	17.5	40.0	175
21 October	3	371	28.5	33.1	15.5	18.1	27.1	197
18 November	3	371	24.3	31.1	11.5	25.3	42.5	586
17 December	3	371	22.1	31.6	8.8	29.9	49.4	726
<b>Estuary</b>								
28 January	4	340–368	0.6–18.6	10.0–30.0	6.0–6.3	36.3–51.7	53.9–3881.3	438
25 February	6	340–363	0.4–16.4	0.5–23.9	5.8–7.0	25.3–47.6	54.4–485.0	641
27 March	6	331–362	1.7–12.6	2.4–18.3	9.3–10.0	20.0–35.2	62.2–1764.3	270
23 April	5	327–364	0.4–20.9	0.5–28.1	12.0–13.9	14.8–76.0	56.0–314.4	159
28 May	6	331–366	0.3–19.6	1.0–22.4	14.7–15.8	32.7–114.4	49.3–1758.0	256
25 June	6	323–354	1.0–20.9	1.5–30.6	18.8–21.7	28.8–76.3	52.9–2662.0	140
22 July	6	324–355	1.2–20.4	1.3–21.2	20.8–22.0	56.0–112.2	74.0–537.3	139
21 August	6	334–365	0.4–19.5	0.5–28.7	21.2–22.6	15.3–144.5	320.0–22890.0	224
18 September	6	326–362	0.8–19.5	0.7–19.7	16.6–17.9	101.1–590.0	392.2–63400.0	132
20 October	5	330–362	0.5–12.9	0.5–19.0	15.0–15.5	47.3–69.5	49.2–371.3	191
18 November	5	337–363	0.5–10.5	0.5–25.0	13.2–14.0	99.6–223.1	185.7–1700.0	586
16 December	6	338–370	0.4–18.5	0.4–30.6	6.9–8.2	38.1–109.8	105.5–12400.0	749

Pk, kilometric point (Paris corresponding to 0 km).

had an important influence on living resources. Suspended matter concentrations reached 15–590 mg l<sup>-1</sup> in surface waters and 50–63400 mg l<sup>-1</sup> near bottom throughout the year (Table 1). In 1996, the longitudinal salinity gradient encompassed values between 0.3 and 20.9 psu in surface waters and 0.4–30.6 psu near the bottom (Mouny, 1998).

For the different sampling sites, temperature fluctuated annually with the lowest temperature in winter (5°C) and the highest in summer (20–22°C). Over the year temperature in the estuary was higher than in the outer part of the estuary (site F) (Table 1).

#### Sampling strategy

All tows were collected with a new version of the Macer-GIROQ sledge (Dauvin & Lorgeré, 1989). This sledge allowed simultaneous sampling of the fauna at four levels between 0.10 and 1.45 m (net 1, 0.10–0.40 m; net 2, 0.45–0.75 m; net 3, 0.80–1.10 m; and net 4, 1.15–1.45 m) above the bottom with four WP2 plankton nets (0.5 mm mesh size). Each net was equipped with a Tsurimi Seiki Ku flowmeter to measure the volume of seawater filtered. Mean speed during the 5 min hauls was 1.5 m s<sup>-1</sup>. Trawling was done against the tide. Sampling occurred monthly during an annual cycle over 1996 with respectively three sledges at site F around the ebb tide to study the compartment of coastal fauna with the freshwater

intrusion and, one sledge at each site of the transect along the salinity gradient in the estuary realized during the flood tide for study the compartment of estuarine fauna with the marine water intrusion. Environmental parameters were recorded at each sampling station such as surface and bottom salinity, temperature, turbidity and dissolved oxygen. The total number of sledges realized at each month is given in Table 1.

Materials collected were fixed with 10% neutral formalin, washed and transferred to 70% ethanol. The organisms were sorted under a dissecting microscope, counted and identified to species level. All species sampling by suprabenthic sledge were studied including suprabenthic fauna such as amphipods, cumaceans, decapods, isopods, mysids and pycnogonids, macrozooplankton such as the chaetognaths *Sagitta elegans* Verrill (1873) and *S. setosa* Müller (1847) and different fish larvae (gobiidae, clupeidae or gadidae), and the ctenophore *Pleurobrachia pileus* (O.F. Müller, 1776) (Mouny, 1998; Vallet & Dauvin, 1998; Zouhiri et al., 1998). The individual dry weight of each taxon at each site was measured after oven-drying at 80°C and the ash-weight after further heating at 550°C for 2 h. The ash-free dry weight (AFDW) is the difference between these two values. The mean total number of individuals collected in the four nets of the sledge and biomass of each species or taxon were standardized to 100 m<sup>-3</sup>.

**Table 2.** List and codes of demersal species (sampled with the suprabenthic sledge) used in the different statistical analyses.

Suprabenthic species		Decapoda	
Amphipoda			
<i>Ampelisca</i> spp.	ampe	<i>Carcinus maenas</i>	cmae
<i>Amphilocheus neapolitanus</i>	anea	<i>Crangon crangon</i>	ccra
<i>Apherusa</i> spp.	aphe	<i>Galathea intermedia</i>	gint
<i>Atylus</i> spp.	atyl	<i>Hippolyte</i> spp.	hypp
<i>Bathyporeia</i> spp.	bath	<i>Liocarcinus pusillus</i>	lpus
<i>Corophium</i> spp.	coro	<i>Palaemon longirostris</i>	plon
<i>Gammarus</i> spp.	gamm	<i>Palaemon serratus</i>	pser
<i>Leucothoe incisa</i>	linci	<i>Pinnotheres pisum</i>	ppis
<i>Megaluropus agilis</i>	magi	<i>Pisidia longicornis</i>	psid
<i>Melita obtusata</i>	mobt	<i>Pontophilus</i> spp.	pbis
<i>Orchomenella nana</i>	onan	<i>Processa nouveli</i>	pnou
<i>Pariambus typicus</i>	ptyp	Fishes	
<i>Perioculodes longimanus</i>	perio	<i>Pomatoschistus microps</i>	pmic
<i>Phthisica marina</i>	pmar	<i>Pomatoschistus minutus</i>	pmin
<i>Stenothoe marina</i>	smar		
Isopoda		<b>Macrozooplanktonic species</b>	
<i>Sphaeroma serratum</i>	sser	Ctenophora	
Mysidacea		<i>Pleurobrachia pileus</i>	ppil
<i>Anchialina agilis</i>	aagi	Chaetognatha	
<i>Gastrosaccus spinifer</i>	gspe	<i>Sagitta elegans</i>	sele
<i>Gastrosaccus</i> spp.	gast	<i>Sagitta setosa</i>	sset
<i>Mesopodopsis slabberi</i>	msla	Fish larvae	
<i>Mysidopsis gibbosa</i>	mgib	Gadidae	lgad
<i>Neomysis integer</i>	nint	Gobiidae	lgob
<i>Paramysis helleri</i>	phel	Clupeidae	lclu
<i>Schistomysis</i> spp.	schis	Pleuronectidae	lple
<i>Siriella jaltensis</i>	sjal	Solidae	lsol
Cumacea		<i>Trisopterus</i> spp.	ltris
<i>Bodotria pulchra</i>	bpul		
<i>Bodotria scorpioides</i>	bsco		
<i>Diastylis</i> spp.	dias		
<i>Endorella trunculata</i>	etru		
<i>Pseudocuma longicornis</i>	pseu		

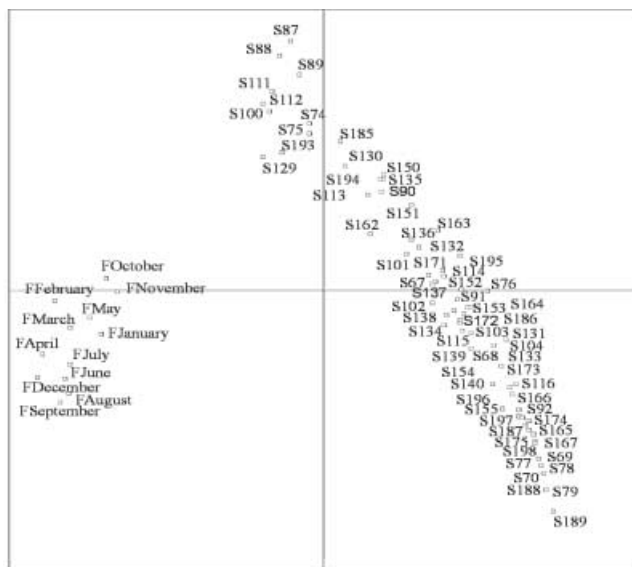
*Data analysis*

Correspondence analysis was used to determine the longitudinal structure of the suprabenthic fauna with a data matrix plotting all sites sampled in 1996 (one value for site F corresponding to the mean of the total number of individuals collected in the three sledges in each month; four to six sites along the estuary: four sites in January, five sites in April, October and November and six sites for the other months in 1996) and 53 taxa characterized by abundance superior with 1 individual per 100 m<sup>-3</sup> (species listed and coded in Table 2). Data were log transformation to minimize the effect of the dominant species (Field et al., 1982). Sites were classified into groups by hierarchical classification using the Bray–Curtis distance (Bruynhooge, 1978; Jambu & Lebeaux, 1978). Correspondence analysis was also performed to determine the seasonal changes in the suprabenthic assemblage at site F (12 months and 46 taxa) and in the estuary (12 months: species abundances averaging on all sites of each monthly longitudinal transect: 21 taxa). Hierarchical classification, with the Bray–Curtis distance, was performed on the same data to define the different temporal assemblages. Correlation analysis and Pearson test (*t*-test, Scherrer, 1984) were used to determine the relation between densities of the main suprabenthic estuarine species and the most important environmental parameters such as salinity, turbidity and dissolved oxygen.

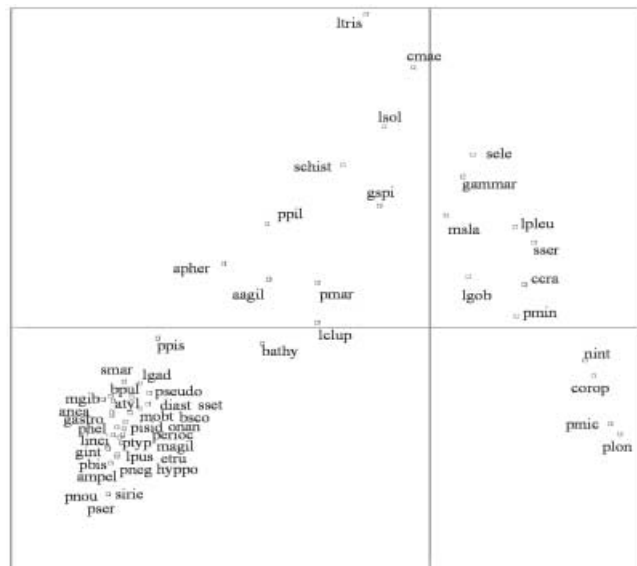
**RESULTS**

*Longitudinal structure of suprabenthic fauna*

Correspondence analysis, performed on all data collected in 1996, distinguished two main groups of sites (Figures 2 & 3). The first assemblage was related to site F. The second assemblage plotted all estuarine sites along a salinity gradient from S87–88 (downstream, high salinity) to S189 (upstream, low salinity).



**Figure 2.** Projection of sites on the first two axes of correspondence analysis performed on species abundances data recorded along the salinity gradient in 1996. FJanuary to FDecember, marine coastal sites (F); S87–S189, estuarine sites.



**Figure 3.** Projection of species on the first two axes of correspondence analysis performed on species abundances data recorded along the salinity gradient in 1996.

The first assemblage was characterized by marine amphipods (*Atylus* spp., *Orchomenella nana*, *Perioculodes longimanus*, *Pariambus typicus*), cumaceans (*Diastylis* spp., *Endorella trunculatulata*), mysids (*Paramysis helleri*, *Gastrosaccus lobatus*) and decapods (*Pontophilus* spp.). The estuarine pattern was essentially characterized by the estuarine mysid *Neomysis integer*, the decapod *Palaemon longirostris* Milne Edwards (1837), the gobiid *Pomatoschistus microps* (Kröyer, 1838) and neritic species using the estuarine zone such as the decapod *Crangon crangon* (L., 1758) and the gobiid *Pomatoschistus minutus* (Figure 3).

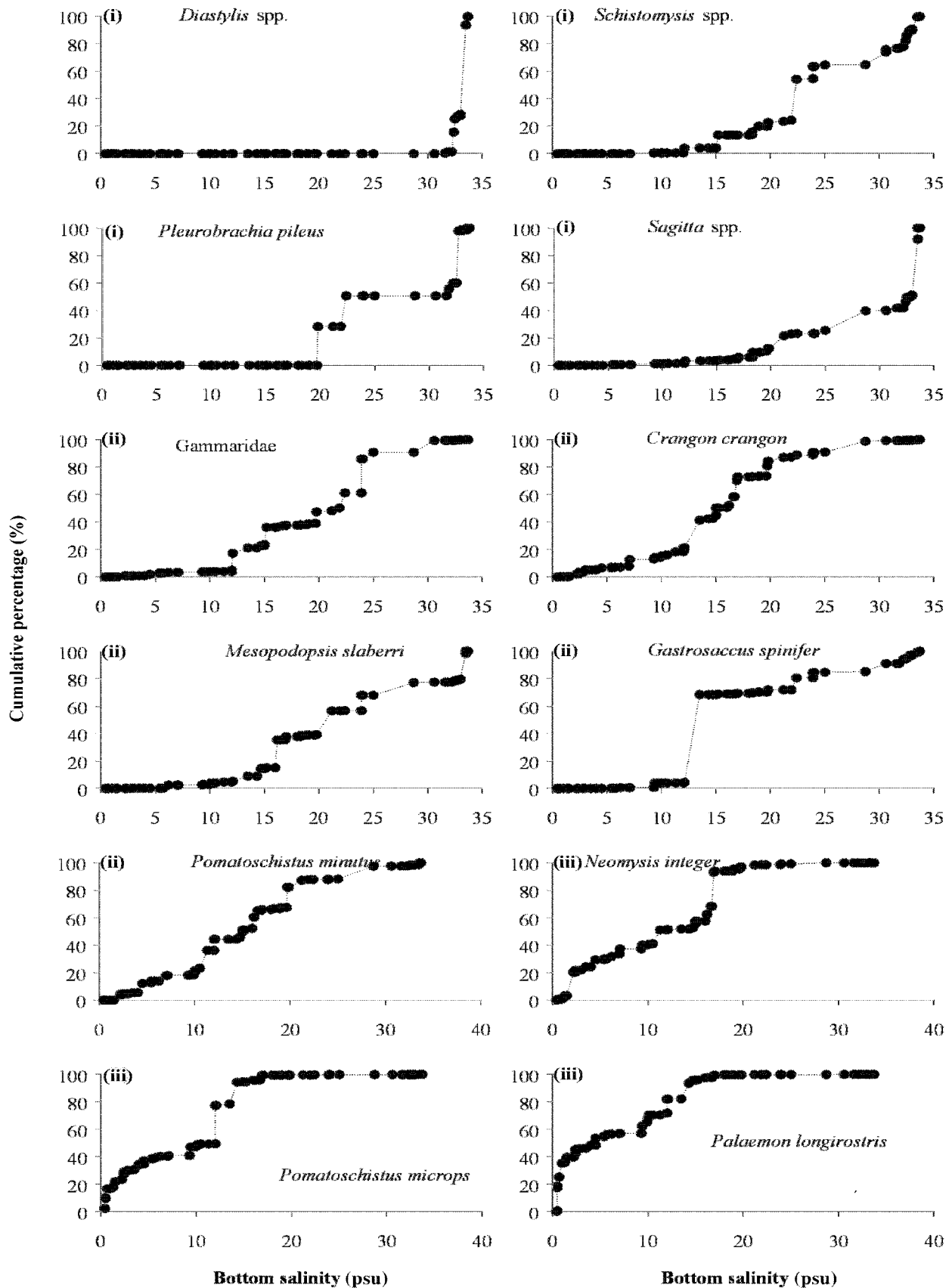
The correlation analysis confirmed the major role of bottom salinity on the longitudinal structure of the dominant suprabenthic species (Table 3). *Neomysis integer* was the single species showing no significant correlation between longitudinal distribution and bottom salinity. However, its distribution was correlated significantly with turbidity as was the distribution of *Palaemon longirostris* and *Pomatoschistus microps*. Species distribution in the Seine Estuary was not correlated with the dissolved oxygen gradient (Table 3).

The trend of cumulative percentages in abundance of the main demersal species as a function of bottom salinity showed three distinct patterns (Figure 4): (i) marine species with high abundances recorded only in marine

**Table 3.** R-value of correlation between densities of demersal species and main bottom environmental factors in the Seine Estuary.

	Salinity	Turbidity	Dissolved oxygen
<i>Mesopodopsis slabberi</i>	0.507*	0.172	0.255
<i>Neomysis integer</i>	0.042	0.586*	0.235
<i>Crangon crangon</i>	0.422*	0.07	0.091
<i>Palaemon longirostris</i>	0.428*	0.525*	0.304
<i>Pomatoschistus microps</i>	0.426*	0.535*	0.256
<i>Pomatoschistus minutus</i>	0.411*	0.111	0.017

\*, statistical significance (Pearson test, *P* < 0.05).



**Figure 4.** Trend of cumulative percentage of the abundances of the main species (plot of all abundances recorded in 1996, site F+ estuarine sites) along the bottom salinity gradient: (i) marine species; (ii) species using estuary only during part of their life; and (iii) estuarine species.

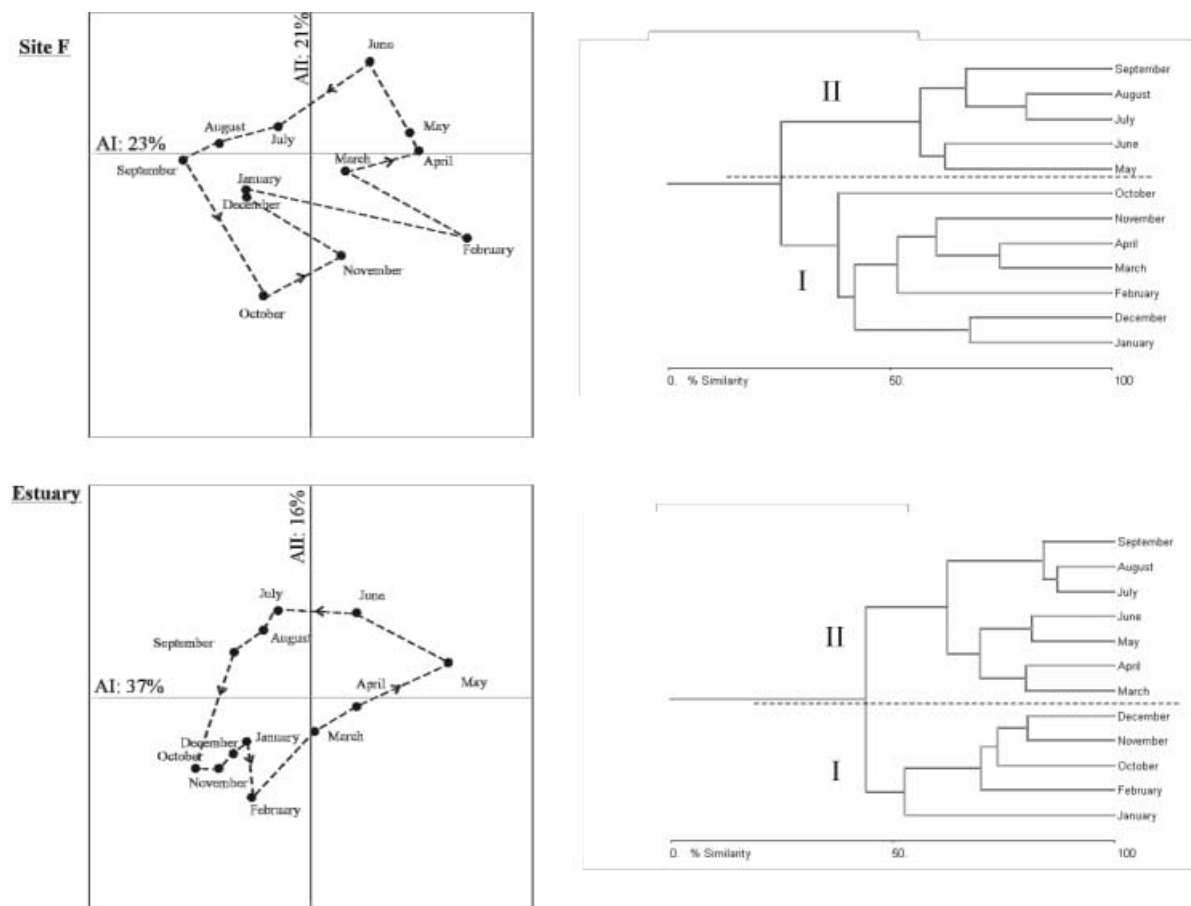
waters (downstream part of the estuary and site F) such as the cumacean *Diastylis* spp., the mysid *Schistomysis* spp. and the ctenophore *Pleurobrachia pileus*. (ii) Species using the estuary only over part of their life cycle with an important population located between 10 and 15 psu: gammaridae, decapod *C. crangon*, mysids *Mesopodopsis slabberi* (Van Beneden, 1861) and *Gastrosaccus spinifer*, and gobiid *Pomatoschistus minutus* (Figure 4). (iii) Typically estuarine species, mysid *N. integer*, gobiid *P. microps* and decapod *Palaemon longirostris*; these two latter species showing maximal abundances in the inner part of the estuary with low salinity range (0–5 psu).

#### Temporal changes—seasonality

The correspondence analysis with data recorded at site F (AI, 23%; AII, 21%) completed by hierarchical

analysis distinguished two different temporal periods (Figure 5). The first period can be subdivided in three other subperiods: (i) winter period (December and January); (ii) beginning of the spring and November; and (iii) October (Figure 5). The second period plotted the spring and summer months with two distinct subperiods: (i) end of spring (May and June); (ii) summer with July, August and September. For the estuarine data, the analysis also described the presence of two periods (AI, 37%; AII, 16%). The first period plotted the autumnal and winter months (October to February) when the second assemblage was related to the spring and summer periods (Figure 5). These classifications seem to be related to the seasonal patterns of suprabenthic species abundances at site F and in the estuary.

The suprabenthic fauna was always more diverse at site F than in the estuary throughout the year with a



**Figure 5.** Correspondence analyses and hierarchical classification performed on densities of demersal species in site F and estuary (mean of densities recorded in all estuarine sites) in the Seine Estuary 1996.

**Table 4.** Seasonal changes of maximum suprabenthos species number collected at site F (pk 371) and in the Seine Estuary.

	Spring		Summer		Autumn		Winter	
	F	Estuary	F	Estuary	F	Estuary	F	Estuary
Amphipoda	17	4	19	2	21	3	25	1
Mysidacea	7	5	8	4	10	2	10	1
Cumacea	7	3	7	0	6	0	5	0
Decapoda	6	2	11	2	8	2	7	2
Total suprabenthos	38	17	46	11	46	9	48	6

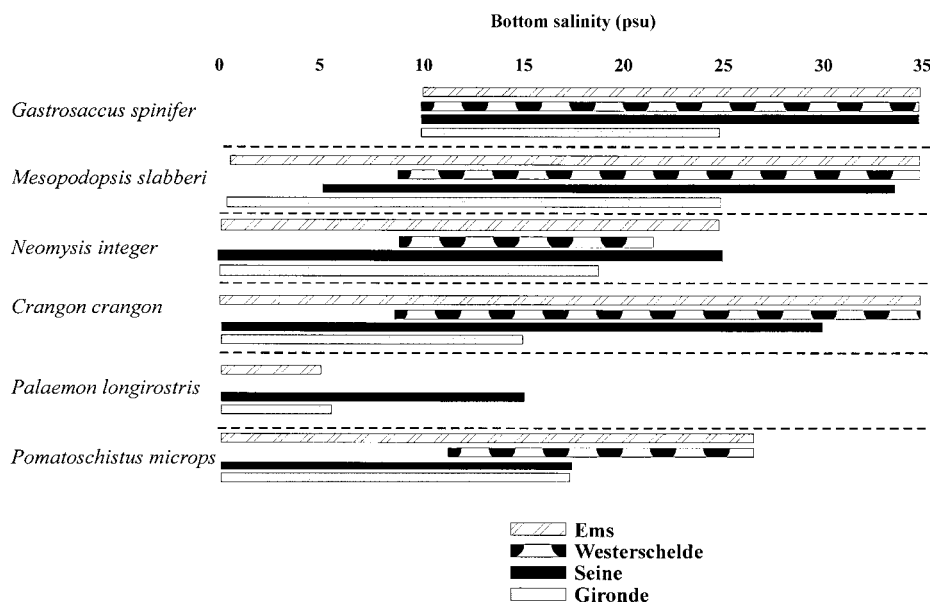
minimum of 38 taxa recorded in spring and the maximal value (48 taxa) observed in winter compared to the estuary where just six taxa were recorded in winter and a maximum of 17 taxa were observed in spring (Table 4).

Amphipods are an important zoological group in the suprabenthic community at site F with 17–25 species observed, followed mysids (7–8), cumaceans (5–7) and decapods (6–11). In the estuary, the suprabenthic commu-

**Table 5.** Percentage composition of the abundance of suprabenthos, macrozooplankton and main suprabenthic species, mean abundances ( $N\ 100\ m^{-3}$ ), mean biomass (mg AFDW  $100\ m^{-3}$ ) in site F (mean of three sledges) and in the Seine Estuary (mean of all stations sampling at each month along the salinity gradient) during 1996.

	J	F	M	A	M	J	J	A	S	O	N	D
Site F (49°26'N 00°01'E)												
Mysidacea												
<i>Gastrosaccus spinifer</i>	–	20	2	–	1	1	–	–	–	1	10	–
<i>Mesopodopsis slabberi</i>	68	–	5	1	1	–	10	8	35	80	4	3
<i>Schistomysis ornata</i>	1	20	16	1	5	1	9	7	2	1	27	18
Cumacean												
<i>Diastylis</i> spp.	15	3	47	37	11	47	68	75	50	1	34	21
Suprabenthos	92	55	85	47	25	76	94	98	97	86	88	93
Macrozooplankton	8	45	15	53	75	24	6	2	3	14	12	7
Mean abundance ( $N\ 100\ m^{-3}$ )	768	718	516	802	5162	4186	4364	6087	40878	1493	440	468
Mean biomass (mg AFDW $100\ m^{-3}$ )	372	252	292	195	636	1129	1241	2306	16282	569	258	179
Estuary												
Mysidacea												
<i>Mesopodopsis slabberi</i>	–	2	29	23	9	16	16	14	1	–	–	4
<i>Neomysis integer</i>	66	19	26	44	49	66	82	69	86	67	9	45
Decapodea												
<i>Crangon crangon</i>	–	1	1	–	–	1	–	1	1	1	1	1
<i>Palaemon longirostris</i>	33	29	12	11	1	1	–	13	8	25	59	21
Fish												
<i>Pomatoschistus microps</i>	1	20	5	4	1	–	–	–	2	6	15	11
<i>Pomatoschistus minutus</i>	–	5	1	–	–	–	1	1	2	1	1	1
Suprabenthos	100	98	93	88	77	78	99	99	99	99	97	98
Macrozooplankton	–	2	7	12	23	22	1	1	1	1	3	2
Mean abundance ( $N\ 100\ m^{-3}$ )	1233	447	1163	2631	8153	25618	25980	26594	9445	4081	2402	664
Mean biomass (mg AFDW $100\ m^{-3}$ )	44301	17300	24374	24720	46682	29676	29278	83357	41267	21137	79098	13470

–, % < 1.



**Figure 6.** Comparative distribution along the bottom salinity gradient of main demersal species in four north European estuaries (Ems, Westerschelde and Gironde, Mees, 1994; Seine, this study).

nity was less diverse with 1–5 mysids, a maximum of three cumacean species and only two decapods: the migrant *C. crangon* and the endemic *P. longirostris*.

Throughout the year, the demersal fauna was more abundant in the estuary than at site F, except in September when abundance at site F (40,878 ind 100 m<sup>-3</sup>) was higher than in the estuary (9445 ind 100 m<sup>-3</sup>) largely related to the maximal abundance of the cumacean *Diastylis* spp. Suprabenthic species biomass were always greatest in the estuary (between 13 and 83 g AFDW 100 m<sup>-3</sup>) than at site F (0.2–16 g AFDW 100 m<sup>-3</sup>) (Table 5). This very important biomass of the suprabenthic community in the estuary can be explained by the presence of important densities of species with high individual biomasses such as the decapod *P. longirostris* and the goby *Pomatoschistus microps*. At site F and in the estuary, suprabenthic species dominated the Benthic Boundary Layer fauna throughout the year, representing 98–99% of total abundance (except in spring (April and May) at site F). In the estuary, the suprabenthic fauna was dominated throughout the year by mysids and especially *N. integer* which represented between 9.4 (November) to 86.1% (September) of the suprabenthic abundances. The two estuarine decapods represented just a maximum of 58.8% for *Palaemon longirostris* and 1.4% for *C. crangon*, of the suprabenthic abundances in the estuary. The suprabenthic gobiids *Pomatoschistus microps* and *P. minutus*, represented respectively a maximum of 19.6 and 5.2% in February of total suprabenthic abundances (Table 5). At site F (marine waters), the suprabenthic community was dominated by cumaceans (*Diastylis* spp., *Pseudocuma longicornis*) and represented between 1% (October) and 75% (August) of the suprabenthic community. Mysids represented the second faunistic group of the boundary layer fauna at site F and formed up to 82% of total abundance in October. The mean annual abundance and biomass were respectively 5490 ind 100 m<sup>-3</sup> and 2.0 g AFDW 100 m<sup>-3</sup> and 9034 ind 100 m<sup>-3</sup> and 37.9 g AFDW 100 m<sup>-3</sup> at site F and estuarine sites.

## DISCUSSION

The first faunal assemblage, determined by correspondence analysis, was related to site F located at the mouth of the estuary associated to high salinity. It was mainly dominated by mysids, cumaceans, amphipods and decapods. This assemblage is similar to those found in the coastal waters of the Voordelta (Netherlands) where demersal fauna is essentially characterized by high densities of *Mesopodopsis slabberi* and *Schistomysis* spp. (Mees & Hamerlinck, 1992; Mees et al., 1993a,b; Mees, 1994). The second assemblage recorded corresponded to species which colonized the different zones of the estuary. Although, the Seine Estuary is relatively short (maximum 30 km from estuary mouth to Tancarville), in comparison with the Gironde Estuary (≈60 km from mouth to Ambès), the longitudinal distribution of main demersal species remain similar to those found in other European estuaries (Figure 6). In the Westerschelde Estuary, the important anoxia of the upstream zone explains the absence of demersal species in this area and particularly estuarine species such as the *Palaemon longirostris* are totally absent from this estuary (Mees,

1994; Mees et al., 1995). The influence of dissolved oxygen was not significant in the Seine Estuary in relation to a temporarily deficit only during the summer period limited in the upstream part of the estuary. The Gironde Estuary is characterized by a weak output of estuarine and neritic demersal species in marine waters as records for *Gastrosaccus spinifer* and *M. slabberi* (Figure 6). On the other hand, as recorded in the Seine Estuary by Mouny (1998), the longitudinal pattern of demersal species is directly influenced by the salinity gradient (Jassby et al., 1995; Locke & Courtenay, 1995). The distribution of suprabenthic species in the Seine Estuary showed no direct influence from turbidity except for the estuarine species (*Neomysis integer*, *Palaemon longirostris* and *Pomatoschistus microps*) remained close to the maximal turbidity zone which could be a favourable zone for nutrition (accumulation of zooplanktonic species as copepod *Eurytemora affinis*).

Three different kinds of species are recorded in the Seine Estuary. Neritic species are located in marine and coastal waters of the Bay of Seine such as the cumacean *Diastylis* spp., the ctenophore *Pleurobrachia pileus* or marine mysids; they present maximal abundances in marine waters near the Seine Estuary or in the Bay of Seine (Wang et al., 1994; Vallet, 1997). The second kind of demersal species, recorded in the Seine Estuary, involves marine or euryhaline species living in the coastal (with estuarine dependant juvenile development) such as the mysid *M. slabberi* (Hamerlinck & Mees, 1991; Moffat & Jones, 1993), the decapod *Crangon crangon* or the goby *Pomatoschistus minutus*. This behaviour suggest that species notably during their juvenile stages must be able to select favourable environmental conditions for their development. The last category of species found in the Seine Estuary includes typically estuarine species such as the mysid *N. integer*, the decapod *Palaemon longirostris* and the goby *Pomatoschistus microps* which live throughout the year in the lowest salinity zone where they show their maximal abundances. They are rarely found in the coastal marine area (site F) and occur mainly during important fresh-water discharge events in autumn and winter. This category was also observed in the Gironde (Sorbe, 1983), the Loire (Marchand, 1981) or the Ythan (Healey, 1972) estuaries.

Several neritic species showed spring and summer migrations in the estuary which found in this zone important densities of mesozooplankton (e.g. *Eurytemora affinis*), favourable to juvenile development. As an example, *M. slabberi* colonized an important part of the estuary up to 5 psu (bottom salinity) in spring while this mysid was located in the downstream part of the estuary (site F) in autumn and winter (maximal abundance recorded in September in this coastal zone). The marine coastal decapod *C. crangon* and suprabenthic fish *P. minutus* showed similar inputs of individuals in the estuarine zone during spring and summer with high abundances of juveniles during these periods (Mouny, 1998). Nevertheless, a majority of the suprabenthic community such as cumaceans or amphipods recorded at site F did not migrate in the estuary. On the other hand, typically estuarine species always were located in the estuary without output in the marine part of the estuary, as the most important estuarine mysid *N. integer*, the decapod *Palaemon longirostris*



and the goby *Pomatoschistus microps* were always located in the upstream part of the estuary along the year ( $S < 10$  psu).

The estimated abundances of the demersal assemblages (site F, estuary) are of the same order of magnitude as those reported by Mees & Jones (1997) for shallow waters and estuaries: 100–80,000 ind  $100\text{ m}^{-3}$ . The ratio between the maximal abundance and minimal abundance reached 93 at site F and 60 in the estuary, and the maximal abundance observed at site F (September) and during summer in the Seine Estuary are amongst the highest values reported in the literature (Mees & Jones, 1997; Dauvin et al., 2000). Nevertheless, these reported values are the mean of three (site F) or four to six (estuary) samples (=sledge); so, the maximum abundance observed in one sledge is sometimes very high, and the maximum abundance observed for the mysid *N. integer* reached 216,000 ind  $100\text{ m}^{-3}$  which is higher than those reported by Mees & Jones (1997) for other European estuaries. Nevertheless, the maximum abundance of *M. slabberi* observed in the Seine Estuary ( $> 34,000$  ind  $100\text{ m}^{-3}$ ) is lower than that observed in spring in the Tamar Estuary ( $> 100,000$  ind  $100\text{ m}^{-3}$ ) (Moffat & Jones, 1993). The maximum abundance reported in the Seine Estuary and site F of the other following species such as the goby *P. microps*, the decapod *Palaemon longirostris* and the cumacean *Diastylis* spp. are amongst the highest reported in the English Channel (Mees & Jones, 1997; Mouny, 1998).

The abundance and the biomass of both assemblages are amongst the highest reported in the literature. In fact, the annual mean abundance of suprabenthic fauna estimated at site F (5490 ind  $100\text{ m}^{-3}$ ) and at the estuary site (9034 ind  $100\text{ m}^{-3}$ ) are amongst the highest values reported in the literature (Mees & Jones, 1997; Dauvin et al., 2000). The estimated mean annual biomass of suprabenthic fauna is very important in comparison with mean annual biomass recorded in marine coastal zone (maximum of 16.4 g AFDW  $100\text{ m}^{-3}$ ). In the estuary, the suprabenthic fauna profits by high phytoplankton biomass and high mesozooplankton biomass which are the main diet of the demersal fauna (Mouny, 1998). So, the suprabenthic fauna appeared as a major link between primary production and the higher level of the trophic chain as fish juveniles such as sea bass *Dicentrarchus labrax* and the flounder *Platichthys flesus* which preferentially eat suprabenthic species such as mysids and decapods (Mouny, 1998; Mouny et al., 1998).

In conclusion, the suprabenthic fauna collected in the Seine Estuary is composed of two main assemblages. In the outer part of the estuary, the fauna is characterized by marine species, several neritic species using the inner part of the estuary for juvenile growth such as *M. slabberi*, *C. crangon* and *Pomatoschistus minutus*. The upstream part of the estuary is dominated by a typically estuarine fauna with *Palaemon longirostris*, *Pomatoschistus microps* and *N. integer*. The most abundant estuarine species, *N. integer*, shows a larger distribution than both the endemic species which colonize only the upstream part of the estuary. The particular morphological characteristics of the Seine Estuary do not influence the distribution of suprabenthic species related to the salinity gradient. This is contrary to the mesozooplanktonic assemblages which show a mixing

of different species in the neritic coastal and estuarine zones (Mouny, 1998). In spite of the important anthropogenic influence (dredging, pollutants), the Seine Estuary, with important densities of zooplanktonic and suprabenthic fauna, seems to hold a preponderant role in the functioning of the Bay of Seine system, as an active nursery for several suprabenthic species. These form important food webs for marine benthic and fish communities of the Bay of Seine (Mouny et al., 1996). The important abundances and biomass found in the Seine Estuary shows that this estuary remains one of the most productive ecosystems of the north European coastal systems.

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