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Biological components from the Seine estuary: first results

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Abstract

The Seine estuary plays an important role in the dynamics of the eastern English Channel ecosystem. Nevertheless, its biological compartment is poorly known. This constitutes an important handicap to establish the precise state of the health of this major European estuary. The objectives of this study were to identify the life resources of the estuary: macrobenthos, mesozooplankton, suprabenthos, and fish populations and to define the main trophic links in two parts of the estuary (i.e. the polyhaline and oligohaline zones). There is an impoverishment of the biological diversity from the polyhaline zone to the oligohaline zone. The benthic and pelagic fauna of the Seine estuary is similar to other North-Eastern Atlantic estuaries. But the pelagic fauna, especially the copepod *Eurytemora affinis* and the shrimp *Palaemon longirostris* seemed to be more abundant in the Seine estuary than in other estuaries. Two macrobenthic communities occurred in the estuary: a diversified and abundant *Abra alba-Pectinaria koreni* community in the outer part of the estuary and a *Macoma balthica* community in the inner part. This latter was especially poor in specific richness, density and biomass, in all areas, except on tidal mud flats. Two trophic chains were identified. In the oligohaline zone corresponding to the maximum turbidity zone (high turbidity, low concentration of oxygen), the trophic chain was exclusively planktonic due to the dredging of the estuary which prevented permanent benthic fauna formation. In this zone, the number of fishes was relatively low in spite of high biomass of mesozooplankton and suprabenthos. In the outer part of the estuary, low turbidity and high concentration of oxygen are more favourable to fish populations which feed especially on benthic fauna.

Introduction

The Seine estuary is the largest macrotidal estuary in the English Channel, with an area of about 150 km^2 at high tide. Freshwater input into the estuary is mainly from the Seine river with a drainage area of approximately 78 650 km^2. The discharge varies seasonally from a maximum of 2 000 $m^3\ s^{-1}$ in winter to a minimum of 100–200 $m^3\ s^{-1}$ in summer. Mean annual discharge ranges from 240 to 625 $m^3\ s^{-1}$ with an average of 380 $m^3\ s^{-1}$ (Avoine, 1986). It is an important area for the French economy, because 1/4 of the French population and 1/3 of the industry and agriculture are concentred along the Seine river.

Several multidisciplinary research programs have occurred in the Bay of Seine (especially during the beginning of the 1980s; Cabioch, 1986). The distribution and dynamics of marine benthic communities in the eastern part of the Bay of Seine were studied (e.g. Gentil et al., 1986; Dauvin & Gillet, 1991; Thiébaut et al., 1997). Data on mesozooplankton and suprabenthos were given later by Wang & Dauvin (1994) and

Wang et al. (1994, 1995) at the mouth of the estuary. The distribution of the ctenophore *Pleurobrachia pileus* was also studied in spring with several sets of spring plankton and suprabenthos samples (Wang et al., 1995).

Nevertheless, knowledge on the composition and distribution of the fauna in the Seine estuary remained very limited, and concerned only the outer part of the estuary during the 'Schéma d'Aptitude à l'Utilisation de la Mer' (at the end of the 1970s, SAUM, 1980). In 1978–1979, quantitative measurement on the distribution of subtidal macrobenthic communities was conducted from the mouth of the estuary to the upstream limit of the salinity intrusion (Proniewski & Elkaim, 1980). The distribution of intertidal macrobenthic communities was also studied by Desprez (1981). In the inner part of the estuary, the distribution of the Maximum Turbidity Zone and environmental parameters, e.g. concentrations of pollutants and dissolved oxygen are well described (Avoine, 1981).

Moreover, the Seine estuary was the main nursery ground of the English Channel (Duval, 1982). Conversely, the data on the fauna from other main estuaries of French coasts and North-Eastern Atlantic was well documented: e.g. Gironde (Castel, 1981; Sorbe, 1981), Loire (Robineau & Marchand, 1984; Marchand, 1981), Schelde (Mees, 1994; Mees et al., 1995; Soetaert & van Rijswijk, 1993), and Ems (Baretta & Malschaert, 1988).

The present study, as a part of the French Seine-Aval program, was initiated in 1995 to examine the life resources and to define the main trophic links within each part of the Seine estuary in order to: (i) to describe the gross taxonomic composition of the main biological compartments, i.e. macrobenthos, mesozooplankon, suprabenthos and ichtyofauna mainly in two seasons spring and autumn, (ii) to describe the main components of the trophic chains in the inner and outer parts of the estuary.

Study site

To assess the distribution of live resources, samples were collected from the mouth of the estuary (East of 0 of longitude) to the upstream limit of the salinity intrusion upstream Pont de Tancarville (see Figure 1).

Sampling strategy and treatment of the samples

Macrobenthos

Three replicates were collected at each station using a Smith McIntyre grab (0.10 m^2), 14 were taken on November 1993 to estimate the specific composition, density and biomass of the macrofauna from the subtidal zone of the mouth of the estuary (Fosse Nord: five stations, and Fosse Sud: five stations, three from the outer part and two from the inner part), and in the navigation channel along a transect of four stations from the mouth of the Seine estuary to the inner part of the estuary near the Pont de Tancarville. Three transects (Pont de Normandie, Marais du Hode and Pont de Tancarville) with four to six stations were sampled in the inner part of the estuary in May and October 1995: 14 stations in May (3 intertidal and 11 subtidal), and 12 subtidal stations in October. The samples were taken with a benthic corer with a surface 0.0625 m^2 (four replicates at each station) at the intertidal stations. A 'Rallier du Baty' dredge was used in the subtidal stations, so that about 30 to 40 l of sediment were preserved for each dredge sample.

After, the sediment was sieved (1 mm mesh), the retained material was sorted twice. The samples were fixed with 10% neutral formalin and identified to specific level. The dry weight (DW) of each species was determined and results were expressed as number of animals or biomass per m^2.

Mesozooplankton

Mesozooplankton were obtained using a WP2 (200 μm mesh size) plankton net with a TSK flowmeter in the mouth part to measure the volume of filtered water. The plankton net was hauled oblique from bottom to the surface against the tide. To assess the spatial distribution of the mesozooplankton in the estuary, a set of samples was taken during a daytime flood tide along a transect of 5 to 6 stations with a salinity gradient from 25.6 to 0.4 P.S.U. (SAPO32/Pk371 to SAPO37/Pk336 upstream Pont de Tancarville) in May 1994 and 12.1 to 0.4 P.S.U. in September 1995 (SAPO96/Pk365 to SAPO100/Pk336) (see Figure 1, Table 1). Materials collected were fixed with 5% neutral formalin 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 subsampling method (Frontier, 1972). The ash-fresh dry weight (AFDW) of each species was determined and results were expressed as number of organisms or AFDW biomass m^{-3}.

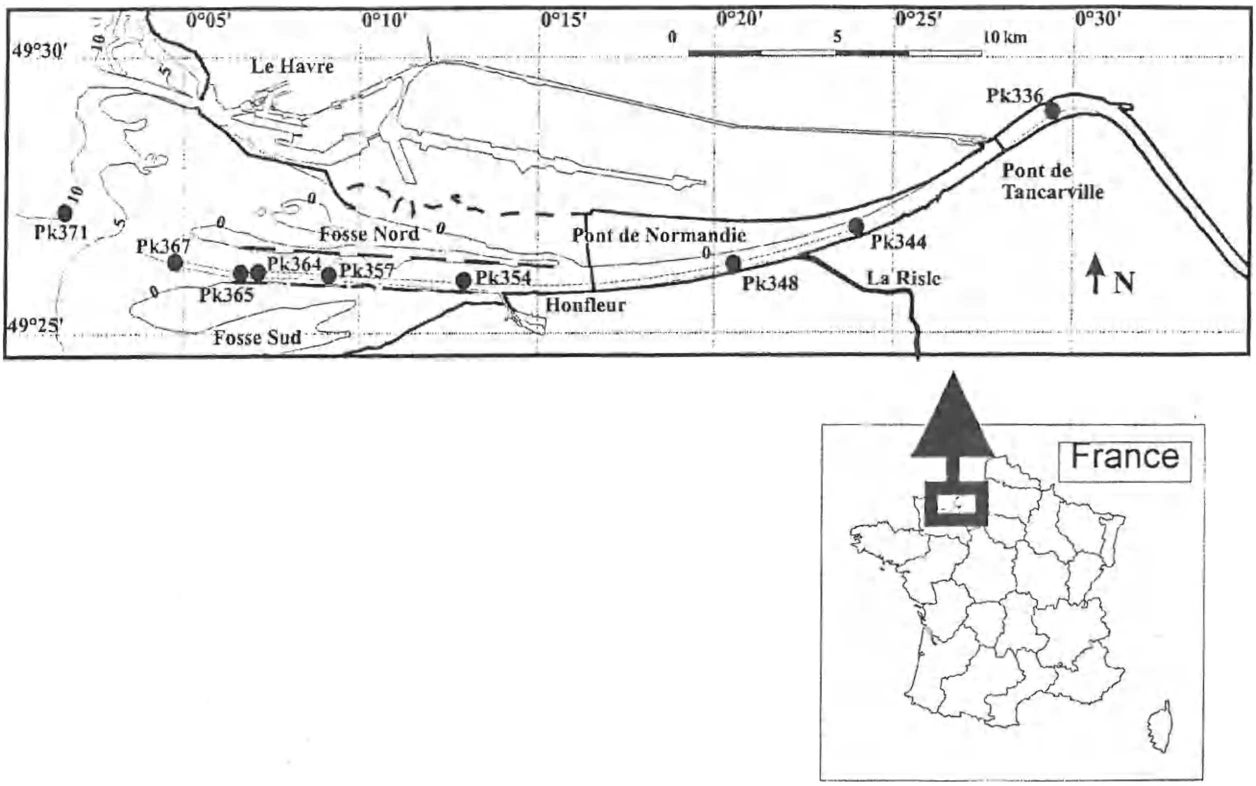

Figure 1. Map of the Seine estuary showing the different sampling stations.

Table 1. Sampling stations for the different areas of the estuary with indication of their environmental characteristic. Nm: number of mesozooplankton sample, Ns: number of suprabenthic sample, Pk: kilometric point (Pk = 0 at Paris), Hr: hour of sampling (HT: High tide at the Havre; May 1994: HT = 15:55, September 1995: HT = 15:55).

	Date	Type	Sampling station				Environmental characteristics	
			Nm	Ns	Pk	Hr (UT+2)	Surface salinity	Temperature (C)
Suprabenthos and Mesozooplankton	May 1994	Transect	SAPO32	SAT11	371	11:00	25.5	13.3
			SAPO33	SAT12	364	12:00	20.3	14.2
			SAPO34	SAT13	357	14:00	12.9	15.5
			SAPO35	SAT14	348	15:00	4.3	16.6
			SAPO36	SAT15	344	16:15	0.7	17.6
			SAPO37	SAT16	336	17:15	0.3	17.8
	September 1995	Transect	SAPO96	SAT44	365	10:30	12.1	17.8
			SAPO97	SAT45	362	11:30	7.7	18.0
			SAPO98	SAT46	354	13:00	4.4	18.2
			SAPO99	SAT47	348	14:00	1.8	18.5
			SAPO100	SAT48	336	15:00	0.4	18.6
Ichtyofauna	May 1995	2 areas: Honfleur	–	–	–	HT	14.0	17.2
		Tancarville	–	–	–	HT	0.5	16.4
	September 1995	3 areas: Bouée Amfard	–	–	367	HT	32.5	17.9
		Honfleur	–	–	–	HT	24.0	16.0
		Tancarville	–	–	–	HT	6.0	16.5

Table 2. Densities of benthic species collected in eight areas from the seine estuary.

Zone	Fosse Sud Outer part	Fosse Sud Inner part	Fosse Nord	Chenal dowstream Honfleur	Chenal upstream Honfleur	Pont de Normandie			Marais du Hode			Pont de Tancarville	
Date	November 93		November 93	November 93	November 93	May 95		October 95	May 95		October 95	May 95	October 95
Number stations	3, subtidal	2, subtidal	5, subtidal	2, subtidal	2, subtidal	1, intertidal	3, subtidal	6, subtidal	2, intertidal	3, subtidal	3, subtidal	6, subtidal	3, subtidal
Species richness	25	13	12	8	4	7	11	14	6	7	9	5	6
N. endobenthic species	23	12	9	4	–	6	5	7	3	2	3	1	2
N. vagile species	2	1	3	4	4	1	6	7	3	5	6	4	4
Endobenthic species													
Abra alba	566	–	–	–	–	–	–	–	–	–	–	–	–
Cerastoderma edule	–	213	13	8	–	–	–	4	–	–	–	–	–
Eteone longa	11	4	4	5	–	10	10	2	–	–	10	–	3
Hediste diversicolor	–	–	4	–	–	615	9	6	42	2	6	16	12
Macoma balthica	3	5	21	9	–	58	18	7	–	–	–	–	–
Nephtys hombergii	66	17	32	1	–	40	11	13	5	2	2	–	–
Owenia fusiformis	345	3	–	–	–	–	–	–	–	–	–	–	–
Pectinaria koreni	344	8	–	–	–	–	–	–	–	–	–	–	–
Other polychaeta	27	8	8	–	–	–	–	8	–	–	–	–	–
Divers	26	7	1	–	–	37	–	–	13	–	–	–	–
Vagile species													
Gastrosaccus spinifer	3	–	–	–	–	–	3	–	–	–	–	–	–
Carcinus maenas	2	–	1	4	–	–	–	1	2	1	–	2	–
Crangon crangon	–	5	2	22	5	–	28	21	–	9	6	–	29
Mesopodopsis slabberi	–	–	4	20	7	–	22	24	–	7	6	–	–
Neomysis integer	–	–	–	–	–	–	8	3	–	33	4	28	25
Palaemon longirostris	–	–	–	–	–	–	17	–	–	22	16	40	3
Amphipoda													
Corophium volutator	–	–	–	–	–	1022	–	–	–	–	–	–	–
Other amphipoda	–	–	–	–	5	–	1	2	3	–	2	2	1
Isopoda	–	–	–	–	4	–	–	–	–	–	–	–	–
Divers	–	–	–	2	–	–	11	12	3	–	–	–	–
Total density m^{-2}	1393	270	90	82	21	2252	138	100	68	76	52	88	73
Total Biomass mg m^{-2}	44961	2366	655	3912	441	6120	1661	1928	221	2878	1206	4545	1928
Endobenthic Biomass mg m^{-2}	44807	2148	389	211	0	5060	193	43	40	40	46	53	43
Vagile Biomasse mg m^{-2}	154	218	266	3701	441	1060	1468	1885	181	2838	1160	4492	1885

Table 3. Densities of mesozooplanktonic species collected along the salinity gradient (oblic samples) in the Seine estuary in May 1994 and September 1994.

Date	May 1994						September 1995				
Samples	SAPO32	SAPO33	SAPO34	SAPO35	SAPO36	SAPO37	SAPO96	SAPO97	SAPO98	SAPO99	SAPO100
Kilometric Point	371	364	357	348	344	336	365	362	354	348	336
Sub-surface Salinity (P.S.U.)	27.6	23.0	17.8	4.2	1.3	0.4	12.1	7.7	4.4	1.8	0.4
Cladocera											
Bosmina spp.	–	–	1	257	218	907	88	–	8	7	2000
Daphnia spp.	–	–	–	16	29	88	–	–	–	–	105
Evadne nordmanni	19	132	174	3	–	–	–	–	–	–	–
Other cladocera	14	3	1	1	21	7	–	7	–	–	158
Copepoda											
Acartia spp.	283	282	6	–	–	–	62941	6897	190	–	–
Eurytemora affinis	–	1	945	47145	157890	1033	853	10414	5337	464	13684
Euterpina acutifrons	5	1	6	–	–	–	853	7	–	–	–
Temora longicornis	56	185	3	–	–	–	–	–	–	–	–
Other copepoda	19	69	3	–	–	–	412	14	24	–	579
Copepodid											
Acartia spp.	274	692	–	–	–	–	1235	62	–	–	–
Eurytemora affinis	–	127	13826	47000	35266	45	–	9172	5159	879	4105
Temora longicornis	27	1104	–	–	–	–	–	–	–	–	–
Other copepodid	7	162	–	–	–	–	–	–	–	–	–
Cirriped larvae	30	812	260	–	10	48	–	–	–	–	–
Mysidacea											
Mesopodopsis slabberi	–	4	437	2	–	–	81	–	–	–	–
Neomysis integer	–	–	–	11	–	–	657	757	104	8	21
Other mysidacea	–	–	–	–	–	–	–	–	–	–	–
Chaetognatha											
Sagitta elegans	–	1	–	–	–	–	35	–	–	–	–
Appendicular											
Oikopleura dioica	65	212	30	–	–	–	–	–	–	–	–
Fish larvae and fishes											
Gobiidae	1	1	3	–	–	–	19	4	8	5	17
Other species	3	1	7	–	–	–	–	–	–	–	–
Decapoda larvae	6	11	7	1	–	–	3	1	1	1	–
Ostracoda	29	113	122	–	–	1	–	7	–	–	–
Amphipoda	–	–	–	–	–	–	–	–	–	–	–
Polychaeta larvae	2	15	3	–	–	–	–	–	–	–	–
Ctenophore						–					
Pleurobrachia pileus	8	10	3	–	–	–	–	–	–	–	–
Other taxa	6	19	27	–	–	–	–	–	–	–	–
Species richness	27	32	25	14	8	14	14	12	9	7	11
Total density (ind m^{-3})	854	3957	15864	94436	193434	2129	67177	27342	10831	1364	20669
Total biomass (mg m^{-3})	5.26	14.97	218.81	536.00	1513.10	11.62	1558.85	1582.24	257.02	21.05	181.52

Suprabenthos

A suprabenthic sledge with a principle similar to the GIROQ version of the MACER sledge was used (Dauvin & Lorgeré, 1989; Dauvin et al., 1995). Four WP2 zooplankton nets (0.5 mm mesh size) were superposed on 0.10–0.40 (net 1), 0.45–0.75 (net 2), 0.80–1.10 (net 3) and 1.15–1.45 m (net 4) above the sea bed. Each net holded a TSK flowmeter to measure the volume of water filtered. Mean trawling speed during the 5-min-long hauls was 1.5 knots against the tide. As for the mesozooplanktonic samples, a set of samples was taken along a transect of six stations (SAT11/Pk371 to SAT16/Pk336) in May 1994, and a transect of five stations in September 1995 (SAT44/pk365 to SAT48/pk336) at the same stations for mesozooplanktonic samples (see Figure 1 and Table 3).

Materials collected were fixed with 10% neutral formalin for approximately one week then the materials were washed and preserved in 70% alcohol. Suprabenthic fauna was examined by a dissecting microscope. The ash fresh dry weight (AFDW) of each species was estimated and the mean of total number of individuals of the four nets or biomass in a haul was standardized to 100 m^3.

Ichthyofauna

Trawling with a prawn trawl (22 mm mesh size) was carried out in May 1995 and in September-October 1995 at stations 'Bouée Amfard/Pk367', Honfleur and Pont de Tancarville (see Figure 1). Fresh fishes were identified, counted and weighted. The weight of fishes sampled were standardized to 1000 m^2.

Trophic chains

To determine the trophic chains, stomach contents of four main fishes collected in the estuary (i.e. the flounder *Platichthys flesus*: 187 stomachs, the sole *Solea vulgaris*: 56 stomachs, the sea perch *Dicentrarchus labrax*: 34 stomachs, the goby *Pomatoschistus microps*: 200 stomachs) and the shrimp *Palaemon longirostris* (420 stomachs) were examined to identify the main prey of these species. Sampling sites were in the meso-oligohaline (downstream Pont de Tancarville) and meso-euhaline (downstream Pont de Normandie) zones. For the goby *P. microps* and the shrimp *P. longirostris*, the number of prey (Np) and the ratio in percentage of number of prey i on the total number of preys (Cn) were calculated. For the demersal fishes the occurrence of prey was only recorded.

Physical environment

The main characteristics of the environment parameters in May and September–October were given in the Table 1. In May the turbidity, near the sea-bed, increased regularly from the outer part of the estuary to the inner part which varied from < 50 mg l^{-1} at Pk371 to 375 mg l^{-1} at Pk344 and then decreased upstream from less than 50 mg l^{-1}. In September there was the same gradient but the Suspended Particule Matter (SPM) concentration exceeded 1000 mg l^{-1} near the Pont de Tancarville (lowest water level of the Seine River).

Results

Macrobenthos

During the autumn (November 1993 and October 1995), 25 species were sampled in the subtidal outer part of the estuary in the 'Fosse Sud' (Table 2). The species richness was lower in Honfleur and 'Marais du Hode' (i.e. 14 and 4 respectively). Total density and biomass showed also a similar pattern which decreased from the outer part of the estuary in the 'Fosse Sud' to the inner part of the estuary in Honfleur. The density was particularly low (< 21 ind m^{-2}) in the channel station near Honfleur; in the other stations the density was near 100 ind m^{-2}. The biomass showed a very high value in the outer part of the 'Fosse Sud' (DW = 45 g m^{-2}) and was lower than 4 g m^{-2} in the other part of the estuary. It was important to notice the contribution of the vagile species (suprabenthic species) at the stations from the navigable channel and the stations upstream Honfleur. In these stations, the biomass of the endobenthic macrofauna was very low (Table 2).

The specific richness, density and biomass at stations of Pont de Normandie, Marais du Hode and Pont de Tancarville showed no seasonal changes.

For the intertidal zone, the 'Pont de Normandie' station showed a low species richness but a high density which was due to the amphipod *Corophium volutator* and the polychaete *Hediste diversicolor* (Table 2). In the 'Marais du Hode' intertidal station, although the density was of the same order of magnitude as the subtidal station, its biomass was very low.

In summary, the benthic macrofauna showed a drastic reduction of species richness, density and biomass from the outer part of the estuary in the 'Fosse

Table 4. Densities of suprabenthic species collected along the salinity gradient in the Seine estuary in May 1994 and September 1995.

Date	May 1994						September 1995				
Samples	SAT11	SAT12	SAT13	SAT14	SAT15	SAT16	SAT44	SAT45	SAT46	SAT47	SAT48
Kilometric Point	371	364	357	348	344	336	365	362	354	348	336
Sub-surface Salinity (P.S.U.)	27.6	23.0	17.8	4.2	1.3	0.4	12.1	7.7	4.4	1.8	0.4
Amphipoda	6	2	1	–	–	–	1300	569	57	12	–
Mysidacea											
Gastrosaccus spinifer	19	1	8	1	–	–	–	–	–	–	–
Mesopodopsis slabberi	1	1	47	522	22	–	34329	12	–	–	–
Neomysis integer	–	–	–	20443	332	4	261	77056	56425	2153	1137
Other Mysids	21	40	11	–	–	–	8	–	–	–	–
Decapoda											
Crangon crangon	81	37	104	1055	43	–	2	555	446	41	–
Palaemon longirostris	–	–	1	157	4	–	–	–	175	1769	776
Other decapoda	1	3	–	–	–	–	116	2	2	–	–
Decapoda larvae	137	34	109	–	–	–	19	69	3	–	–
Cumacea	14	–	–	–	–	–	55	–	–	–	–
Chaetognatha											
Sagitta elegans	1	–	–	–	–	–	71	–	6	–	–
Fishes											
Pomatoschistus microps	649	630	862	1588	26	–	61	59	209	251	992
Pomatoschistus minutus	–	–	–	45	–	–	141	126	435	14	2
Other fishes	–	–	–	–	–	1	2	2	7	1	1
Clupeidae larvae	240	283	58	10	–	–	3	–	–	–	–
Gadidae larvae	36	7	3	1	–	–	–	–	–	–	–
Gobiidae larvae	–	–	–	–	–	–	614	81	24	1	65
Pleuronectidae larvae	5	1	8	5	–	–	–		–	–	–
Soleidae larvae	28	9	1	1	–	–	–		–	–	–
Other larvae	5	1	6	3	–	–	–		–	–	–
Total richness	26	19	18	13	5	2	20	11	15	9	6
Total density (ind 100 m^{-3})	1244	1049	1219	23831	427	5	36982	78531	57789	4242	2973
Total biomass (mg 100 m^{-3})	75749	72892	93922	224631	4139	72	57341	100634	142037	216774	188864

Sud' to the channel especially in the part between Honfleur and Pont de Tancarville. In this zone, the contribution of the vagile fauna was important. No seasonal changes was observed in the channel stations.

Mesozooplankton

For both seasons, spring and autumn, the mesozooplankton community showed the same changes along the salinity gradient (Table 3). The species richness decreased from the outer part to the inner part of the estuary; the maximum value in May (i.e. 32 species) was recorded for a salinity of 23.0 P.S.U. and the minimum value in September (i.e. 14 species) was in a salinity zone of 12.1 P.S.U. The lowest species richness was recorded in May for a salinity of 1.3 (i.e. 8 species) and in September for a salinity of 1.8 P.S.U. (i.e. 7 species). Upstream, the species richness increased with the increasing of freshwater species (cladocerans).

The mesozooplankton community showed three distinct patterns (Table 3). In the polyhaline zone (18–30 P.S.U., Venice system of classification of saline waters; Anonymous, 1959) the community was characterized by marine copepods (*Pseudocalanus elongatus, Paracalanus parvus* and *Temora longicornis*), ostracods and the ctenophore *Pleurobrachia pileus*. In the mesohaline zone (5–18 P.S.U.) the community was characterized by the copepod *Acartia* (64,176 ind m^{-3} in autumn) and the mysid *Neomysis integer*. In

Table 5. Biomass (g fresh weight/1000 m^{-2}) of fishes collected by trawls in three areas of the Seine estuary.

Species	Pont de Tancarville Pk 340 May	Pont de Tancarville Pk 340 October	Honfleur Pk 356 May	Honfleur Pk 356 October	Bouée Amfard Pk 367 September
Anguilla anguilla (L., 1758)	–	–	–	–	206
Agonus cataphractus (L., 1758)	–	–	–	–	13
Buglossidium luteum (Risso, 1810)	–	–	–	–	434
Callionymus lyra L., 1758	–	–	–	–	561
Ciliata mustela (L., 1758)	–	–	–	45	–
Clupea harengus L., 1758	–	2	130	955	710
Dicentrarchus labrax (L., 1758)	99	5	–	105	34
Gobiidae	–	–	–	–	1
Limanda limanda (L., 1758)	–	–	–	–	392
Merlangius merlangus (L., 1758)	–	–	–	843	21
Mugilidae	–	8	–	–	–
Platichthys flesus (L., 1758)	131	228	860	473	239
Pleuronectes platessa L., 1758	–	–	–	–	156
Pomatoschistus microps (Kröyer, 1838)	–	1	35	39	57
Solea vulgaris Quensel, 1806	–	–	–	–	40
Sprattus sprattus (L., 1758)	–	1	206	–	138
Trachinus draco L., 1758	–	–	–	1	13
Trachurus trachurus (L., 1758)	–	–	–	24	307
Trigla lucerna L., 1758	–	–	–	44	1
Trisopterus luscus L., 1758	–	–	639	360	238
Species richness	2	6	5	10	18
Biomass (g fresh weight/1000 m^2)	230	245	1870	2889	3561

the oligohaline zone (0.5–5 P.S.U.), the community was characterized by the dominance of the copepod *Eurytemora affinis* ($\cong$ 190,000 ind m^{-3} in May) and the presence of freshwater cladocerans (*Bosmina* spp.). In the oligohaline zone, the density and biomass reached their maximum in May with the values of 193,434 ind m^{-3} and 1,513 mg m^{-3} respectively, while in the mesohaline zone in September they were 67,177 ind m^{-3} and 1,582 mg m^{-3} respectively. During spring, the biomass in the polyhaline zone was lower than those found in the meso- and oligohaline zones (Table 3).

Suprabenthos

At both seasons, the specific richness decreased as the salinity decreased. The maximum species richness was 26 species in May and 20 in September for salinities of 27.6 P.S.U and 12.1 P.S.U. respectively, while few species were reported in the low salinity zone (i.e. only two species in May and six species in September for a salinity of 0.4 P.S.U. (Table 4).

The suprabenthic community was characterized by six dominant species: the mysids *Mesopodopsis slabberi* and *Neomysis integer*, the decapods *Crangon crangon* and *Palaemon longirostris*, the gobies *Pomatoschistus minutus* and *P. microps*. The quantitative composition of this compartment varied between the mesohaline zone which was dominated by *M. slabberi* (34,330 ind 100 m^{-3} in September), *C. crangon* (104 ind 100 m^{-3} in May) and the young gobies (860 ind 100 m^{-3}) in spring and the oligohaline zone which was characterized by the dominance of *N. integer*, *P. longirostris* and *P. microps*, with maximal densities of 77 000, 1 769 and 991 ind 100 m^{-3} respectively in September (Table 4).

The total density of suprabenthic community was always higher in the oligohaline zone than in the mesohaline zone (Table 4). The biomass was higher in the summer than in the spring. At both seasons the

Table 6. Diet of three size classes of the gobiidae *Pomatoschistus microps* in the oligohaline zone of the Seine estuary in May 1994 and September 1995. Np: Number of prey; CN: Ratio in percentage of number of prey i on the number of total prey; L1: 10–29 mm; L2: 29–39 mm; L3: 39–50 mm.

	May 1994					
	L1		L2		L3	
Number of stomach	34		34		33	
Stomachs with prey	33		34		33	
Total number of prey	308		2029		2766	
Mean number of prey per stomach	9.1	59.7	83.8			
	Np	Cn	Np	Cn	Np	Cn
Copepoda						
Eurytemora affinis	308	100	2023	99.6	2741	99.1
Other copepoda	–	–	–	–	9	0.3
Cladocera						
Bosmina spp.	–	–	4	0.30	3	0.1
Mysidacea						
Neomysis integer	–	–	–	–	6	0.2
Mesopodopsis slabberi	–	–	–	–	3	0.1
Decapoda						
Crangon crangon	–	–	1	0.05	–	–
Other decapoda	–	–	–	–	1	0.04
Decapoda larvae	–	–	–	–	1	0.04
Ostracoda	–	–	1	0.05	–	–
Pleuronectidae larvae	–	–	–	–	1	0.04
Chironomidae larvae	–	–	–	–	1	0.04
	September 1995					
	L1		L2		L3	
Number of stomach	53		44		3	
Stomachs with prey	38		35		3	
Total number of prey	207		192		21	
Mean number of prey per stomach	5.4		5.5		7.0	
	Np	Cn	Np	Cn	Np	Cn
Copepoda						
Eurytemora affinis	186	89.9	162	84.4	9	42.9
Mysidacea						
Neomysis integer	21	10.1	29	15.1	12	57.1
Mesopodopsis slabberi	–	–	1	0.5	–	–

biomass was maximum in the salinity zone around 4 P.S.U. (Table 4).

Ichthyofauna

A total of 20 fish species was identified from all trawls. The major ichtyofauna components of the Seine estuary were the flounder *Platichthys flesus*, the sole *Solea vulgaris*, the sea perch *Dicentrarchus labrax*, the herring *Clupea harengus* and the sprat *Sprattus sprattus* (Table 5).

The species richness in the outer part of the estuary was 5 in May and 10 in October at downstream Honfleur, and 18 in September at Bouée Amfard. By contrast, low species richness as 2 in May and 6 in October at Pont de Tancarville was observed in the inner part of the estuary (Table 5). The biomass showed the same pattern as 3561 and only 245 g of fresh weight.

Table 7. Diet of two size classes of the decapoda *Palaemon longirostris* in the oligohaline zone of the Seine estuary. Np: Number of prey; Cn: ratio in percentage of number of prey i on the number of total prey. L1: 20–29 mm; L2: > 29 mm.

	May 1994			
	L1		L2	
Number of stomach	159		77	
Stomachs with prey	29		16	
Total number of prey	26		17	
Mean number of prey per stomach	0.9		1.1	
	Np	Cn	Np	Cn
Copepoda				
Eurytemora affinis	8	30.8	9	52.9
Other copepoda	4	15.4	–	–
Mysidacea				
Neomysis integer	7	26.7	4	23.5
Other mysid	6	23.1	2	11.8
Decapoda				
Crangon crangon	–	–	1	5.9
Other decapoda	1	0.04	1	5.9
Number of stomach with Detritus	29	–	9	–
	September 1995			
	L1		L2	
Number of stomach	121		63	
Stomachs with prey	42		27	
Total number of prey	145		62	
Mean number of prey per stomach	3.5		2.3	
	Np	Cn	Np	Cn
Cladocera				
Bosmina spp.	3	2.1	–	–
Other cladocera	1	0.7	–	–
Copepoda				
Eurytemora affinis	134	92	54	87.1
Other copepoda	5	3	4	6.5
Mysidacea				
Neomysis integer	–	–	1	1.6
Other mysid	2	1.4	3	5
Number of stomach with detritus	42	–	27	–

1000 m^{-2} for respective by the outer and the inner parts of the estuary in October. Comparatively speaking, species richness and total biomass were higher in autumn than in spring. For example at Honfleur, 10 species were present in autumn for a total biomass of 2889 g of fresh weight 1000 m^{-2} while in spring only 5 species were sampled for a total biomass of 1870g of fresh weight 1000 m^{-2}.

Inner part trophic chain

The stomach contents analysis showed that the copepod *Eurytemora affinis* was the main prey of the goby *Pomatoschistus microps* (Table 6). The diet of the young goby (Length < 30 mm) was based exclusively on this copepod in spring, while some *Neomysis integer* were present in the diet in autumn. The diet of the large *P. microps* (length > 30 mm) was not so specific, including the decapod *Crangon crangon* and cladocerans (Cn: 0.1 to 0.3). In spring, the mean number of preys per stomach in large goby was higher than the small ones (L2: 59.7 and L3: 83.8). However, it was similar for the three size classes in autumn (5.4 to 7.0). In general, the copepod *E. affinis* was a dominant diet component at both seasons, although mysids were also found in autumn (Table 6).

In the decapod *Palaemon longirostris* (Table 7) as in the *P. microps*, the copepod *E. affinis* was also the major food component of the diet (Cn 30.8 to 92.0%). The mysid *N. integer* composed the secondary diet (Cn: 1.6 to 26.7%). Detritus was always present in the stomach of *P. longirostris*. No seasonal change of the diet was observed, but the mean number of prey per stomach was higher in autumn than in spring.

Outer part trophic chain

Table 8 showed the analysis of stomach contents of three main fishes sampled in the lower estuary. An important number of stomachs with prey was recorded: 100% for the three size class of *D. labrax*, 93.3 to 100% for *P. flesus* and 6.3 to 92.3% for *S. vulgaris*. The flatfishes *P. flesus* and *S. vulgaris* showed more benthic diet than *D. labrax*. The suprabenthic Decapoda Caridea were the major diet component of the three species. The diet of *D. labrax* and *P. flesus* were more diverse (respectively 5 and 6 preys) than *S. vulgaris* (3 preys). There was also an intraspecific variability of the diet: the juveniles of *P. flesus* and *D. labrax* presented a more diverse diet than adults which preferred planktonic copepods and mysids. The diet of young *D. labrax* was characterized by mysids (Cn:

68%) while copepods represented 31% of the diet of the young *P. flesus*. Generally, the benthic preys in the diet increased with the size of the fish. For example, benthos formed 33% of the juvenile and 92% of the adult *S. vulgaris* diets.

Discussion

This present study furnished the first quantitative data on the mesozooplankton, suprabenthos and the first quantitative data for the subtidal macrobenthos in the mesohaline and oligohaline areas of the Seine estuary at only two seasons spring and autumn. It gave also supplementary data on fish composition and analysis on 5 dominant suprabenthic species with accomplishment of the food chains in two parts of the estuary. Among the abundant literature on estuaries, data were mainly compared with these available on four other north-eastern Atlantic estuaries, the Ems and the Schelde (The Netherlands), and the Loire and the Gironde (France) (see Heip & Herman, 1995).

Faunistic composition and spatio-temporal distribution

Macrobenthos. The fauna belongs to two distinct benthic communities. (i) In the outer part of the Fosse Sud, it was an *Abra alba-Pectinaria koreni* community which occurred in the eastern part of the Bay of Seine on muddy fine sand (Gentil et al., 1986; Thiébaut et al., 1997). It was dominated by the bivalve *Abra alba*, and the polychaetes *Pectinaria koreni*, *Owenia fusiformis*, and *Nephtys hombergii* which exhibited high density and biomass (Table 2). (ii) In the other parts of the estuary, it was a *Macoma balthica* community which commonly occurs in the north-eastern Atlantic estuaries (Bachelet, 1979; Robineau & Marchand, 1984; Meire et al., 1991). In the Seine estuary, the *Macoma balthica* community showed a very low number of species in relation to the salinity gradient. Very low density and biomass were also found, except on intertidal stations near the Pont de Normandie where *Hediste diversicolor* and *Corophium volutator* were important species in density. Nevertheless, as a 1 mm mesh size sieve was used, the densities of small species like the Oligochaeta which may constitute very high densities in the less haline zone of the estuaries was not estimated. In the Seine estuary on 1 mm mesh size sieve, the density of the *Macoma balthica* was nearly 100 ind m^{-2} and the biomass ranged from 0.2 to 6 g m^{-2}, while the maximum density and biomass exceeded 10 000 ind m^{-2} and 10 g m^{-2} in the other estuaries (Bachelet, 1979; Robineau & Marchand, 1984; Meire et al., 1991). Our results agreed with the previous study from Proniewski & Elkaim (1980) on the subtidal macrofauna of the Seine estuary, who described both communities and underlined the absence of typical oligohaline fauna in this estuary. The commonest species was the polychaete *Hediste diversicolor* which occurred along the salinity gradient. In the Fosse Nord and Fosse Sud (Figure 1), the community was dominated by the bivalves *Cerastoderma edule* and *Macoma balthica*. In contrast, in the inner part of the estuary, the mysid and decapod suprabenthic species were dominant. This distribution patterns with two distinct zones was due to a strong abiotic limitation of maximum SPM concentration and oxygen deficiency in the inner estuary compared to the outer part with low turbidity and high concentration of oxygen, and to a regular dredging of the channel which prevented the settlement of species in the channel. In the outer part of the Fosse Sud (Figure 1), the *Abra alba-Pectinaria koreni* exhibited a high density and biomass which indicated an eutrophic condition without anoxia (Gentil et al., 1986).

Mesozooplankton. In the Seine estuary, the gross composition of the mesozooplankton was similar to those found in the other north-European estuaries (Castel, 1981; Bakker, 1994; Sautour & Castel, 1995) which included 3 different zones. (i) A polyhaline zone (18 to 30 P.S.U.) where neritic copepods *Temora longicornis*, *Euterpina acutifrons*, *Pseudocalanus elongatus* and *Paracalanus parvus*, and the cladocera *Evadne nordmanni* were common. In spring, copepod abundance was in the same order of magnitude as in other estuaries (maximum values: 2 600 ind m^{-3} in the Seine, 3 800 ind m^{-3} in the Ems, 2 300 ind m^{-3} in the Gironde and 5 100 ind m^{-3} in the Schelde, Sautour & Castel, 1995). (ii) A mesohaline zone, with the salinity between 5 and 18 P.S.U., was dominated by the copepods *Acartia* spp. especially in autumn, but *Eurytemora affinis* could also develop a dense population at both seasons. In spring, copepod abundance reached to 15 000 ind m^{-3} while in autumn it exceeded 62 000 ind m^{-3}. The density of *Acartia* spp. was very low in winter and autumn ($\approx$300 ind m^{-3}) (Mouny et al., 1996). In spring, the maximum density of *Acartia* spp. in the Seine estuary (1 000 ind m^{-3}) was in the same order of magnitude as in the Gironde (1 100 ind m^{-3}) but lower than found in the West-

Table 8. Occurrence of prey items in the stomach of 3 size classes of *Dicentrarchus labrax* (D.l.), *Platichthys flesus* (P.f.) and *Solea vulgaris* (S.v.) from May and October hauls in the downstream Seine estuary (Pk 340, Pk 356 and Pk 367) (L1 = 9–15 cm; L2 = 16–21 cm; L3 > 21 cm).

	D.l.			P.f.			S.v.		
	L1	L2	L3	L1	L2	L3	L1	L2	L3
Number of stomachs	15	16	3	137	30	20	16	27	13
% of Stomachs with prey	100	100	100	95.6	93.3	100	6.3	77.7	92.3
Copepod	8	–	–	31	7	–	–	–	–
Mysid	68	9	–	1	4	–	–	–	–
Decapod Caridea	12	57	66	4	40	40	60	26	8
Benthic preys	4	6	–	7	19	20	33	74	92
Fishes	–	8	–	2	4	–	–	–	–
Other preys	12	20	33	22	22	40	7	–	–
Detritus	–	–	–	33	4	–	–	–	–

Table 9. Comparative densities of mesozooplankton and suprabenthos from four North-European Atlantic estuaries (Gironde, Schelde and Ems: Mesozooplankton data: Sautour & Castel, 1995; Suprabenthic data: Mess et al., 1995; Seine: this study).

	Gironde	Seine	Schelde	Ems
Mesozooplankton				
Type of samples	Surface/Bottom	oblique	oblique	oblique
Gyre	WP2 net (200 μm)	WP2 net (200 μm)	WP2 net (200 μm)	WP2 net (200 μm)
Date of sampling	March to June	May	March, April and June	March and May
Maximum spring density (ind m^{-3}) of				
Acartia spp.	1100	1000	2800	18200
Eurytemora affinis	14500	193160	11500	16800
Suprabenthos				
Gyre	Sledge (mesh size: 2–1 mm) (Hamerlynck & Mees, 1991)	Sledge (mesh size: 500 μm) (Dauvin & Lorgeré, 1989)	Sledge (mesh size: 2–1 mm) (Hamerlynck & Mees, 1991)	Sledge (mesh size: 2–1 mm) (Hamerlynck & Mees, 1991)
Date of sampling	August	September	August	August
Maximum summer density (ind m^{-2})				
Neomysis integer	30	240	200	20
Palaemon longirostris	224	6000	0	1
Pomatoschistus spp.	6300	4000	5	435

erschelde (2800 ind m^{-3}) and the Ems (18200 ind m^{-3}) (Table 9). (iii) An oligohaline zone (0.5 to 5 P.S.U.) which was dominated by the copepod *Eurytemora affinis*. The spring peak of abundance of *E. affinis* in the Seine estuary was more than ten time higher than those found in Gironde, Schelde and Ems estuaries (Table 9). The density of *Eurytemora affinis* remained relatively high during the autumn and the winter (16000 to 27000 ind m^{-3}) (Mouny et al., 1996).

Suprabenthos. The suprabenthic fauna was composed of 39 species in May and 34 species in September. There was a decrease in the number of species along the salinity gradient from the polyhaline zone (> 20 species), the mesohaline zone (11–20 species), to the oligohaline zone (< 15 species). In the eu-

Table 10. Comparative fish species richness in four north-european estuaries (fishes sampled with a suprabenthic sledge). Gironde, Schelde & Ems: Mees et al., 1995; Seine: this study.

Material	Gironde Sledge (mesh size: 2–1 mm) (Hamerlynck & Mees, 1991)	Seine Sledge (mesh size: 500 μm) (Dauvin & Lorgeré, 1989)	Schelde Sledge (mesh size: 2–1 mm) (Hamerlynck & Mees, 1991)	Ems Sledge (mesh size: 2–1 mm) (Hamerlynck & Mees, 1991)
Species				
Anguilla anguilla	*	*		
Callionymus lyra		*		
Callionymus reticulatus		*		
Ciliata mustela		*		
Clupea harengus		*	*	*
Dicentrarchus labrax		*		
Gasterosteus aculeatus	*	*	*	
Gobius niger		*		
Gymnocephalus cernuus				*
Lampetra fluviatilis		*		
Limanda limanda				*
Liparis liparis				*
Merlangius merlangus		*		
Osmerus eperlanus	*			*
Platichthys flesus		*		
Pleuronectes platessa				*
Pomatoschistus lozanoi	*		*	*
Pomatoschistus microps	*	*	*	*
Pomatoschistus minutus	*	*	*	*
Solea spp.	*	*		*
Sprattus sprattus	*	*	*	*
Syngnathus spp.	*	*	*	*
Trisopterus luscus				*
Zoarces viviparus				*
Total number of fish species	9	16	7	14

haline zone of the Seine estuary (Wang & Dauvin, 1994), the suprabenthos was more diverse than in the estuarine zones, with 46 species of Decapoda and Peracarida sampled, especially amphipods, mysids, and cumaceans, and 19 other macrozooplankton taxa (Wang et al., 1994). Spatial changes of the suprabenthos fauna were less pronounced than the mesozooplankton because some species, e.g. the decapod caridea *Crangon crangon* and the mysid *Mesopodopsis slabberi* showed seasonal migrations between the bay and the estuary. However, dominant species presented their maximal abundance in the mesohaline zone: the mysids *Mesopodopsis slabberi* and *Neomyis integer*, or in the oligohaline zone: the decapods *Palaemon longirotris* and *Crangon crangon*, and the goby *Pomatoschistus microps*. The maximum density in spring increased from the polyhaline zone to the oligohaline zone (Table 4), but the density of the fauna decreased dramatically if the salinity below 1.0 P.S.U. In the euhaline zone, the suprabenthic fauna was dominated by the ctenophore *Pleurobrachia pileus* and fishes larvae in spring (Wang et al., 1994, 1995). In summer, the abundance of *Palaemon longirostris* in the Seine estuary was higher than found in the Gironde, Schelde and Ems estuaries (Table 9). The abundance of *Neomysis integer* in the Seine was similar to the Schelde estuaries. *Pomatoschistus* spp. was in the same order of magnitude in the Gironde and the Seine estuaries (Table 9).

Ichtyofauna. The fish composition of the Seine estuary was relatively similar to those found in the Loire (Lardeux, 1986), the Forth and the Tyne estuaries (Pomfret et al., 1991), and the Gironde, Schelde and Ems estuaries (Mees et al, 1995). Comparative sampling of fishes by suprabenthic sledge was available for four estuaries (Table 10), the number of species recorded was in the same order of magnitude in the Seine and Ems estuaries, and higher than Schelde and Gironde estuaries.

Trophic chains

In the Seine estuary, two trophic chains were identified.

Upstream of Pont de Normandie, the shrimp *Palaemon longirostris* and the goby *Pomatoschistus microps* preyed on the pelagic compartment exclusively (copepods and mysids) (Tables 6 & 7). In this zone, the dominant copepod *Eurytemora affinis* was the main prey for both species. But, *Pomatoschistus* spp. (in the Ythan estuary, North Sea) and *P. longirostris* (in the Loire estuary) had a diet mainly on benthic preys (Healey, 1972; Marchand, 1981). However, the diet of the shrimp *Palaemon* in the Loire estuary included also pelagic prey (*N. integer*); the role of the detritus which should be an important source of organic materials found in the stomach of the shrimp in the Seine estuary and the Loire estuary should be elucidated. In the Ythan estuary, the diet of the common goby showed seasonal changes with a more diverse diet in spring than in autumn, coinciding with the availability of preys (Healey, 1972). Conversely, no seasonal changes of the diet of the Palaemonidae was observed in the Loire estuary. The difference between the Seine estuary and the other estuaries might be due to the dredging of the navigation channel of the Seine estuary which prevented the formation of a permanent benthic fauna.

The diet of fishes downstream of Honfleur showed a classical change of diet with age: juveniles eating mainly on planktonic prey (copepods, mysids and decapods) and adults eating benthic prey (polychaetes and bivalves). The benthic prey were especially important for *Solea vulgaris*. This result agreed with those of studies that the diet of the demersal fishes especially the flounder *Platichthys flesus* (Arntz, 1977) was mainly based on the benthic fauna. In summary, in the oligohaline zone (high turbidity, low concentration of oxygen) the diversity and density of fishes are relatively low in spite of high biomass of mesozooplankton and suprabenthos. In the outer part of the estuary, low turbidity and high concentration of oxygen are favourable of older fish populations which especially eat benthic fauna. In this area, a high macrozoobenthic biomass and a weak planktonic biomass are found.

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