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The suprabenthic crustacean fauna of the infralittoral fine sand community from the Bay of Seine (Eastern English Channel) : composition, swimming activity and diurnal variation

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Abstract : The suprabenthic fauna of a station located in the outer part of the estuary of the Seine (Eastern English Channel) was sampled with a modified Macer-GIROQ suprabenthic sledge. Thirty-eight hauls were collected in two series of hourly sampling ; they provided a first quantitative description of the suprabenthic crustacean fauna from this area. Species composition of the fauna, swimming activities and diurnal vertical migrations of the main species were studied. A total of forty-six crustacean species were collected. Mysids and cumaceans were the most abundant species of the fauna. The dominant species were *Schistomysis kervillei, Mesopodopsis slabberi, Diastylis bradyi* and *Pseudocuma longicornis.* All principal species of the fauna regularly performed a nocturnal vertical migration.

Résumé : La faune suprabenthique d'une station située au débouché en mer de la Seine (Manche orientale) a été échantillonnée avec un traîneau suprabenthique Macer-GIROQ modifié. Trente-huit échantillons horaires ont été récoltés en deux séries de prélèvements ; ils permettent de décrire pour la première fois la faune suprabenthique de cette région. La composition faunistique, les activités natatoires, et les migrations nyctémérales des principales espèces sont décrites. Un total de 46 espèces de crustacés a été identifié. Les espèces dominantes de la communauté sont *Schistomysis kervillei, Mesodopsis slabberi, Diastylis bradyi* et *Pseudocuma longicornis.* Toutes les espèces présentent une migration verticale nocturne.

INTRODUCTION

The suprabenthic fauna, often called hyperbenthos, demersal zooplankton or benthopelagic plankton, includes all swimming bottom-dependent animals - mainly crustaceans - which perform, with varying amplitude, intensity and regularity, seasonal or daily vertical migrations above the sea-floor (Brunel *et al.*, 1978 ; Sainte Marie & Brunel, 1985). Since swimming peracarids and decapods are known to be an important food source for demersal fishes (see for instance Sorbe, 1981, 1984 ; Kleppel *et al.*, 1980 ; Mauchline, 1982 ; Dauvin, 1988), studies of the infralittoral and circalittoral suprabenthic fauna are of great interest and are carried out in several regions. In the English Channel, the first information on the suprabenthos was provided by Dauvin on the coarse sand community off Roscoff (Western English Channel) (Dauvin & Lorgeré, 1989 ; Dauvin *et al.*, 1991 ; Dauvin *et al.*, 1994). The present study is the first description of the suprabenthic fauna in the eastern part of the Bay of Seine (Eastern English Channel). The species composition, densities, swimming activities and diurnal variations of the principal species are described and the results are discussed in comparison with those available for other infralittoral suprabenthic communities.

MATERIAL AND METHODS

Study site

The Bay of Seine is located in the south of the eastern basin of the English Channel. Its eastern part is directly influenced by the Seine estuary with an average annual flow of 380 $m^3. s^{-1}$ in the mouth region (Avoine, 1986). This fluviative flow produces a haline circulation : the brackish surface water flows to the north-east while marine bottom water converges into the estuary.

The sampling station F (49°26.26' N, 0°01.30' E) was located at the center of the fine-sand *Abra alba-Pectinaria koreni* community (Gentil *et al.*, 1986 ; Dauvin & Gillet, 1991), in the outer side of the estuary of the Seine (Fig. 1). Sampling depth varied between 8-13 m according to the tidal cycle. The sediment was muddy fine sand. During the study period, the hydrological conditions were characterised by the existence of a thermocline and a halocline. The near-bottom salinity was 33.00-34.00 g. l^{-1} and the sub-surface salinity was 29.00-30.00 g. l^{-1}. During the sampling period of June 1-2, 1992, temperature was 14.5-17.0 °C in the sub-surface water layer and 12-13 °C near the bottom ; the current speed varied between 20 cm. s^{-1} around high tide and 60 cm. s^{-1} an hour after low tide (Wang, *et al.*, 1994). During the sampling period of June 13, 1992, temperature was 15.0-17.7 °C in the sub-surface water layer and 14.9-15.3 °C near the bottom ; the current speed varied between 20 cm. s^{-1} around high tide and 50 cm. s^{-1} two hours after low tide (Wang, 1993). There was no slack water at low tide. The north component of the tidal currents was strong at the end of the flood tide and around high tide. Inversely, during the ebb tide and around low tide, the water mass was transported toward the south. Marine water entered the estuary during the flood tide when the east component of the tidal current was strong and went out from there during the ebb tide when the west component was strong. The flood tide had a shorter duration than the ebb tide, but the tidal current was stronger during the flood tide (Wang, *et al.*, 1994).

Sampling

A modified MACER-GIROQ suprabenthic sledge (Brunel *et al.*, 1978 ; Dauvin & Lorgeré, 1989) was used for sampling. This sledge allowed us to collect samples of the suprabenthic fauna simultaneously at four levels : 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 bottom. The mesh size was 0.5 mm. A TSK flowmeter fixed at the center of each net measured the volume of water filtered.

Two series of hauls were collected every one hour. On June 1-2, 1992, when it was the period of spring tide (tide coefficient : 88-90), 24 samples were collected from 9h on June 1 to 9h on June 2. No sampling was undertaken at 4h on June 2 due to technical problems. On

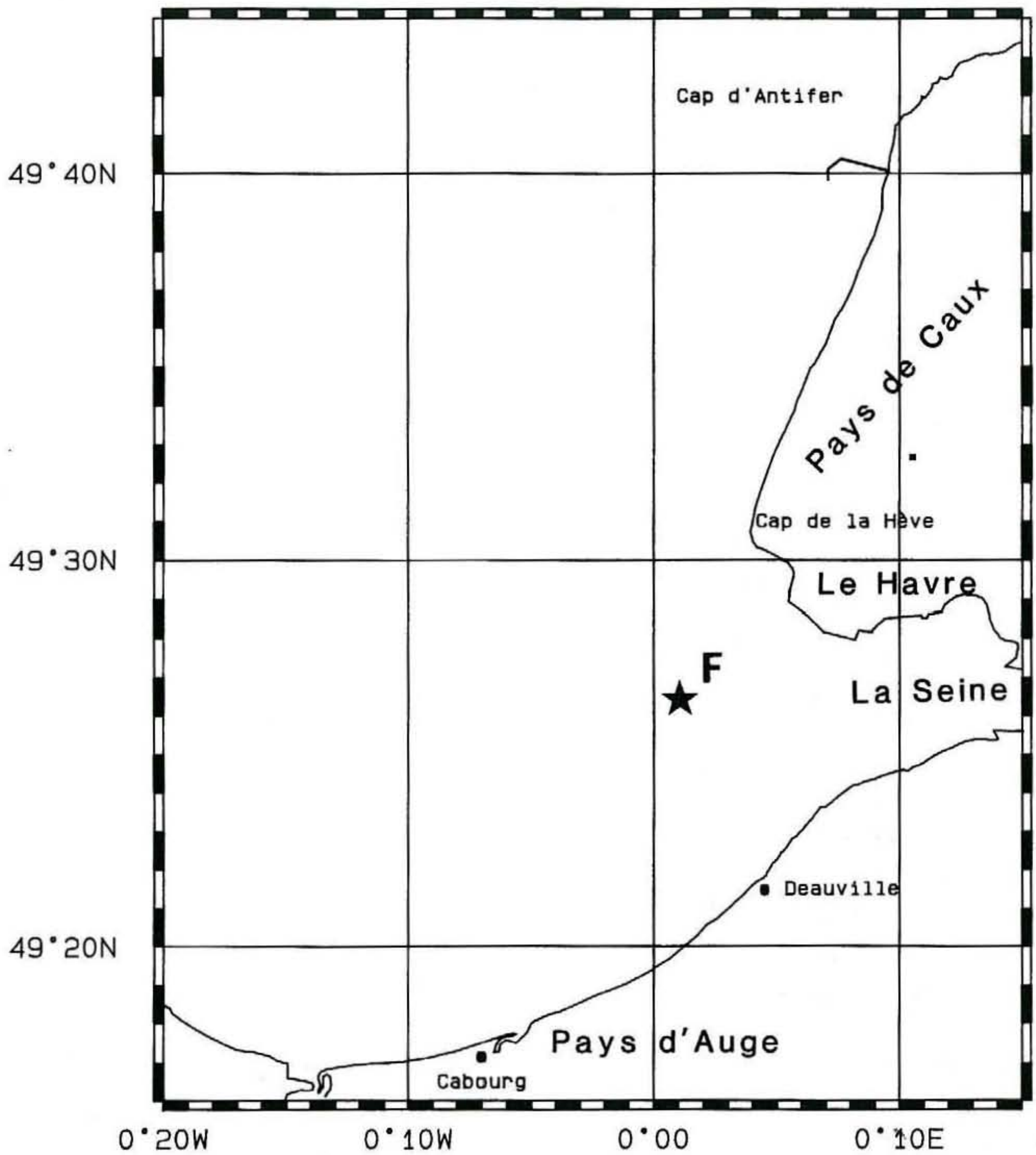

Fig. 1 : Sampling station F in the eastern part of the Bay of Seine.

June 13, 1992, when it was the period of neap tide (tide coefficient : 70), 14 samples were collected. For each haul, the sledge was towed along the sea bed against the tidal current at a speed of about 1.5 knots for 5 minutes. The water volume filtered by each net varied between 54 and 111 m^3, with 10 % less than 60 m^3, 31 % between 60 and 69 m^3, 33 % between 70 and 79 m^3, 16 % between 80 and 89 m^3, and 9 % more than 90 m^3 (Table I). Organisms collected by each net were separately fixed in 10 % neutral formalin.

TABLE I

Data on sampling

Haul	Date	Hour	Day/ Night	Volume of water filtered (m^3)				Mean volume (m^3)	Sampled area (m^2)
				Net 1	Net 2	Net 3	Net 4		
F3	06/01/1992	09:00	D	73	61	71	72	69.3 ± 5.6	230
F4	06/01/1992	10:00	D	76	66	76	77	73.8 ± 5.2	247
F5	06/01/1992	11:00	D	69	61	57	58	61.3 ± 6.6	203
F6	06/01/1992	12:00	D	76	69	79	75	74.7 ± 5.1	250
F7	06/01/1992	13:00	D	76	76	77	75	76.0 ± 1.0	253
F8	06/01/1992	14:00	D	68	64	55	69	64.0 ± 7.8	213
F9	06/01/1992	15:00	D	69	64	69	69	67.3 ± 2.9	223
F10	06/01/1992	16:00	D	97	101	111	103	103.0 ±7.2	343
F11	06/01/1992	17:00	D	92	82	89	87	87.5 ± 4.2	290
F12	06/01/1992	18:00	D	82	74	81	79	79.0 ± 4.4	263
F13	06/01/1992	19:00	D	74	63	71	66	68.5 ± 5.0	227
F14	06/01/1992	20:00	D	77	72	77	79	76.3 ± 3.0	253
F15	06/01/1992	21:00	D	61	58	61	60	60.0 ± 1.7	200
F16	06/01/1992	22:00	N	60	56	60	59	58.7 ± 2.3	197
F17	06/01/1992	23:00	N	61	56	65	68	62.5 ± 5.2	207
F18	06/02/1992	00:00	N	67	59	63	63	63.0 ± 3.3	210
F19	06/02/1992	01:00	N	72	67	70	70	69.6 ±2.5	233
F20	06/02/1992	02:00	N	71	66	65	63	66.3 ± 4.2	220
F21	06/02/1992	03:00	N	63	68	66	59	64.0 ± 3.9	210
F22	06/02/1992	05:00	N	89	88	94	80	87.6 ± 7.1	293
F23	06/02/1992	06:00	D	69	65	69	68	67.7 ± 2.3	227
F24	06/02/1992	07:00	D	77	72	85	85	80.0 ± 6.4	267
F25	06/02/1992	08:00	D	77	68	80	79	76.0 ± 5.5	253
F26	06/02/1992	09:00	D	68	58	67	63	64.0 ± 4.5	213
F35	06/13/1992	07:25	D	77	72	78	78	76.3 ± 2.9	253
F36	06/13/1992	08:10	D	74	69	74	80	74.3 ± 5.5	247
F37	06/13/1992	09:00	D	56	61	59	61	59.3 ± 2.9	197
F38	06/13/1992	10:00	D	57	54	57	60	57.0 ± 3.0	190
F39	06/13/1992	11:00	D	64	66	66	68	66.0 ± 2.0	220
F40	06/13/1992	12:00	D	69	68	72	79	72.0 ± 6.1	240
F41	06/13/1992	13:00	D	65	57	67	78	66.7 ± 10.6	223
F42	06/13/1992	14:00	D	75	88	86	96	86.3 ± 10.6	287
F43	06/13/1992	15:00	D	86	84	87	91	87.0 ± 3.6	290
F44	06/13/1992	16:00	D	76	71	81	77	76.3 ± 5.0	253
F45	06/13/1992	17:00	D	90	80	100	95	91.3 ± 8.5	303
F46	06/13/1992	18:00	D	80	79	82	86	81.7 ± 3.8	273
F47	06/13/1992	18:50	D	88	79	86	90	85.7 ± 5.9	287
F48	06/13/1992	19:45	D	71	71	72	74	72.0 ± 1.7	240

Sorting

A total of 38 hauls, or 152 nets were examined. After rinsing on a 1 mm sieve, all animals were sorted, counted and identified under a binocular microscope. For each net, the numbers of individuals of each species were standardized into mean densities in 100 m^{-3}.

Mean densities per 100 m^{-3} of the total of four nets in each sample and average day-night densities were also calculated.

Analysis

The swimming activity was measured with three coefficients adapted from Brunel (1972) and reported by Elizalde *et al.* (1991) : Kl = Nf2/Nt, K2 = Nf3/Nt, and K3 = Nf4/Nt, with Nf2 = density. 100 m^{-3} in net 2, Nf3 = density. 100 m^{-3} in net 3, Nf4 = density. 100 m^{-3} in net 4 and Nt = total density. 400 m^{-3} in the four nets.

A test of Wilcoxon-Mann-Whitney (U test) (Scherrer, 1984) was used to determine if there was a significant difference between day and night densities.

RESULTS

Faunistic composition

One hundred and eight species/groups were collected in the samples. Among them, there were forty-one benthic species/groups, mainly gastropods and bivalves, and twenty-one macroplanktonic species/groups, mainly copepods and crustacean larvae. These groups were studied otherwise (Vallet, 1993 ; Wang *et al.*, 1994). The present study only deals with a total of forty-six suprabenthic crustacean and pycnogonid species (Table II).

In the samples of June 1-2, a total of 41 species were identified : seven species of Mysidacea, four species of Cumacea, six species of Decapoda, twenty-three species of Amphipoda and one species of Isopoda (Table II). According to their abundances, these species were classified into three groups :

1. Twelve principal species of the fauna, whose average total densities were higher than 1.0 ind. 100 m^{-3} (daytime samples and night samples were respectively taken as a whole) : *Schistomysis kervillei, Mesopodopsis slabberi, Gastrosaccus spinifer, Schistomysis spiritus, Diastylis bradyi, Pseudocuma longicornis, Bodotria scorpioides, Diastylis laevis, Crangon crangon, Liocarcinus pusillus, Megaluropus agilis* and *Atylus falcatus* (Table II).

2. Sixteen common species which were present in most of the samples with an average total density less than 1.0 ind. 100 m^{-3} : *Hippolyte varians, Orchomenella nana, Atylus swammerdami, Perioculodes longimanus, Pariambus typicus, Bathyporeia elegans, Melita obtusata, Leucothoe incisa, Amphilochus neapolitanus, Atylus vedlomensis, Melphidipella macra, Stenothoe marina, Ischyrocerus anguipes, Ampelisca brevicornis, Gammarus sp.* and *Pontocrates altamarinus* (Table II).

3. Thirteen rare species which were present in one or a few samples with only one or few individuals : *Acanthomysis longicornis, Siriella clausii, Anchialina agilis, Pinnotheres pisum, Corystes cassivelaunus, Pandalus montagui, Argissa hamatipes, Cressa dubia, Apherusa cirrus, Guernea coalita, Gammaropsis maculata, Phtisica marina* and *Astacilla sp.* (Table II).

TABLE II

Average day-night densities (N. ind. 100 m^{-3}) of the principal species of the suprabenthic fauna

Sampling date		June 1-2, 1992		June 13, 1992
		Day	Night	Day
Number of hauls		17	7	14
Volume of water filtered (m^3)		4988	1888	4204
Mysidacea		64.5	72.5	55.4
Schistomysis kervillei	(G.O. Sars, 1865)	51.9	52.3	7.3
Mesopodopsis slabberi	(Van Beneden, 1861)	5.0	15.1	44.1
Gastrosaccus spinifer	(Goës, 1864)	3.0	2.5	+
Schistomysis spiritus	(Norman, 1860)	2.2	2.5	3.5
Acanthomysis longicornis	(Milne-Edwards, 1839)	-	-	-
Siriella clausii	G.O. Sars, 1876	-		-
Anchialina agilis	(Sars, 1877)	-	-	
Cumacea		47.8	352.6	50.1
Diastylis bradyi	Norman, 1879	30.2	207.6	41.8
Pseudocuma longicornis	(Bate, 1858)	15.5	137.5	7.3
Bodotria scorpioides	(Montagu, 1804)	3.9	5.7	+
Diastylis laevis	Norman, 1879		1.6	+
Eudorella truncatula	Bate, 1856			-
Decapoda		3.9	19.6	2.0
Crangon crangon	(Linnaeus, 1758)	3.1	17.2	1.7
Liocarcinus pusillus	(Leach, 1815)	+	1.7	+
Hippolyte varians	Leach, 1814	+	+	-
Pinnotheres pisum	(Linnaeus. 1767)		-	-
Corystes cassivelaunus	Pennant, 1777	-		
Macropodia rostrata	Linnaeus, 1761			-
Pandalus montagui	Leach, 1814	-	-	-
Amphipoda		3.0	31.7	1.8
Megaluropus agilis	Hoek, 1889	+	21.0	+
Atylus falcatus	Metzger, 1871	-	1.5	
Orchomenella nana	(Kröyer, 1846)	-	+	-
Atylus swammerdami	(Milne-Edwards, 1830)	-	+	
Perioculodes longimanus	(Bate & Westwood, 1868)	-	+	-
Pariambus typicus	Kröyer, 1846	-	+	-
Bathyporeia elegans	Watkin, 1938	-	+	
Melita obtusata	(Montagu, 1813)	-	+	-
Leucothoe incisa	Robertson, 1892	-	+	-
Amphilochus neapolitanus	Della Valle, 1893	-	+	
Atylus vedlomensis	(Bate & Westwood, 1862)	-	+	
Melphidipella macra	(Norman, 1869)	-	+	
Stenothoe marina	(Bate, 1856)	-	+	-
Ischyrocerus anguipes	Kröyer, 1838	-	+	-
Ampelisca brevicornis	(A. Costa, 1853)		+	-
Gammarus sp.		-	+	
Pontocrates altamarinus	Bate & Westwood, 1862	-	+	
Argissa hamatipes	(Norrnan, 1869)		-	
Cressa dubia	(Bate, 1857)		-	
Apherusa cirrus	(Bate, 1856)	-		
Guernea coalita	(Norman, 1868)		-	
Gammaropsis maculata	(Johnston, 1828)	-		
Phtisica marina	Slabber, 1769	-		
Urothoe poseidonis	Reibisch, 1902			-
Acidostoma obesum	Bate & Westwood, 1861			-
Isopoda				
Astacilla sp.			-	
Pycnogonida				
Nymphon rubrum	Hodge, 1865			-

Note : + indicates that the mean density was less than 1.0 ind. 100 m^{-3}.
- indicates that only one or few specimen were found in all the sample.
daytime = 6h-21 h, night 22h-5h.

In the samples of June 13, 1992, a total of 29 species were identified : six species of Mysidacea, five species of Cumacea, six species of Decapoda, eleven species of Amphipoda and one species of Pycnogonida (Table II). Compared with the daytime samples of June 1-2, the species composition was similar. Except for *Atylus falcatus* which was only present during the night of June 1-2 with a density of 1.5 ind. 100 m^{-3}, all the principal species were also present in the samples of June 13. However, some of them were present with different densities : *Schistomysis kervillei* was much more abundant on June 1-2 (51.9 ind. 100 m^{-3}) than on June 13 (7.3 ind. 100 m^{-3}), while the density of *Mesopodopsis slabberi* increased from 5.0 ind. 100 m^{-3} on June 1-2 to 44.1 ind. 100 m^{-3} on June 13.

The majority of rare species and some common species in the samples of June 1-2 had disappeared from the samples of June 13 : *Anchialina agilis, Corystes cassivelaunus, Atylus swammerdami, Bathyporeia elegans, Amphilochus neapolitanus, Atylus vedlomensis, Melphidipella macra, Gammarus sp., Pontocrates altamarinus, Argissa hamatipes, Cressa dubia, Apherusa cirrus, Guernea coalita, Gammaropsis maculata*, and *Phtisica marina*. Inversely, four rare species were only present in the samples of June 13 with low densities : *Eudorella truncatula, Macropodia rostrata, Urothoe poseidonis* and *Acidostoma obesum.*

Total density

The total faunal density and species composition in the samples of June 1-2 varied drastically through the day. At 9h in the morning of June 1 (haul F3), the total faunal density collected by the sledge was only 2.2 ind. 100 m^{-3} ; at 2h (haul F20), the faunal density reached its maximum : 824 ind. 100 m^{-3} and the fauna was dominated by two species of cumaceans *Diaslylis bradyi* and *Pseudocuma longicornis* which represented 79 % of the individuals collected. Then at 6h (haul F23), density was 586 ind. 100 m^{-3} ; the mysids *Schistomysis kervillei* represented 70 % of the individuals collected. The average daytime faunal density was 266.4 ind. 100 m^{-3} in net 1 (55.9 %), 98.5 ind. 100 m^{-3} in net 2 (20.7 %), 59.2 ind. 100 m^{-3} in net 3 (12.4 %) and 52.6 ind. 100 m^{-3} in net 4 (11.0 %). The average of daytime densities of the four nets was 119.2 ind. 100 m^{-3}. The average night faunal density was 634.2 ind. 100 m^{-3} in net 1 (33.3 %), 483.8 ind. 100 m^{-3} in net 2 (25.4 %), 409.7 ind. 100 m^{-3} in net 3 (21.5 %) and 376.9 ind. 100 m^{-3} in net 4 (19.8 %). The average of night densities of the four nets was 476.2 ind. 100 m^{-3}. The daily average faunal density was 223.0 ind. 100 m^{-3} (Table III).

In the samples of June 13, the faunal density varied from 26 ind. 100 m^{-3} (haul F36) to 254 ind. 100 m^{-3} (haul F44) and the fauna was dominated by *Diastylis bradyi, Schistomysis kervillei* and *Mesopodopsis slabberi* which represented 78 % of all individuals collected. The average faunal density was 153.7 ind. 100 m^{-3} in net 1 (35.1 %), 118.2 ind. 100 m^{-3} in net 2 (27.0 %), 81.2 ind. 100 m^{-3} in net 3 (18.6 %) and 84.2 ind. 100 m^{-3} in net 4 (19.3 %). The average of the total density of the four nets was 109.3 ind. 100 m^{-3}, and was thus close to the daytime density observed in the samples of June 1-2 (Table III).

Swimming activity

According to their coefficients of swimming activity (Table IV), the 12 principal species of the suprabenthic fauna were classified in three groups as follow :

TABLE III

Mean densities (N. ind. 100 m^{-3}) of principal taxa in the four nets

Sampling date	June 1-2, 1992										June 13, 1992				
	Day					Night					Day				
Net	net 1	net 2	net 3	net 4	Mean	net 1	net 2	net 3	net 4	Mean	net 1	net 2	net 3	net 4	Mean
Mysidacea	165.5	35.2	23.3	34.1	64.5	98.7	68.0	63.6	59.4	72.5	58.8	46.2	49.3	67.5	57.9
Cumacea	88.0	56.3	30.7	16.1	47.8	468.5	354.8	301.3	285.3	352.6	86.2	68.8	29.8	15.5	50.1
Decapoda	7.4	3.6	2.9	1.7	3.9	33.7	16.5	15.2	12.9	19.6	5.4	1.5	1.1	0.1	2.0
Amphipoda	5.5	3.4	2.3	0.7	3.0	33.3	44.5	29.6	19.3	31.7	3.3	1.7	1.0	1.1	1.8
total	266.4	98.5	59.2	52.6	119.2	634.2	483.8	409.7	376.9	476.2	153.7	118.2	81.2	84.2	109.3
%	55.9	20.7	12.4	11.0		33.3	25.4	21.5	19.8		35.1	27.0	18.6	19.3	

TABLE IV

Coefficients of swimming activity K1, K2 & K3 of the principal species of the suprabenthic fauna

Sampling date		Day			Night			Day	
				June 1 - 2, 1992			June 13, 1992		
Number of hauls		17			7			14	
Volume of water filtered (m^3)		4988			1888			4204	
	K1	K2	K3	K1	K2	K3	K1	K2	K3
Mysidacea									
Schistomysis kervillei	0.13	0.07	0.07	0.24	0.21	0.18	0.19	0.05	0.07
Mesopodopsis slabberi	0.21	0.24	0.34	0.26	0.25	0.31	0.22	0.27	0.37
Gastrosaccus spinifer	0.23	0.21	0.21	0.18	0.29	0.12	-	-	-
Schistomysis spiritus	0.17	0.10	0.20	0.16	0.19	0.21	-	-	-
Cumacea									
Diastylis bradyi									
Males	0.30	0.28	0.04	0.24	0.25	0.25	0.42	0.14	0.09
Females & juveniles	0.28	0.17	0.08	0.27	0.25	0.24	0.35	0.15	0.08
Pseudocuma longicornis									
Males	0.26	0.16	0.08	0.20	0.09	0.08	0.29	0.20	0.06
Females & juveniles	0.30	0.13	0.08	0.28	0.22	0.19	0.35	0.15	0.07
Bodotria scorpioides	0.40	0.19	0.21	0.22	0.31	0.32	-	-	-
Diastylis laevis	-	-	-	0.18	0.07	0.47	-	-	-
Decapoda									
Crangon crangon	0.22	0.14	0.11	0.20	0.19	0.16	-	-	-
Liocarcinus pusillus	-	-	-	0.32	0.30	0.29	-	-	-
Amphipoda									
Megaluropus agilis	0.32	0.11	0.09	0.35	0.21	0.15	0.35	0.20	0.15
Atylus falcatus	0.29	0.11	0.04	0.32	0.30	0.12	-	-	-

Note : daytime = 6 h - 21 h, night = 22 h - 5 h.

1. Upper suprabenthic species with a strong swimming activity who swam in the water column above the bottom all the time : K1 < K2 < K3, K3 > 0.30. One species : *Mesopodopsis slabberi*.

2. Suprabenthic species with a strong activity which stayed near the bottom during the day : Kl > K2 > K3, and swam upward in the water column at night : Kl ≈ K2 ≈ K3 ≈ 0.25 or even Kl < K2 < K3. Four species : *Schistomysis spiritus, Diastyli bradyi* (males and females), *Bodotria scorpioides* and D*iastylis laevis*. Compared with the females and juveniles, the males of *Diastylis bradyi* were more concentrated in the lower net during the daytime. At night, both males and females were regularly distributed in the four nets. Thus the males were more active than the females and juveniles.

3. Lower suprabenthic species with a limited swimming activity which were more abundant in the lower nets both during day and night : Kl > K2 > K3. Still, densities observed at

night in the upper nets were slightly higher. Seven species : *Schistomysis kervillei, Gastrosaccus spinifer, Pseudocuma longicornis, Crangon crangon, Liocarcinus pusillus, Megaluropus agilis*, and *Atylus falcatus*. All the time, the males of *Pseudocuma longicornis* were more abundant than the females and juveniles in the lower nets. That means that the males tended to stay near the bottom and the amplitude of their swimming activity was more limited than that of the females and juveniles.

Nycthemeral migration

Only some species were present in the samples with a density high enough to allow us to study their migratory activities in detail (Table II).

Mysidacea

There was no significant difference between the density of *Schistomysis kervillei* in the daytime and at night ($p > 0.05$). The density was always highest in net 1, which contained 64 to 73 % of the individuals collected during the day and 38 % of those collected at night (Fig. 2a, b). The densities in the three upper nets were higher at night. This means that they performed a nocturnal vertical migration from the near-bottom water layer to the overlaying water.

The density of *Mesopodopsis slabberi* was higher at night than in the daytime ($p < 0.01$). Its abundance decreased gradually from net 4 to net 1 (Fig. 2c, d). Thus it seemed to be a pelagic species with a photophobe reaction : the individuals swim down to the vicinity of the bottom at night. However, *Mesopodopsis slabberi* is known to be a very good swimmer and to form schools. The lower catches during daytime could also be, more or less, due to the effect of the visual net-avoiding activity and the change of schooling behaviour.

Cumacea

Cumaceans are known to hide in the sediment during the day and to perform an active vertical migration at night (Corey, 1970 ; Granger, 1974 ; Hethagen, 1973). This was confirmed by our observations.

The densities of *Diastylis bradyi* and *Pseudocuma longicornis* were both higher at night than in the daytime ($p < 0.001$). During the day, few individuals were collected and their densities decreased gradually from net 1 to net 4. At night, *Diastylis bradyi* was regularly distributed over the four nets of the sledge. Thus, an active vertical migration occurred : the individuals moved from the bottom to the upper water layers. The males were almost totally absent in the daytime but were regularly present in the four nets at night. Thus they performed a more active vertical migration than the females and juveniles (Fig. 3a, b). *Pseudocuma longicornis* was always more abundant in the lower net than in the upper nets, especially the males. Both in the daytime and at night, about 50 % of all individuals collected were found in net 1. However, its higher density at night indicated that a vertical migration took place and that the individuals moved from the bottom to the water layer immediately above it. The density of the males was lower than that of the females and juveniles in the daytime. But they were more abundant at night, especially in net 1 where the males

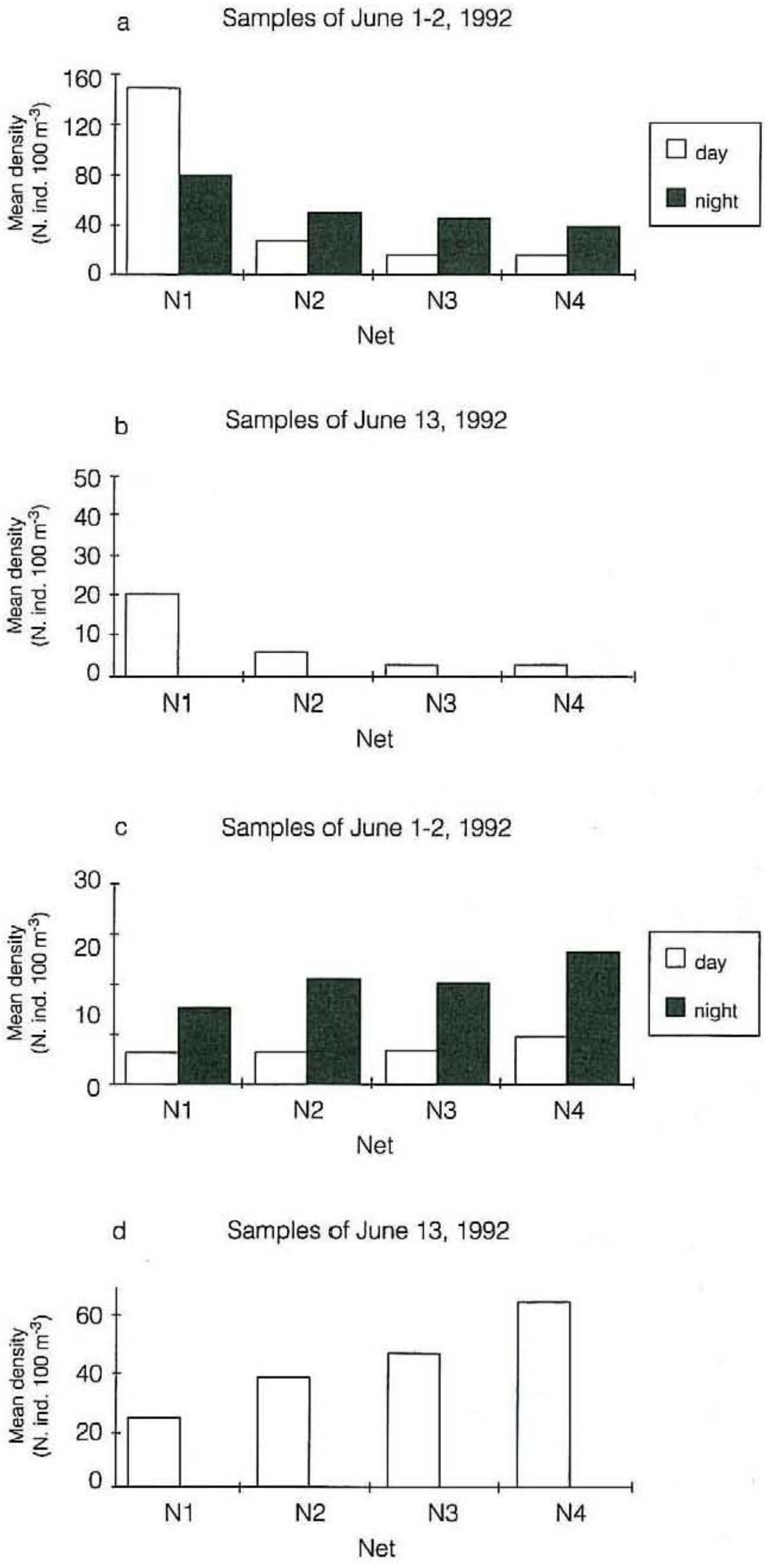

Fig. 2 : Daytime/night mean densities (N. ind. 100 m^{-3}) of mysids in the four nets (N1 = net 1, N2 = net 2, N3 = net 3, N4 = net 4), a, b : *Schistomysis kervillei* ; c, d : *Mesopodopsis slabberi*. daytime = 6 h - 21 h, night = 22 h - 5 h.

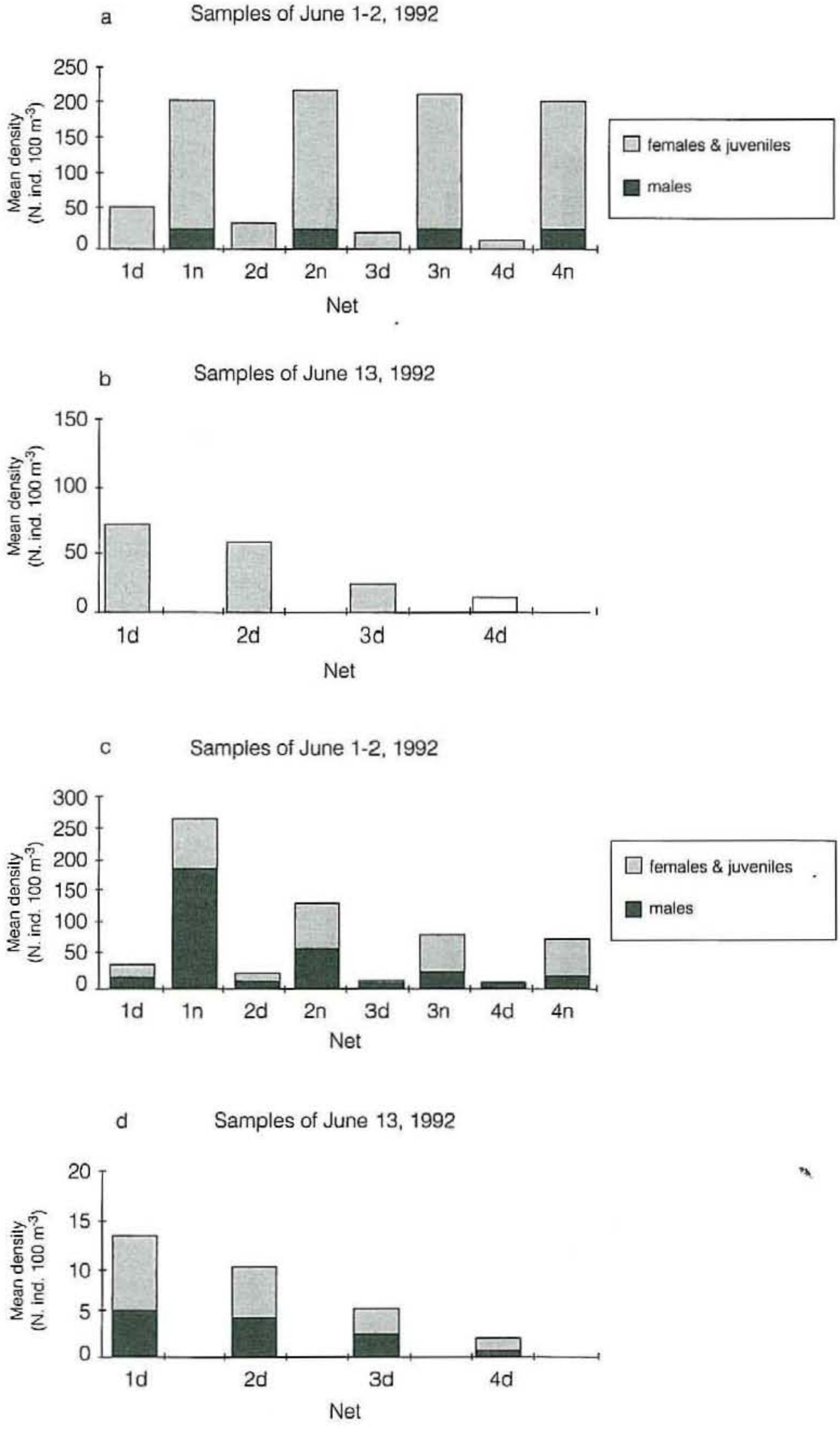

Fig. 3 : Daytime/night mean densities (N. ind. 100 m^{-3}) of cumaceans in the four nets (d = day, n = night, 1 = net 1, 2 = net 2, 3 = net 3, 4 = net 4 a, b : *Diastylis bradyi* ; c, d : *Pseudocuma longicornis*. daytime = 6 h - 21 h, night = 22 h - 5 h.

represented 65 % of the individuals collected. Thus, although the moving range was limited, the vertical migration of the males was more active than that of the females and juveniles (Fig. 3c, d).

Decapoda

Like cumaceans, most individuals of *Crangon crangon* were hidden in or on the sediment during the daytime and few of them were collected. At night, their density was significantly higher ($p < 0.001$) with most specimens (45 %) found in net 1. Thus they performed a nocturnal vertical migration in the same way as *Pseudocuma longicornis* : from the bottom to the water layer immediately above it (Fig. 4).

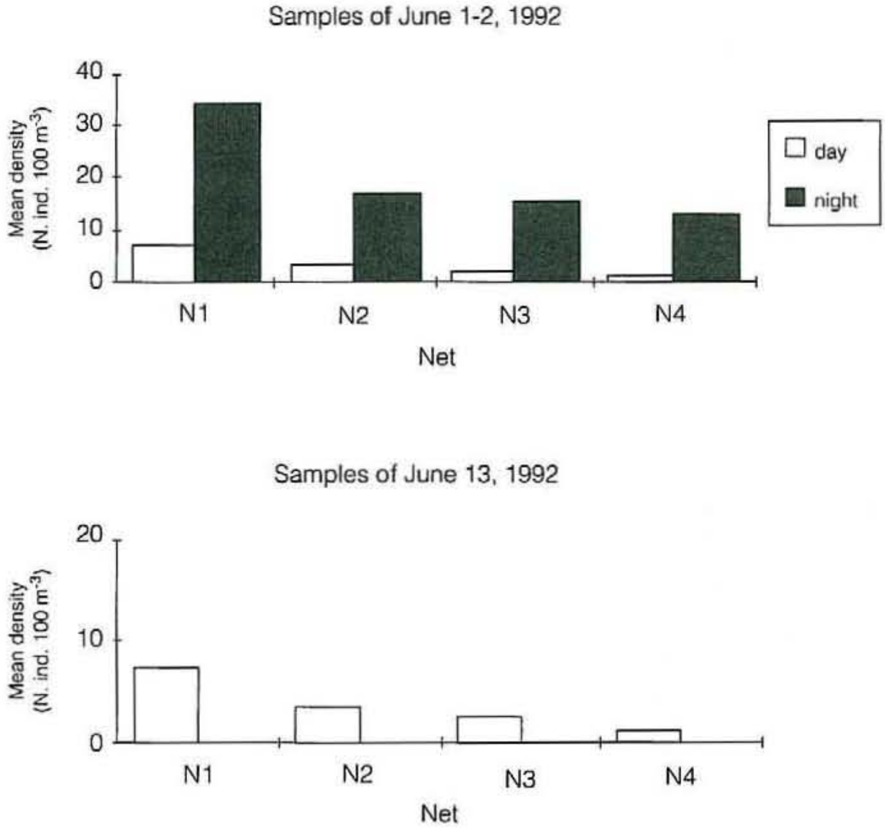

Fig. 4 : Daytime/night mean densities (N. ind. 100^{-3}) of *Crangon crangon* in the four nets (N1 = net 1, N2 = net 2, N3 = net 3, N4 = net 4), daytime = 6 h - 21 h, night = 22 h - 5 h.

Amphipoda

The amphipod *Megaluropus agilis* was also found to be endobenthic during the day as they were almost entirely absent from our samples. After dusk, they moved up to the near-bottom water column with most individuals reaching the water layer of net 2 ; then they returned to the bottom before dawn (Fig. 5). Thus the difference of the density of *Megaluropus agilis* (the only amphipod species with the densities high enough to allow for stastistical testing) between the day and the night was very significant ($p < 0.001$).

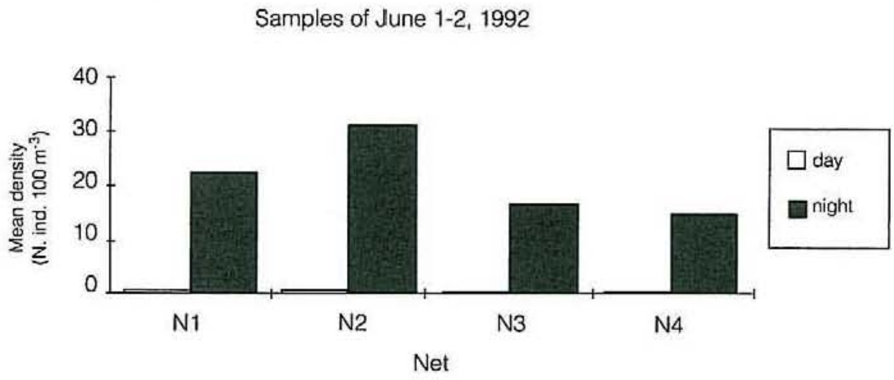

Fig. 5 : Daytime/night mean densities (N. ind. 100 m^{-3}) of *Megaluropus agilis* in the four nets (N1 = net 1, N2 = net 2, N3, N4 = net 4). daytime = 6 h - 21 h, night = 2 2h - 5 h.

Diurnal variation

Mysidacea

In the samples of June 1-2, *Schistomysis kervillei* was present with very low densities (0-30 ind. 100 m^{-3}), both in the daytime and during the night. It showed its maximal densities only at sunset (167 ind. 100 m^{-3}) and at sunrise (412 ind. 100 m^{-3}) (Fig. 6a). In the samples of June 13, *Schistomysis kervillei* was less abundant and its maximal density was not more than 26 ind. 100 m^{-3}.

The swimming species *Mesopodopsis slabberi* showed its density peaks (64-79 ind. 100 m^{-3}) during the ebb tide in the samples of June 1-2 when the estuarine water mass went out from the estuary to return to the open sea. And in the samples of June 13, when it was the period of neap tide and marine water masses were more important, it was very abundant and showed its maximal densities when the current was strong. Therefore it seemed that this swimming species preferred marine salted water (Fig. 6b, c).

Cumacea

In the samples of June 1-2, *Diastylis bradyi* and *Pseudocuma longicornis* were present essentially at night. The density of *Diastylis bradyi* went up progressively after sunset and reached its maximum of 462 ind. 100 m^{-3} after midnight. Then densities went down progressively with a slight increase at sunrise, after which the species disappeared from the samples (Fig. 7a). The density of *Pseudocuma longicornis* increased abruptly around sunset, between 21h and 22h, increased rapidly to a maximum of about 190 ind. 100 m^{-3} and remained abundant until 2h. Then its densities decreased to about 70 ind. 100 m^{-3} during the last few hours of the night and the species disappeared almost totally from the samples after 9h (Fig. 7b).

Decapoda

Crangon crangon was only present at night. In the samples of June 1-2, the individuals emerged rapidly to reach a maximal density of 46 ind. 100 m^{-3} just after sunset. During the

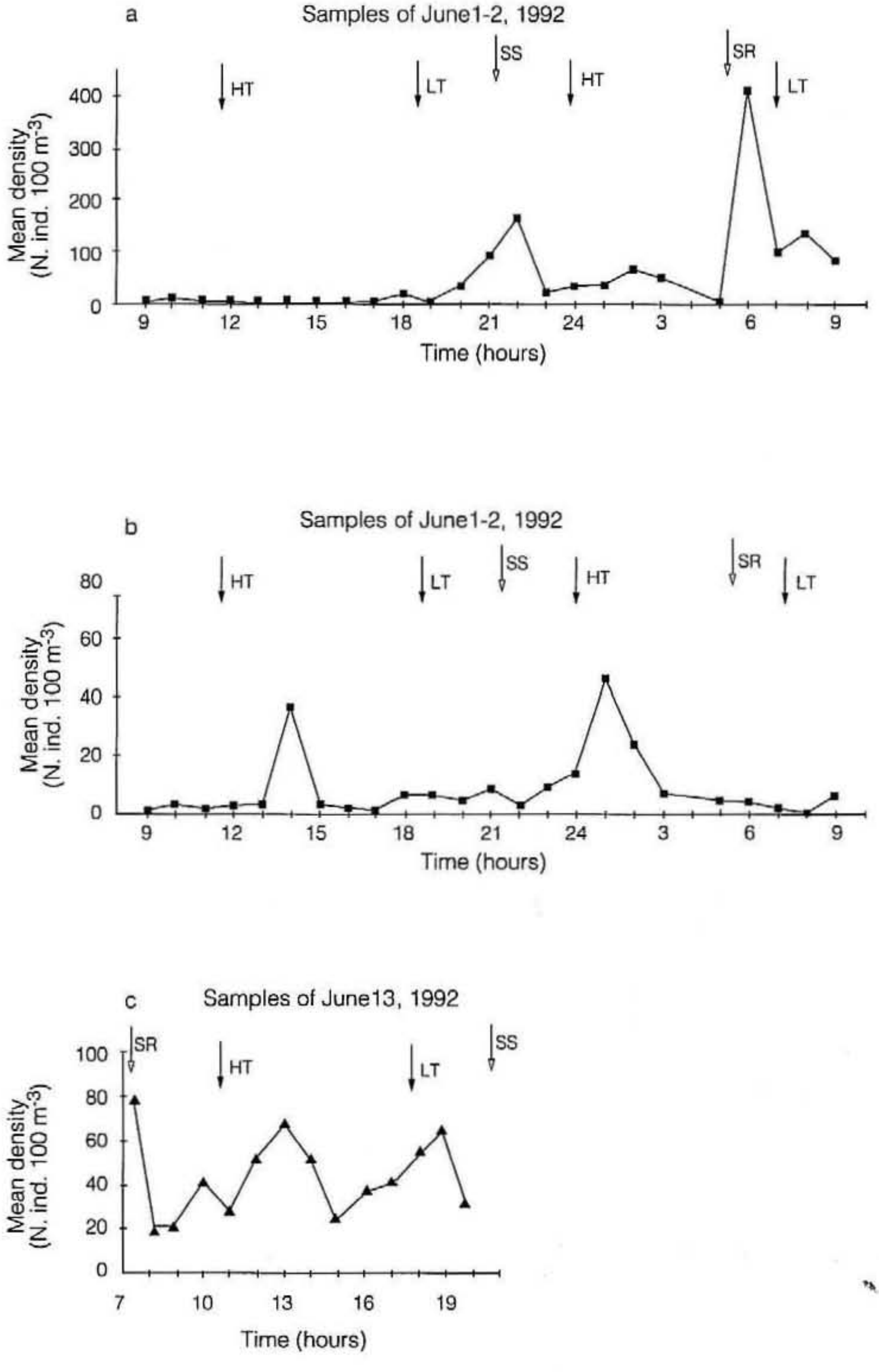

Fig. 6 : Diurnal variation of the density of *Schistomysis kervillei* (a) and *Mesopodopsis slabberi* (b, c) daytime = 6 h - 21 h, night = 22 h - 5 h. HT = high tide, LT = low tide, SS = sunset, SR = sunrise.

night hours, its density fluctuated irregularly and then went down. The species disappeared from the samples after sunrise (Fig. 8a).

Amphipoda

Megaluropus agilis seemed to be a very sensitive photophobic species. It performed a clear nocturnal vertical migration. It was only present during a few dark hours. The migratory activity began at sunset, its density reached a maximum of 43 ind. 100 m^{-3} around midnight and decreased rapidly between 2h and 3h. The species disappeared from the samples before sunrise (Fig. 8b).

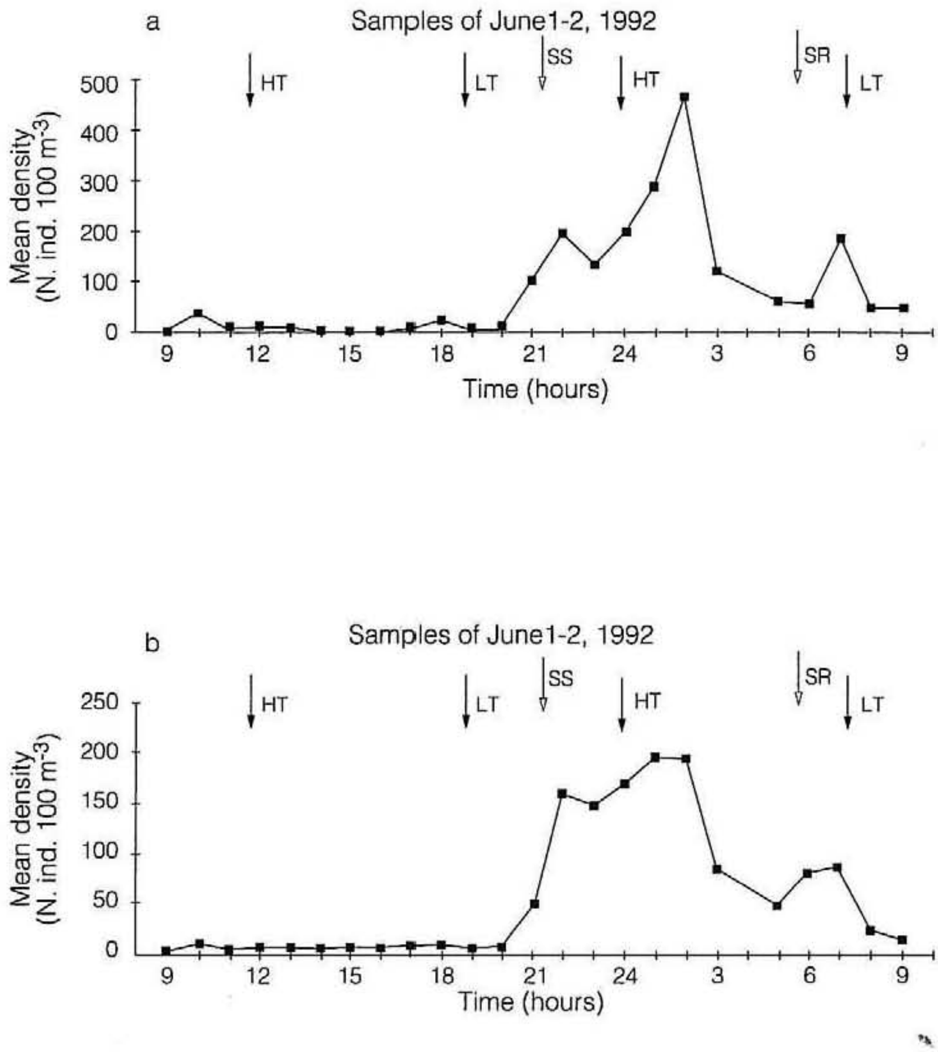

Fig. 7 : Diurnal variation of the density of *Diastylis bradyi (a)* and *Pseudocuma longicornis (b)* daytime = 6 h - 21 h, night = 22 h - 5 h. HT = high tide, LT = low tide, SS = sunset, SR = sunrise.

DISCUSSION

Faunistic composition

Because of the existence of a halocline and the maintenance of a high salinity near the bottom (33.00-34.00 g. l^{-1}) (Wang, *et al.* 1994), the suprabenthic crustacean fauna was

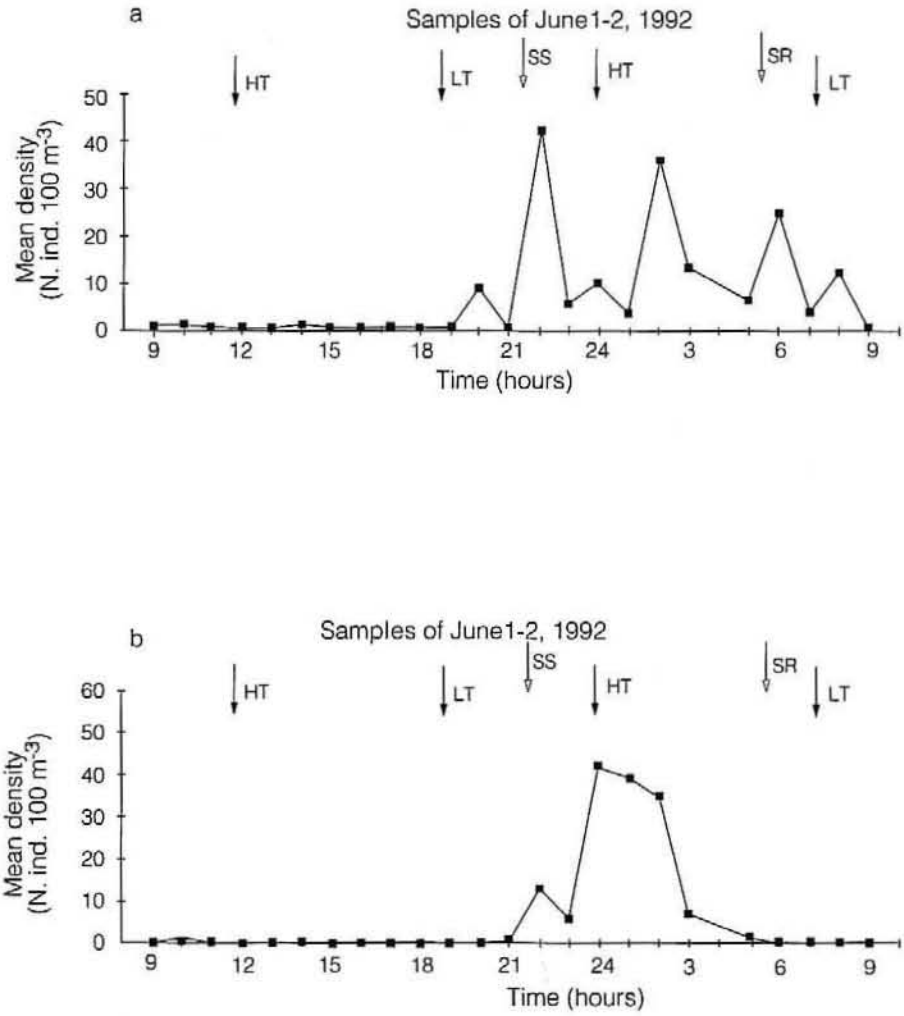

Fig. 8 : Diurnal variation of the density of *Crangon crangon* (a) and *Megaluropus agilis* (b) daytime = 6 h - 21 h, night = 22 h - 5 h. HT : high tide, LT = low tide, SS = sunset, Sr = sunrise.

essentially a marine one. However, some elements of the fauna might be euryhaline species. For example, *Schistomysis spiritus, Mesopodopsis slabberi, Schistomysis kervillei, Gastrosaccus spinifer, Atylus swammerdami* and *Gammarus crinicornis* were dominant species in the estuary of Westerschelde (especially in the marine part) where salinity varied between 15.00 and 20.00 g. l^{-1} in different seasons (Mees *et al.*, 1993 ; Cattrijsse *et al.*, 1993).

The suprabenthic fauna of the Bay of Seine is dominated by cumaceans (63.3 %) and mysids (27.5 %). Amphipods were present with low abundance (5.1 %) and high diversity (Table II). The same taxa also dominated the suprabenthic fauna in other regions : Kiel Bight (Boysen, 1975 ; Hesthagen, 1973), Norwegian and Swedish coasts (Kaartvedt, 1985, 1989 ; Buhl-Jensen, 1986 ; Buhl-Jensen & Fossa, 1991), Dutch and Belgian deltas and estuaries (Hamerlynck & Mees, 1991 ; Mees & Hamerlynck, 1992 ; Mees *et al.*, 1993 ; Cattrijsse *et al.*, 1993). The species composition and densities of the present fauna was similar to that found in the Bay of Biscay : in regions of fine sand bottom, a similar dominance of cumaceans and mysids was observed (Sorbe, 1984). But it was different from the fauna near coarse sand bottoms where amphipods dominated overall (Dauvin *et al.*, 1994). In the Bay of Fundy, the Bay of Chaleurs, the estuaries of Saint Lawrence and Schelde, in the circalittoral area, near the bottom of moving sediments, amphipods were also found to be dominant (Sainte-Marie & Brunel, 1985 ; Chevrier *et al.*, 1991 ; Cattrijsse *et al.*, 1993). In shallow water regions, for example, Browns Bank (Wildish *et al.*, 1992) and Gullarfjord (Buhl-Jensen & Fosså, 1991), amphipods and mysids were often found to be dominant.

The daily average faunal density of the suprabenthos was 223 ind. 100 m^{-3}. This value was a little lower than that of the shallow water of the Western English Channel (about 240 ind. 100 m^{-3}) and a little higher than that of Browns Bank (about 75 ind. 100 m^{-3}). But it was far from the richness of the fauna present in Gullmarfjord and the Bay of Biscay, where average faunal density was often more than 3 000 ind. 100 m^{-3}. On the contrary, in the circalittoral and infralittoral area of Schelde estuary, the average faunal density was less than 50 ind. 100 m^{-3}, except in certain seasons and in some stations (Table V). Therefore, the present suprabenthic fauna was not among the richest ones reported to date, but it is still relatively important.

Although the time interval between the two series of samples was no more than 12 days, some differences, as well as many similarities, could be detected between them. Among the forty-one species found in the samples of June 1-2, 16 species were absent in the samples of June 13. On the other hand, 5 other species appeared. When the samples collected in the daytime only were considered, 34 species were present on June 1-2, and 29 species on June 13.

Certain species, such as *Schistomysis spiritus, Diastylis bradyi, Pseudocuma longicornis* and *Crangon crangon*, were present in both series of samples with comparable densities. This means that in June, weak fluctuations of these species took place. It is possible that in the spring they are permanent species of the suprabenthic fauna of the region. The densities of some other species changed largely : *Schistomysis kervillei, Gastrosaccus spinifer* and *Megaluropus agilis* were more abundant on June 1-2, while *Mesopodopsis slabberi* was more abundant on June 13 (Table II). These results showed that there was a quantitative change of the fauna related to the alternation of the spring tide/neap tide cycle which changed the proportions of brackish and saline water.

Diurnal variation

The diurnal quantitative variation of the suprabenthic crustacean fauna is a result of two mechanisms operating at the same time : passive advection with tidal currents and active nocturnal vertical migrations from the endobenthos to the water column or from the near-bottom layer to the upper layers, or inversely from the upper layer to the near bottom layer.

A number of researchers have studied the nycthemeral vertical migrations of cumaceans, mysids, amphipods and decapods. They revealed that many species were endobenthic during the day and suprabenthic at night. Some authors concluded that the change of light was the most important factor determining migratory activities (Corey, 1970 ; Hesthagen,

TABLE V

Densities (N. ind. 100 m^{-3}) of near-bottom amphipods and mysids in several regions
• density calculated from available author data

Type of sled	Region	Depth (m) Taxa	Height above the sediment (cm) Mean density (N. ind. 100 m^{-3})				Remarks	Reference
MACER-GIROQ	Eastern English Channel NE Atlantic	8-13	10-40	45-75	80-110	115-145	one station daily average	This study
		Amphipods	14	15	10	6		
		Mysids	146	45	35	42		
		Total	374	211	161	147		
MACER-GIROQ	Western English Channel NE Atlantic	75	10-40	45-75	80-110	115-145	annual average	Dauvin *et al.*, 1994
		Amphipods	138	194	180	202		
		Mysids	51	57	55	48		
		Total	204	257	242	256		
MACER-GIROQ	Browns Bank NW Atlantic	about 80		33-73		109-149	34 stations	Wildish *et al.*, 1992
		Amphipods		53		12		
		Mysids		10		1		
		Total		113		36		
R. P. sledge	Gullmarfjord shallow fjord NE Atlantic	33-41		29-59			3 stations	Buhl-Jensen & Fossa, 1991
		Amphipods		1700*				
		Mysids		1616*				
		Total		3360*				
R. P. sledge	Gullmarfjord Sill NE Atlantic	40-42		29-59			2 stations	Buhl-Jensen & Fossa, 1991
		Amphipods		2769*				
		Mysids		679*				
		Total		3606*				
Sorbe sledge	Bay of Biscay NE Atlantic	31	0-50		50-100		1 station annual average	Sorbe, 1984
		Amphipods	5922		812			
		Total	8633		3134			
hyperbenthic	Schelde estuary NE Atlantic Voor Delta	< 15		20-100			several stations winter average	Mees & Hamerlyncks, 1992
		Total		21*				
hyperbenthic sledge	Schelde estuary NE Atlantic Westerschelde	2-10		20-100			several stations winter average	Mees & Hamerlynck 1992
		Total		451*				
hyperbenthic sledge	Schelde estuary NE Atlantic Voor Delta	5-10		20-100			several stations annual average	Cattrijsse *et al.*, 1993 Mees *et al.*, 1993
		Amphipods		≃5*				
		Mysids		≃0.5*				
		Total		≃6*				
hyperbenthic sledge	Schelde estuary NE Atlantic Westerschelde	10		20-100			several stations annual average	Cattrijsse *et al.*, 1993 Mees *et al.*, 1993
		Amphipods		≃3*				
		Mysids		≃20*				
		Total		≃25*				
McIvor & Odum fyke net	salt marsh NE Atlantic Westerschelde	intertidal					2 stations annual average	Cattrijsse *et al.*, 1993 Mees *et al.*, 1993
		Amphipods		≃30*				
		Mysids		≃8*				
		Total		≃50*				

1973 ; Anger & Valentin, 1976 ; Macquart-Moulin, 1984 ; Kaartvedt, 1985, 1989 ; Macquart-Moulin *et al.*, 1987 ; Elizalde *et al.*, 1991). The present study confirmed these observations and showed that in the infralittoral area, except for swimming species, the tidal circulation hardly influenced the distribution of suprabenthic organisms.

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