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Diel changes of the Benthic Boundary Layer macrofauna over coarse sand sediment in the western English Channel

Macrofauna
Benthic Boundary Layer
Diel changes
Coarse sand
Western English Channel

Macrofaune
Couche d'eau adjacente au fond
Migrations nycthémérales
Sable grossier
Manche occidentale

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ABSTRACT

The Benthic Boundary Layer (BBL) macrofauna over a coarse sand community at Trezen Vraz (western English Channel) was sampled with a modified Macer-GIROQ hyperbenthic sledge to analyse its diel changes on two occasions, in November 1988 (9 hauls), and in July 1990 (11 hauls). Species composition of the fauna, swimming activities, daily vertical migrations, biomass of the principal taxa, and biomass exchanges between the BBL, the benthos, and the pelagos were studied. Sixty-one taxa in November and 129 taxa in July were sorted, counted, and classified into three groups: mesozooplankton, macrozooplankton, and hyperbenthos. In the mesozooplankton, copepods and crustacean larvae were very abundant in July. In the macrozooplankton, the chaetognath *Sagitta elegans* was abundant in both sets of samples, while the euphausiids were only abundant in November, and fish larvae and the amphipod *Apherusa clevei* were only abundant in July. In both sets of samples the most abundant taxon of the hyperbenthos was the mysid *Anchialina agilis*. The densities of all collected taxa fluctuated with daily vertical migrations: higher densities of mysids and euphausiids were present in daytime, whereas amphipods and decapods were more abundant at night. The biomasses in each haul varied from 72 to 303 mg/100 m^3 (mean: 154 mg/100 m^3) in November, and from 160 to 1943 mg/100 m^3 (mean: 638 mg/100 m^3) in July. Biomass exchanges between pelagos, BBL and benthos appeared important around sunset and sunrise.

RÉSUMÉ

Variations nycthémérales de la macrofaune de la couche d'eau adjacente au fond du peuplement de sables grossiers de la Manche occidentale.

La macrofaune hyperbenthique du peuplement des sables grossiers de la station Trezen Vraz (Manche occidentale) a été échantillonnée avec une nouvelle version du traîneau Macer-GIROQ en deux occasions, en novembre 1988 (9 traits) et juillet 1990 (11 traits) afin d'en étudier ses variations nycthémérales. La composition spécifique de la faune collectée, son activité natatoire et ses migrations nycthémérales, la biomasse des principaux taxons, et les échanges de biomasses entre la couche d'eau adjacente au fond, le benthos et le pélagos, ont été précisés. Les taxons identifiés, 61 en novembre et 129 en juillet, ont été répartis en trois grands groupes : le mésozooplancton, le macrozooplancton, et l'hyperbenthos. Les Copépodes et les larves de Crustacés sont très abondants en juillet ; dans le macrozooplancton, les Chaetognathes sont abondants dans les deux séries, tandis que les Euphausiacés ne sont abondants qu'au mois de novembre et les larves de Poissons et l'Amphipode *Apherusa clevei* qu'en été. Dans les deux séries, le Mysidacé *Anchialina agilis* est l'espèce dominante de l'hyperbenthos. Les densités montrent des variations journalières : celles des Mysidacés et des Euphausiacés sont plus élevées le jour, et à l'inverse celles des Amphipodes et des Décapodes sont plus élevées la nuit. Les biomasses mesurées dans chaque trait varient entre 72 et 303 mg/100 m^3 (moyenne 154 mg/100 m^3) en novembre, et entre 160 et 1943 mg/100 m^3 (moyenne 638 mg/100 m^3) en juillet. Les échanges de biomasse entre la couche d'eau adjacente au fond, le benthos et le pélagos ne semblent importants qu'au crépuscule et à l'aube.

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INTRODUCTION

Several studies have shown that there is a particular biological compartment in the Benthic Boundary Layer (BBL), dominated by Peracarida and Decapoda crustaceans which are food sources for demersal fishes. So the BBL fauna probably constitutes an important link in the food web of the coarse sand community which covers a large area in the English Channel. This fauna has been defined using different terms: nectobenthos, benthopelagic plankton, benthoplankton, demersal zooplankton, hyperbenthos, suprabenthos, and BBL fauna (*see* reviews in Sorbe, 1984 and Mees, 1994). Brunel *et al.* (1978) included in the suprabenthos (= hyperbenthos, Mees, 1994) all swimming, bottom-dependent animals; mainly crustaceans which perform, with varying amplitude, intensity and regularity, seasonal or daily vertical migrations above the sea-floor. Wildish *et al.* (1992) included in the BBL macrofauna, the epi-endofauna, zooplankton, fish larvae and all the species considered by Brunel *et al.* (1978) as suprabenthos. In the English Channel, the first information on the hyperbenthos was provided by Dauvin and Lorgeré (1989), and Dauvin *et al.* (1994) on the coarse sand community off Roscoff (western English Channel), excluding the planktonic components. Wang and Dauvin (1994) and Wang *et al.* (1994) provided data on the hyperbenthic and demersal macrozooplanktonic community from a station offshore from the Seine estuary (eastern English Channel). The objectives of the present study of an offshore coarse sand community in the western English Channel were: (1) to describe the fauna in the BBL sampled with a modified Macer-GIROQ between 0.10 and 1.45 cm above the sea-floor; (2) to assess the diurnal vertical migrations of the dominant species; (3) to estimate densities and biomasses of the BBL macrofauna; and (4) to use the available information to calculate biomass exchanges between benthic and pelagic environments separated by the BBL.

MATERIAL AND METHODS

Study site

The station "Trezen Vraz" (48° 51.20' N; 3° 53.42' W), located in the north of Roscoff harbour, consists of bioclastic coarse sand with a benthic macrofauna belonging to the *Venus fasciata* community (Dauvin *et al.*, 1994). The station depth is about 75 m and it lies within a thermohomogenous area characterized by low annual variations in salinity, without a thermocline. Bottom-water temperature is about 8°C in winter and 15.5°C in summer (annual mean = 12°C), and the salinity varies from 34.80 in winter to 35.30 at the beginning of autumn (Dauvin *et al.*, 1989, 1991).

Sampling and analysis

The samples were collected with a modified Macer-GIROQ hyperbenthic sledge (Brunel *et al.*, 1978; Dauvin and Lorgeré, 1989; Dauvin *et al.*, 1995). This sledge simultaneously sampled the fauna at four levels: 0.10-0.40 (net N1), 0.45-0.75 (net N2), 0.80-1.10 (net N3) and 1.15-1.45 m (net N4) above the sea-floor. Each net (WP2, 0.5 mm mesh size) was equipped with a "T.S.K." flowmeter to measure the volume of filtered water.

Two sets of hauls were made, the first on 14-15 November 1988 with nine hauls (TV01-TV09) and the second on 17-18 July 1990 with 11 hauls (TV22-TV32). The water volume filtered by each net varied from 203 to 254 m^3 for the first set and from 177 to 254 m^3 for the second (Tab.1). Organisms collected in each net were separately fixed in 10% neutral formalin immediately on board. A week later, the samples were washed and transferred to 70% ethanol. All the individuals were sorted, counted and determined to the species level (when possible), except for the adult copepods and for the crustacean larvae which were very numerous. Their densities were estimated using the following steps: (1) measure of the biovolume of each sample after extracting individuals of the other species; (2) count of copepods and crustacean larvae in three duplicates of 1 ml; and (3) multiplication of the mean number per ml by the biovolume of the sample. The numbers of individuals in each net were standardized to 100 m^3 [mean density in the four nets = (ΣDN1 + DN2 + DN3 + DN4)/4; DN1, DN2, DN3, DN4, density values (ind./100 m^3) in nets N1, N2, N3, and N4] and the total number in a haul (4 nets) was standardized to 400 m^3.

Swimming activities during the day and night were measured with three coefficients: K1 = DN2/tD, K2 = DN3/tD, K3 = DN4/tD, with DN2, DN3, DN4: density values (ind./100 m^3) in nets N2, N3, N4, and tD = total density (ind./400 m^3) in the four nets of the sledge (Dauvin *et al.*, 1994). The Wilcoxon-Mann-Whitney U test (Scherrer, 1984) was used to determine whether there was a significant difference between daytime and night-time densities.

Table 1

Information for samples collected, and volume of water filtered by the nets. D: day, N: night, SS: sunset, SR: sunrise. (1): volume not measured in these nets, and considered as equal to the mean volume of the 11/14/1988 hauls.

Principales caractéristiques de l'échantillonnage, et volume d'eau filtrée par les filets. D : jour, N : nuit, SS : crépuscule, SR : aube. (1) volume d'eau filtrée non disponible et considéré comme étant égal au volume moyen d'eau filtrée au cours de la campagne du 14 novembre 1988.

				Volume of filtered water				
Hauts	Date	Hour	Day/night	Net1	Net 2	Net 3	Net 4	
TV01	11/14/1988	15h45	D	(1)	(1)	(1)	(1)	251
TV02	11/14/1988	17h30	D	(1)	(1)	(1)	(1)	251
TV03	11/14/1988	18h30	SS	262	236	265	284	261
TV04	11/14/1988	19h30	N	237	203	238	271	237
TV05	11/14/1988	24h00	N	255	260	220	284	254
TV06	11/15/1988	6h00	N	239	214	233	271	239
TV07	11/15/1988	7h00	N	241	240	220	262	241
TV08	11/15/1988	7h50	SR	256	232	275	261	256
TV09	11/15/1988	8h30	D	234	205	268	228	233
TV22	07/17/1990	17h15	D	200	177	186	177	185
TV23	07/17/1990	18h45	D	196	179	203	196	193
TV24	07/17/1990	20h45	D	243	201	216	213	218
TV25	07/17/1990	22h00	SS	223	205	222	216	216
TV26	07/17/1990	23h00	N	232	219	245	267	241
TV27	07/17/1990	24h00	N	212	181	202	194	197
TV28	07/18/1990	4h45	N	207	186	207	200	200
TV29	07/18/1990	5h35	N	191	202	209	213	204
TV30	07/18/1990	6h45	SR	240	211	224	228	226
TV31	07/18/1990	8h45	D	254	226	234	231	236
TV32	07/18/1990	10h45	D	242	222	201	230	223

The dry weight of each taxon was measured after oven-drying at 80°C for 48 h and the ash weight after further heating at 550°C for 2 h. Both weights were measured with a precision of 0.001 mg. The ash-free dry weight (AFDW) was the difference between these two values. Biomasses of each species or taxon in each net were calculated and expressed in mg of AFDW per 100 m^3 [mean biomass in the four nets = (ΣBN1 + BN2 + BN3 + BN4)/4; BN1, BN2, BN3 et BN4, biomass mg AFDW/100 m^3 in nets N1, N2, N3, and N4].

Vertical biomass (mean biomass in the four nets in mg AFDW/100 m^3) exchanges between pelagos (water column above the hyperbenthic environment) and BBL (water layer sampled by the sledge), corresponding to migration of planktonic organisms, and between BBL and benthos, corresponding to migration of benthic organisms, were estimated by comparing biomasses of successive hauls. We considered positive exchanges when the biomasses in the BBL increased, and negative exchanges when the biomasses in the BBL decreased.

RESULTS

Faunistic composition

Sixty-one taxa were collected in the samples of November 1988 and 129 taxa in the samples of July 1990 (Zouhiri, 1993), for a total of 133 taxa (Tab. 2). The fauna could be classified into three groups of organisms according to their size and their bottom dependence: (1) two mesozooplanktonic taxa, Copepoda and crustacean larvae; (2) 24 macrozooplanktonic taxa, Chaetognatha, Euphausiacea, the holopelagic amphipod *Apherusa clevei*, which was present throughout the water column in the Roscoff area (Toulmond and Truchot, 1964), Mollusca Cephalopoda and fish larvae; and (3) 102 hyperbenthic taxa: Amphipoda, Mysidacea, Isopoda, Pycnogonida, and Leptostracea.

In November 1988, Copepoda, crustacean larvae, Euphausiacea, Chaetognatha, four families of fish larvae, 31 species of Amphipoda, 10 species of Mysidacea, two species of Cumacea, four species of Isopoda, five species of Decapoda, and one species of Leptostracea were collected in nine hauls (Tab. 2). A total of 75,653 individuals were counted, excluding copepods and crustacean larvae. Macrozooplanctonic taxa, Euphausiacea and Chaetognatha, were dominant. Three other species accounted for more than 500 individuals: *Anchialina agilis, Apherusa clevei,* and *Eusirus longipes*. Only four taxa were found in all samples, and 12 taxa had a frequency higher than 50%. Four taxa were present in the nine lower nets, and 12 taxa were found in at least five of the lower nets.

In July 1990, the fauna was more diversified: Copepoda, crustacean larvae, Euphausiacea, Chaetognatha, 19 families of fish larvae, 57 species of Amphipoda, 16 species of Decapoda, 15 species of Mysidacea, eight species of Isopoda, five species of Cumacea, two species of Mollusca Cephalopoda, two species of Pycnogonida and one species of Leptostracea were collected in 11 hauls (Tab. 2). A total of 751,497 individuals were counted, excluding copepods and crustacean larvae. The *Apherusa* species, and *Sagitta elegans* were dominant, 12 other taxa accounted for more than 1000 individuals (Tab. 2). Five taxa were found in all samples, and 22 taxa had a frequency ≥ 50%. Seven taxa were present in all 11 lower nets, and 26 taxa were found in at least six of the lower nets. In both series of hauls, the most diversified group was Amphipoda; a great number of taxa was collected but abundances were low, often fewer than 10 individuals (Tab. 2).

Density

The density of meso- and macrozooplankton showed an increase from the lower to the upper net. Inversely, hyperbenthos was more abundant in the lower net (Tab. 3). The density of organisms varied greatly from one haul to another and from one net to another (Tab. 2, 3). In July, the mean density of organisms was much higher than those of November (10,018 ind./100 m^3 *vs.* 1164 ind./100 m^3).

Macrozooplanktonic organisms dominated in both series; they represented 69.1% of the total organisms in November (mean density: 804 ind./100 m^3), and more than 55.7% in July (mean density: 5,777 ind./100 m^3). The proportions of mesozooplanktonic organisms were respectively 25.7% (mean density: 299 ind./100 m^3) in November and 34.9% (mean density: 3494 ind./100 m^3) in July, and hyperbenthic organisms 5.2% (mean density: 61 ind./100 m^3) in November and 9.4% (mean density: 947 ind./100 m^3) in July. In November, higher densities, especially for macrozooplanktonic organisms, were found during daytime (Tab. 4), whereas in July the higher densities were found during darkness (Tab. 5). The highest values of mesozooplankton and hyperbenthos in the July hauls were observed

Table 2

Frequency of occurrence (F), number (N) and density of collected specimens in July 1990 and November 1988. tD: ind./400 m^3, cumulative values from the four nets of the sledge. DN1: ind./100 m^3, density in N1. Amp., Amphipoda, Cep., Cephalopoda, Cha., Chaetognatha, Cum., Cumacea, Iso., Isopoda, Dec., Decapoda, Eup. Euphausiacea, Lep., Leptostracea, Mys., Mysidacea, Pis., Pisces, Pyc., Pycnogonida.

Fréquence de capture de 0 à 1, nombre (N) et densité des espèces collectées en juillet 1990 et novembre 1988. tD : ind./400 m^3, cumul des densités des quatre filets du traîneau, DN1 : ind./100 m^3 densité dans le filet 1.

			17-18 July 1990						14-15 November 1988					
			ΣN1N2N3N4 (44 nets)			N1(11 nets)			ΣN1N2N3N4 (36 nets)			N1 (9 nets)		
			F	N	tD	F	N	DN1	F	N	tD	F	N	DN1
Apherusa clevei	Sars, 1904	Amp.	1,00	450019	14702,90	1,00	56701	2360,00	1,00	2258	101,60	1,00	288	15,57
Sagitta elegans	Verrill, 1873	Cha.	1,00	158076	7128,00	1,00	49991	2017,00	1,00	46181	2111,80	1,00	10902	496,60
Anchialina agilis	(Sars, 1877)	Mys.	1,00	29594	1327,30	1,00	8523	340,06	1,00	3066	138,60	1,00	612	30,23
Stenothoe marina	(Bate, 1856)	Amp.	1,00	12564	592,70	1,00	3129	280,00	0,94	148	6,73	0,88	47	2,13
Leptomysis gracilis	(Sars, 1864)	Mys.	1,00	2311	98,76	1,00	1081	44,75	0,77	99	4,44	0,77	38	1,92
Gastrosaccus normani	Sars, 1877	Mys.	0,97	8026	349,78	0,90	1625	72,42	0,97	257	11,98	0,88	72	2,80
Siriella jaltensis	Czerniavsky, 1868	Mys.	0,93	1348	59,02	0,90	341	13,86	0,14	6	0,25	0,11	2	0,08
Paramysis nouveli	Labat, 1953	Mys.	0,93	986	42,18	1,00	550	22,62	0,86	177	8,56	0,88	45	2,72
Nyctiphanes couchi	(Bell, 1853)	Eup.	0,90	2164	91,38	0,90	504	20,12	1,00	21754	1010.33	1,00	6413	295,60
Gobiidae		Pis.	0,88	501	23,80	0,90	3	0,12	0,00	0	0,00	0,00	0	0,00
Clupeidae		Pis.	0,81	3246	340,43	0,45	577	91,79	0,50	32	1,41	0,11	2	0,08
Mullidae		Pis.	0,77	240	10,41	0,81	63	3,40	0,02	1	0,08	0,00	0	0,00
Pseudocuma longicornis	(Bate, 1858)	Cum.	0,77	176	7,03	0,90	56	2,28	0,14	8	0,41	0,11	2	0,08
Melphidippella macra	(Norman, 1869)	Amp.	0,72	2193	117,51	0,81	417	24,24	0,69	332	15,24	0,88	50	2,98
Atylus vedlomensis	(Bate & Westwood, 1862)	Amp.	0,72	493	32,40	0,72	123	7,70	0,39	34	1,57	0,22	5	0,21
Sepiola atlantica	Orbigny, 1939	Cep.	0,63	96	4,06	0,72	38	1,63	0,00	0	0,00	0,00	0	0,00
Pandalina brevirostris	(Rathke, 1843)	Dec.	0,61	1450	63,60	1,00	600	27,41	0,47	50	2,51	0,33	10	0,43
Mysidopsis angusta	Sars, 1864	Mys.	0,61	259	11,71	0,81	148	6,16	0,00	0	0,00	0,00	0	0,00
Gadidae		Pis.	0,59	152	8,68	0,54	36	1,47	0,02	1	0.04	0,00	0	0,00
Siriella norvegica	Sars, 1869	Mys.	0,56	287	12,50	0,63	129	5,34	0,00	0	0,00	0,00	0	0,00
Eusirus longipes	Boeck, 1861	Amp.	0,52	1659	48,36	0,63	584	16.93	0,75	788	35,34	0,77	186	8,13
Iphimedia obesa	Rathke, 1843	Amp.	0,50	203	8,80	0,45	99	1,20	0.19	10	0.46	0,33	4	0,18
Atylus swammerdami	(Milne-Edwards, 1830)	Amp.	0,47	207	8.15	0,54	60	2,80	0,00	0	0,00	0,00	0	0,00
Phtisica marina	Slabber, 1769	Amp.	0,47	51	2,17	0,72	27	0,16	0,00	0	0,00	0,00	0	0,00
Apherusa bispinosa	(Bate, 1856)	Amp.	0,45	67326	671,60	0,45	1570	103,10	0,60	141	5,85	0,88	40	1,80
Apherusa cirrus	Bate, 1862	Amp.	0,45	5978	230,28	0,45	616	38,90	0,00	0	0,00	0,00	0	0,00
Callionymus reticulatus	Valenciennes, 1834	Pis.	0,45	80	3,24	0,45	24	0,96	0,00	0	0,00	0,00	0	0,00
Guernea coalita	(Norman, 1868)	Amp.	0,45	44	1,55	0,45	13	0,72	0,36	43	2,36	0,55	25	1,33
Loligo forbesii	Steentrup, 1856	Cep.	0,45	34	1,47	0,45	6	0,25	0,00	0	0,00	0,00	0	0,00
Pisidia longicornis	(L., 1767)	Dec.	0,43	294	10,31	0,54	77	1,25	0,00	0	0,00	0,00	0	0,00
Synchelidium maculatum	Stebbing, 1906	Amp.	0,40	192	7,30	0,45	51	2,20	0,36	37	1,65	0,22	13	0,36
Eurydice pulchra	Leach, 1815	Iso.	0,36	122	5,58	0,27	44	2,01	0,05	2	0,08	0,11	1	0,04
Pontophilus sculptus	(Bell, 1853)	Dec.	0,36	33	2,06	0,54	10	0,86	0,05	2	0,09	0,00	0	0,00
Megamphopus cornutus	(Johnston, 1828)	Amp.	0,31	58	2,23	0,72	45	1,65	0,14	8	0,34	0,22	5	0,22
Orchomene nana	Kröyer, 1846	Amp.	0,31	31	1,34	0,45	17	0,76	0,16	13	0,54	0,11	5	0,22
Galathea intermedia	Lilljeborg, 1851	Dec.	0,29	95	4,12	0,36	17	0,72	0,03	1	0,04	0,00	0	0,00
Mysidopsis gibbosa	Sars, 1864	Mys.	0,29	30	1,36	0,27	13	0,59	0,19	8	0,35	0,22	3	0.12
Pontocrates arenarius	(Bate, 1858)	Amp.	0,29	28	1,35	0,45	13	0,56	0,03	2	0,08	0,11	2	0,08
Erythrops elegans	Sars, 1876	Mys.	0,27	50	2,10	0,45	29	1.22	0,08	3	0,15	0,00	0	0,00
Bodotria scorpioides	(Montagu, 1804)	Cum.	0,27	20	0,75	0,45	4	0,12	0,00	0	0,00	0,00	0	0,00
Trachinus draco	L., 1758	Pis.	0,27	14	0,60	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Gammaropsis maculata	Norman, 1869	Amp.	0,25	68	1,91	0,54	49	1,27	0,14	17	0,77	0,44	15	0,68
Gastrosaccus lobatus	Nouvel, 1951	Mys.	0,25	31	1,77	0,18	9	0,42	0,16	7	0,44	0,11	1	0,04
Pseudoprotella phasma	(Montagu, 1804)	Amp.	0,22	38	1,81	0,45	26	1,30	0,00	0	0,00	0.00	0	0,00
Sphaeromatidae sp2		Iso.	0,22	16	0,64	0,36	4	0,17	0,00	0	0,00	0,00	0	0,00
Calipallene brevirostris	(Johnston, 1837)	Pyc.	0,22	15	0,48	0,36	6	0,19	0,00	0	0,00	0,00	0	0,00
Nymphon brevirostris	Hodge, 1863	Pyc.	0,22	9	0,55	0,09	2	0,07	0,00	0	0,00	0,00	0	0,00
Labrus mixtus	L., 1758	Pis.	0,20	54	2,16	0,18	17	0,68	0,00	0	0,00	0,00	0	0,00
Gnathia oxyuraea	(Lilljeborg, 1855)	Iso.	0,20	15	0,53	0,27	5	0.20	0,16	6	0,26	0,22	2	0,09
Gitana sarsi	Boeck, 1871	Amp.	0,20	13	0,55	0,45	8	0,33	0,14	7	0,35	0,33	3	0.14
Amphilochus neapolitanus	Della Valle, 1893	Amp.	0,20	11	0,46	0,27	5	0,17	0,03	1	0,04	0,00	0	0,00
Syngnathidae		Pis.	0,20	10	0,40	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Cheirocratus assimilis	(Lilljeborg, 1852)	Amp.	0,18	23	0,71	0,45	13	0,72	0,27	27	1,18	0,33	10	0,46
Astacilla longicornis	(Sowerby)(Sars, 1899)	Iso.	0,18	11	0,41	0,36	5	0,20	0,00	0	0,00	0,00	0	0,00
Ampelisca spinipes	Boeck, 1861	Amp.	0,18	8	0,33	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Liocarcinus pusillus	(Leach, 1816)	Dec.	0,15	41	0,73	0,27	11	0,43	0,16	11	0,48	0,00	0	0,00
Leptomysis lingvura	(Sars, 1866)	Mys.	0,15	38	1,55	0,27	9	0,37	0,25	13	0,58	0,33	6	0,26
Dicentrachus labrax	L., 1758	Pis.	0,15	27	1,08	0,18	4	0,16	0,00	0	0,00	0,00	0	0,00
Monoculodes carinatus	(Bate, 1856)	Amp.	0,15	19	0,82	0,18	2	0,08	0,08	2	0,13	0,00	0	0,00
Pontophilus trispinosus	Hailstone, 1835	Dec.	0,13	12	0,75	0,09	4	0,17	0,00	0	0,00	0,00	0	0,00
Callionymus lyra	L., 1758	Pis.	0,13	10	0,40	0,18	3	0,12	0,00	0	0,00	0,00	0	0,00
Tmetonyx similis	Sars, 1891	Amp.	0,13	9	0,38	0,27	5	0,22	0,00	0	0,00	0,00	0	0,00

			17-18 July 1990						14-15 November 1988					
			ΣN1N2N3N4 (44 nets)			N1(11 nets)			ΣN1N2N3N4 (36 nets)			N1 (9 nets)		
			F	N	tD	F	N	DN1	F	N	tD	F	N	DN1
Tmetonyx similis	Sars, 1891	Amp.	0,13	9	0,38	0,27	5	0,22	0,00	0	0,00	0,00	0	0,00
Macropodia tenuirostris	(Leach, 1814)	Dec.	0,13	6	0,52	0,18	5	0.21	0,00	0	0,00	0,00	0	0,00
Processa nouveli holthuisi	Al-Adhub & Williamson, 1975	Dec.	0,13	5	0,25	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Conilera cylindracea	(Montagu, 1803)	Iso.	0,11	26	0,71	0,18	19	0,48	0,05	2	0,08	0,11	1	0,04
Hippomedon denticulatus	(Bate, 1857)	Amp.	0,11	16	0,50	0,27	13	0,37	0,05	2	0,13	0,11	2	0,08
Hippolyte varians	Leach, 1814	Dec.	0,11	13	0,58	0,09	4	0,19	0,00	0	0,00	0,00	0	0,00
Parametopa kervillei	Chevreux, 1901	Amp.	0,11	6	0,22	0,18	2	0,07	0,11	5	0,20	0,22	2	0,08
Eurydice spinigera	Hansen, 1890	Iso.	0,11	5	0,19	0,00	0	0,00	0,11	5	0,21	0,11	1	0,04
Iphimedia nexa	(Myers & McGrath, 1982)	Amp.	0,11	4	0,24	0,27	3	0.14	0,03	1	0,04	0,00	0	0,00
Leucothoe spinicarpa	(Abildgaard, 1789)	Amp.	0,09	15	0,30	0,09	7	0.26	0,16	12	0,53	0,33	6	0,26
Socarnes filicornis	(Heller, 1866)	Amp.	0,09	8	0,34	0,36	8	0,34	0,00	0	0,00	0,00	0	0,00
Ischyrocerus anguipes	Kröyer, 1838	Amp.	0,09	5	0,20	0,18	3	0,12	0,00	0	0,00	0,00	0	0,00
Urothoe elegans	(Bate, 1856)	Amp.	0,09	4	0,16	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Nannastacus brevicaudatus	Calman, 1905	Cum.	0,09	4	0.18	0,09	2	0,08	0,00	0	0,00	0,00	0	0,00
Soleidae		Pis.	0,09	4	0.18	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Aora typica	Kröyer, 1845	Amp.	0,06	25	0,44	0,18	18	0,11	0,00	0	0,00	0,00	0	0,00
Schistomysis spiritus	Norman, 1860	Mys.	0,06	15	0,68	0,09	11	0,47	0,00	0	0,00	0,00	0	0,00
Tritaeta gibbosa	(Bate, 1862)	Amp.	0,06	7	0.28	0,09	1	0,03	0,00	0	0,00	0,00	0	0,00
Leucothoe incisa	Robertson, 1892	Amp.	0,06	5	0.22	0,09	1	0,03	0,11	3	0.13	0,00	0	0,00
Anthura gracilis	(Montagu)(Sexton, 1914)	Iso.	0,06	5	0.25	0,27	5	0,21	0,00	0	0,00	0,00	0	0,00
Ericthonius punctatus	(Bate, 1857)	Amp.	0,06	4	0.22	0,06	4	0,20	0,00	0	0,00	0,00	0	0,00
Tryphosella minima	Lilljeborg, 1852	Amp.	0,06	4	0.26	0,18	2	0.09	0,00	0	0,00	0,00	0	0,00
Ammodytidae		Pis.	0,06	4	0.20	0,09	3	0,12	0,22	18	0,80	0,22	2	0,08
Argentinidae		Pis.	0,06	4	0.20	0,09	3	0,12	0,00	0	0,00	0,00	0	0,00
Iphimedia eblanae	Bate, 1857	Amp.	0,06	3	0.14	0,27	3	0,16	0,00	0	0,00	0,00	0	0,00
Argissa hamatipes	Norman, 1869	Amp.	0,06	3	0.12	0,09	1	0,04	0,08	3	0.13	0,11	2	0,09
Atylus falcatus	Metzger, 1871	Amp.	0,06	3	0,12	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Processa edulis	Nouvel & Hothuis, 1957	Dec.	0,04	8	0,31	0,18	7	0,31	0,00	0	0,00	0,00	0	0,00
Iphimedia spatula	(Myers & McGrath, 1982)	Amp.	0,04	2	0,06	0,09	1	0,03	0,00	0	0,00	0,00	0	0,00
Lysianassa ceratina	Walker, 1889	Amp.	0,04	2	0,08	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Normanion chevreuxi	Diviacco & Vader, 1988	Amp.	0,04	2	0,08	0,18	2	0,08	0,03	1	0,04	0,11	1	0,04
Perrierella audouiniana	(Bate, 1857)	Amp.	0,04	2	0,11	0,09	1	0,04	0,08	2	0,14	0,00	0	0,00
Perioculodes longimanus	(Bate & Westwood, 1868)	Amp.	0,04	2	0,08	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Stenopleustes nodifer	(Sars, 1882)	Amp.	0,04	2	0,08	0,00	0	0,00	0,14	6	0.24	0,22	3	0,13
Siriella clausii	Sars, 1876	Mys.	0,04	2	0,08	0,09	1	0,04	0,16	10	0,43	0,11	2	0,08
Iphinoe trispinosa	(Goodsir, 1843)	Cum.	0,04	2	0,08	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Nannastacus unguiculatus	(Bate, 1859)	Cum.	0,04	2	0,08	0,00	0,00	0,00	0,00	0	0,00	0,00	0	0,00
Pagurus bernhardus	(L., 1758)	Dec.	0,04	2	0,08	0,18	2	0,08	0,00	0	0,00	0,00	0	0,00
Nebalia bipes	(Fabricius, 1780)	Lep.	0,04	2	0.11	0,18	2	0,13	0,05	2	0,08	0,11	1	0,04
Ampelisca spooneri	Dauvin & Bellan-Santini, 1982	Amp.	0,04	1	0.04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Scomber scomber	L., 1758	Pis.	0,02	17	0,68	0,18	3	0,12	0,00	0	0,00	0,00	0	0,00
Schistomysis parkeri	Norman, 1860	Mys.	0,02	11	0,47	0,09	11	0,47	0,00	0	0,00	0,00	0	0,00
Aspitrigla cuculus	L., 1758	Pis.	0,02	3	0.12	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Gastrosaccus spinifer	(Goes, 1864)	Mys.	0,02	2	0,08	0,09	2	0,08	0,00	0	0,00	0,00	0	0,00
Iphimedia minuta	Sars, 1882	Amp.	0,02	1	0,03	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Ampelisca diadema	Costa, 1853	Amp.	0,02	1	0,03	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Leptocheirus bispinosus	Norman, 1908	Amp.	0,02	1	0,04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Leptocheirus pectinatus	Norman, 1869	Amp.	0,02	1	0,03	0,09	1	0,03	0,00	0	0,00	0,00	0	0,00
Ceradocus semiserratus	(Bate, 1862)	Amp.	0,02	1	0,04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Liljeborgia pallida	(Bate, 1857)	Amp.	0,02	1	0,04	0,00	0	0,00	0,03	1	0,04	0,11	1	0,40
Lysianassa plumosa	Boeck, 1871	Amp.	0,02	1	0,03	0,09	1	0,03	0,00	0	0,00	0,00	0	0,00
Lysianassa sp.		Amp.	0,02	1	0,04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Orchomene humilis	(Costa, 1853)	Amp.	0,02	1	0,04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Austrosyrrhoe fimbriatus	(Stebbing & Robertson, 1891)	Amp.	0,02	1	0,04	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Metaphoxus fultoni	(Scott, 1890)	Amp.	0,02	1	0,03	0,00	0	0,00	0,03	1	0,04	0,11	1	0,04
Colomastrix pusilla	Grube, 1861	Amp.	0,02	1	0,04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Sphaeromatidae sp1		Iso.	0,02	1	0,03	0,09	1	0,03	0,00	0	0,00	0,00	0	0,00
Pagurus prideauxi	Leach, 1815	Dec.	0,02	1	0,04	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Achaeus cranchii	Leach, 1815	Dec.	0,02	1	0,04	0,00	0	0,00	0,03	1	0,04	0,00	0	0,00
Ebalia tuberosa	(Pennant, 1777)	Dec.	0,02	1	0,04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Liocarcinus depurator	(L., 1758)	Dec.	0,02	1	0,04	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Pinnotheres pisum	(L., 1767)	Dec.	0,02	1	0,04	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Liparis liparis	(L., 1766)	Pis.	0,02	1	0,04	0,81	63	3,40	0,00	0	0,00	0,00	0	0,00
Hippoglosoides platessoides	Bloch, 1787	Pis.	0,02	1	0,04	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Myoxocephalus scorpius	(L., 1758)	Pis.	0,02	1	0,04	0,09	1	0,04	0,00	0	0,00	0,00	0	0,00
Zeus faber	L., 1758	Pis.	0,02	1	0,04	0,00	0	0,00	0,00	0	0,00	0,00	0	0,00
Urothoe marina	(Bate, 1857)	Amp.	0,00	0	0,00	0,00	0	0,00	0,08	3	0,14	0,11	1	0,04
Maerella tenuimana	(Bate, 1862)	Amp.	0,00	0	0,00	0,00	0	0,00	0,11	5	0,22	0,11	1	0,04
Scopelocheirus hopei	(Costa, 1851)	Amp.	0,00	0	0,00	0,00	0	0,00	0,30	16	0,70	0,33	4	0,17
Campylapsis legendrei	Fage, 1951	Cum.	0,00	0	0,00	0,00	0	0,00	0,03	1	0,04	0,00	0	0,00

Table 3

Minimum (Dmin), mean (Dm) and maximum (Dmax) densities (ind./100 m³) of organisms collected in the four nets during the two sets of hauls in November 1988 and July 1990. N1: net 1, N2: net 2, N3: net 3, and N4: net 4.

Densité minimale (Dmin), maximale(Dmax) et moyenne (Dm)(N. ind./100 m³) des individus récoltés dans chacun des quatre filets au cours des deux séries de traits en novembre 1988 et juillet 1990. N1 : filet 1, N2 : filet 2 ; N3 : filet 3 et N4 filet 4.

		14-15 November 1988				17-18 July 1990			
		N1	**N2**	**N3**	**N4**	**N1**	**N2**	**N3**	**N4**
Mesozooplankton	Dmin	23	37	29	37	86	97	683	989
	Dm	**101**	**408**	**294**	**393**	**1797**	**3794**	**4260**	**4510**
	Dmax	246	1135	540	1554	3704	7310	9304	12212
Macrozooplankton	Dmin	201	388	267	420	871	669	1932	1952
	Dm	**805**	**911**	**931**	**761**	**4504**	**5335**	**6249**	**5781**
	Dmax	2095	1954	2918	1558	11993	14303	13944	9821
Hyperbenthos	Dmin	20	24	17	22	332	70	58	48
	Dm	**61**	**70**	**59**	**53**	**1400**	**1003**	**840**	**733**
	Dmax	113	138	117	101	4256	3551	1531	1644
Total	Dmin	226	578	507	567	3228	4956	6942	4063
	Dm	**967**	**1390**	**1284**	**1208**	**7701**	**10132**	**11348**	**11023**
	Dmax	2342	2812	3081	3013	13598	16391	16197	21971

around sunset and sunrise, while in November hyperbenthos abundances were more variable (Tab. 4, 5).

Swimming activity and vertical distribution

Table 6 gives the swimming activity coefficients in day and night hauls of the 19 dominant macrozooplanktonic, mesozooplanktonic and hyperbenthic taxa with a mean density higher than 1 ind./100 m³ which were found in one or both sets of samples. These taxa could be classified into four groups according to their swimming behaviour and their vertical distribution in the BBL (Dauvin *et al.*, 1994).

Group 1: organisms with a strong swimming activity occupying the whole BBL, K1 ≈ K2 ≈ K3 ≈ 0.25 all day although some of them had slightly higher abundances in the lower nets in July night hauls.

Group 1 included chaetognaths (Fig. 1*a, b*), *Anchialina agilis* (Fig. 1*c, d*), *Eusirus longipes* (Fig. 1*e, f*), *Gastrosaccus normani*, and *Siriella jaltensis*.

Group 2: upper hyperbenthic species with an exceptionally strong swimming activity were found mainly in the upper nets, K1+K2+K3 > 0.80. Abundances were low in net 1, and they could be concentrated in different upper nets depending on the time of collection. Group 2 included Euphausiacea

Table 4

Mean density D (ind./100 m³) and mean biomass B (mg AFDW/100 m³) of organisms collected in the four nets during the November sampling.

Densité moyenne D (ind./100 m³) et biomasse moyenne B (Poids Sec Libre de Cendres en mg/100 m³) des organismes collectés dans les quatre filets du traîneau au cours de la campagne de novembre 1988.

Haul	TV01		TV02		TV03		TV04		TV05		TV06		TV07		TV08		TV09	
Taxa	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**
Sagitta elegans	840,00	63,00	709,75	53,23	364,00	27,30	298,00	22,40	456,00	34,20	480,00	36,00	327,00	24,56	614,00	46,10	663,00	49,76
Apherusa clevei	13,00	0,58	17,21	0,79	19,00	0,86	44,00	2,03	28,00	1,31	17,00	0,77	20,00	0,91	14,00	0,63	56,40	2,59
Stenothoe marina	1,00	0,04	0,62	0,02	2,20	0,09	0,54	0,02	5,26	0,21	1,35	0,05	1,45	0,06	0,60	0,02	2,13	0,09
Others amphipoda	1,24	0,56	0,40	0,18	47,78	6,83	17,77	2,60	55,47	7,84	12,48	2,54	8,64	0,98	0,60	0,09	1,14	0,06
Cumacea	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,67	2,19	0,20	0,64	0,00	0,00	0,40	0,30	0,00	0,00
Isopoda	0,41	2,07	0,10	0,11	0,50	1,43	0,25	2,51	0,40	3,93	0,00	0,00	0,10	1,06	0,09	0,96	0,00	0,00
Anchialina agilis	66,00	6,00	58,00	3,59	18,00	1,60	19,00	1,70	10,00	0,90	13,00	1,20	13,00	1,20	38,00	3,43	77,00	7,00
Others Mysidacea	12,00	1,07	6,73	0,76	8,20	1,22	5,02	0,42	5,76	1,53	6,51	0,62	5,70	0,77	4,32	3,94	7,54	0,65
Pandalina brevirostris	0,00	0,00	0,00	0,00	2,25	13,13	0,55	3,20	1,15	6,70	1,40	8,10	0,30	1,73	0,00	0,00	0,00	0,00
Others Decapoda	0,00	0,00	0,00	0,00	0,21	3,65	0,23	0,86	0,69	1,45	0,27	0,09	0,19	0,07	0,10	0,04	0,09	0,03
Euphausiacea adult	790,00	132,70	310,75	42,72	15,50	2,60	72,50	12,18	21,00	3,53	62,25	10,46	65,75	11,05	561,00	94,25	347,50	58,38
Euphausiacea larvae	61,00	15,20	30,25	7,62	9,75	2,43	25,50	6,40	41,50	10,40	39,75	9,90	67,00	16,70	99,75	24,94	430,75	107,68
Copepoda	52,70	7,40	21,75	3,04	44,70	5,14	170,00	23,80	65,70	9,20	275,70	38,60	412,75	57,78	213,20	29,85	370,70	51,90
Crustacean larvae	13,75	4,80	8,51	3,00	14,00	4,90	31,75	11,11	21,25	7,44	35,00	12,25	44,75	15,66	21,75	7,61	67,25	23,54
Mollusca Cephalopoda	0,00	0,00	0,00	0,00	0,00	0,00	0,56	0,92	0,20	0,33	0,10	0,15	0,93	1,48	0,30	0,48	0,00	0,00
Fish larvae	0,00	0,00	0,00	0,00	0,45	1,18	1,78	3,77	1,45	1,83	1,14	2,24	1,75	3,46	0,48	0,32	0,69	1,48
Total	1851,10	233,42	1164,07	115,06	546,54	72,36	687,45	93,92	714,50	92,99	946,15	123,61	969,31	137,47	1568,59	212,96	2024,19	303,16
Macrozooplankton	1643,00	196,28	1037,71	96,74	398,95	31,94	416,84	41,30	506,65	41,20	560,49	49,62	415,43	41,46	1189,78	141,78	1067,59	112,21
Mesoplankton	127,45	27,40	60,51	13,66	68,45	12,47	227,25	41,31	128,45	27,04	350,45	60,75	524,50	90,14	334,70	62,40	868,70	183,12
Hyperbenthos	80,65	9,74	65,85	4,66	79,14	27,95	43,36	11,31	79,40	24,75	35,21	13,24	29,38	5,87	44,11	8,78	87,90	7,83

Table 5

Mean density D (ind./100 m^3) and mean biomass B (mg AFDW/100 m^3) of organisms collected in the four nets during the July sampling.

Densité moyenne D (ind./100 m^3) et biomasse moyenne B (Poids Sec Libre de Cendres en mg/100 m^3) des organismes collectés dans les quatre filets du traîneau au cours de la campagne de juillet 1990.

	TV22		TV23		TV24		TV25		TV26		TV27		TV28		TV29		TV30		TV31		TV32	
Sagitta elegans	1981,00	7,90	3031,00	12,10	1557,00	4,60	926,00	3,70	1336,00	7,30	2862,00	11,50	938,00	3,75	699,00	2,80	273,00	1,60	1980,00	7,90	4020,00	16,10
Apherusa clevei	753,00	52,70	1173,00	82,10	1599,00	111,90	6723,00	470,60	8157,00	545,70	10081,00	705,80	2117,00	148,20	2927,00	204,90	1000,00	70,00	2811,00	196,80	3092,00	216,40
Stenothoe marina	12,00	0,60	22,00	1,00	48,00	2,30	127,00	5,90	187,00	8,80	321,00	15,20	400,00	18,80	397,00	18,70	90,00	4,20	12,00	0,60	14,00	0,70
Others Amphipoda	4,00	0,40	3,80	0,10	5,98	0,07	708,64	118,60	821,60	195,70	996,60	199,10	278,00	217,90	408,90	63,30	30,20	18,75	4,90	0,03	0,60	0,00
Cumacea	0,40	0,04	1,20	0,10	0,50	0,05	1,70	0,20	0,80	0,08	3,20	0,30	1,70	0,20	3,90	0,40	3,80	0,40	2,20	0,20	0,00	0,00
Isopoda	0,00	0,00	0,00	0,00	0,00	0,00	0,30	0,50	0,60	0,70	1,10	12,30	3,10	17,40	0,60	1,90	0,90	0,07	0,40	0,80	0,00	0,00
Anchialina agilis	63,00	1,40	475,00	10,90	342,00	7,90	578,00	85,50	32,00	4,80	9,00	1,30	10,00	1,50	33,00	4,90	1738,00	39,90	346,00	7,90	24,00	0,90
Others mysidacea	93,00	6,50	159,40	17,40	153,40	9,90	208,90	114,30	44,70	57,15	59,20	8,50	29,50	8,90	95,10	36,00	415,40	28,60	296,90	20,10	43,10	4,00
Pandalina brevirostris	3,00	0,50	2,00	0,40	3,00	0,50	3,00	0,50	83,00	13,30	49,00	7,90	19,00	3,10	11,00	1,70	1,00	0,08	0,00	0,00	1,00	0,08
Others Decapoda	5,10	0,60	2,80	0,04	0,00	0,00	3,20	0,50	7,10	9,60	7,30	5,90	25,30	4,90	6,20	14,40	9,80	8,10	0,60	0,20	0,00	0,00
Euphausiacea	91,00	11,80	6,00	0,80	1,00	0,10	0,30	0,04	1,00	0,06	2,00	0,20	2,00	0,20	1,00	0,20	9,00	1,20	52,00	6,70	86,00	11,20
Clupeidae	0,00	0,00	2,00	3,80	30,00	59,70	540,00	1074,90	23,00	46,20	13,00	25,40	20,00	39,70	54,00	106,80	214,00	426,70	5,00	9,20	2,00	3,50
Others fish larvae	5,70	1,00	10,30	6,50	7,80	6,90	18,90	8,90	10,80	8,80	17,90	6,40	7,70	6,00	18,20	12,10	13,20	12,10	17,90	12,30	9,60	11,90
Pycnogonida	0,00	0,00	0,41	0,04	0,11	0,01	0,00	0,00	0,10	0,01	0,90	0,07	0,61	0,05	0,47	0,04	0,33	0,03	0,31	0,03	0,30	0,03
Mollusca Cephalopoda	0,28	0,62	0,00	0,00	0,69	1,51	4,30	9,52	1,83	4,03	1,37	2,87	1,17	2,23	2,37	5,16	1,22	2,63	1,83	3,89	0,22	0,51
Copepoda	2799,70	47,59	1493,70	25,39	3172,70	53,93	1404,00	23,86	580,50	9,86	363,70	6,18	979,50	16,65	1034,20	17,58	2784,00	47,32	4577,70	77,82	3026,50	51,45
Crustacean larvae	1416,00	28,32	1968,50	39,37	2581,70	51,63	1245,00	24,90	153,00	3,06	165,70	3,31	377,70	7,55	830,70	16,61	2797,20	55,94	3135,20	62,70	1550,20	31,00
Total	7227,18	159,97	8351,11	200,04	9502,88	311,01	12492,24	1942,42	11440,03	915,14	14953,97	1012,23	5210,28	497,03	6522,64	507,49	9381,05	717,62	13243,94	407,17	11869,52	347,77
Macrozooplankton	2830,98	74,02	4222,30	105,30	3195,49	184,71	8212,50	1567,66	9529,63	612,09	12977,27	752,17	3085,87	200,08	3701,57	331,96	1510,42	514,23	4867,73	236,79	7209,82	259,61
Mesozooplankton	4215,70	75,91	3462,20	64,76	5754,40	105,56	2649,00	48,76	733,50	12,92	529,40	9,49	1357,20	24,20	1864,90	34,19	5581,20	103,26	7712,90	140,52	4576,70	82,45
Hyperbenthos	180,50	10,04	666,61	29,98	552,99	20,73	1630,74	326,00	1176,90	290,14	1447,30	250,57	767,21	272,75	956,17	141,34	2289,43	100,13	663,31	29,86	83,00	5,71

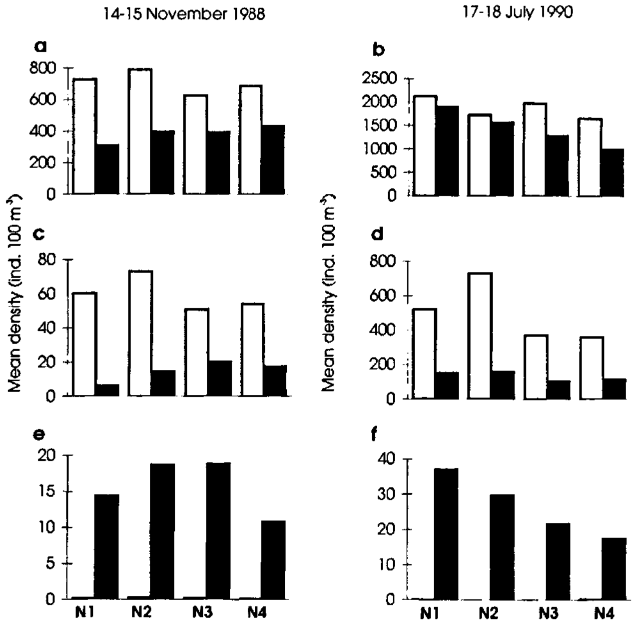

Figure 1

Day/night mean densities of Sagitta elegans: *(*a, b*);* Anchialina agilis: *(*c, d*);* Eusirus longipes*: (*e, f*) s.* □ *day;* ■ *night. N1, N2, N3, and N4: net1, net 2, net 3 and net 4.*

Densités diurnes ou nocturnes (ind./100 m^3) de : *Sagitta elegans* (*a, b*); *Anchialina agilis* (*c, d*); *Eusirus longipes* (*e, f*). □ jour; ■ nuit. N1, N2, N3, et N4 : filet 1, filet 2, filet 3 et filet 4.

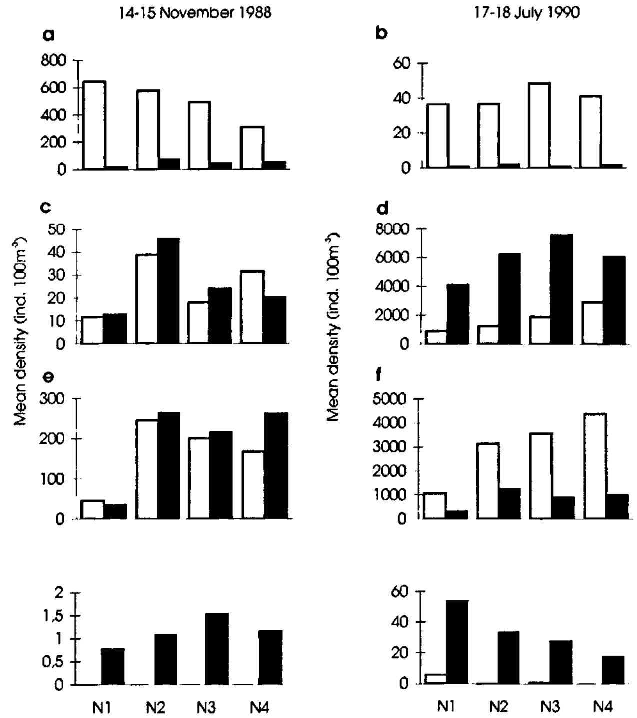

Figure 2

*Day/night mean densities (ind./100 m^3) of Euphausiacea: (*a, b*);* Apherusa clevei: *(*c, d*); Copepoda (*e, f*), and* Pandalina brevirostris *(*g, h*).* □ *day;* ■ *night. N1, N2, N3, and N4: net1, net 2, net 3, and net 4.*

Densités diurnes ou nocturnes (ind./100 m^3) de : Euphausiacés (*a, b*); *Apherusa clevei* (*c, d*); copépodes (*e, f*); *Pandalina brevirostris* (*g, h*). □ jour ; ■ nuit. N1, N2, N3, et N4 : filet 1, filet 2, filet 3 et filet 4.

(Fig. 2*a, b*), *Apherusa clevei* (Fig. 2*c, d*), Copepoda (Fig. 2*e, f*), *Atylus vedlomensis* and crustacean larvae.

Group 3: lower hyperbenthic species with a limited swimming activity which were more abundant in the two lower nets, K1 > K2 > K3, K1 + K2 + K3 < 0.60 including *Leptomysis gracilis, Mysidopsis angusta, Paramysis nouveli, Melphidipella macra, Stenothoe marina* and *Pandalina brevirostris* (Fig. 2*g, h*). The latter showed a strong swimming activity in the November night samples.

Group 4: organisms with strong swimming activity which occupied the whole BBL during the daytime with K1 ≈ K2 ≈ K3 ≈ 0.25 and concentrated in the lower nets at night with K1 + K2 + K3 < 0.70. Group 4 included Clupeidae, Gobiidae, and Mullidae larvae.

Daily changes

Organisms showed active vertical migrations from the endobenthos to the water column, or from the BBL to the pelagos. Three main patterns of daily changes could be identified:

Pattern 1: taxa with high abundances during the day, and low abundances during the night. Their abundances increased at sunrise to a maximum during the day then decreased at sunset. This behaviour was found in chaetognaths, euphausiids (Fig. 3*a, b*) and larvae, and two species of mysids *Anchialina agilis* (Fig. 3*c, d*) and *Gastrosaccus normani*. Nevertheless, in July, *A. agilis* showed two peaks of abundance at sunset and at sunrise, and very low abundances in dark hauls (Fig. 3*d*). Abundances during daytime were generally significantly higher than those observed at night (Tab. 6).

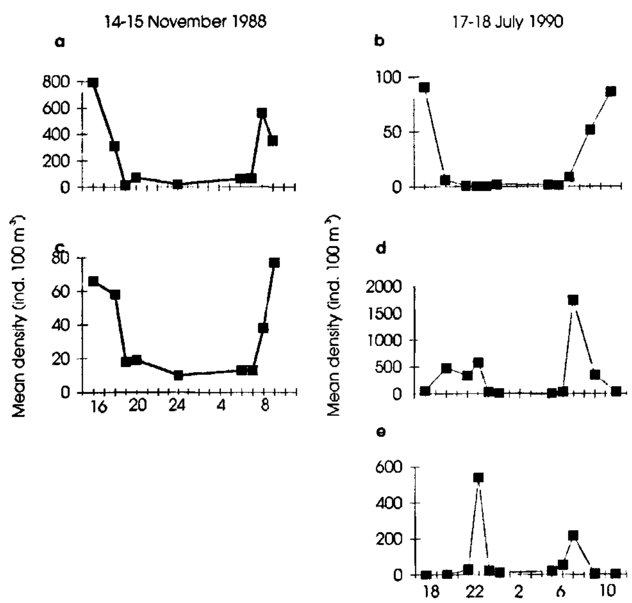

Figure 3

*Daily variation of mean density in the four nets (ind./100 m^3) of Euphausiacea: (*a, b*);* Anchialina agilis *(*c, d*), and (*e*):* clupeidae larvae.

Variations nycthémérales de la densité moyenne (ind./100 m^3) dans les quatre filets du traîneau de : Euphausiacés (*a, b*); *Anchialina agilis* (*c, d*) et (*e*) larves de clupeidés.

Table 6

*Coefficients of swimming activity K1, K2 and K3 for dominant species, and U test: * significant at 5% level, ** significant at 1% level. D: day; N: night*

Coefficients d'activité natatoire K1, K2 et K3 des espèces dominantes et test U: * significatif à 5 %, ** significatif à 1 %. D: jour ; N: nuit.

Sampling date	14-15 November 1988							17-18 July 1990						
	Day			Night			U test	Day			Night			U test
Number of samples	4			5			D/N	6			5			D/N
Volume of filtered water (m³)	5150			4233				3883			4935			
	K1	K2	K3	K1	K2	K3		K1	K2	K3	K1	K2	K3	
Chaetognatha														
Sagitta elegans	0,28	0,22	0,24	0,26	0,25	0,28	D>N*	0,23	0,26	0,22	0,27	0,22	0,17	NS
Euphauciacea														
Euphauciacea adult	0,28	0,24	0,15	0,39	0,24	0,27	D>N**	0,22	0,29	0,25	0,40	0,16	0,30	D>N**
Euphauciacea larvae	0,27	0,12	0,44	0,33	0,30	0,29	D>N**	-	-	-	-	-	-	-
Mysidacea														
Anchialina agilis	0,31	0,21	0,23	0,25	0,35	0,30	D>N**	0,37	0,18	0,18	0,30	0,20	0,22	D>N**
Gastrosaccus normani	0,30	0,17	0,22	0,39	0,33	0,19	D>N**	0,31	0,22	0,28	0,25	0,25	0,21	D>N**
Leptomysis gracilis	0,19	0,18	0,20	0,22	0,19	0,16	N>D*	0,19	0,18	0,19	0,20	0,18	0,10	N>D*
Mysidopsis angusta	-	-	-	-	-	-	-	0,22	0,19	0,10	0,13	0,18	0,08	N>D**
Paramysis nouveli	0,33	0,10	0,07	0,22	0,32	0,25	NS	0,22	0,07	0,05	0,26	0,11	0,08	NS
Siriella jaltensis	-	-	-	-	-	-	-	0,24	0,26	0,26	0,46	0,20	0,12	NS
Decapoda														
Pandalina brevirostris	-	-	-	0,24	0,34	0,25	N>D**	0,01	0,09	0,00	0,25	0,21	0,13	N>D**
Fish larvae														
Clupeidae	-	-	-	-	-	-	-	0,25	0,27	0,31	0,26	0,24	0,17	N>D**
Gobiidae	-	-	-	-	-	-	-	0,21	0,25	0,33	0,28	0,17	0,23	NS
Mullidae	-	-	-	-	-	-	-	0,31	0,18	0,24	0,23	0,16	0,14	NS
Amphipoda														
Apherusa clevei	0,38	0,18	0,31	0,44	0,23	0,19	NS	0,18	0,27	0,41	0,26	0,31	0,25	N>D**
Atylus vedlomensis	-	-	-	0,40	0,22	0,23	N>D**	0,49	0,18	0,14	0,29	0,24	0,23	N>D**
Eusirus longipes	-	-	-	0,30	0,30	0,17	N>D**	-	-	-	0,28	0,20	0,16	N>D**
Melphidippella macra	0,28	0,12	0,00	0,21	0,36	0,25	N>D**	0,22	0,22	0,16	0,37	0,25	0,02	N>D**
Stenothoe marina	0,35	0,09	0,28	0,33	0,22	0,12	N>D**	0,27	0,12	0,17	0,26	0,17	0,09	N>D**
Copepoda	0,37	0,30	0,25	0,34	0,28	0,34	NS	0,26	0,29	0,35	0,36	0,26	0,29	D>N**
Crustacean larvae	0,56	0,16	0,16	0,32	0,27	0,30	N>D*	0,24	0,30	0,26	0,24	0,30	0,28	D>N**

Pattern 2: fish larvae which performed an active migration and were present in the BBL only at sunrise and sunset. In addition to these movements, they swam in the upper water column and showed low abundances in the BBL: *e.g.* clupeid larvae were present with high abundances (around sunrise and sunset) in July hauls (Fig. 3*e*). The night abundance was significantly higher than the day abundance only in clupeid larvae (Tab. 6).

Pattern 3: the reverse of pattern 1, these taxa were present in the BBL during darkness. They migrated actively from the bottom to the BBL at sunset, their abundances reached a maximum around midnight and then decreased at sunrise. Four mysids *Leptomysis gracilis, Mysidopsis angusta, Paramysis nouveli,* and *Siriella jaltensis, Pandalina brevirostris,* and two amphipods: *e.g. Eusirus longipes* (Fig. 4*a, b*) and *Stenothoe marina* showed this behaviour (Fig. 4*c, d*). Night densities were generally significantly higher than those observed during the daytime (Tab. 6).

Copepods and crustacean larvae showed different behaviour in the two sets of samples. In November, no daily change was observed, similar low abundances were found in all samples (Fig. 4*e*). In July, daily changes were found in the BBL, highest abundances being observed during the daytime and only low abundances at night (Fig. 4*f*), as in pattern 1. The abundances were thus significantly higher during the daytime than at night (Tab. 6).

Biomasses

Biomasses of each taxon (species or family) in both sets of samples are shown in table 7. For the mysids *Anchialina agilis* and *Gastrosaccus normani*, day and night biomasses were measured separately because individual sizes of collected organisms varied greatly. During the daytime, individuals were smaller, mainly comprising juveniles, while at night, they were larger and mainly composed of adults.

Generally, the biomass was higher in November than in July. This means that the population was composed of adults in November and juveniles in July. Nevertheless, in some cases, *e.g.* amphipods *Cheirocratus assimilis* and *Stenothoe marina*, the biomass was higher in July.

The mean total biomass (Tab. 4, 5) in each haul varied from 72 to 303 mg/100 m^3 (mean: 154 mg/100 m^3) in November and from 160 to 1943 mg/100 m^3 (mean: 638 mg/100 m^3) in July. The mean biomasses of mesoplankton were similar in the two sets: 58 mg/100 m^3 in November and 64 mg/100 m^3 in July. In contrast, the mean biomass of macrozooplankton was five times higher

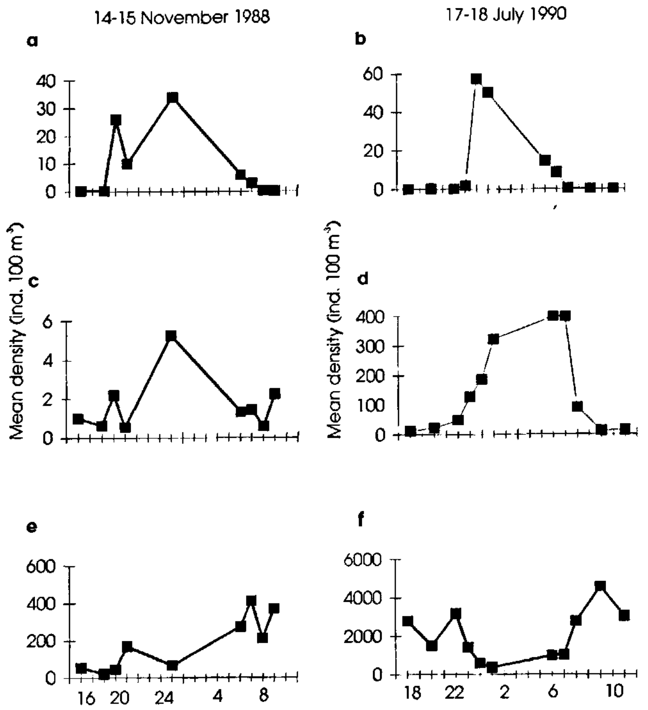

Figure 4

Daily variation of mean density in the four nets (ind./100 m^3) of Eusirus longipes *(*a, b*);* Stenothoe marina*: (*c, d*), and copepoda: (*e, f*).*

Variations nycthémérales de la densité moyenne (ind./100 m^3) dans les quatre filets du traîneau de *Eusirus longipes* (*a, b*); *Stenothoe marina* (*c, d*), et des copépodes (*e, f*).

in July than in November (84 *vs.* 440 mg/100 m^3), and the mean biomass of hyperbenthos was 10 times higher in July than in November (13 *vs.* 134 mg/100 m^3, Tab. 8). In July the high biomass of hyperbenthos at night was due to the presence of the mysid *Anchialina agilis.* There were two peaks of total biomass in July: one at sunset (TV25 = 1943 mg/100 m^3) and the other at sunrise (TV30 = 718 mg/100 m^3), corresponding to biomass peaks of the macrozooplankton, especially clupeid larvae and *Apherusa clevei.* In November, when the higher values of total biomass were found during daytime, a large number of mesoplanktonic organisms was present in the BBL.

Biomass exchanges

In both sets of hauls, total mesozooplankton biomass exchanges between the pelagic environment and the BBL sampled by the sledge were positive: respectively 157 mg/100 m^3 in November and 6.5 mg/100 m^3 in July (Fig. 5*a, b*). In November, except for an important positive exchange of mesozooplankton biomass between the water column and the BBL sampled by the sledge (about 120 mg/100 m^3, between 8 and 9 *a.m.*), exchanges were very low. In July, there were alternately positive and negative exchanges (around 40 to 60 mg/100 m^3), at sunset and sunrise (Fig. 5*b*).

The total macrozooplankton biomass exchanges between the pelagic environment and the BBL sampled by the sledge (Fig. 5*c, d*) were negative in November (84 mg/100 m^3) and positive in July (185 mg/100 m^3). In November, there was an important exchange of macrozooplankton biomass from the BBL to the water column around sunset ($\approx$100 mg/100 m^3), and a positive biomass exchange around sunrise ($\approx$100 mg/100 m^3). In July, a positive biomass exchange occurred at sunset (>1300 mg/100 m^3) due to the migration of Clupeidae larvae, followed by a negative biomass exchange ($\approx$1000 mg/100 m^3), at the beginning of the night (Fig. 5*b*), and then a second one later at night. Low positive and negative biomass exchanges were also observed around sunrise.

Conversely, total biomass exchanges between the BBL sampled by the sledge and the benthic environment were slightly negative in the two series, respectively 1.9 mg/100 m^3 in November and 2.3 mg/100 m^3 in July. This means that there is a daily balance between the input and the ouput of hyperbenthic organisms in the BBL. Nevertheless the values of the biomass exchanges were more important in July, *e.g.* the maximum positive biomass exchange reached 300 mg/100 m^3 in July and only

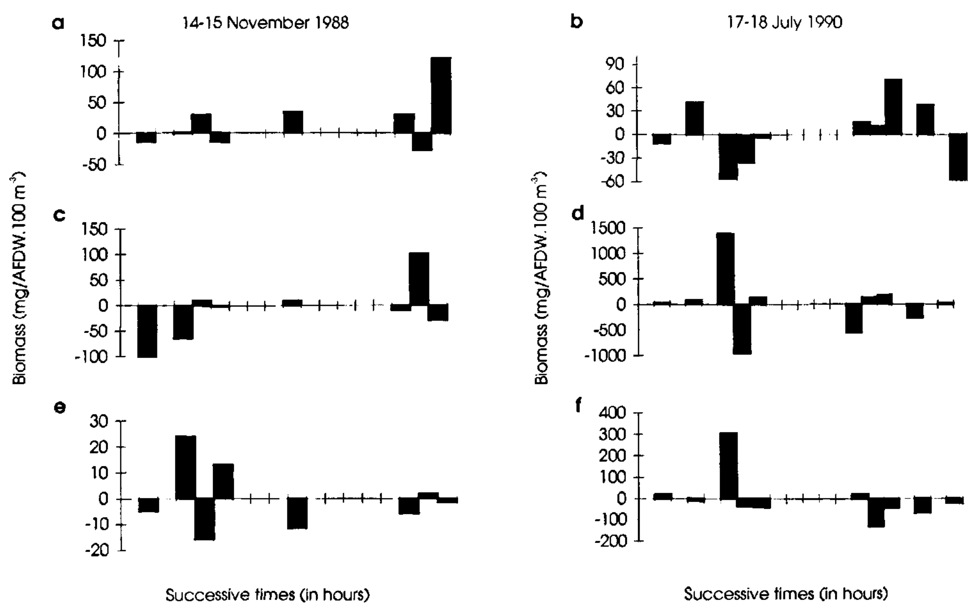

Figure 5

Biomass exchanges in November 1988 and July 1990 during successive time intervals in hours between pelagos, BBL sampled by the sledge and benthos: a, b, *mesozooplankton;* c, d, *macrozooplankton, and* e, f, *hyperbenthos. Biomasses in mg AFDW/100 m^3.*

Transfert de biomasses entre le pélagos, la couche d'eau adjacente au fond échantillonnée par le traîneau et le benthos (en mg de Poids Sec Libre de Cendres par 100 m^3) durant des intervalles de temps successifs en heures, en novembre 1988 et juillet 1990. *a, b* : mésozooplancton; *c, d* : macrozooplancton, et *e, f*: hyperbenthos.

25 mg/100 m^3 in November. At sunrise, important exchanges between the two compartments were found in both series. In November, positive and negative biomass exchanges occurred alternately around sunset (Fig. 5*e*) due to the swimming activity of amphipods and the decapod *Pandalina brevirostris*. In July, there was an important positive biomass exchange when peracarids and decapods migrated into the BBL (Fig. 5*f*). The following negative biomass exchanges lasted several hours the next morning.

DISCUSSION

Fauna composition

The BBL fauna collected at Trezen Vraz was composed of three groups of organisms: (1) mesozooplankton; (2) macrozooplankton, both groups of these organisms possessing good swimming ability and concentrated in the BBL in daytime then migrating up into the water column at night; and (3) hyperbenthic organisms which showed nocturnal migration in the near-bottom water. The BBL macrofauna of Trezen Vraz sampled by the Macer-GIROQ sledge was as diversified as the fauna in the Bay of Biscay described by Sorbe (1984), and more diversified than that found in the Bay of Seine (Wang and Dauvin, 1994; Wang *et al.*, 1994) and on Browns Banks, off the coast of Nova Scotia (Wildish *et al.*, 1992).

Swimming activity and daily changes

Daily vertical migrations and swimming activities of many zooplanktonic species were thoroughly documented by Sainte-Marie and Brunel (1985). By studying our samples four models of swimming behaviour and vertical distribution could be identified in the BBL fauna: (1) occupying the entire BBL; (2) found essentially in the upper nets; (3) concentrating near the bottom; and (4), occupying the entire BBL during the day and concentrating near the bottom during the night. Two main types of daily changes were observed: (1) amphipods, decapods and some mysids migrated from the bottom to the BBL at sunset and during the night; while (2) planktonic organisms such as euphausiids, copepods and the dominant mysid *Anchialina agilis* and *Gastrosaccus normani* concentrated near the bottom during the day and migrated from the BBL to the water column at night. This daily rhythm has been often observed in the BBL (*e.g* Sorbe, 1984; Fosså, 1986; Kaartvedt, 1985; Wang and Dauvin, 1994). Change in light intensity was the most important factor determining migratory activities (Hesthagen, 1973; Anger *et al.*, 1976; Macquart-Moulin, 1973; Sainte-Marie and Brunel, 1985; Macquart-Moulin *et al.*, 1987; Kaartvedt 1989; Elizalde *et al.* 1991). It was probably the determinant factor in diel changes of Trezen Vraz BBL macrofauna; but changes in intensity on the sea bottom and in the water column should be measured in order to determine their relationship to diel change of the BBL macrofauna. Other factors, such as food (Hesthagen, 1973; Brunel, 1979; Sorbe, 1984; Jones,1986; Silbert, 1981), sex (Elizalde *et al.*, 1991, 1993), and maturity state (Elizalde *et al.*, 1991; Macquart-Moulin *et al.*, 1987) were also important in explaining daily and seasonal changes of the BBL macrofauna in other areas.

Table 7

Individual biomass of main species mg AFDW in November 1988 and July 1990 hauls ; d = day ; n = night.

Biomasse individuelle des principales espèces en mg de Poids Sec Libre de Cendres dans les deux séries de novembre 1988 et juillet 1990 ; d = jour ; n = nuit.

	14-15 November 1988	17-18 July 1990
Chaetognatha		
Sagitta elegans	0.075	0.004
Euphausiacea		
Euphausiacea adult	0.160	0.130
Mysidacea		
Anchialina agilis (d)	0.062	0.023
Anchialina agilis (n)	0.114	0.148
Gastrosaccus normani (d)	0.028	0.066
Gastrosaccus normani (n)	0.068	0.225
Other Mysidacea	0.974	0.339
Decapoda		
Pandalina brevirostris	5.820	0.160
Galathea intermedia	10,8	0.140
Hippolyte varians	-	0.620
Pontophilus sculptus	3.800	2.010
Pontophilus trispinosus	-	0.930
Processa sp.	-	6.500
Fish larvae		
Clupeidae	0.820	1.990
Gobiidae	2.860	0.640
Others	1.370	2.670
Amphipoda		
Apherusa clevei	0.046	0.070
Atylus vedlomensis	0.073	0.008
Cheirocratus assimilis	0.170	0.440
Eusirus longipes	0.190	0.036
Gammaropsis maculata	0.700	0.230
Hippomedon denticulatus	2.230	2.410
Melphidippella macra	0.043	0.007
Stenothoe marina	0.040	0.470
Others amphipoda	0.092	0.078
Cumacea	1.012	0.092
Isopoda	1,130	1.670
Mollusca Cephalopoda	1.555	2.073
Copepoda	0.040	0,070
Crustacean larvae	0.350	0.020

Density and biomass

In November, the mean total faunal density in the four nets varied between 547 and 2,024 ind./100 m^3 (mean: 1164 ind./100 m^3), while in July, it varied between 5,210 and 14,954 ind./100 m^3 (mean: 10,018 ind./100 m^3). The total density of BBL macrofauna collected with a hyperbenthic sledge and a 0.5 mm sieve mesh varied strongly from one area to another. High densities were present in areas with important nutrient flux. In the Bay of Seine, in an area about 10 m deep, under the influence of the high input of nutrients from the Seine, the total density varied

Table 8

Mean biomass in the four nets (mg AFDW/100 m³) of the three groups of organisms and of the total fauna in the two sets of hauls.

Biomasses moyennes dans les quatre filets du traîneau des trois principaux groupes d'organismes et biomasses totales (mg en Poids Sec Libre de Cendres/100 m³) de la faune collectée en novembre 1988 et juillet 1990.

	November 1988	July 1990
Macrozooplankton	83.6	440.0
Mesozooplankton	57.6	63.8
Hyperbenthos	12.7	134.3
Total organisms	153.9	638.0

between 3.8 and 85.9 × 10^3 ind./100 m³ with a daily mean reaching 21.6 × 10^3 ind./100 m³ in June (Wang *et al.*, 1994). On Browns Banks (34 stations sampled in summer during daytime at the depth of about 80 m), the total density varied between 187 and 26,894 ind./100 m³, the overall mean was 3,574 ind./100 m³ (Wildish *et al.*, 1992). On the Atlantic seamount, the summer density was very low on Josephine Bank with daily mean of seven stations, 199-271 m deep: 187 ind./100 m³, but higher on Meteor Bank with daily mean of eight stations, 290-313 m deep: 1,111 ind./100 m³ (Hesthagen, 1970). The values of available density of the BBL zooplankton more or less close to the ocean floor estimated by reentry trap and 95-153 µm sieve mesh were recorded by Cahoon and Tronzo (1992). They varied strongly from one area to another from 23 and 54,000 ind. m^{-2}, mostly between 2 and 20 × 10^3 ind. m^{-2}. The abundances observed in this study, respectively 3.5 ind. m^{-2} in November and 30 ind. m^{-2} in July, were among the lowest probably because the use of 0.5 mm mesh underestimated demersal zooplankton abundances. Nevertheless, above the coarse bottom, fish larvae were quite abundant in July hauls, a maximum of 570 ind./100 m³ being collected around sunset. In the Bay of Seine, fish larvae were also abundant around sunset with a density higher than 1000 ind./100 m³ (Wang *et al.*, 1994). Such high concentrations of fish larvae near the sea bottom have not been reported in other studies.

The average faunal density of hyperbenthos in the four nets was 58 ind./100 m³ in November 1988 and 947 ind./100 m³ in July. The most abundant species was the mysid *Anchialina agilis*. The abundance of hyperbenthic organisms has been reported more often than abundances of the total BBL fauna. Total BBL fauna also varied strongly from one area to another, being highest on muddy substrata (Dauvin *et al.*, 1994; Wang and Dauvin, 1994). The mean annual values found by Dauvin *et al.* (1994) on the Trezen Vraz station were 240 ind./100 m³. The abundance of summer hauls (July) was higher than those reported by Wildish *et al.* (1992) on Browns Banks (about 75 ind./100 m³) and by Wang and Dauvin (1994), in the Bay of Seine (476 ind./100 m³ but it was lower than the faunal density in Gullmarfjord and Bay of Biscay where the abundance reached about 3,000 ind./100 m³ (Buhl-Jensen and Fosså, 1991; Elizalde *et al.*, 1993).

Mean total biomass in the four nets showed temporal changes, being respectively 154 and 638 mg AFDW/100 m³ in November and July (185 and 766 mg DW/100 m³). Biomasses were lower than at the Browns Banks stations where summer biomass varied between 118 and 15,047 mg DW/100 m³, with an overall mean of 2,944 mg/100 m³ (Wildish *et al.*, 1992), and those estimated by Sorbe (1984) at a 31 m depth: 2,130 mg DW/100 m³, and at a a 91 m depth station: 1,050 (daytime) and 3,120 (nighttime) mg DW/100 m³ (annual mean values). At the Trezen Vraz station, the biomass found in July was of the same order of magnitude as the biomass of zooplankton sampled with a WP2 net with a 0.5 mm mesh size in the water column in June 1992: 1,400 mg DW/100 m³ (Le Hoerff, pers. comm.).

In the western English Channel , the BBL macrofauna on coarse sand community was affected by seasonal variation of density and biomass, as were the benthic community (Dauvin, 1988) and the zooplankton (Colebrook, 1986), in relation to the concentration of the period of recruitment and growth of organisms in Spring (May-June), and high mortality of organisms at the beginning of Autumn (October-November).

Vertical biomass exchange

Interactions among the BBL macrofauna, benthos and pelagos are very important in the study of pelago-benthic flux (Sainte-Marie and Brunel, 1985; Chevrier *et al.*, 1991). In this study, the biomass exchanges of live matter between the water column and the benthos, and the BBL sampled by the sledge were estimated for the first time. The biomass exchanges between the three compartments (benthic, BBL and pelagos) occurred mostly at sunset and sunrise. Other than at these times, the biomass exchanges were limited, *e.g.* in July the biomass of macrozooplankton sampled in the BBL was multiplied by 6 around sunset, and the biomass exchanges was higher than 1,600 mg/100 m³ within an hour. But the lack of hauls collected in the middle of the night did not permit determination of the intensity of nocturnal exchanges of biomasses. Positive biomass exchanges between benthos and BBL were 39 mg/100 m³ (0.1 mg m^{-2}) in November and 347 mg/100 m³ (1.0 mg m^{-2}) in July. Positive biomass exchanges between pelagos and BBL were 317 mg/100 m³ (0.9 mg m^{-2}) in November and 2,142 mg/100 m³ in July (6.4 mg m^{-2}). These values were of an order of magnitude lower than those estimated by Hammer (1981) who, by using emergence traps (153 µm sieve mesh), found a mean total biomass of 94.2 mg AFDW m^{-2} of total demersal zooplankton emerged from the sand substrate in a kelp forest over a diel cycle. As the organisms of the BBL are known to be important food sources for demersal fishes, it is clear that these available prey changed considerably between day and night, both qualitatively and quantitatively. Our future objectives will be to quantify the impact of such changes of the BBL macrofauna on demersal fishes and on the whole community.

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