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Preliminary data on the near-bottom meso- and macrozooplanktonic fauna from the eastern Bay of Seine : faunistic composition, vertical distribution and density variation

Z. Wang*, J.-C. Dauvin* & E. Thiébaut**
* Laboratoire de Biologie des Invertébrés Marins et Malacologie
Muséum National d'Histoire Naturelle CNRS URA 699,
57, rue Cuvier 75231 Paris Cedex 05, France
** Station Biologique de Roscoff, Université P. et M. Curie
et CNRS UPR 4601, 29680 Roscoff, France

Abstract : In the eastern Bay of Seine, just in front of the Seine estuary, two series of samples were collected in June 1992 with a new version of the Macer-GIROQ suprabenthic sledge, using 0.5 mm mesh size plankton nets. Chaetognaths, ctenophores and copepods (holoplankton), fish postlarvae, polychaete and crustacean larvae (meroplankton) were sorted, counted and identified. The most abundant taxa of the near-bottom meso- and macrozooplanktonic fauna were copepods, the ctenophore *Pleurobrachia pileus,* larvae of crustaceans and the polychaete *Lanice conchilega,* postlarvae of clupeids, gobiids. Three patterns of density variations were found : (1) dominance of diurnal vertical migrations, with high abundances near the bottom around sunset and sunrise, e.g. clupeid postlarvae ; (2) dominance of tidal advections, with maximal abundances during flood tide, e.g. gobiid postlarvae, or during ebb tide, e.g. *Pleurobrachia pileus ;* and (3) a combination of tidal advections and diurnal migrations, e.g. copepods.

Résumé : Deux séries d'échantillons planctoniques ont été récoltés en juin 1992 dans une station située au débouché de la Seine (Manche orientale) avec une nouvelle version du traîneau suprabenthique Macer-GIROQ muni de filets à plancton de 0.5 mm de vide de maille. Chaetognathes, Cténaires et Copépodes (holoplancton), postlarves de poissons, larves de Polychètes et de Crustacés (méroplancton) ont été triés, comptés et identifiés. Les taxa plus abondants de la faune méso- et macrozooplanctonique proche du fond sont les Copépodes, le Cténaire *Pleurobrachia pileus,* les larves de Crustacés et de la Polychète *Lanice conchilega,* les postlarves de Clupéidés et Gobiidés. Trois principaux schémas de variations d'abondance sont décrits : (1) dominance des migration nycthémérales verticales avec fortes abondances au fond au crépuscule et à l'aube, e.g. postlarves de Clupéidés ; (2) dominance de l'advection tidale avec maximums de densité lors du flot, e.g. postlarves de Gobiidés, ou lors du jusant, e.g. *Pleurobrachia pileus ;* (3) mélange de migration nycthémérale et d'advection tidale, e.g. Copépodes.

INTRODUCTION

The near-bottom zooplanktonic fauna has rarely been studied due to sampling problems. This fauna is sometimes considered as a part of the suprabenthic community under the term of "temporary suprabenthos" (Hesthagen, 1973 ; Boysen, 1975a & b ; Hamerlynck & Mees, 1991) since these organisms pass a part of their life in the benthic boundary layer just above the sediment, along with the permanent suprabenthos such as mysids, cumaceans and amphipods which migrate from the benthos to the boundary layer throughout the whole year. Some of them may even be elements of the permanent suprabenthos, for example, demersal postlarval fishes like gobies. But most of them are pelagic species which are often excluded from the suprabenthic community (e.g. Cornet *et al.*, 1983 ; Sorbe, 1989).

The present investigation gives a first description of the near-bottom meso- and macro-zooplanktonic fauna in the infralittoral area from the eastern part of the Bay of Seine in June 1992.

MATERIAL AND METHODS

Sampling

The sampling station F (49°26.60' N, 0°01.30' E) is located in the outer part of the Seine estuary (Wang & Dauvin, 1994), in the middle of the *Abra alba-Pectinaria koreni* community (Gentil *et al.*, 1986). The sediment was muddy fine sand. Sampling depth was 8-13 meters.

All the material was collected with a new version of Macer-GIROQ suprabenthic sledge (Brunel *et al.*, 1978 ; Dauvin & Lorgeré, 1989), which is equipped with four boxes 0.10-0.40, 0.45-0.75, 0.80-1.10 and 1.15-1.45 m above the bottom. Each box is fitted with a WP2 zooplankton net (0.5 mm mesh size). The lowest net is called net 1, then net 2, net 3 and finally the uppermost net, net 4. Each box holds a "T.S.K" flowmeter to measure and register the volume of water filtered through the net.

On June 1-2, 1992, during a period of 24 hours, and on June 13, 1992, during a period of 14 hours, hauls were collected every hour (there was no sampling at 4h on June 2 due to technical problems). For each haul, the sledge was towed against the tidal current at a speed of approximately 1.5 knots for 5 minutes. The volume of water filtered by each net varied from 54 to 111 m^3. Sampling characteristics are given in detail in Wang & Dauvin (1994). Little sediment was collected by net 1. All samples were preserved in 10 % neutral formalin.

Data on temperature and current speed were collected with an Aanderaa Current Meter at two meters above the sea bed near the sampling station. The temperature of the subsurface sea water (-1.6 m) was measured with a sonde aboard the "N.O. Pluteus II".

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} (Wang, 1993).

Sorting

Material of 38 samples, or 152 nets, was rinsed and filtered through three sieves with mesh sizes of 2, 1 and 0.5 mm. The material retained on the 2 mm screen was composed mainly of the ctenophore *Pleurobrachia pileus* and fish postlarvae. The quantity of ctenophores was estimated by the measure of its biovolume in ml with a mean density of 77 ± 4 ind. ml^{-1} which was based on ten counts of 1 ml of organisms. Except for copepods and crustacean larvae, all animals bigger than 1 mm were sorted, counted and identified under a binocular microscope. The remaining fraction was rinsed on a 0.5 mm sieve. Then Frontier's subsampling method (1972) was used to estimate the densities of copepods and crustacean larvae : the sample was brought in 200 ml of water, homogenised, and 1/10 aliquot was pipetted into a reticulated Dolfuss receptacle composed of 200 distinct cells. Organisms were randomly distributed in the receptacle. Two to ten aliquots were used to count and pick out 100 copepods and 100 crustacean larvae per sample in order to obtain a density estimate of these two mesozooplanktonic taxa (Frontier, 1972).

Individual numbers of each taxon of the meso- and macrozooplanktonic fauna in a net were standardized to mean densities per 100 m^{-3}. Average densities per 100 m^{-3} of the total of daytime and night samples were also calculated.

The vertical distribution was measured with three coefficients of swimming activity adapted from Brunel (1972) and used 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 = density. 400 m^{-3} in the four nets.

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

RESULTS

Sea water temperature and bottom currents

During the sampling period on June 1-2, 1992, the sub-surface temperature fluctuated between 14.5 and 17.0 °C. Near the bottom, the temperature varied between 13.6 and 14.8 °C along with the tidal cycle : minimum values were measured around high tide and maximum values around low tide. Since it was the period of spring tide (tide coefficient : 88-90), the tidal current was quite strong. There was no slack water at low tide. The current speed varied regularly according to the tidal cycle : the minimum was 20 cm. s^{-1} one hour after the high tide, the maximum was 63 cm. s^{-1} one hour after the low tide. The northern component of the tidal currents was strong around the high tide and at the beginning of the ebb tide, corresponding to the Verhaule current (Salomon, 1986). The southern component of the tidal currents was more important at the end of the ebb tide and around the low tide. Marine water entered the estuary when the eastern component of the tidal currents was strong and left the estuary during the ebb tide when the western component of the tidal currents was strong. The flood tide had a shorter duration than the ebb tide, but the tidal current was stronger during the flood tide (Fig. 1).

During the sampling period on June 13, 1992, the sub-surface temperature fluctuated between 15.5 and 17.5 °C. Near the bottom, the temperature was around 15.0 °C with very weak variation. It was the period of neap tide (tide coefficient : 70). The tidal current was weak during the ebb tide with a minimal current speed of about 20 cm. s^{-1} for five hours. As observed on June 1-2, the northern component of the tidal currents was strong around the high tide and at the beginning of the ebb tide. The southern component of the tidal currents was more important at the end of the ebb tide and around the low tide. During the flood tide, the eastern component of the tidal currents reached its maximum of 40 cm. s^{-1}.

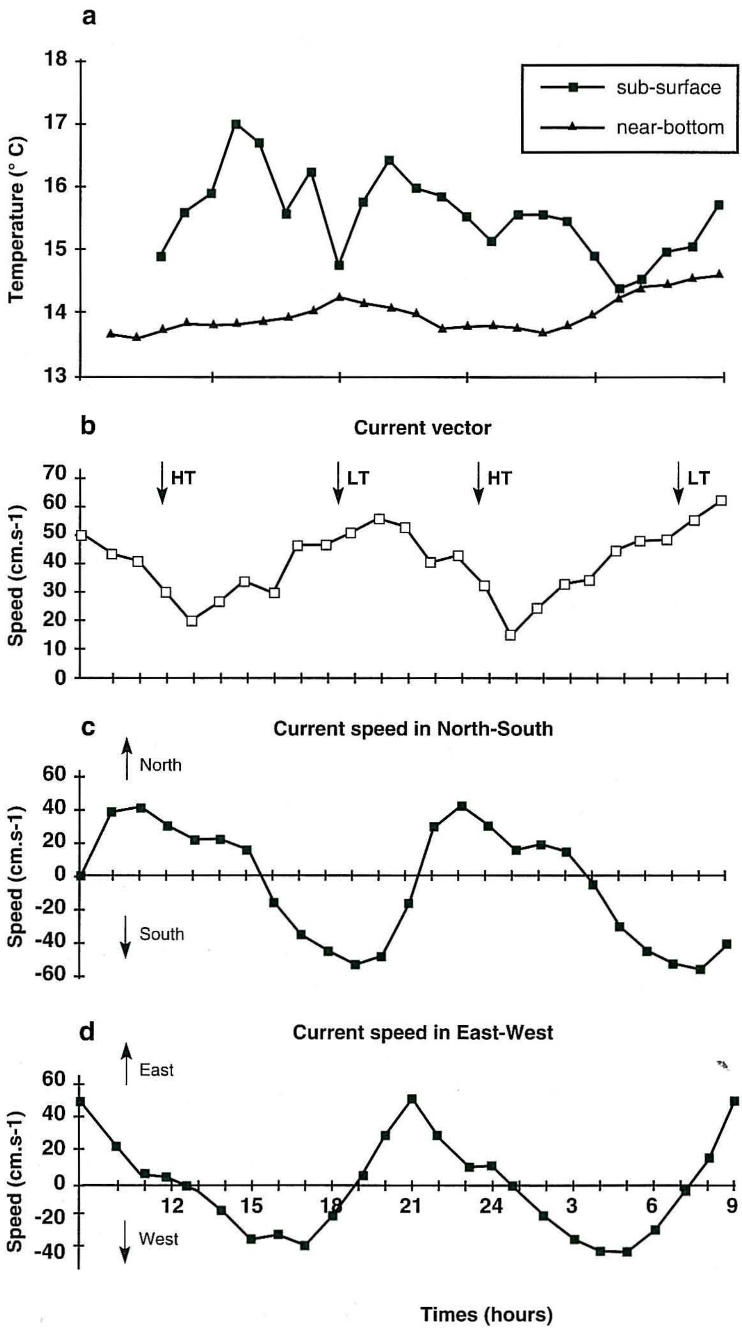


Fig. 1 : Temperature condition (a) and speed and direction of the current 2 m above the sea bed during the sampling period of June 1-2, 1992.

The maximum value of the western component of the tidal currents was less then 20 cm. s^{-1} and was recorded during the ebb tide. Thus more marine water entered the estuary on June 13 (Fig. 2).

Faunistic composition

A total of one hundred and eight species or taxa were found in the samples (Wang, 1993). Among them, 41 taxa were post-larvae, juveniles or adults of benthic organisms which performed diurnal migrations or had active mechanisms of resuspension (Vallet, 1993). Other 46 species of amphipods, cumaceans, isopods, mysids, decapods and pycnogonids formed the permanent suprabenthic fauna (Wang & Dauvin, 1994). The present study concerned 21 species or taxa of meso- and macrozooplanktonic animals from the holo- and meroplankton. Because of the relatively large mesh aperture of the net, i.e. 0.5 mm, the majority of copepods caught in the samples were calanoid adults. Two species, *Temora longicornis* and *Centropages hamatus* were found to be dominant. All copepodes were taken as a whole. Densities of these copepod species, were not calculated separately. Zoeae of Brachyura were the dominant forms of crustacean larvae.

In the samples of June 1-2, 1992, nine families of fish postlarvae, one chaetognath species, one ctenophore species, one polychaete species (syllid epitokes), six species/families of polychaete larvae, copepods and crustacean larvae were found. Among them, the most abundant taxa were copepods, ctenophore *Pleurobrachia pileus* and the larvae of crustaceans and *Lanice conchilega*, postlarvae of clupeids and gobiids (Table I).

In the samples of June 13, 1992, seven families of fish postlarvae, one chaetognath species, one ctenophore species, one polychaete species (syllid epitokes), four taxa of polychaete larvae, copepods and crustacean larvae were found. The most abundant taxa were the same as in the former samples (Table I).

According to their abundances in daytime and night samples, these taxa were classified into three groups (Table I) :

1. Seven taxa whose average day and night densities were both higher than 1.0 ind. 100 m^{-3} (daytime and night samples were respectively taken as a whole) in two series of samples : mesozooplankton, i.e. copepods and crustacean larvae, and macrozooplankton, i.e. the ctenophore *Pleurobrachia pileus*, Clupeidae, Gobiidae and Callionymidae fish postlarvae, and larvae of polychaete *Lanice conchilega*. They were considered to be principal elements of the fauna.

2. Four taxa which were only present in daytime or night samples or in one of the two series of samples with a density higher than 1.0 ind. 100 m^{-3} : Gadidae and Soleidae postlarvae, the chaetognath *Sagitta elegans* and syllid epitokes. They were considered to be common elements of the fauna.

3. Ten taxa which were present in one or a few samples with an average density lower than 1.0 ind. 100 m^{-3} all the time : Pleuronectidae, Agonidae, Syngnathidae and Bothidae postlarvae ; larvae of the polychaetes *Arenicola marina, Poecilochaetus serpens,* Harmothoidae, Spionidae, Phyllodocidae and Nereidae. They were considered to be rare

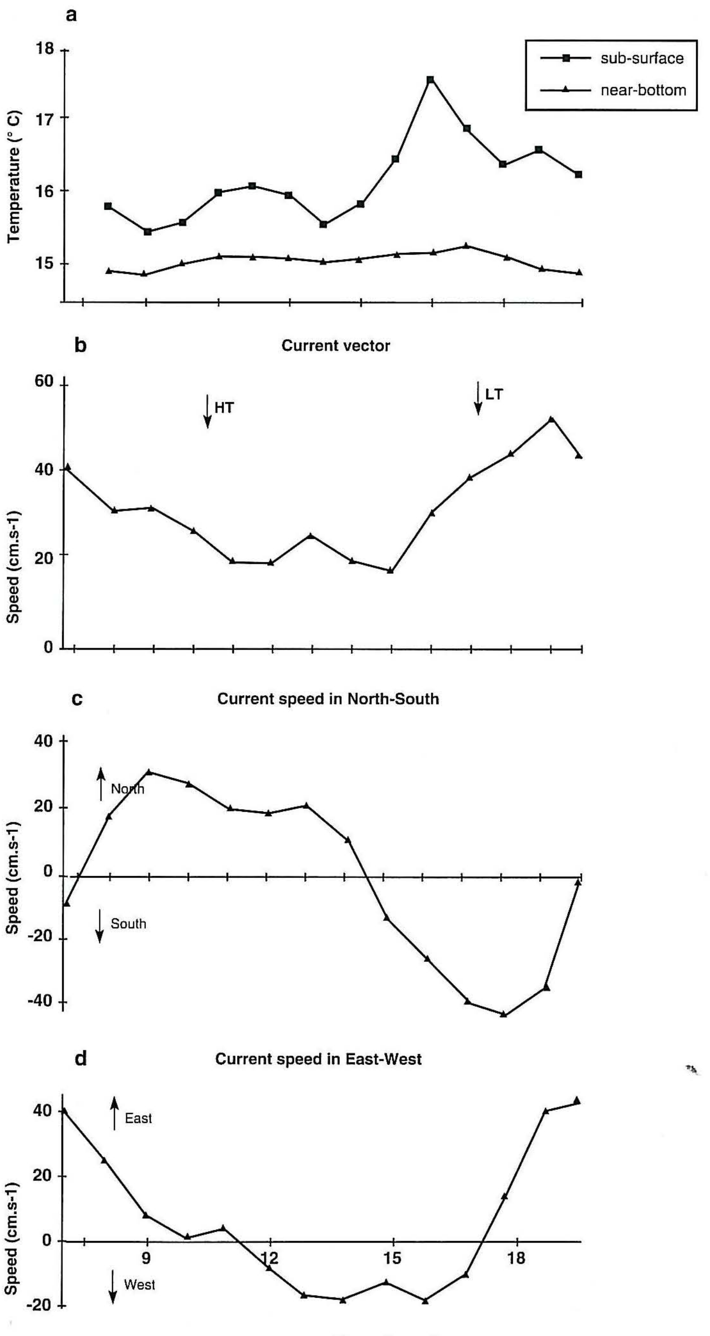


Fig. 2 : Temperature condition (a) and speed and direction of the current 2 m above the sea bed during the sampling period of June 13, 1992.

elements of the fauna. Some of them, such as fish postlarvae of Agonidae and Bothidae, Polychaetes *Arenicola marina* and Nereidae, were only present with a low density in the samples of one campaign (Table I).

TABLE I

Mean density (N. ind. 100 m^{-3}) of the principal species and taxa of the near-bottom planktonic 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
Fish larvae	280.7	505.0	214.3
Clupeidae	102.4	378.1	87.7
Gobiidae	145.3	101.8	120.1
Callionymidae	11.4	13.2	3.6
Soleidae	17.5	8.7	+
Gadidae	3.5	+	1.6
Pleuronectidae	+	+	-
Agonidae	+	-	
Syngnathidae	-	-	+
Bothidae	-		
Chaetognatha			
Sagitta elegans	5.1	+	14.9
Ctenophora (x10^3)			
Pleurobrachia pileus	4.0	2.1	0.5
Syllid epitokes	2.1	+	3.6
Polychaete larvae	15.0	12.0	343.0
Lanice conchilega	14.6	9.9	343.0
Arenicola marina	+	+	
Harmothoidae	+	+	-
Poecilochaetus serpens	+	+	
Spionidae	+	-	
Phyllodocidae	-		-
Nereidae			-
Copepoda (x10^3)	8.5	26.5	0.6
Crustacean larvae (x10^3)	3.8	3.0	11.1

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

Total density

In the samples of June 1-2, the total faunal density varied highly. At 6 h in the morning of June 2 (sample F23) total faunal density was minimum: 3.8 x 10^3 ind. 100 m^{-3}, dominated by the ctenophore *Pleurobrachia pileus* which represented 66 % of the number of organisms collected. At 21 h on June 1 (sample F15), the faunal density reached its maximum of 85.9 x 10^3 ind. 100 m^{-3}, dominated by copepods and crustacean larvae which represented

99 % of the number of organisms collected. In fact, these three taxa dominated the fauna all the time. Excluding them, the faunal density varied between 35 ind. 100 m^{-3} (sample F06, collected at 12 h on June 1) and 1550 ind. 100 m^{-3} (sample F16, collected at 22 h on June 1), dominated by clupeid and gobiid postlarvae which represented 71-95 % of the number of organisms collected ; maximal densities were reached between 21 h and 6 h. The daytime faunal density was 8.8 x 10^3 ind. 100 m^{-3} in net 1 (13.3 %), 25.7 x 10^3 ind. 100 m^{-3} in net 2 (37.8 %), 12.6 x 10^3 ind. 100 m^{-3} in net 3 (19.0 %) and 19.2 x 10^3 ind. 100 m^{-3} in net 4 (29.0 %). The average of daytime densities of the four nets was 16.6 x 10^3 ind. 100 m^{-3}. The night faunal density was 13.4 x 10^3 ind. 100 m^{-3} in net 1 (24.7 %), 42.9 x 10^3 ind. 100 m^{-3} in net 2 (31.8 %), 19.1 x 10^3 ind. 100 m^{-3} in net 3 (14.2 %) and 59.5 x 10^3 ind. 100 m^{-3} in net 4 (44.1 %). The average of night densities of the four nets was 33.7 x 10^3 ind. 100 m^{-3}. The daily average faunal density was 21.6 x 10^3 ind. 100 m^{-3} (Table II).

In the samples of June 13, the total faunal density varied between a minimum of 1.3 x 10^3 (sample F41, collected at 13 h), dominated by *Pleurobrachia pileus* and mesozooplankton copepods and crustacean larvae which represented 80 % of the number of organisms collected, and a maximum of 57 x 10^3 ind. 100 m^{-3} (sample F35, collected at 7 h 25), dominated by crustacean larvae which represented 96.1 % of the number of organisms collected. Excluding the same three dominant groups as before, the density fluctuated from 80 ind. 100 m^{-3} (sample F43, collected at 15 h) to 2270 ind. 100 m^{-3} (sample F38, collected at 10 h), dominated by the larvae of *Lanice conchilega* which represented 19-97 % of the number of organisms collected ; maximal densities were present at the beginning and at the end of the sampling period. The faunal density was 9.8 x 10^3 ind. 100 m^{-3} in net 1 (17.4 %), 14.7 x 10^3 ind. 100 m^{-3} in net 2 (26.2 %), 17.3 x 10^3 ind. 100 m^{-3} in net 3 (30.8 %) and 14.4 x 10^3 ind. 100 m^{-3} in net 4 (25.6 %). The average density of the four nets was 14.1 x 10^3 ind. 100 m^{-3} (Table II).

Vertical distribution

According to their coefficients of swimming activity of the daytime and the night (Table III), the main taxa of the near-bottom zooplanktonic fauna were classified into three groups as follows :

1. Upper nectonic organisms with regular swimming activities which occupied the upper water layer during the day : $K1 \approx K2 \approx K3 \approx 0.25$, and swam down to the vicinity of the bottom during the night : $K1 \approx K2 \approx K3 > 0.25$. Two taxa : Clupeidae and Callionymidae postlarvae. Clupeid postlarvae were the most abundant fish postlarvae of the fauna. They were present in the samples rather at night than in daytime (Table II). Thus their vertical migration was quite strong.

2. Boundary nectonic organisms with regular swimming activities which stayed near the bottom during the day : $K1 > K2 > K3$, $K1 \leqslant 0.25$, and moved up to the water column during the night : $K1 \approx K2 \approx K3 \approx 0.25$. Three taxa : Gobiidae, Soleidae and Gadidae postlarvae. But there was no significant difference between their densities of the daytime and

TABLE II

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

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	U test	net 1	net 2	net 3	net 4	Mean
Fish larvae																
Clupeidae	127.3	98.6	93.9	90.0	102.4	178.5	420.2	456.9	456.9	378.1	**	97.6	97.9	75.2	80.3	87.7
Gobiidae	323.7	93.1	94.5	69.7	145.3	130.5	95.6	97.5	83.6	101.8	-	241.3	66.0	78.6	94.7	120.1
Callionymidae	12.3	12.3	9.9	11.0	11.4	4.6	14.7	18.2	15.4	13.2	-	2.0	5.4	3.3	3.7	3.6
Soleidae	27.5	19.1	12.1	11.4	17.5	9.3	7.8	8.5	9.3	0.9	-	0.6	0.9	0.7	0.9	0.8
Chaetognatha																
Sagitta elegans	5.3	5.2	5.2	4.9	5.1	0.2	0.2	0.4	0.0	0.2	**	16.3	18.7	15.1	9.6	14.9
Polychaete larvae																
Syllidae	0.9	2.5	2.6	2.5	2.1	0.0	0.6	1.5	0.6	0.7	*	1.9	4.3	4.4	3.7	3.6
Lanice conchilega	13.1	13.1	15.5	16.6	14.6	10.4	8.3	13.4	7.7	9.9	-	204.4	523.3	310.6	333.7	343.0
Ctenophora (x10^3)																
Pleurobrachia pileus	2.8	5.9	3.7	3.6	4.0	1.4	2.4	1.8	2.6	2.1	-	0.4	0.5	0.5	0.6	0.5
Copepoda (x10^3)	4.1	15.7	4.5	9.6	8.5	8.1	36.2	12.2	49.4	26.5	*	0.3	1.2	0.3	0.7	0.6
Crustacean larvae (x10^3)	1.4	3.8	4.2	5.8	3.8	1.5	3.8	4.5	6.9	4.2	-	8.4	12.3	11.4	12.5	11.1
Total (10^3)	8.8	25.7	12.6	19.2	16.6	13.4	42.9	19.1	59.5	33.7		9.8	14.7	17.3	14.4	14.1
%	13.3	37.8	19.0	29.0		24.7	31.8	14.2	44.1			17.4	26.2	30.8	25.6	

Notes :
- ** very significant, $p < 0.01$
- * significant, $p < 0.05$
- - not significant, $p > 0.05$

those of the night. Only their vertical distribution over the four nets changed. That means that their vertical movements were only of a small amplitude (Table II).

3. Planktonic organisms. Five taxa : copepods, crustacean larvae, *Pleurobrachia pileus*, syllid epitokes and the larvae of *Lanice conchilega*. Some of them were essentially present in the upper water layers : all the time K1 < K2 < K3 with K1 ≥ 0.25, like crustacean larvae. The others did not show regular swimming activities ; their vertical distributions varied from day to night and from one day to the other, with highest abundances in one of the three upper nets : K1 or K2 or K3 > 0.30. Nevertheless, the sledge sampling did not permit the description of the vertical migration pattern in the whole water column.

The chaetognath *Sagitta elegans* was present essentially in the daytime samples (Table II). Their coefficients of swimming activity did not arrow for the identification of a vertical migration pattern (Table III).

TABLE III

Coefficients of swimming activity K1, K2 & K3 of the principal taxa of the planktonic fauna

Species	Serie 1						Serie 2		
	Day			Night			Day		
	K1	K2	K3	K1	K2	K3	K1	K2	K3
Fish larvae									
Clupeidae	0.24	0.23	0.22	0.28	0.30	0.30	0.28	0.21	0.23
Gobiidae	0.16	0.16	0.12	0.24	0.24	0.21	0.14	0.16	0.20
Callionymidae	0.27	0.22	0.24	0.28	0.34	0.29	0.37	0.23	0.26
Soleidae	0.27	0.17	0.16	0.22	0.24	0.27	0.30	0.24	0.28
Gadidae	0.26	0.19	0.21	0.26	0.24	0.23	0.29	0.24	0.30
Copepoda	0.46	0.13	0.29	0.34	0.12	0.47	0.48	0.12	0.27
Chaetognatha									
Sagitta elegans	0.25	0.26	0.24	–	–	–	0.31	0.25	0.16
Crustacean larvae	0.25	0.28	0.38	0.25	0.25	0.28	0.28	0.26	0.28
Ctenophora									
Pleurobrachia pileus	0.37	0.23	0.23	0.29	0.22	0.32	0.25	0.25	0.30
Polychaete larvae									
Lanice conchilega	0.23	0.27	0.29	0.21	0.34	0.20	0.38	0.23	0.24
Syllidae epitokes	0.29	0.31	0.30	0.23	0.47	0.31	0.31	0.31	0.26

Density variations

Most taxa of the meso- and macrozooplanktonic fauna were pelagic. Therefore, the tidal current of the region (Figs. 1, 2) could certainly influence their spatial distribution. Our hourly samples allowed us to reveal the relation between the density variation and the tidal cycle. On the other hand, some of these taxa would perform more or less diurnal vertical migrations. Since our sledge simultaneously sampled at four vertical levels, we should also be able to see the possible existence of vertical migrations.

However, only a few taxa were abundant enough to allow us to take these studies in detail (Table I). According to the regularity of density variation during the sampling period, four patterns of density variations were found :

1. Pattern of clupeid postlarvae.

For the greater part of the day, clupeid postlarvae kept swimming in the upper water column and were almost absent from the samples. Around sunset and sunrise, they performed an active vertical migration and concentrated in the vicinity of the bottom (Figs. 3a, b).

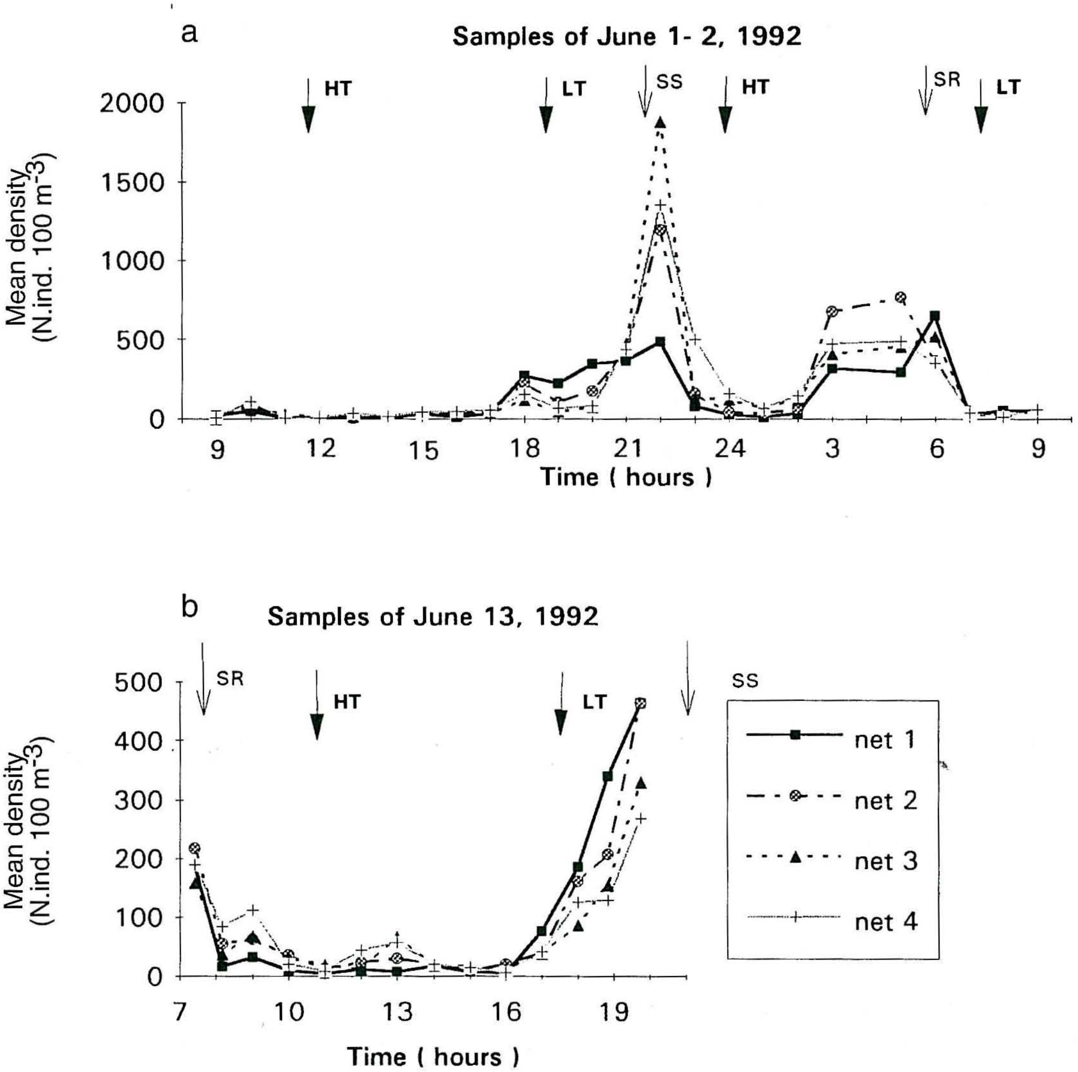


Fig. 3 : Diurnal variation of the density of Clupeidae postlarvae. daytime = 6 h - 21 h, night = 22 h - 5 h. HT = high tide, LT = low tide, SR = sunrise, SS = sunset.

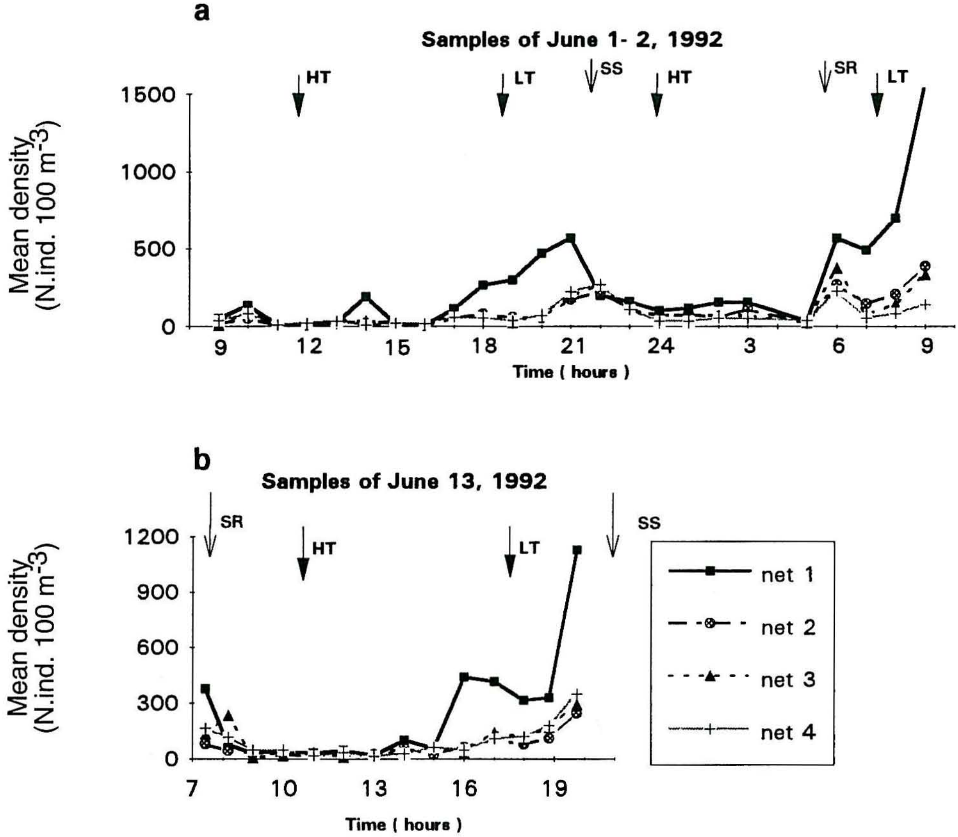


Fig. 4, continued p. 169

Most individuals were caught in the three upper nets, but they could also sometimes be found close to the bottom. For example, they were most abundant in the lower nets of sample F48 which was collected at 19 h 45 on June 13. Tidal currents showed no influence on the distribution of these good swimmers (Figs. 3a, b).

2. Pattern of gobiid postlarvae.

The postlarvae gobiids, *Callionymus* and soles, the chaetognath *Sagitta elegans* and crustacean larvae were more abundant during the flood tide. Their densities peaked every twelve hours along with the tidal cycle (Figs. 4, 5). These density peaks corresponded to the beginning of the flood tide when the current speed reached its maximum in eastern direction and was negligible in the direction north-south (Figs. 1, 2). Therefore, they were marine animals which entered the estuary with the saline water. The postlarvae of *Callionymus*, which are known to be swimming animals, showed no difference in density of individuals caught by the four nets of the sledge, while the postlarvae of gobiids and soles, which are demersal fishes, were mainly caught by net 1 (Fig. 4).

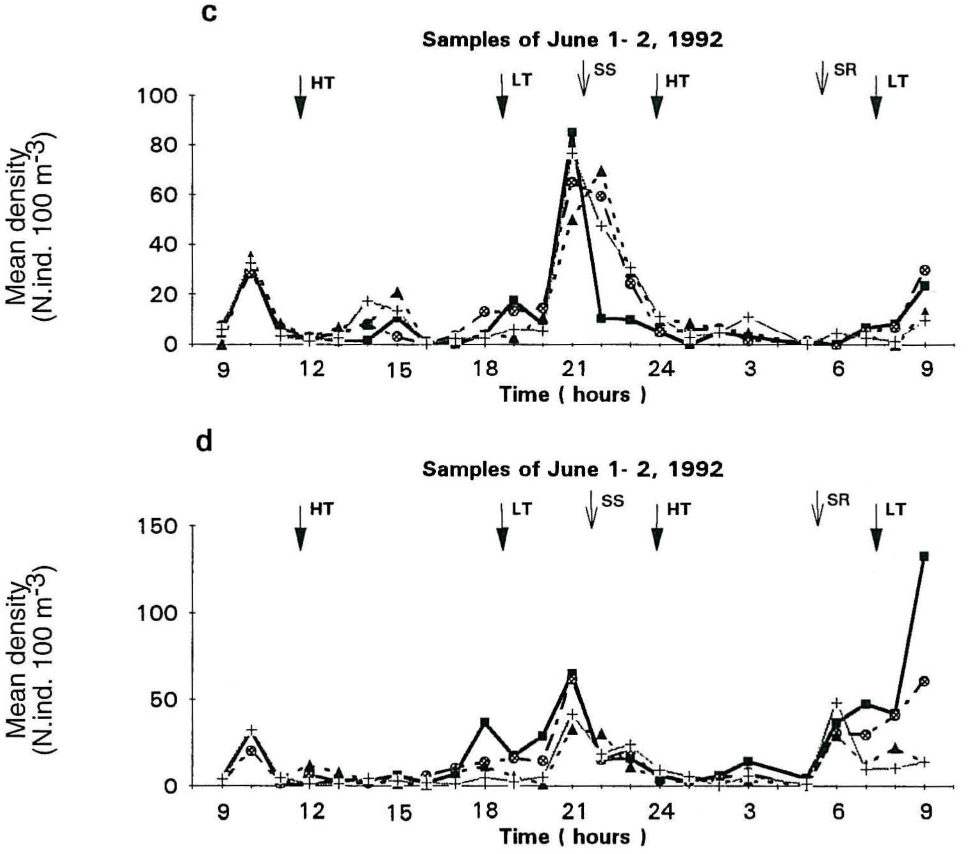


Fig. 4 : Diurnal variation of the density of Gobiidae (a, b), Callionymidae (c) and Soleidae (d) postlarvae ; daytime = 6 h - 21 h, night = 22 h - 5 h. HT = high tide, LT = low tide, SS = sunset, SR = sunrise.

3. Pattern of *Pleurobrachia pileus*.

In the samples of June 1-2, the ctenophore *Pleurobrachia pileus* and polychaete larvae *Lanice conchilega* showed density peaks every 12 hours during the ebb tide when the current speed reached its maximum in western direction and was negligible in the direction north-south (Figs. 1 ; 6a, b). Thus they were neritic animals which went out from the Bay of Seine passively with the estuarine water. No active vertical migration could be detected. Since it was the period of neap tide on June 13 and the marine water mass was more important at the sampling station, *Pleurobrachia pileus* was present with a very low density. Nevertheless, *Lanice conchilega* larvae showed an important density peak at the beginning of the flood tide when the current speed was negligible in direction east-west and maximal in northern direction (Fig. 6c).

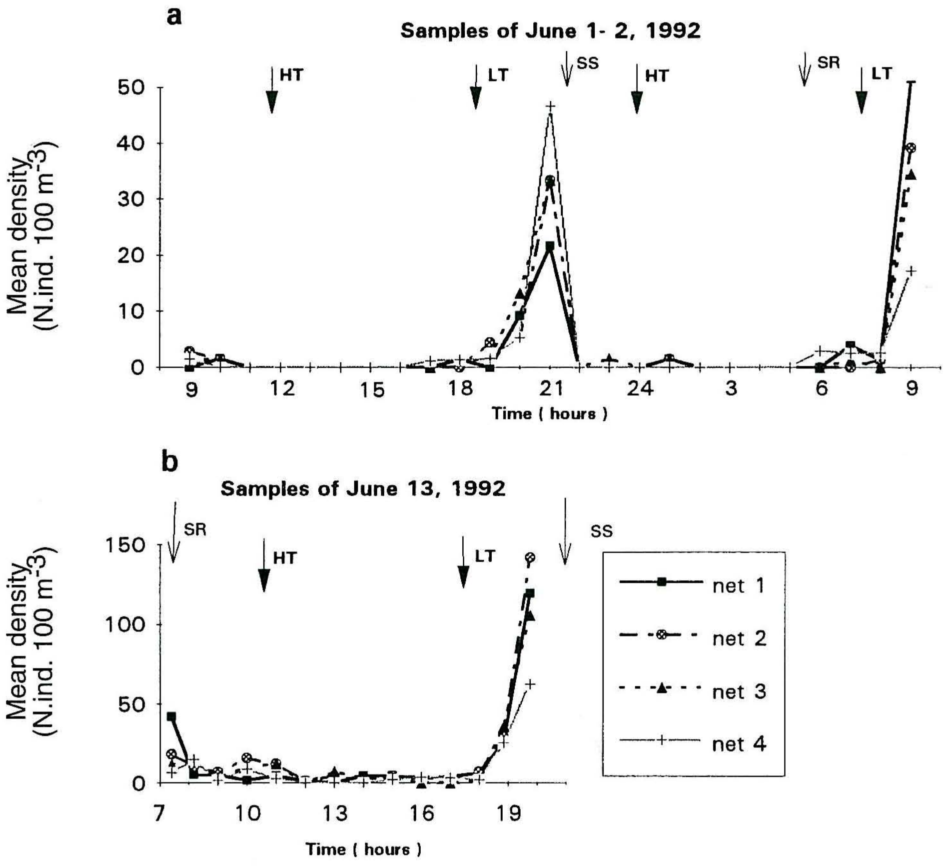
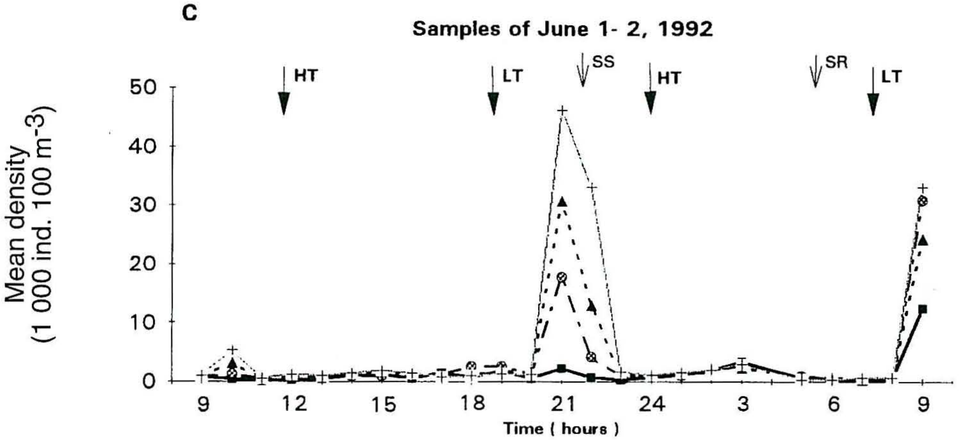


Fig. 5, continued p. 171

4. Pattern of copepods.

The density variation of copepods was a combination of two mechanisms : advection and migration. In the samples of June 1-2, they showed density peaks every twelve hours, following the tidal currents in eastern direction during the flood tide. In addition, in the middle of the dark hours, they reached an important density peak ; a vertical migration from the upper water column to the near-bottom water layer seemed to occur. That was probably the so-called "midnight sinking" (Fig. 7a). It was also the cause of their significantly higher densities at night (Table II). They were less abundant in the samples of June 13 but showed the same pattern (Fig. 7b). The higher densities of individuals caught by nets 2 and 4 might be due to different behaviour of dominant species (Fig. 7).



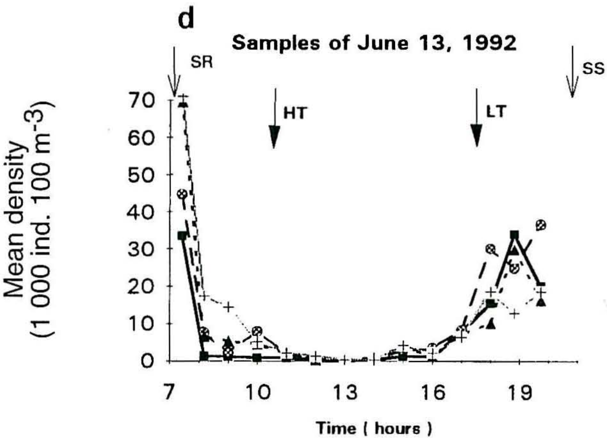


Fig. 5 : Diurnal variation of the density of chaetognaths (a, b) and crustacean larvae (c, d) daytime = 6 h - 21 h, night = 22 h - 5 h. HT = high tide, LT = low tide, SS = sunset, SR = sunrise.

DISCUSSION

Faunistic composition and density

The zooplanktonic fauna was composed of two main groups : mesozooplankton (mainly copepods and crustacean larvae) and macrozooplankton (mainly the ctenophore *Pleurobrachia pileus* and fish postlarvae). Characteristic of this fauna was the high abundance of the mesozooplankton : average total density of copepods and crustacean larvae was more than 10 x 10^3 ind. 100 m^{-3} throughout the whole day (Table I ; Figs. 5c, d, 7). The maximal density of copepods was 120 x 10^3 ind. 100 m^{-3}, present in net 4 at 2 h on June 2. The daytime density of copepods decreased sharply from 8.5 x 10^3 ind. 100 m^{-3} on June 1-2 to 0.6 x 10^3 ind. 100 m^{-3} on June 13, this may be due to their patchy distribution.

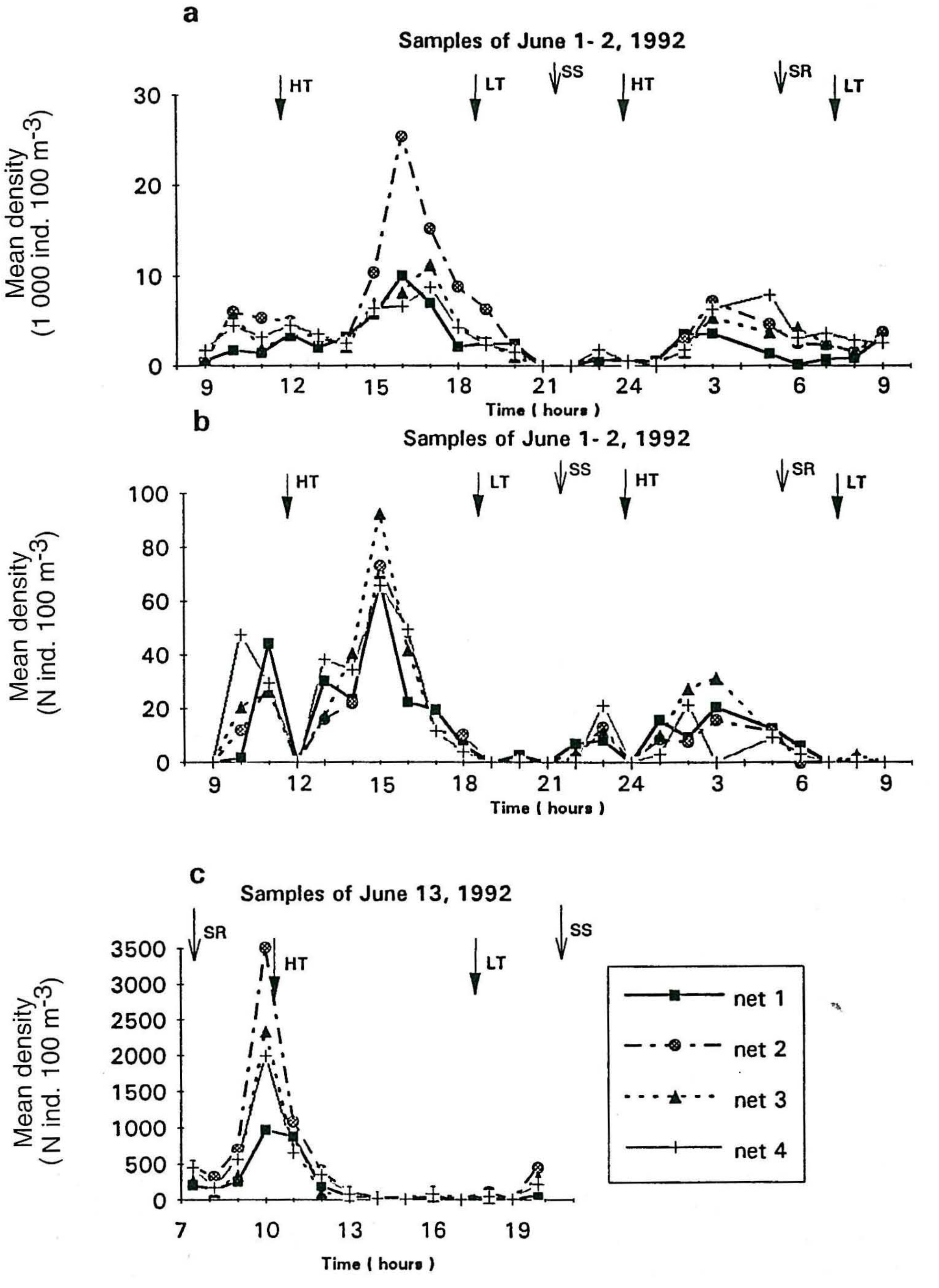
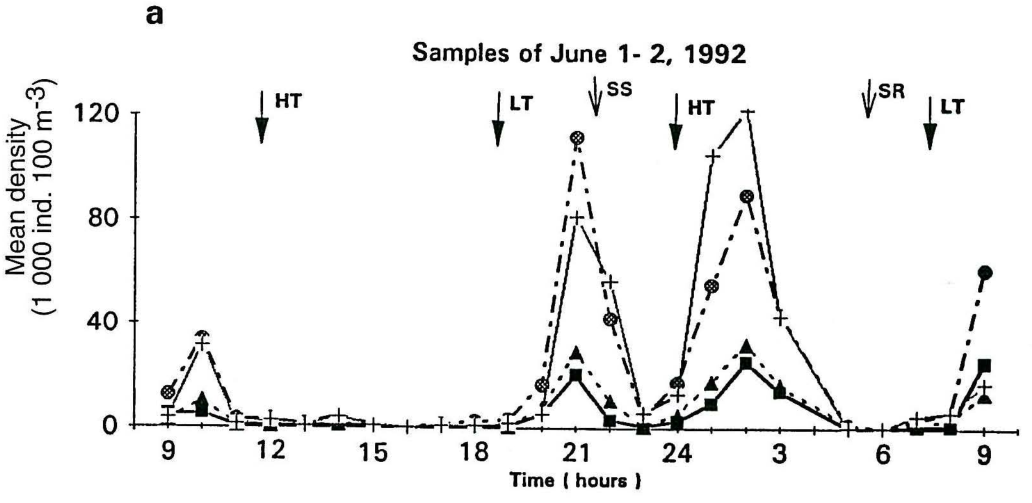


Fig. 6 : Diurnal variation of the density of *Pleurobrachia pileus* (a) and the larvae of *Lanice conchilega* (b, c) daytime = 6 h - 21 h, night = 22 h - 5 h. HT = high tide, LT = low tide, SS = sunset, SR = sunrise.



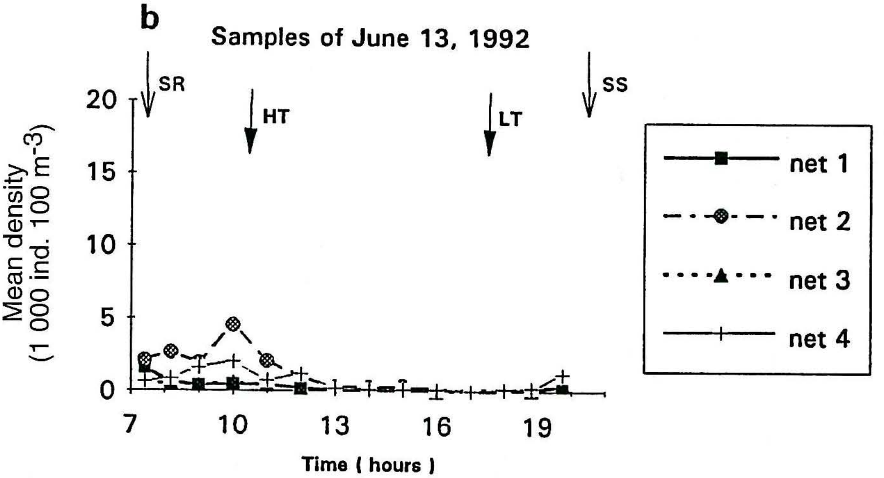


Fig. 7 : Diurnal variation of the density of copepods. daytime = 6 h - 21 h, night = 22 h - 5 h. HT = high tide, LT = low tide, SS = sunset, SR = sunrise.

Still, compared with the values of copepods found in some other near-bottom areas, the present copepod densities are among the highest reported to date : in Browns Bank (Northwest Atlantic, depth 25-90 m), the summer density was 2800 ind. 100 m^{-3} (Wildish *et al.*, 1992) ; in the inner Oslofjord (Northeast Atlantic, depth 112-115 m), the daily mean density of several samples collected in May 1973 was less than 500 ind. 100 m^{-3} (Hesthagen & Gjermundsen, 1978) ; in Josephine Seamount (North Atlantic, depth 199-268 m) and Great

Meteor Seamount (depth 290-313 m), the mean densities of the samples collected in several stations in July 1967 were 150 and 880 ind. 100 m^{-3}, with maxima of 383 and 2932 ind. 100 m^{-3} (Hesthagen, 1970). The increase in numbers of crustacean larvae in the samples of June 13 was associated with the advection of the marine water mass which was more important during this sampling period.

Although the macrozooplankton was less abundant in the samples (average total density between 700 and 4300 ind. 100 m^{-3} (Table I)), it was of essential importance in the fauna because of their much larger body size and higher biomass. In spring, the ctenophore *Pleurobrachia pileus* is abundant near the bottom in the Bay of Seine (Thiébaut, unpublished observations). They were more abundant in the samples of June 1-2 (2-4 x 10^3 ind. 100 m^{-3}) than in those of June 13 (0.5 x 10^3 ind. 100 m^{-3}) (Table I).

Density variations

The density variation of the near-bottom zooplanktonic fauna was due to a combination of two mechanisms : active vertical migration and passive advection with the tidal currents. As active swimmers, clupeid postlarvae performed a vertical migration from the water column to the vicinity of the bottom around sunset and sunrise, and showed no correlation with the tidal cycle. The same rhythm was observed in the suprabenthic samples collected in July 1990 from another station situated in the Western English Channel at 65-80 m depth on coarse sand (Zouhiri, 1993).

All the other animals of the fauna were mainly transported by the tidal currents. In the Newport River estuary (North Carolina, USA), the distribution of the larvae of the crab *Rhithropanopeus harrisii* was found to be associated with the tidal currents (Cronin, 1982). Levin (1986) reported that polychaete larvae, mainly spionids, moved passively within the water mass in Mission Bay, southern California. However, some of them seem to perform more or less a migratory activity. For example, the "midnight sinking" of copepods seemed strong and was evident from our samples (Fig. 7a). Still, it seems that the phenomenon also depends on the species composition of the copepod population and on their respective habitats. The bottom-living copepods in Northumberland and Kiel Bight usually performed an active diurnal vertical migration upward at night and downward in the morning, but no "midnight sinking" was found (Bossanyi, 1957 ; Hesthagen, 1973). In Great Meteor Seamount, the copepod population was also found to display the same diurnal rhythm, with maximal densities present at noon and absent around midnight (Hesthagen, 1970). Different species of copepods probably show different behaviours. Further studies are needed to examine their specific components and migratory activities.

As estuarine planktonic animals (Thiébaut, unpublished observations), the distribution of *Pleurobrachia pileus* was determined by the transport of tidal currents and associated with the advection of brackish estuarine water mass which was stronger on June 1-2.

The abruptly increasing numbers of the larvae of *Lanice conchilega* in several samples of June 13 might be due to a breeding activity of this species taking place between June 2 and June 13 which resulted in an important larval patch coupled with the advection of the estuarine water mass.

Swimming fish postlarvae were abundant in both series of samples with a total of 200-500 ind. 100 m^{-3} throughout the whole day (Table I). This could be due to the fact that in this area, their preys, mainly mesozooplanktonic and suprabenthic animals, were abundant and so the environment was favorable for them (Wang & Dauvin, 1994). The same was observed in the estuary of Saint Lawrence, where a lot of larval rainbow smelt *Osmerus mordax* (Osmeridae) stayed in the turbidity center associated with amphipods, mysids and the shrimp *Crangon septemspinosus* (Dodson *et al.*, 1989). The more they went close to the maximal turbidity center, where there was a high concentration of food organisms, the better they could develop (Dauvin & Dodson, 1990). Similar results of the postlarvae of *Osmerus eperlanus* in the Loire estuary were reported by Lardeux (1987).

On the other hand, the increase in the numbers of postlarval gobiids and soles caught by net 1 at the beginning of the night and in the next morning could correspond to their migration from the bottom to the adjacent water layer (Figs. 4a, b, d). Moreover, in the samples of June 1-2, the chaetognath *Sagitta elegans* showed two density peaks. The first peak was present at 21 h on June 1, with the density of collected individuals increasing gradually from net 1 to net 4. The second was observed at 9 h the next morning, with the density of collected individuals increasing inversely from net 4 to net 1. In fact, they were only then present in the samples (Figs. 5a, b). Therefore, it seemed that the chaetognaths performed a regular diurnal rhythm : they stayed in the near-bottom water layer during the day ; around sunset they actively migrated to the upper part of the water column and disappeared from suprabenthic samples ; then in next morning, after sunrise, they rapidly returned to the vicinity of the bottom. Hesthagen (1973), in his studies of the hyperbenthos of Kieler Bight, where tidal currents were negligible, also found a very pronounced diurnal vertical migration of *Sagitta elegans* in the near-bottom water, and he suggested that this could be correlated to the change of daylight. More observations are needed to reveal the relative importance of active migration and passive advection in the distribution.

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