Jeep 92

Major Biological Processes in European Tidal Estuaries

Mast

DESIGN – ANA RODRIGUES

JEEP 92 MAST PROJECT

Joint European Estuarine research Project

PROGRESS REPORT

PART I

Comparative studies: Gironde estuary

PART II

Biological Processes: Biology of the water column

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Introduction

The objective of the studies undertaken during the last 18 months (*) was to investigate the biological processes that influence the fate of organic matter in tidal estuaries by:

i/ comparison of the ecological structure of two major European tidal estuaries: the WesternSchelde and the Gironde,

ii/ specific coordinated studies on the rates of major processes on short and medium time scales in the field in Schelde and Gironde, and in laboratory experiments.

The present report is divided in two parts dealing with the above aspects i.e. Part I: Comparative studies: Gironde estuary, and Part II: Biological processes: Biology of the water column.

In complement to the JEEP 92-MAST project, several programmes or specific actions helped our work in the Gironde estuary:

- The first one is a National programme sponsored by IFREMER: "Surveillance écologique sur le site du CPN Le Blayais". It concerns the general survey of the estuary. It guarantees a number of cruises along the estuary and the measurements of the basic parameters (in collaboration with the Institut de Géologie du Bassin d'Aquitaine and the Laboratoire Municipal de Bordeaux).

- The second one is through a European network of laboratories sponsored by the French Ministry of Research and Technology. The laboratories concerned are from Arcachon, Bordeaux, Yerseke, Brussel and Lisbon. The name of the network is EPEE : "Ecologie du Plancton dans les Estuaires Européens". Mainly travels are paid by this programme.

- Ship time on the R/V Côte d'Aquitaine was provided by CNRS (Centre National de la Recherche Scientifique) for the JEEP project.

(*)The work began just after the acceptance of the project (March 1990), i.e. well before the signature of the contract.

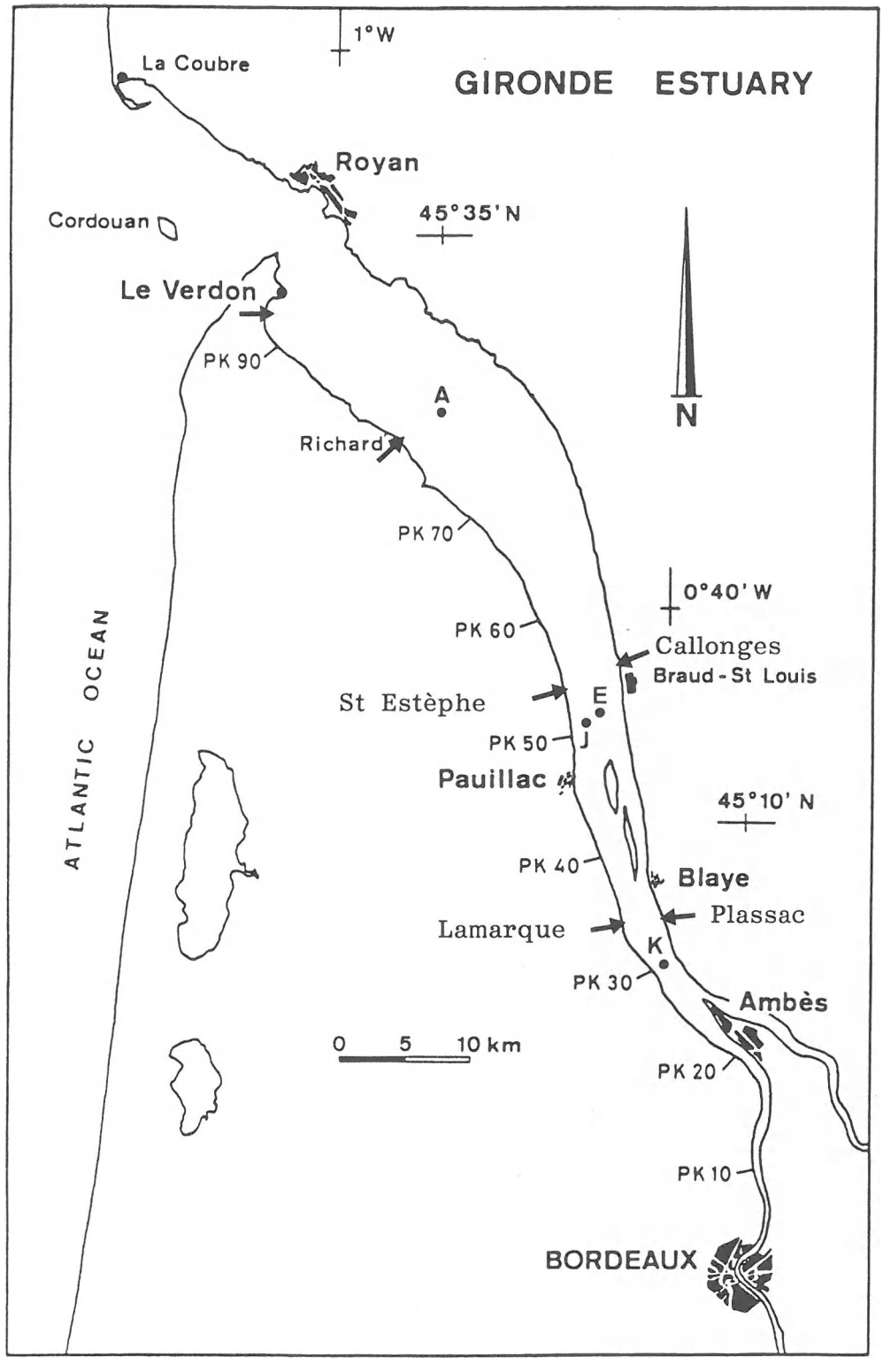

Figure 1: Map of the Gironde estuary showing the sampling stations. Stations E, J & K: general survey. Stations J and A: intensive field measurements. Arrows show the stations corresponding to the benthic survey. PK refers to the distance, in km, from the city of Bordeaux. Garonne river on the left side, Dordogne river on the right side.

PART I

COMPARATIVE FIELD STUDY OF THE ECOLOGICAL STRUCTURE OF MAJOR EUROPEAN TIDAL ESTUARIES: THE GIRONDE ESTUARY.

This part of the programme is not directly funded by the MAST project and is covered on a volontary basis. The surveys and the analyses were sponsored by other sources, and the following organizations contributed to the measurements:

- Institut de Biologie Marine, Université de Bordeaux I, Arcachon (I. Auby, G. Bachelet, J. Castel, X. Irigoien, P. Santos): zooplankton and zoobenthos
- Institut de Géologie du Bassin d'Aquitaine, Université de Bordeaux I, Talence: hydrology
- Laboratoire Municipal de Bordeaux: nutrients and chlorophyll
- IFREMER, Centre de Toulon, La Seyne s/ Mer general support

1. WATER COLUMN

Monthly samplings were made between March and November 1990, and then between March and November 1991 at three stations (E, J and K) situated in the oligo- and mesohaline zones of the Gironde estuary (Figure 1). The following variables were measured: temperature, salinity, current velocity, suspended particulate matter, dissolved oxygen concentration, chlorophyll and pheopigments, and nutrients. Nutrients and chlorophyll were also analysed in the fluvial part of the estuary, in both Garonne and Dordogne rivers.

Hydrological variables were measured at water surface and near bottom, every 2 h during a tidal cycle (12h30) whereas samples for chlorophyll and nutrients were taken just below the water surface at high tide, mid-tide and low tide. All analyses were made according to the "Manual on sampling and analytical procedures of tidal estuarine waters" (Kramer K.J.M., Warwick R.M. & Brockmann U., eds). For technical reasons, most results of the 1991 campaigns are not yet available.

1.1. Salinity (Figure 2)

In 1990 salinity varied from 0.13‰ to 19.08‰ and in 1991 the salinity range was 0.19‰-15.75‰. Waters of the Gironde estuary are not very stratified; during the 1990 and 1991 field campaigns the difference between surface and bottom salinity was generally 0.5-1.5 ‰ and did not exceed 2.5‰. Seasonal variations in salinity are clearly related to river discharge (see fig. 4 for the year 1990): minimum salinities were recorded in spring and maximum values occurred in October.

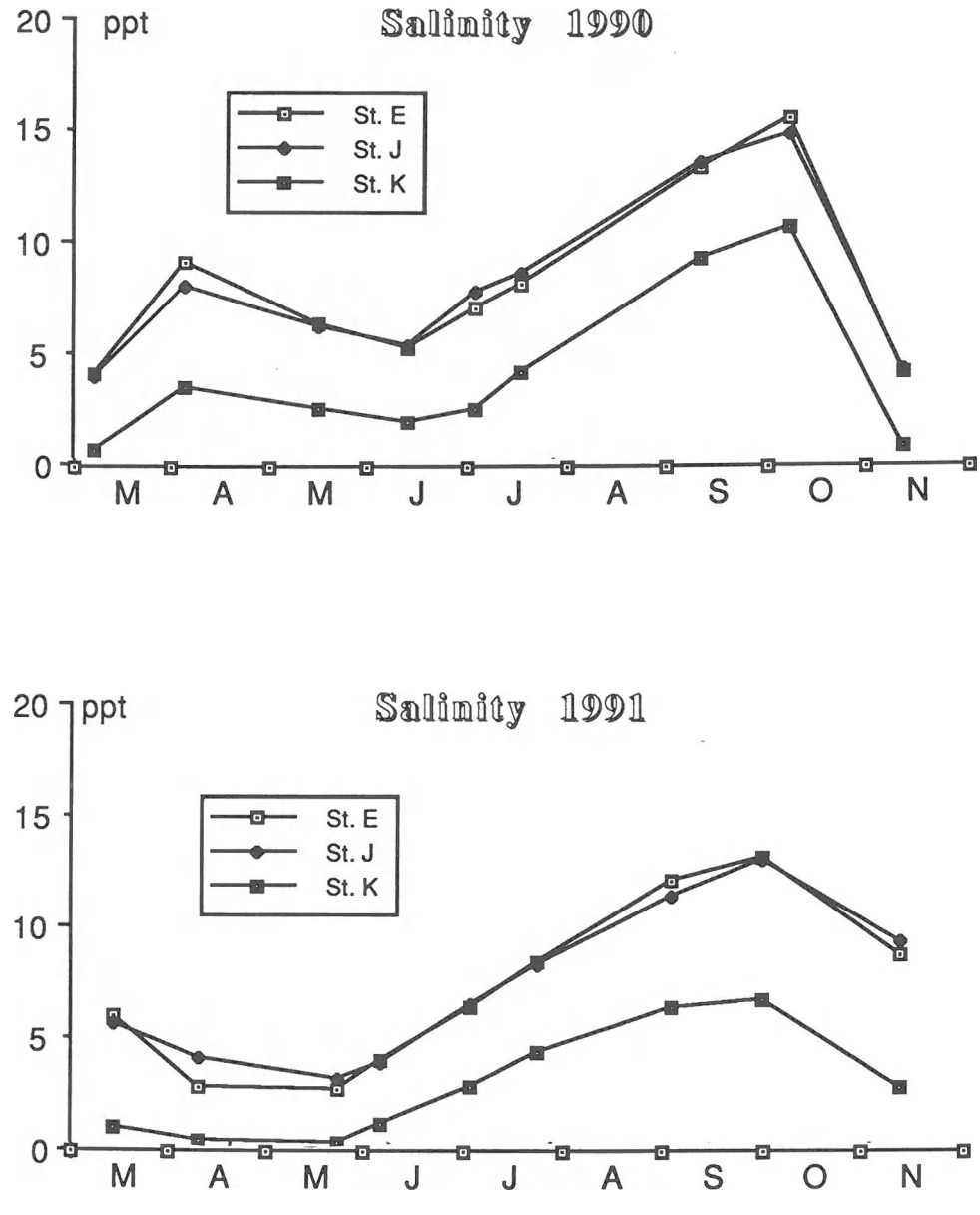

Figure 2: Salinity variation in the Gironde estuary. Each point represents the mean of ten measurements (5 in surface water, 5 near the bottom) over a tidal cycle.

1.2. Suspended particulate matter (Figure 3)

The Gironde estuary is a highly turbid estuary with particulate concentrations that are tidally resuspended and that may exceed 1 g/l. A maximum value of 7.4 g/l was measured in the bottom water at St. K in October 1990.

SPM concentrations were always higher in the upper reach of the estuary (St. K) than in the more saline zone (St. E and St. J). On a seasonal basis, highest mean values were recorded in spring and autumn, i.e. during periods of high river flow (Figure 4).

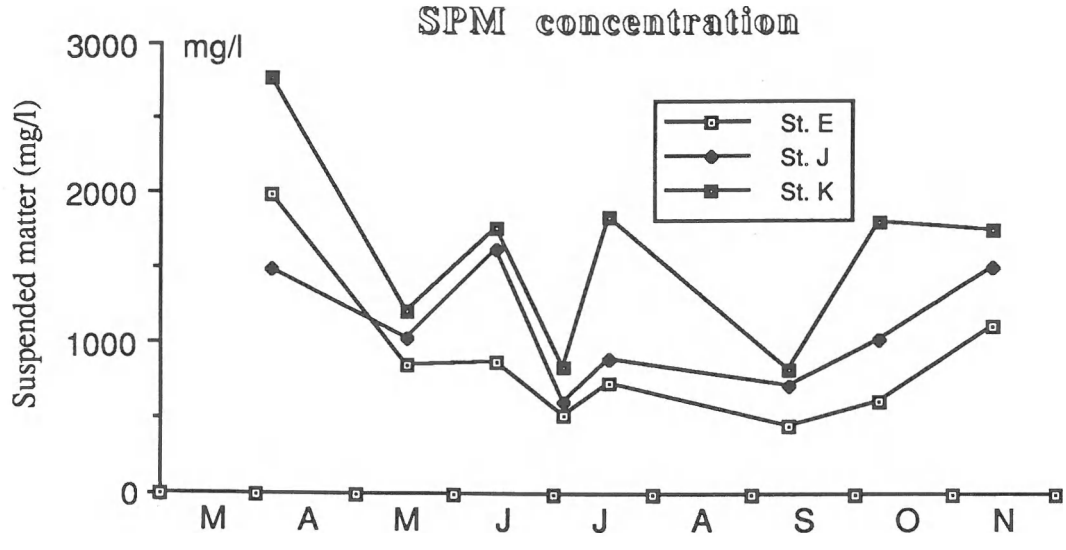

Figure 3: Suspended particulate matter concentration in the Gironde estuary during the year 1990. Each point represents the mean of ten samples (5 at water surface and 5 near the bottom) over a tidal cycle.

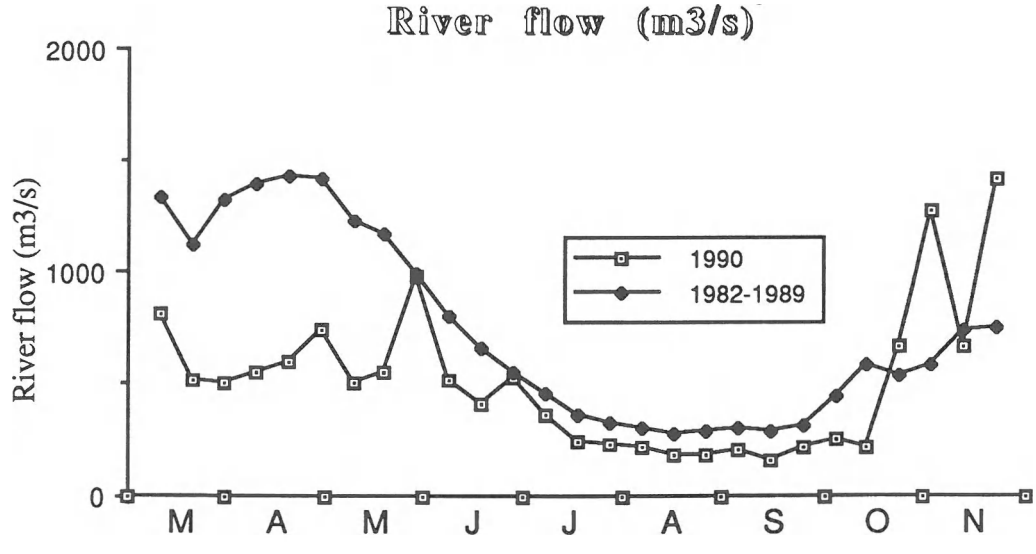

Figure 4: River flow of the Garonne + Dordogne for the year 1990 and comparison with the period 1982-1989. Data are averaged over periods of ten days.

1.3. Oxygen concentration (Figure 5)

Oxygen concentration is not a limiting factor in the Gironde estuary since the waters are rather well-mixed. Minimum concentrations were observed in summer but they did not reached lethal values for the biota. Percentage saturation was not lower than 67 % (Figure 6).

On average, waters of the upper estuary station K were less oxygenated than waters of St. E and St. J, probably because of the high load in suspended matter.

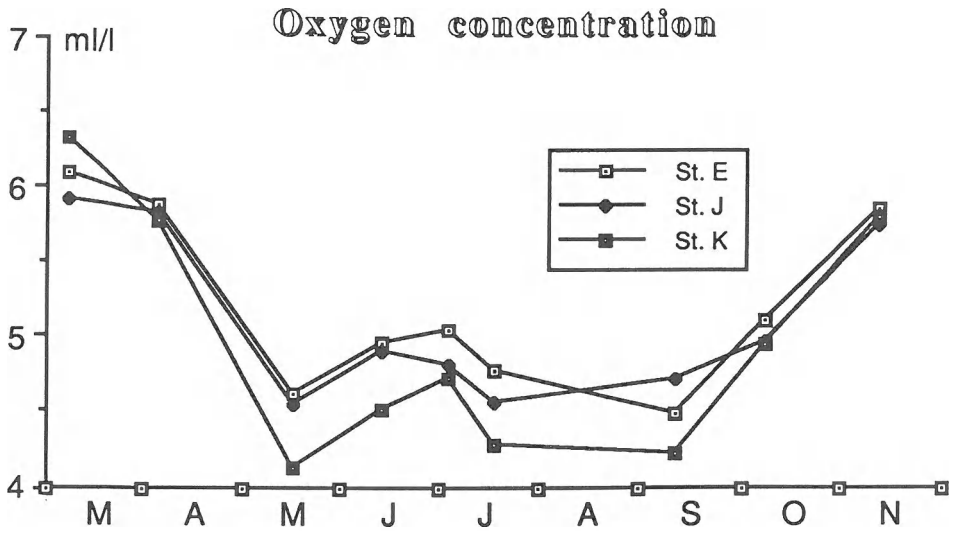

Figure 5: Dissolved oxygen concentration in the Gironde estuary during the year 1990. Each point represents the mean of ten measurements (5 at water surface and 5 near the bottom) over a tidal cycle.

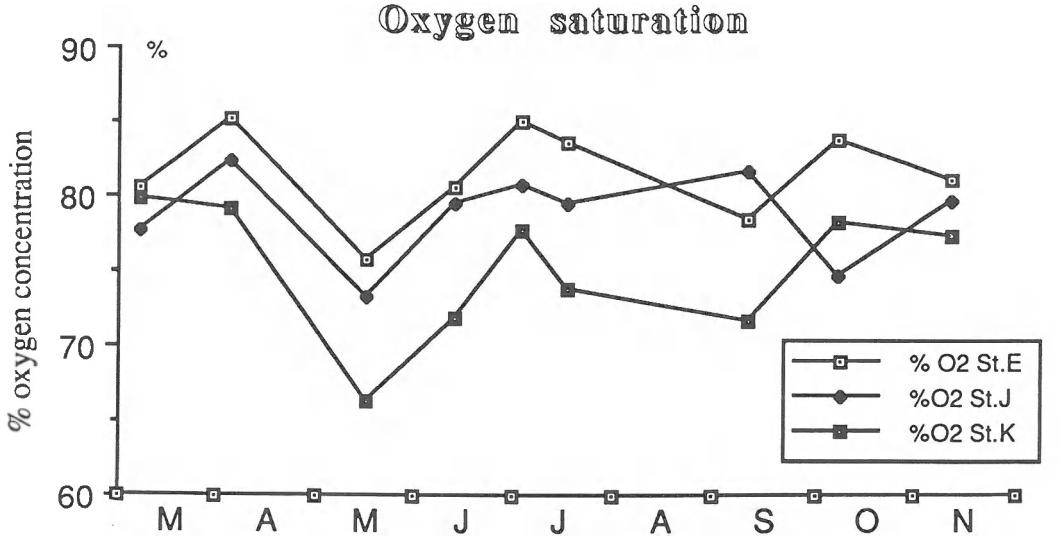

Figure 6: Percentage saturation of dissolved oxygen in the Gironde estuary during the year 1990. Each point represents the mean of ten measurements (5 at water surface and 5 near the bottom) over a tidal cycle.

1.4. Nitrates (Figure 7)

In the Gironde estuary nitrates clearly represent the predominant (98 %) form of inorganic nitrogen.

Due to the consumption by primary producers, nitrates measured in the rivers showed minimum concentrations in May and September 1990. The concentrations recorded in the estuarine stations seemed to be influenced by the riverine input, as shown by the parallelism of the seasonal variations.

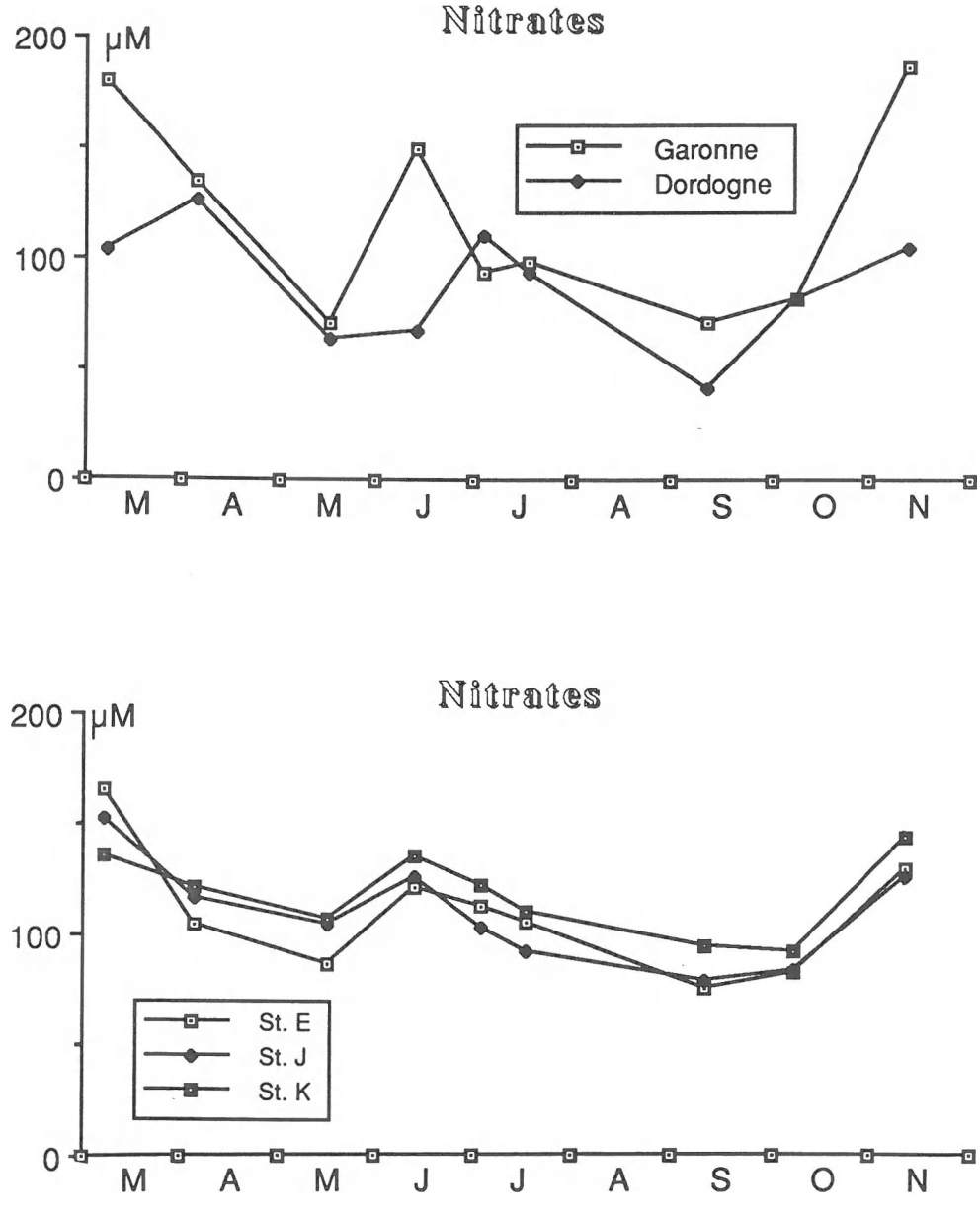

Figure 7: Variation of nitrate concentrations in the Gironde estuary during the year 1990. Each point represents the mean of 3 samples taken at water surface (HT, MT, LT).

1.5. Phosphates (Figure 8)

Very low phosphate concentrations were measured in the Dordogne river. Conversely, in the Garonne river, a value of 7 µM was reached in October 1990. This could be due to the draining of the soils after the storms that took place in September 1990. The influence of the river input on the estuary seems to be low. In the estuary, phosphate concentrations increased during summer and decreased from September onwards.

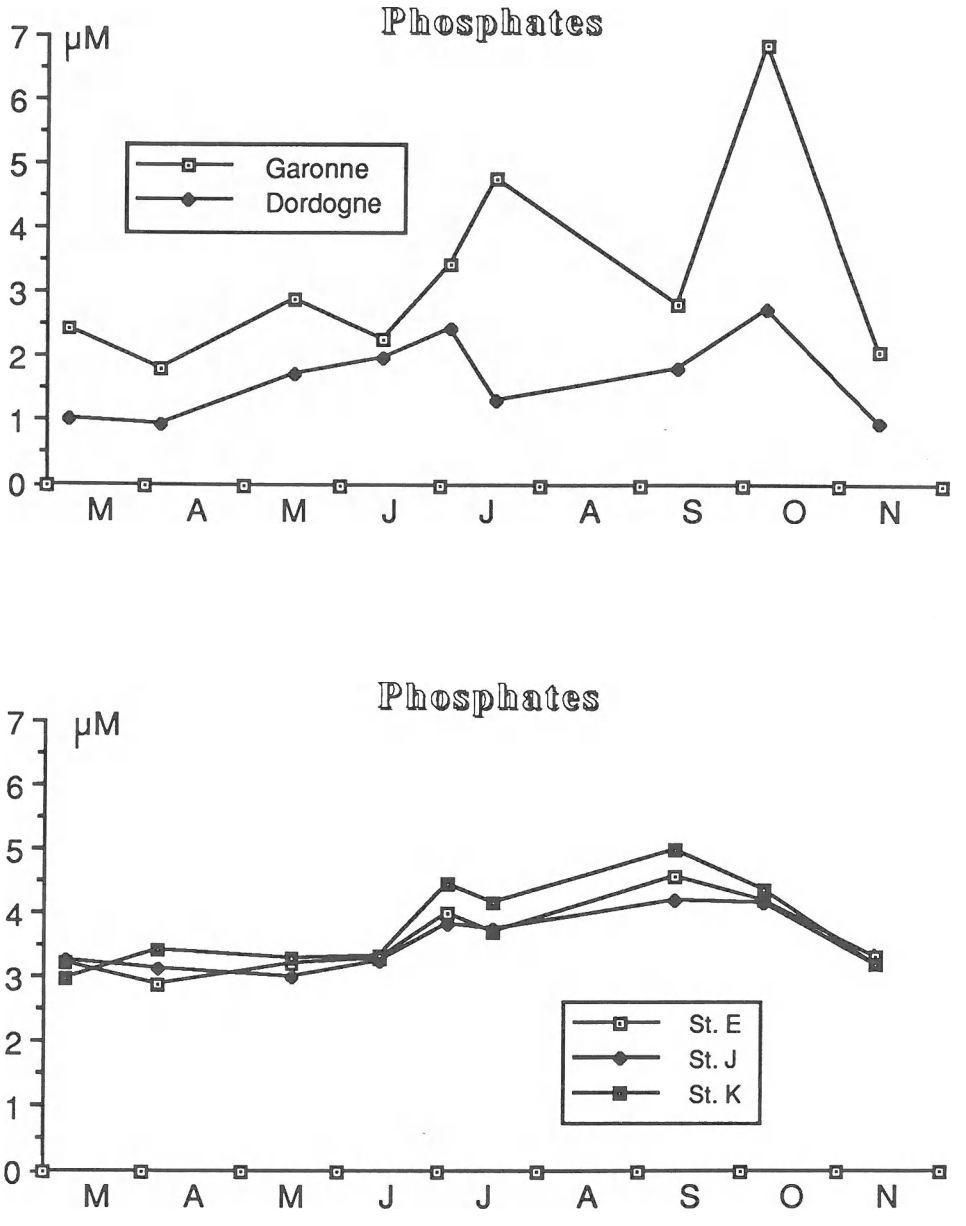

Figure 8: Variation of phosphate concentrations in the Gironde estuary during the year 1990. Each point represents the mean of 3 samples taken at water surface (LT, MT, HT).

1.6. Chlorophyll (Figure 9)

The ratio chlorophyll *a* / total pigments can be considered as an index of potential activity of the phytoplankton biomass. In the rivers, the % chlorophyll showed two peaks: one in May and another in September. In the estuary proper, the upstream St. K showed seasonal variations identical to that of the rivers. Conversely, at St. E and St. K only the September bloom was recorded.

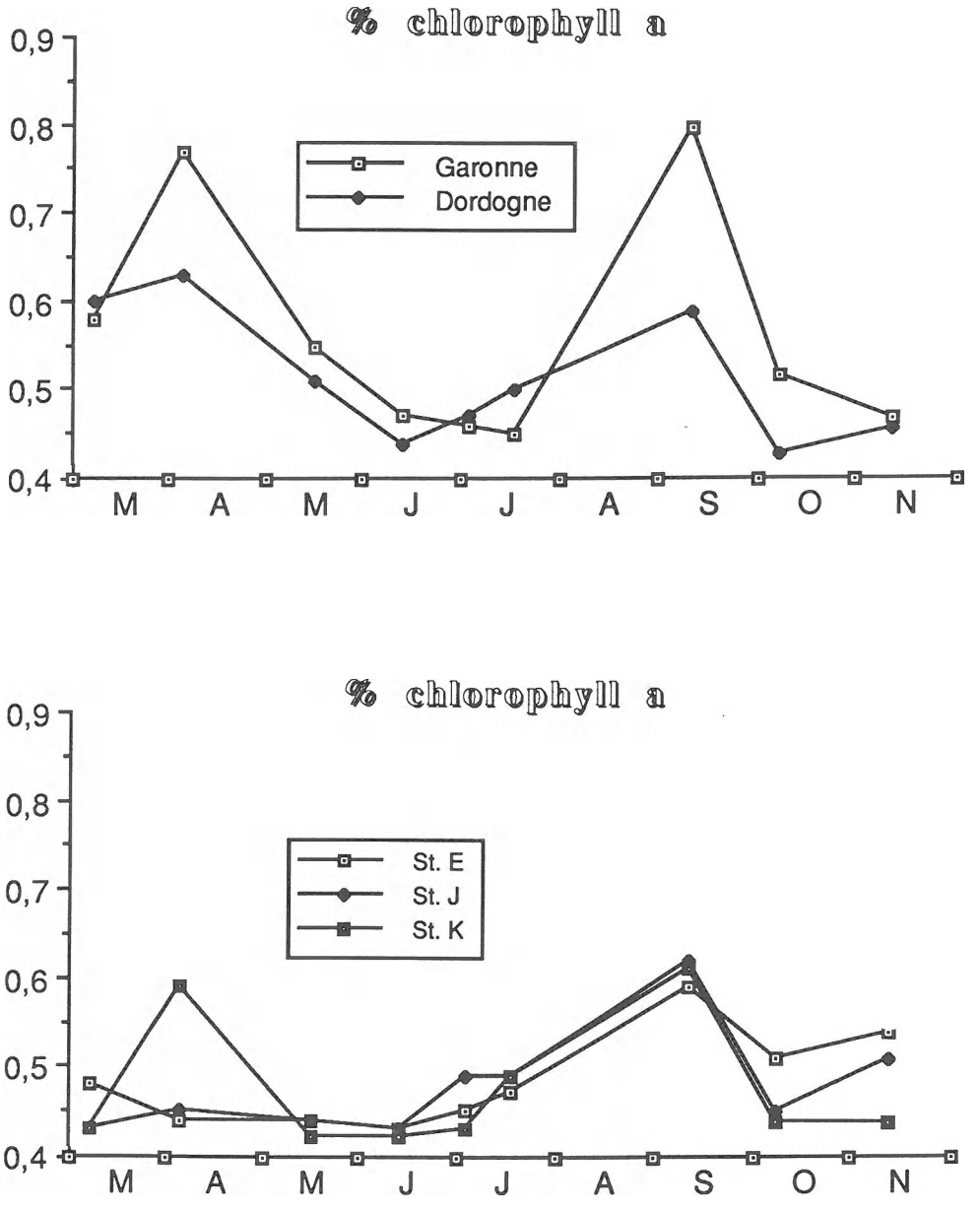

Figure 9: Variation of the percentgae chlorophyll *a* in the Gironde estuary during the year 1990. Each point represents the mean of 3 samples taken at water surface (HT, MT, LT).

2. ZOOPLANKTON

Monthly sampling was made between March and November 1990, and then between March and November 1991 at three stations (E, J and K) situated in the oligo- and mesohaline zone (Figure 1). Zooplankton was collected with a standard WP_2 nylon net (200 µm). Samples (surface and bottom) were obtained at approx. 2h intervals during a tidal cycle.

2.1. *Eurytemora affinis*

The zooplankton community is dominated by copepods and more specifically by *Eurytemora affinis*. Maximum abundance was observed in spring (March-May) (Figure 10) which is usual for this species in most European estuaries. The summer minimum was clearly related to the salinity intrusion (maximum salinity: 15-19 ‰ in the study area). On average, the abundance was higher in 1991 than in 1990, except in autumn.

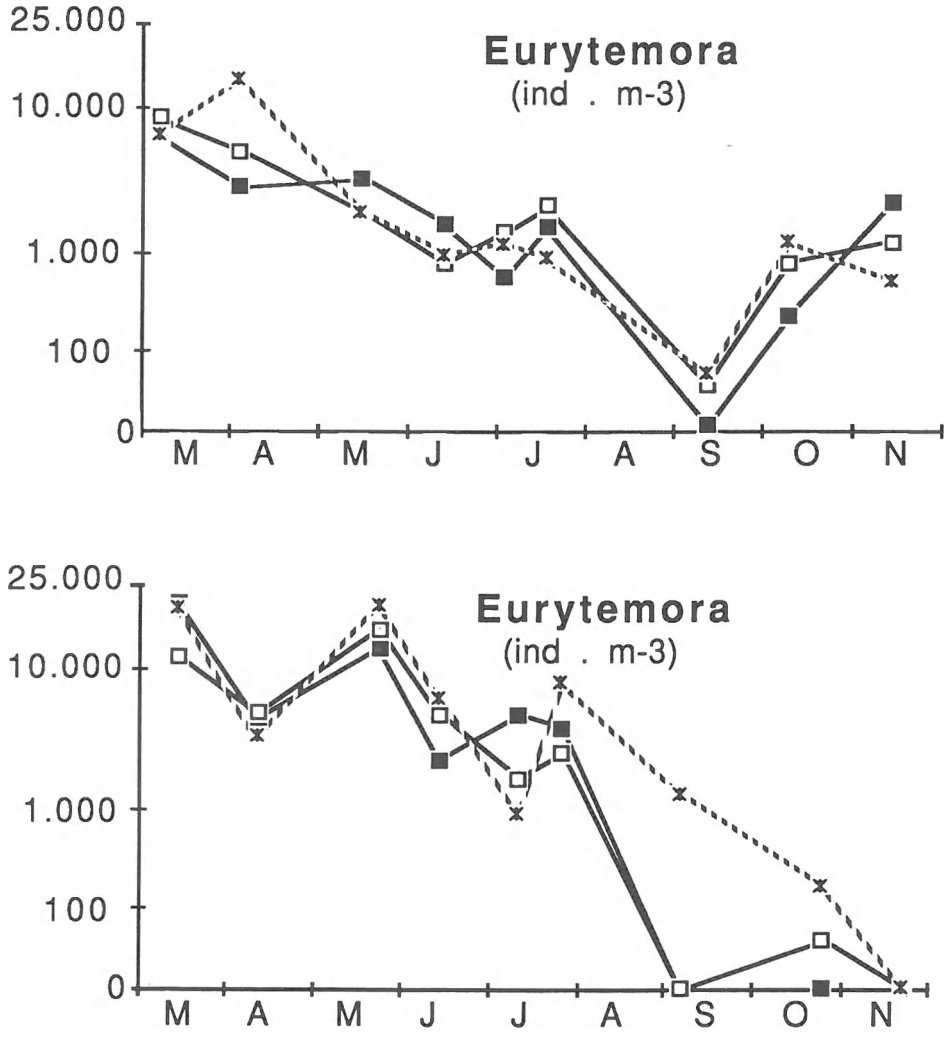

Figure 10: *Eurytemora affinis*. Variations of abundance at stations E (■), J (□) and K (x) of the Gironde estuary in 1990 (upper) and 1991 (lower). Each point represents the mean of ten samples (5 at water surface and 5 near the bottom) over a tidal cycle.

1.2. *Acartia bifilosa*

Acartia bifilosa is the second important species, showing a maximum abundance in summer (Figure 11), i.e. during the period of high salinity. Previous studies have shown that the center of distribution of *Acartia* is situated downstream, in the meso-polyhaline zone for optimum salinity between 15 and 22 ‰ and optimum temperature between 17-22 °C.

No significant difference was observed in mean abundance between both years 1990 and 1991. However low numbers counted in April and May 1991 could be due to the low salinity recorded in this period compared with 1990.

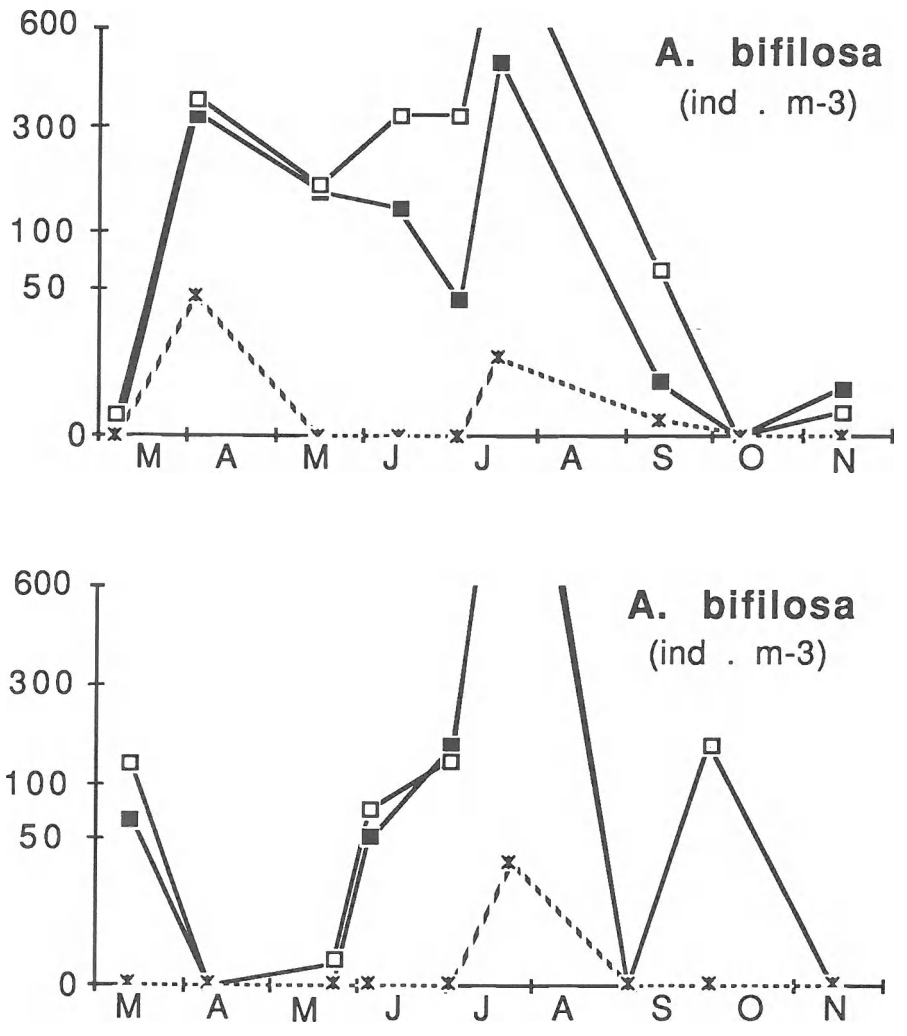

Figure 11: *Acartia bifilosa*. Variations of abundance at stations E (■), J (▫) and K (x) of the Gironde estuary in 1990 (upper) and 1991 (lower). Each point represents the mean of ten samples (5 at water surface and 5 near bottom) over a tidal cycle.

1.3. *Acartia tonsa*

Acartia tonsa which is a polyhaline and thermophilous species was recorded in late summer and early autumn in the study area (Figure 12), when *Eurytemora affinis* and *Acartia bifilosa* were in very small numbers. As for *Acartia bifilosa* the abundance of *A. tonsa* was much lower at the upstream station K than at stations E and J.

On average, no significant difference in abundance could be detected between both years 1990 and 1991.

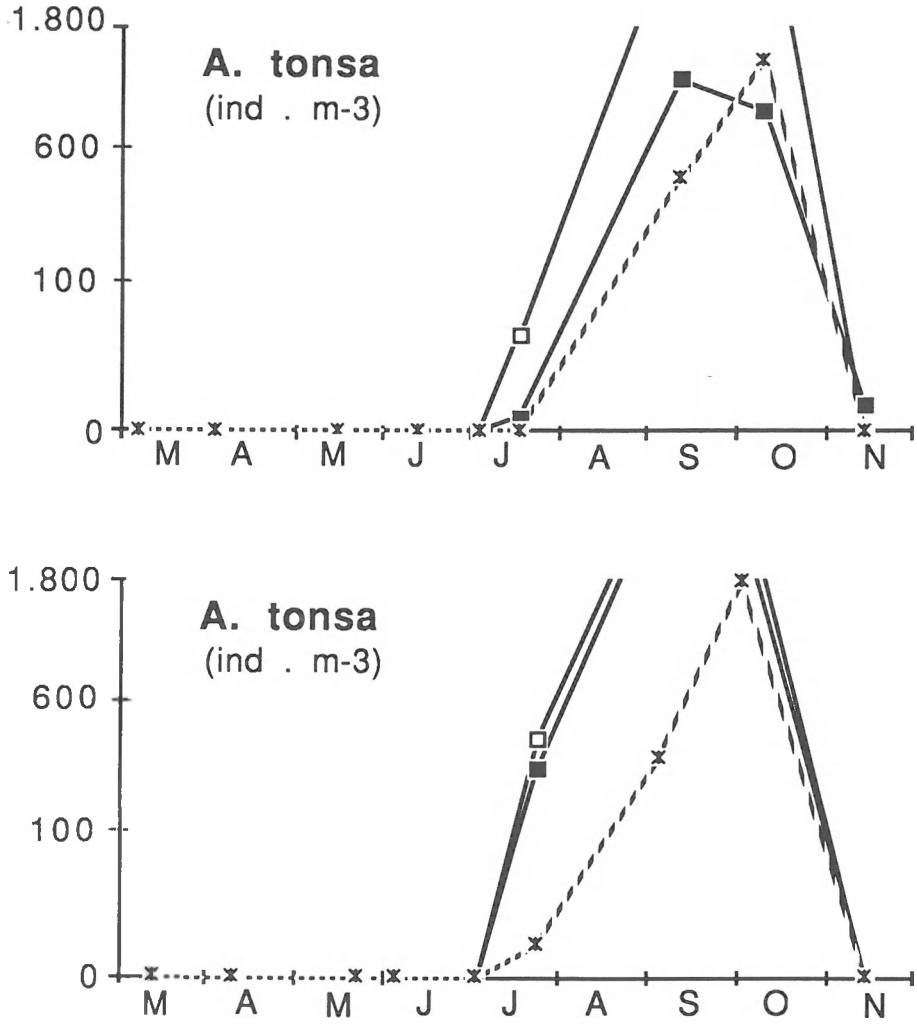

Figure 12: *Acartia tonsa.* Variations of abundance at stations E (■), J (▫) and K (x) of the Gironde estuary in 1990 (upper) and 1991 (lower). Each point represents the mean of ten samples (5 at water surface and 5 near bottom) over a tidal cycle.

3. HYPERBENTHOS

During the zooplankton surveys large numbers of hyperbenthic individuals were caught by the net and were counted. They mainly comprised juveniles of the mysids *Neomysis integer* (Figure 13) and *Mesopodopsis slabberi* (Figure 14). Both species showed a clear separation in time, *Neomysis* being most abundant in May-June or July (Figure 13) and *Mesopodopsis* dominating during the summer period (July-September). They were less abundant at the upstream St. K than at St. E and St. J.

3.1. *Neomysis integer*

On an average, *Neomysis* was slightly more abundant in 1991 than in 1990, probably because of the difference in salinity regime. Previous studies have shown that this species lives mainly in the middle estuary and does not endure high salinity.

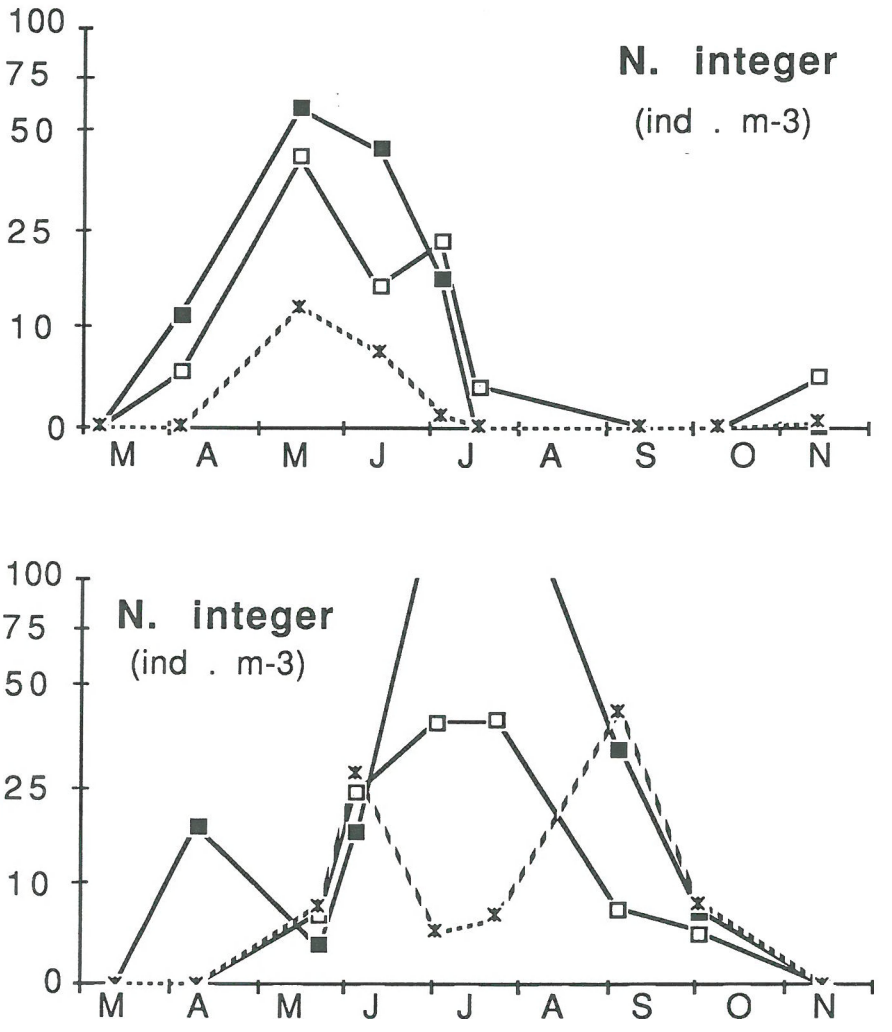

Figure 13: *Neomysis integer*. Variations of abundance at stations E (■), J (□) and K (X) of the Gironde estuary in 1990 (upper) and 1991 (lower). Each point represents the mean of ten samples (5 at water surface and 5 near the bottom) over a tidal cycle.

3.2. *Mesopodopsis slabberi*

It is a polyhaline species living in the same distribution area as *Acartia bifilosa*. The high abundance recorded in 1990 is probably due to relatively high salinities compared with the year 1991.

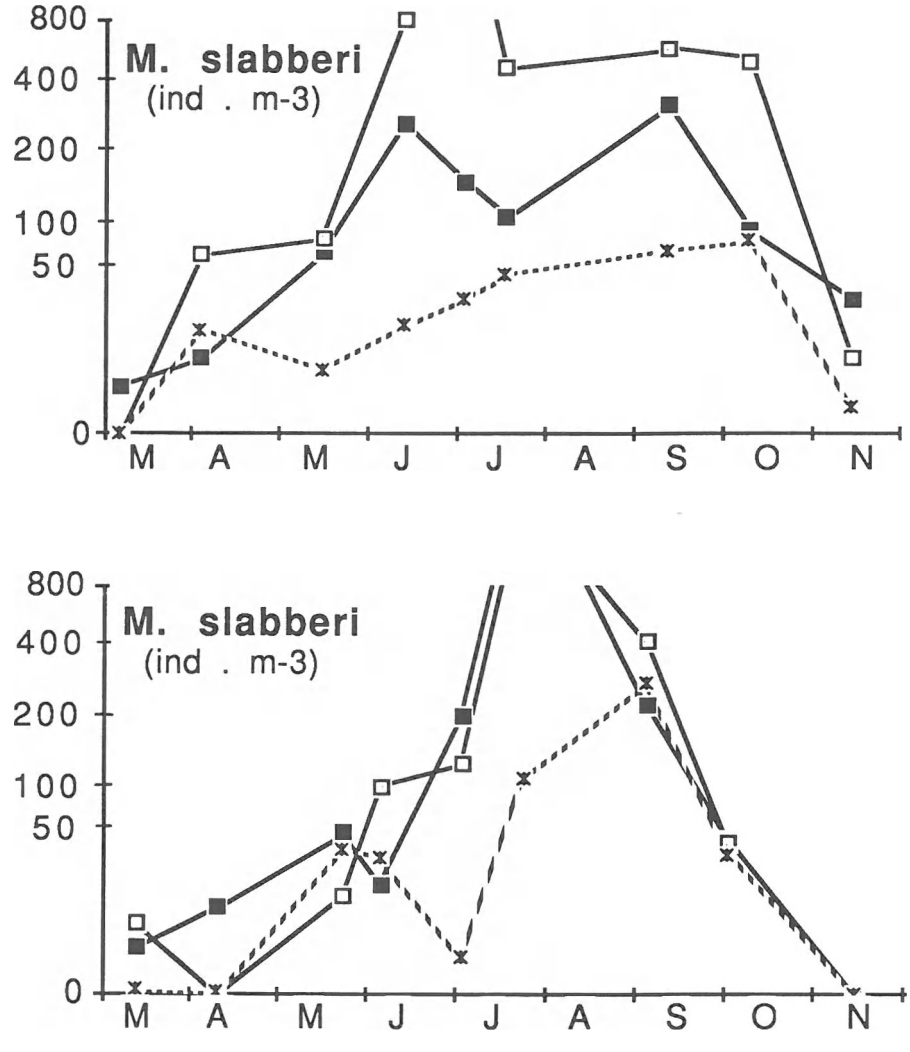

Figure 14: *Mesopodopsis slabberi*. Variations of abundance at stations E (■), J (□) and K (x) of the Gironde estuary in 1990 (upper) and 1991 (lower). Each point represents the mean of ten samples (5 at water surface and 5 near the bottom) over a tidal cycle.

This part of the project has been enlarged during 1991. Jan Mees (Univ. Ghent, Belgium) made an intensive survey in August 1991 in the Gironde. Another campaign is planned by February 1992.

4. BENTHOS

Benthic surveys were undertaken in April 1991 (02/04/91, 15/04/91 and 18/04/91) and in October 1991 (24-25/10/91 and 29/10/91). Only the intertidal zone was sampled since the benthic fauna is very poor in the channels. Six stations were chosen (2 on the right bank and 4 on the left one, see fig. 1). Samples were taken across the tidal area at HTL, MTL and LTL, except for station Plassac where only HTL could be sampled. The following variables were taken into account : silt fraction (< 63µm), organic carbon, chlorophyll, meiobenthos and macrobenthos. All samples were taken and were analysed according to the "Manual on sampling and analytical procedures of tidal estuarine waters" (Kramer K.J.M., Warwick R.M. & Brockmann U., eds). The present results refer to the first campaign.

4.1. Microphytobenthos

The station with greatest marine influence (Le Verdon) presented the highest values for chlorophyll *a* and pheopigments, which decreased from low-water (LW) and mid-water (MW) to high-water (HW) level.(Table 1) A similar pattern, though with lower values, was observed for the second outer station, Richard.

For the inner stations, the values normally decreased from HW to LW level. At these stations the values were low (less than 15 µg chlorophyll equivalent per gram of sediment) except at Lamarque where high values were found.

Active chlorophyll was higher at Le Verdon (all tidal levels) and Lamarque HW with values near 50 %, intermediate at Lamarque MW and LW and Richard LW (mean 37 %) and lower at the other stations (ranging from 20 to 33 %).

Bank	Station	Tidal level	Chlo a (µg/g) ± S.E.	Phéo (µg/g) ± S.E.
LEFT	LE VERDON	HW	14,43 ± 0,76	16,28 ± 1,13
		MW	18,51 ± 1,08	15,01± 2,92
		LW	5,70 ± 1,59	5,24 ± 0,80
	RICHARD	HW	5,03	12,69
		MW	5,09 ± 0,42	15,84 ± 0,37
		LW	5,25 ± 0,12	8,31 ± 1,18
	St ESTEPHE	HW	3,34 ± 0,26	8,58 ± 0,48
		MW	1,29 ± 0,19	4,01 ± 0,06
		LW	1,51 ± 0,12	5,58 ± 0,29
	LAMARQUE	HW	15,03 ± 1,14	10,95 ± 0,43
		MW	2,88 ± 0,10	5,08 ± 0,20
		LW	5,03 ± 0,12	8,37 ± 0,13
RIGHT	CALLONGES	HW	3,89	8,26
		MW	1,21 ± 0,05	4,87 ± 0,30
		LW	1,65 ± 0,25	6,11 ± 0,72
	PLASSAC	MW	1,45 ± 0,42	5,97 ± 0,85

Table 1: Gironde estuary (April 1991). Mean concentrations (± standard error) of chlorophyll and pheopigments.

4.2. Meiofauna

The nematode group dominated over all other taxa with densities ranging from 45 to 2282 ind 10 cm^{-2} for the top 5 cm. A significant difference was observed for the abundance of this group between the top 0-1 cm and the lower 1-5 cm: mean densities were 944 and 267 ind 10 cm^{-2} respectively.

Different patterns of nematode abundance were recorded for each tidal level, according to the station. At Callonges and Lamarque nematode abudance decreased from HW to LW, at Richard the pattern was inverse (LW>MW>HW) and at St Estèphe and Le Verdon the mid-water level presented the highest densities. As a general pattern, the nematode densities decreased from the outer estuary (St Estèphe being the exception with distinct low densities of nematodes and increased abundances of oligochaetes, especially at HW and MW).

Copepods were the second dominant group at most stations (Lamarque being the exception with higher densities of polychaetes and archiannelids). The pattern observed for nematodes between the strata and between the stations was followed by copepods. The differences between the levels were similar for most stations (St Estèphe, Callonges and Lamarque), with MW densities greater than HW, the lowest values being found at low-water level. A quite similar pattern was observed for Le Verdon (HW>MW>LW). The station Richard was very different with higher densities at LW, followed by MW level.

A cluster analysis (Figure 15) was used to distinguish the associations between the different taxa, using as attributes the different location, level, stratum abundances of each taxa. The analysis indicated the existence of two associations :

- a copepod dominated association (copepods, nauplii and others)
- a polychaete dominated association (polychaetes, archiannelids and bivalves), and isolated nematodes and oligochaetes.

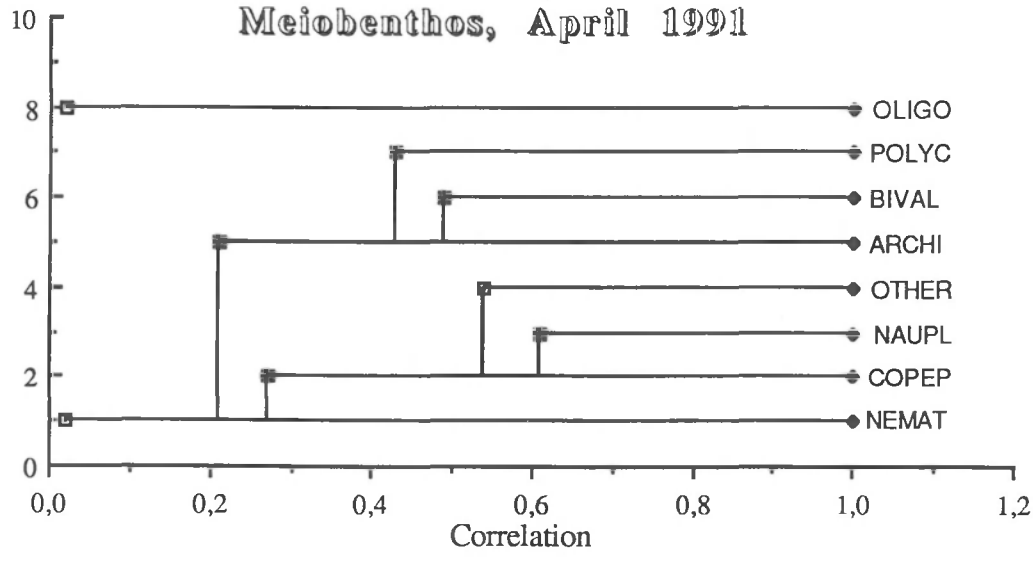

Figure 15: Gironde estuary. Cluster analysis of the dominant meiobenthic taxa from samples taken in April 1991.

4.3. Spatial structure and interactions

The interaction between the dominant meiofaunal taxa (nematodes and copepods) and the microphytobenthos (expressed by the variables chlorophyll *a*, pheopigments and active chlorophyll) was analyzed by means of a correlation analysis. A significant positive correlation was observed between nematode abundance and the chlorophyll *a* and pheopigments values. For copepods no significant correlation was found with the phytobenthos, although a significant positive correlation was found between copepods and nematodes. A detailed analysis for each level showed that the significant correlation between nematodes and microphybenthos occurred only at mid-water level, while the correlation between nematodes and copepods was significant only at the other levels.

The distribution of the nematode to copepod ratio (herein N/C ratio) for the different stations and levels (Figure 16) showed an interesting pattern with higher values at the most extreme stations along the salinity gradient (Le Verdon and Lamarque). Considering all stations, the N/C ratio presented a significant positive correlation with the active chlorophyll. Without the stations Le Verdon and Lamarque (which presented the highest values for both variables) the relation disappeared.

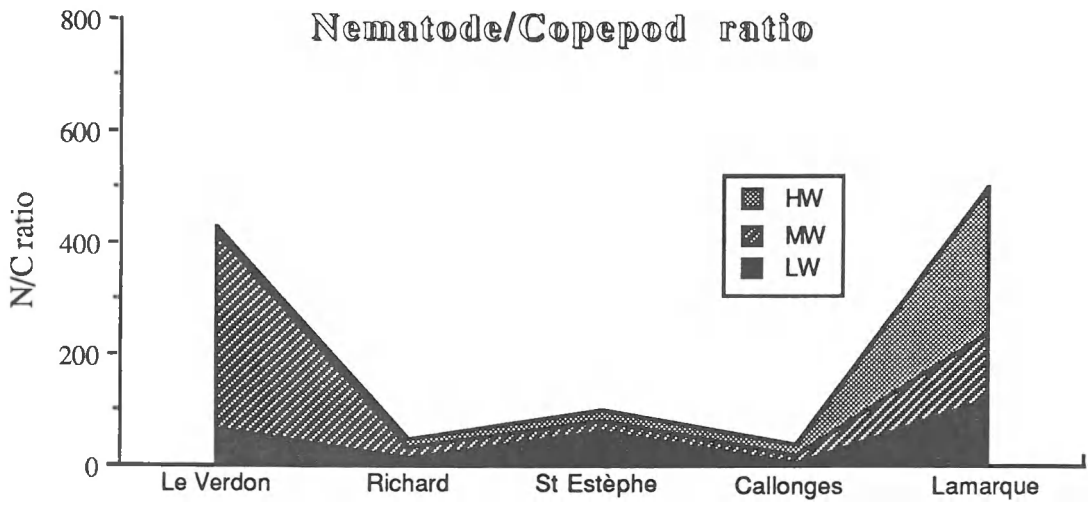

Figure 16: Gironde estuary. Evolution of the Nematode/copepod ratio in April 1991.

The classification of the stations using a cluster analysis and taking as attributes the density of the different taxa, showed the existence of 3 groups. A first one formed by the stations with high marine influence (Le Verdon and Richard) and characterized by the high-water, and two complementary groups that distinguish the top 0-1 cm from the lower 1-5 cm samples. Le Verdon and Richard stations being excluded, four groups were separated. Two groups corresponded to the two different strata, a third one was formed by St Estèphe 0-1cm

LW and MW, and a fourth group with the samples from St Estèphe HW (0-1 and 1-5 cm). This classification differentiated St Estèphe as a separate entity in the inner estuary.

A correspondence factor analysis using as attributes chlorophyll *a*, pheopigments, nematode and copepod values, showed as principal organizing factor the N/C ratio (as expressed by the first and second axes representing respectively 57.1 and 38.3 % of the total variability). Active chlorophyll was a complementary factor (axes 1 and 3, the latter representing only 4.5 % of the total variance).

A discriminant analysis was used to evaluate the significance of these factors in the separation of the station groups, taking as explicative variables the log of N/C ratio and the active chlorophyll. The analysis preserved the originally given groups (Figure 17) with significance levels <<0.01 for the derivate functions. Group 1 formed by samples with both high quantity of active chlorophyll and high N/C ratio, is composed by the stations situated at the extremity of the salinity gradient: Le Verdon and Lamarque. Group 2 formed by only two samples (St Estèphe LW and Plassac MW) is characterized by moderate values of the N/C ratio and low active chlorophyll. The third group (3) also formed by only two samples (Le Verdon HW and Richard LW) presents high value of active chlorophyll and a low N/C ratio (mainly due to high abundance of copepods). The last group (4) is formed by all Callonges samples, and St Estèphe and Richard HW + MW; it is characterized by low values of both active chlorophyll and N/C ratio.

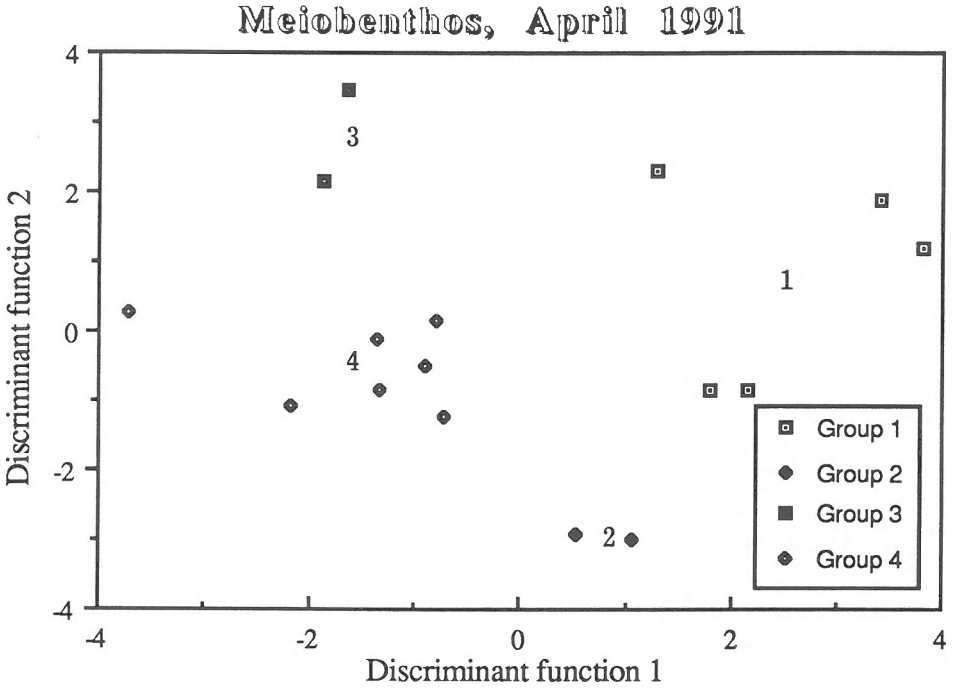

Figure 17: Gironde estuary. Discriminant analysis of the samples taken in April 1991.

Unstandardized Discriminant Function Coefficients

	1	2
log N/C	3.67129	-2.50139
active chlorophyll	0.56806	17.3284
CONSTANT	-5.76144	-2.09424

GROUPS	1	2	3	4
COUNTS	5	2	2	7
MEANS				
log N/C	2.18589	1.74792	1.03091	1.11154
active chlorophyll	0.47779	0.20420	0.42852	0.25464
STD DEVIATIONS				
log N/C	0.29012	0.9847	0.03051	0.29024
active chlorophyll	0.10185	0.01242	0.05849	0.04266

Table 2: Discriminant analysis of benthic data (explanation in the text).

4.4. Macrobenthos

Highest mean abundances were recorded at the outer stations Le Verdon and Richard. These stations also showed highest number of species (Table 3 and 4). At Le Verdon the fauna was dominated by *Streblospio, Heteromastus, Hydrobia* and Oligochaets. Both abundance and diversity were highest at HTL. The patterns of abundance and distribution of the species were different at Richard. The most abundant species were *Streblospio, Tharyx, Corophium, Hydrobia* and Oligochaets. *Streblospio, Tharyx* and *Hydrobia* were found in greatest abundance at LTL, contrary to the observations made at Le Verdon, whereas *Corophium* and Oligochaets were found mainly at HTL.

Species	HTL	MTL	LTL
Oligochaets	1144 ± 713	90 ± 90	30 ± 30
Eteone sp	30 ± 30		
Heteromastus filiformis	2199 ± 719	211 ± 58	60 ± 35
Nephtys hombergii	211 ± 103	331 ± 134	271 ± 58
Nereis diversicolor	602 ± 523		
Pygospio elegans	512 ± 316	1476 ± 376	90 ± 58
Streblospio shrubsolii	4548 ± 1122	1054 ± 395	60 ± 35
Tharyx marioni	30 ± 30		
Hydrobia ulvae	1596 ± 651	452 ± 301	181 ± 78
Abra tenuis	30 ± 30	30 ± 30	
Macoma balthica	151 ± 76	90 ± 58	30 ± 30
Scrobicularia plana	301 ± 143	60 ± 60	
Corophium volutator	30 ± 30		30 ± 30
Cyathura carinata	121 ± 49		
Insects (larvae)	30 ± 30		90 ± 90

Table 3: Le Verdon, April 1991. Mean abundance (ind. m^{-2}) ± S.E. of macrobenthic taxa.

Species	HTL	MTL	LTL
Oligochaets	975 ± 656	94 ± 39	6 ± 6
Capitella capitata	6 ± 6		
Heteromastus filiformis		6 ± 6	138 ± 63
Manayunkia aestuarina	31 ± 12	6 ± 6	
Neanthes succinea	419 ± 295	288 ± 135	31 ± 12
Nephtys hombergii		38 ± 16	150 ± 35
Pseudopolydora pulchra		12 ± 7	244 ± 66
Pygospio elegans	25 ± 14	6 ± 6	94 ± 21
Streblospio shrubsolii	6150 ± 5625	8900 ± 1957	8781 ± 1164
Tharyx marioni	31 ± 6	775 ± 220	7000 ± 322
Hydrobia ulvae	638 ± 491	875 ± 414	4088 ± 596
Abra tenuis	25 ± 10	13 ± 7	163 ± 38
Macoma balthica	13 ± 13	31 ± 12	300 ± 20
Scrobicularia plana		6 ± 6	44 ± 6
Corophium volutator	5450 ± 1150	950 ± 356	250 ± 51
Cyathura carinata	31 ± 16		163 ± 30
Insects (larvae)	31 ± 12		

Table 4: Richard, April 1991. Mean abundance (ind. m^{-2}) ± S.E. of macrobenthic taxa.

At stations St Estèphe and Callonges, situated at the same distance from the inlet (see Figure 1), the dominant taxa were Oligochaets and *Nereis* (Tables 5 and 7). Oligochaets were most abundant at the lower tidal level (MTL and LTL) whereas *Nereis* was distributed at the upper levels (HTL and MTL). The partitioning between both taxa was clearer at Callonges than at St Estèphe.

Species	HTL	MTL	LTL
Oligochaets	450 ± 57	3125 ± 325	1869 ± 683
Nereis diversicolor	1413 ± 211	1338 ± 63	94 ± 26
Streblospio shrubsolii	25 ± 10	213 ± 38	244 ± 131
Tharyx marioni	6 ± 6		
Hydrobia ulvae	13 ± 13		
Corophium volutator	25 ± 18	38 ± 13	6 ± 6
Cythura carinata		50 ± 25	19 ± 6
Insects (larvae)	6 ± 6		6 ± 6

Table 5: St Estèphe, April 1991. Mean abundance (ind. m^{-2}) ± S.E. of macrobenthic taxa.

The fauna was very poor at Lamarque and Plassac, the most oligohaline stations (Tables 6 and 8). At Lamarque, Insect larvae were most abundant at HTL and Oligochaets dominated at MTL.

Species	HTL	MTL	LTL
Oligochaets spX	6 ± 6	838 ± 104	81 ± 33
Oligochaets spL	2775 ± 1263	5588 ± 469	244 ± 41
Nereis diversicolor	6 ± 6		
Streblospio shubsolii	6 ± 6		6 ± 6
Insects (larvae)	531 ± 167	38 ± 13	

Table 6: Lamarque, April 1991. Mean abundance (ind. m^{-2}) ± S.E. of macrobenthic taxa.

Species	HTL	MTL	LTL
Oligochaets spA	175 ± 45	956 ± 187	
Oligochaets spX			106 ± 47
Oligochaets spY			8975 ± 2071
Nereis diversicolor	325 ± 53	13 ± 7	25 ± 18
Streblospio shrubsolii	44 ± 44	50 ± 23	13 ± 13
Hydrobia ulvae		19 ± 12	
Macoma balthica			6 ± 6
Corophium volutator	13 ± 7	19 ± 6	6 ± 6
Cyathura carinata	6 ± 6	13 ± 7	

Table 7: Callonges, April 1991. Mean abundance (ind. m^{-2}) ± S.E. of macrobenthic taxa.

Species	HTL	MTL	LTL
Oligochaets spL	181 ± 26		
Oligochaets sp X	19 ± 12		
Nereis diversicolor	31 ± 6		
Streblospio shubsolii	63 ± 47		
Tharyx marioni	13 ± 13		
Cyathura carinata	6 ± 6		
Insects (larvae)	6 ± 6		

Table 8: Plassac, April 1991. Mean abundance (ind. m^{-2}) ± S.E. of macrobenthic taxa.

In terms of biomass (Figure 18) a strong decreasing gradient was found from the marine polyhaline zone to the upper estuary. Generally, highest biomass was recorded at HTL, then at MTL and at LTL. The station Richard was an exception, with lowest biomass at MTL.

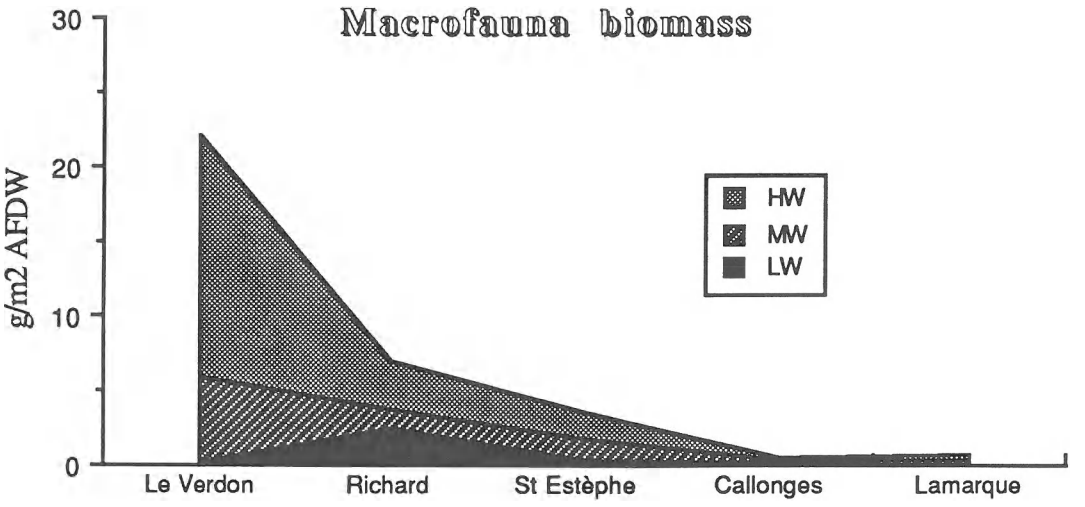

Figure 18: Gironde estuary, April 1991. Mean biomass (g m-2 AFDW) of macrobenthos for each tidal level.

PART II

MAJOR BIOLOGICAL PROCESS STUDIES: BIOLOGY OF THE WATER COLUMN.

This part of the programme is specifically related to the JEEP 92-MAST Project.

Participants:

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1. INTENSIVE FIELD MEASUREMENTS

In May 1990 two sampling stations (see figure 1) were studied during 24 h: station J in the oligohaline zone where *Eurytemora affinis* lives , and station A in the mesohaline zone where *Acartia bifilosa* is dominant. In October 1990 (low river flow) and March 1991 (high river flow), only the station J was investigated during 48 h. In April 1991 station A was studied during 48 h. A number of stations were studied during 14h in July and October 1991 but the results are not presented here.

During each survey, the following variables were measured every 2 hour (surface and near bottom): temperature, salinity, suspended matter, chlorophyll, gut fluorescence of copepods. Additional samples were taken for zooplankton abundance and biomass. Furthermore, in April 1991, incubations of copepods were made onboard using two methodologies: ^{14}C labelled algae and gut fluorescence (Brussel and Arcachon teams). Results are presented separately.

1.1. Water column

Whatever the stations or the period of the year, the tidal cycle of salinity is always strongly pronounced (Figures 19-24). The difference in salinity between high tide and low tide generally exceeded 5 ‰ and could reach 10 ‰ (April 1991, Figure 23). The waters were not highly stratified: the difference between surface and bottom water was generally less than 2 ‰ (see §1.1, Part I).

The concentration of suspended particulate matter (SPM) although variable, was generally high (up to several grammes per litre) especially in the turbidity maximum zone. During the tidal cycle, maximum SPM concentrations were found at low tide (Figures 19, 21, 23) indicating that most of the suspended sediment originated from the upper reach of the estuary. Two series of measurements made along the estuary in August and October 1991 indicated that the turbidity maximum was situated in the upstream part of the Gironde,

65-70 km from the inlet (Figures 25-26). It has been demonstrated that, in period of high river flow, the turbidity maximum migrates downstream and can be observed near the inlet.

The turbidity cloud is composed of fine material. The mean diameter of the particles is between 4 and 9 µm. The Figures 27-28 represent the extreme situations encountered during the study period. More than 50 % of the particles have a diameter between 1.5 and 5.5 µm, the maximum frequency being recorded for the size class 1.5-2.5 µm. During a tidal cycle the mean diameter of the particles followed the variation of SPM concentration (Figures 29-30). This means that SPM concentration, here measured as the weight of all particles per liter, is a function of both particle number and particle size. As highest SPM concentrations were observed at low tide, biggest particles will be found also at low tide.

The chlorophyll concentration is strongly linked to SPM, showing maxima at low tide (example given in Figure 21). Conversely the percentage of chlorophyll *a* (relative to total pigments) is very low at low tide and increases significantly at high tide (not shown). These observations indicated that the autochthonous primary production is weak; most of the pigments are imported from the upper reaches of the estuary and are degraded in the zone of high SPM concentration.

On average, there was a good correlation between pheopigments and SPM concentrations (Table 9) indicating the detrital nature of the pigments found in the turbidity cloud. Chlorophyll *a* was also correlated with SPM concentrations except during periods of blooms. Such exceptions were noted in July and August 1991 at the outer stations where huge quantities of (undetermined) diatoms were observed. From a practical point of view the correlation between chlorophyll and SPM concentrations could be used to determine the limit between the inner estuarine system and the zone submitted to marine influence.

DATE	point	chl-SPM	r	pheo-SPM	r
MAY 90	A	y=1.87x+2.51	0.84	y=2.21x-0.61	0.96
MAY 90	J	y=2.25x+1.19	0.96	y=2.23x-0.16	0.96
OCTOBER 90	J	y=0.98x+1.01	0.93	y=2.99x+0.22	0.98
MARCH 91	J	y=0.77x+0.23	0.89	y=4.09x+1.31	0.95
APRIL 91	A	y=1.41x+0.30	0.79	y=3.53x+0.10	0.90
JULY 91	PK72	y=-0.23x+2.97	**-0.03**	y=3.38x-0.01	0.91
JULY 91	PK65	y=-3.56x+3.33	**-0.33**	y=3.98x-0.08	0.94
JULY 91	PK40	y=1.48x+0.75	0.92	y=4.10x-0.05	0.97
AUGUST 91	Transect	y=-3.63x+6.90	**-0.37**	y=4.10x+0.58	0.90
OCTOBER 91	PK50	y=0.76x+1.79	0.74	y=2.33x+0.28	0.95
OCTOBER 91	PK72	y=3.36x+0.91	0.92	y=2.31x+0.35	0.85
OCTOBER 91	Transect	y=1.39x+1.07	0.73	y=3.53x-0.33	0.97

Table 9: Correlation between chlorophyll *a* and SPM concentrations, and between pheopigments and SPM concentration in the Gironde estuary. Stations A and J are indicated on Figure 1. The other stations are defined by their distance (in km) downstream from the city of Bordeaux. Transect = stations covering the whole salinity gradient.

Although chlorophyll *a* and SPM concentrations were generally correlated, their ratio varied in large proportion. In general the ratio chl *a* / SPM increased with salinity (Figures 20, 22, 24) indicating that (living) chlorophyll had mainly a marine origin.

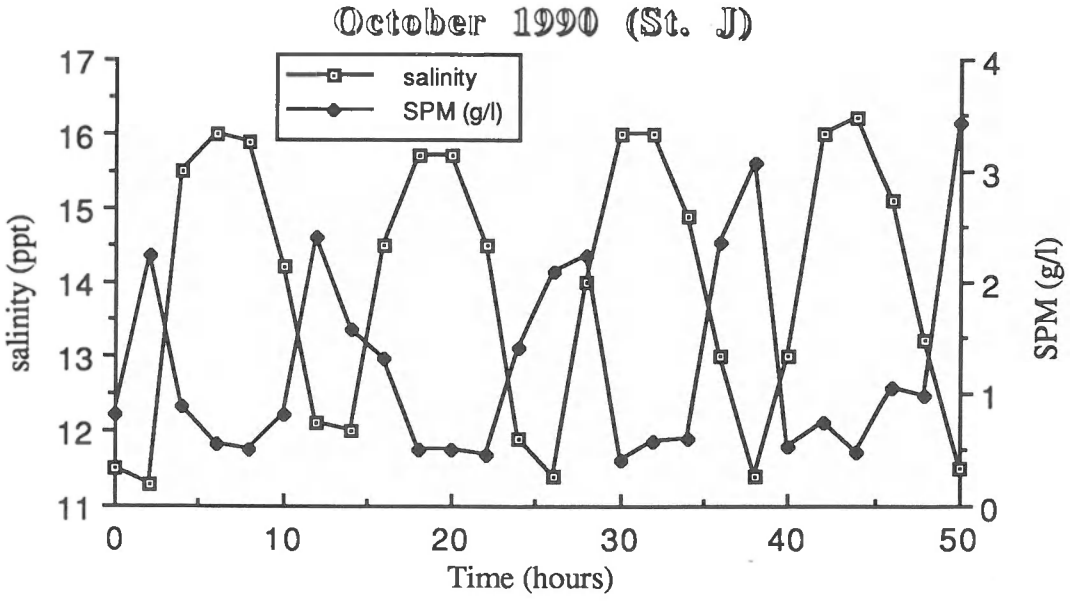


Figure 19: Gironde estuary. Variation of salinity and SPM concentration during a 48h period.

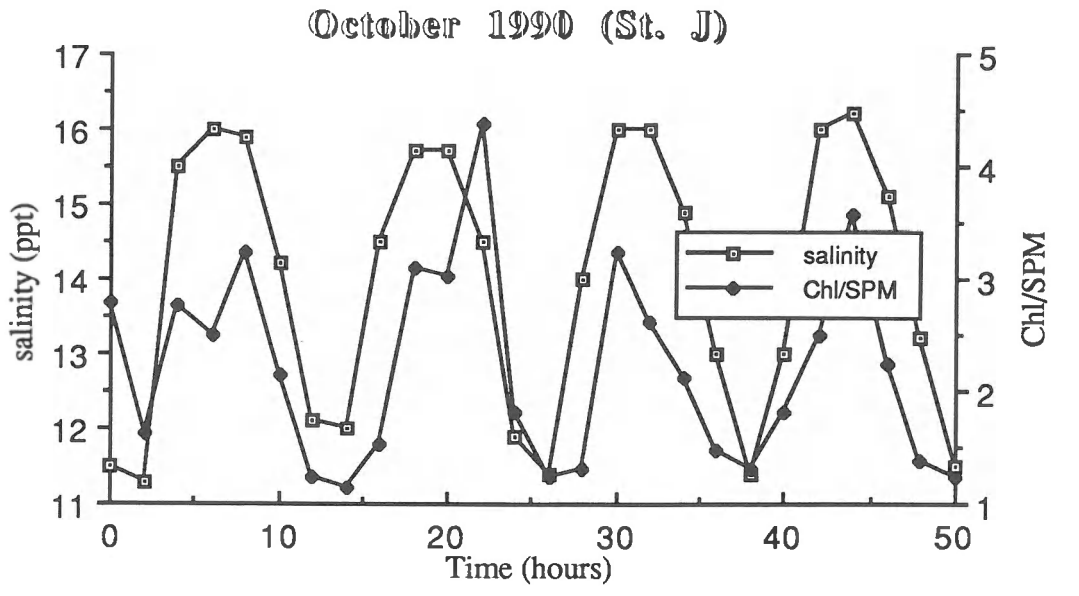


Figure 20: Gironde estuary. Variation of salinity and Chlorophyll/SPM ratio during a 48 h period.

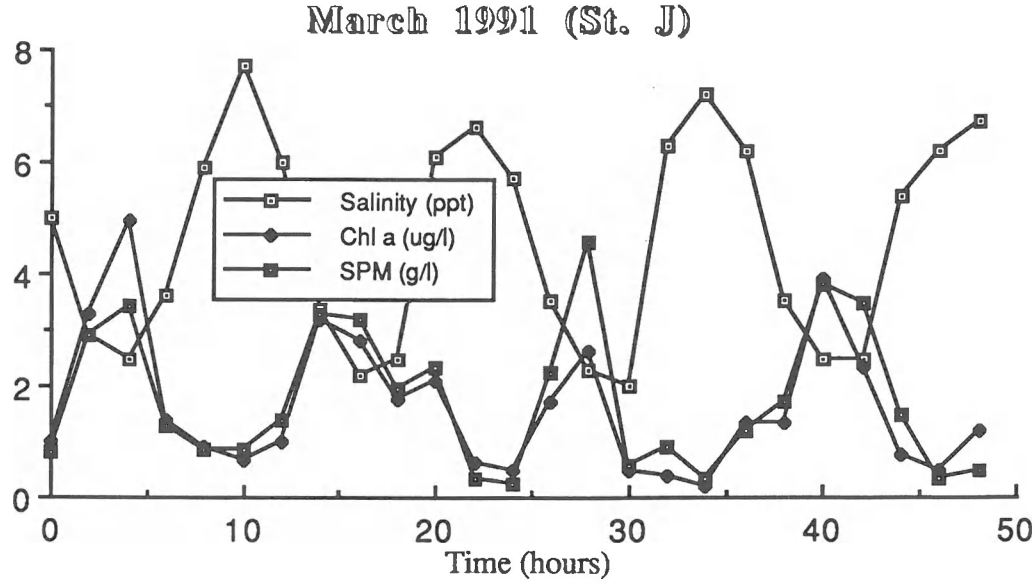


Figure 21: Gironde estuary. Variation of salinity, Chlorophyll *a* and SPM concentrations during a 48h period.

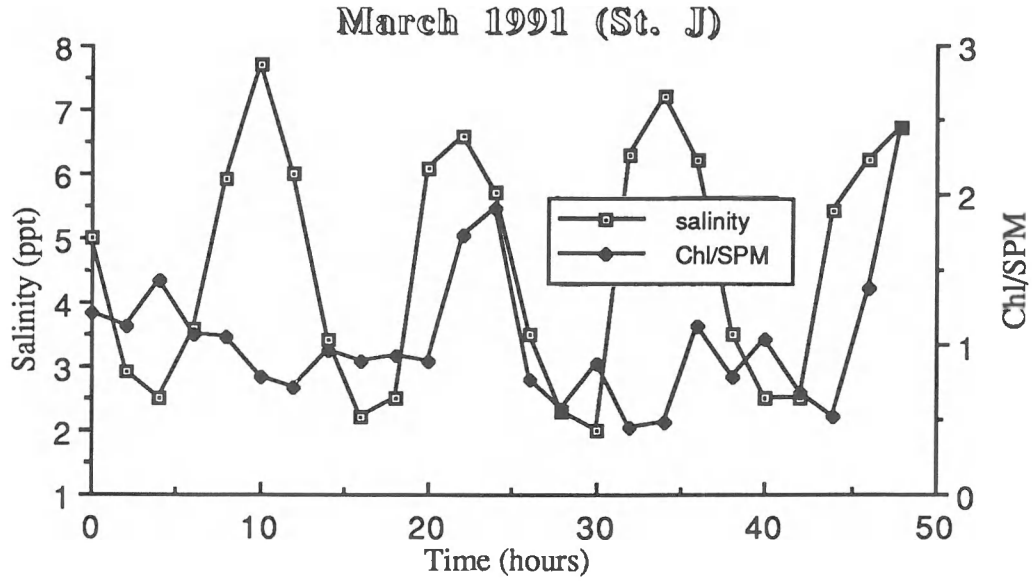


Figure 22: Gironde estuary. Variation of salinity and Chlorophyll / SPM ratio during a 48h period.

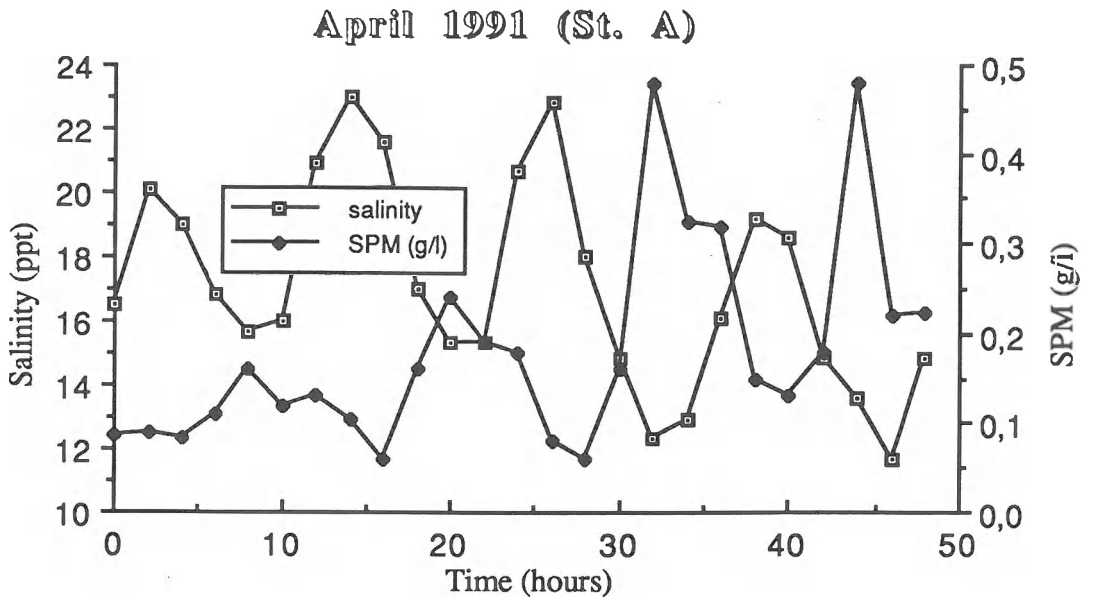


Figure 23: Gironde estuary. Variation of salinity and SPM concentration during a 48h period.

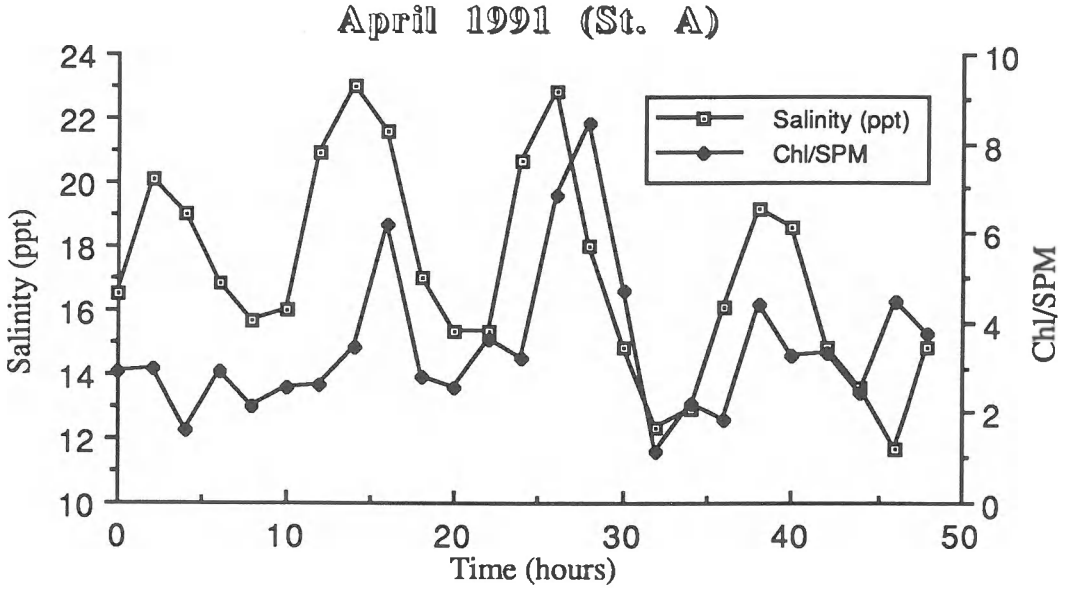


Figure 24: Gironde estuary. Variation of salinity and Chlorophyll/SPM ratio during a 48h period.

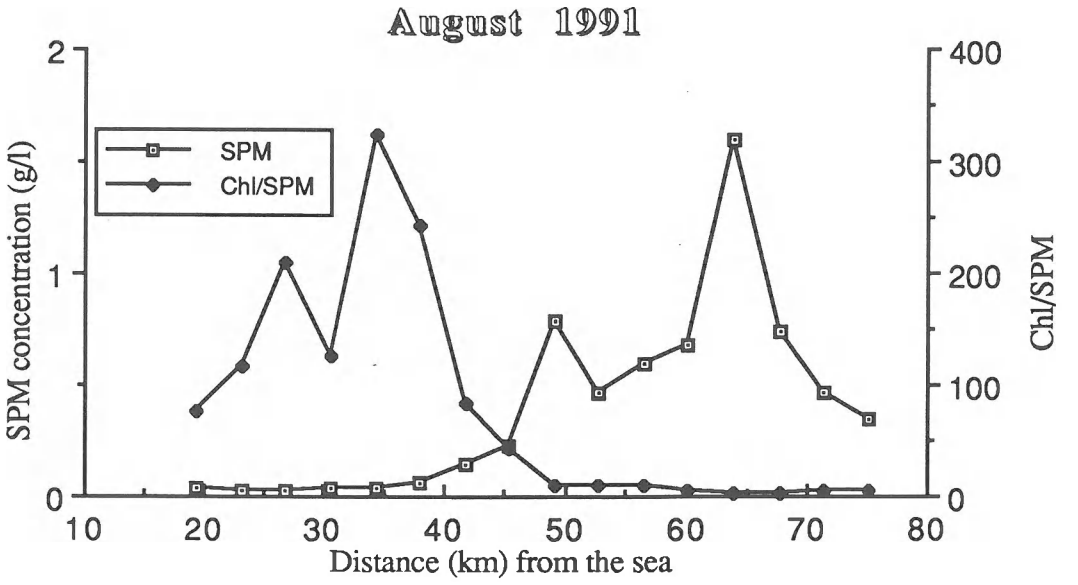


Figure 25: Evolution of SPM concentration and chlorophyll/SPM ratio along the Gironde estuary. Samples were taken every 2 nautic mile at ebb tide.

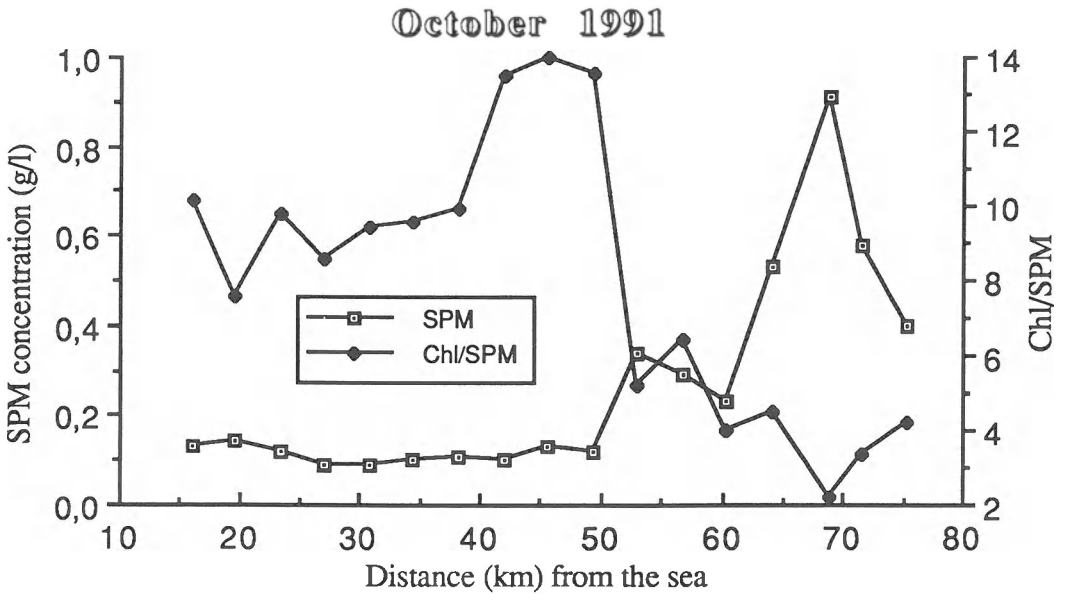


Figure 26: Evolution of SPM concentration and chlorophyll/SPM ratio along the Gironde estuary. Samples were taken every 2 nautic mile at flood tide.

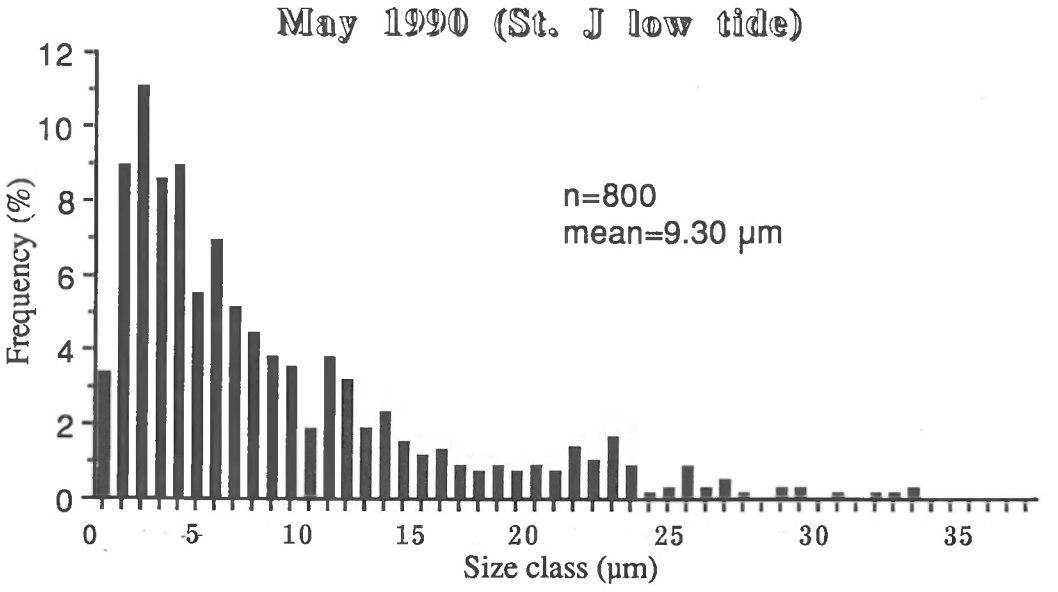


Figure 27: Gironde estuary. Example of size frequency distribution of suspended particles ("coarse particles").

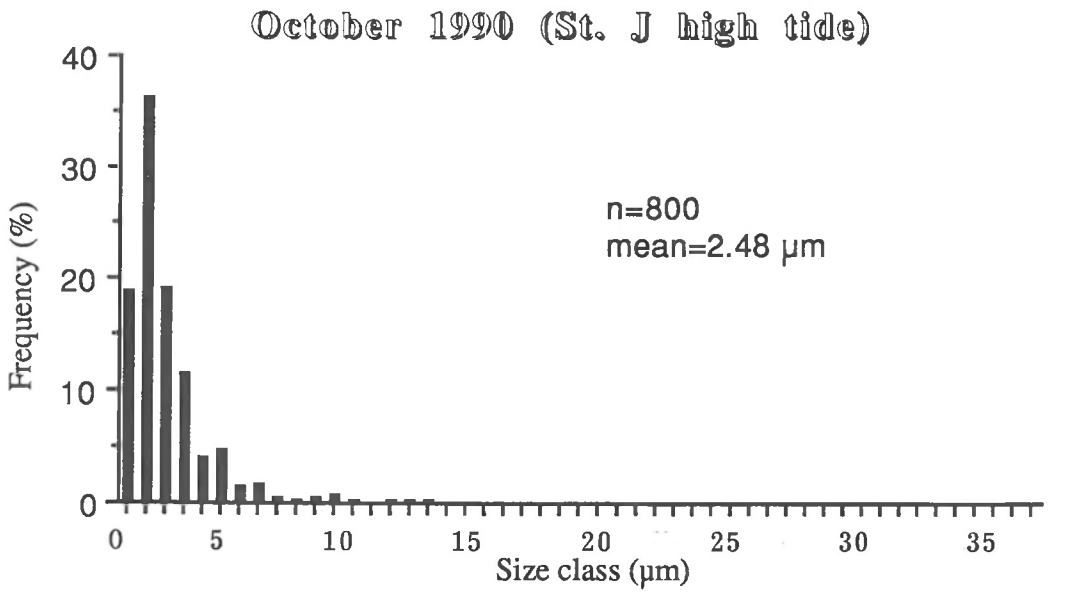


Figure 28: Gironde estuary. Example of size frequency distribution of suspended particles ("fine particles").

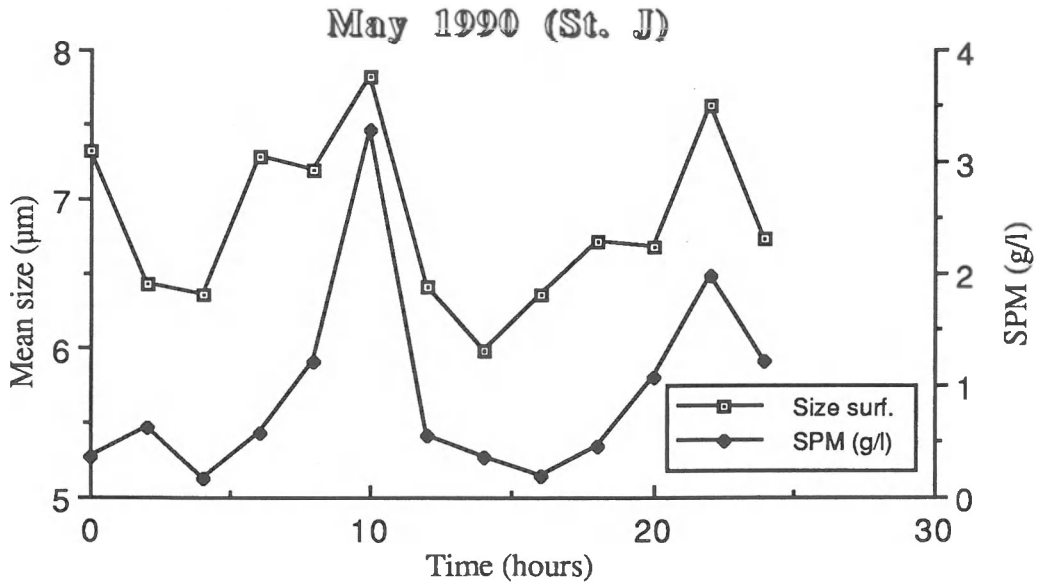


Figure 29: Gironde estuary. Variation of the mean size of suspended particles and SPM concentration during a 24h period (water surface).

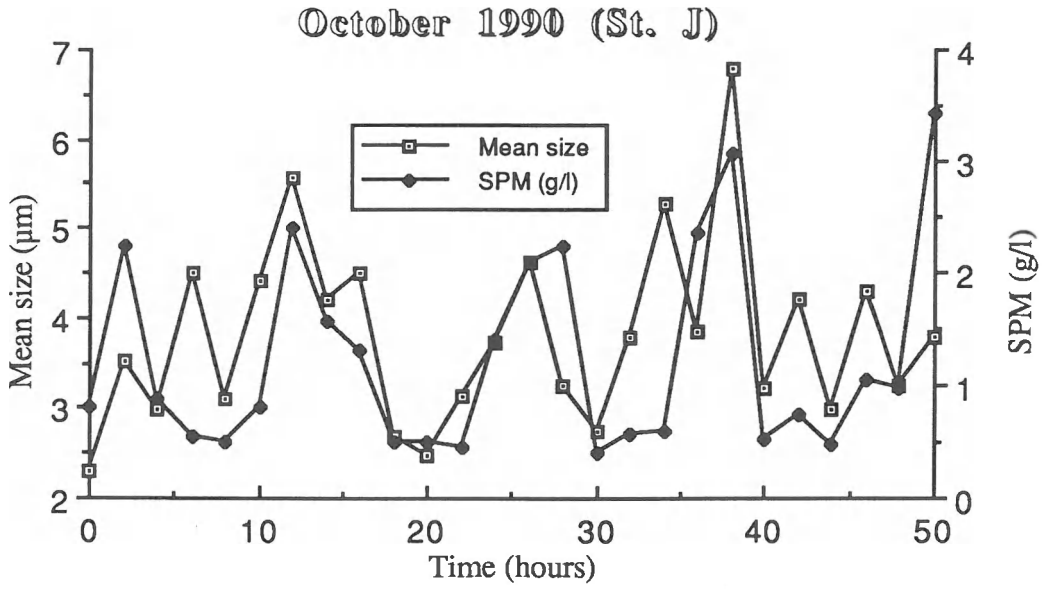


Figure 30: Gironde estuary. Variation of the mean size of suspended particles and SPM concentration during a 48h period (water surface).

1.2.Grazing activity of zooplankton

One purpose of the study was to determine the possibility to put in evidence some rhythms of nutrition of the copepods. Two basic rhythms may occur : one due to the tidal cycle, on the one hand, and the second due to the day-night cycle on the other hand. Only one aspect of the nutrition was taken into account : the quantity of chlorophyll by copepod as measured by fluorometry.

May 1990

No significant cyclic variation was found for *Eurytemora* (Figure 31). In contrast, for *Acartia*, a more obvious cycle was observed (Figure 32) but it was not strongly linked to the tidal phase. The peaks were correlated with the percentages of active chlorophyll *a*.. These observations suggest that *Acartia* prefers a less detritic food source than *Eurytemora*.

No correlation was found between gut fluorescence and concentration of chlorophyll in the water. However, a positive correlation existed between gut fluorescence of both species and the ratio total pigments / suspended particulate matter, at least for *Eurytemora* (Figure 33). This indicates that the copepods ingest particles of adequate size, without discrimination.

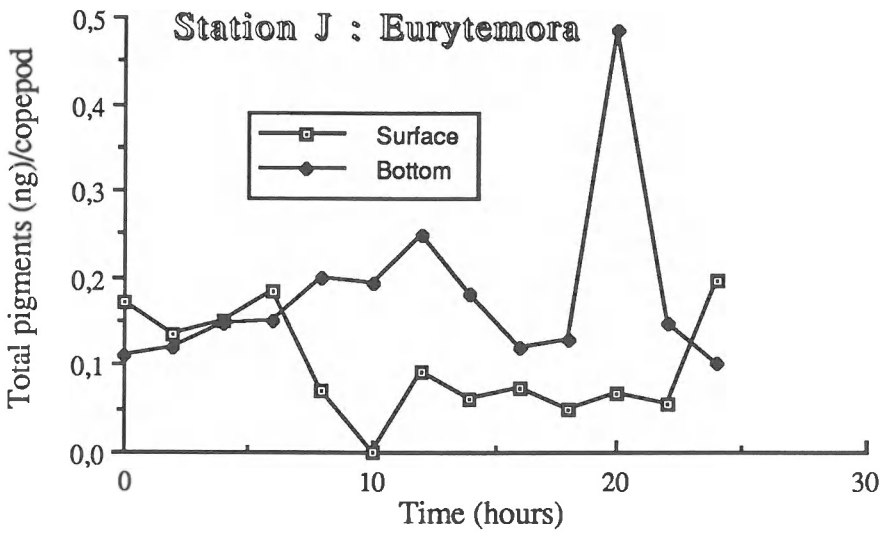


Figure 31: *Eurytemora affinis*. Gut fluorescence analysis from Gironde estuary population (May 1990).

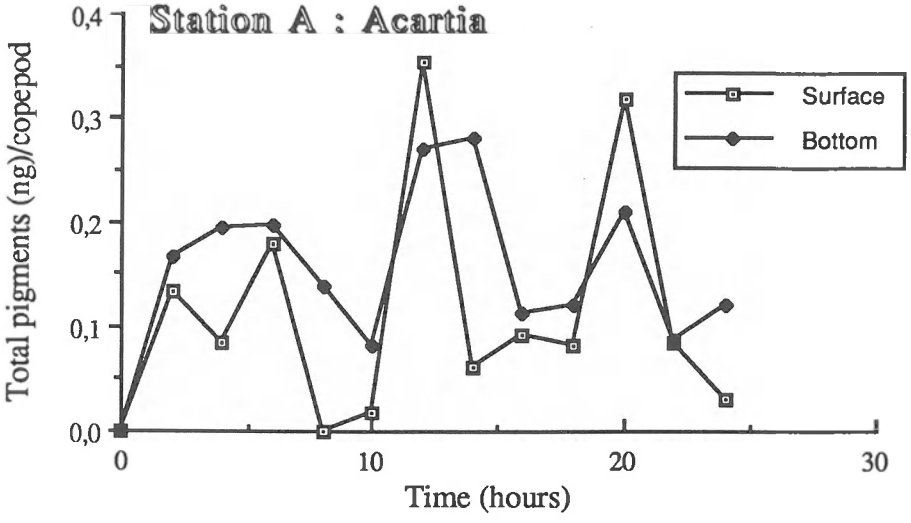


Figure 32: *Acartia bifilosa*. Gut fluorescence analysis from Gironde estuary population (May 1990).

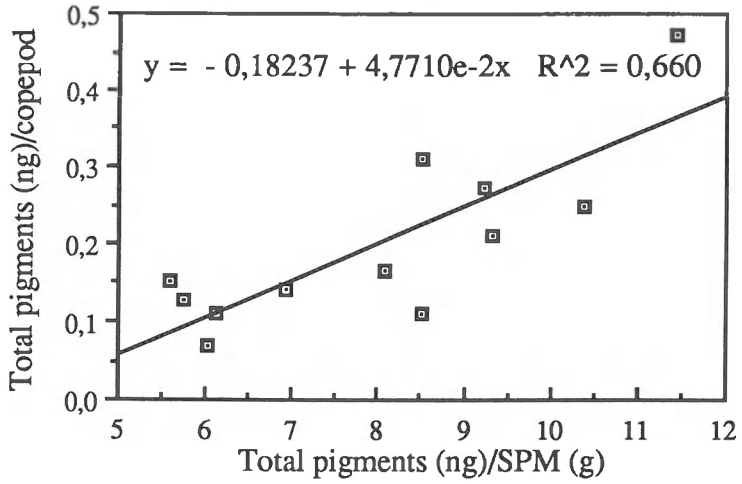


Figure 33: Correlation between gut fluorescence of *Eurytemora affinis* and the potential nutritional values of suspended matter.

October 1990

As in May 1990, *Eurytemora* did not show a clear cycle of feeding activity (Figure 34). Several peaks of gut fluorescence corresponded to an increase of the chlorophyll/SPM ratio, but the overall correlation between both variables was weak.

In contrast, *Acartia tonsa* showed a clear rhythm of feeding activity (expressed as gut content) which was related to the chlorophyll/SPM ratio (Figure 35).

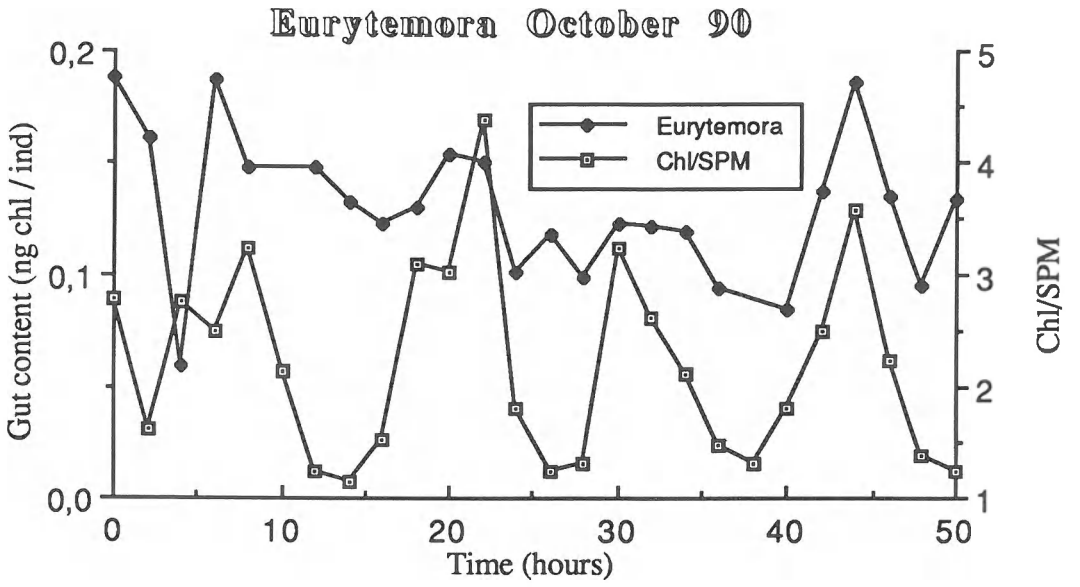


Figure 34: *Eurytemora affinis*. Gut fluorescence analysis and chlorophyll/SPM ratio in the water during a 48h period (station J, water surface).

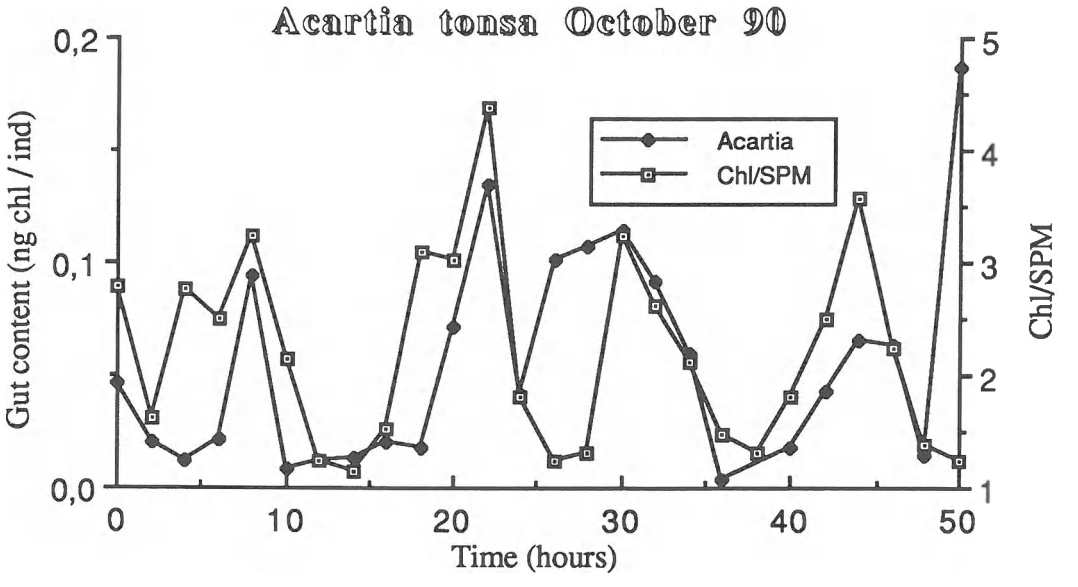


Figure 35: *Acartia tonsa*. Gut fluorescence analysis and chlorophyll/SPM ratio in the water during a 48h period (station J, water surface).

March-April 1991

In March 1991 a cyclic pattern of gut fluorescence was found for *Eurytemora* with a maximum every 12h (i.e. at low tide). This corresponded to cyclic variations of chlorophyll *a* (Figure 36). The variation of gut fluorescence seemed independent from that of chlorophyll/SPM ratio (Figure 37). For *Acartia bifilosa*, sampled in April 1991, no feeding pattern was observed (Figure 38). The gut fluorescence variation was independent from both chlorophyll concentration and chlorophyll/SPM ratio (Figure 39).

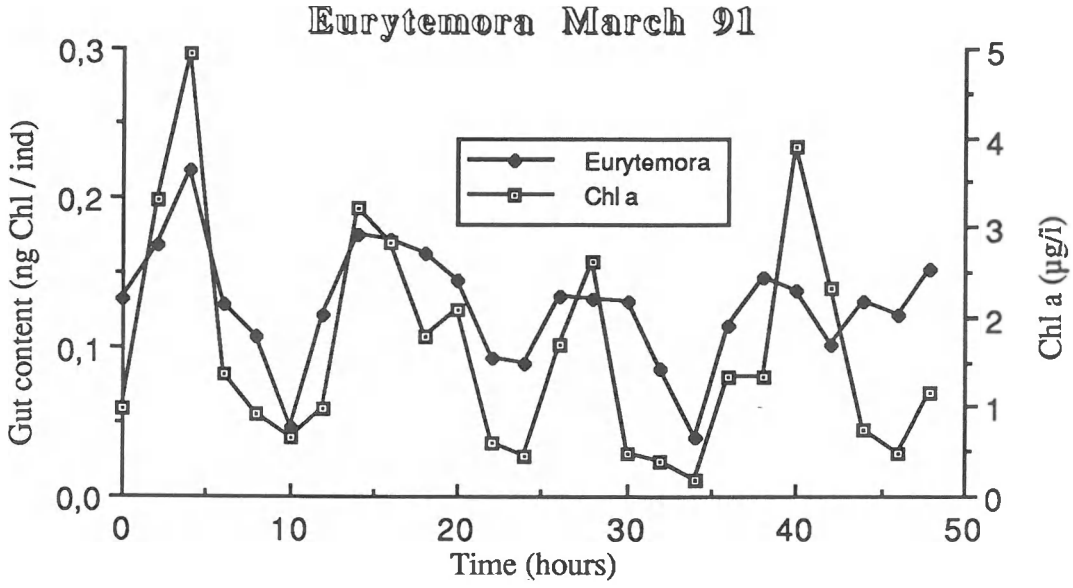


Figure 36: *Eurytemora affinis*. Gut fluorescence analysis and chlorophyll *a* concentration in the water during a 48h period (station J, water surface).

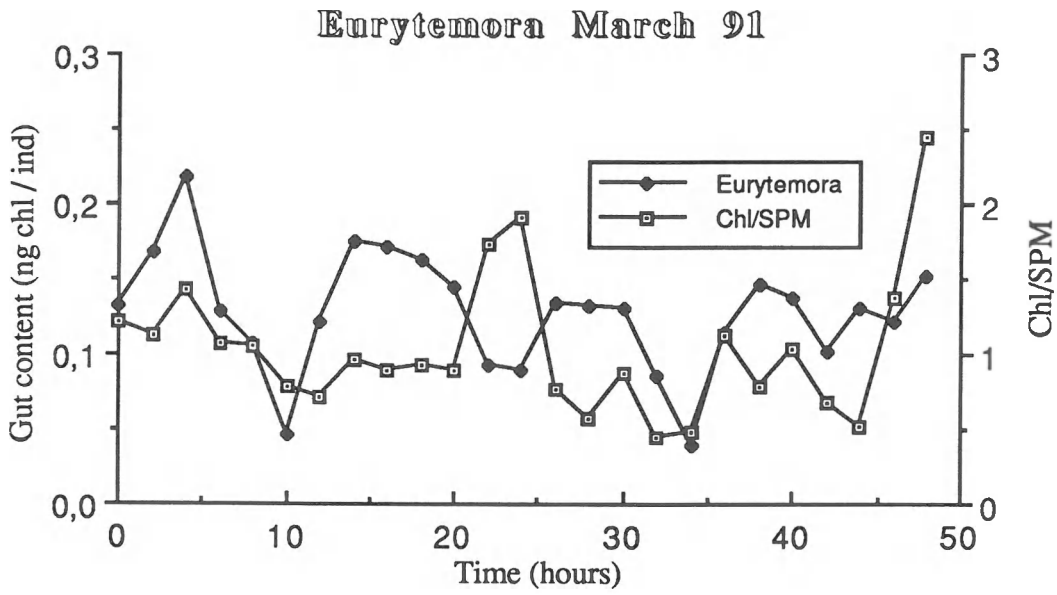


Figure 37: *Eurytemora affinis*. Gut fluorescence analysis and chlorophyll/SPM ratio in the water during a 48h period (station J, water surface).

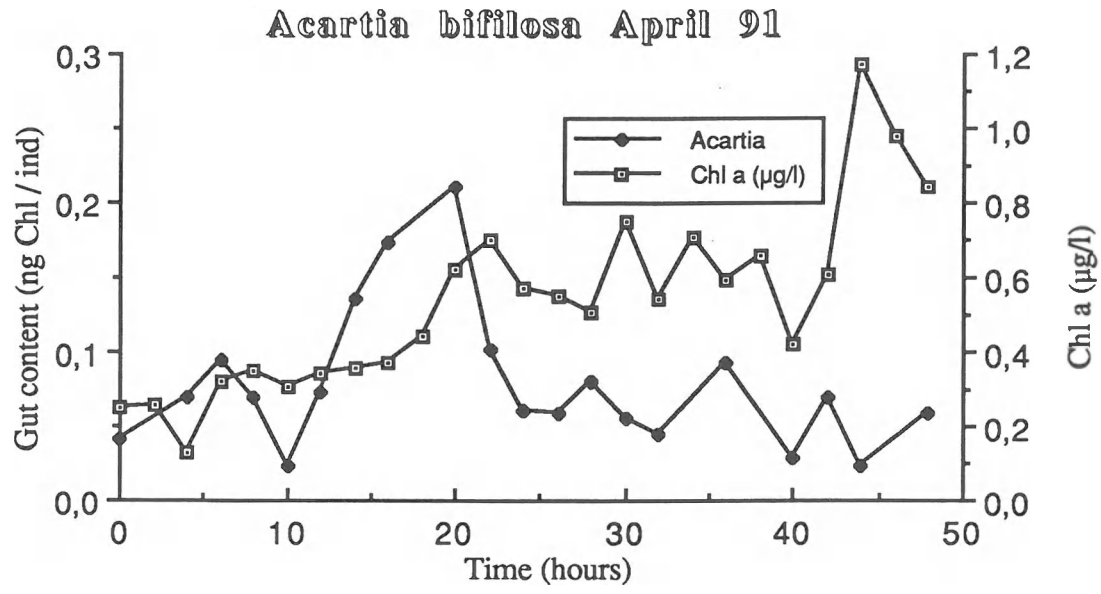


Figure 38: *Acartia bifilosa*. Gut fluorescence analysis and chlorophyll *a* concentration in the water during a 48h period (station A, surface water).

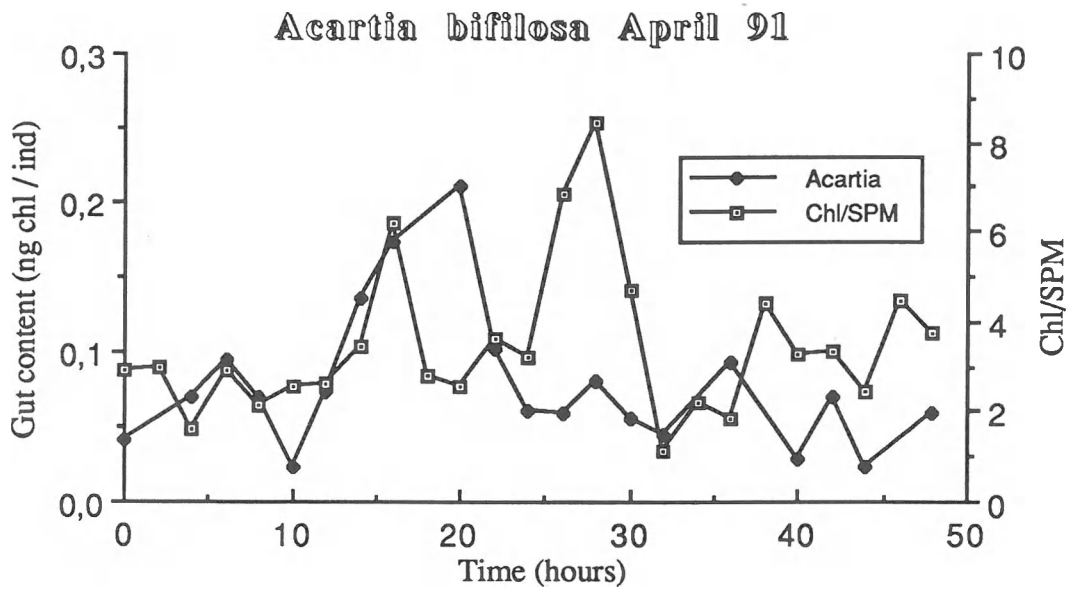


Figure 39: *Acartia bifilosa*. Gut fluorescence analysis and chlorophyllSPM ratio in the water during a 48h period (station A, water surface).

Conclusion

Whatever the species, a cyclic pattern of feeding activity is not a constant feature throughout the year. The absence of cyclic pattern is observed when the considered species is far from its optimum temperature and/or salinity (e.g. *Eurytemora,* October 1990, *Acartia,* April 1991). When observed, the cyclic pattern is related to either chlorophyll concentration or chlorophyll/SPM ratio. In this case, the species live in their optimal salinity-temperature range and develop abundant populations (see §2, part I).

2. LABORATORY FEEDING EXPERIMENTS

2.1. Feeding ethology of *Eurytemora affinis*

Introduction

The major food item for the *Eurytemora affinis* population is generally considered to be allochthonous organic matter, present in the form of detritus. In recent years, high speed cinematographic studies on copepod feeding mechanisms have revealed that the capacity for phytoplankton selection by calanoids was underestimated in the past. If *E. affinis* is able to select living phytoplankton to a considerable degree, or to feed on microzooplankton, it could play a considerable role in the cycling of the local primary production in the brakish water zone.

The food habits of copepods can be deduced from the morphological structure of their feeding appendages. Relating quantitatively the morphology of feeding appendages to the food habits of calanoid copepods Itoh (1970) summarized the difference between the feeding habits of copepods using an edge index (Ei). With this index the spacing between adjacent teeth (hi) and the spacing between them (Wi) in relation to the total width (W) and the longest distances between tip and base (H) of the mandibular blade is considered (Figure 40). The following equation gives the relation:

$$Ei = \Sigma(wi\ hi\ W^{-1}\ H^{-1} * 10^4)\ N^{-1}$$

N being the number of teeth. Itoh defines three groups of copepods based on the value of the Edge index. Filtering herbivorous species are characterized by an Ei less than 500, omnivorous species have an index between 500 and 900, and carnivorous species show an index higher than 900.

In the present report some observations on the mandible structure of *E. affinis*, collected from both the Westerschelde and the Gironde estuary are shown.

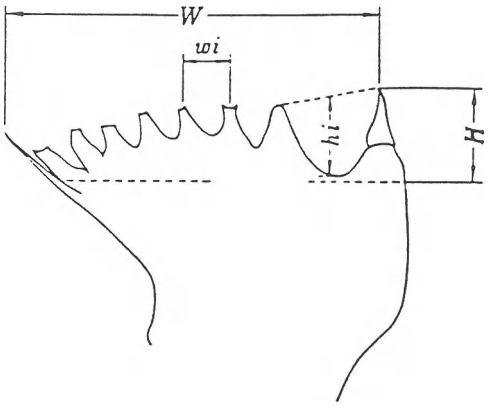


Figure 40: Schematic illustration of the edge index for the cutting edge of a mandible, after Itoh (1970).

Material and methods

Mandibles were dissected from adult *E. affinis* specimens collected in the Westerschelde which were first deep-frozen and then stored in buffered 5 % formaldehyde. The mandibles were mounted in polyvinyllactophenol, dyed with rose bengal. After drying, the mouth parts were studied under microscope and drawings were made using a camera lucida.

Specimens from the Gironde estuary were stored in 5 % buffered formaldehyde. For light microscope observations, mandibles were treated in the same way as for specimens from the Westerschelde. For scanning electron microscopy (SEM), specimens were rinsed in distilled water. Each mandible was air-dried and glued to aluminium support with adhesive tape, then coated with 60:40 gold:palladium applied by vacuum evaporation.

The different variables (wi, hi, W, and N) necessary for computing the Itoh's index were measured on the drawings. The edge index Ei was calculated for each mandible.

Summary of results and discussion

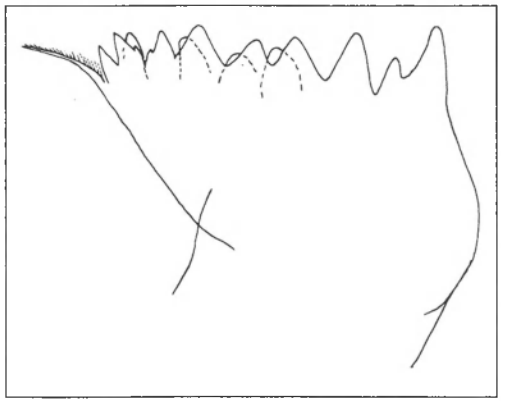
Observations of the mandible structure of female *E. affinis* (Fig. 41 a,b,c) showed that it does not consist of a single row of cutting edges, but that the teeth have a molar like structure. The first two teeth, from the ventral end, have a hyaline structure (Fig. 41, 42) giving a more "transparent" appearance than the others. SEM photographs (Fig. 41) suggest that these teeth correspond to siliceous teeth which are very generally observed in marine copepods.

Observations made on male specimens showed the same structure but give the impression that the teeth are less sharp than those observed in females (Fig. 42 a,b,c). In addition, egg bearing females tended to have somewhat more blunt teeth than females without eggs (not figured).

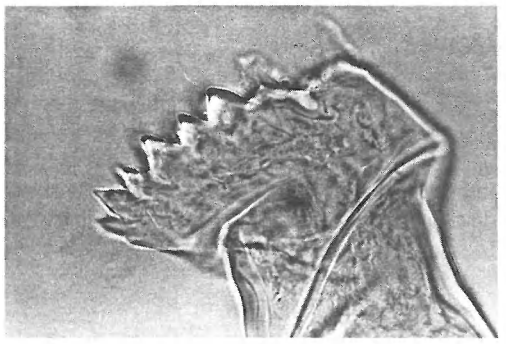
The copepodites stage V, females as well as males, had smaller mandible blades than the adults and they were ornamented with small sharp teeth.

Measurements were carried out only on mandible blades of adult females without eggs and the Edge index was calculated from these results. Calculation of Itoh's index from observations on female species without eggs yielded a mean value of 540 (n=5, s.e.=10) for the specimens collected from the Westerschelde, and of 522 (n=5, s.e.=33) for specimens collected from the Gironde. Thus *E. affinis* can be classified as an omnivore.

Fig. 44a shows the ventral tooth of an adult specimen being detached. It is probably a siliceous tooth crown which was cemented on the gnathobase. The observation corresponds to the description of the morphogenesis of opal teeth in calanoid copepods by Miller *et al.* (1990) : "Fibrous molds in the shapes of the new teeth (during molting) are extruded onto the epidermal surface. Tooth molds are linked to a gland in the proximal part of the gnathobase by ducts. Silification follows. Opal is laid down at the outer periphery of the mold then thickens toward the attachment of the mold to newly formed chitin at its base."



a



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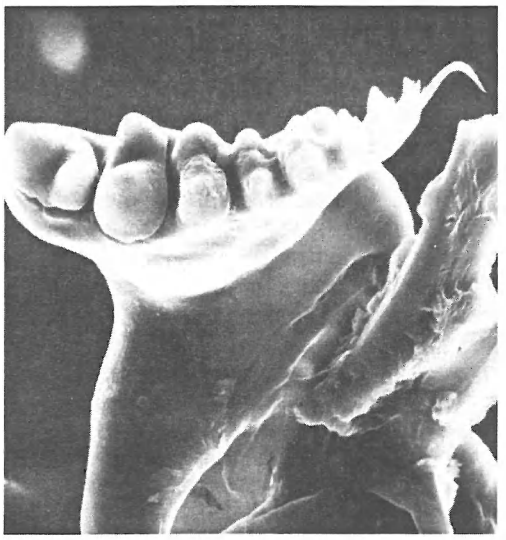

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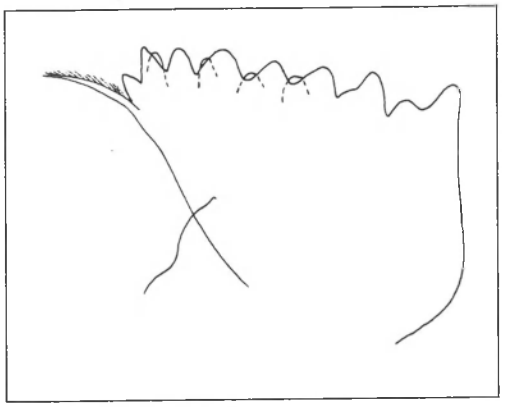

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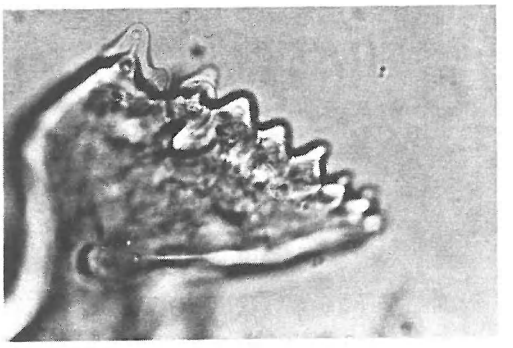

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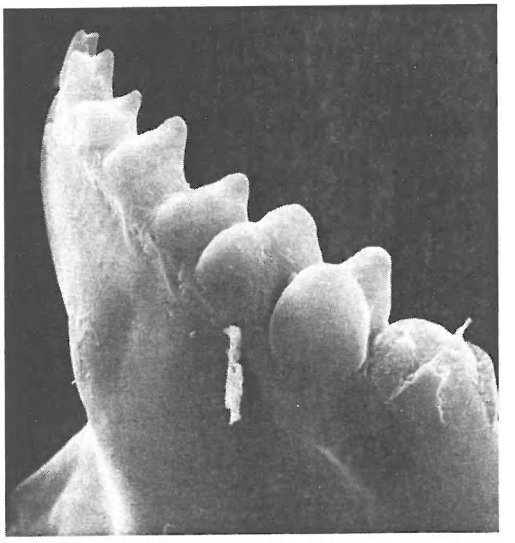

c

Figure 41 (left): a. Schematic drawing; b. photograph of the mandible of *E. affinis* adult female collected from the Westerschelde; c. SEM microphotograph of the mandible of *E. affinis* adult female collected from the Gironde.

Figure 42 (right): a. Schematic drawing; b. photograph of the mandible of *E. affinis* adult male collected from the Westerschelde; SEM microphotograph of the mandible of *E. affinis* adult male collected from the Gironde.

On Figure 43 b the crown is completely removed. From the gnathobase protrude spine-like structures, corresponding in position to the punctuations observed on the tooth in Fig. 42c. These structures are probably "salivary ducts" that connect small dermal glands with pores in the sides of the opal teeth. Presumably the glands secrete a substance into food newly broken by the teeth. This substance could be an aid to digestion.

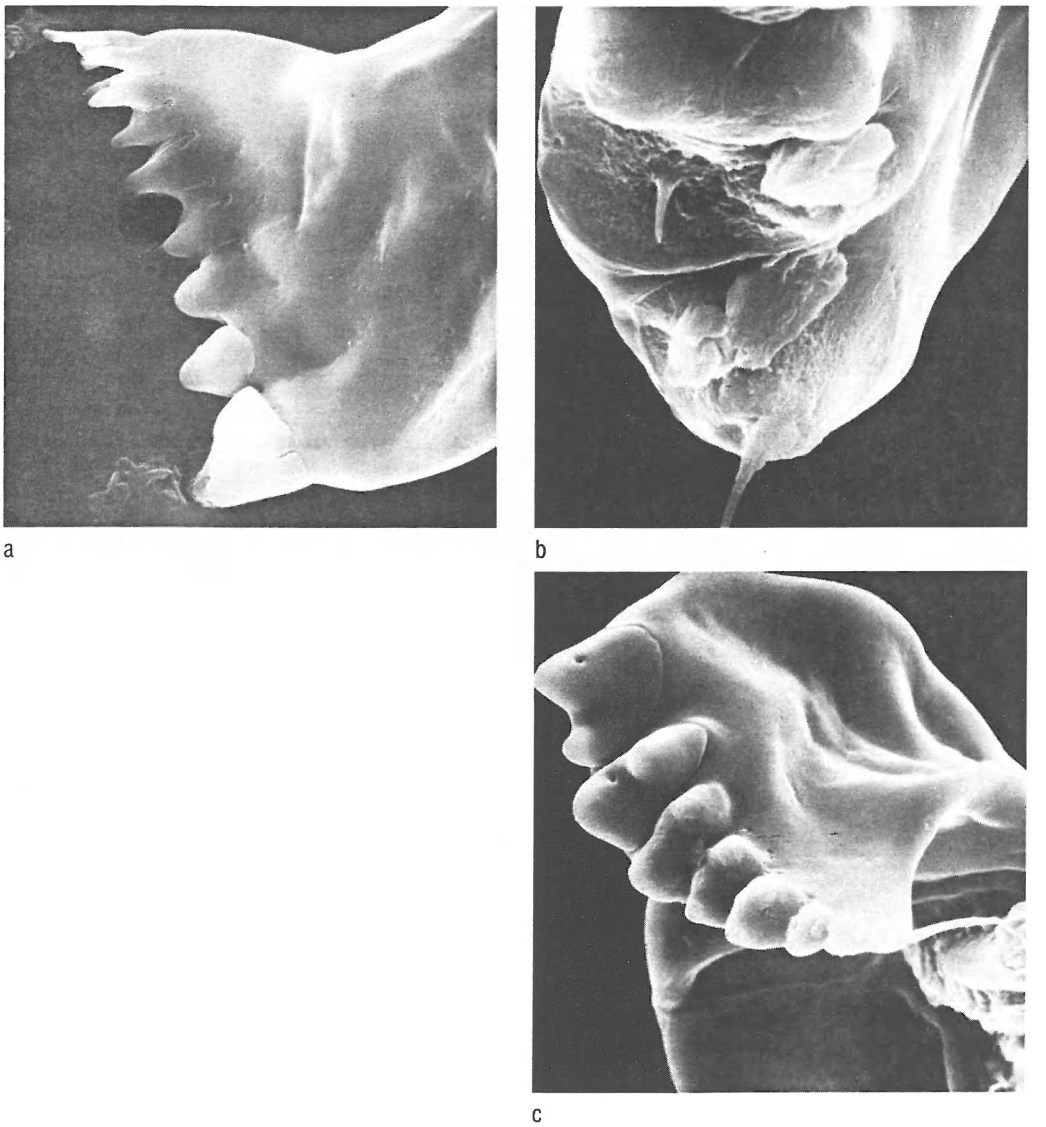

Figure 43: a. *E. affinis* from the Gironde, left mandible. SEM microphotograph showing the ventral opal tooth being detached; b. Right mandible with opal teeth removed revailing two 'salivary ducts'; c. Punctuations in ventral teeth.

2.2. Diel variation in copepod feeding activity (*Eurytemora affinis* and *Acartia bifilosa*)

Introduction

Diel feeding rhythms have been widely reported among planktonic copepods. Maximum feeding intensity usually occurs at night or at dusk. Although diel feeding rhythms are often associated with diel vertical migrations, the two behaviours appear to be controlled independently. Diel feeding rhythms ave been observed in non-migratory species and in non-migrating populations of migratory species. Furthermore, endogenous diel rhythms of feeding and respiration of zooplankton have been demonstrated in the absence of light.

Direct evidence for *in situ* cyclic feeding is difficult to obtain in turbid water (see §1. above). This is mainly due to high concentrations of particulate matter which reduce light penetration, and to water movements mixing the populations. So laboratory experiments are required. In the present report, diel changes in feeding behaviour in adult *Eurytemora affinis* and *Acartia bifilosa* were investigated in relation to day/night cycle. Feeding activity was estimated by the production of fecal pellets.

Principle of the method

For copepods there is a direct relationship between ingestion and production of fecal pellets. Thus the production of fecal pellets per unit of time is considered as an index of grazing activity. In the present experiments, the number of fecal pellets produced by isolated individuals was determined by direct count and the mean time between production of fecal pellets calculated. Gut evacuation rate (1/residence time of one pellet) was expressed in units of min^{-1}.

Summary of results

In a first experiment, freshly caught copepods were maintained in aquaria and were submitted to an illumination cycle (12h day, 12h night). Copepods were fed *Chlamydomonas* sp produced from natural estuarine water. Evacuation rates were determined by counting the fecal pellets produced by individual. Five *Eurytemora* and five *Acartia* were isolated in 40 ml dishes during 24h at a temperature of 18°C. Fecal pellets were counted and removed every 2h. The experiment was repeated twice. The results (Figure 44) showed a clear increase in feeding activity during night for both species. The ratio nocturnal/diurnal (N/D) evacuation rate was 1.43 for *Eurytemora* and 1.73 for *Acartia*. However, the mean evacuation rate averaged over 24h was the same (0.043 min^{-1}) for both species.

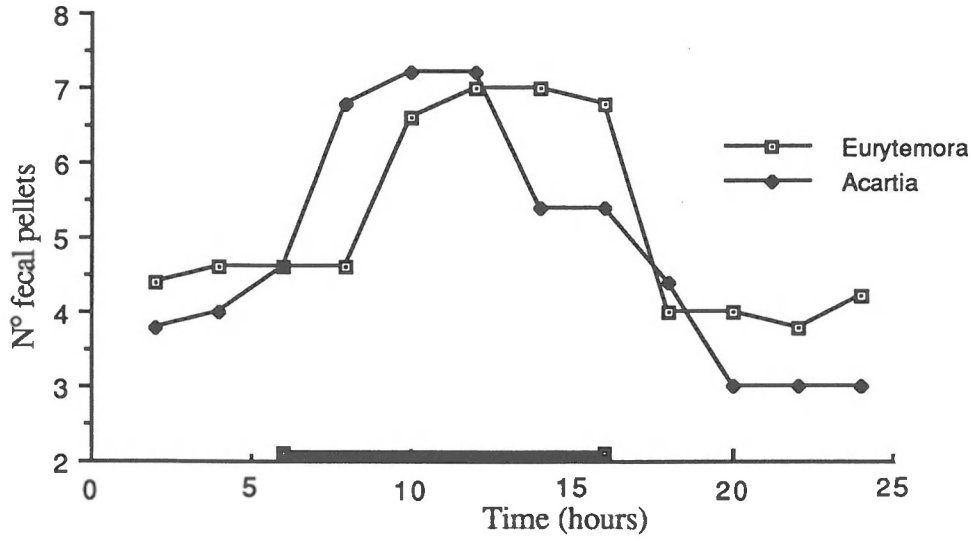

Figure 44: Production of fecal pellets every 2h during 24h. Horizontal bar indicates the dark period ("normal" day/night cycle).

In order to determine if the feeding rhythm is light-induced or if it is endogenous, a second experiment was conducted. Copepods were kept in total obscurity for 5 days at 18°C and evacuation rate was determined using two series of 5 individuals for both *Eurytemora* and *Acartia* fed *Chlamydomonas*. Results (Figure 45) indicated that the feeding rhythm disappeared for *Eurytemora* (N/D = 0.94) whereas it persisted for *Acartia* (N/D = 1.92). It is concluded that an endogenous feeding rhythm is likely to exist for *Acartia bifilosa* whereas the rhythm is induced by light for *Eurytemora affinis*.

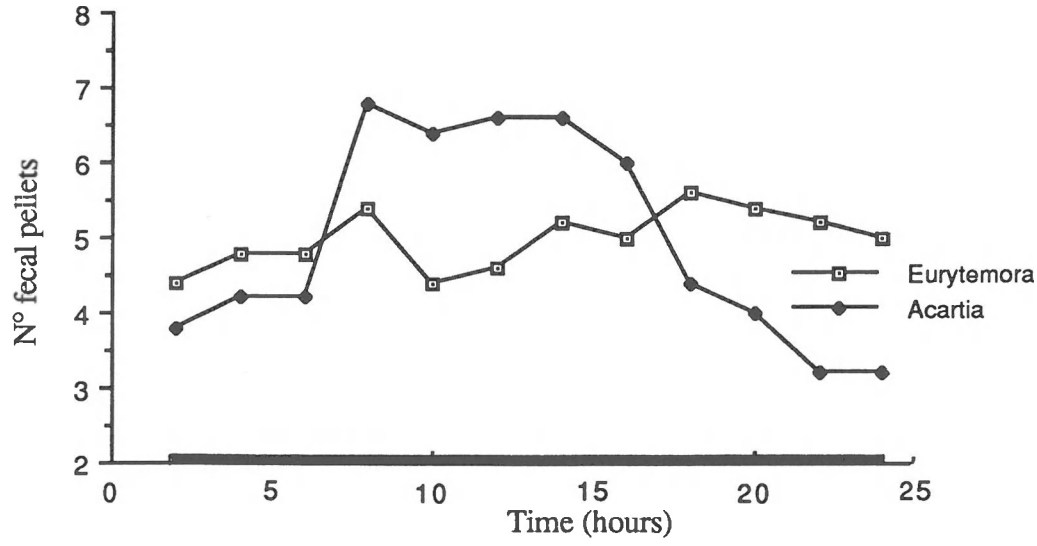

Figure 45: Production of fecal pellets every 2h during 24h. Horizontal bar indicates the dark period (no day/night cycle).

The mean evacuation rates were almost identical for both species (0.042 and 0.043 min^{-1} respectively) and were not significantly different from the first experiment. For *Eurytemora* this could indicate a compensation mechanism when exposed to day-night cycle: strong increase of ingestion rate during night in order to balance the low feeding activity during daytime. In that way a mean daily ration would be maintained.

In a third experiment, the induction power of light was investigated by inverting the day-night cycle (Figure 46). Copepods were placed in water from the estuary and were submitted to an reverse photoperiod (12h dark, 12h light) during 5 days prior to the experiment (T = 18°C). Both species displayed a rhythm in evacuation rate with higher production of fecal pellets during the artificial night than during the illuminated period (N/D = 1.42 and 1.45 respectively). Mean evacuation rates averaged over 24h were 0.038 and 0.041 min^{-1} for *Eurytemora* and *Acartia* respectively.

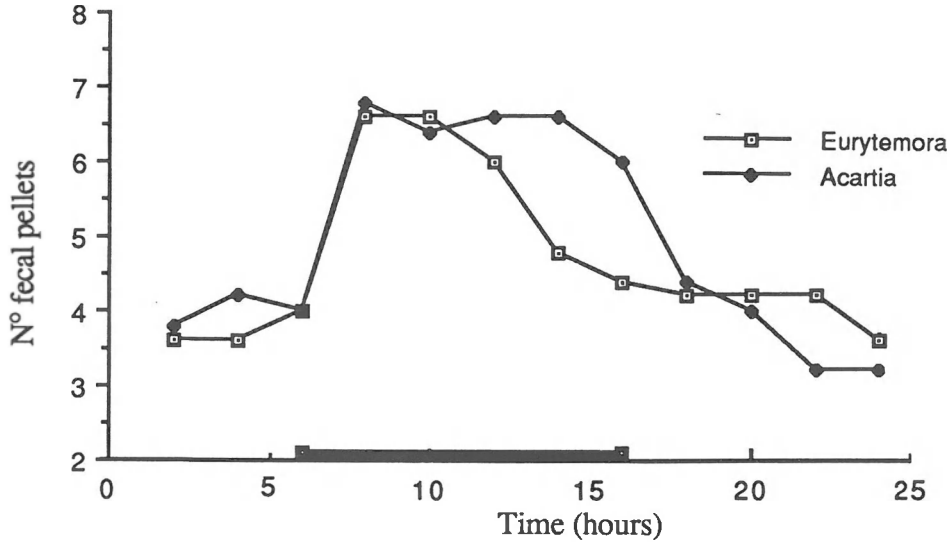

Figure 46: Production of fecal pellets every 2h during 24h. Horizontal bar indicates the dark period ("reverse" photoperiod).

In conclusion, it is clear that light induces a decrease of ingestion rate for the copepods *E. affinis* and *A. bifilosa*. Inversion of the feeding activity can be obtained by modifying the day-night cycle. Visual observations indicate that their locomotory activity is increased by light. This could result in a decrease of energy spent for feeding. Rhythmic feeding activity is maintained for *Acartia* kept in the dark; it is not the case for *Eurytemora*. These observations could reflect the influence of the environment on the behaviour of the species. *Eurytemora* lives in the turbidity maximum zone where the light does not diffuse at the water surface below a few cm. Conversely, *Acartia bifilosa* is found in the dowstream polyhaline zone where light penetration and thus nychtemeral rhythms are much more important.

2.3. Ingestion rates of *Eurytemora affinis* and *Acartia bifilosa*

Operations

The gut fullness can be used as an index of feeding activity, but to calculate ingestion rate it must be multiplied by a gut evacuation rate. The latter was measured in the laboratory using *Isochrysis galbana*. Prior to experiments, the animals were fed for 6-10 h at high algal concentration. At time zero the copepods were placed in filtered seawater at constant temperature (17 °C) and the evacuation of pigments from the gut was followed by fluorescence.

Summary of the results

The gut content declined during time. Examples are shown in Figures 47 and 48. The results from the regressions showed that the residuals were the lowest for the exponential model, which, therefore, was used in subsequent calculations of instantaneous evacuation rates.

After 1 h, the gut evacuation rate was found to be constant. In the examples given in Figures 47 and 48, the values were 0.028 min^{-1} for *Eurytemora* and 0.020 min^{-1} for *Acartia*. From the masurements of gut fluorescence made in May 1990 during the two 24h cycles at the same temperature, the quantity of chlorophyll (expressed as carbon) ingested by copepod was computed: 313 ng C day^{-1} for *Eurytemora* and 224 ng C day^{-1} for *Acartia*.

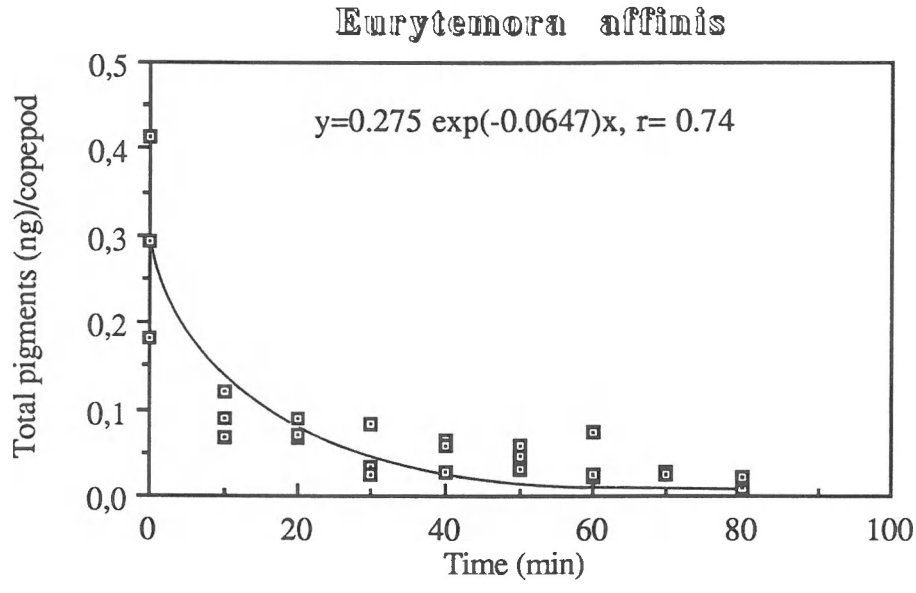

Figure 47: Time-dependent changes in the gut content of *E. affinis*.

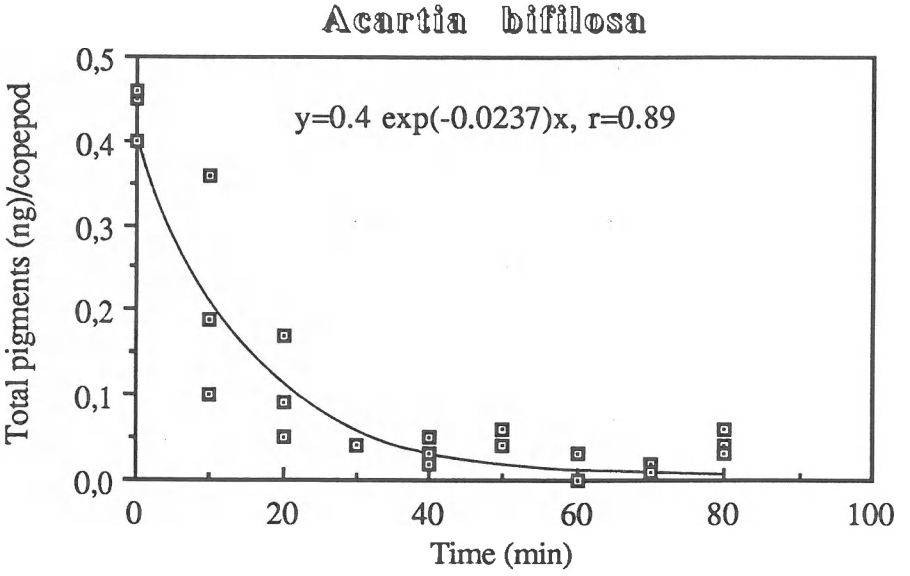

Figure 48: Time-dependent changes in the gut content of *A. bifilosa*.

The influence of temperature on the gut evacuation rate was estimated using two methods: the production of fecal pellets (*Eurytemora* and *Acartia*) and the loss of gut fluorescence (*Eurytemora* only). For both *Acartia* and *Eurytemora*, the gut evacuation rate clearly increased from 6 to 22°C (Figure 49). At higher temperature (26°C) the evacuation rate was constant for *Acartia* and decreased for *Eurytemora*.

The evacuation rate computed from the production of fecal pellets was slightly higher than the evacuation rate measured as the loss of gut fluorescence. Nevertheless, the kinetics of the influence of temperature on evacuation rate was identical in both series of experiments.

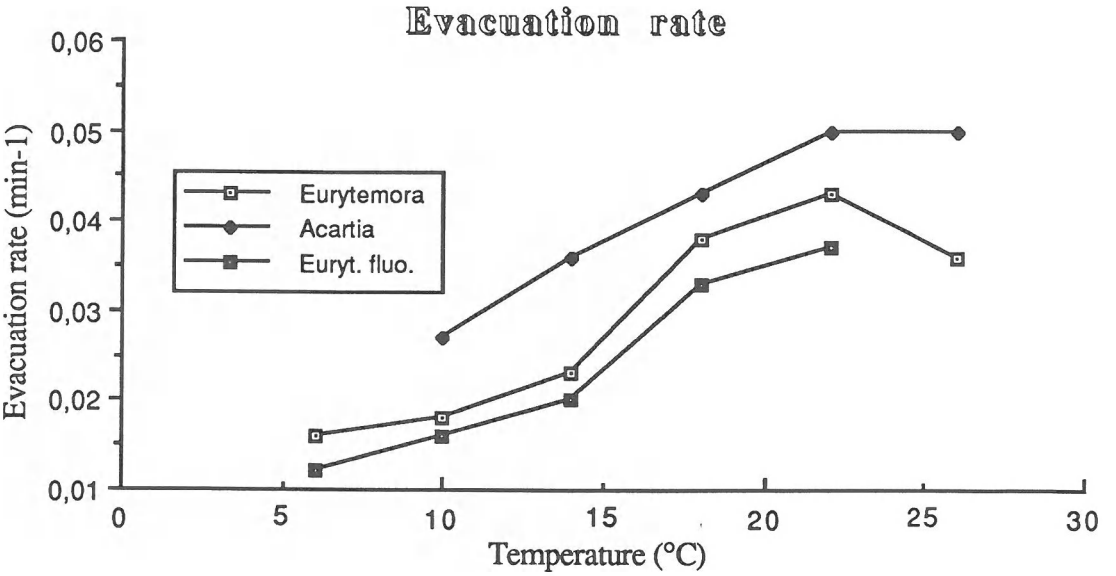

Figure 49: Influence of temperature on the gut evacuation rate of *E. affinis* and *A. bifilosa* computed from the production of fecal pellets. The gut fluorescence method was also used for *Eurytemora*.

3. PRODUCTION EXPERIMENTS

3.1. Oxygen consumption of *Eurytemora affinis*

Material and methods

The oxygen consumption of *E. affinis* was determined using a manometric method. The animals were collected from the habitat. The temperature during storage and experiments differed by no more than 5°C. Nevertheless, prior to the experiments, the animals were acclimated at the experimental temperature for at least 24h. The salinity ranged from 0 to 5 ‰. The oxygen uptake was measured using a standard manometric technique on a Gilson differential respirometer. The 15 ml experimental vessels had an external arm into which was placed 0.4 ml of 10 % NaOH. About 50 copepods were placed in 8 ml of water from the habitat. The temperature was stabilized for one hour before the experiment started. The results were calculated in $\mu l\ O_2\ h^{-1}$ for the average size of individuals and for each exposure temperature (10, 12.5, 15, 17.5, 20, 22.5 and 25°C). The duration of each experiment was 6h.

Summary of the results

Our purpose was not to undertake a refine ecophysiological study of respiration but to determine the influence of temperature on the global metabolism of an average population. Equations relating the oxygen consumption to the weight are given in Table 10.

Temperature (°C)	Regression	Correlation
10	log R = 0.79 + 0.78 log W	r=0.37, n=19
12.5	log R = 0.92 + 0.83 log W	r=0.83, n= 9
15	log R = 0.90 + 1.14 log W	r=0.82, n=28
17.5	log R = 1.02 + 1.10 log W	r=0.82, n=12
20	log R = 1.10 + 1.06 log W	r=0.70, n=15
22.5	log R = 1.25 + 0.73 log W	r=0.53, n=15
25	log R = 1.07 + 1.32 log W	r=0.86, n=10

Table 10: *E. affinis*.Log-log regressions between oxygen consumption R (nl $ind^{-1}\ h^{-1}$) and dry weight W (µg). n: number of experiments.

The values of the b coefficient (0.73-1.32) of the log-log regressions relating the oxygen consumption to the weight are comparable to the values given in the literature. For instance, Conover (1959) indicated a range of 0.81 to 1.00 for several marine species of copepods. Klekowski & Shushkina (1966) found values from 0.27 to 1.23 for various stages of the cyclopoid *Macrocyclops albidus*.

For *E. affinis*, the optimum level of oxygen consumption was situated at 15°C. This confirmed previous results (Castel *et al.*, 1983; Escaravage, 1991) obtained in culture experiments and showing a maximum growth rate at 15-17°C.

The increase in oxygen consumption by unit of weight, as a function of temperature (Figure 50) was nearly linear between 10 and 20°C, then a plateau was observed between 20 and 25°C. Gylllenberg (1973) also showed a respiratory compensation plateau for *E. affinis* from the Baltic sea, but it was between 4 and 15°C. At upper temperature, near the lethal limit, the respiration increased three-fold. The difference between both studies could be explained by mechanisms of acclimation either to a cold situation (Finland) or to a warm temperate zone (Gironde).

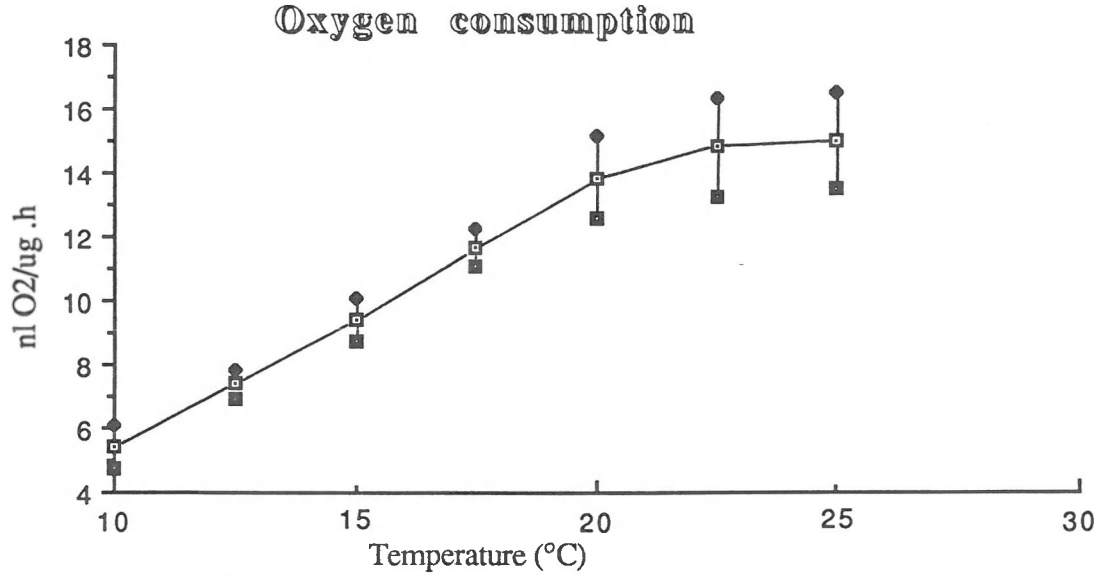

Figure 50: *E. affinis*. Influence of temperature on the weight-specific oxygen consumption rate (± S.E.). Mean weight of the individuals = 3.4 µg d.w.

More generally, the kinetics of temperature influence on the oxygen consumption for *Eurytemora* appears to be related to the latitude (Table 11). The increase in respiratory metabolism as a function of temperature is the highest in the Gironde, the most southern area whereas studies undertaken in Finland indicate the lowest values.

Temperature (°C)					Sources
5	10	15	20	25	
2.40	2.80	3.60	9.60		Gyllenberg, 1973 (Finland)
3.80	4.00	5.08			Gyllenberg & Lundqvist, 1979 (F.)
6.50	8.30	10.00	11.50	13.00	Boak & Goulder, 1983 (U.K.)
3.39	6.44	7.80	9.83	11.53	Roddie *et al.*, 1984 (U.K.)
	5.43	9.42	13.90	14.99	Present study (France)

Table 11: *E. affinis*. Weight-specific oxygen consumption (µl O_2 mg^{-1} h^{-1}) as a function of temperature (adults + last copepodid stages).

3.2. Development rate of *Eurytemora affinis*

Introduction

A quantitative approach of copepod productivity requires precise knwoledge about the *in situ* dynamics of the populations. Unfortunately, the existence of mixed cohorts resulting from a continuous reproduction, makes it hard to elucidate the population dynamics of the species even through a high frequency field sampling. Thus one has to resort to laboratory cultures. The two main variables controlling population dynamics in the field are temperature and food availability. In cultures devoted to a description of field processes, one has to keep a high correspondence between culture and field conditions concerning temperature and food availability. If such conditions are reproduced within the cultures, one may expect the copepods to express a similar metabolism than in the field.

For the present project, our purpose consisted essentially in defining copepod growth rates in so called 'field simulated' conditions of temperature and food availability. These growth rates were then used in a developmental model reproducing what had been observed in the cultures. The final purpose of the model is to be incorporated into a more general mathematical structure simulating *E. affinis* population dynamics in the field.

Methods

The copepods were isolated from the brackish part of the Western Schelde estuary in April and June 1990, and in March 1991. The temperature ranges used in the cultures were chosen according to the corresponding field temperatures. Each week about 40 l of water were collected in the same area as the copepods. This water was used as a culture medium stock after being filtered on a 55µm mesh size sieve and maintained at the field temperature. Copepods were cultured from adult to adult in 100 ml glass beakers filled with 40 ml of culture medium. The culture medium was renewed every 2 day. The copepods were checked every 2 day and their state of development was noted. Some extra experiments were performed for naupliar development. Here, an artificial cohort (synchronized birth) was followed and sampled at regular intervals.

The ultimate goal of this study was to provide a simple model describing *E. affinis* development through the different stages. Mean development rate can be expressed as a simple temperature function. Heip (1974) suggested the use of the following equation: $D = a * T^b$ (D: development time, T: temperature, a and b: parameters). Fitting such equation to culture results provide mean residence time (D_i) in each development stages (i) within a continuous thermic range.

Based on the mean residence time in several developmental stages (i) one can develop a simple model of copepod growing population formulated as:

$dN_i/dt = N_{i-1} - N_i/D_i$, where dN_i is the change in number of individuals in stage (i) during the time interval dt. The major inconvenient of this kind of formulation is the

'numerical diffusion' allowing a fraction of copepods to complete their development (from stage 1 to n) within the time interval covered by n integration steps. As the integration steps used in modelling copepod development rarely exceed a fraction of day, this formulation will make some copepods to develop from egg to adults within about 1 or 2 days when the minimal development time obtained at 20°C was 9 days. Moreover, in this kind of model the age distribution within each stage is assumed to be uniform, an unlikely situation in nature.

These two drawbacks, numerical diffusion and abusive uniform age distribution can be avoided by subdividing each development stage in age classes. The subdivision of stages into classes inforces the featured copepods to molt to the next stage only after stayed in the stage the duration necessary for their development. The number of classes is given by $m_i = D_i^2/SD_i^2$, where SD_i is the standard deviation associated to D_i. The model reduces to a set of two derivative equations calculating for each development stage i (1 to n), then density changes (dN) in each age classes j (1 to m_i) for each integration step (dt):

1. For i=1 to n, j=1 (first class of each stage) and supposing $N_{0,m(0)}=0$ (no recruitment in $N_{1,1}$, 1st class of nauplii)

$dN_{i,1}/dt = (N_{i-1,mi-1} * Trp_{i-1}) - (N_{i,1} * Trp_i)$

2. For i=1 to n, j=2 to m_i (other classes)

$dN_{i,j}/dt = (N_{ij-1} * Trp_i) - (N_{ij} * Trp_i)$

The transition probability (Trp_i) from one age class to the next equals the inverse of the residence time in this class.

By introducing copepods in the first class of the first stage (newly hatched nauplii) at the stimulation start, a 'wave of copepods' is initiated progressing through development from class to class and consequently from stage to stage until reaching adulthood.

Solving the derivative equations and calibrating the model has been done within the SENECA programme (Simulation ENvironment for ECological Application) developed by the Delta Institute for Hydrobiological Research.

Summary of the results

In the extra experiments especially designed to describe the naupliar development, small nauplii (N1+N2) were distinguished from large nauplii (N3-N6). Whereas from 14 to 20°C residence time in these both groups were rather similar, at 5 and 8°C large nauplii developed much slower than small nauplii (Figure 51). Moreover at 2°C, it was impossible to obtain a transition to the first copepodite stage, even for copepods having stayed more than 5 weeks as nauplii.

It was not possible to obtain a complete copepodite development at 5°C as no copepod succeeded to molt to the fifth copepodite stage even after 60 days counted from hatching. Moreover, it seems that the fourth copepodid stage represented a critical part of the development even for higher temperature.

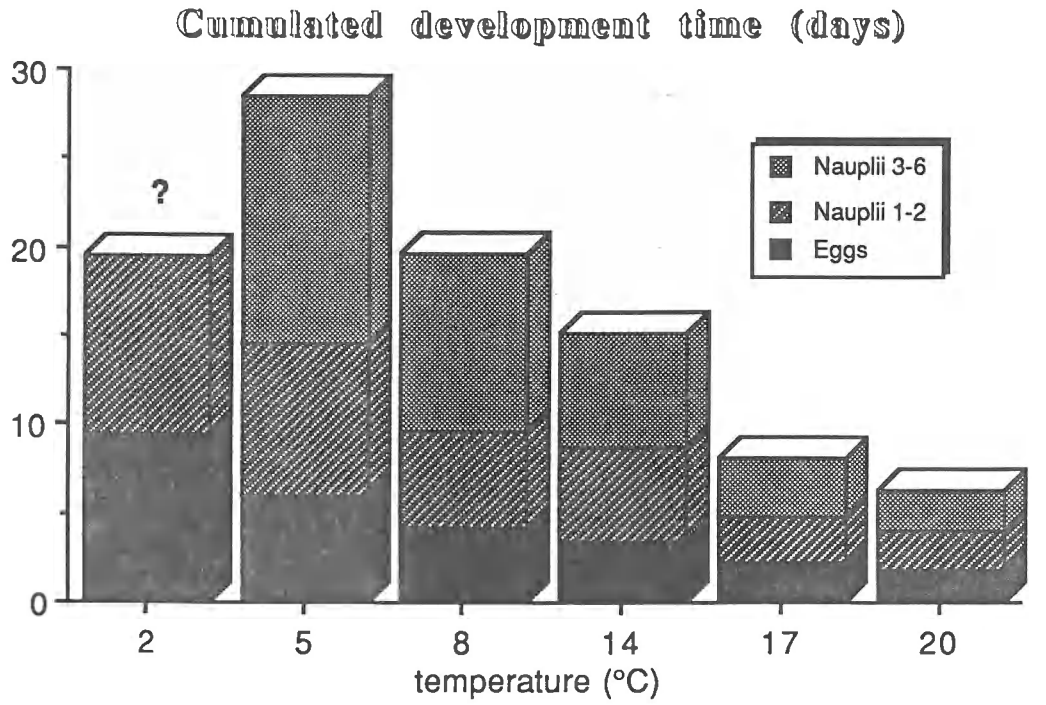

Figure 51: *Eurytemora affinis*. Development time of eggs and nauplii as a function of temperature.

The cultures showed a distinct relationship between total development time and temperature (Figure 52). Development sharply accelerated from 8 to 17°C. From 17 to 20°C this trend was less pronounced giving similar development time for these both temperatures.

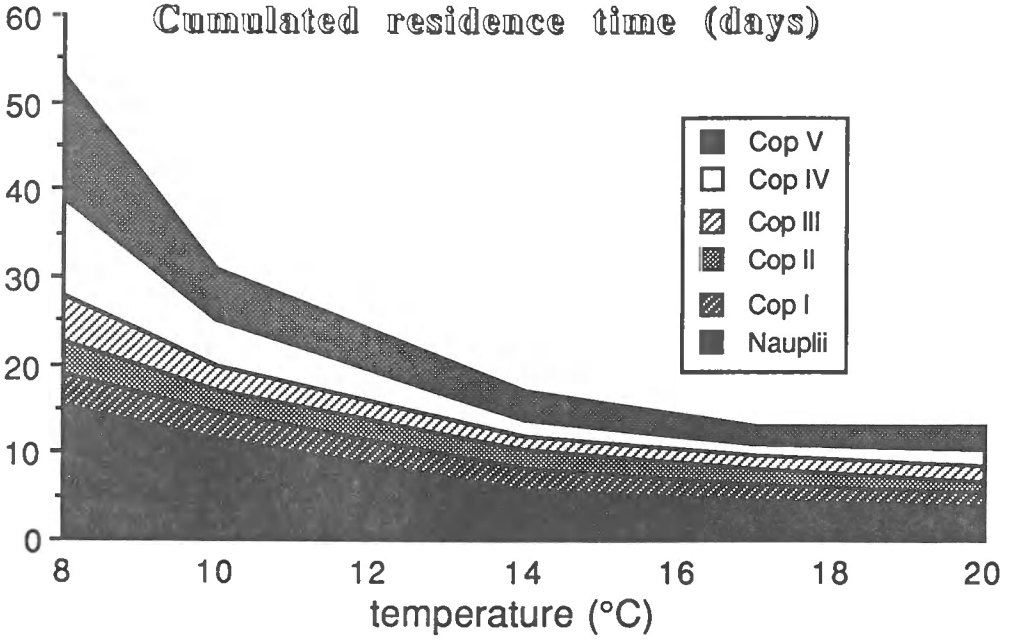

Figure 52: *Eurytemora affinis*. Development time of nauplii and copepodid stages as a function of temperature.

In the temperature function chosen to fit to *E. affinis* development rate $D = aT^b$, the relative changes in development time versus temperature is defined by **b**, when **a** mainly controls its absolute value. According to the observations made above, it seemed more realistic to adjust stage specific temperature functions as certain periods of development seemed to be distinguishable following their sensitivity to temperature (Table 12).

Development stages	N° age classes (m_i)	b_i	a_i
Small Nauplii (NI-NII)	36	-1.05	47.011
Large Nauplii (NIII-NVI)	14	-1.50	161.00
Total Nauplii	38	-1.60	448.781
Copepodite I	9	-1.30	62.429
Copepodite II	6	-1.30	64.832
Copepodite III	6	-1.30	74.992
Copepodite IV	3	-1.96	530.682
Coepodite V	5	-1.96	791.096

Table 12: *E. affinis* development time. Model parameters calibrated with SENECA.

The first procedure engaged with SENECA consisted in the calibration of the parameters used in the model. The b_i values estimated by simple regressions were introduced in the model as fixed parameters and the calibration concerned only with the a_i values and the number of classes m_i. The final simulation produced a satisfactory goodness of fit. However, the modelling performance was not uniform among the experiments. As an example the rather good outputs obtained for the 8°C culture shown in Figure 53A can be compared with the less succesful 14°C simulation (Figure 53B). The main divergence shown in this last simulation consisted with the too large broadness of the copepodites IV and V peaks when their 'emergence' time and heights fitted well with the observed data.

Discussion

In some previous studies *E. affinis* was cultured in an excess of algal food (Heinle & Flemer, 1975; Vuorinen, 1982), or as in our case with natural food directly collected in the field (Poli & Castel, 1983). The models corresponding to cultures supplied with algal food are exceptionally similar (Figure 54) which can lead these both experiments (Heinle & Flemer, 1975 and Vuorinen, 1982) reproduced true standardized optimal food conditions. The developments shown by *E. affinis* in Poli & Castel (1983) and in the present study are quite different compared together and with the two other ones (Figure 54). These differences could result from the various quality of food used in these experiments.

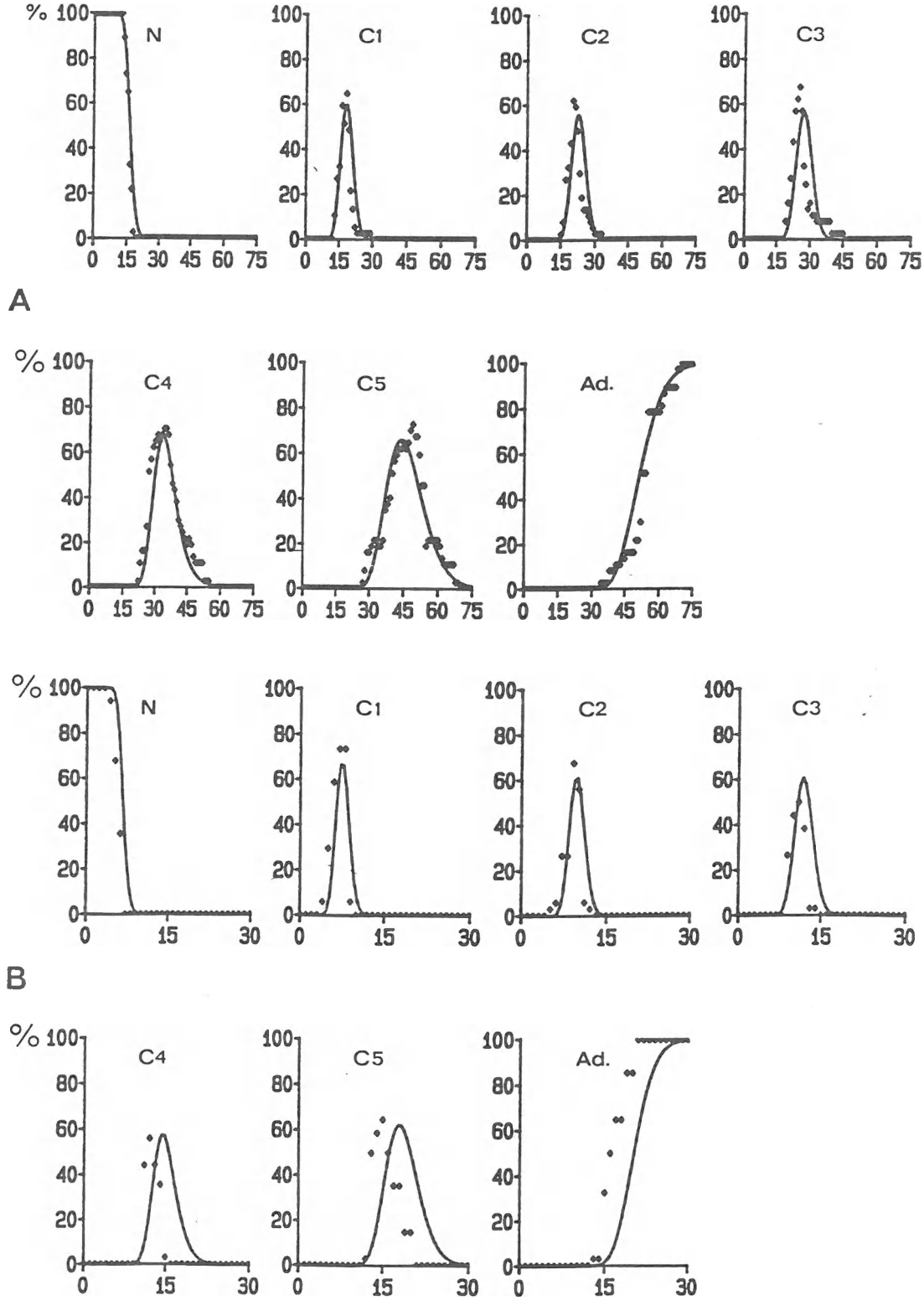

Figure 53: Relative abundances in each stage versus time counted from hatching. (---) = simulation outputs, (+) corresponding experimental data obtained at 8°C (in A) and at 14°C (in B).

In most copepod models, integration is done with a fixed time step, and the number of classes is adjusted so as to obtain a residence time within each class which is close to the integration step. The programming environment SENECA uses an adjustable time step so as to keep the changes in state variables (densities in each class) within preset ranges. As a consequence, there is a decoupling of the residence time within a stage and the number of classes in this stage.

Some failures did appear in the modelling performance as shown for the 14°C experiment. These failures are likely to originate from the unability of the reduced number of parameters used here to reproduce exactly the observed data. Temperature is the only independent variable in this set of experiments (food factor supposed to be uniform). In order to get a better fit with the observed data, we could have try to increase the number of parameters involved in the temperature dependent development rate. But considering that only two variables are involved in this model (development time and temperature) an increase in the parameters number would probably improve local agreement with the experiments but also decrease the statistical and biological consistency of the outcomes.

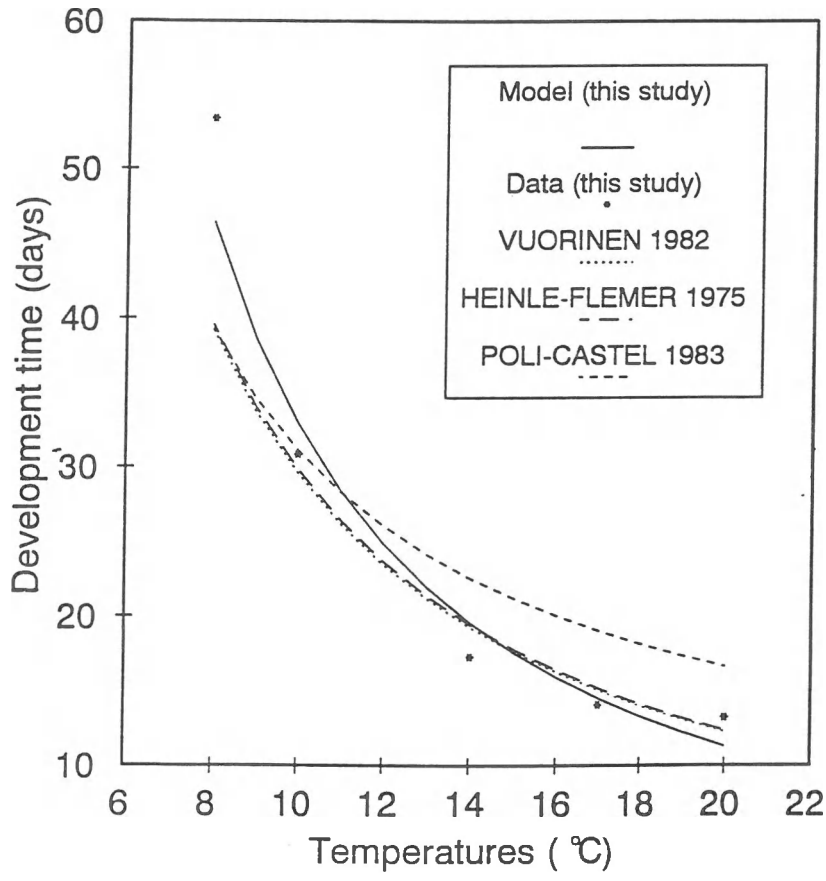

Figure 54: Comparison with other models for *E. affinis* development time from hatching to adulthood.

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