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Seasonal dynamics of the zoobenthic communities in the mesohaline zone of the Loire estuary (France)

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Abstract

The application of correspondence factorial analysis to four types of sediment in the upper reaches of the Loire estuary enabled the significance of environmental factors in the spatial distribution, abundance and seasonal dynamics of the biotic communities to be determined. In coarse sand, the communities are stable but species are few in number and population densities are low. In muddy sediments (from muddy sand to fluid mud) population densities are high but undergo seasonal fluctuations due to changes in the hydrological regime (especially the dissolved oxygen regime). This is true for the composition of the biotic communities. The oligohaline phase, in which the fluvial element is predominant, is characterized by abundance maxima due to freshwater species. The mesohaline phase, in which the marine element is predominant, exerts a restrictive action on population densities; certain species are supplanted by others, their development being governed by the quality of the environment.

Introduction

In an estuary, the boundaries between the various haline zones are variable and depend on the combined action of the river and tides. In temperate regions with wide tidal ranges, a particular area can experience great fluctuations not only in haline conditions but also in temperature and oxygen content. This is particularly true of the mesohaline zone (5–18‰) which is found at the interface of the river-dominated limnic-oligohaline environment and the polyhaline zone which is more subject to marine influences. In this zone, in which the waters are turbid and silt deposits abundant, the communities must adapt to these fluctuations by modifying their specific composition and abundance.

This paper examines and analyses the structure and functioning of the intertidal benthic communities of the mesohaline zone of the Loire estuary in correlation with the hydrological and sedimentary conditions experienced over a full annual cycle. Moreover, an attempt has been made to highlight the main factors affecting the seasonal evolution of these communities.

Area of investigation

The area of investigation was situated 20 miles upstream from the river mouth at St. Nazaire and was limited to the northern side of the estuary, close to the main navigational fairway (Figs. 1 and 2). The four sampling stations, with water depths between 1 and 2 metres, had different substrata varying be-

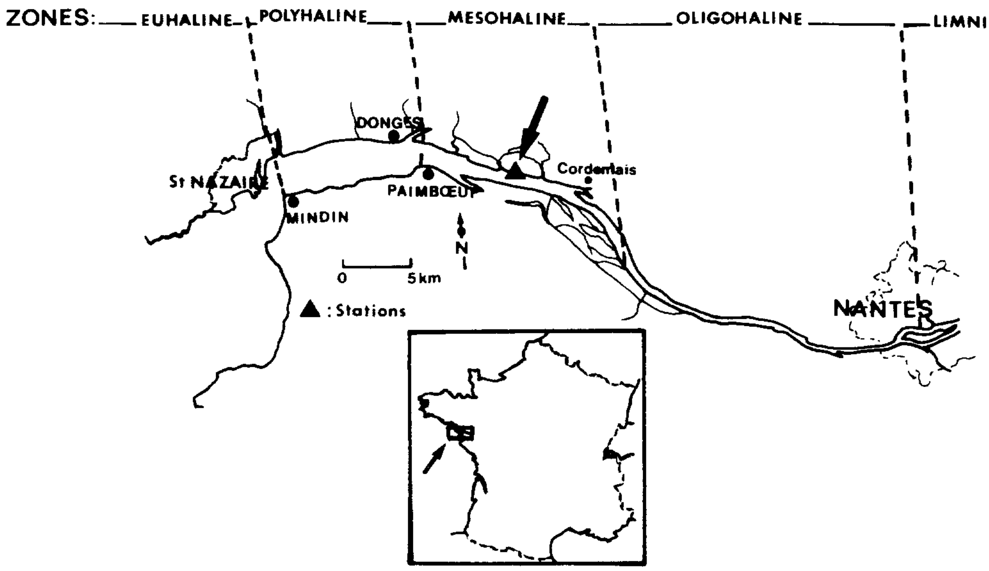

Fig. 1. Map of the Loire estuary with the localization of the sampling stations.

tween fluid silt and clean sand. Recent cartographical studies of the animal communities in this area have shown that the low specific diversity index is due to the predominance of two Oligochaetes: *Limnodrilus hoffmeisteri* Clarapede and *Monopylephorus rubroniveus* Levinsen (Robineau & Marchand, 1985).

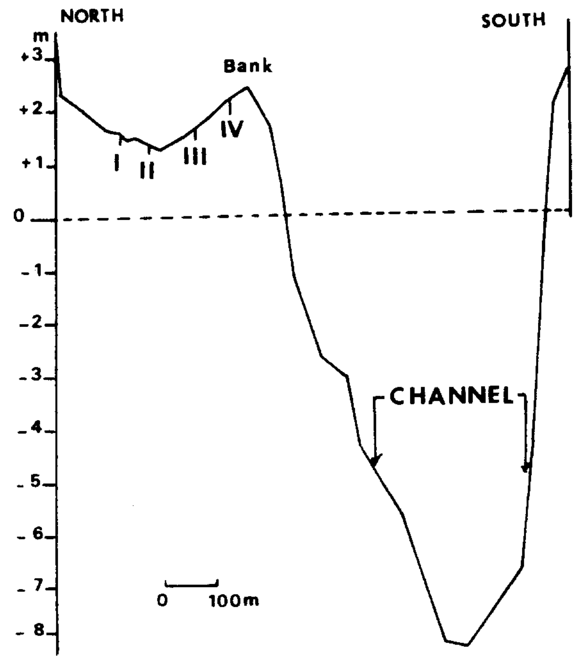

Fig. 2. Localization of the sampling stations on the transect in the mesohaline zone of the estuary.

The hydrological conditions of the mesohaline zone are determined mainly by the flow rate of the river which can vary between 100 $m^3 \cdot s^{-1}$ at low water to 5500 $m^3 \cdot s^{-1}$ when the river is in spate. During the study period (October 1981 to November 1982), four successive hydrological phases were observed (Fig. 3):

- a limnic phase (less than 0,5‰) from January to February with cold, well oxygenated water (5 °C, 80% O_2);
- an alpha-oligohaline phase (3 to 5‰) in March and again from October to December with temperatures varying between 7° and 14 °C and an oxygen content above 60%: it is a highly stratified estuary;
- a beta-mesohaline phase (5 to 10‰) in April and May with water temperatures increasing (18 °C) and dissolved oxygen levels decreasing (75 to 35%): the estuary is partially mixed;
- an alpha-mesohaline phase (10 to 15‰) from June to September with high water temperatures (18° to 24 °C) and poorly oxygenated water (less than 30%): the estuary is homogeneous.

The annual cycle under study differs from that of

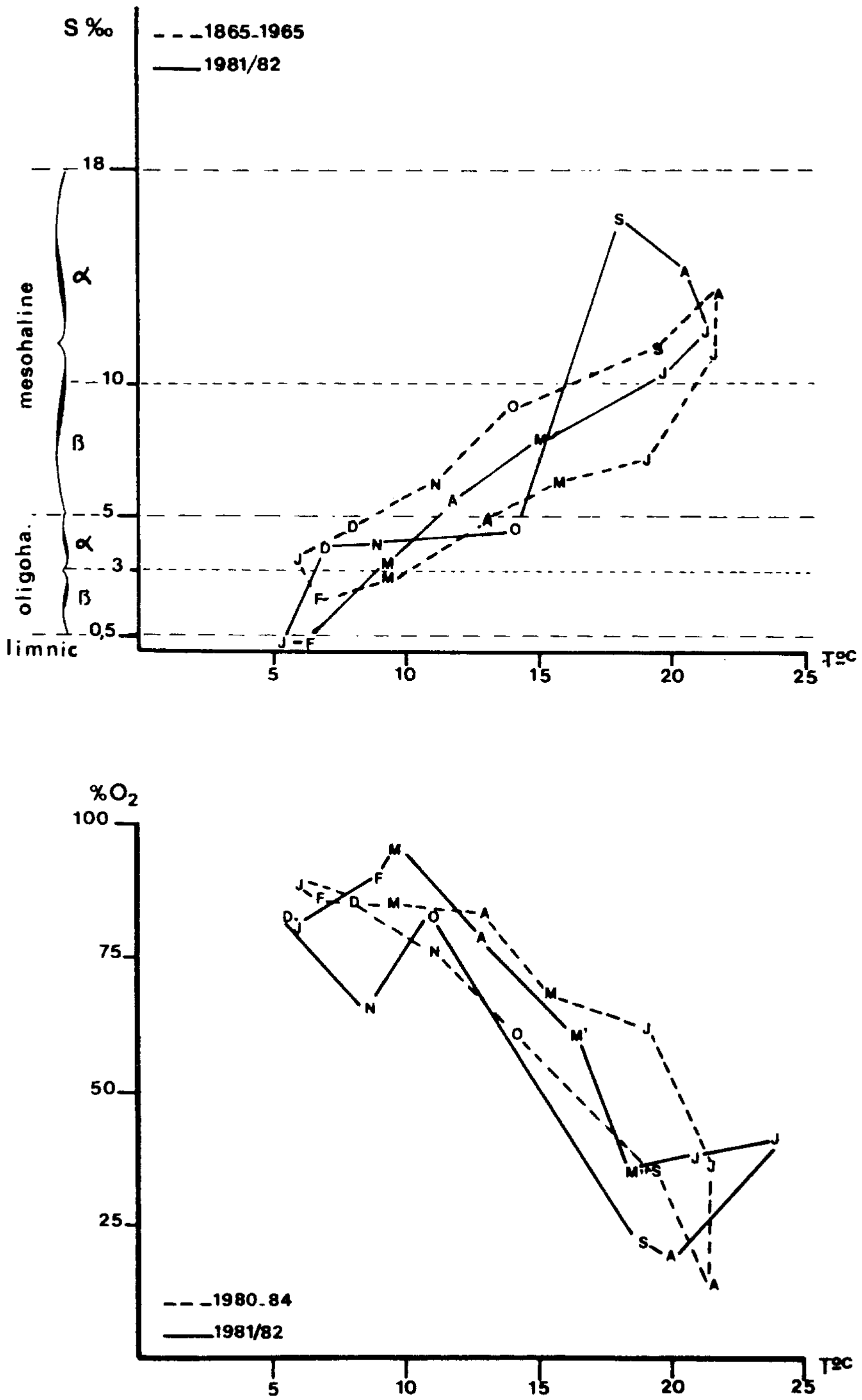

Fig. 3. Seasonal evolution of the principal environmental factors: salinity, temperature and dissolved oxygen content in the water column (1865–1965: salinity data estimated from the mean monthly river flow calculated on a hundred years) (1980–1984: average of monthly dissolved oxygen data).

other years (1980, 1983, 1984) in the following ways:
- there was an exceptional period of spate during the winter resulting in the complete dechlorination of the environment for a period of two months;
- the mesohaline period lasted for six and a half months and was characterized by salinity levels in excess of those which are normally observed in April and September.

Methods and materials

From October 1981 until November 1982, core samples were taken at monthly intervals at the four sampling sites over an area of 208 cm^2 to a depth of 25 cm. These were then sieved over a 0.5 mm mesh. The macrofauna were fixed in 5% formalin. For purposes of identification the Oligochaetes were cleaned in Amman chloral lactophenol: they were then identified according to Brinkhurts's method (1982). After counting, specific diversity and evenness were calculated using Shannon's method.

Possible predators (fish and crustacea) of the benthic fauna were sampled monthly using an experimental beam trawl (20 mm mesh) (Marchand & Elie, 1983).

On site, the temperatures of the sediment (at the surface and at a depth of 7 cm) and of the water column were noted, as well as the depth of the oxydized layer. The upper layer of sediment (2 cm) was sampled to enable granulometric analysis to be effected and total organic matter content (by incineration at 600 °C) and microphytobenthic biomass to be measured (according to Plante-Cluny, 1974). The hydrological parameters of the area were also considered: river flow rate, tidal coefficient, salinity at high water and dissolved oxygen content in the water column, the presence or otherwise of the 'turbidity maximum'.

Multidimensional analyses were carried out on the 48 samples (4 stations 12 months), each of which was characterized by:
- its specific densities;
- the 13 environmental parameters (abiotic and biotic);
- the values of 7 of the abiotic parameters divided into modalities (2 or 4) giving 7 new discontinuous variables.

The analysis of these descriptors was effected using the SPAD programmes (Lebert & Morineau, 1982) on a Mini 6 Gill Honeywell Bull computer at the Ecole Nationale Superieure d'Agronomie in Rennes. There were 4 stages:

a description of the 4 stations using the most characteristic variables;

b correspondence factorial analysis enabling the inertia, factorial axes and factorial coordinates of the samples to be calculated from their classification by specific density; we took:
  - the densities as active continuous variables;
  - the environmental parameters as illustrative continuous variables or illustrative nominal variables if they were modalities;

c cluster analysis of the samples from their coordinates on the first three factorial axes;

Table 1. Sediment and faunistic mean characteristics of the four stations during the period studied.

Sediment parameters	Stations			
	I	II	III	IV
Mean diameter (Md μm)	152	258	258	477
Silts (%S)	76.5	45.3	57.1	18.8
Oxydized layer (O.L. cm)	7	8	12	27
Organic matter (O.M. %)	3.4	3.0	2.0	1.0
Microphyto-benthic biomass (Mpb $\mu g\ m^{2-1}$)	118	107	66	30
Species	N m^{2-1}	N m^{2-1}	N m^{2-1}	N m^{2-1}
L. hoffmeisteri	8,336	4,194	162	60
M. rubroniveus	1,715	940	171	289
B. ligerica	310	158	8	16
S. shrubsolii	84	12	6	8
N. diversicolor	20	36	26	0
M. balthica	4	–	–	–
S. plana	32	4	–	–
Total	10,501	5,344	373	373

d calculation of the correlation matrix on the samples of the most characteristic station in the sector, changing the density scale by logarithmic transformation (Frontier, 1983).

Results

In the mesohaline zone, the four stations studied show mean differing faunistic and sedimentary characteristics (calculated on the year cycle) (Table 1). Station I can be contrasted with others as it is the only one to have muddy sediments with low median granulometry, rich in silts with a shallow oxidized layer. The animal community is made up of 7 species with *Limnodrilus hoffmeisteri*, present in high densities, predominating. Station II with sandy-silt sediments is characterized by a community comprising 6 species and an identical specific diversity index to that of station I. Station III seems to be representative of the area with no parameter being particularly distinctive compared to the average values, although densities are low and specific diversity is maximum in this zone. Station IV is characterized by coarse sediments with little silt, a fairly deep oxydized layer and limited microphytobenthic biomasses. Specific diversity is limited to 4 species in which *Nereis diversicolor* is no longer present.

The correspondence factorial analysis of the 48 samples based on the densities of the 7 species shows the proportion of cumulative inertia as given by the three axes, is as follows (Fig. 4):

- axis 1 : 59.5%;
- Axes 1 & 2 : 83.3%;
- axes 1 to 3 : 95.1%.

Axis 1 compares samples taken during periods of high river flow rates in which *L. hoffmeisteri* is the dominant species with those taken during periods of medium and low flow rates in which *M. rubroniveus*

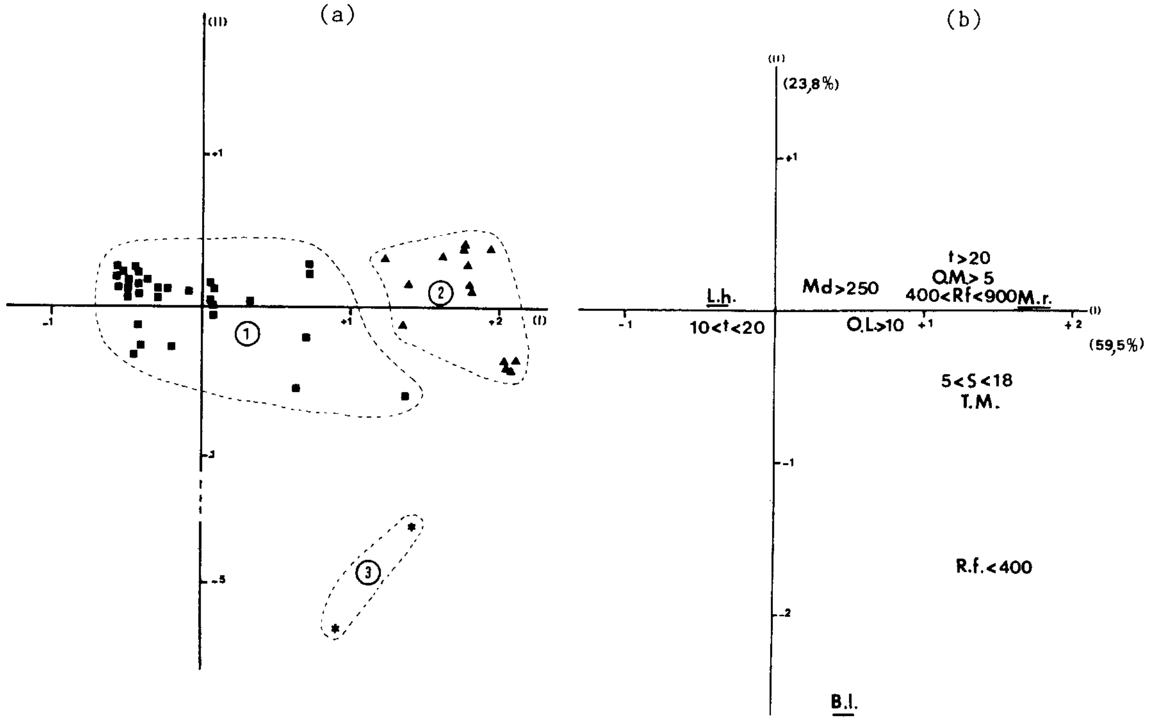

Fig. 4. Positions of the 48 samples (a) and of the principal modalities and species (b) on the two axis from the correspondence analysis. *L.h.* = *Limnodrilus hoffmeisteri; M.r.* = *Monopylephorus rubroniveus; B.I.* = *Boccardia ligerica;* t = temperature (°C); Md = mean diameter (μm); O.L. = oxydized layer (cm); O.M. = organic matter (%); R.f. = river flow (m^3s^{-1}); T.M. = turbidity maxima; S = salinity (‰).

is the leader species. Axis 2 is constructed from the specific character of two samples taken in September. This axis is difficult to interpret and would seem to be due to the random nature of the faunal composition of the samples.

Population dynamics for each one of the four stations (Fig. 5) (Table 2) differs according to the type of substrata. The populations of the muddy sediments (stations 1 to 3) go through approximately the same seasonal variations. The winter transition between class 2 (December) and class 1 (January) was very rapid due principally to the sudden arrival of large quantities of flood water. The spring transition, on the other hand, (class 1 – class 2) was gradual: the samples taken between May and July overlap and can be placed in one class or the other, according to the substratum considered or the manner of effecting the analysis (with or without the September data). In clean sand (station 4), the dynamics of the biotic community are completely independent of the hydrological situation; its biotic characteristics place it in class 1 whatever the season (except in November 1982).

Cluster analysis of the samples from their positions on the first three factorial axes enables the classes to be characterized as follows (Table 2):

Class 1 includes the 33 samples taken between January and May, that is, from the beginning of the limnic phase to the end of the beta-mesohaline phase in spring. This latter phase begins when the river is in spate (flow rate: 5500 $m^3 \cdot s^{-1}$) which means that the environment is well oxygenated, and ends when

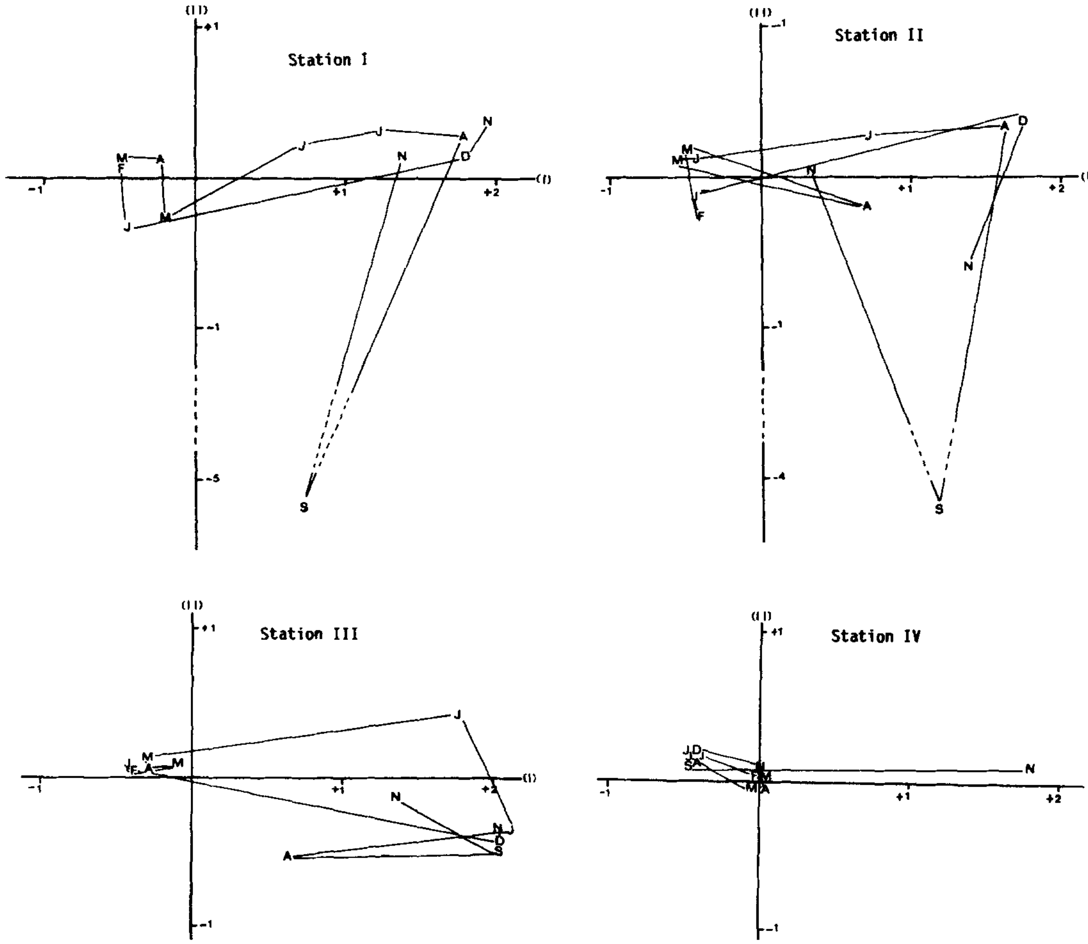

Fig. 5. For each station, projection of the observations (dates of sampling) in the plane of axis 1 and 2 from the correspondence analysis.

Table 2. Characteristics of the clusters from the correspondence analysis with the species (mean densities) and the modalities of the environmental factors.

Species	Classes (CLA)			
	Class 1 (N m2s – 1)	Class 2 (N m2s – 1)	Class 3 (N m2s – 1)	Mean values (N m2s – 1)
L. hoffmeisteri	4,543	241	0	3,188
M. rubroniveus	159	2,442	193	779
B. ligerica	96	78	867	123
S. shrubsolii	9	74	24	28
N. diversicolor	24	15	0	20
M. balthica	0	0	24	1
S. plana	0	0	217	9
Total	4,831	2,850	1,345	4,148
H_N (diversity)	0.55	0.55	1.15	0.57
E_N (eveness)	0.35	0.34	0.83	0.37
Modalities of environmental parameters (MOD)	% CLA/MOD	%CLA/MOD	%CLA/MOD	Number of samples by modality
River flow (Rf m^3s^{-1})				
Rf>2000	100	–	–	4
900<Rf<2000	85	–	–	20
Rf<400	–	–	16.7	12
Salinity (S‰)				
0,5<S‰<5	82.1	–	–	28
5<S‰<18	–	40	10	20
Temperature (t°C)				
10<t<20	–	–	10	20
Dissolved Oxygen ($\%O_2$)				
$\%O_2>75$	82.1	–	–	28
$\%O_2<25$	–	40	10	20
Organic matter (O.M.%)				
O.M.>5	–	75	–	4
O.M.<3	74.4	–	–	39
Oxydized layer (O.L.cm)				
O.L.<3	–	–	20	10
Number of samples	33	13	2	Total = 48

the oxygen content drops below a level of 5 $mg \cdot l^{-1}$. The increase in temperature and decrease in the river flow rate correspond to the arrival of the mud plug. This class of samples concerns all four stations the sediment of which is deficient in organic matter during this period. The densities of *L. hoffmeisteri* reach their maximum values (up to 53000 individuals per m^2 and more in February at station 1) with a number of individuals in their reproductive phase (Fig. 6). Because of the high rate of river flow, bottom predators are scarce and there is little predatory activity (Fig. 7).

Class 2 consists of 13 samples from the alpha-mesohaline phase with oxygen deficient water (less

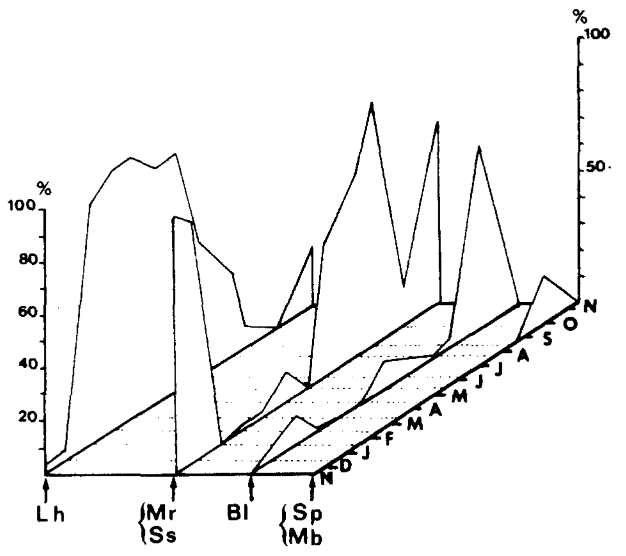

Fig. 6. Seasonal succession of the macrobenthic populations during the period studied.

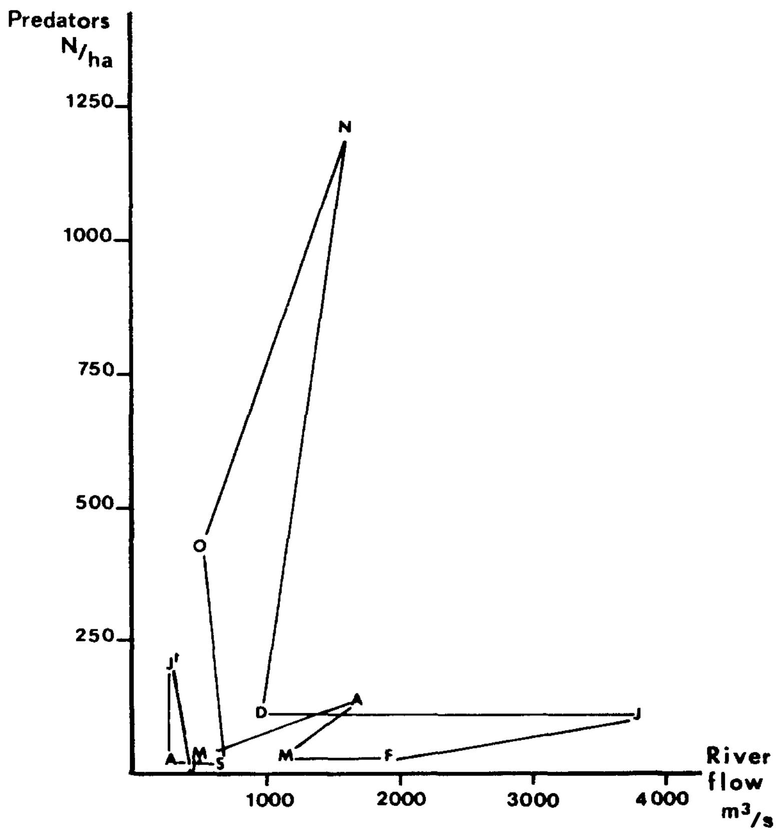

Fig. 7. Seasonal evolution of the abundance of predators in relation with the river flow.

than 20%) on the one hand, and from the beta-mesohaline phase in autumn in which the oxygen content rises to a more acceptable level (50%) on the other hand. The sediments which are rich in organic matter are peopled by a community with *M. rubroniveus* as the dominant species although densities do not exceed 4000 individuals per m^2 (Fig. 6). This class concerns only stations 1 and 2. Predators are scarce at the beginning of summer but become much more abundant in autumn (with maximum numbers in November) (Fig. 7) and predatory activity on the river bottom is intense. These first two classes have in common their low specific composition due to the almost total predominance of one species (Table 2).

The third class concerns only stations 1 and 2 and is limited to September only. Salinity is maximum (16‰) and the environment is oxygen deficient with less than 2 $mg \cdot l^{-1}$ dissolved oxygen content, the oxydized layer being less than 1 cm in depth. The populations had a high diversity index but none was exceptionally abundant, with *Boccardia ligerica* Ferroniere as leader species together with *Scrobicularia plana* (Da Costa) and *M. rubroniveus* (Fig. 6). Analysis shows that it is the association of *B. ligerica*, *S. plana* and *Macoma balthica* (Linne) which is responsible for the specific character of this class. Predatory activity was nil as the predators were absent from this inhospitable zone during this period (Fig. 7).

Because of the large proportion of muddy substrata in the mesohaline zone (95% of the intertidal flats), the correlation matrix between species and the environmental parameters were only established for station 1 (Table 3). Moreover, this station is the only one to show significant seasonal variations when compared to those of the biotope. A significant correlation (with 99.9% reliability) exists between the abundance of *L. hoffmeisteri* and the dissolved oxygen content value (in $mg \cdot l^{-1}$ or as a percentage of saturation). Maximum productivity for this species occurs with a dissolved oxygen level of 10 $mg \cdot l^{-1}$ (in February and March), i.e. 90–95% saturation. The species loses ground if the dissolved oxygen content level falls below 5 $mg \cdot l^{-1}$ and disappears if this value drops below 2 $mg \cdot l^{-1}$. The correlation between abundance and salinity is less well defined ($r = -0.75$), as is that between abundance and temperature ($r = -0.69$). The same is true for abundance in the whole community when its de-

Table 3. Correlations between species and environmental factors according to three significance levels.

	Significance level (p)					
	p<0.001 (r>0.82)		p<0.01 (r>0.71)		p<0.05 (r>0.58)	
df = 10	DATA	r	DATA	r	DATA	r
Correlations between species densities and environmental factors	L.h./O_2	0.85	L.h./S‰	−0.75	L.h./Rf20d	0.58
	L.h./%O_2	0.84	M.r./Rf4d	−0.71	Total/O_2	0.65
			B.l./Mpb	−0.73	H_N/S‰	0.67
					H_N/t	0.67
					L.h./t	−0.69
					M.r./Rf10d	−0.67
					M.r./Rf20d	−0.64
					Total/t	−0.61
					Total/Mpb	−0.64
Correlations between environmental factors	t/S‰	0.89	t/%O_2	−0.79		
	t/O_2	−0.90	t/Rf20d	−0.79		
	O_2/S‰	−0.88	%O_2/S‰	−0.80		
	Md/%S	−0.88	S‰/Rf20d	−0.81		
			O_2/Rf20d	−0.71		

(Rf4d, Rf10d, Rf20d = River flow calculated over 4, 10 or 20 days before sampling).

velopment is plotted against temperature variation ($r = -0.61$) and that of the microphytobenthic pigments. The correlations are less significant for the other species with the exception of *M. rubroniveus*, the abundance of which varies inversely as the increase in the flow rate of the river (especially that calculated over the 4 days before sampling).

Discussion

In the upper reaches of the estuary, the seasonal dynamics of the biotic communities vary according to the type of sediment. Communities are stable but few in number on clean, coarse sand, the movement of which, due to hydrodynamic effects, prevents any colonization. In muddy sediments which are physically more stable than sands, the communities go through three seasonal stages, showing their greater sensitivity to variations in their environment. Their abundance and faunal composition are in close correlation with the 'hydrological' factor which depends on river flow. Such correlations have been observed in other estuaries such as the Thames (Birtwell & Arthur, 1980) or in rivers like the Po (Paoletti & Sambugar, 1984). One of the fundamental aspects of river flow is the effect it has on the estuarine flushing time and its consequences on the biotic community. When the Loire is in spate, a given volume of fresh water can travel 50 kilometres in 24 hours while at low water levels, the flushing time may be as much as 20 days (Ottmann, 1978). The way in which the river bed is colonized by the various species is related to these variations in river flow. In periods of high river flow, the communities of *L. hoffmeisteri* are displaced rapidly through drifting by bed load transport (Birtwell & Arthur, 1980). When the river flow rate is low, the euryhaline marine species are all the more prevalent as the period of low water is more marked and longer. This is true for the newly hatched members of *M. balthica* and *S. plana* which settle momentarily in the muddy sediments in the months of September and October. As far as the typically estuarine species, such as *M. rubroniveus*, are concerned, their communities develop as soon as the haline conditions are favourable but their growth remains limited due to the oxygen deficiency of the biotope during the summer. Such passive and involuntary migrations in a fluctuating environment have already been observed by Chapman & Brinkhurst (1981), Birtwell (1972) and MacLusky (1968). They give rise to a succession of oligospecific associations in which the communities of the leader species cannot attain full development unless the hydrosedimentary parameters correspond in every way to their requirements. The dissolved oxygen regime would seem to be the decisive factor, particularly for *L. hoffmeisteri*, whose capacity for survival in anaerobic conditions has already been demonstrated (Pfannkuche, 1980). In a fresh water environment, Uzunov (1982a, b) has shown the very close interdependence which exists between the dissolved oxygen level, saprobity and the abundance of Oligochaetes: *L. hoffmeisteri*, which is a polysaprobic species, disappears if the dissolved oxygen value falls below 3 to 4 $mg \cdot l^{-1}$ but can survive for a month in anaerobic conditions if the temperature range is favourable. In the Loire, the anaerobic period is coupled with high temperatures and salinity levels (above 20 °C and more than 15‰) as well as considerable turbidity. In autumn, the increase in the river flow rate causes the mud plug to disappear and a few tidal cycles are sufficient for the dissolved oxygen level to rise again to a fairly high level (more than 80%), enabling *L. hoffmeisteri* to settle again in the muddy sediments of the sector. It can thus be observed that the sedimentary parameters (organic matter, oxydized layer) do not play a decisive role in the seasonal dynamics of the biotic communities. The same can be said of their prey (microphytobenthos) and predators (flounder, bream, etc.) the abundance of which is also closely linked to the hydrological regime. The development and growth of plant life is maximum during the summer when the animal communities are fewest in numbers. Fish and crustacea only make their presence felt as predators after the increase in fluvial input in autumn.

Conclusion

Principal component analysis of the parameters of the benthic communities of the upper reaches of the Loire estuary shows that the substratum is an abiotic factor which plays a significant role in their spatial distribution and abundance. The seasonal dynamics of the faunal parameters are governed mainly by the hydrological factors and more especially by the dissolved oxygen regime, itself closely correlated to the river flow rate. The biotic communities of the muddy sediments in which the species characteristic of the environment succeed each other, are more sensitive to abiotic conditions than those of the sandy sediments. Their annual cycle comprises three phases:

- an oligohaline phase of intense colonization during the periods of high river flow rate with displacement of the freshwater species through drifting;
- a mesohaline phase during the summer with degradation of the environment leading to modification and regression of the biotic communities;
- a phase of 'recovery' in autumn linked to the increase in the river flow rate.

References

Birtwell, I. K., 1972. Ecophysiological aspects of Tubificids in the Thames estuary. Ph. D. Thesis, University of London, 504 pp.

Birtwell, I. K. & D. R. Arthur, 1980. The ecology of Tubificids in the Thames estuary with particular references to Tubifex costatus (Clarapede). In R. O. Brinkhurst & D. G. Cook (eds). Aquatic Oligochaete Biology. Plenum Press, New York: 331–381.

Brinkhurst, R. O., 1982. British and other marine and estuarine Oligochaetes. In D. M. Kermack & R. S. K. Barnes (eds), Synopses of the British Fauna (new series). Cambridge University Press 21: 127 pp.

Chapman, P. M. & R. O. Brinkhurst, 1981. Salinity tolerance in some selected Oligochaetes. Int. Revue ges. Hydrobiol. 65: 499–505.

Daget, J., 1976. Les modèles mathématiques en écologie. In Masson (ed.), Paris, Collection d'écologie 8: 172 pp.

Frontier, S., 1983. Stratégies d'échantillonnage en écologie. In Masson (ed.), Paris, Collection d'écologie 17: 494 pp.

Lebart, L. & A. Morineau, 1982. SPAD, système portable pour l'analyse des données. Cesia (ed.), Paris: 244 pp.

Maclusky, D. S., 1968. Some effects of salinity on the distribution and abundance of Corophium volutator in the Ythan estuary. J. mar. biol. Ass. U.K. 48: 443–454.

Marchand, J. & P. Elie, 1984. Contribution a l'étude des ressources benthodemersales de l'estuaire de la Loire: biologie et écologie des principales espèces. In CNRS-CNEXO (ed.), Rapport final du CSEEL. Rapp. Scient. Techn. 55: 89–100.

Ottman, F., 1978. Résumé des conditions hydrologiques et caractéristiques des eaux dans l'estuaire de la Loire. Rapport interne, Université de Nantes: 63.

Paoletti, A. & B. Samburgar, 1984. Oligochaeta of the middle Po river (Italy): principal component analysis of the benthic data. Hydrobiologia 115: 145–152.

Pfannkuche, O., 1980. Distribution and abundance of Tubificidae and Naididae (Oligochaeta) in a brackish-water fjord, with special reference to the α-mesohaline zone. Neth. J. Sea Res. 14: 78–93.

Plante-Cuny, M. R., 1974. Evaluation par spectrophotométrie des teneurs en chlorophylle a fonctionnelle et en phéopigments des substrats meubles marins. In ORSTOM (ed.), Nosy-Be. Doc. Sci. 45: 1–76.

Robineau, B. & J. Marchand, 1984. Distribution des communautés macrozoobenthiques des substrats meubles de l'estuaire interne de la Loire (France). J. Rech. Oceanogr. 9: 146–149.

Tenore, K. R., 1972. Macrobenthos of the Pamlico river estuary N. C. Ecol. Monogr. 42: 51–69.

Uzunov, J. I., 1982a. Dissolved oxygen and saprobity as factors for the distribution of aquatic Oligochaetes in rivers. Hydrobiology 16: 20–30.

Uzunov, J. I., 1982b. Statistical assessment of the significance of both bottom substrata for the distribution of aquatic Oligochaetes in rivers. Limnologica 14: 353–361.