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Long-term Changes in a Mediterranean Benthic Community: Relationships Between the Polychaete Assemblages and Hydrological Variations of the Rhône River

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ABSTRACT: Long-term changes in a macrobenthic, muddy community of the French Mediterranean coast, near the mouth of the Rhône River, were studied using 14 samples collected between 1963 and 1996 at 70-m depth. No drastic change in the community was observed over this time period. A factor correspondence analysis (FCA) performed with the most frequent polychaete species revealed that 3 sample groups were related to trends in the Rhône River discharge. Between 1965 and 1976, the effects of dumping events close to the study site acted in synergy with river drought leading to a drop in the abundance of the most common species of the community (e.g., *Sternaspis scutata*). Floods were observed to be the main factor structuring the polychaete assemblages. These floods were subsequently followed, over a period of several years, by peaks of opportunistic species (*Heteromastus filiformis*, *Prionospio cirrifera*) and, with a time lag of 1 or 2 yr, by peaks of *S. scutata*. Autumn and early winter floods were mainly the result of heavy rainfalls on the Mediterranean part of the drainage basin. They transported large amounts of mineral and particulate organic matter that increased the surface and subsurface deposit feeders assemblages. Late winter and spring floods originated from the north of the basin. They proportionally brought more dissolved material and were followed by developments of suspension and surface deposit feeders. Eutrophication of the area due to increased nitrate concentrations in the river is suggested to be responsible for the abundance, since the 1980s, of small-sized deposit feeders. There is a good parallel between the cumulative mean deviations of the river discharge and the quantity of soles caught in the area with a time lag of 4 yr between these two curves. These results may be of value to the management of the regional resources.

Introduction

Most soft bottom, macrobenthic marine communities along the French Mediterranean coast were described between 1960 and 1970 by Pérès and Picard (1964) and their co-workers, for the Marseille' region, and by Guille (1970) to the west of this area. Since then, these communities have been subjected to severe anthropogenic disturbancies (e.g., harbor installations, domestic and industrial sewages). Following these perturbations, impact studies have been carried out on point sources (Salen-Picard et al. 1997; Massé 1998; Bellan et al. 1999) but no long-term continuous monitoring has been performed. Data on temporal changes of these Mediterranean benthic communities are not available in contrast to data collected from other marine areas: the Baltic Sea (Bonsdorff et al. 1997), Chesapeake Bay (Dauer 1997), the North Sea, and the Channel French coast (Dauvin and Ibanez 1986; Carpentier et al. 1997). Owing to this lack of data, relationships between changes due to anthropogenic perturbations and changes due to more global events (such as climatic changes) are poorly understood. In a previous study (Salen-Picard et al. 1997), it was suggested that the circalittoral muddy bottom community of the Marseille' region had changed as a result of both the construction of an important port and the variations in the outflow of the Rhône River during the investigated period (1963–1993). We hypothetized that changes observed at the deeper site were mainly due to hydrological changes of the river. In order to confirm this hypothesis, annual sampling of this deeper site was performed from the summer of 1993 to the summer of 1996. The aim of the present study was to assess the long-term changes (1963–1996) that occurred in the macrobenthic community and to determine their relation to hydrological variations of the Rhône River.

Materials and Methods

AREA OF INVESTIGATION AND SAMPLING SITE

The area of investigation is situated in the eastern part of the Gulf of Lion, 3.2 nautical miles east of the Rhône River mouth (Fig. 1). Fluvial waters initially flow out northwest-southeast and are subsequently diverted to the southwest by the Liguro-Provenço-Catalan current, which controls water circulation in the northwestern Mediterranean basin (Millot 1990). The size and position of the river

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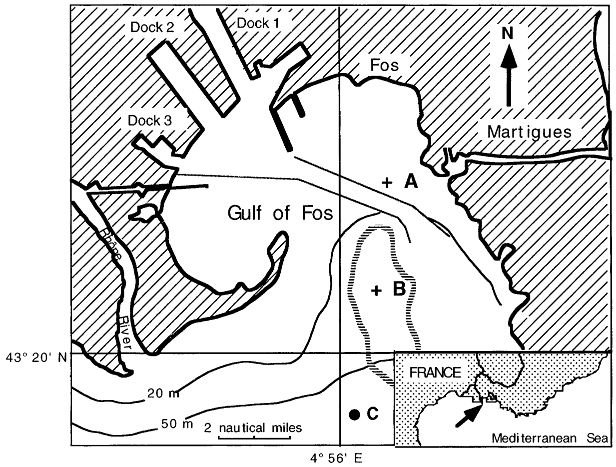

Fig. 1. Location of the study site. Three sites (A, B, and C) have been the object of a previous study (Salen-Picard et al. 1997). Site C (●, 70 m depth, 43°18′36″N, 4°56′85″E) was chosen to assess the relationships between the macrobenthic community and hydrological variations of the Rhône River. ▤ = dumping area.

plume are influenced by the flow rate of the river and the strength and direction of the winds, with 45% of these winds blowing from the northwest (Lochet and Leveau 1990). River flow data were obtained from the Compagnie Nationale du Rhône, and measurements were taken at Beaucaire, 65 km from the river mouth. Annual mean flow over the period 1920–1996 was 1,697 m^3 s^{-1}. The regime exhibits maximum flows from November to March and minimum flows in summer. The regime varies from less than 500 m^3 s^{-1} in summer to more than 10,000 m^3 s^{-1} during flooding periods. A flood is usually defined as a discharge of over 3,000 m^3 s^{-1}. The river is the main source of sediment for the continental shelf of the Gulf (Zuo et al. 1991), the solid discharge being estimated at 1.4×10^6 to 16.4×10^6 t yr^{-1} (Pont 1997). The sediment on the continental shelf, at depths between 10 and 120 m, is made of very fine mud with a silt content of more than 90% of the total dry weight. The macrofauna benthic community was first described as ''biocénose de la Vase Terrigène Côtière'' by Pérès and Picard (1964, p. 94). The maximum richness in term of characteristic species, sensu Picard (1965), and individuals was observed at depth between 40 and 80 m (Salen-Picard 1982). From 1965 to 1977, the area was affected by the dredging of the docks and the access channel of the port of Fos and by the dumping of the dredged material at sea. Dumping was performed from 1965 to 1977 with an interruption of one year in 1975. This dumping led to dramatic changes in the benthic community both in shallow water (site A, 15 m depth, Fig. 1) and in the dumping area (site B, 30–60 m depth; Salen-Picard 1981; Salen-Picard et al. 1997). In order to determine the relationship existing between changes in the community and the hydrological variations of the Rhône River, the site choosen in the present study (site C, 70 m depth) was situated outside of the dumping area.

FAUNISTIC DATA

Macrofauna samples were obtained in either spring or summer in 1963, before the beginning of the construction of the port, during the dumping period (1969, 1972, and 1976), during a dumping interruption (1975), and then every year, from 1984 to 1986 and from 1993 to 1996. The first four samples (1963, 1969, 1972, and 1975) were performed using a Charcot-Picard dredge. In order to collect the main species, a sediment volume of 50 L was required (Picard 1965). For each sampling event, this volume of sediment was washed through a 1.5-mm mesh size. From 1976 onward, samples were taken using a Smith Mac Intyre grab. With this grab, four replicates were needed to obtain the appropriate volume of sediment which were then washed through a 1-mm mesh size. Samples were immediately fixed in 10% neutral formalin. All individuals were sorted under a binocular microscope. Only annelid polychaetes were studied. They represented 65% to 75% of the species present and 80% to 95% of individuals. The change in mesh size required that, for most species, a correction factor be applied as described by Salen-Picard et al. (1997). Small species such as Paraonids, Cossurids, Pilargids, numerous Cirratulids, and some Spionids such as *Prionospio fallax* were never collected on the 1.5-mm mesh size sieve, so it was not possible to calculate a correction factor for these smaller organisms.

DATA ANALYSIS

A factor correspondence analysis (FCA) was performed after having encoded species abundance as follows: 0 = 0, 1 = 1, 2 to 10 = 2, 11 to 100 = 3, 100 to 1,000 = 4, and 1,000 to 10,000 = 5. Rare species were removed from the FCA as described by Ibanez et al. (1993). Small species, for which we could not calculate a correction factor, were also removed. Monthly deficits or excesses of the river discharge over the 12 mo before the sampling dates were used as additional variables. These values were coded in the same way as were the abundances. Relationships between Rhône flow data and the abundances of certain species were studied using a simple graphic method. This method was also applied to assess the relationship between flow data and the percentages of feeding types. Species were allocated to three feeding types: mixed (suspension and surface deposit feeders), subsurface

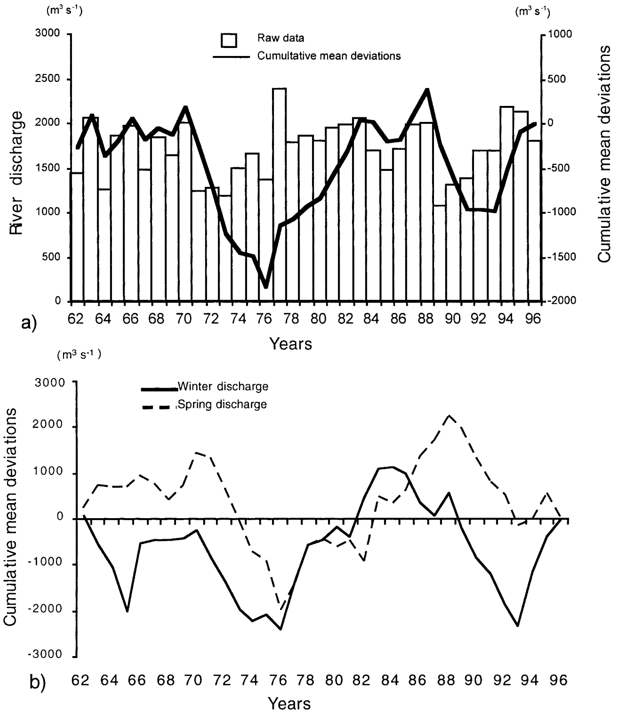

Fig. 2. The Rhône River flow from 1962 to 1996. a) The mean annual discharge (raw data) and the trends displayed by the cumulative mean deviations (the mean value was 1,703 m^3 s^{-1}). b) Trends in winter and spring discharges (the mean values were 2,011 and 1,947 m^3 s^{-1}, respectively).

deposit feeders, and carnivores-omnivores (Fauchald and Jumars 1979; Ibanez and Dauvin 1988). In samples obtained using the same method (i.e., since 1976), species ranks were attributed as a function of abundance. The cumulative mean deviations were used to display the trends in the Rhône River discharge. The reference value was the annual discharge of the river calculated over the 1962–1996 period of time.

Results

RHÔNE DISCHARGE TENDENCIES

The mean Rhône discharge during the period spanning from 1962 to 1996 was 1,703 m^3 s^{-1}. Mean annual discharge (Fig. 2a) was at a maximum in 1977 (2,388 m^3 s^{-1}) and a minimum in 1989 (1,074 m^3 s^{-1}). The long-term trend of the mean annual discharge exhibited a period of relative stability (1962–1970) and two periods of decreased discharge (1970–1976 and 1988–1993) which were followed by increases (1976–1988 and 1993–1996). These upward tendencies were due to several important floods. Floods occurred mainly in winter (November to February) or spring (March to June). The 1976–1988 upward tendency (Fig. 2b) was related, for a period of 6 yr (1976–1982), to both winter and spring discharges. Following this 6-yr period, the spring discharge was almost exclusively responsible for the changes. The upward tendency observed in the 1990s was mainly due to winter discharges.

FCA ANALYSIS

Fifty-five polychaete species were collected. FCA was performed with 27 of these species that were present in at least six samples. The three first axes described 60.9% of the total inertia. Only the first two axes (29.8% and 18.5% of the total inertia, respectively) were retained for the interpretation. On these two axes, 9 samples and 12 species presented a contribution higher than that generated by the hypothesis of an equal contribution of each sample or species to one axis (CTR = 7.1% and 3.7%, respectively). Axis I and II separated three groups (Fig. 3a). Position of axis I was determined from samples collected in 1994 to 1996 (ΣCTR = 54%). This group was characterized by *Ophiodromus flexuosus, Nerinides tridentata, Prionospio cirrifera, Prionospio ehlersi, Poecilochaetus serpens,* and *Heteromastus filiformis* (Fig. 3b). Projections of January and, to a lesser extent, October and December flow excesses clustered with this group. Two groups were associated with negative values of axis I and were separated along axis II. The more homogenous of these two groups was made up of samples obtained during the years 1975, 1978, and 1979 (ΣCTR on axis II = 31.7%). Projections of spring flow excesses clustered close to this last group, and *Diplocirrus glaucus* and *Magelona alleni* were its characteristic species. Although it weakly contributed to the position of the first two axis, the 1985 sample had its best correlation on axis II (R^2 = square cosine = 0.387) and was added to this group. The third group included samples which contributed to either axis I (1976: 18.9%) or axis II (1963: 30.1%, 1972: 12.1%). Only flow deficits clustered with this group which also included samples taken during the dumping period. *Clymene gracilis* and *Paraprionospio pinnata* were the most characteristic species of this last group.

CHANGES IN ABUNDANCE

According to the FCA analysis, species which contributed to the position of axis I (positive values) were more abundant during years of high winter flow (Fig. 4a). In contrast, *Clymene gracilis* (Fig. 4b; negative values of axis I) was never sampled during the years 1994 to 1996, a period characterized by a very high winter flow. This was also the case of *Notomastus latericeus,* although the contribution of this last species to the first axis was low. *D. glaucus,* which contributed to the position of axis II (negative values), was abundant when spring

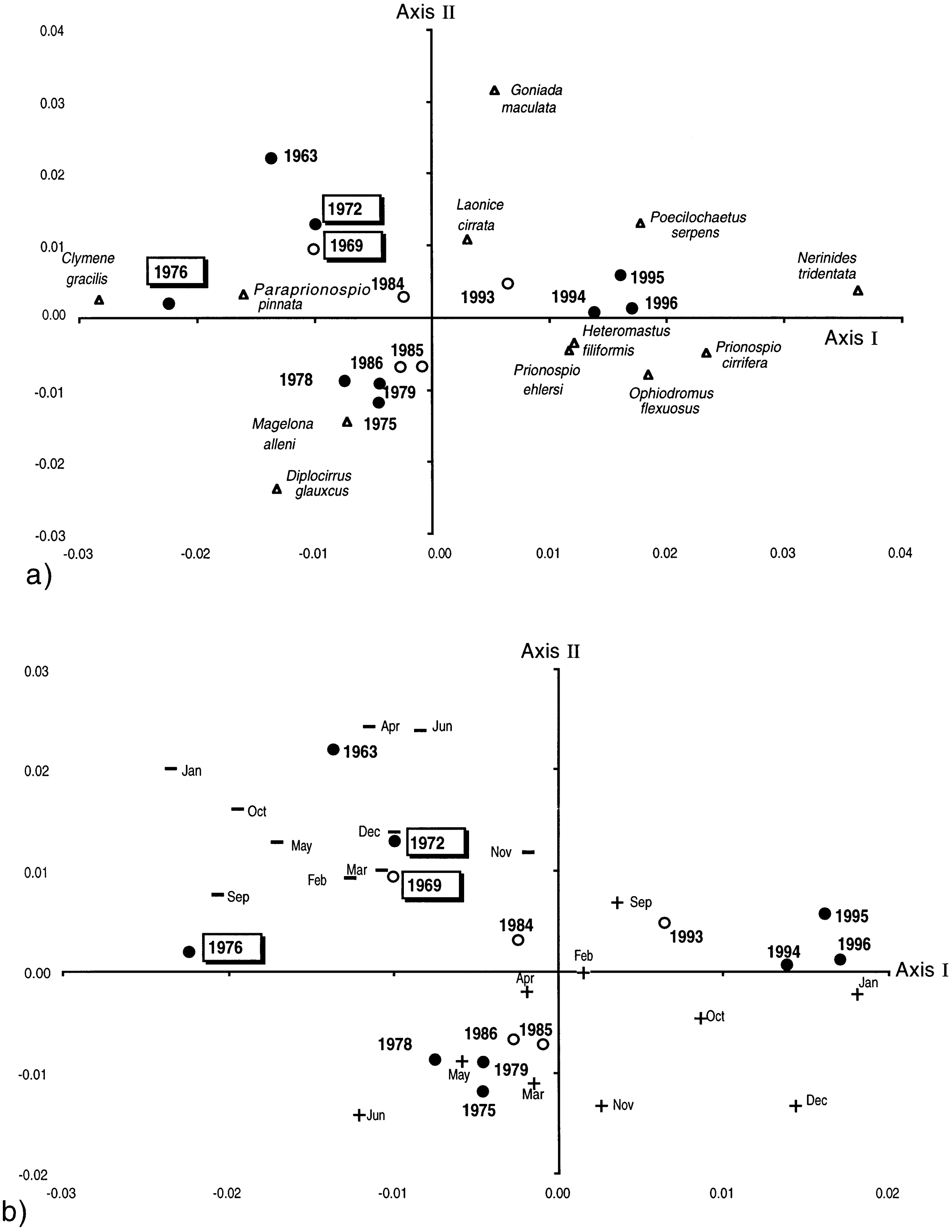

Fig. 3. FCA of the fourteen samples. Projection in the plane of factorial axis I and II of a) structuring species (△) and structuring samples (●). ○·: samples which weakly contribute to the two first axis. b) of samples (● and ○) and additional variables: monthly deficits (−) or excesses (+) of the river discharge. Excesses and deficits from July and August were not used. Dumping years are in boxes.

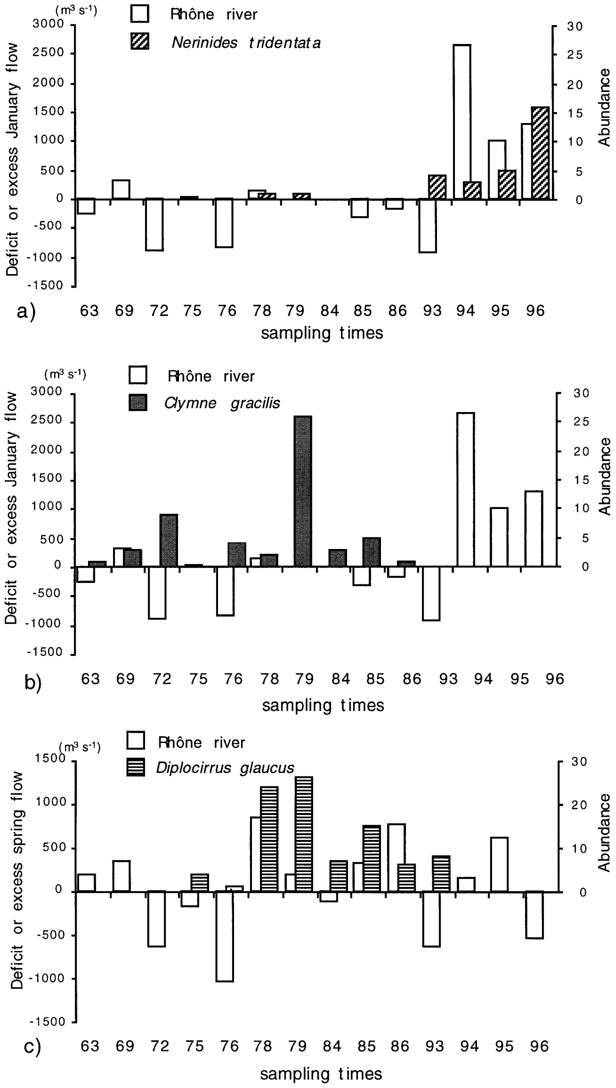

Fig. 4. Abundance, in 50 L of sediment, of a) *Nerinides tridentata* and b) *Clymene gracilis* compared with the Rhône River flow for the month of January preceding the sampling period; c) abundance of *Diplocirrus glaucus* compared with the Rhône River flow during spring (March to June) before the sampling period.

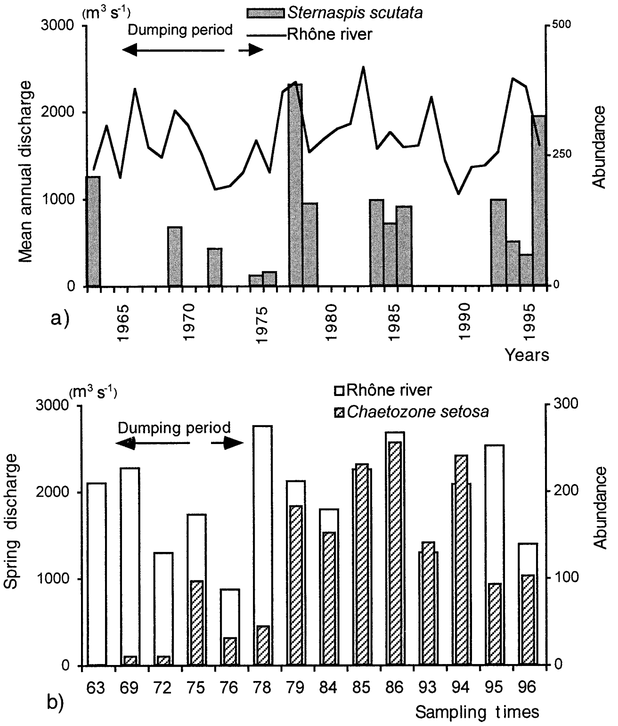

Fig. 5. Abundance, in 50 L of sediment, of the two most abundant species in the community during the study. a) *Sternaspis scutata* abundance was compared with the mean annual discharge of the Rhône River, b) *Chaetozone setosa* abundance was compared with the spring discharge of the river before the sampling period.

flow was in excess: years 1978, 1979, and 1985 (Fig. 4c). *Chaetozone setosa* and *Sternaspis scutata* were the two most abundant species in the community during the survey. Present in almost all samples, these species did not contribute to inertia. *S. scutata* abundance was compared with the mean annual discharge of the river (Fig. 5a). Minimum abundance values for this species (1975–1976 and 1995) were observed after several years of drought (1970 to 1976 and 1988 to 1993). Peaks of *S. scutata* (years 1978 and 1996) occurred after several years of high annual discharge (1977–1978 and 1994–1995). *C. setosa* was seldom collected before 1975. Changes in its abundance reflect those of mean spring flow (Fig. 5b).

RANKING OF SPECIES

For each sample, the five most important species in order of abundance are listed in Table 1. These five species represented at least 50% of the sample abundance. Before 1976, *S. scutata* was the top-ranked species. From 1976 onward, this species tended to be outnumbered by *C. setosa* and, in the 1990s, by *Levinsenia* sp. Nine other species were frequent throughout the survey. *Glycera rouxii, Nephtys hystricis, Ninoe armoricana, Anobothrus gracilis,* and *Terebellides stroemi* were present in all samples and *Lumbrineris latreilli, Lumbrineris emandibulata mabiti, Prionospio dubia,* and *Tharyx heterochaeta* were in 93% of these. With the exception of *T. heterochaeta,* the abundance of all these species was higher after flooding than after drought and reached a maximum after the 1978–1979 floods. Most of these nine species were temporarily among the five first top ranked species. Several small-sized species entered the top five group during the 1980s (*Levinsenia* sp. and *P. fallax*) and 1990s (*P. cirrifera* and *H. filiformis*).

TABLE 1. Ranking of the five most important polychaete species in order of abundance in each sample taken since 1976.

Species	1976	1978	1979	1984	1985	1986	1993	1994	1995	1996
Chaetozone setosa	1	4	1	2	1	1	2	1	2	2
Sternaspis scutata	2	1	2	1	2	2	1	4	3	1
Ninoe armoricana	3		4						5	
Nephthys hystricis	4									
Lumbrineris latreilli	5	2	3	5	5		4			
Prionospio dubia		3								
Anobothrus gracilis		5	5							
Tharyx sp.				3	4		3	5	5	
Tharyx heterochaeta				4	3	3		3	4	
Prionospio fallax						4			5	
Levinsenia sp.						5		2	1	4
Lumbrineris emandibulata mabiti							5			
Prionospio ehlersi							5			
Prionospio cirrifera										2
Heteromastus filiformis										5

Trophic Categories

The proportions of feeding types were compared with the seasonal discharges of the river. The proportion of mixed species (suspension and surface deposit feeders, Fig. 6a) was high in 1975, the year during which dumping was interrupted, and subsequently, tended to change with spring discharge. Following the cessation of the port construction activities, variations in the percentage of subsurface deposit feeders seeemed to be related to winter discharge (Fig. 6b). Carnivorous and omnivorous species never exceeded 20% of total individuals, except during the dumping period: 35.3% in 1972 and 36.8% in 1976.

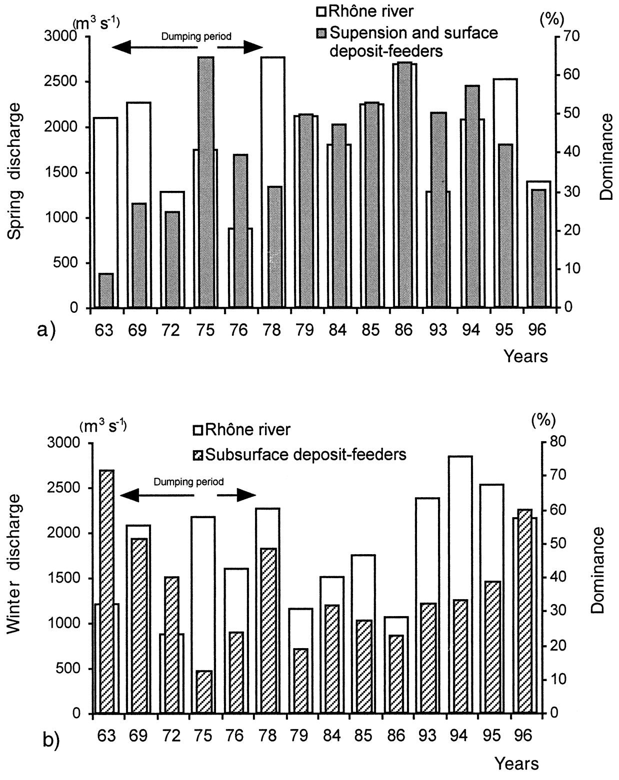

Fig. 6. a) Dominance (expressed as percent) of suspension and surface deposit feeders compared with the mean flow of the river during late winter and spring (February to June) preceding the sampling period. b) Dominance of subsurface deposit feeders compared with the mean flow of the river during autumn and early winter (October to January) preceding the sampling time.

Discussion

CHANGES IN THE POLYCHAETE ASSEMBLAGE AND HYDROLOGICAL VARIATIONS OF THE RHÔNE RIVER

As shown by projections and contributions of samples and additional variables in the plane of the first two axes of the FCA, the macrobenthic community off the Rhône delta responded to the hydrological changes of the river. Changes in community structure would appear to be related to hydrological periods of the Rhône: period of relative stability in annual yield or of drought (1963 to 1976) and periods of upward tendencies (1977 to 1988 and 1993 to 1996). Upward tendencies were due to successive and severe floods. Floods occurred mainly in late winter and spring between 1977 and 1988 and in autumn and early winter from 1993 to 1996 (Table 2). Samples taken during these two periods were well separated. It is clear that the response of the community varied according to the flooding season.

Numerous studies performed in estuarine areas deal with physical and physiological disturbances that are enhanced by low salinity and low dissolved oxygen levels (Jones 1987; Palacin et al. 1991; Schiedek and Schöttler 1991; Le Bris and Glémarec 1995; Tahey et al. 1996). Others have focussed on the consequences of eutrophication on a large temporal scale (Beukema 1991; Dauer 1997). Effects of small temporal changes in river inputs and

TABLE 2. The most important floods of the Rhône River between 1962 and 1996.

Years	Flooding Months
1977	February and May
1978	February and March
1979	February
1983	April and May
1986	April and May
1992	November
1993	October
1994	January and November
1995	January to June
1996	January, November, and December

the links between these inputs and deeper marine benthic infauna communities are less known. Following severe floods, Moverley et al. (1986) observed colonization in Australian estuaries by either the same species (e.g., *S. scutata*) or species related to those which were observed to be abundant off the Rhône delta (e.g., *Mediomastus* sp., *Cossura* sp., and Spionids). In the Skagerrak-Kattegat area, Josefson et al. (1993) examined the changes occurring in benthic communities and concluded that the faunal changes were a response to sedimentation of pelagic production, this pelagic production being enhanced by land runoff. They also admitted the possibility of the influence of other factors such as changes in temperature and salinity. The site of the present study is located beneath the Rhône plume. According to both sampling depth and the absence of turbulence induced by tides (Broche et al. 1998), salinity within the bottom layer is high and remains contained between 37.5 and 38 (Salen-Picard unpublished data). The input of nutrients and mineral material from the river into the Mediterranean Sea is particularly high during flood periods (Cauwet 1995; Pont 1997; Moutin et al. 1998). Floods can provide organic matter that is directly available to the benthic fauna. In addition, as is true of all hydrological fronts (Largier 1993; Josefson and Conley 1997), the river plume is an area of high in-situ production (Kirchman et al. 1989; Gaudy et al. 1996) which can, after having settled, enhance benthic production. From 1993 onward, the percentage of organic matter in the superficial sediment was seen to vary from 7.5 to 12.5, the highest value being reached after the floods of October 1993 (daily flow on October 10: 9,450 $m^3 s^{-1}$) and January 1994 (daily flow on January 8: 10,610 $m^3 s^{-1}$). Changes observed in the benthic community may be a result of changes in the organic matter input.

ECOLOGICAL STRATEGIES AND SPECIES RESPONSES

All of the polychaete species observed to be abundant within the community over the survey period are known to live in environments rich in organic matter and are able to exploit these resources (Pearson and Rosenberg 1978). Among them, at least two types of ecological behavior, reflecting a particular demographic strategy, have been recognized. The first kind of behavior is observed for opportunistic species such as *P. cirrifera, N. tridentata, H. filiformis,* and *D. glaucus.* These species have a high growth rate and are able to adapt their reproductive features in order to rapidly exploit pulses of organic matter. In the present study, they responded at least during the 12 mo following a given flood. Their abundance changed with monthly or seasonal river flow. Being present or dominant only for several months following the floods (''série à lacune'' according to Ibanez and Fromentin 1997, p. 13), their contribution to inertia was high. The permanent and abundant species of the community, such as *S. scutata,* exhibited a different pattern of behavior, which was characterized by a low growth rate and long reproductive period. Population increases of these last species were observed later (1 or 2 yr after the beginning of a given flooding period). Maximum abundances of these species were maintained over several years (''série à tendance monotone'' according to Ibanez and Fromentin 1997, p. 13). Their abundance changed like variations of the annual discharge of the river. Moverley et al. (1986) also described plateau densities of macrobenthic species after flooding, although they recorded a time lag of 5 yr. These last authors described a recolonization pattern following the disappearance of the initial communities by flood-induced scouring. This may explain the discrepancy between their results and those of the present study. Our results are in agreement with those of Josefson et al. (1993) who found that the best correlation between macrofauna parameters and land runoff were obtained when the benthic variables lagged runoff with 1 and 2 yr. In the same way, according to Beukema (1991), the zoobenthic biomass in the Wadden Sea responded to changes in chlorophyll concentration with an expected time lag of nearly 2 yr.

COMMUNITY RESPONSES AND FLOODING SEASON

Community responses to floods differed as a function of flooding season. After winter floods, subsurface deposit feeders were numerically dominant in the community, whereas, after spring floods, suspension and surface deposit feeders prevailed. The catchment area of the river is subject to various hydroclimatic influences (Vivian 1989). Pont (1997) recognized two main flood types. The Mediterranean type is the result of heavy rainfalls on the southern part of the basin. Floods are sudden and violent and bring to the sea most of the annual particulate organic and mineral input (Cauwet 1995; Pont 1997). For the Oceanic flood type, the floods are due to rainfall from the Atlantic Ocean falling on the upper part of the basin. These floods transport small quantities of suspended matter to the sea. These floods bring, proportionally, more dissolved material than do Mediterranean floods. They take place in late winter and spring, just before or during spring water warming, and enhance marine phytoplanktonic and microphytobenthic blooms. Suspension feeders such as *A. gracilis* and *T. stroemi,* in addition to species that feed at the water-sediment interface such as *D. glaucus, M. alleni, C. setosa,* and other Cirratulids, preferentially use this food resource. The three sample groups separated along the first two axes of the FCA (Fig. 3a) corresponded to samples taken following high Mediterranean floods (positive values of axis I), samples taken after high Oceanic floods (negative values of axis I and axis II), and samples taken after several years of drought (negative values of axis I and positive values of axis II). From the positive to negative values of axis I and from axis I to axis II of the FCA, there was a decrease in the quantity of the particulate organic matter brought to the sea by the Rhône River.

Mediterranean floods occur mainly in autumn and early winter. Because of their high mineral load, they may inhibit suspension feeders and non free-living polychaetes such as *C. gracilis* and juveniles of *N. latericeus* (Wilson 1937, in Fauchald and Jumars 1979). Particulate organic matter arriving to the sea during this type of flood is constituted of detritus removed from soils by erosion, detritus from freshwater production, and anthropogenic wastes (Cauwet 1995). Development of blooms in situ is also possible. Despite the fact that the particulate organic matter brought by rivers is weakly biodegradable (Cauwet 1995), surface deposit feeders (e.g., the Spionids *N. tridentata, P. cirrifera,* and *P. fallax*) and free-living subsurface deposit feeders (e.g., *S. scutata, H. filiformis,* and Paronids) seem to be able to take advantage of these inputs with a time lag that depends on their reproductive features. We do not know the degree to which this food resource is available to consumers, but it may help explain the benthic successional dynamics and lags observed: surface and small subsurface deposit feeders living close to the surface are the first to use this resource, whereas deeper burrowing subsurface deposit feeders make use of it later and over a longer time frame (Moverley et al. 1986; Blake 1993).

Effects of Other Disturbance Factors: Dumping Operations, Eutrophication, and Pollution

During the dumping periods, organisms that feed at the water sediment interface were inhibited by both the turbidity and instability of the superficial layer. Subsurface deposit feeders were not, as was seen after floods, stimulated by the sedimentation of a material probably possessing a low organic matter content. Inhibition of the larval settlement and high juvenile mortality (Rosenberg 1977) led, as was seen during drought periods, to low abundances, the minimum being reached in 1976, when drought and dumping acted in synergy. Numerous small-sized, deposit-feeding species have become more abundant since the 1980s. Despite the difference of methods and differences in the Rhône regime, this observation may be attributable to the global eutrophication of coastal marine areas (Beukema 1991; Josefson et al. 1993; Bonsdorff et al. 1997), the mean annual nitrate concentration in the Rhône having increased by about 50% during the last two decades (Moutin et al. 1998). The Rhône flow also controls the arrival of pollutants such as heavy metals (Chiffoleau et al. 1995), radionuclides (Thomas and Noël 1995), pesticides, and hydrocarbons (Milano et al. 1986). These pollutants react with nutrients in an antagonistic way. Field studies do not permit us to assess their impact. Most of the dominant species of the present study are more abundant near the river mouth than at the study site (Salen-Picard unpublished data), which would tend to suggest that they have a low sensitivity to pollutants transported by the river.

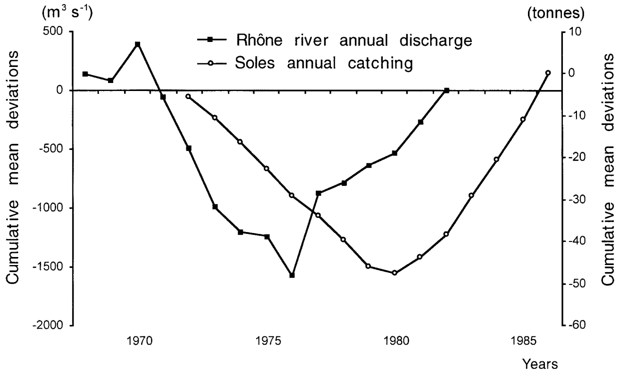

Fig. 7. The Rhône River trends from 1968 to 1982 and trends in the quantity of soles landed in the port of Martigues from 1972 to 1986.

Consequences on Other Components of the Food Web

We calculated the cumulative mean deviations of both the mean annual Rhône flow and the weight of soles landed in Martigues (Fig. 1) from 1972 to 1986, period of constant fishing effort. The tendency of these two parameters (Fig. 7) presents a good parallel with a time lag of about 4 yr (Spearman correlation rank = 0.907, $p < 1$‰). The minimum fishing size authorized for *Solea solea* is 24 cm (European Economic Community, July 10, 1986). According to the growth curve of this species (Quéro 1997), a time lag of 4 yr would correspond to the time necessary for the fish to reach this fishing size. Sutcliffe (1972) demonstrated correlations between St. Lawrence River discharge and catches of several commercial species with a 5 to 10 yr slip and suggested that land runoff was perhaps affecting larval survival or growth. As polychaetes are the main food source for adults of *S. solea* (Quéro 1997), an increase in available food could also stimulate their reproduction. Long-term data collection and confirmatory statistics are required to determine environmental effects on fisheries (Drinkwater and Myers 1987).

Conclusions

The macrobenthic, muddy community of the continental shelf under the Rhône River plume exhibits variations closely related to both flow variation and levels of eutrophication. River floods are observed to be the main factor structuring the community. The community response differs according to the geographic origin of the flood. These floods act on the different components of the food web as pulses of organic matter. These pulses are available to the benthic community with time lags that depend on the feeding ethology and biology of the species. It is clear that new data sets must be generated to increase our knowledge and understanding of the biological responses to these inputs. The question of whether such knowledge will aid in the sound management of regional marine resources remains to be determined.

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