

# Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean)

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Harmelin–Vivien, M. L., Bănaru, D., Dierking, J., Hermand, R., Letourneur, Y. & Salen–Picard, C., 2009. Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean). *Animal Biodiversity and Conservation*, 32.2: 135–145.

## Abstract

*Linking benthic biodiversity to the functioning of coastal ecosystems subjected to river runoff (NW Mediterranean).*— Continental particulate organic matter (POM) plays a major role in the functioning of coastal marine ecosystems as a disturbance as well as an input of nutrients. Relationships linking continental inputs from the Rhone River to biodiversity of the coastal benthic ecosystem and fishery production were investigated in the Golfe du Lion (NW Mediterranean Sea). Macrobenthic community diversity decreased when continental inputs of organic matter increased, whereas ecosystem production, measured by common sole (*Solea solea*) fishery yields in the area, increased. Decreases in macrobenthic diversity were mainly related to an increasing abundance of species with specific functional traits, particularly deposit–feeding polychaetes. The decrease in macrobenthic diversity did not result in a decrease, but an increase in ecosystem production, as it enhanced the transfer of continental POM into marine food webs. The present study showed that it is necessary to consider functional traits of species, direct and indirect links between species, and feedback loops to understand the effects of biodiversity on ecosystem functioning and productivity.

Key words: Diversity, Production, Polychaetes, Common sole (*Solea solea*), Fisheries.

## Resumen

*Relación de la biodiversidad bentónica con el funcionamiento de los ecosistemas costeros sujetos a las descargas fluviales (NO del Mediterráneo).*— La materia orgánica particulada (MOP) continental juega un papel principal en el funcionamiento de los ecosistemas marinos costeros, tanto como factor perturbador como en forma de input de nutrientes. Se han investigado las relaciones entre los inputs continentales aportados por el río Ródano con la biodiversidad de los ecosistemas bentónicos costeros y la producción de las pesquerías en el golfo de León (NO del Mediterráneo). La diversidad de la comunidad macrobentónica disminuía cuando aumentaban los inputs continentales de materia orgánica, mientras que la producción del ecosistema, medida mediante el rendimiento pesquero del lenguado común (*Solea solea*) según las capturas en dicha zona, aumentaba. El descenso de la diversidad macrobentónica se relacionó principalmente con la abundancia de especies con rasgos funcionales específicos, particularmente de poliquetos depositívoros. Dicha disminución de la diversidad macrobentónica no tuvo como resultado un descenso, sino un aumento de la producción del ecosistema, estimulada por la aportación de MOP continental a las redes tróficas marinas. Este estudio pone de manifiesto que es necesario considerar los rasgos funcionales de las especies, las relaciones directas e indirectas entre las especies, y los bucles de retroalimentación, para entender los efectos de la biodiversidad sobre la productividad y el funcionamiento de los ecosistemas.

Palabras clave: Diversidad, Producción, Poliquetos, Lenguado común (*Solea solea*), Pesquerías.

(Received: 25 V 09; Conditional acceptance: 16 X 09; Final acceptance: 28 X 09)

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## Introduction

Relationships between biodiversity, disturbance, and production differ from one ecosystem to another and are complex and difficult to untangle. Understanding these relationships is a major challenge in the context of global warming and rapid climatic change because disturbances are presumed to increase in frequency and intensity (Loreau et al., 2001; Schmitz et al., 2003). The functional aspects of biodiversity and the impact of changes in species diversity on relationships within communities and on energy transfer and productivity in food webs are a question of debate (Loreau, 2000; Worm & Duffy, 2003). Marine coastal ecosystems are open systems subjected to fluctuations in environmental factors. Such variability can constrain the above-mentioned relationships, as discussed by Loreau (2000), Hulot et al. (2000) and Worm et al. (2002). In this context, estuarine and deltaic areas are of particular interest, as they are subjected to highly variable environmental conditions (salinity, sedimentation, nutrient concentration) due to fluctuations in river inputs, which are in turn controlled by precipitation and climatic conditions (Nohara et al., 2006). Continental matter brought by rivers to the sea plays a major part in the functioning of coastal marine ecosystems (Caddy, 2000; Cartes et al., 2007). Importantly, it can represent both a disturbance due to high sedimentation rates, and a resource supply in form of inputs of dissolved and particulate organic matter (Cloern, 2001). An important question in this setting is how changes in biodiversity affect the transfer of energy in such ecosystems.

In this study, our objective was to investigate the relationships between biodiversity of macrobenthic communities, transfer of continental particulate organic matter (POM) and secondary production in a coastal marine benthic system subjected to high continental inputs, using variations in river flow as a natural experiment. This paper is a synthesis of several studies on macrobenthic communities (Salen-Picard & Arlhac, 2002; Salen-Picard et al., 1997, 2003; Hermand et al., 2008) on the role of continental POM in the functioning of coastal ecosystems (Darnaude, 2005; Darnaude et al., 2004a, 2004b), and on demersal fish catches (Campillo, 1992; Salen-Picard et al., 2002) performed in the Golfe du Lion (NW Mediterranean Sea), an area subjected to inputs of the Rhone River.

## Materials and methods

Detailed descriptions of methodologies and data analyses are available in the references cited.

### Study site

All studies were conducted in the northern part of the Golfe du Lion from the Bay of Marseille to the Rhone River mouth, 30 km westwards (43° 08' – 43° 27' N, 4° 00' – 4° 56' E) (fig. 1). Since the damming of the Nile River in the 1970s, the Rhone has been the largest river flowing into the Mediterranean Sea, with a mean

water discharge of 1,700 m<sup>3</sup> s<sup>-1</sup>. During strong flooding events the Rhone discharge can exceed 11,000 m<sup>3</sup> s<sup>-1</sup>, as observed during winter 2003 (Antonelli et al., 2008). The mean annual solids discharge is estimated at 7.4 10<sup>6</sup> t year<sup>-1</sup> and can reach 22.7 10<sup>6</sup> t in years with strong flooding events (Pont et al., 2002). Mean annual sedimentation rates vary from 0.15 g cm<sup>-2</sup> year<sup>-1</sup> on the mid-shelf to 40 g cm<sup>-2</sup> year<sup>-1</sup> near the river mouth, with a maximum between 30 and 50 m depth (Zuo et al., 1997; Durrieu de Madron et al., 2000). Decreases in salinity due to mixing with freshwater in the river plume is observed only in surface water (0–6 m) (Naudin et al., 2001) and does not affect soft-bottom communities located deeper.

### Macrobenthic community

The macrobenthic community of the Golfe du Lion at 50–70 m depth was characteristic of coastal terrigenous muddy bottoms, with low overall species richness and a dominance of polychaetes (Salen-Picard et al., 2003; Labrune et al., 2007). Polychaetes represent 60–80% of the total number of species and 70–98% of individual abundance in the study area (Salen-Picard & Arlhac 2002; Salen-Picard et al., 2003; Hermand et al., 2008). Community biodiversity was investigated in terms of species richness (S, number of species) and diversity (E, expected number of species for a given sample size). E takes into account individual abundance. It was estimated by the rarefaction method of Sanders, modified by Hurlbert (1971). The rarefaction method calculates the expected number of species in fractions of the main samples and permits comparison of samples of different sizes (Rygg, 1985). Samples of the macrobenthic community were collected using a Smith-McIntyre grab (three 0.1 m<sup>2</sup> replicates at each site) along a longitudinal transect from the Bay of Marseille to the Rhone mouth, and a depth transect in front of the river delta between 10 and 80 m depth (transects 1 and 2, fig. 1). To analyse community changes in time, samples were collected seasonally from 1993 to 1998 at a fixed site located at 70 m depth near the river mouth (Salen-Picard et al., 2003). Due to their dominance, polychaetes only were considered in this temporal survey. Moreover, polychaetes, as one of the most characteristic groups of soft-bottom communities, are considered a good surrogate of species richness and structure of macrobenthic assemblages (Olsgard et al., 2003).

### Tracers of continental organic matter

Chlorophyll *b* is a pigment characteristic of chlorophytes (Lionard et al., 2008) and represents a good marker of continental POM, as chlorophytes are the second-most important component of river phytoplankton after diatoms (Lemaire et al., 2002). Chlorophyll *b* was then quantified in surface sediment (upper 5 cm) at 50–70 m depth along the longitudinal transect from the Bay of Marseille to the Rhone mouth to delineate the area influenced by river inputs (Alliot et al., 2003). Carbohydrate, lipid, and protein contents of surface sediment were also determined in order

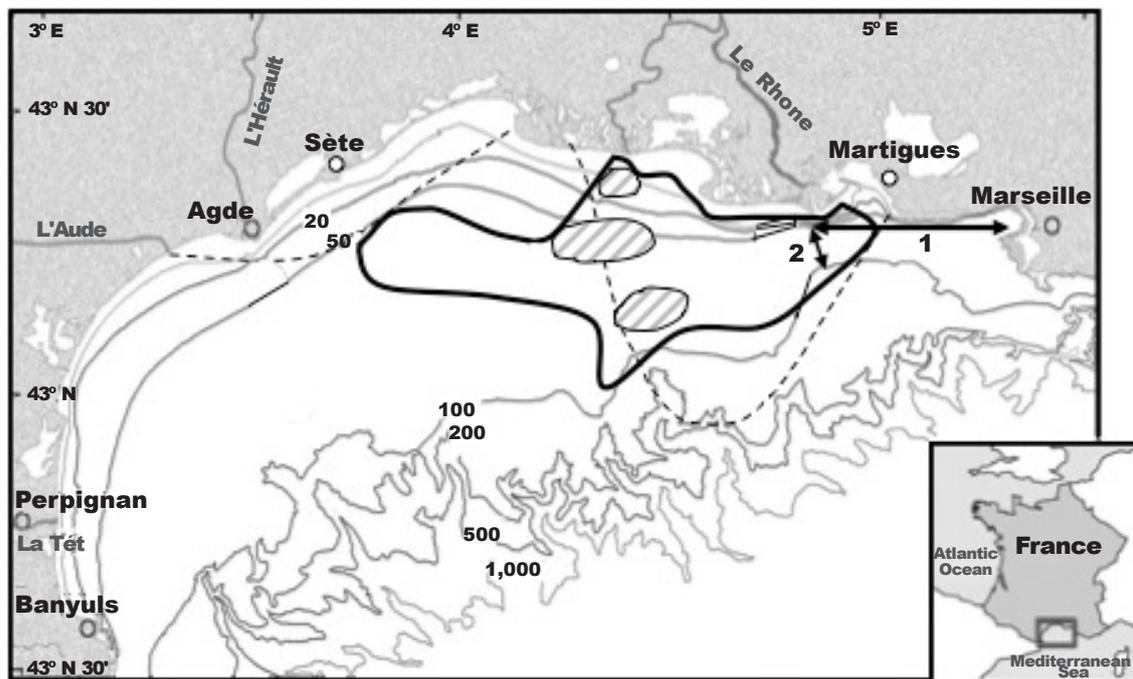


Fig. 1. Map of the Golfe du Lion. The two-way arrows indicate the longitudinal transect (1) and the depth transect (2) studied. The dashed line gives the average extension of the Rhone River water dilution zone (courtesy X. Durrieu de Madron), and the bold dark line indicates the localisation of *Solea solea* populations (from Campillo, 1992). Dashed zones correspond to the areas with the highest common sole abundance.

Fig. 1. Mapa del golfo de León. Las flechas bidireccionales indican el transecto longitudinal (1) y de profundidad (2) estudiados. La línea de puntos da la extensión media de la zona de dilución del agua del Ródano (cortesía de X. Durrieu de Madron), y la línea gruesa indica la localización de las poblaciones de *Solea solea* (de Campillo, 1992). Las zonas rayadas corresponden a las áreas con mayor abundancia de lenguado común.

to measure the nutritive quality of the settled POM (Dell'Anno et al., 2002). Sampling design and analysis protocols are detailed in Alliot et al. (2003). Biochemical composition of sediments was used to trace the mean extension of the influence of the dilution plume on the soft-bottom benthic community (Hernand et al., 2008). These data were then related to surface water salinity time-series records collected between 1996 and 2000. Similar biogeochemical analyses were performed on surface sediments along the depth transect (10–80 m depth) located perpendicular to the coast off the Rhone mouth.

#### Stable isotope analyses

To trace the transfer of continental POM into the coastal marine ecosystem, carbon stable isotopes were analysed in Rhone POM, marine surface water POM, surface sediments, and in prey animals on different trophic levels in the food web of the common sole, *Solea solea* (see Darnaude et al., 2004a and 2004b for sampling design and analysis

protocols). In particular, as continental POM carried by rivers is characterized by lower  $\delta^{13}\text{C}$  values than marine phytoplankton, its transfer into coastal food webs can be traced (Harmelin-Vivien et al., 2008). Specifically, significant differences ( $t$ -test,  $p < 0.001$ ) in  $\delta^{13}\text{C}$  between the Rhone POM ( $-26.11 \pm 0.23\text{‰}$ ) and marine phytoplankton outside the river influence ( $-22.36 \pm 0.24\text{‰}$ ) allowed the determination of their relative importance in surface sediment and within benthic food webs (Darnaude et al., 2004a). To evaluate the importance of continental POM as a carbon source for macrobenthic communities at different depths, the percentage of continental carbon (F%) in surface sediment was calculated using the following mixing equation (Harrigan et al., 1989):

$$F\% = [(\delta^{13}\text{C}_{\text{Sed}} - \delta^{13}\text{C}_{\text{M}}) / (\delta^{13}\text{C}_{\text{R}} - \delta^{13}\text{C}_{\text{M}})] \times 100$$

where  $\delta^{13}\text{C}_{\text{Sed}}$  was the signature of surface sediment organic matter at each investigated depth,  $\delta^{13}\text{C}_{\text{M}}$  the signature of marine phytoplankton and  $\delta^{13}\text{C}_{\text{R}}$  the signature of Rhone POM.

The carbon stable isotope ratios of polychaetes, the main group of macrobenthic communities, and the common sole, their most important predator, were investigated in three depth ranges (0–20 m, 30–50 m, 70–100 m). Signatures were then used as a proxy of the importance of continental POM in surface sediment, with low  $\delta^{13}\text{C}$  values indicating a high contribution of continental carbon (Darnaude et al., 2004a).

#### Sole fishery

Fishery yield of the common sole was used as a proxy of benthic ecosystem production since no data on macrobenthic production in this area were available at the time of this study in spite of data on community structure (Salen-Picard & Arlhac, 2002; Labrunet et al., 2007). Though an indirect measure, sole landings should be a good estimator of production, considering that previous studies demonstrated strong relationships between river inputs, polychaete abundance and common sole landings (Salen-Picard et al., 2002; Darnaude et al., 2004b). The common sole is among the most abundant and economically valuable demersal fish species in the Golfe du Lion (Campillo, 1992), and its populations are located mainly in the area directly influenced by the Rhone plume down to 100 m depth (Gaertner et al., 1999) (fig. 1). To estimate sole fishery production along transect 1, we analysed sole landing data (1972–1999) from two harbours, Martigues, located close to the Rhone mouth, and Marseille, located 30 km eastwards in an area not influenced by the river outflow (Campillo, 1992). Fishing grounds of the two fishing communities do not overlap as fishermen from Martigues work mainly off the river mouth, while those from Marseille do not venture so far west. To correlate fishery yields to the Rhone flow in the temporal study, we analysed the common sole landings obtained from the French Fisheries Statistics Department (Centre Administratif des Affaires Maritimes de Saint-Malo) at Martigues and Sète for the period 1972–1999. These two fishing harbours are both located close to the Rhone delta (east and west respectively) and accounted for 82% of the sole landings from the Golfe du Lion (Salen-Picard et al., 2002).

## Results

#### Longitudinal transect

From the Bay of Marseille to the Rhone mouth, surface water salinity decreased from east to west, reaching a minimum off the river mouth, whereas chlorophyll *b* concentration increased in surface sediments (fig. 2). Mean surface water salinity and chlorophyll *b* content in the sediment were significantly negatively correlated (linear correlation,  $r = -0.97$ ,  $p < 0.001$ ). Similarly, carbohydrates, lipids and proteins in the sediment were also significantly negatively correlated with salinity, and like chlorophyll *b* exhibited their highest values near the river mouth

(table 1). Carbohydrate and protein concentrations were 2.2 times higher near the Rhone mouth than near Marseille, and lipid concentrations were 3.6 times higher, demonstrating a higher nutritive quality of the settled POM in the area influenced by the river.

Species richness (S) of the macrobenthic community exhibited a 27% decrease from Marseille to the Rhone mouth (78 vs 57 species) and diversity (E), which accounted for individual abundance, decreased even more markedly (–55%) (fig. 2). Decrease in macrobenthic diversity was significantly positively related to surface water salinity (linear correlation  $r = 0.94$ ,  $p < 0.001$ ) and negatively to chlorophyll *b* concentration in surface sediments ( $r = -0.97$ ,  $p < 0.001$ ) (fig. 2). This latter relationship was due to an increase in population abundance of depositivorous polychaetes, particularly *Laonice cirrata*, *Mediomastus* sp., *Cossura* sp., *Sternaspis scutata* and *Polycirrus* sp. In terms of individual abundance, the mean density of macrobenthic organisms increased significantly from Marseille ( $3,603 \pm 406$  indiv  $\text{m}^{-2}$ ) to the Rhone mouth ( $24,513 \pm 5,723$  indiv  $\text{m}^{-2}$ ) (*t*-test,  $p < 0.001$ ). This 6.8 fold increase in macrobenthic density was also linked to an increase in the relative numerical abundance of polychaetes (78% of total community by number near Marseille to 98% near the Rhone).

Regarding sole fishery production, significantly higher sole landings were observed in Martigues than Marseille (*t*-test,  $p < 0.001$ ) (fig. 3). During the period analysed (1972–1999), 42% of the total annual catches from the Golfe du Lion were landed at Martigues, the fishing harbour located closest to the Rhone mouth ( $134.6 \pm 85.3$  t  $\text{year}^{-1}$ ), and only 7% at Marseille ( $23.1 \pm 9.1$  t  $\text{year}^{-1}$ ). More significantly, mean annual yields per boat were higher at Martigues than at Marseille (0.90 vs 0.25 t  $\text{year}^{-1}$  boat $^{-1}$  respectively).

#### Depth transect

Along the depth transect (10–80 m) near the river mouth, chlorophyll *b* concentration in surface sediment increased with increasing depth until a peak at 30 m, and then decreased from 30–80 m (fig. 4). Similar distribution patterns were observed for carbohydrates and proteins, which were respectively 4.9 and 2.3 times higher between 30 and 60 m depth than in shallower and deeper waters. Conversely, both the species richness (S) and diversity (E) of the macrobenthic community reached a minimum at 30–50 m depth (fig. 4). Diversity decrease was related to a strong increase in abundances of populations of a few depositivorous polychaetes (*Aricidea claudiae*, *Cossura* sp. and *Lumbrineris latreilli* at 30 m, *Sternaspis scutata* and *Lumbrineris latreilli* at 50 m).

As data relating fishery landings to fishing depth were not available, we estimated the influence of continental inputs on macrobenthic community and common sole dynamics by their  $\delta^{13}\text{C}$  signatures. Significantly lower  $\delta^{13}\text{C}$  values were recorded in polychaetes and common soles in the 30–50 m depth

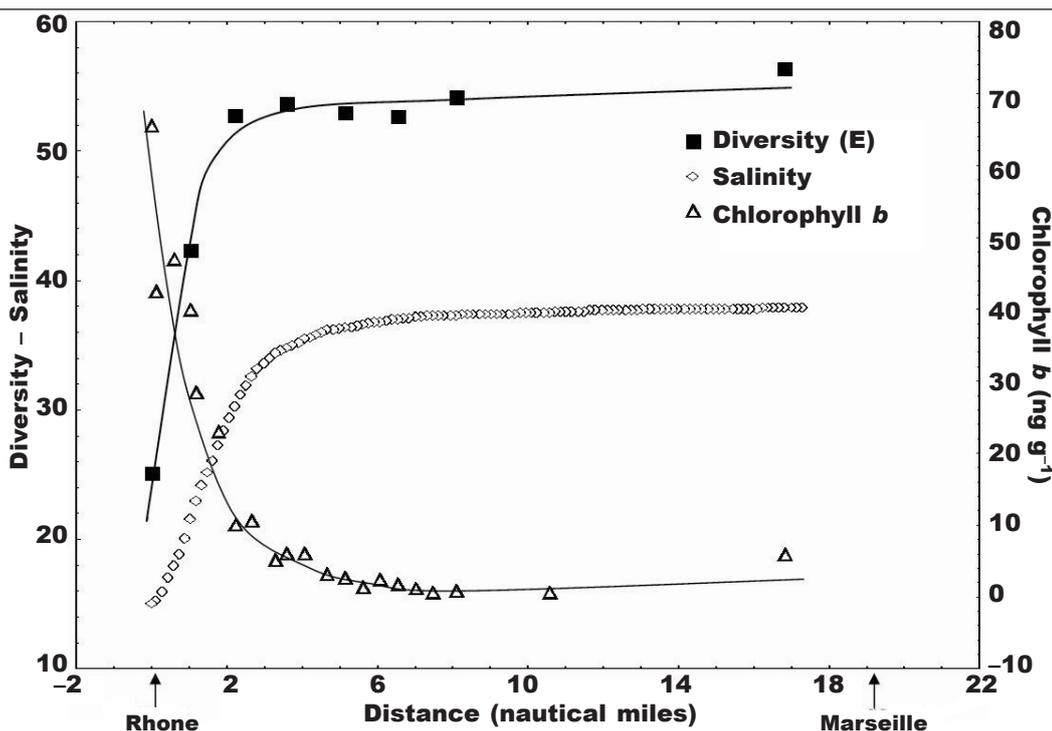


Fig. 2. Decrease in diversity (E) of macrobenthic community from the Bay of Marseille (marine site) to the Rhone River mouth (site impacted by river inputs). Influence of the river plume is reflected on surface water by a decreasing salinity gradient towards the river mouth (mean salinity for the period 1996–2000) and on surface sediment by an increase in chlorophyll *b* (from Alliot et al., 2003).

Fig. 2. Descenso de la diversidad (E) de la comunidad macrobentónica desde la bahía de Marsella (enclave marino) a la desembocadura del Ródano (enclave con impacto de los inputs fluviales). La influencia de la corriente fluvial se refleja en la superficie del agua mediante un descenso del gradiente de salinidad en dirección a la desembocadura (salinidad media en el periodo 1996–2000) y en la superficie sedimentaria por un aumento de la clorofila *b* (de Alliot et al., 2003).

range compared to those in shallower or deeper waters (ANOVA,  $p < 0.05$  for both) (table 2). This indicated that continental POM transfer in the food

webs up to the common sole was at its maximum between 30 and 50 m depth, where the percentage of carbon from continental origin was maximum.

Table 1. Mean concentrations ( $\mu\text{g mg}^{-1}$  dry sediment) of carbohydrates, proteins and lipids in surface sediments in the Bay of Marseille and off the Rhone River mouth, linear regression coefficient ( $r$ ) and probability ( $p$ ) with surface water salinity (from Alliot et al., 2003).

Tabla 1. Concentraciones medias ( $\mu\text{g mg}^{-1}$  de sedimento seco) de carbohidratos, proteínas y lípidos en los sedimentos superficiales de la bahía de Marsella y frente a las costas de la desembocadura del Ródano, coeficiente de regresión lineal ( $r$ ) y probabilidad ( $p$ ), con la salinidad del agua superficial (de Alliot et al., 2003).

	Bay of Marseille	Rhone River mouth	Regression with salinity
Carbohydrates	2.714 ± 0.528	5.683 ± 0.914	$r = -0.93, p < 0.001$
Proteins	0.614 ± 0.135	1.351 ± 0.139	$r = -0.80, p < 0.001$
Lipids	0.532 ± 0.444	1.891 ± 0.348	$r = -0.77, p < 0.001$

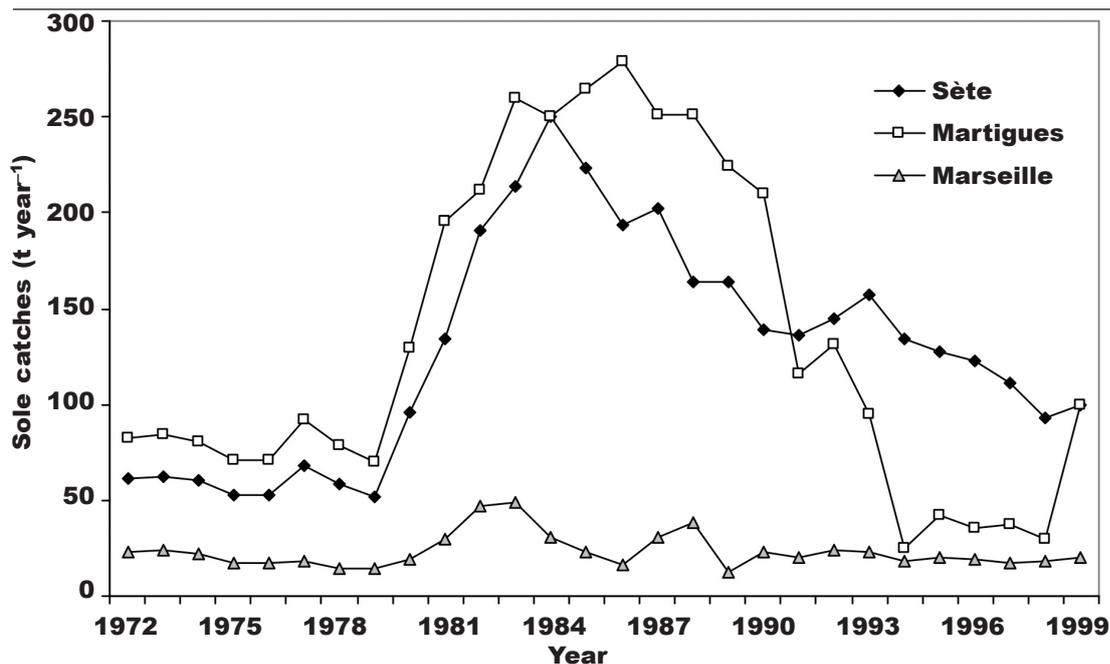


Fig. 3. Annual sole landings ( $\text{t year}^{-1}$ ) at Sète, Martigues and Marseille during the period 1972–1999 (data from Campillo, 1992 and Centre Administratif des Affaires Maritimes de Saint-Malo).

Fig. 3. Desembarques anuales de lenguados ( $\text{t año}^{-1}$ ) en Sète, Martigues y Marsella durante el período 1972–1999 (datos de Campillo, 1992 y el Centre Administratif des Affaires Maritimes de Saint-Malo).

#### Time series

The diversity (E) of the polychaete community located at 70 m depth off the Rhone mouth was inversely related to the mean annual river flow between 1993 and 1998 (fig. 5). When river flow was in excess ( $> 1,700 \text{ m}^3 \text{ s}^{-1}$ ), as in 1994 and 1995, polychaete diversity decreased, whereas it increased when the river flow was in deficit ( $< 1,700 \text{ m}^3 \text{ s}^{-1}$ ), as in 1997 and 1998. However, no significant change in species richness occurred over the study period as a whole, with a mean of  $46 \pm 2$  species recorded each year. The decrease in polychaete diversity observed from 1993 to 1995 was due to an increase in abundance of some depositivorous polychaetes (*Mediomastus* sp., *Cossura* sp., *Lumbrineris latreilli*, *Laonice cirrata*, *Polycirrus* sp., *Aricidea claudiae*), which resulted in a three-fold increase in total polychaete density during this period (from 2,390 to 8,630  $\text{indiv m}^{-2}$ ). In 1998, after two years of deficit in river flow, polychaete abundance was reduced by 40% compared to 1994–1995 (5,180  $\text{indiv m}^{-2}$ ), whereas diversity increased to its pre-flooding value. At a longer time scale (1972–1999), sole fishery yields in the river mouth area were significantly positively correlated with the mean annual Rhone flow for the two fishing harbours located closest to the river delta, Martigues ( $r = 0.84$ ,  $p < 0.01$ ) and Sète ( $r = 0.93$ ,  $p < 0.001$ ) with a five year time lag, whereas no correlation was observed at Marseille

( $r = -0.06$ ,  $p > 0.05$ ). An increase in Rhone flow thus resulted in an increase in polychaete abundance and a delayed increase in sole catches.

#### Discussion

In coastal marine environments subjected to river inputs, flooding events can be considered as natural disturbance experiments, of variable but *a posteriori* known intensity and periodicity (Akoumianaki & Nicolaidou, 2007). They may thus provide insights into the relationships linking community parameters, species biology and ecosystem production. Markers of continental particulate organic matter (POM) in surface sediments, in this case chlorophyll *b*, allowed us to delineate the area in which soft bottom communities were influenced by the Rhone plume (Alliot et al., 2003). Sediments under river influence were characterised by low  $\delta^{13}\text{C}$  values (Darnaude et al., 2004b; Hermand et al., 2008), and enrichment in organic matter was shown by the quantity of carbohydrates, lipids and proteins (Alliot et al., 2003). Such enrichment has different impacts on macrobenthic community parameters, such as species richness, diversity and abundance. Specifically, our data indicated that Rhone POM inputs negatively influenced the diversity of the macrobenthic community in the Gulf of Lions, but positively influenced both macrobenthos abundan-

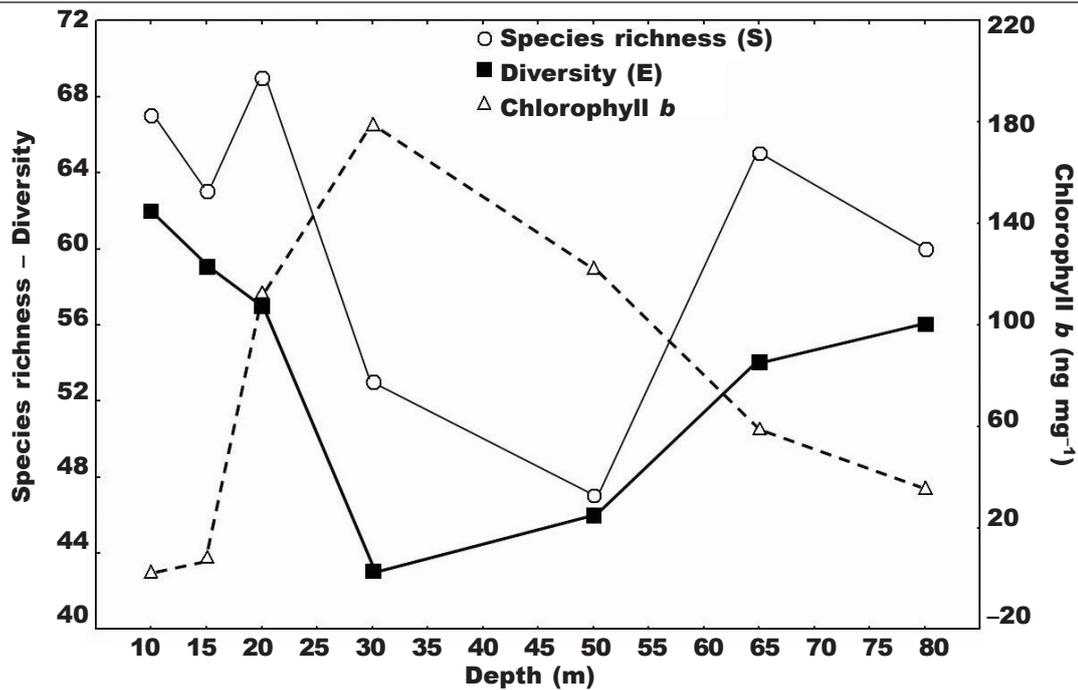


Fig. 4. Changes in macrobenthic species richness (S), diversity (E), and chlorophyll *b* content in surface sediment on a depth gradient off the Rhone River mouth. Chlorophyll *b* concentrations are a measure of river input intensity.

Fig. 4. Cambios en la riqueza de especies macrobentónicas (S), la diversidad (E) y el contenido de clorofila *b* en la superficie de los sedimentos en un gradiente de profundidades frente a la desembocadura del Ródano. Las concentraciones de clorofila *b* constituyen una medida de la intensidad de input fluvial.

ce and ecosystem production quantified by sole fishery yields.

River inputs of particulate matter (organic and inorganic) acted both as a disturbance and as a source of nutrients (fig. 6). As a disturbance, sedimentation induced a decrease in species richness of the macrobenthic community (direct negative link). As

a source of nutrients, it increased the populations of species with specific adaptative traits, here the ability to consume continental POM (direct positive link). A feedback loop linked the two, as an increase in populations of particular species in itself results in a decrease of the measure of species diversity (fig. 6). Increases in specific populations of macrobenthic

Table 2. Mean percentage ( $\pm$  SD) of carbon of continental origin in surface sediment and mean  $\delta^{13}\text{C}$  ( $\pm$  SD) of polychaetes and the common sole, *Solea solea*, according to depth in front of the Rhone River (from Darnaude et al., 2004a): n. Number of individuals analysed in each depth range.

Tabla 2. Porcentaje medio ( $\pm$  DE) de carbono de origen continental en la superficie de los sedimentos y  $\delta^{13}\text{C}$  media ( $\pm$  DE) de los poliquetos y el lenguado común (*Solea solea*), según la profundidad, frente al río Ródano (de Danaude et al., 2004a): n. Número de individuos analizados en cada rango de profundidades.

Depth range	% continental C (n = 9)	$\delta^{13}\text{C}$ Polychaetes (‰) (n = 6)	$\delta^{13}\text{C}$ <i>Solea solea</i> (‰) (n = 10)
0–20 m	81.2 $\pm$ 13.0	-22.65 $\pm$ 0.17	-19.07 $\pm$ 0.23
30–50 m	86.6 $\pm$ 13.7	-23.36 $\pm$ 0.17	-22.36 $\pm$ 0.36
70–100 m	64.3 $\pm$ 11.4	-21.54 $\pm$ 0.07	-20.06 $\pm$ 0.67

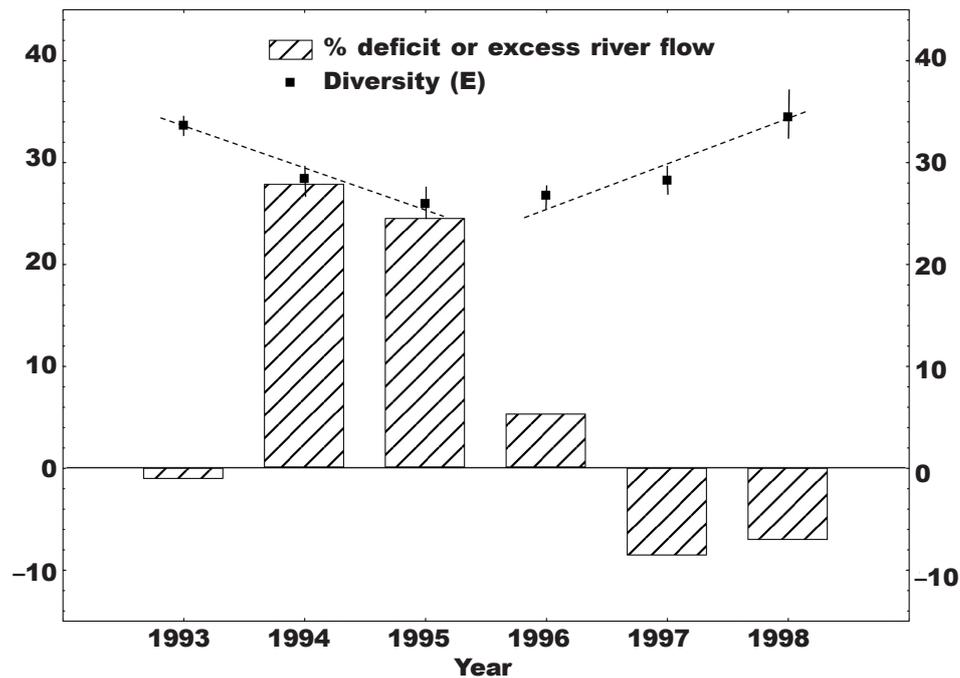


Fig. 5. Temporal changes in macrobenthic diversity (E) off the Rhone River according to excess or deficit of river flow (% on annual means). Macrobenthic diversity decreased from 1993 to 1995 with flow excess and increased from 1996 to 1998 with flow deficit.

*Fig. 5. Cambios temporales en la diversidad macrobentónica (E) frente al Ródano, según el exceso o déficit del caudal del río (% de medias anuales). La diversidad macrobentónica disminuyó del 1993 al 1995 con un exceso de caudal, y aumentó del 1996 al 1998 con un déficit de caudal.*

invertebrates (depositivorous polychaetes) in turn led to an increase in specific predator populations (the common sole) (direct positive effect and presumed feedback loop of prey regulation). Finally, the increase in predator populations was reflected in increased fishery yields of some benthic fish species (common sole fisheries) (direct positive effect). The relationship between river flow and sole fisheries production was therefore an indirect link, explained by the transfer pathway of continental POM within coastal marine food webs.

Off the Rhone mouth, decreased macrobenthic diversity was not associated with a decrease but with an increase in system productivity. As discussed by Loreau (2000), the positive effect of an environmental factor on productivity may prevail over its negative effect on biodiversity. As changes in species abundance have crucial consequences for ecosystem functioning (Yachi & Loreau, 1999; Dangles & Malmquist, 2004; Schmitz, 2004), diversity indices that take species abundance into account should be considered in addition to species number. This was underscored in the present study by the stronger variation in species diversity E than in species richness S, due to the fact that E incorporated the large changes in abundance that occurred in the study area

and which affected community structure. Changes in the total abundances of species in the macrobenthic community were thus at the basis of fluctuations in ecosystem productivity.

The effects of increased nutrient supply, mainly from organic pollution, on community structure and diversity of macrobenthic communities have long been studied (Pearson & Rosenberg, 1978; Rygg, 1985; Labruno et al., 2008). Increases in organic matter induce a decrease in diversity caused by high dominance of a limited number of opportunistic species capable of reaching high densities under the new environmental conditions. The effects of changes in biodiversity depend on specific biological traits or functional roles of individual species. Understanding the flow of matter among the functional compartments of an ecosystem thus requires knowledge of the biological components and their roles as consumers and transformers (Loreau, 1995).

In combining biological information on macrobenthos and demersal fish species with information on the biogeochemical and stable isotope composition of organic matter, we established that continental POM in the study area was transferred up to the benthic fish predator common sole. The crucial link for the integration of POM in the sole foodweb was surface

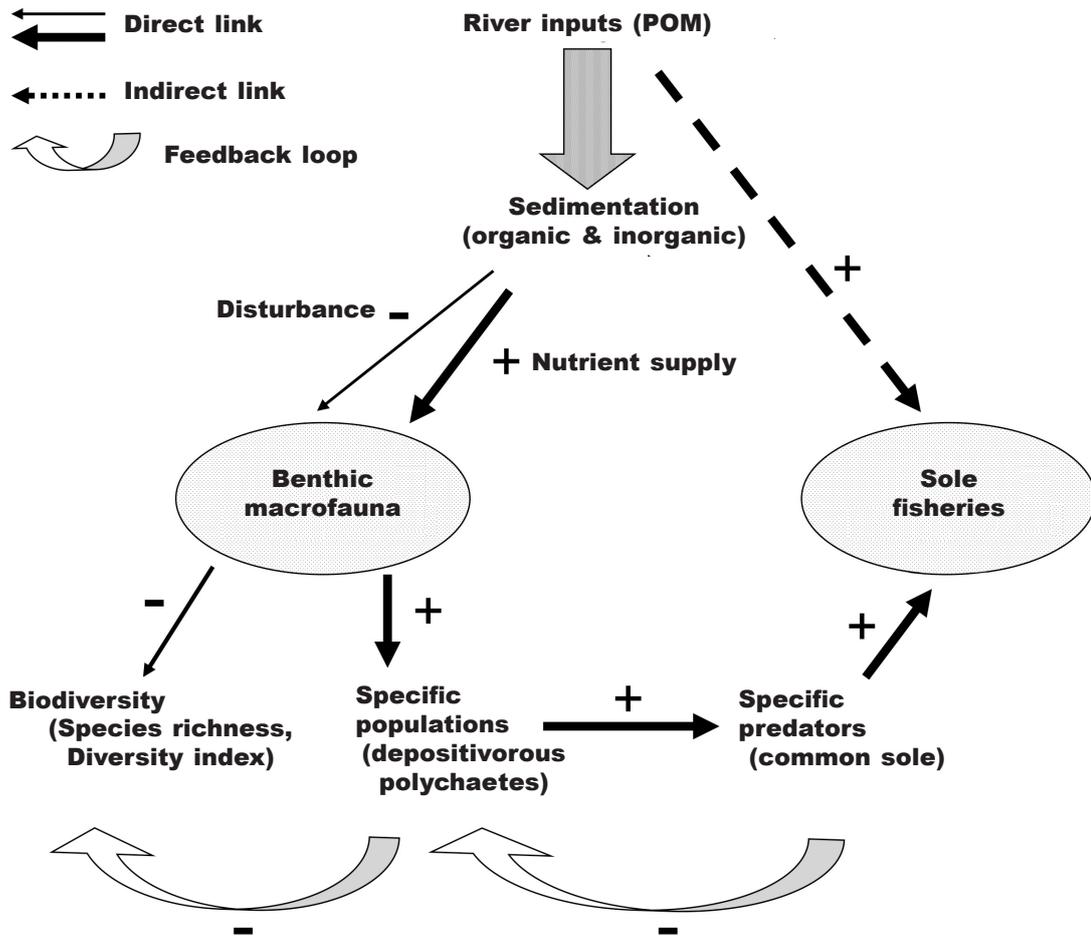


Fig. 6. Conceptual model of potential relationships explaining patterns in river inputs, diversity of macrobenthic communities, and fisheries production in the study area in the Golfe du Lion. As a disturbance, sedimentation induced a decrease in macrofaunal species richness (direct negative link). As a nutrient supply, continental POM was transferred through the system by direct positive links. Continental POM increase induced an increase in populations of species with particular functional traits (depositivorous polychaetes) which in turn led to an increase in specific predator populations (common sole) and related fisheries. Feedback loops existed between specific population abundance and macrobenthic diversity, and presumably between predator (sole) and prey (depositivorous polychaetes) abundance.

Fig. 6. Modelo conceptual de las posibles relaciones que explican los patrones de los inputs fluviales, la diversidad de las comunidades macrobentónicas y la producción de las pesquerías en la zona de estudio del golfo de León. La perturbación que constituye la sedimentación produce un descenso de la riqueza de especies de la macrofauna (relación negativa directa). Como suministro de nutrientes, la MOP continental se transfiere a través del sistema mediante relaciones positivas directas. El aumento de la MOP continental induce un aumento de las poblaciones de especies con unos rasgos funcionales particulares (poliquetos depositívoros), que a su vez conduce a un aumento de las poblaciones de depredadores específicos (lenguado común) y las pesquerías relacionadas. Se dan bucles de retroalimentación entre la abundancia específica de poblaciones y la diversidad macrobentónica, y presumiblemente entre las abundancias del depredador (el lenguado) y la presa (los poliquetos depositívoros).

and subsurface depositivorous polychaetes feeding on this matter. As the common sole mainly preyed on depositivorous polychaetes, its population dynamics were influenced by river inputs. The increase in sole

landings with river flow which peaked with a 5-year time lag, is a two-step biological process (increase in juvenile survival and female fecundity with a 2–3 year delay) combined with the mean age of individuals in

catches (2–3 years) (Salen–Picard et al., 2002). Positive relationships between river inputs and recruitment abundance of *Solea solea* were also observed in the Bristol Channel (Henderson & Seaby, 2005) and the Vilaine Bay (Le Pape et al., 2003).

In the Golfe du Lion Salen–Picard et al. (2003) subtle differences previously observed in the feeding behaviour, life cycle and position in the sediment of depositivorous polychaetes resulted in a succession of peaks of abundance for several species, accelerating and maximising continental carbon transfer into the benthic ecosystem. These traits allowed the system not only to perform (have a high production), but also to persist. This suggests that in the absence of macrobenthic species adapted to rapidly consume the available continental POM, coastal marine ecosystems could become highly eutrophic after flooding and might collapse, as observed in front of un-treated urban sewages (Bellan & Bourcier, 1990). Recycling of large quantities of continental POM by benthic microorganisms would be a longer and less efficient pathway, resulting in a lower productivity of the system. In conclusion, our study suggests that the specific adaptative functional traits exhibited by depositivorous polychaetes in using continental POM resulted in an increase in coastal benthic production near the Rhone mouth after flooding events in spite of a decrease in macrobenthic diversity.

### Acknowledgements

This study was supported by the French National Programme on Coastal Ecology (PNEC). J. D. was supported by the Okeanos Foundation (Germany). Thanks are expressed to Elisabeth Alliot, Audrey Darnaude, Jean–Claude Romano and Wallid Youness for their contributions and to David Pollard for valuable comments and English text revisions. Two anonymous reviewers are acknowledged for critical improvement of the manuscript.

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