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Review

The food web in the lower part of the Seine estuary: a synthesis of existing knowledge

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Abstract

The Seine estuary illustrates the alterations to estuaries due to human activities: heavy releases of pollutants of various origins and significant morphological changes beginning in the middle of the 19th century. The intertidal mudflat surface has been seriously reduced (<30 km^2) since the channels of the Seine River came under management. While the role of the Seine estuary in the dynamics of the eastern English Channel ecosystem is recognized as important, the biological characteristics of the estuary remained relatively unknown until the 1990s. Biological diversity was progressively impoverished from the polyhaline zone to the oligohaline zone. In spite of a heavily contaminated environment, the macrobenthic and planktonic fauna of the Seine estuary remains similar to those of other northeastern Atlantic estuaries. The fauna exhibit clear contrasts between areas with very high abundance and others with very low abundance. The pelagic fauna, especially the copepod *Eurytemora affinis* and the shrimp *Palaemon longirostris,* are more abundant in the Seine estuary than in other estuaries. Diversified and abundant, *Abra alba-Pectinaria koreni* and *Macoma balthica* benthic communities occur, respectively, in the outer and inner parts of the estuary. In subtidal flats, benthic fauna is especially poor in terms of specific richness, abundance and biomass. Paradoxically, considering the high abundance of prey, fish are particularly scarce. Two food webs have been identified. In the oligohaline zone, where turbidity is maximum, the food web is exclusively planktonic, due to dredging that prevented benthic fauna from settling. In the polyhaline zone, fish populations that feed particularly on benthic fauna benefit from low turbidity and high oxygen concentrations. So, in spite of heavy organic and metallic contamination and human activities, the Seine estuary remains a highly productive ecosystem, which provides a nursery for marine fish and feeding grounds for migratory birds. A global management plan appears to be necessary in order to guarantee that the Seine estuary continues to function as it currently does.

Introduction

The Seine estuary is the largest megatidal estuary in the English Channel, covering about 150 km^2 at high tide. The average tidal range, at the mouth, is about 8.5 m for spring tides and 4 m for neap tides. The influence of marine water is increased by the estuarine morphology: the tide penetrates 170 km in from the coastline (to the Barrage de Poses at PK 202; PK0: Notre Dame de Paris). Freshwater enters the estuary mainly from the Seine River with a drainage area of approximately 78 650 km^2, 80% of which is in the urban areas of the estuary. River discharge varies seasonally, from a maximum of 2000 m^3 s^{-1} in winter to a minimum of 100–200 m^3 s^{-1} in summer (Guézennec, 1999). As for many European macrotidal estuaries, the Seine estuary is characterized by a zone of maximal turbidity with suspended matter concentrations of 1 g l^{-1}, generally located in the upper part of the estuary. Given that 25% of the French population and 40% of her industry and agriculture are concentrated along either bank, the Seine estuary is economically important.

Several multidisciplinary research programs were carried out in the Bay of the Seine over the two last decades, particularly the 'Baie de Seine' program (Cabioch, 1986) and the 'Baie de Seine' site of the National Coastal Environment Program (Ménesguen, 2002). The 'Schéma d'Aptitude à l'Utilisation de la Mer' (at the end of the 1970s, SAUM, 1980) had given information about the faunal composition and distribution in the lower part of the Seine estuary. In the 1990s, the scientific Seine-Aval program significantly increased the knowledge of this estuary. The aims of the Seine-Aval program, which continues today, were to assess the ecological situation of the estuary and to understand how the estuary functions. For this, an integrated scientific approach was employed. This approach first took the various compartments of the system into account, and then, after consultation with users and decision-makers, organized the implementation of the operational tools (Lafite & Romaña, 2001). In November 1999, a colloquium on the estuary, entitled 'The Seine Estuary: Features and Perspectives, took place in Rouen, focusing on the principal results of the first phase of the program. A special issue of *Estuaries* (Vol. 24, No. 6B) summarizes the contents of the 14 scientific papers presented. In addition, 17 fascicules directed towards the general public were published between 1999 and 2002, illustrating the primary knowledge of this heavily managed estuary. Additional scientific papers from a global viewpoint describe the present situation of the Seine estuary.

The objectives of this paper, which focuses on the lower part of the estuary (i.e. from the polyhaline to the oligohaline zones included between PK 370 and PK 325, ≅45 km), are: (1) to summarize the main characteristics of the living resources (zooplankton, suprabenthos, macrobenthos, and fish populations) in relation to the environmental factors and, (2) to describe the principal food webs observed in this part of the Seine estuary.

Environmental characteristics of the lower part of the Seine estuary

General morphology

The estuarine morphology is mostly artificial, resulting from man-made modifications. Since the mid-19th century, industrial activity and development has taken place in the lower part of the Seine. These extensive activities/public works operations have led to a decrease in the river channel section as well as in the exchanges of seawater. Its width and cross-section decrease exponentially upstream from the mouth, with a maximum width of 9 km, and the width of the Navigational Channel decreases from 1000 m at the mouth to only 200 m, 30 km upstream (Fig. 1). The Seine has been canalized and dredged 120 km upstream from the mouth to allow navigation from the sea to the inland port of Rouen. At the mouth, intensive dredging (≅5 millions t y^{-1}) is necessary to maintain water depth at 5–6 m below the zero sea level. Due to the successive construction of dykes, the intertidal zone had been reduced from 130 km^2 at the middle of the 19th century to < 30 km^2 in 2000. Now, intertidal mudflats and salt marshes are restricted to the northern bank of the estuary, and muddy sand is found only in the South Channel downstream from Honfleur (Fig. 1). The present-day estuary displays a classic funnel shape. Elongated sandbars that are typical of tide-dominated estuaries have developed in the inlet (Lesourd et al., 2001). At the mouth of the estuary, superficial sediments become more and more muddy (Lesourd et al., 2001). Mud also dominates the subtidal zones of both the North and South Channels, with the exception of the Ratier Bank in the South Channel and Amflard bank in the North Channel where sand dominates. As a result of permanent dredging, sediment in the Navigational Channel is dominated by sand downstream from Honfleur and by gravel upstream from Honfleur (Lesourd et al., 2001).

Physical characteristics

Figure 2 summarizes the physical constraints interacting in the lower part of the estuary. The mean annual particulate discharge has been evaluated at around 500 000 t as suspended matter comes upstream from freshwaters. The maximum turbidity zone (MTZ) is now located at the mouth of the estuary between the 'Pont de Tancarville' (PK337) and Honfleur (PK 357) (Fig. 2), but can be pushed into the Bay of the Seine during swelling (Le Hir et al., 2001). In the MTZ, the bottom turbidity, often lower than

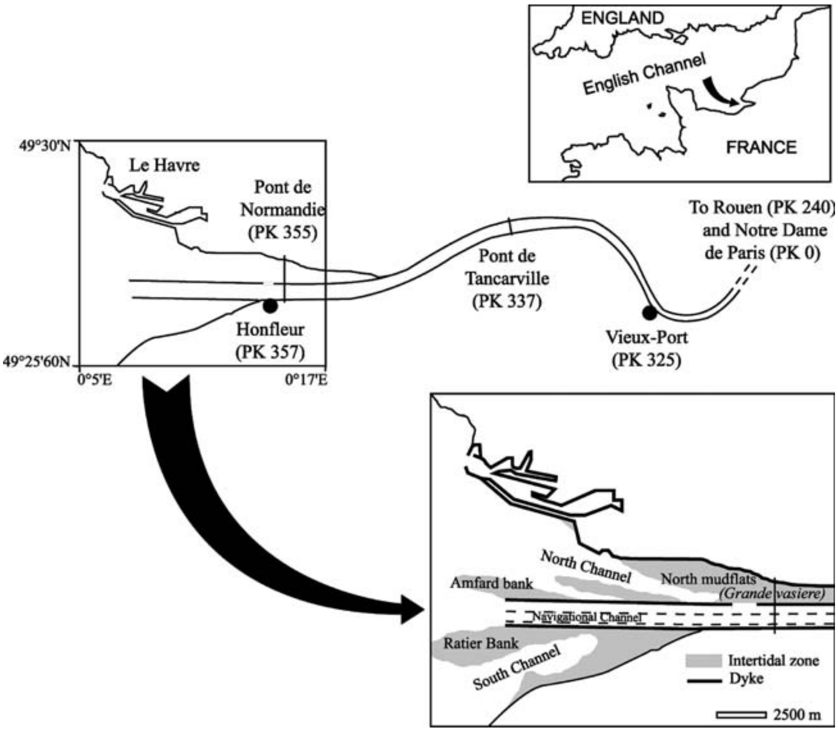

Figure 1. Map showing the different sections of the lower part of the Seine estuary (from Dauvin et al., 2002).

2 g l^{-1}, can occasionally surpass 10 g l^{-1} and has reached as high as 63 g l^{-1} (Mouny & Dauvin, 2002). Rarely higher than 0.1 g, the surface turbidity is most often ≅0.05 g l^{-1}. Although low oxygen concentrations of <2 ml l^{-1} have been observed near the sea bottom in spring and summer, oxygen concentration usually remains >5 ml l^{-1} during other seasons in most of the other parts of the lower estuary (Mouny, 1998).

The salinity decreases from the mouth of the estuary (PK 370; salinity ≅30) towards the upper levels (Fig. 2). Although found upstream as far as PK 320 during spring tide and periods of low freshwater discharges, the isohaline (≅0.5) is usually located between the 'Pont de Tancarville' (PK 337) and the 'Pont de Normandie' (PK 355), according to the discharge of the Seine. The Seine estuary is characterized by a high level of water column mixing. Nevertheless, the water column can be stratified at the mouth of the estuary during ebb and low tide, when the discharge of freshwater is >500 m^{-3} s^{-1} (Mouny, 1998).

Pollutants

Heavy metal concentrations, particularly of cadmium and lead, make the Seine estuary the most contaminated in Europe. A comparison of metal concentrations in estuarine species collected on contaminated and non-contaminated sites and in the Seine estuary, shows a high level of copper, zinc, and lead contamination in the Seine estuary (Miramand et al., 2001). These authors showed that bivalves were mainly affected by Cd, and high concentrations of copper were found in copepods, shrimp and fish. Lead was concentrated mainly in planktonic species living in the Seine channel, especially in the dominant copepod *Eurytemora affinis*, as well as benthic deposit-feeders. Elevated levels of zinc were also measured in all species in the Seine estuary, from invertebrates to fish (Miramand et al., 2001).

In addition, the level of organic contaminants (PAHs, PCBs, and pesticides) coming from continental sources place the Seine estuary among the most contaminated of European estuaries

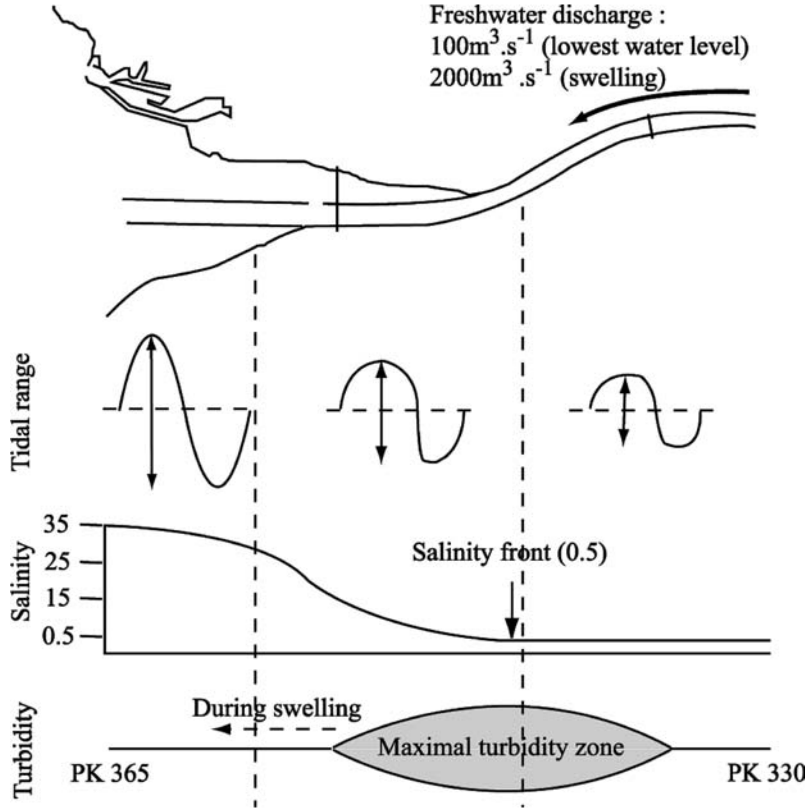

Figure 2. Summary of the physical interaction factors in the lower part of the Seine estuary (from Dauvin et al., 2002).

(Tronczynski, 1999). An internal source of PAHs has also been identified; chronic, high levels of organic contamination in the Seine estuary pose a problem because of the effects on organisms and ecological resources. For example, PCBs contamination increases with the trophic level; the highest concentrations were found in the oldest sea bass individuals, and a steady-state model of PCBs bioaccumulation shows that feeding is the principal route for contamination (Loizeau et al., 2001).

Characteristics of the biological components

Mesozooplankton

General patterns

As has been observed in other estuaries (Collins & Williams, 1981, 1982; Baretta & Malschaert, 1988; Soetaert & van Rijswik, 1993; Laprise & Dodson, 1994), mesozooplankton is spatially distributed in the Seine estuary according to the salinity gradient (Mouny & Dauvin, 2002). The MTZ plays a restricted role in the spatial structure of the pelagic components (Mouny & Dauvin, 2002).

The polyhaline zone (surface salinity >18.0) is characterized by the dominance of copepods *Temora longicornis, Acartia* spp. and *Centropages* spp. and the cladoceran *Evadne nordmanni* (Dauvin et al., 1998). These marine species can however penetrate upstream in the estuary up to salinity levels of 10.0.

The mesohaline zone (5.0 < surface salinity <18.0) is dominated in abundance by the estuarine copepods *Acartia* spp., recorded in salinity levels up to 7.0, and *Eurytemora affinis*.

The oligohaline zone (S < 5.0) is dominated by the copepod *E. affinis* and the freshwater cladoceran *Bosmina* spp. and *Daphnia* spp.

As observed in American estuaries (Bulger et al., 1993), these different zooplanktons largely overlap along the salinity gradient. As suggested by Attrill & Rundle (2002), this pattern corresponds to an ecocline, a continuum of faunal assemblages in estuaries.

Seasonal changes in dominant species

Eurytemora affinis is dominant throughout the year, representing 52–99.9% of mesozooplankton abundance at salinities <18. In the mesohaline and oligohaline zones, abundance increases during the winter, is maximal during spring (≅ 190 000 ind m^{-3}), and rapidly declines to reach low levels in summer and autumn (< 10 000 ind m^{-3}). Although, the spring maximum abundance period recorded for the Seine estuary occurs at the same period as in the other major megatidal European estuaries (Sautour & Castel, 1995), *E. affinis* shows abundance figures 10 times higher in the Seine (Fig. 3). This difference could be due to (i) a higher production of this copepod in the Seine estuary and/or (ii) a higher concentration of individuals given that the Seine estuary is canalized and has a smaller surface than other European estuaries. In the polyhaline and mesohaline zones, the neritic copepods *Acartia* spp. increases in abundance during the spring and exhibits two peaks, one in June and one in September. The magnitude of the peak is different depending on the zone where it occurs (June: 2800 ind m^{-3} and 1000 ind m^{-3} for the polyhaline and for the mesohaline and September: 1500 ind m^{-3} and 850 ind m^{-3} for the polyhaline and for the mesohaline). The maximal abundance of other neritic species is always lower than 200 ind m^{-3} (Mouny & Dauvin, 2002). Maximal numbers of freshwater species (*Bosmina* spp., *Daphnia* spp. and *Acanthocyclos robustus*) are always < 2200 ind m^{-3} (Mouny & Dauvin, 2002).

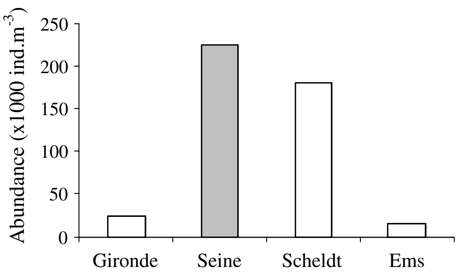

Figure 3. Maximal spring abundance of the dominant estuarine copepod *Eurytemora affinis* (x 1000 ind m^{-3}) in the oligohaline zone of four major European estuaries (from Mouny, 1998).

Macrozooplankton

Other than in spring, macrozooplankton abundance remains very low (Mouny et al., 2000). It is weakly diversified and is organized in two main groups. Neritic marine species, such as the chaetognaths *Sagitta elegans* and *S. setosa*, the ctenophore *Pleurobrachia pileus* and different fish larvae (callionymidae, clupeidae, gadidae gobiidae, and soleidae), are distributed in the outer part of the estuary. In the mesohaline and oligohaline zones of the Navigational Channel, maximum spring abundances of the macrozooplankton are often < 1 ind m^{-3} (Mouny, 1998), though only gobiidae larvae are recorded. In the outer part of the polyhaline zone of the estuary, maximum spring abundances of clupeidae can exceed 1 ind 1 m^{-3} (Wang et al., 1994). Although gobiidae larvae can occasionally reach abundance levels up to 4.2 ind m^{-3}, their abundance levels are more often found between 1 and 5 ind m^{-3} (Mouny, 1998; Mouny et al., 2000). More abundant in the Seine estuary than in any other European shallow waters, *Pleurobrachia pileus* shows very high spring abundances (May–June) in salinity levels > 15, with a maximum abundance >800 ind m^{-3}. Nevertheless, mean spring averaged abundance levels are ≅30 ind m^{-3} (Wang et al., 1995).

Suprabenthos

General patterns

The suprabenthic samples are collected with a new version of the Macer-Giroq sledge (Wang & Dauvin, 1994). This sledge allows the simultaneous sampling of the fauna at four levels between 0.10 and 1.45 m above the bottom, using four WP2 plankton nets (0.5 mm mesh size).

Two main species assemblages are identified along the salinity gradient (Wang & Dauvin, 1994; Mouny et al., 2000).

(1) a marine assemblage located in the downstream part of the estuary, diversified, and dominated by amphipods and mysids *Mesopodopsis slabberi*, *Schistomysis* spp. and *Gastrosaccus* spp.
(2) an estuarine assemblage essentially dominated by the mysid *Neomysis integer*, recorded along the salinity gradient with a maximal abundance observed between 10 and 15.

The marine assemblage shows high abundances from May to September (>50 ind m^{-2}), with a single peak in September (490 ind m^{-2}); then, the abundance decreases rapidly in October (≅18 ind m^{-2}) and remains lower than 12 ind m^{-2} the rest of the year. The annual mean abundance is 66 ind m^{-2}. The biomass varies between 2.4 and 7.2 mg AFDW m^{-2} from October to May, surpasses 12 mg AFDW m^{-2} from June to August and is maximal in September (195 mg AFDW m^{-2}). The annual mean biomass varies around 25 mg AFDW 100^{-2}.

The estuarine assemblage also presents high abundances from May to September (>100 ind m^{-2}), with maximal values (310–320 ind m^{-2}) reached from June to August. The abundance level decreases rapidly in October (≅50 ind m^{-2}) and remains lower than 30 ind m^{-2} throughout the rest of the year, with a winter minimum in February (<5 ind m^{-2}). The mean annual abundance is >100 ind m^{-2}. Biomass always remains very high (>200 mg. AFDW m^{-2}), with peaks in August (1000 mg AFDW m^{-2}) and in October (950 mg. AFDW m^{-2}) for an annual mean of ≅450 mg AFDW m^{-2}.

The estimated abundance levels of the suprabenthos of both assemblages are similar to values reported by Mees & Jones (1997) for estuaries, and are among the highest reported in the literature for shallow and deep-water suprabenthic assemblages (Mees & Jones, 1997; Dauvin et al., 2000).

Seasonal changes in dominant species

The decapod *Palaemon longirostris* and the goby *Pomatoschistus microps* are located only in the upstream part of the estuary when they present high maximal abundances. Some species, e.g. the decapod *Crangon crangon,* are present in the estuary only during their juvenile development. The maximal abundance reported in the Seine estuary for the three mentioned species are amongst the highest reported anywhere (Fig. 4) (Mees et al., 1995; Dauvin et al., 2000).

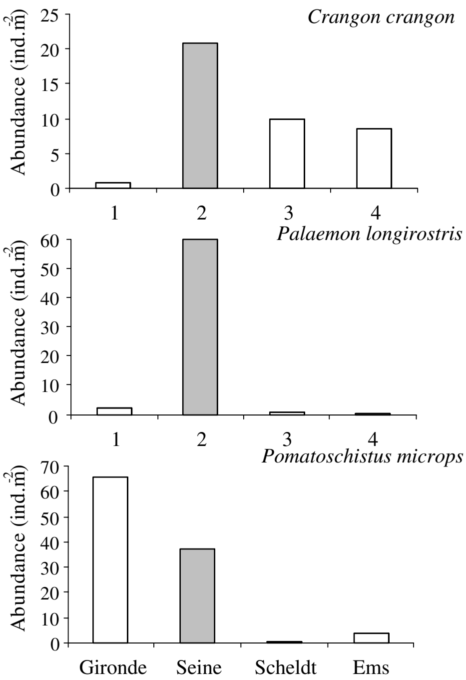

Figure 4. Maximal abundance of three dominant suprabenthic species – *Crangon crangon*, *Palaemon longirostris* and, *Pomatoschistus microps* – (ind m^{-2}) in four major European estuaries (from Mouny, 1998).

Intertidal macrobenthos

Two main communities are found on the intertidal flats (Desprez, 1981; Bessineton, 1998; Dauvin, 2002). The first, a *Nephtys cirrosa* fine sand community dominated by amphipods, such as the *Urothoe brevicornis* and *Bathyporeia* spp., is present in the marine part of the estuary. It is characterized by high specific richness (≅50) and low abundance (≅300 ind m^{-2}) (Desprez, 1981). The second, a *Macoma balthica* community, occupies the mudflats of both the North and South Channels and the border of the Navigational Channel. Desprez (1981) has identified two sub-communities of the *Macoma balthica* community in relation to the bathymetric level of the tidal flats and the location in the estuary. In the lower part of the estuary, the *Macoma balthica* community is more diversified (≅30 species) and shows moderate abundance (2400 ind m^{-2}). The biomass expressed in simple dry weight reaches 20 g DW m^{-2} in summer. The amphipod *Corophium volutator* and the polychaete *Hediste diversicolor* exhibit abundance levels of >1000 ind m^{-2} and >600 ind m^{-2} respectively. In the upper part, the community is weakly diversified (<10 species); conversely the mean abundances reach 10 000 ind m^{-2} and biomasses 12 g DW m^{-2}

respectively. The oligochaetes *Tubifex* spp. and the polychaete *Manayunkia aestuarina* are dominant.

In the mesohaline and oligohaline zones of the Navigational Channel, the macrobenthic fauna of the mudflats is particularly poor (<6 species, abundance <100 ind ind m^{-2}, and biomass <0.25 g DW m^{-2}) (Mouny et al., 1998). The mean biomass observed for the 'Grande Vasière' *Macoma balthica* community (Fig. 5) is on the same order of magnitude of those observed on mudflats of other northeastern Atlantic estuaries (Wilson, 2002). Nevertheless, this biomass remains two times lower than those measured in the Humber estuary (North Sea) and in the Somme Bay (eastern English Channel), where mean biomass exceeds >25 g DW m^{-2}.

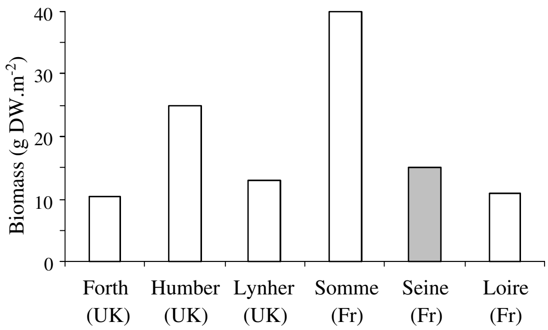

Figure 5. Comparison of mean biomasses on the intertidal mudflat *Macoma balthica* community in some northeastern Atlantic estuaries.

Subtidal macrobenthos

Two main subtidal communities have been identified in the lower part of the Seine estuary (Fig. 6) (Proniewki & Elkaim, 1980; Elkaim et al., 1982; Thiébaut et al., 1997; Mouny et al., 1998; Dauvin, 2002).

1. An *Abra alba – Pectinaria koreni* muddy sand community occupies the external part of the estuary and the entrance to the North and South Channels. Four facies impoverished by the penetration in the estuary, have been described in relation to the sediment silt content. The *Pectinaria koreni* and *Acrocnida brachiata* facies is the most diversified (≅100 species), characterized by the polychaetes *P. koreni*, *Owenia fusiformis*, *Lanice conchilega*, *Nephtys hombergii*, the bivalves *Mysella bidentata* and *A. alba*, and the echinoderms *Acrocnida brachiata* and *Ophiura ophiura*. The three other facies are impoverished in terms of species, especially the *Donax vittatus – Spio martinenis* that is usually located on clean fine sand. The total abundance and biomass levels exhibit a very high spatial heterogeneity (Thiébaut et al., 1997). Maximal abundance levels (annual mean >3000 ind m^{-2}; spring–summer maximum >20 000 ind m^{-2}) and biomass levels (annual mean ≅50 g DW m^{-2}; maximum >200 g DW m^{-2}) have been observed in three permanent sites situated (1) along the coast of *Pays de Caux*, (2) between Cabourg and Deauville and in the South Channel, and (3) seaward off the Seine Estuary (Thiébaut et al., 1997).

Except for the very high biomass observed at the Gravelines site (southern Bight of the North Sea), the mean biomass observed for the *Abra alba* community of the Seine estuary is 5–10 times higher than values generally recorded in the North Sea and the English Channel (Fig. 7).

2. A *Macoma balthica* community inhabits inner subtidal bottoms in the North, South and Navigational Channels. Species diversity (<15 species), abundance (<200 ind m^{-2}) and biomass (<1 g DW m^{-2}) levels are moderate, and the community has been heavily impoverished in the North and Navigational Channels where permanent dredging has prevented macrofaunal colonization. The dominant species are the bivalves *Cerastoderma edule* and *Macoma balthica,* and the polychaetes *Nephtys hombergii* and *Hediste diversicolor*. However, abundance and biomass values observed for the subtidal *Macoma balthica* community are similar to values observed in the mesohaline part of the Schelde Estuary (Ysebaert et al., 2000).

Ichtyofauna

Data on the ichtyofauna from the lower part of the estuary are scattered. As studies are generally carried out both in the Bay of the Seine and the Seine Estuary, it is difficult to identify what is specific to the estuary. Nevertheless, using the results of Rochard et al. (1997), Mouny et al. (1998) and Dauvin (2002) completed by additional personal observations, it is possible to give a general idea of the composition of the fish population in the lower part of the Seine estuary.

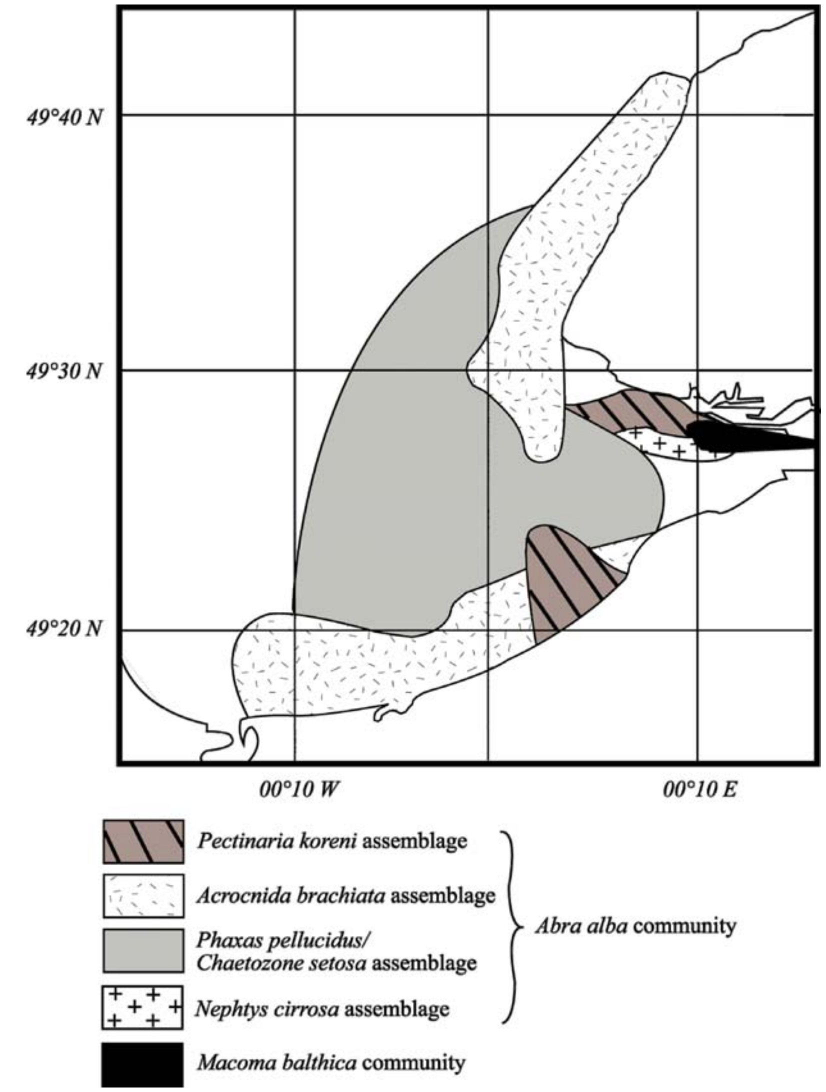

Figure 6. Macrobenthic subtidal assemblages in the eastern part of the Bay of the Seine (from Dauvin, 2002 and unpublished data).

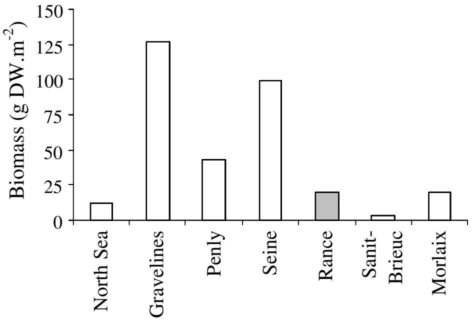

Figure 7. Comparison of mean biomasses on the subtidal, fine sand *Abra alba* community in the North Sea and the English Channel.

Eleven species *Anguilla anguilla*, *Ciliata mustela*, *Clupea harengus, Dicenthrarchus labrax, Platichthys flesus, Pleuronectes platessa, Callionymus lyra, Pomatoschistus microps*, *Pomatoschistus minutus*, *Solea vulgaris,* and *Sprattus sprattus* have been observed to be constant. They belong to two main assemblages.

(1) An estuarine assemblage located in the Navigational and North Channels dominated by *Osmerus eperlanus*, *Platichthys flesus, Pomatoschistus minutus*, *Pomatoschistus microps* and juveniles of *Dicentrarchus labrax, Platichthys flesus*, and *Solea vulgaris*.

(2) A marine assemblage located in the external part of the estuary and the South Channel, dominated by *Callionymus lyra, Pleuronectes platessa, Trisopterus luscus,* and *Solea vulgaris.*

Eight migrant species are also present in the Seine estuary: *Alosa fallax, Anguilla anguilla, Lampetra fluviatilis, Liza ramada, Osmerus eperlanus, Petromyzon marinus, Platichthys flesus* and *Salmo trutta*. However, three migrant species appear to be missing at the end of the 20th century: *Alosa alosa, Acipenser sturio* and *Salmo salar*.

The total species richness reaches 50 species, and the species numbers vary from a maximum of 33 in summer to a minimum of 19 in winter. Maximal abundance (≅10 ind 1000 m^3) has been observed in the oligohaline zone in summer and in the polyhaline zone in winter. By comparison, values for mean abundance and biomass (e.g. 3 ind 1000 m^3 and 2.6 g DW 1000 m^3) are lower in the summer in the Seine estuary than in the Gironde (10–100 ind 1000 m^3 and, 10–100 g DW 1000 m^3) (Rochard et al., 1997). However, the overall small size of individuals would seem to indicate that juveniles mainly occupy the Seine estuary.

Avifauna

The Seine estuary is located on a main migratory route of the Western Europe, connecting north-western European nesting areas to wintering zones located in southern Europe and Africa. About 250 different species of birds visit the estuary, which 164 are regular visitors, 101 are breeding species and 52 are wintering species. From 80 000 to 120 000 water birds regularly stop in the estuary to feed or rest (GONm, 1989). These characteristics confer to the estuary a national importance for several species of water birds, which *Calidris alpina*, *Numenius arquata*, *N. phaeopus*, *Philomachus pugnax*, *Recurvirostra avosseta*, *Tadorna tadorna*

Table 1. Number of species in the different biological compartments from the euhaline to the freshwater zones in the Seine estuary (from Dauvin et al., 2002)

	Euhaline	Polyhaline	Mesohaline	Oligohaline	Freshwater
Macrobenthos	170	60	30	15	75
Suprabenthos	90	50	15	10	10
Mesozooplankton	40	15	10	30	40
Macrozooplankton	30	15	10	5	–
Fish	50	40	20	10	15
Total	380	180	85	70	140

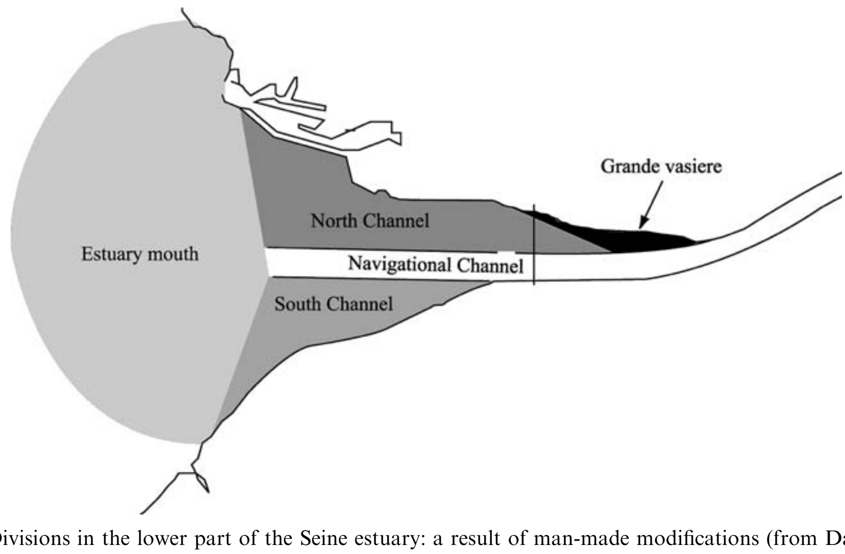

Figure 8. Divisions in the lower part of the Seine estuary: a result of man-made modifications (from Dauvin, 2002).

Table 2. Summary of the spring biomasses (g. Dry Weight m^{-2}) of the main biological compartments in principal sections of the lower part of the Seine estuary (from Dauvin, 2002)

	Macrobenthos	Suprabenthos	Mesozooplankton
Navigational channel	<1–0	15–60	0.5–1.5
North Channel	1.5	0.2	<0.01
'Grande Vasière'	>9	–	–
South Channel	>10–50	–	<0.01
Estuary mouth	>2–100	0.2	<0.01

and *Tringa totanus*, and an international importance for *Anas acuta*, *Haematopus astralegus* and *Platalea leucorodia*.

Biological structure of the Seine estuary

A continuum of planktonic, suprabenthic and benthic assemblages has been described in the Seine estuary along the salinity gradient from the freshwater Seine River to the marine part of the Bay of the Seine. This patterns fits the ecocline model recently proposed by Attrill & Rundle (2002) for estuaries. The number of marine species decreases from the outer to the inner estuary, while the opposite is true of freshwater species. As a result, the total number of species decreases from the euhaline to the oligohaline zones, and increases from the oligohaline to the freshwater zones (Table 1) according to the Remane diagram, revisited by Attrill & Rundle (2002).

A superimposed partitioning of biological zones has been identified in the lower part of the Seine estuary, probably as a result of the man-made modifications over the past 150 years. The lower part of the estuary can be divided into five main compartments of high interest for the trophic chains: the Navigational Channel, the North Channel, the 'Grande vasière', the South Channel and the Estuary mouth (Fig. 8). The macrobenthos compartment exhibits high or very high biomass in the intertidal zone for the *Macoma balthica* muddy community in the 'Grande Vasière' as well as in the subtidal *Abra alba* – *Pectinaria koreni* community located in the South Channel and at the estuary mouth (Table 2). Suprabenthos and mesozooplankton biomasses are high in the Navigational Channel, especially in the oligohaline zone (Table 2). In the Navigational Channel, benthic macrofauna is prevented from settling by the permanent dredging of the riverbed to allow large ships access to Rouen Harbor.

In summary, the lower part of the Seine Estuary is characterized by (1) a high contrast between zones with high and low abundance and biomass, (2) a balance between benthic and planktonic biomasses in the different zones of the estuary, and (3) the relative impoverishment of benthos and plankton in the North Channel.

Trophic chains

The spatial pattern of the benthic and planktonic resources induces a strong interaction between ichtyofauna and their habitats. Two food webs

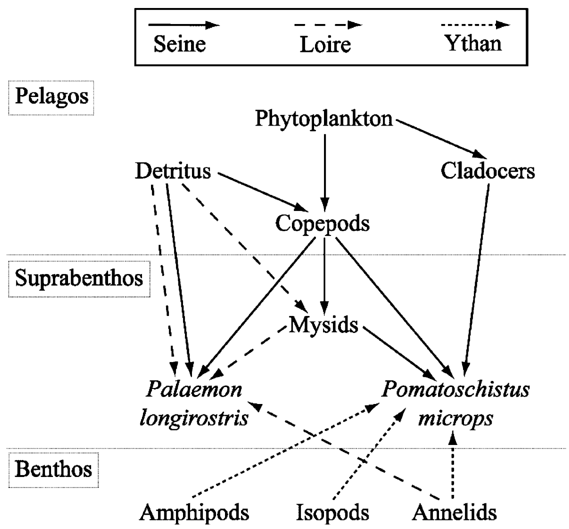

Figure 9. Main prey of *Palaemon longirostris* (Mine Edwards, 1837) and *Pomatoschistus microps* (Kröyer, 1838) in three European estuaries (from Mouny, 1998).

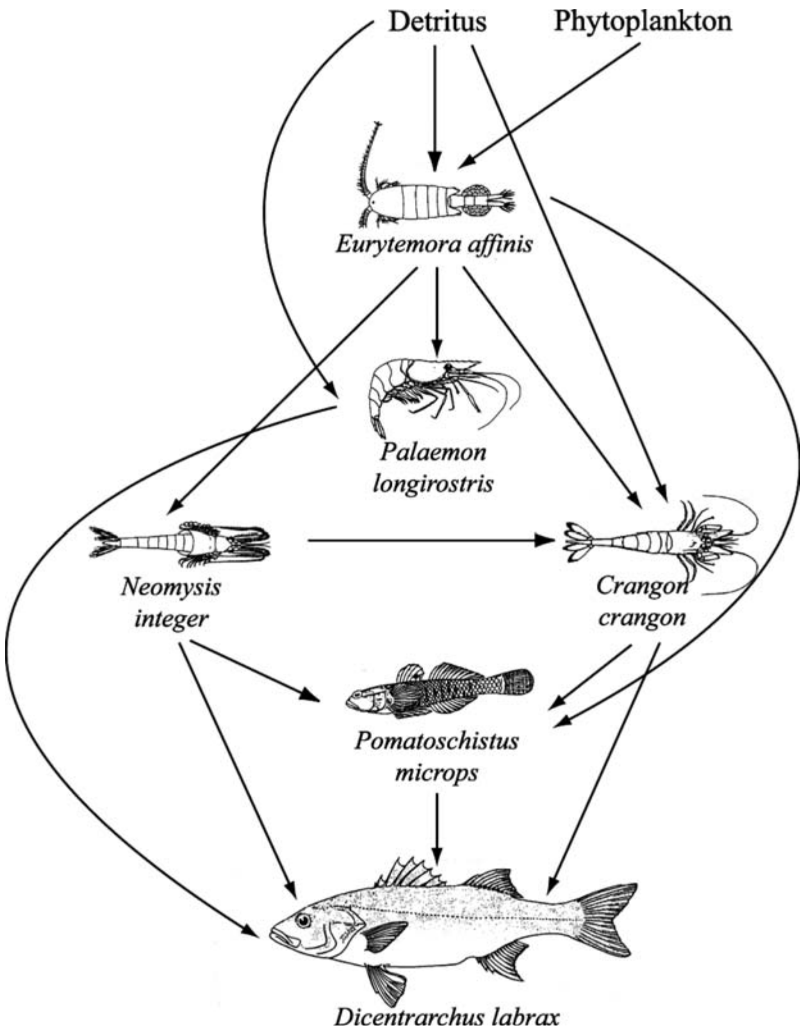

Figure 10. The food web of the sea bass *Dicenthrarchus labrax* (L., 1758) in the lower part of the Seine estuary (from Loizeau, Ifremer Brest in Dauvin, 2002).

have been identified in the lower part of the seine estuary.

1. Using fatty acids and sterol biomarkers, Thoumelin et al. (2000) have shown that *Eurytemora affinis* mainly feed on freshwater phytoplankton in the oligohaline zone of the Navigational Channel. Detritric particles produced by either terrestrial plants or from sewage effluents, are not ingested. Bacteria that develop on detritic particles do not seem to be a significant food source (Thoumelin et al., 2000). In this part of the estuary, accurate functioning depends on the upper freshwater estuarine zone. Stomach analysis of both decapod *Palaemon longirostris* and fish *Pomatoschistus microps* shows these species feed mainly and exclusively on mesozooplanktonic copepod *Eurytemora affinis,* the first throughout the year and the second in spring (Mouny, 1998). Other suprabenthic prey (mysid *Neomysis integer*), and mesozooplanktonic prey (ostracoda, cladocera, decapoda larvae) diversify the diet; nevertheless, during autumn *N. integer* is an alternative resource for both species (Fig. 9). In other estuaries (e.g. Loire, France, Marchand, 1981 or Ythan, UK, Healey, 1972), both species that feed on benthic amphipods, isopods, and polychaetes are able to adapt their diet to the availability of benthic or planktonic prey (Fig. 9).

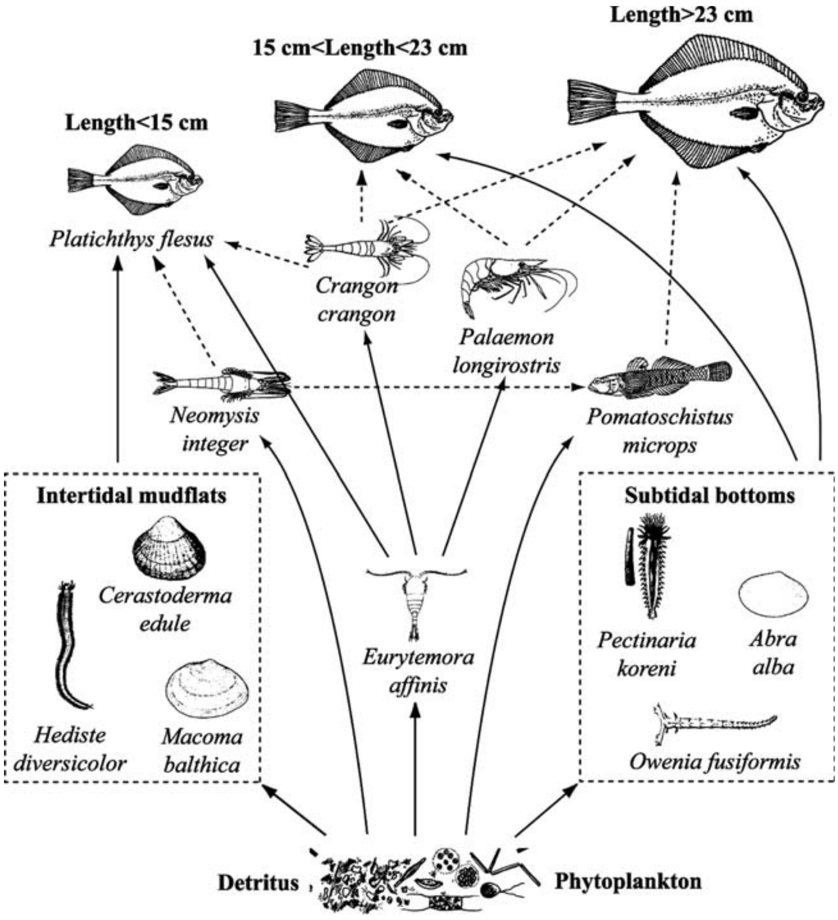

Figure 11. The food web of the flatfish *Platichthys flesus* (L., 1758) in the lower part of the Seine estuary (from Loizeau, Ifremer Brest in Dauvin, 2002). Full line: main prey; dotted line: secondary prey.

Dicentrarchus labrax and *Platichthys flesus* juveniles (0–1 year old), common in this part of estuary, exclusively eat *E. affinis* and *M. integer* (Mouny et al., 1998).

2. In the polyhaline zone, older specimens (2+) of the sea bass *Dicentrarchus labrax* diversify their diet with benthos prey and fish, but suprabenthic decapoda, like *Crangon crangon* and other Caridea, remain primary food sources (Mouny et al., 1998) (Fig. 10). The diet of the flounder *Platichthys flesus* is more diversified (Fig. 11). Juveniles feed on suprabenthic prey like mysids, decapods, intertidal polychaetes and bivalves, whereas adults (total length > 15 cm) consume decapods, fish and subtidal macrobenthic prey from the *Abra alba* community (Fig. 11). Benthic prey to the flounder diet increases with the growth of fish (Mouny et al., 1998). Figure 12 shows a conceptual model of how the North Channel compartment functions, at two tidal periods. At high and low tide, respectively, juvenile fish feed mainly on the intertidal *Macoma bathica* community, and the suprabenthic community.

Conclusions

The lower part of the Seine estuary exhibits contrasted zones characterized either by high biomass or low biomass for each of the biological components studied, e.g. mesozooplankton, suprabenthos and macrobenthos. There has been considerable partitioning of the lower part of the Seine estuary as a result of the man-made modifications, and it will be necessary in the future to establish a model that explains the principal

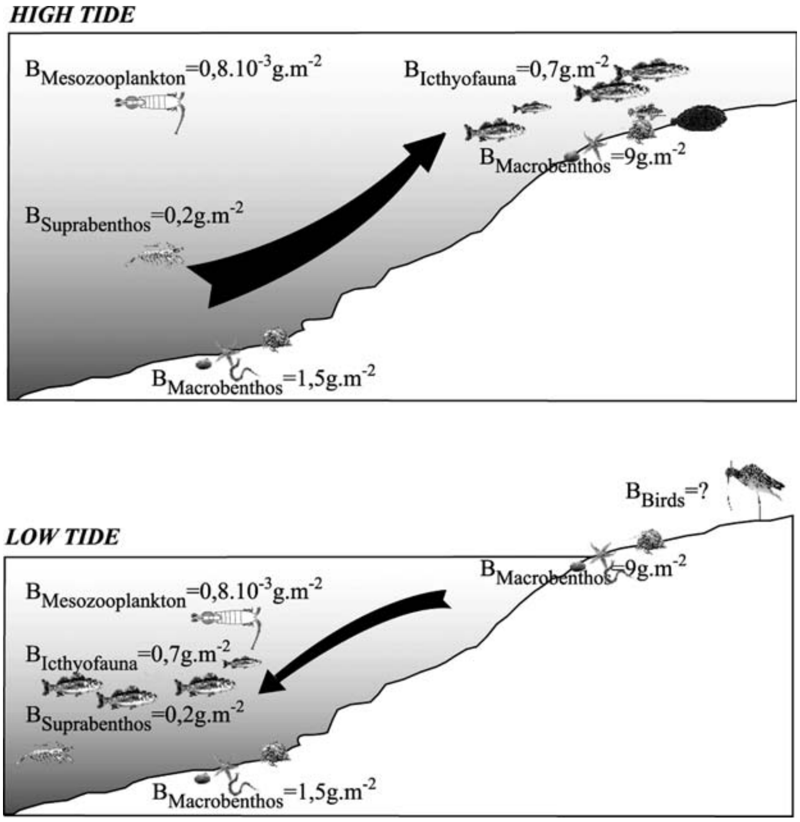

Figure 12. Schematic representation of the food web in the North Channel of the lower part of the Seine estuary.

relationships between the different compartments of the estuary. The biological function of the estuary is highly dependant on the mesozooplanktonic and suprabenthic fauna from the Navigational Channel and on the benthic biomass of the intertidal *Macoma balthica* and subtidal *Abra alba* communities. As maximum abundance and biomass of the prey components are among the highest observed in the other North-East Atlantic estuaries, food availability does not appear to be a limiting factor for fish. Nevertheless, low fish biomass is observed in spite of this abundance of prey. The paucity of food can not be evoked as the cause of the absence of migrant species as can the level of contamination (Miramand et al., 2001). This absence can probably be attributed to man-made modifications, such as the destruction of habitats by dredging or the constructions of lock gates (Dauvin, 2002). The lower part of the Seine estuary remains an important nursery for marine fish like the sea bass and the sole (Dauvin, 2002), and the Seine estuary maintains its attractiveness for wildlife, despite industrialization and land-claim, because estuarine habitats are the most resilient habitats on earth (Elliott & McLusky, 2002). As with other estuaries (Elliott & McLusky, 2002), the Seine estuary provides unique ecosystem services to benefit mankind and maintain the health of the eastern English Channel marine ecosystem, by trapping contaminants in its sediment, whilst also providing nurseries for marine fish and feeding grounds for migratory birds. The restoration of habitats and the reduction of chemical contamination are challenges that must be met in order to preserve current biological processes in the estuary and to ensure the return of migrant fish to the Seine. The extension of the port in Le Havre (France) will have consequences on the sedimentation of the external estuary by increasing fine particle sedimentation, thus reducing the intertidal zone in the North Channel, and will cause further damage to the Seine estuary as a whole. Some compensatory measures, such as the construction of an artificial island for birds, and the dredging of a new canal in the upper part of the North Channel to maintain seawater circulation, have been decided in order to limit the negative ecological effects of this new man-made modification of the Seine estuary (Dauvin, 2002). At the same time, a committee of scientific and technical experts has been created under the responsibility of the 'Prefecture de Haute Normandie' to ensure the sustainable development of the Seine estuary. Though sometimes considered rather subjective, the concept of sustainability seeks to establish consensus between widely diverse points of view – flood defense, navigation, water quality, conservation and recreation – in an attempt to balance the economic, social and environmental considerations that will result in a solution that satisfies everyone. In this context, the Seine estuary, like other estuaries (Jones et al., 2002), presents a daunting challenge for legislators, territorial planners and the scientific community as they struggle to formulate plans for future estuarine management.

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