Establishing trends in trophic functioning of the Sélune River megatidal estuary prior to dam removal

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Abstract

Restoration of the ecological continuity of rivers has become a strong ecological issue. In some cases, it may lead to the dismantling of dams, but ecological consequences for estuarine ecosystems are poorly known. Notably, by increasing sediment and nutrient retention in reservoirs, dams can alter the influx of terrestrial subsidies to estuarine food webs. Here, we assessed the trophic functioning of the megatidal estuary of the river Sélune (bay of Mont-Saint-Michel, France) before the removal of two large dams on the river. Both estuarine benthic invertebrate and bentho-demersal fish faunas were characterized at two periods (spring and autumn 2017) and food web described by means of stable isotope (nitrogen and carbon) and fish gut analyses. Macrobenthic fauna was typical of European estuaries, with low species richness because of high physical constraints (highly variable salinity, strong currents, high altitude) prevailing in the area. High abundances and biomasses were observed in the two downstream sectors under the bay influence providing them a feeding interest for juvenile fish. Two species of gobies (*Pomatoschistus microps* and *Pomatoschistus minutus*), juvenile sea bass (*Dicentrarchus labrax*) and juvenile flounder (*Platichthys flesus*) dominated the fish fauna. Food web was mostly fueled by local primary production, predominantly microphytobenthos. Macrobenthic invertebrates (*Corophium arenarium* or *Bathyporeia pilosa*) but also harpacticoid copepods and mysids in autumn were the major prey and constitute the primary consumer level of the food web, the fish being at the top as secondary consumers. The analysis of the trophic niche of fish and their overlaps gave elements on the respective feeding strategies and inter-specific competitions.

Key words: estuary, trophic ecology, stable isotope analysis, gut contents analysis, Mont-Saint-Michel Bay

Introduction

Although coastal and estuarine ecosystems (CEE) represent only 6% of the marine surface, they are among the most productive systems on earth (Costanza et al., 1997). Several studies underline the essential nursery role that these ecosystems play by serving as feeding areas or as a simple refuge for many species, including fish (Pasquaud et al., 2012). They are essential to the functioning of the marine environment, as well as for human welfare (Costanza et al., 1997). However, CEE are threatened by human activities, notably overfishing, aquaculture, tourism, and pollution (Worm et al., 2006; Halpern et al., 2007). Anthropogenic pressure on CEE often, if not systematically, decreases biodiversity (animal and plant), alters ecosystem functions and ecological state (Hammerschlag et al., 2019), leading to a possible loss of some ecosystem services.

The construction of dams for producing electricity, securing freshwater resources, controlling flood or improving upstream navigability is one of such disturbances that cause meaningful changes to downstream ecosystems such as CEE (Ly, 1980; Nixon, 2004; Morais, 2008, Zhang et al. 2022). Schaffer et al. (2017) estimated that 40,000 to 47,000 large-scale dams have significant impacts on watershed and marine ecosystems worldwide. Over two-thirds of the largest rivers in Europe have major discontinuities due to large dams. These dams were mostly constructed during the second half of the 20^{th} century (Duarte et al. 2020). It is well known that large-scale dams (>15 m in height) change hydrologic regimes, alter sediment and nutrient loads downstream (Rollet et al. 2014; Dethier et al. 2022), with potential impacts aquatic communities and ecosystem functioning (Schaffer et al., 2017, Zhang et al. 2022, Morais et al. 2009). Therefore, congruently with an increasing effort to restore degraded aquatic ecosystems, large dam removal projects have emerged as an important ecosystem restauration tool during the past 20 years (Schaffer et al., 2017).

Depending on the context, dam removal can have significant outcomes on CEE (Foley et al. 2017). Notably, the restoration of natural tidal and river flow patterns enhances the interaction between freshwater and saltwater, re-creating a dynamic environment with more diverse habitats (Bednarek, 2001). The natural balance between sediment deposition and erosion also restores critical habitats for plant and animal communities (Figueroa et al., 2022). Moreover, some species that use both marine and freshwater habitats during their life cycle are favoured by the removal of obstructions to flow in estuaries and rivers (Hill et al., 2019; Wippelhauser 2021). Conversely, the sudden release of trapped sediment following dam removal operations and water can however lead to short-term disruptions in the estuarine ecosystem (Warrick et al. 2015; Shaffer et al. 2018), by causing turbidity peaks, affecting light penetration and potentially affecting some species (Bednarek, 2001). However, these disruptions are usually transient, and the ecosystem tends to recover and readjust to natural conditions over time (Bednarek, 2001).

Looking beyond direct effects on continuity and aquatic habitats through hydraulic and geomorphological processes, dam removal can induce major, indirect impacts on ecosystem functions in CEE too. Indeed, large-dam reservoirs have a meaningful effect of retention of organic matter and dissolved nutrients (Dethier et al. 2022; Maavara et al. 2020), which are important subsidies for CEE food webs. For instance, it has been shown that particulate organic matter from terrestrial origin conveyed by the river Vilaine (bay of Biscay, France) fuels coastal benthic food webs, highlighting that the river discharge has a central role in determining the carrying capacity of a main nursery habitat for flatfish (Kostecki et al. 2010). Moreover, following the construction of the Aswan High Dam on the Nile River, terrestrial water and nutrient supply to CEE decreased by 90%, and a major effect on fishery performance (mostly finfish, shrimp and prawns) was reported along the Egyptian Mediterranean coast (Nixon 2003, and references therein). Therefore, by restoring the downstream transfer of terrestrial subsidies to marine habitats, dam removal operations can induce structural and functional changes in CEE food webs. The underlying processes are known, however, the probable effect of river continuity restoration on CEE food webs have not been clearly reported yet.

The Sélune River is a short coastal stream that discharges into the Bay of Mont Saint-Michel, France. The downstream transfers of sediments and solutes from catchment to CEE has been altered by the presence of two large hydropower dams since the early 20th century. The amount of sediment stored in reservoirs was estimated to reach 3,000 tons.y^{-1} in 2015-2016, including organic matter particles from terrestrial origins (Fovet et al. 2020, Roussel et al. submitted). Similarly, a significant decrease in nutrient concentrations in water has been reported downstream of the reservoirs (Fovet et al 2020), notably silicon which is key element for the growth of benthic diatoms. The bay of Mont Saint-Michel is a wide, shallow system with a high tidal range (up to 15 m) and that mostly consists of mudflats and intertidal salt marshes. It is a remarkable nursery habitat for many marine fish species of commercial interest, among which sea bass *Dicentrarchus labrax*, common sole *Solea solea*, plaice *Pleuronectes platessa* and flounder *Platichthys flesus*. Previous studies on benthic food webs in the bay have showed that primary production is largely based on salt marshes and benthic diatoms (Lefeuvre et al. 2000, Arbach Leloup et al. 2008), and the prevalent role of microphytobenthos as primary food source for juvenile fish and benthic food webs has been outlined (Kostecki et al 2012). Trends in food webs functioning in the megatidal estuary of the Sélune river, however, is mostly unknown, while this mainly intertidal ecosystem is the first to receive terrestrial organic matter and dissolved nutrients from the river.

The present study was launched after the decommissioning of dams on the Sélune river has been confirmed in 2017. Considering that transfer of organic sediments and dissolved nutrients fluxes are the major changes expected after restoration of the downstream on its estuary, the objective of the study is i) to establish its bentho-demersal food web prior to dam removal and ii) to discuss on assumed effects of these changes on the trophic functioning of the estuary and on its contribution to the function of nursery of the bay of Mont-Saint-Michel. In this objective, bentho-demersal fish as main secondary consumers and macro-benthic invertebrates as potential fish prey were considered and characterized. They were sampled using trawl and hand-held corer. Trophic relationships, energy sources and transfers through benthic food web were investigated by means of fish digestive contents and stable isotope analyses (DCA and SIA, respectively) as complementary approaches.

Material and methods

Study site

The estuarine area is located in the North-West of France (Figure 1). It opens in the bay of Mont-Saint-Michel and exhibits a semi-diurnal system with a high tidal range (15 m). It covers ca 45 km^2 partly shared with the estuary of the Sée river and is characterized by intertidal flats veined with channels which locations vary with high hydrodynamical conditions. A schorre is observed in its higher parts (supralittoral). Four sectors were distinguished according to geomorphological traits along an east-west estuarine gradient (Figure 1). The “Upper Sélune estuary” is in the continuity of the Sélune river bed, the “Middle estuary” is an enlarged part shared with main channel of the Sée estuary and the “Open estuary” is the wider part of the estuary forming the transition with the bay of Mont-Saint-Michel. The “Sée estuary” situated in the north of the study site constitutes another sector.

Sampling

As biological and trophic characteristics were assumed to change within a year, two surveys were conducted in order to sample the benthic invertebrate macrofauna and the bentho-demersal ichtyofauna: the first one at the end of March / beginning of April 2017 (spring) and the second, at the end of September / beginning of October 2017 (autumn).

Fauna, sediment and water

Sampling of ichtyofauna took place at high tide during spring tides using a beam trawl (146 cm wide x 45 cm high) towed for 10 to 15 minutes (depending on bottom configurations) at a speed of two knots. Beam trawl hauls were realized in channels according to bathymetric constraints. A total of seven trawl stations were sampled (Figure 1). At each trawl station, temperature, salinity and oxygen were recorded with a CTD probe. Samples were kept in cold until their analysis in laboratory. Benthic sampling was carried out using a hand-corer (0.029 m²) at a sediment depth of 20 cm, at eleven sampling sites near the channels (Figure 1). At each site, nine samples (*i.e.* 0.261 m² per station), collected to characterize macrobenthos, were gently washed *in situ* through a 1 mm sieve. In addition, two samples of the top centimeters of the sediment (10 cm and 1 cm) were taken to determine the particle size and organic matter content of the sediment, respectively.

Sources

At trawled sampling sites, three samples of 1L of sub-surface seawater were taken to characterize the isotopic signature of the estuarine particulate organic matter (POM) and three freshwater samples from the Sée and the Sélune rivers were collected for the river POM. The microphytobenthos (MPB) was sampled, when present, by scraping directly with a spatula the few millimeters of surficial sediment. The samples were tripled during the autumn campaign, in order to calculate an average representative of the isotopic composition. Invertebrates of several benthic species and fish were additionally collected during benthic and fish sampling surveys for isotopic analyses. Fish, macro invertebrates and sources samples were stored in coolers until their return to the laboratory.

Laboratory analyses

Sediment

An aliquot of each sediment sample was removed, weighed a first time after drying (48 hours at 60°C) and a second time after burning (6h at 450°C). The difference between the two weights gave the organic content.

For granulometric analysis, sediment samples were rinsed through a 63 µm sieve with filtered seawater. The fraction smaller than 63 µm was dried for 48 hours at 60°C and weighed giving the mud rate. The remainder was dried for 48 hours at 60°C before being sieved on a vibrating column composed of 26 AFNOR standard sieves and each sieve oversize, weighed in order to assess the Trask sediment sorting index.

Fauna

At the laboratory, macrobenthic samples were preserved in 4.5 % buffered formalin before being sorted, identified for the smallest with a binocular magnifying glass at the most precise taxonomic level possible, counted and weighted wet. In the few hours following sampling, the fish were identified, counted, measured and weighted wet. The digestive tracts of four species of fish currently observed (*Dicentrarchus labrax*, *Platichthys flesus*, *Pomatoschistus microps* and *Pomatoschistus minutus*) were removed and fixed in a buffered formaldehyde solution (3.5%). They were weighed full and emptied, and the species present were identified with a binocular magnifying glass at the most precise taxonomic level possible and counted.

Isotopic analysis preparation

Marine and freshwater POM were extracted by filtration of 250 to 500 mL (depending on the turbidity) through a GF/F filter previously calcined (500°C – 1 hour). The filters were then decalcified with hydrochloric acid (1N HCl) and rinsed with distilled water. Microphytobenthos (MPB) was extracted from the sediment by migration through a 60 µm nylon mesh. The mesh used for the migration was washed with filtered seawater and the residue filtered on a GF/F filter previously calcined (500°C – 1 hour), decalcified with 1N HCl and rinsed with distilled water. The leaves of the phanerogam species sampled were rinsed with filtered seawater, decalcified with hydrochloric acid (1N HCl) and rinsed with distilled water. Digestive tracts of polychaete annelids collected in macrobenthic samples were removed so that only the muscles were analyzed. Shells and digestive gland of bivalve mollusks were removed, in order to analyze only the muscles, mantle and foot. For crustaceans, (i) amphipod were pooled to have enough material for analysis and one half of them was kept as such, and the other half was decalcified (1N HCl) and rinsed with distilled water and (ii) Mysids crustaceans (Mysida) were previously decalcified (1N HCl) and rinsed with distilled water. Finally, a sample of the dorsal muscle of fish was taken from five individuals for each of the four species chosen (see above) and per trawl station.

After their previous preparation, samples were stored in the freezer at a temperature of -20°C, then freeze-dried. The analysis of the isotopic compositions of the samples was carried out at the Stable Isotopes in Nature Laboratory (SINLAB, University of New Brunswick, Canada). The values of the stable isotopes have been converted into ratios (denoted δ):

$$\delta X = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 10^3 (‰)$$

with R=$^{13}C/^{12}C$ or $^{15}N/^{14}N$. The references of the international standards are Pee Dee Belemnite carbonate (PDB) for $\delta^{13}C$ and atmospheric nitrogen (AIR) for $\delta^{15}N$.

The complementarity of these two approaches (digestive contents and isotopic analyses) makes possible to better understand the ecological processes involved. DCA is classically used in trophic ecology (Amundsen, P. A., & Sánchez-Hernández, 2019) but only gives an instantaneous picture of ingested food. SIA of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) provides integrated information on food sources assimilated over the long term (a few weeks) by a consumer (Phillips et al., 2014) but is less informative about the precise prey spectra.

Data analysis

Statistical analyses were performed with Rstudio software (version 3.0.1+) and several R packages (See below).

Environmental data

A Principal Component Analysis (PCA) was used to characterize the study area, for both seasons. Parameters selected were, for sediments: organic matter rate, Trask's index, mud content; and for water: dissolved oxygen, salinity and temperature.

Stable isotope analysis

Isotopic niche

In order to visualize the species isotopic niche, Standard Ellipse Areas (SEAs) were plotted for each species in a bi-plot $\delta^{15}N/\delta^{13}C$ per survey [spring and autumn (Parnell et al., 2010; Jackson et al., 2012)]. SEA represents the isotopic niche of each species by integrating 40% of its variance. To avoid problems of underestimation of SEAs when the number of samples per species is less than 30, a correction factor has been applied, as follows:

$$SEAc = SEA \times (n-1)(n-2)^{-1}(‰^2)$$

This estimator, called corrected Standard Ellipse Area (SEAc), quickly reaches an asymptote and eliminates the influence of the individual number.

From the SEAc, a second estimator has been developed by a Bayesian approach to the area of the standard ellipse (bayesian Standard Ellipse Area - SEAb), which makes possible to compare the isotopic niches of each species, by maximizing the uncertainty linked to the area calculated for groups of small numbers (Jackson et al., 2011). Calculation of surfaces refers to *a posteriori* probability distribution model of estimation of the ellipse area (based on Monte-Carlo methods by Markov chains from 20 000 iterations).

The width of each isotopic niche was compared (*p*-value of 0.05), considering as hypothesis H0 that the area of the standard ellipse $SEAb_i$ is smaller than the area of the standard ellipse $SEAb_j$. Finally, isotopic niche overlaps were estimated and expressed as the percentage of the standard ellipse corrected area (SEAc) of isotopic niche i overlapping the ellipse corrected area of isotopic niche j (Package "Siber" of R, Parnell et al., 2010).

Mixing model

From mixing models, the contribution level of multiple sources for each consumer can be estimated. We focused here on the main fish. The estimate is based on the values of sources and consumers, according to the trophic enrichment factor (TEF or Δ). Mixing models were applied to estimate the proportions of contributions of main basal sources of the food web (MPB and freshwater and marine POM). Classic TEF values are of 1.3‰ (± 0.4 SD) for $\Delta\delta^{13}C$ and 3.4‰ (± 1.0 SD) for $\Delta\delta^{15}N$ for the passage of a trophic level (Post, 2002). Based on the study conducted by Kostecki (2012) in the bay of Mont-Saint-Michel, TEF values of 2.00 (± 1.30SD) for $\Delta\delta^{13}C$ and 5.60 (± 1.00SD) for $\Delta\delta^{15}N$ were retained between basal sources and fish in our study. All mixing models were performed using the R package 'SimmR' (Parnell et al., 2010).

Digestive content analysis

The study of fish diet was based on the calculation of relative abundance of prey. This metrics was chosen over "bulk" type methods, as it is statistically more robust (Baker et al., 2014).

Results

Environmental characterization of the study site

Following axis 1 of PCA performed on environmental variables shows clear differences between the two periods and more particularly for the upstream sectors (Sée estuary and Upper; Figure 2). Water salinity and temperature on one side and Upper sector at the opposite mainly contribute to this axis. The estuarine gradient from open to upstream sectors is mainly observed on axis 2 with a high contribution of the mud content of sediment and the two upstream sectors in autumn.

Macrobenthic invertebrate fauna

A total of 35 taxa, for most of them identified at the species level, were observed. Annelids (mainly polychaetes: 10 species) as well as crustaceans (10 species) dominate the taxonomic spectrum. Insects (7 species, mainly under nymphea stages) and mollusks (4 species) were also recorded. The taxonomic richness shows a general increase trend from upstream to more open sectors (Figure SM1) whatever the period (from minimum 1 to maximum 14 taxa). Abundance was higher in the Middle sector whatever the period and shows higher values in the upstream stations in autumn compared to spring. Biomass presents a clear increase from Sée to Middle sectors in spring. This trend is not observed in autumn, despite the existence of a minimum in the station F (Figure SM1).

In the taxa recorded in the study site, four species strongly dominate numerically. Their densities vary according to sectors and periods (Figure 3). Thus, the amphipod crustacean *Corophium arenarium* dominated in the Sée estuary and the Middle sectors in spring with changes in autumn with the leading of the polychaete annelid *Hediste diversicolor* and the amphipod *Bathyporeia pilosa*, respectively in stations E and C. *H. diversicolor* characterizes the Upper sector, station G forming transition with the Middle sector. In the Open sector, the dominance between these species and the bivalve mollusk *Macoma balthica* seems more balanced in spring than in autumn for stations A and B where *C. arenarium* and *B. pilosa* were not observed. Thus, in regards to the spatial distributions of dominant species in spring and autumn, two general trends are observed: *C. arenarium* and *H. diversicolor* are present on the whole gradient while *B. pilosa* and *M. balthica* occur only on the downstream part of the area (mainly Middle and Open sectors).

Available prey [i.e. individual weight < 0,66 $g.ind.^{-1}$ WW, Day et al, (2020)] biomass (Figure 4) mainly concerns the suspension & deposit feeder group and to a lesser extent the omnivore group only represented by *H. diversicolor*. Other groups (suspension feeders, deposit-feeders, carnivore & scavenger, carnivore) are generally less important and herbivore group is almost absent. High available biomass values are observed in the Open and Middle sectors (mainly the suspension & deposit feeder group), while they are low in the Upper sector (mainly the omnivore group) and insignificant in the Sée sector. In autumn, biomass shows a net decrease the Middle sector while it increases in the Upper sector and also in one station of the Sée sector. Isotopic analysis that follows will allow to assess the position of the different trophic groups within the food chain.

Bentho-demersal fish

A total of 10 bentho-demersal fish species were collected in the study. No clear spatial trend was observed in the estuarine gradient for the specific richness (Figure SM2). The abundance decreases from up to downstream whatever the period. It is generally higher in autumn than in spring. The same feature is observed for the biomass. Four fish species were strongly dominant whatever the period considered (Figure 5): two gobies (*Pomatoschistus microps* and *Pomatoschistus minutus*), juvenile bass (*Dicentrarchus labrax*) and juvenile flounder (*Platichthys flesus*). Gobies and bass occur on the whole gradient whatever the period. Flounder was absent in the Open sector in spring and the Open and Middle sectors in autumn.

Digestive contents of fish

Of all the digestive contents examined, few were empty whatever the season: mean rates of emptiness were of 1.7 ± 4.0% and of 2.26 ± 3.5% in spring and in autumn respectively. The prey identified do not only belong to macrobenthos (mainly amphipods) but also to meiobenthos (size < 1 mm, exclusively harpacticoid copepods), predominant in spring, and suprabenthos (exclusively mysids) appearing in autumn.

D. labrax (242 analyses, total length = 8.3 ± 1.4 cm and 7.2 ± 1.9 cm SD, in spring and autumn respectively).

In spring, whatever the sector, 90% of the digestive content of *D. labrax* were composed of amphipods, *C. arenarium* representing at least 78% of the diet and *B. pilosa*, from 4% to 18% (Figure 6). In autumn, except in the Sée sector where the diet was dominated by a gnathiidae (isopod), the sea bass diversified its diet although the amphipod *C. arenarium* remained the main prey, the contribution of mysids increased for each sector.

P. minutus (282 analyses, total length = 4.7 ± 0.8 cm and 4.5 ± 0.9 cm SD, in spring and autumn respectively)

The digestive contents of *P. minutus* showed strong variations between the two periods. In spring, *C. arenarium* and *B. pilosa* represented 62 to 79% of its diet (Figure 6), except in the Open sector where cumaceans represented 80% of prey. In autumn, although *C. arenarium* still represented 29 to 57% of the diet, mysids (*Mesodopsis slabberi* and especially *Schistomysis spiritus*), constituted 23 to 70% of prey.

P. microps (395 analyses, total length = 3.9 ± 0.6 cm and 3.6 ± 0.6 cm SD, in spring and autumn respectively)

The diet of *P. microps* showed little seasonal variation, this species feeding largely on harpacticoid copepods (abundance >45%) and *C. arenarium* [between 20 and 40% of prey (Figure 6)].

P. flesus (82 analyses, total length = 5.7 ± 1.6 cm and 5.3 ± 2.5 cm SD, in spring and autumn respectively)

In spring, the digestive content of *P. flesus* was based on two main prey: *C. arenarium* (with a proportion ranging between 43% and 72%) and harpacticoid copepods [up to 95% in the Sée zone (Figure 6)]. In autumn, the prey diversity was reduced and copepods were the almost exclusive prey (between 87 and 95% of prey) depending on the zone.

Trophic food web provided by the isotopic analysis

As preliminary analyses did not show any significant isotopic contrast between sectors for sources (estuarine POM and MPB) and secondary consumers (fish), isotopic data were grouped in order to give a global view of the food chain of the study site for the two periods. The sources appear at the bottom of the of the $\delta^{15}N/\delta^{13}C$ biplot (Figure 7) mainly varying according to the $\delta^{13}C$ axis with large SEAc except for estuarine POM in autumn. River POM appears as the most ^{13}C depleted. A slight increase of MPB through the $\delta^{15}N$ axis is observed in autumn compared to spring. Above these sources, are located bivalve mollusks (Cardiida) and amphipods crustaceans (Amphipoda) as strict or flexible deposit or suspension feeders (primary consumers) showing narrow SEAc. As observed above (Figure 4) they represent the major part of the biomass available for juvenile fish. They show a slight increase between spring and autumn. The fish, *P. microps*, *P. minutus* and *D. labrax* as predators (secondary consumers) are positioned at the top of the chain with narrow SEAc and SEAb (Figure 8) whatever the period with a clear overlap (Table 1) between gobies in spring. The overlap (>25%) between these three fish is stronger in autumn (Table 1) than in spring. *P. flesus* clearly differs from the other fish in regards of its depleted ^{13}C composition and its highly variable ^{15}N composition in spring and autumn, giving wide SEAc and SEAb (Figure 9) with rather poor overlaps (<15%) with other fish. Between the primary and secondary consumers are the *Hediste diversicolor* and the mysids (only collected in spring), reflecting their omnivorous diet. As primary consumers, *H. diversicolor* shows a slight increase in autumn compared to spring.

Isotopic niche width and overlap

Values of SEAb and SEAc exhibit good correspondences, attesting a good isotopic representation for each fish (figure 5). *P. flesus* had the widest SEAb whatever the season, whereas *D. labrax* and *P. microps* had the narrowest in spring and autumn respectively. SEAb of *P. flesus* and *P. minutus* were significantly stable between the two seasons (p>0.05) contrary to *D. labrax* and *P. microps* (p<0.01). Few overlaps of the SEAc were observed in spring (figure 3 and table 4): the SEAc of *P. microps* overlaped 23% of that of *P. minutus* and 14% of that of *P. flesus*. Conversely, in autumn, overlaps became important between the SEAc of *D. labrax* and the two species of *Pomatoschistus* (*P. minutus* – 50% and *P. microps* – 39%). Overlap between the SEAc of the two goby species remained of the same order of magnitude (28%).

Contribution of sources

At the scale of the study site, contributions of MPB, estuarine POM and river POM are similar for the two periods studied. Results of mixing models identify the MPB as the preferred source of energy transiting to the four dominant fish species (with a lower contribution for *P. flesus*) and the river POM as the least used source (Figure SM3).

Discussion

Benthic features driven by high environmental constraints

The study of benthic communities in the megatidal Sélune estuary provides essential information on this ecosystem prior to dam removal. Macrobenthic fauna is dominated by amphipods, mainly represented by *Corophium arenarium* and to a lesser extent by *Bathyporeia pilosa*, two species with a high recruitment capacity. These species are closely related to euryhaline environments, regarding to their ability to dig into the sediment to maintain a microcosm corresponding to their ecological preferences (Preece, 1970). These species hierarchy is original compared to other estuaries in northern Europe, where annelids and molluscs are often dominant (Josefson and Hansen, 2004; Thorman, 1986). With the species observed, the "open estuary sector" of the estuary corresponds to the *Macoma balthica* community defined by Trigui (2009) in the high intertidal flats of the eastern part of the bay of Mont St Michel. The "Middle estuary sector" appears as transitional between upper Sélune estuary and the bay.

The bentho-demersal fish fauna of the estuary is dominated by four species only: flounder (*Platichthys flesus*), sea bass (*Dicentrarchus labrax*) and two gobies (*Pomatoschistus microps* and *P. minutus*). They are euryhaline bentho-demersal species withstanding salinity variations (Kelsall and Balment, 1998). Gobies have poor swimming capacities, but they use strong hydrodynamic conditions to move (Laffaille et al., 2001; Pasquaud et al., 2004; Raffaelli et al., 1990). Between the Sélune estuary and the bay du Mont Saint Michel, differences appear in the main bentho-demersal fish species according to the study of Laffaille et al. (2000). Thus, *Gastrosteus acculeatus* (stickleback) and *Pleuronectes platessa* (plaice) are absent in the estuary. Similarly, *Solea solea* (common sole) recorded in the bay are anecdotal in the Sélune estuary. On the other hand, the *P. flesus* gains in dominance in the estuary compared to the bay.

The taxonomic richness of the estuary is low (35 macrobenthic invertebrate taxa and 10 fish species in total) despite a substantial effort (14 and 18 sampling stations for macrobenthos and fish respectively in total with two different periods). This feature is a common pattern shared by estuaries compared to freshwater and marine ecosystems (Whitfield et al. 2012) because of high environmental constraints. The habitat of the Sélune estuary is an alternation of deposit and erosion stages of muddy sands imposed by the strong hydrological constraints, which leads to the frequent relocation of banks and channels visible at low tide (Ehrhold, 1999). The altitude of intertidal flats is added to these constraints. Such environment conditions, are observed in some other macrotidal estuaries in Europe (Josefson and Hansen, 2004; Nicolas et al., 2010) and play on the poor taxonomic richness observed. Its decrease for macrobenthos from “open” to “upper estuary” sectors of our study traduces an increasing stress gradient.

In this gradient, abundance of macro-invertebrates shows a maximum in the “middle” sector whatever the period with a decrease in the upstream sectors (“Upper” and “Sée”). Biomasses are highest in the downstream sectors (“Open” and “Middle”). This combined with small size of macroinvertebrate offer a preferential area for feeding juveniles fish. The higher biomasses in autumn in the upstream sectors suggest that they may be more profitable for fish feeding at this time of the year than in spring. The up to downstream slight decreasing trends in abundance and biomass of fish in spring is not observed in autumn. Whatever the sector, abundance and biomass are higher in autumn, assuming that this period follows summer periods where salinity is more stable and temperature of the surrounding water mass is high, that favor the juvenile occurrence and growth (Marchand, 1993). Therefore, one can logically wonder whether the Sélune estuary as an appendix of the bay du Mont Saint Michel contributes to its nursey function (Kostecki et al., 2012), especially for juvenile sea bass and flounder.

The Selune river with dams: a simple bentho-demersal estuarine food web

The food web of the Sélune estuary is not very diverse as a consequence of the low taxonomic richness observed. Mixing models showed that it was predominantly fed by the microphytobenthos (composed mainly of benthic diatoms) that grows on the intertidal muddy sand banks (Jesus et al., 2009; Riera, 2007) whatever the period. This is similar to what has already been described in the whole intertidal area of the bay du Mont Saint Michel (Kostecki et al., 2012).

According to the fish digestive content analysis the prey taxa do not only belong to macrobenthos but also to suprabenthos (mysids) and meiobenthos (harpacticoids) not sampled by the grab or the beam trawl used in our study. These two benthic components may therefore be significant food resources for these fish (Couch, 1989). Amphipods (*C. arenarium* and *B. pilosa*) which are suspension & deposit feeders (Clare et al. 2022) and clearly primary consumers in the isotopic analysis. They are the predominant prey of juvenile sea bass and *P. minutus* but less in *P. microps* which prefers harpacticoids. In view of the trophic position and the overlaps observed between these species, this suggests that the harpacticoids, are located at a trophic level comparable to that of the amphipods. Mysids as prey are mainly found in autumn in *P. minutus* and in juvenile sea bass. The main species recorded in the digestif tract was *Mesopodopsis slaberri* which can be considered as primary consumer owing its phytoplanktonic feeding (Webb et al., 1987). It differs from the mysids present in the food web figure of spring of our study (Figure 8): *Neomysis integer* and *Schistomysis spiritus* (collected in spring by our beam trawl) that are omnivore (Bremer et al., 1982; Mauchline, 1967) and logically positioned near *H. diversicolor*.

The two species of gobies clearly occupy the top of the food chain while the flounder, slightly beyond at the two periods. The juveniles of the four species of fish in our study have a high food plasticity (in particular *P. flesus*), and are able to take advantage of the most abundant prey and to better adapt to variations in their environment (Andersen et al., 2005; Cabral and Costa, 2001; Leclerc et al., 2013; Pasquaud et al., 2004). In regards of the poor diversity of potential prey and the isotopic niche widths observed, one can assume that the juvenile sea bass and gobies feed on prey of the same isotopic composition as described above. Compared to the other fish, flounder has a wider isotopic niche covering a high range of $\delta^{15}N$ (9.24 to 14.92 ‰ in spring, 9.44 to 14.16 ‰ in autumn) suggesting the feeding on a greater variety of prey of various trophic level not observed in the snapshot analysis of their digestive content. Their range of $\delta^{13}C$ (-22.01 to -15.18 ‰ in spring, -25.75 to -15.51 ‰ in autumn) and the higher contribution of the river POM than for the other fish, probably traduce the capacity of moving to feeding towards the very upstream parts of the estuary since it tolerates or prefers low salinities (O'Neil et al. 2011). This behavior may reduce trophic competition with the other fish species. Considering the isotopic niche overlap and prey spectra, this inter-specific competition will be lower between the two gobies, than between sea bass and *P. minutus* especially on mysids, prey shared by these two species (Laffaille et al., 2001; Leitão et al., 2006).

Conclusions on the potential effects of a restoration of ecological continuity of the Sélune river will be drawn only after a post-removal study. Sampling reproduced under the same spatial and temporal conditions as in the present study will make it possible to assess changes in benthic assemblages and trophic functioning of this part of the bay of Mont Saint-Michel.

Acknowledgements

This work was funded by the Seine-Normandie Water Agency. The authors gratefully acknowledge Julien Chevé, Julien Guillaudeau, Manuel Rouquette and Alexandre Robert for their valuable help in field surveys.

Bibliography

Amundsen P. A. & Sánchez-Hernández, J., 2019. Feeding studies take guts–critical review and recommendations of methods for stomach contents analysis in fish. Journal of Fish Biology, 95(6), 1364-1373.

Andersen B.S., Carl J.D., Grønkjaer P., Støttrup J.G., 2005. Feeding ecology and growth of age 0 year *Platichthys flesus* (L.) in a vegetated and a bare sand habitat in a nutrient rich fjord. Journal of Fish Biology 66, 531–552. https://doi.org/10.1111/j.0022-1112.2005.00620.x

Anonyme 1981. Baie du Mont-Saint-Michel : Maintien du caractère maritime aux abords du Mont. Rapport d'étude CNEXO, LCHF & MNHN. 47 p

ARTELIA Group, 2014, Etude d'impact : 2. Etat Initial du site et de son environnement, Etudes liées aux procédures d'autorisation du démantèlement des barrages de Vezins et La Roche Qui Boit, 260p.

Baker R., Buckland A. & Sheaves M., 2014. Fish gut content analysis: robust measures of diet composition. Fish and Fisheries 15, 170–177. https://doi.org/10.1111/faf.12026

Bednarek A., 2001. Undamming Rivers: A Review of the Ecological Impacts of Dam Removal. Environmental Management 27, 803–814. https://doi.org/10.1007/s002670010189

Bremer, P. & Vijverberg, J. (1982). Production, population biology and diet of *Neomysis integer* (Leach) in a shallow Frisian lake (The Netherlands). *Hydrobiologia*, *93*, 41-51.

Clare D.S., Bolam S.G., McIlwaine P.S., Garcia C., Murray J.M. & Eggleton, J.D., 2022. Biological traits of marine benthic invertebrates in Northwest Europe. *Scientific Data*, *9*(1), 339.

Couch C.A., 1989. Carbon and nitrogen stable isotopes of meiobenthos and their food resources. Estuarine, Coastal and Shelf Science 28, 433–441. https://doi.org/10.1016/0272-7714(89)90090-5

Dadswell M. J. 1996. The removal of Edwards Dam, Kennebec River, Maine: Its effects on the restoration of anadromous fishes. Draft environmental impact statement, Kennebec River, Maine, Appendices 1–3, 92 pp

Day L., Le Bris H., Saulnier E., Pinsivy L., & Brind'Amour A., 2020. Benthic prey production index estimated from trawl survey supports the food limitation hypothesis in coastal fish nurseries. *Estuarine, Coastal and Shelf Science*, *235*, 106594.

De Niro M.J. & Epstein S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42, 495–506. https://doi.org/10.1016/0016-7037(78)90199-0

Dethier E.V., Renshaw C.E. & Magilligan F.J., 2022. Rapid changes to global river suspended sediment flux by humans. Science 376: 1447-1452. https://doi.org/10.1126/science.abn7980Dolbeth, M., Martinho, F., Leitão, R., Cabral, H., Pardal, M.A., 2008. Feeding patterns of the dominant benthic and demersal fish community in a temperate estuary. Journal of Fish Biology 72, 2500–2517. https://doi.org/10.1111/j.1095-8649.2008.01856.x

Duarte G., Segurado P., Haidvogl G., Pont D., Ferreira M.T. & Branco P., 2020. Damn those damn dams: fluvial longitudinal connectivity impairment for European diadromous fish throughout the 20th century. Science of the Total Environment, https://doi.org/10.1016/j.scitotenv.2020.143293

Ehrhold A., 1999. Dynamique de comblement d'un bassin sédimentaire soumis à un régime mégatidal : Exemple de la Baie du Mont-Saint-Michel 303. Thèse de l'Université de Caen.

Figueroa S.M., Soon M. & Lee G.H., 2022. Effect of estuarine dam location and discharge interval on estuarine hydrodynamics, sediment dynamics, and morphodynamics. Frontiers in Marine Science, 9. https://doi.org/10.3389/fmars.2022.1035501

Foley M.M., Bellmore J.R., O'Connor J.E., Duda J.J., East A.E., Grant G. E., Anderson C.W., Bountry J.A., Collins M.J., Connolly P.J., Craig L.S., Evans J.E., Greene S.L., Magilligan F.J., Magirl C.S., Major J.J., Pess G.R., Randle T.J., Shafroth P.B., Torgersen C.E., Tullos D. & Wilcox, A.C., 2017. Dam removal: Listening in. Water Resources Research, 53(7): 5229-5246. https://agupubs.onlinelibrary.wiley.com/doi/pdf/10.1002/2017WR020457

Foley M.M., Warrick J.A., Ritchie A., Stevens A.W., Shafroth P.B., Duda J.J., Beirne M.M., Paradis R., Gelfenbaum G., McCoy R. & Cubley, E.S., 2017. Coastal habitat and biological community response to dam removal on the Elwha River. Ecological Monographs 87. https:doi.org/10.1002/ecm.1268

Fovet O., Ndom,M., Crave, A. & Pannard,A., 2020. Influence of dams on river water-quality signatures at event and seasonal scales: the Séune river (France) case study. River Research Applications, 36: 1267-1278. https://doi.org/10.1002/rra.3618

Hammerschlag N., Schmitz O.J., Flecker A.S., Lafferty K.D., Sih A., Atwood T.B., Gallagher A.J., Irschick D.J., Skubel R. & Cooke S, 2019. Ecosystem function and services of aquatic predators in the anthropocene. Trends in Ecology and Evolution : 34:369–83.

Hill M. J., Long E. A. & Hardin, S., 1993. Effects of dam removal on Dead Lake, Chipola River, Florida. Apalachicola River Watershed Investigations, Florida Game and Fresh Water Fish Commission. A Wallop-Breaux Project F-39-R, 12 pp.

Hill N.L., Trueman J.R., Prevost A.D., Fraser D.J., Ardren W.R. & Grant J.W.A., 2019. Effect of dam removal on habitat use by spawning Atlantic salmon ? Journal of great lakes research, 45(2) : 394-399.

Hureau J. C., 1970- Biologie comparée de quelques poisons antarctiques (Nototheniidae). Buletin de l'Institut Océanographique de Monaco, 68 (1391) : 1-224.

Hyndes G.A., Platell M.E. & Potter, I.C., 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Marine Biology 128, 585–598. https://doi.org/10.1007/s002270050125

Hyslop E.J., 1980. Stomach contents analysis-a review of methods and their application. Journal of Fish Biology 17, 411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x

Jackson A.L., Inger R., Parnell A.C. & Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson M.C., Donohue I., Jackson A.L., Britton J.R., Harper D.M. & Grey, J., 2012. Population-Level Metrics of Trophic Structure Based on Stable Isotopes and Their Application to Invasion Ecology. PLoS ONE 7, e31757. https://doi.org/10.1371/journal.pone.0031757

Jesus B., Brotas V., Ribeiro L., Mendes C.R., Cartaxana P. & Paterson D.M., 2009. Adaptations of microphytobenthos assemblages to sediment type and tidal position. Continental Shelf Research 29, 1624–1634. https://doi.org/10.1016/j.csr.2009.05.006

Josefson A.B. & Hansen J.L.S., 2004. Species richness of benthic macrofauna in Danish estuaries and coastal areas. Global Ecology and Biogeography 13, 273–288. https://doi.org/10.1111/j.1466-822X.2004.00091.x

Kelsall C.J. & Balment R.J., 1998. Native Urotensins Influence Cortisol Secretion and Plasma Cortisol Concentration in the Euryhaline Flounder, *Platichthys flesus*. General and Comparative Endocrinology 112, 210–219. https://doi.org/10.1006/gcen.1998.7166

Laffaille P., Lefeuvre J.-C., Schricke M.T. & Feunteun E., 2001. Feeding Ecology of 0-Group Sea Bass, Dicentrarchus labrax, in Salt Marshes of Mont Saint Michel Bay (France). Estuaries 24, 116. https://doi.org/10.2307/1352818

Leitão R., Martinho F., Neto J.M., Cabral H., Marques J.C. & Pardal M.A., 2006. Feeding ecology, population structure and distribution of Pomatoschistus microps (Krøyer, 1838) and Pomatoschistus minutus (Pallas, 1770) in a temperate estuary, Portugal. Estuarine, Coastal and Shelf Science 66, 231–239. https://doi.org/10.1016/j.ecss.2005.08.012

Kostecki C., Roussel J., Desroy N., Roussel G., Lanshere J., Le Bris H. & Le Pape O., 2012. Trophic ecology of juvenile flatfish in a coastal nursery ground: contributions of intertidal primary production and freshwater particulate organic matter. Marine Ecology Progress Series 449, 221–232. https://doi.org/10.3354/meps09563

Kruge M.A., 2017. Dam Removal in the USA: Effects on River Water Quality. Department of Earth and Environmental Studies Faculty Scholarship and Creative Works. https://digitalcommons.montclair.edu/earth-environ-studies-facpubs/67

Ly C.K., 1980. - The role of the Akosombo Dam on the Volta river in causing coastal erosion in central and eastern Ghana (West Africa). Marine Geology, 37, 323-332.

Maavara T., Chen Q., Van Meter K., Brown L.E., Zhang J. & Zarfl C., 2020. River dam impacts on biogeochemical cycling. Nature Reviews Earth Environment 1: 103–116. https://doi.org/10.1038/s43017-019-0019-0

Marchand J., 1993. The influence of seasonal salinity and turbidity maximum variations on the nursery function of the Loire estuary (France). Netherlands Journal of Aquatic Ecology 27, 427–436. https://doi.org/10.1007/BF02334804

Mauchline J., 1967. The biology of *Schistomysis spiritus* [Crustacea, Mysidacea]. *Journal of the Marine Biological Association of the United Kingdom*, *47*(2), 383-396.

Mendes C., Ramos S. & Bordalo A.A., 2014. Feeding ecology of juvenile flounder *Platichthys flesus* in an estuarine nursery habitat: Influence of prey–predator interactions. Journal of Experimental Marine Biology and Ecology 461, 458–468. https://doi.org/10.1016/j.jembe.2014.09.016

Meziane T., Bodineau L., Retiere C. & Thoumelin G., 1997. The use of lipid markers to define sources of organic matter in sediment and food web of the intertidal salt-marsh-flat ecosystem of Mont-Saint-Michel Bay, France. Journal of Sea Research 38, 47–58. https://doi.org/10.1016/S1385-1101(97)00035-X

Morais P., 2008. Review on the major ecosystem impacts caused by damming and watershed development in an Iberian basin (SW-Europe): focus on the Guadiana estuary. Ann. Limnol. – Int. J. Lim. 44(2): 105-117

Morais P., Chícharo M.A. & Chícharo L., 2009. Changes in a temperate estuary during the filling of the biggest European dam. Science of The Total Environment, Volume 407 (7) : 2245-2259. https://doi.org/10.1016/j.scitotenv.2008.11.037.

Moulin N., Gresselin F., Dardaillon B. & Zahra T., 2022. River temperature analysis with a new way of using Independant Component Analysis. Frontiers in Earth Science, 100. https://doi=10.3389/feart.2022.1033673

Nicolas D., Lobry J., Lepage M., Sautour B., Le Pape O., Cabral H., Uriarte A. & Boët, P., 2010. Fish under influence: a macroecological analysis of relations between fish species richness and environmental gradients among European tidal estuaries. Estuarine, Coastal and Shelf Science 86, 137–147.

Nixon S.W., 2003. Replacing the Nile: are anthropogenic nutrients providing the fertility once brought to the Mediterranean by a great river? Ambio 32, 30–40.

Nixon, S.W., 2004. - The artificial Nile. Am. Sci., 92, 158-165.

O'Neill B., De Raedemaecker F., McGrath D. & Brophy D., 2011. An experimental investigation of salinity effects on growth, development and condition in the European flounder (Platichthys flesus. L.). *Journal of Experimental Marine Biology and Ecology*, *410*, 39-44.

Parnell A.C., Inger R., Bearhop S. & Jackson A.L., 2010. Source Partitioning Using Stable Isotopes: Coping with Too Much Variation. PLoS ONE 5, e9672. https://doi.org/10.1371/journal.pone.0009672

Pasquaud S., Béguer M., Larsen M.H., Chaalali A., Cabral H. & Lobry, J., 2012. Increase of marine juvenile fish abundances in the middle Gironde estuary related to warmer and more saline waters, due to global changes. Estuarine, Coastal and Shelf Science 104–105, 46–53. https://doi.org/10.1016/j.ecss.2012.03.021

Post D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Phillips D.L., Inger R., Bearhop S., Jackson A.L., Moore J.W. ParnellA.C., Semmens B.X. & Ward E.J., 2014. Best practices for use of stable isotope mixing models in food-web studies. Canadian Journal of Zoology 92, 823–835. https://doi.org/10.1139/cjz-2014-0127

Preece G.S., 1970. Salinity and survival in *Bathyporeia pilosa* Lindström and *B. Pelagica* (Bate). Journal of Experimental Marine Biology and Ecology 5, 234–245. https://doi.org/10.1016/0022-0981(70)90002-X

Quezada-Romegialli C., Jackson A.L., Hayden B., Kahilainen K.K., Lopes C. & Harrod C., 2017. TrophicPosition, an r package for the Bayesian estimation of trophic position from consumer stable isotope ratios. Methods in Ecology and Evolution. https://doi.org/10.1111/2041-210X.13009

Raffaelli D., Richner H., Summers R. & Northcott S., 1990. Tidal migrations in the flounder *(Platichthys flesus)*. Marine Behaviour and Physiology 16, 249–260. https://doi.org/10.1080/10236249009378753

Riera P., 2007. Trophic subsidies of *Crassostrea gigas*, *Mytilus edulis* and *Crepidula fornicata* in the Bay of Mont Saint Michel (France): A δ^{13}C and δ^{15}N investigation. Estuarine, Coastal and Shelf Science 72, 33–41. https://doi.org/10.1016/j.ecss.2006.10.002

Rollet A.J., Piégay H., Dufour S., Bornette G. & Persat, H., 2014. Assessment of consequences of sediment deficit on a gravel river bed downstream of dams in restoration perspectives: application of a multicriteria, hierarchical and spatially explicit diagnosis. River Research and Applications, 30(8): 939-953. https://onlinelibrary.wiley.com/doi/pdf/10.1002/rra.2689

Sala E. & Sugihara G., 2005. Food-web theory provides guidelines for marine conservation. In Aquatic food webs: an ecosytem approach. A. Belgrano et al. (Eds). 170-183. https://doi.org/10.1093/acprof:oso/9780198564836.003.0014

Schaffer J.A., Higgs E., Walls C. & Juanes F., 2017. Large-scale Dam Removals and Nearshore Ecological Restoration: Lessons Learned from the Elwha Dam Removals. Ecological restauration, 35 (2): 87-101. DOI : 100.3368/er.35.2.87

Shaffer J.A., Munsch S. & Juanes F., 2018. Functional diversity responses of a nearshore fish community to restoration driven by large-scale dam removal. Estuarine, Coastal and Shelf Science, 213: 245-252. https://doi.org/10.1016/j.ecss.2018.08.030.

Schoener T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology, 51, 408–418

Simons R.K. & Simons D.B., 1991. Sediment problems associated with dam removal-Muskegon River, Michigan. Pages 680–685 *in Hydraulic engineering, Proceedings of the 1991 national conference of the American Society of Civil Engineers*, 29 July–2 August. American Society of Civil Engineers, Nashville, Tennessee.

Tokeshi M., 1991. Graphical analysis of predator feeding strategy and prey importance. Freshwater. Forum, 1: 179-183.

Thorman S., 1986. Seasonal colonisation and effects of salinity and temperature on species richness and abundance of fish of some brackish and estuarine shallow waters in Sweden. Ecography 9, 126–132. https://doi.org/10.1111/j.1600-0587.1986.tb01201.x

Treguer P.J. & De La Rocha, 2013. The world ocean silica cycle. Annual Review of Marine Science, 5: 477-501. https://10.1146/annurev-marine-121211-172346

Trigui R.J., 2009. Influence des facteurs environnementaux et anthropiques sur la structure et le fonctionnement des peuplements benthiques du Golfe Normano-Breton. Thèse du Muséum National d'Histoire Naturelle, 532 pp.

Viguier J., De Croutte E. & Hamm L., 2002. Hydrosedimentary studies to restore the maritime character of Mont-Saint-Michel. Proceedings of the 28th conference on coastal engineering, Cardiff. World Scientific, New-Jerzy, USA : 3285-3297.

Warrick J.A., Bountry JA.A, East A.E., Magirl CS.S, Randle T.J., Gelfenbaum G., Ritchie A.C., Pess G.R., Leung V. & Duda J.J., 2015. Large-scale dam removal on the Elwha River, Washington, USA: Source-to-sink sediment budget and synthesis. Geomorphology, 246: 729-750. https://doi.org/10.1016/j.geomorph.2015.01.010.

Webb P., Perissinotto, R. & Wooldridge T.H., 1987. Feeding of *Mesopodopsis slabberi* (Crustacea, Mysidacea) on naturally occurring phytoplankton. *Marine Ecology Progress Series*, *38*, 115-123.

Winter, B. D. 1990. A brief review of dam removal efforts in Washington, Oregon, Idaho, and California. US Department of Commerce, NOAA Tech. Memo. NMFS F/NWR-28, 13 pp.

Whitfield A.K., Elliott M., Basset A., Blaber S.J.M., & West R.J., 2012. Paradigms in estuarine ecology–a review of the Remane diagram with a suggested revised model for estuaries. *Estuarine, Coastal and Shelf Science*, *97*, 78-90.

Zhang X., Changling F., Yuan W., Xiaoyi L., Ying S. & Dongmei H., 2022. Review of effects of dam construction on the ecosystems of river estuary and nearby marine areas. Sustainability 14: 5974. https://doi.org/10.3390/su14105974

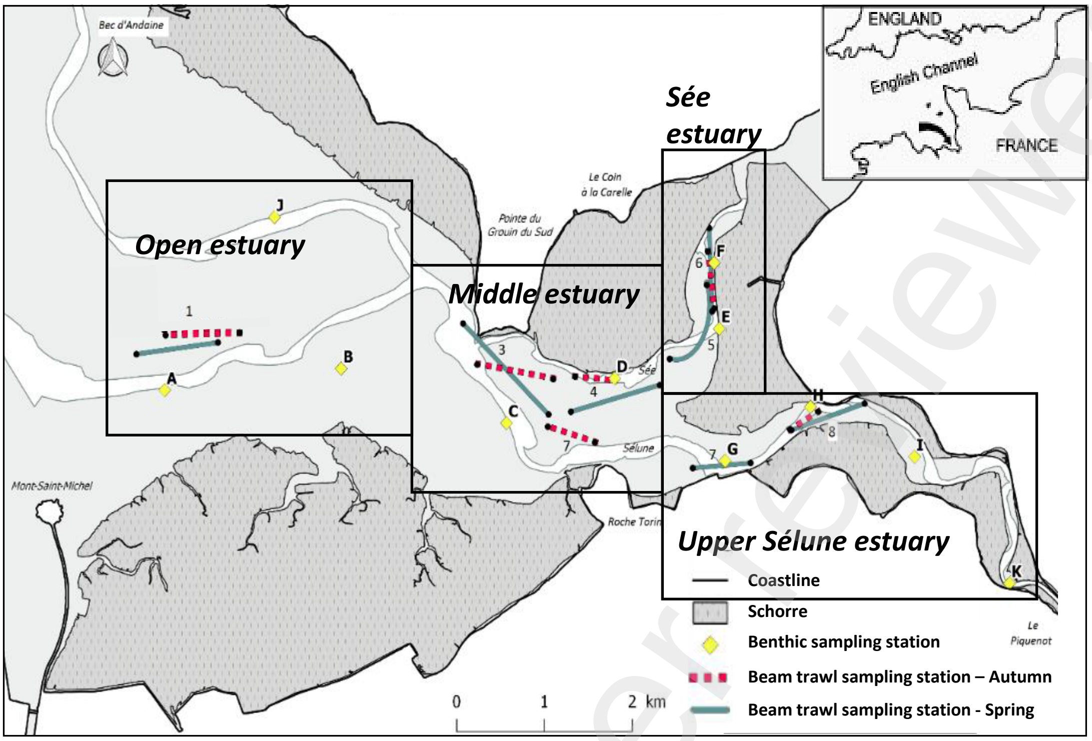

Figure 1: Sectors of the study site and location of sampling stations (spring and autumn 2017)

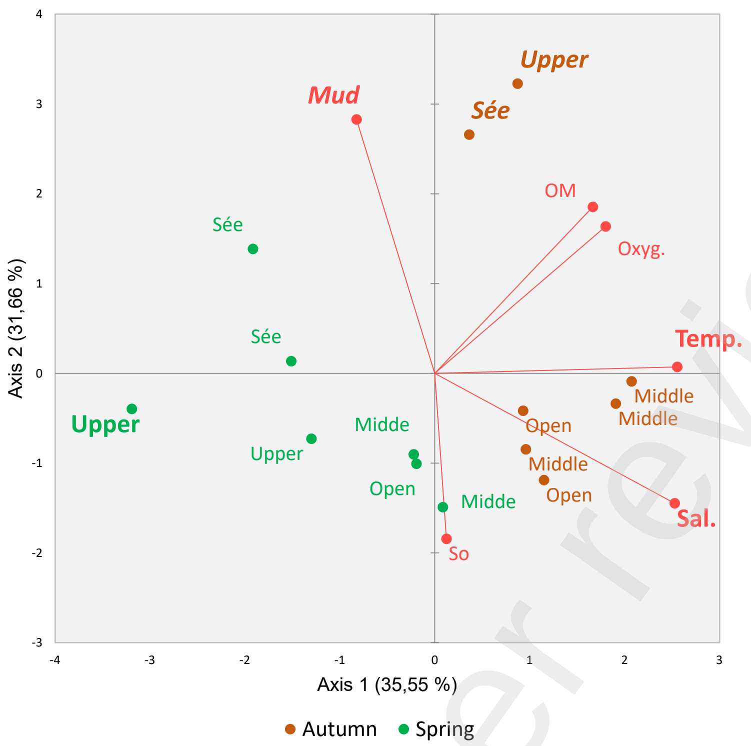

Figure 2. Principal components analysis. Environmental variables (in red) recorded in the study sites sectors in spring and autumn: Mud = granulometric fraction < 63µm, OM = Organic Matter content of sediment, Oxyg. = Oxygen concentration in water, Temp. = Water temperature, Sal. = Water salinity, So = Sediment sorting Index). Bold = main contributors to the axis 1, Bold and Italic = main contributors to axis 2.

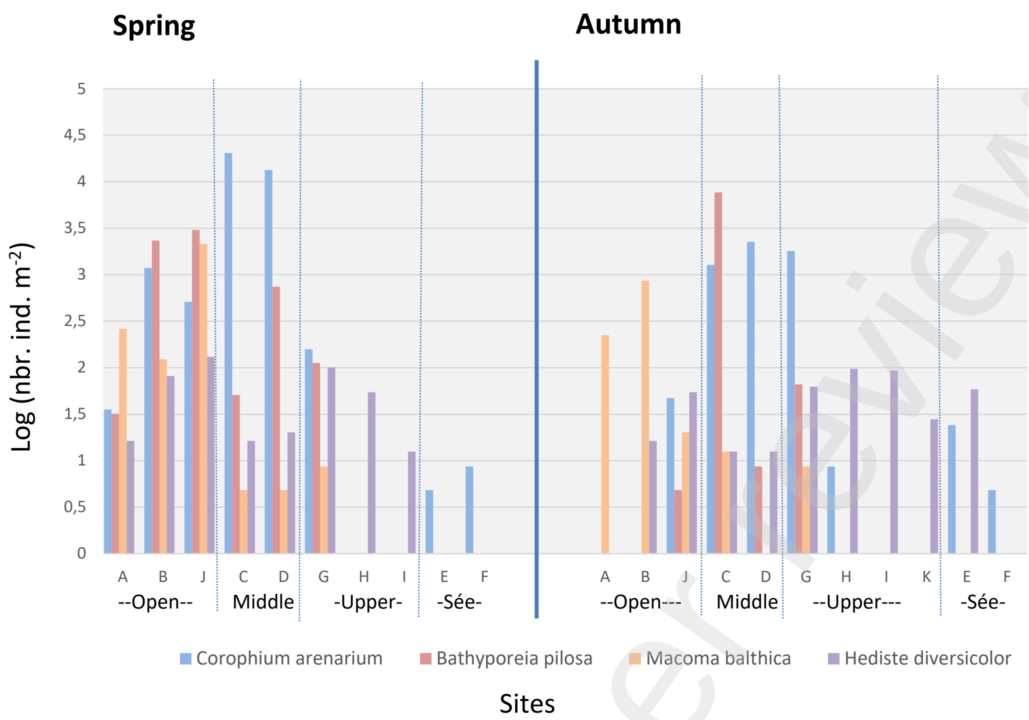

Figure 3. Densities of four main macrobenthic species (polychaete - *H. diversicolor*, mollusk – *M. balthica*, crustaceans – *B. pilosa* and *C volutator*) within the four sectors of the study site in spring and autumn

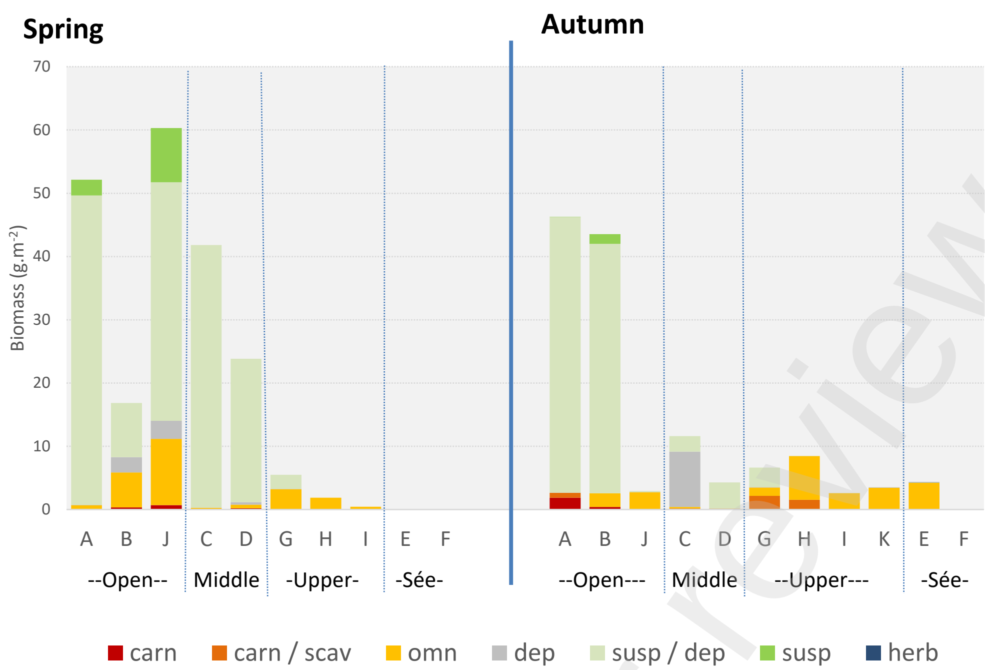

Figure 4. Available prey biomass according to trophic groups of benthic macrofauna in the sampling stations in spring and autumn (carn = carnivore, carn/scav = carnivore & scavenger, omn = omnivore, dep = deposit feeder, susp / dep = suspension & deposit feeder, susp = suspension feeder, herb = herbivore).

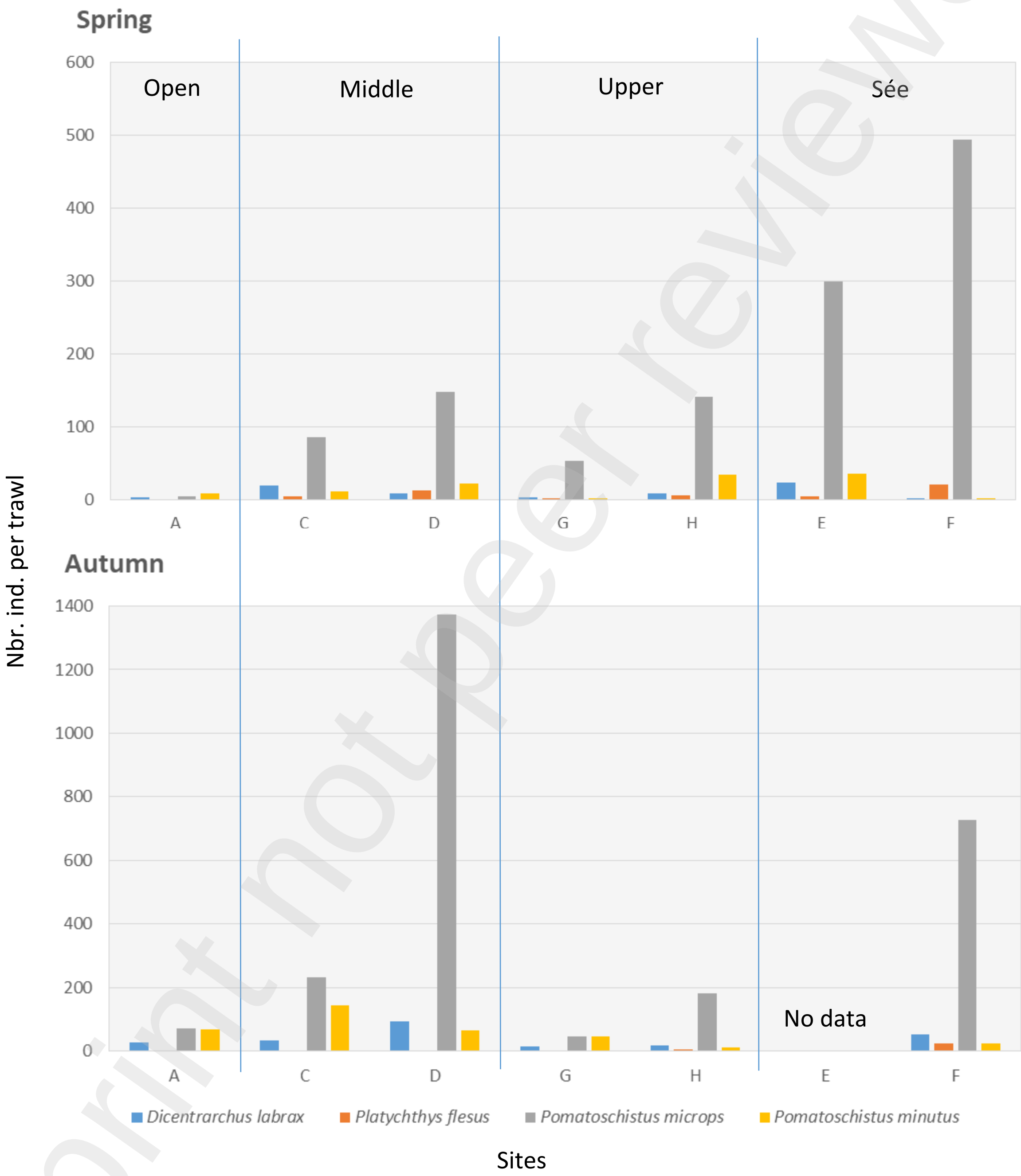

Figure 5. Number of individuals of four main bentho-demersal fish species within the four sectors of the study site in spring and autumn

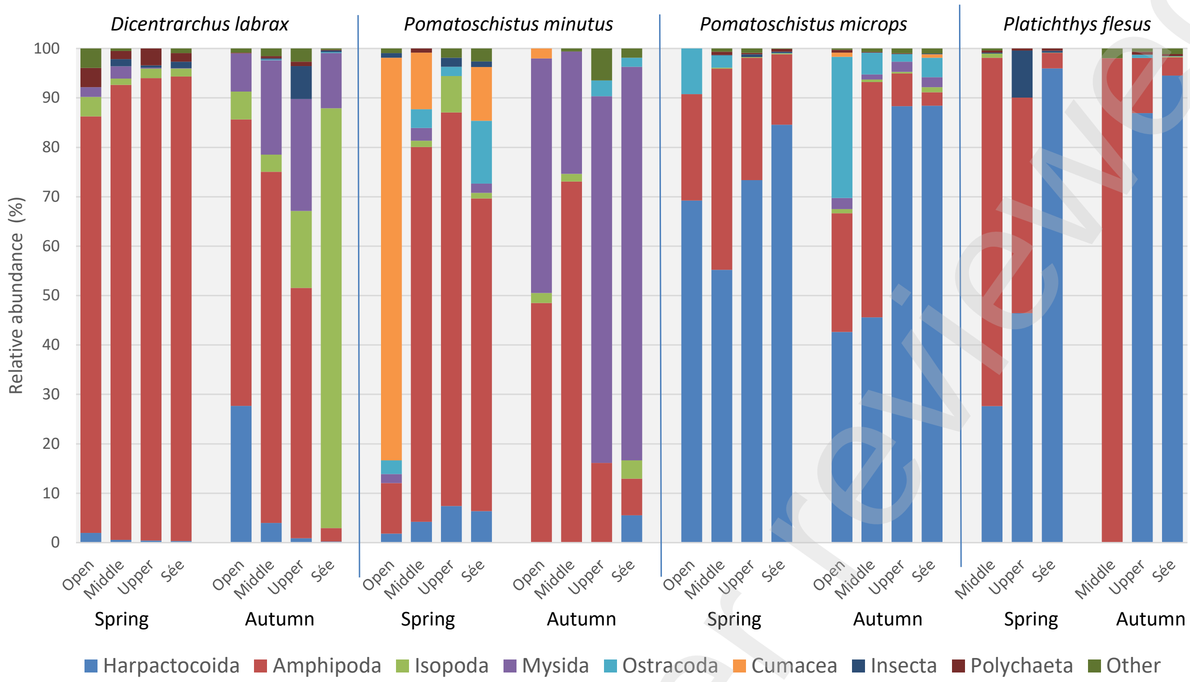

Figure 6. Relative abundance of taxonomic groups of prey identified in the digestive contents of the four main fish species

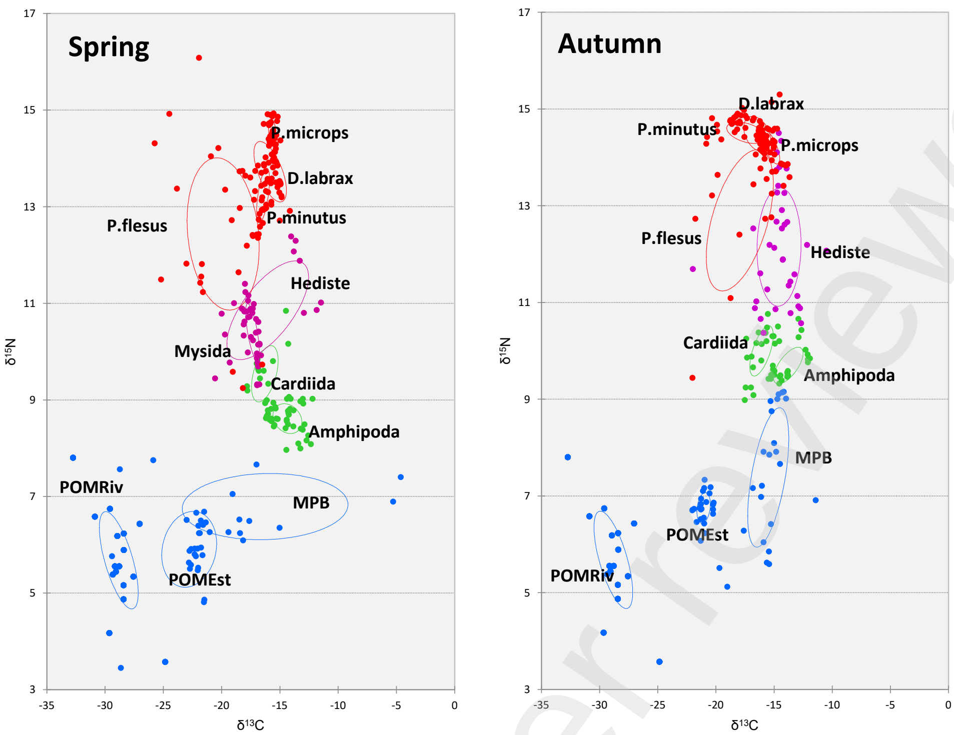

Figure 7. Area corrected for standard ellipses (SEAc) of $\delta^{15}N$ and $\delta^{13}C$ for each species sampled in spring and autumn. Sources (blue): POM Riv = river particulate organic matter, POM Est = estuarine particulate organic matter, MPB = Microphytobenthos. Primary consumers (green): Amphipoda (*B. pilosa* & *Corophium arenarium*), Cardida (*Macoma balthica* & *Cerastoderma edule*), *Arenicola marina*. Omnivore (purple): Mysida (*Neomysis integer* & *Schistomysis spiritus*), *Hediste diversicolor*. Secondary consumers (red): *Platichthys flesus, Pomatoschistus minutus, Pomatoschistus microps, Dicentrarchus labrax*)

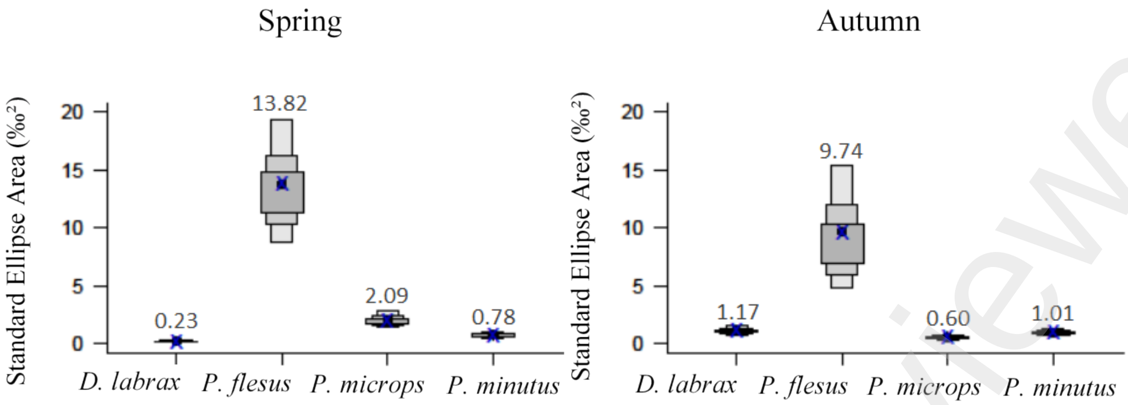

Figure 8: Representation of SEAb (mean in ‰^{2}) of fish (gray) at both seasons and of SEAc (blue cross).

Table 1: Overlap (%) between fish SEAc (normal = spring, italic = autumn, bold = high values).

	D. labrax	*P. flesus*	*P. microps*	*P. minutus*
D. labrax		*12.09*	***39.51***	***50.23***
P. flesus	1.55		*6.04*	*9.36*
P. microps	8.54	14.02		***28.58***
P. minutus	9.81	5.55	**23.27**	

Supplementary material

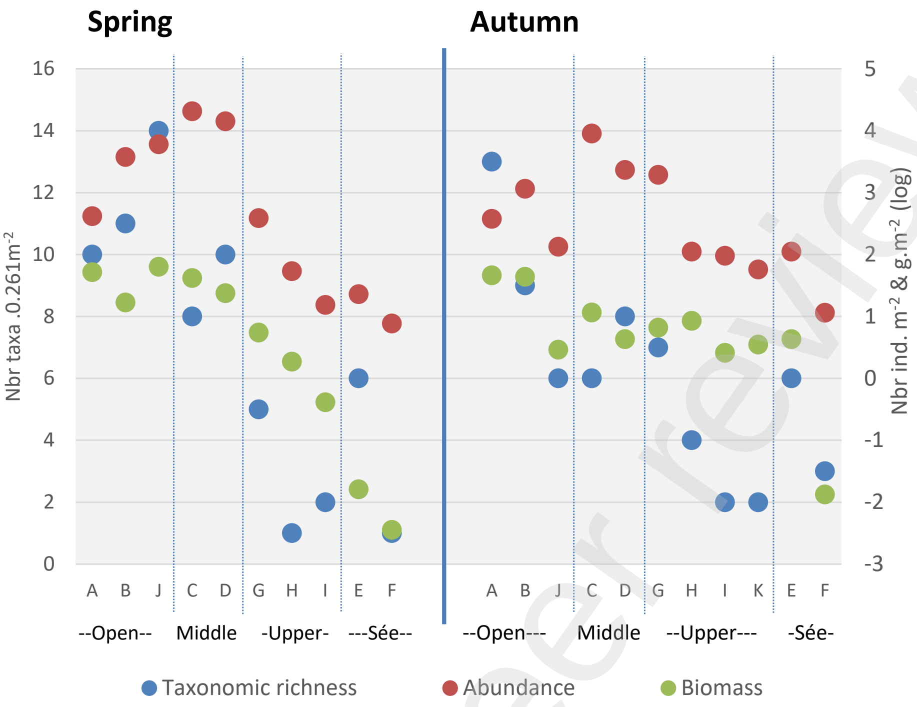

Figure SM1. Taxonomic richness, abundance and biomass of invertebrate macrofauna in spring and autumn

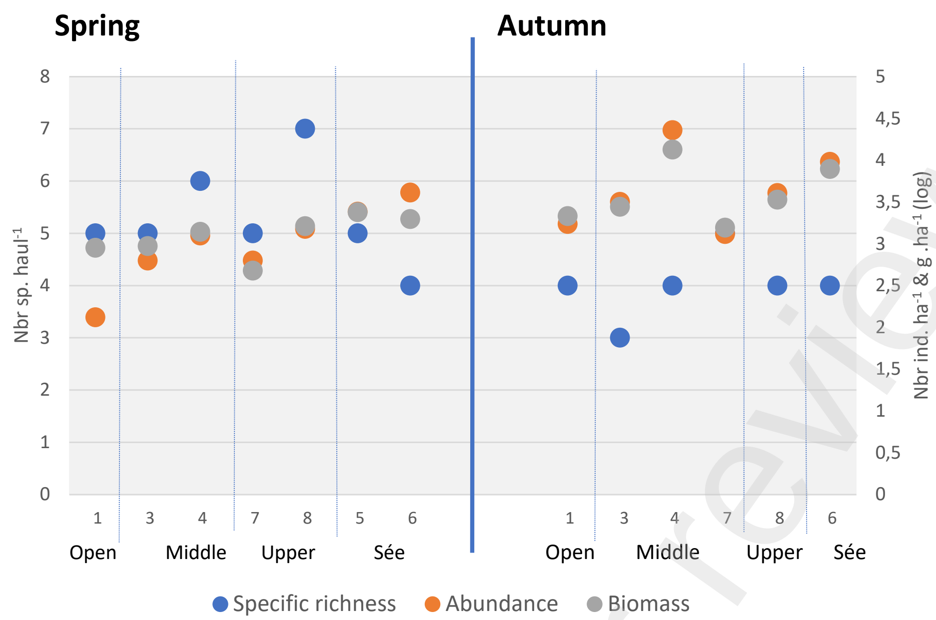

Figure SM2. Taxonomic richness, abundance and biomass of bentho-demersal fish in spring and autumn

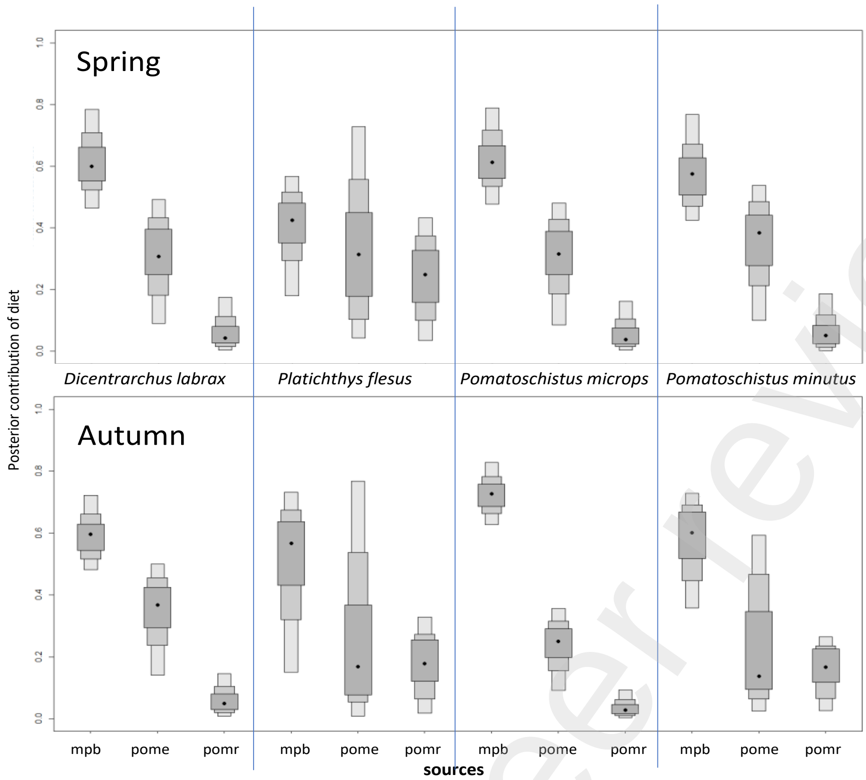

Figure SM3. Estimated contributions of microphytobenthos (mpb), estuarine particulate organic matter (pome) and river particulate organic matter (pomr) to the diet of the main fish species

Table SM1: δ13C and δ15N isotope compositions (mean ± SD), SEAc (corrected standard ellipse area) and SEAb (Bayesian estimator of the standard ellipse area, mean ± SD) of the main fish species collected at the two periods

Period	Species	Nb samples	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	SEAc	SEAb
Spring	*D. labrax*	30	-15.56 ± 0.30	14.55 ± 0.24	0.23	0.23 ± 0.05
	P. flesus	18	-19.80 ± 2.89	12.44 ± 1.48	13.84	13.82 ± 2.76
	P. microps	36	-15.81 ± 1.34	13.72 ± 0.60	2.05	2.09 ± 0.37
	P. minutus	29	-16.35 ± 0.54	13.23 ± 0.54	0.77	0.78 ± 0.15
Autumn	*D. labrax*	37	-16.31 ± 1.11	14.48 ± 0.35	1.17	1.17 ± 0.20
	P. flesus	13	-17.84 ± 2.55	12.70 ± 1.28	9.65	9.74 ± 2.96
	P. microps	37	-15.24 ± 0.74	14.22 ± 0.34	0.58	0.60 ± 0.10
	P. minutus	37	-17.30 ± 1.62	14.51 ± 0.21	1.00	1.01 ± 0.18