

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

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### ARTICLE INFO

#### Keywords:

Estuary  
Trophic ecology  
Stable isotope analysis  
Gut contents analysis  
Mont-Saint-Michel bay

### 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 benthic-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. Macro-benthic 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 marine 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. Macro-benthic invertebrates (*Corophium arenarium* or *Bathyporeia pilosa*) and harpacticoid copepods and mysids in autumn were the major prey (primary consumer level) for secondary consumers. The analysis of the trophic niche of fish and their overlaps gave elements on the respective feeding strategies and inter-specific competitions. Expected long-term effects of dam removal on food web, benthic estuarine ecosystem and nursery function are clarified and discussed.

### 1. 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., 2014). 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., 2014). However, CEE are threatened by human activities, notably overfishing, aquaculture, tourism, and pollution (Halpern et al., 2008). 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 40,000–47,000 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 20th 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

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increasing effort to restore degraded aquatic ecosystems, large dam removal projects have emerged as an important ecosystem restoration 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; Schaffer 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).

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 3000 tons.y<sup>-1</sup> in 2015–2016, including organic matter particles from terrestrial origins (Roussel, personal communication, Fovet et al., 2020). Similarly, a significant decrease in nutrient concentrations in water has

been reported downstream of the reservoirs (Fovet et al., 2020), notably silica 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 to establish its benthic-demersal food web prior to dam removal. Trophic relationships, energy sources and transfers through benthic food web were investigated by digestive contents and stable isotope analyses.

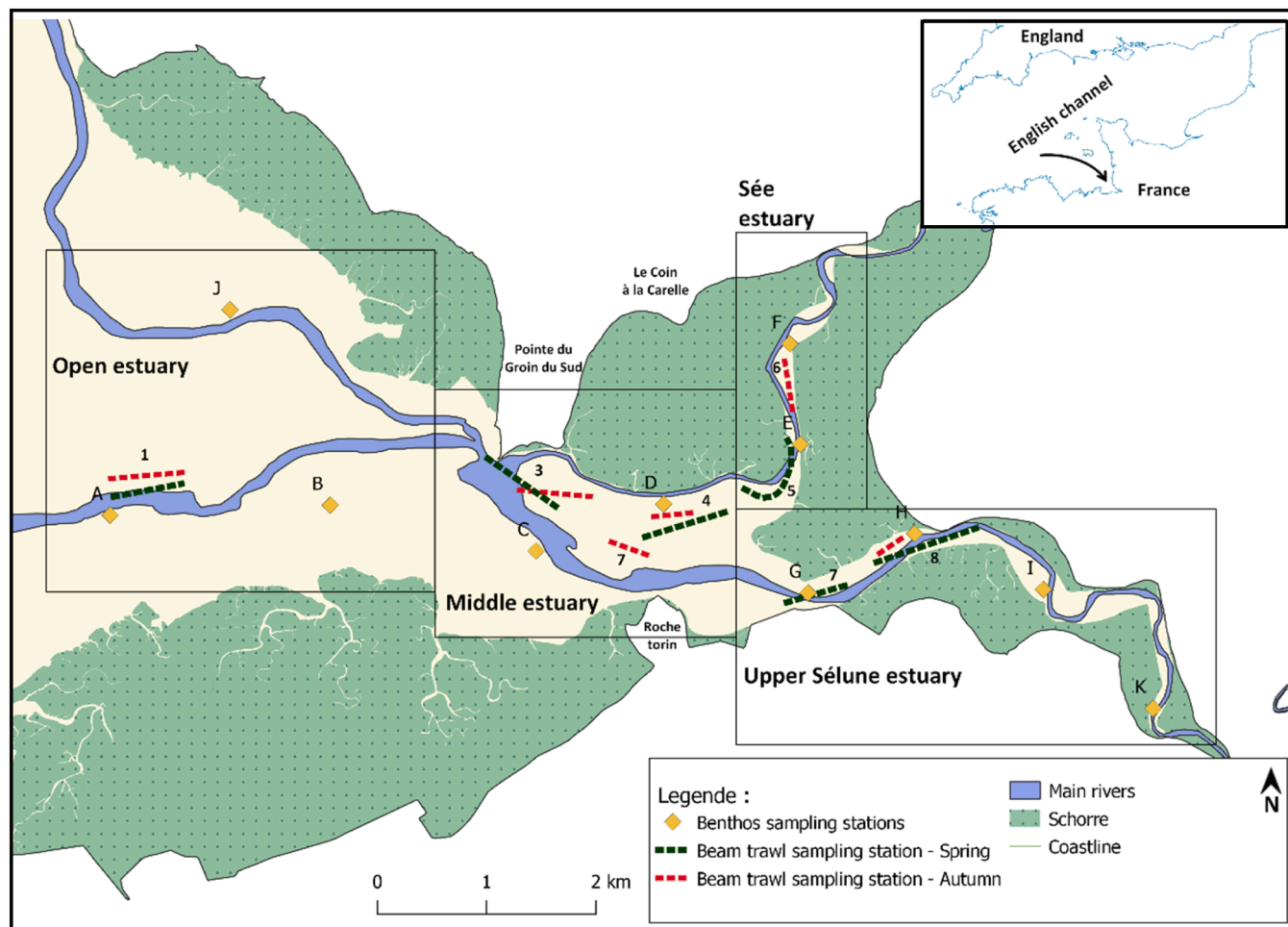


Fig. 1. Sectors of the study site and location of sampling stations (spring and autumn 2017).

## 2. Material and methods

### 2.1. Study site

The estuarine area is located in the North-West of France (Fig. 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 45 km<sup>2</sup> 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).

The Sée, Couesnon and Sélune are the three rivers of the estuarine part of the Mont-Saint-Michel bay, with average annual flows of around 2.0 m<sup>3</sup>.s<sup>-1</sup>, 4.8 m<sup>3</sup>.s<sup>-1</sup> and 11.0 m<sup>3</sup>.s<sup>-1</sup> respectively (Ehrhold, 1999). Although these river's flows represent 86 % of the freshwater inflows of this area (Meziane et al., 1997), they nevertheless remain very modest compared to the marine inflows induced by the megatidal regime of the bay (Ehrhold, 1999, Meziane et al., 1997). If the salinity varies little across the bay, between 34 and 35 psu (Meziane et al., 1997), a local but notable desalination is observed at the mouth of the Sée, Couesnon and Sélune coastal rivers, with values varying between 21 and 34 psu. The turbidity of the water can be high and locally reach 1000 mg.l<sup>-1</sup> (Meziane et al., 1997).

Four sectors were distinguished according to geomorphological traits along an east-west estuarine gradient (Fig. 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.

### 2.2. 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 benthic-demersal ichthyofauna: 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).

#### 2.2.1. Fauna, sediment and water

Benthic sampling was carried out using a hand-corer (0.029 m<sup>2</sup>) at a sediment depth of 20 cm, at eleven sampling sites near the channels (Fig. 1). At each site, nine samples (i.e. 0.261 m<sup>2</sup> 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. Sampling of ichthyofauna took place at high tide during spring tides using a beam trawl (146 cm wide x 45 cm high) towed for 10–15 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 (Fig. 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.

#### 2.2.2. Sources

At trawled sampling sites, three samples of 1 L 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 specifically 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.

### 2.3. Laboratory analyses

#### 2.3.1. Sediment and fauna

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. An aliquot of each sample was previously removed to define the organic content rate. The difference between weights after drying (48 hours at 60°C) and after burning (6 h at 450°C) gave the organic content.

Macrobenthic samples were i) preserved in 4.5 % buffered formalin at the laboratory before being sorted, ii) identified for the smallest with a binocular magnifying glass at the most precise taxonomic level possible, iii) counted and iiiii) weighted wet. In the few hours following sampling, the fish were identified, counted, measured and weighted wet before being frozen (for isotopic sampling). 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.

#### 2.3.2. Isotopic analysis preparation

Samples dedicated to isotopic analysis were frozen at the laboratory before being prepared. Marine and freshwater POM were extracted by filtration of 250–500 mL (depending on the turbidity) through a GF/F filter previously calcined (500 °C – 1 h). The filters were then decalcified with hydrochloric acid (1 N HCl) and rinsed with distilled water. 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 h), decalcified with 1 N 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 and mysids were pooled to have enough material for analysis and one half of them was kept as such, and the other half was decalcified (1 N 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):

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

with R = <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N. The references of the international standards are Pee Dee Belemnite carbonate (PDB) for δ<sup>13</sup>C and atmospheric nitrogen (AIR) for δ<sup>15</sup>N.

The complementarity of these two approaches (digestive contents and isotopic analyses) makes possible to better understand the ecological processes involved. Digestive content analysis is classically used in trophic ecology (Amundsen and Sánchez-Hernández, 2019) but only gives an instantaneous picture of ingested food. SIA of carbon and nitrogen (δ<sup>13</sup>C and δ<sup>15</sup>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.

#### 2.4. Data analysis

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

##### 2.4.1. 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, silt, sand and gravel content; and for water: dissolved oxygen, salinity and temperature. Influence 1) of the season and the zone and 2) of environmental variables on species richness, abundance and diversity of macrofauna and of fish were tested with a Permanova.

##### 2.4.2. Stable isotope analysis

In order to visualize the species isotopic niche, Standard Ellipse Areas (SEAs) were plotted for each species in a bi-plot of  $\delta^{15}\text{N}/\delta^{13}\text{C}$  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:

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

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 *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<sub>i</sub> is smaller than the area of the standard ellipse SEAb<sub>j</sub>. 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). The contribution level of sources for each consumer (with a focus on main fish) were estimated from mixing models (SIAR). SIAR mixing model has been developed to trace sources of organic matter from stable isotopes accounting for uncertainties in TEF (Parnell et al., 2010). The estimate is based on the values of sources and consumers, according to the trophic enrichment factor (TEF or  $\Delta$ ). 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  $\Delta\delta^{13}\text{C}$  and 3.4 ‰ (± 1.0 SD) for  $\Delta\delta^{15}\text{N}$  for the passage of a trophic level (Post, 2002). Based on the study conducted by Kostecki et al. (2012) in the bay of Mont-Saint-Michel, TEF values of 2.00 (± 1.30 SD) for  $\Delta\delta^{13}\text{C}$  and 5.60 (± 1.00 SD) for  $\Delta\delta^{15}\text{N}$  were retained between basal sources and fish in our study. All mixing models were performed using the R package 'SimmR' (Parnell et al., 2010). This approach was completed by digestive content analysis and 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).

### 3. Results

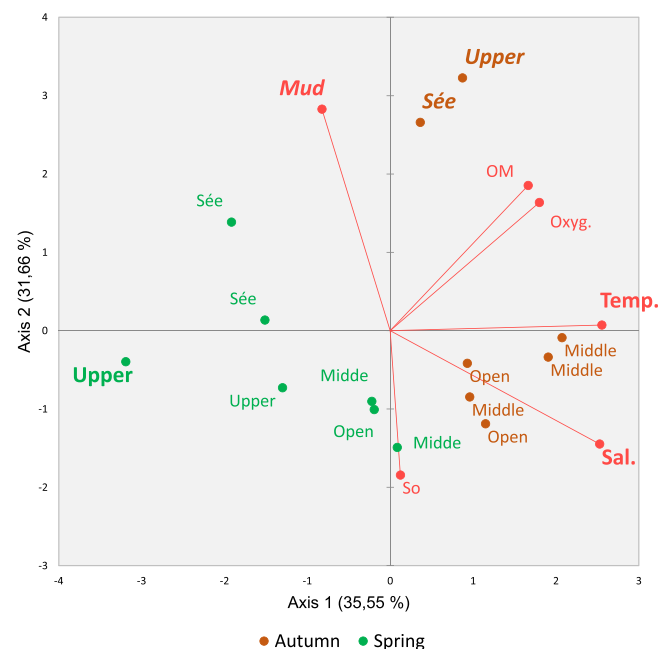
#### 3.1. Environmental characterization of the study site

The sedimentary cover of the study site is homogeneous over time, with a dominance of coarse sands in the most exposed places (stations A, B, C and J) and muddy sands near the river channels (D, E, F, G, H, I and K). The sediments are well to moderately classified, with a clear dominance of the finest fractions.

Axis 1 of the PCA performed on environmental variables showed clear changes in the environment due to seasonality, by differencing the two sampling seasons and more particularly for the upstream sectors (Sée estuary and Upper; Fig. 2). Water salinity and temperature on one side and Upper sector at the opposite mainly contributed 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. Axis 2 identifies two groups of stations located i) in riverine sectors (situated upstream in the Sée and Sélune channels) and ii) downstream (with the exception of station G in September). For macrofauna, the zone significantly affected the species richness ( $p < 0001$ ), abundance ( $p < 0,01$ ) and Shannon index ( $p < 0,01$ ). Trask index significantly interacted with the abundance ( $p < 0,01$ ) and sand and gravel contents had significant effect on species richness (respectively  $p < 0,05$  and  $p < 0,01$ ). For fish, only the abundance ( $p < 0,01$ ) is significantly affected by the season. The zone, and the interaction zone x season had no significant effect on species richness, abundance or Shannon index.

#### 3.2. Fauna richness, abundance and biomass

A total of 35 macrobenthic taxa was observed. Annelids (mainly polychaetes: 10 species) as well as crustaceans (10 species) dominated the taxonomic spectrum. Insects (7 species, mainly under nymphae stages) and mollusks (4 species) were also recorded. The taxonomic richness showed a general increase trend (1–14 taxa) from upstream to



**Fig. 2.** Principal components analysis. Environmental variables (in red) recorded in the study sites sectors in spring and autumn: Mud = granulometric fraction < 63  $\mu\text{m}$ , 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 Italic = main contributors to axis 2.

more open sectors (Figure SM1) whatever the period.

Abundance was higher in the Middle sector whatever the period and showed higher values in the upstream stations in autumn compared to spring. Values ranged between 0 and 20574 ind.m<sup>-2</sup> in spring and 7 and 9000 ind.m<sup>-2</sup> in autumn. Biomass increased from Sée to Middle sectors in spring, but not in autumn, despite the existence of a minimum value in the station F (Figure SM1). Four species strongly dominated numerically, with densities varying according to sectors and periods (Fig. 3). In regards to their spatial distributions of dominant species in spring and autumn, two general trends are observed: *C. arenarium* and *H. diversicolor* were present on the whole gradient while *B. pilosa* and *M. balthica* occurred only on the downstream part of the area (mainly Middle and Open sectors).

Available prey [i.e. individual weight < 0,66 g.ind.<sup>-1</sup> WW, Day et al. (2020)] biomass mainly concerned the suspension deposit feeder group and to a lesser extent the omnivore group, only represented by *H. diversicolor* (Fig. 4). Other groups (suspension feeders, deposit-feeders, carnivore scavenger, carnivore) were generally less important and herbivore group was almost absent. Globally, biomass values were high in the Open (spring and autumn) and Middle (autumn) sectors, low in the Upper sector and insignificant in the Sée sector.

A total of 10 benthic-demersal fish species were collected. No clear spatial trend of specific richness was observed (Figure SM2). Abundance decreased from up to downstream whatever the period and were generally higher in autumn than in spring. The same trend is observed for biomass values. The number of species varied from 4 to 7 in spring and from 4 to 5 in autumn (Figure SM2). In autumn, abundance and biomass followed an upstream-downstream gradient, contrary to spring where no gradient can be detected. Four fish species were strongly dominant whatever the period considered: two gobies (*Pomatoschistus microps* and *Pomatoschistus minutus*), juvenile bass (*Dicentrarchus labrax*) and juvenile flounder (*Platichthys flesus*). Gobies and bass occurred on the whole gradient whatever the period whereas flounder was preferentially located upstream.

### 3.3. Trophic food web

At the scale of the study site, 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 POM from

the Sélune, as the least used source (Table 1). Contributions of MPB, estuarine POM and POM from the Sélune were similar for the two periods studied. Whatever the season, *D. labrax* had the highest trophic position among fish and *P. flesus*, the lowest (at the same level as *C. crangon*, Fig. 5). For fish, except the decrease of the trophic position value of *D. labrax* in autumn, no significant differences were observed over the year (pairwise comparison,  $p < 0.01$ ). Trophic position of the invertebrates *M. balthica* and *H. diversicolor*, potential prey for fish, decreased in autumn (Fig. 4).

Few digestive tracts were empty whatever the season: mean rates of emptiness were of  $1.7 \pm 4.0$  % and of  $2.26 \pm 3.5$  % in spring and in autumn respectively. The prey identified belonged to macrobenthos (mainly amphipods) whatever the season, meiobenthos (exclusively harpacticoid copepods), in spring, and suprabenthos (exclusively mysids) in autumn. The digestive content of *D. labrax* (242 samples) was composed in spring at 90 % of amphipods, whatever the sector. *C. arenarium* represented at least 78 % of the diet and *B. pilosa*, from 4 % to 18 % (Fig. 6). In autumn, although the amphipod *C. arenarium* remained the main prey the sea bass diversified its diet (notably with the ingestion of mysids in each sector).

The digestive contents of *P. minutus* (282 analyses) showed strong variations between the two seasons. In spring, *C. arenarium* and *B. pilosa* represented 62–79 % of its diet (Fig. 6), except in the Open sector where cumaceans represented 80 % of prey. In autumn, although *C. arenarium* still represented 29–57 % of the diet, the contribution of mysids increased (23–70 % of prey).

The digestive content of *P. microps* (395 analyses) showed little seasonal variation, this species feeding largely on harpacticoid copepods (abundance >45 %) and *C. arenarium* [between 20 % and 40 % of prey (Fig. 6)].

The digestive content of *P. flesus* (82 analyses) was based in spring, on two main prey: *C. arenarium* (with a proportion ranging between 43 % and 72 %) and harpacticoid copepods [up to 95 % in the Sée zone (Fig. 6)]. In autumn, harpacticoid copepods were the almost exclusive prey (between 87 % and 95 % of prey), depending on the zone.

These results were confirmed by isotopic analysis. The fish, *P. microps*, *P. minutus* and *D. labrax* were positioned at the top of the chain with narrow SEAc and SEAb, whatever the period (Fig. 7). Values of SEAb and SEAc exhibited good correspondences, attesting a good isotopic representation for each fish. The overlap (>25 %) between

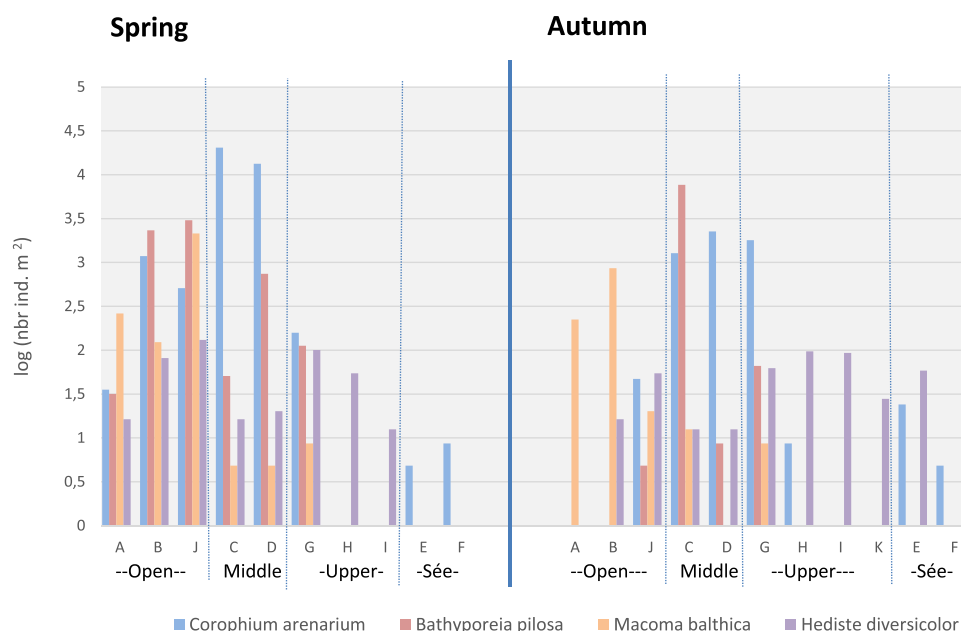
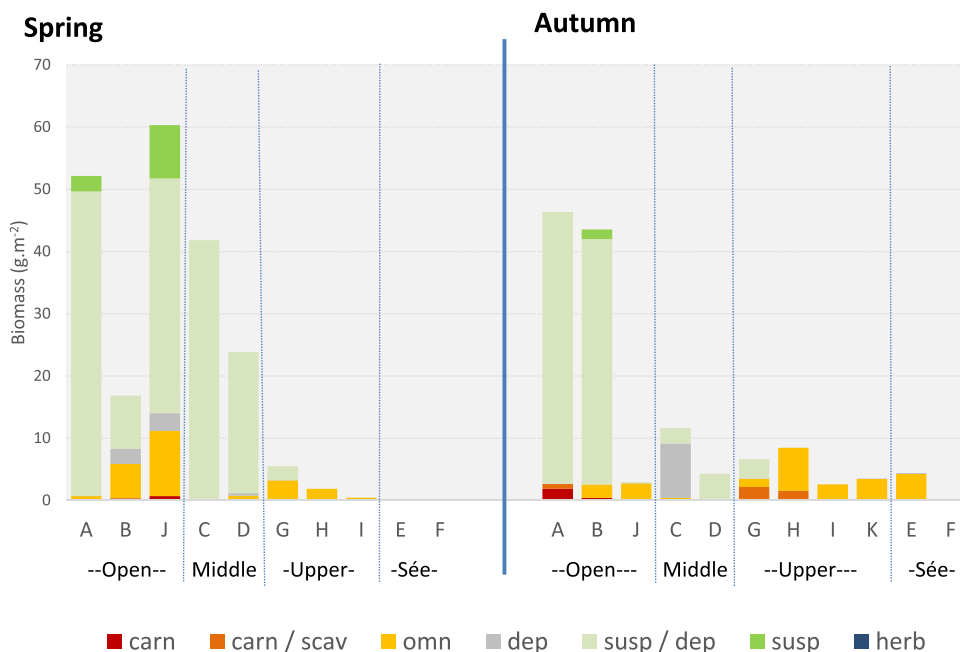


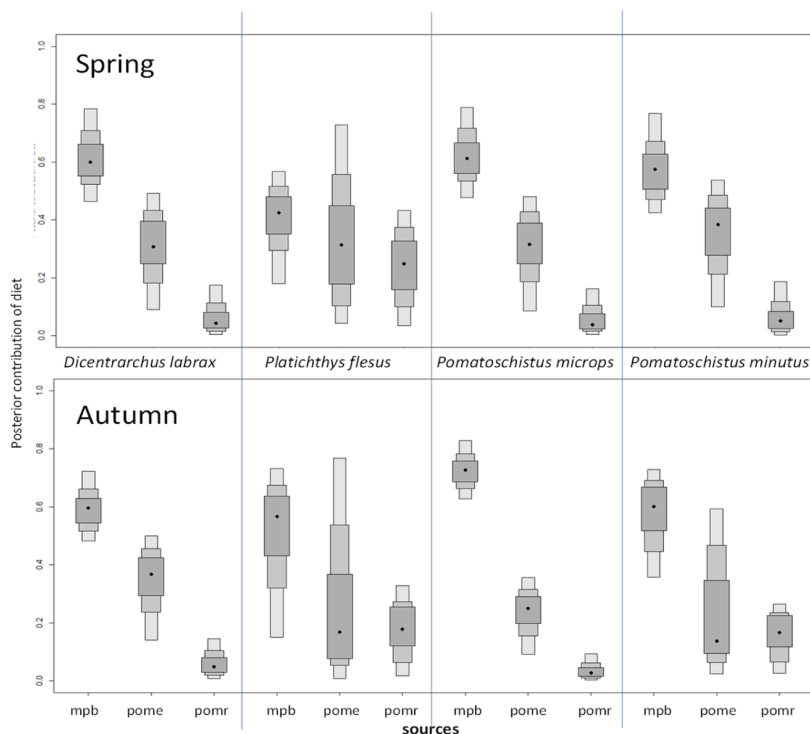
Fig. 3. Densities of four main macrobenthic species within the four sectors of the study site in spring and autumn. A-I correspond to the sampling stations.



**Fig. 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). A-I correspond to the sampling stations.

**Table 1**

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



these three fish was stronger in autumn (Table 1). *P. flesus* clearly differed from the three other fish (overlap <15 %) in regards of its depleted <sup>13</sup>C composition and its highly variable <sup>15</sup>N composition in spring and autumn, giving wide SEAc and SEAb (Table 2 and Table SM1). *P. flesus* had the widest SEAb whatever the season, whereas

*D. labrax* and *P. microps* had the narrowest in spring and autumn respectively (Fig. 7). SEAb of *P. flesus* and *P. minutus* were significantly stable between the two seasons ( $p > 0.05$ ) contrary to *D. labrax* and *P. microps* ( $p < 0.01$ ). Reflecting their omnivorous diet, *H. diversicolor* and the mysids (only collected in spring) ensured the transition between

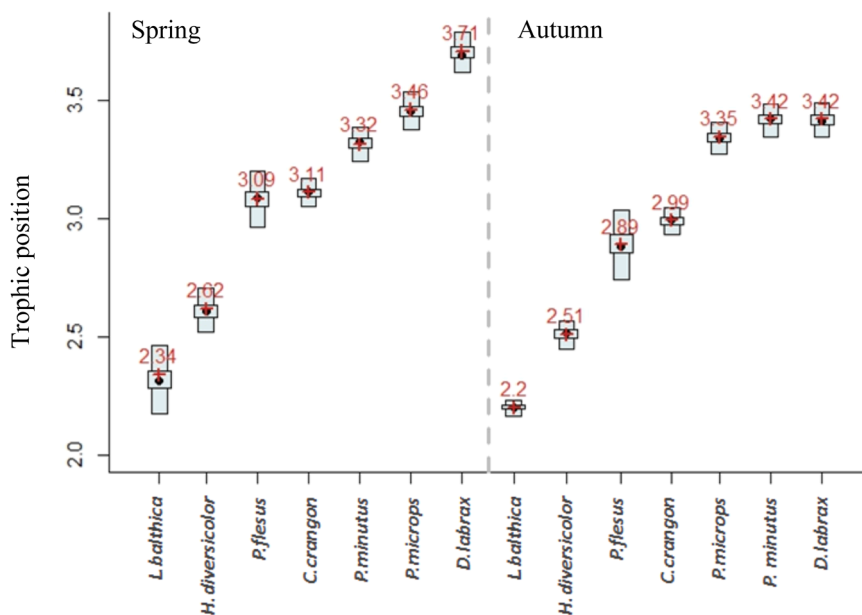


Fig. 5. Trophic position of invertebrate and fish consumers at each season. Boxplots represent the mode and the quartiles (1 and 3) of the trophic position and the red cross, the average trophic position.

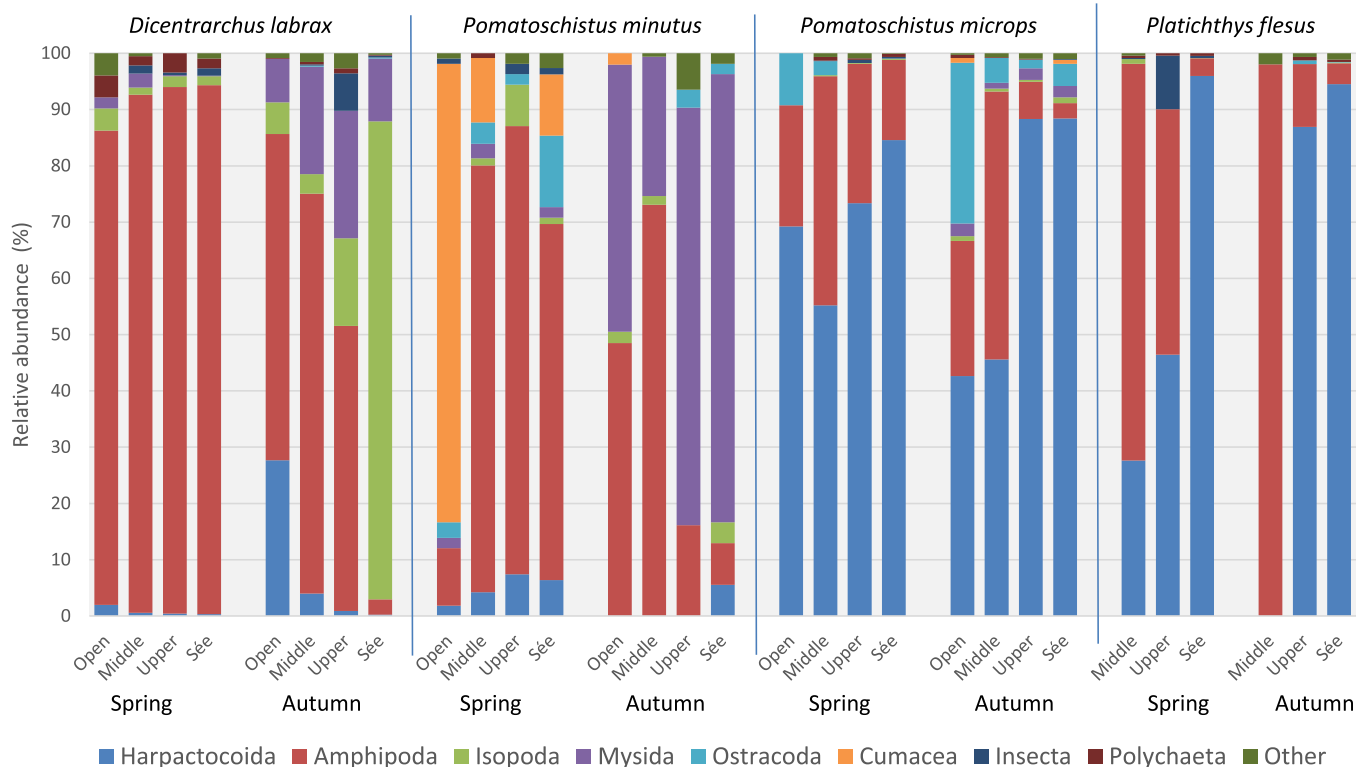


Fig. 6. Relative abundance of taxonomic groups of prey identified in the digestive contents of the four main fish species.

the secondary and the primary consumers, i.e. bivalve mollusks (*Cardiida*) and amphipods, which exhibit narrow SEAc (Fig. 8). As observed above (Fig. 4), they represented the major part of the biomass available for juvenile fish. Primary consumers fed on POM and MPB as sources. Sources mainly varied according to the  $\delta^{13}\text{C}$  axis and exhibit large SEAc, except for estuarine POM in autumn (Fig. 8). River POM was the most  $^{13}\text{C}$  depleted (see Table SM2 for isotopic values). A slight increase of MPB through the  $\delta^{15}\text{N}$  axis is observed in autumn compared to spring. 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).

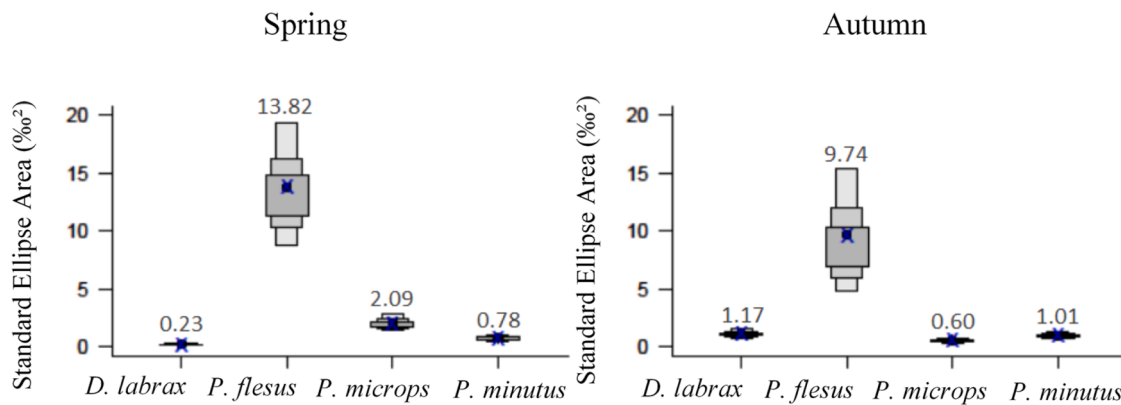


Fig. 7. Representation of SEAb (mean in %<sup>2</sup>) of fish (gray) at both seasons and of SEAc (blue cross).

Table 2

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

	<i>D. labrax</i>	<i>P. flesus</i>	<i>P. microps</i>	<i>P. minutus</i>
<i>D. labrax</i>		12.09	<b>39.51</b>	<b>50.23</b>
<i>P. flesus</i>	1.55		6.04	9.36
<i>P. microps</i>	8.54	14.02		<b>28.58</b>
<i>P. minutus</i>	9.81	5.55	23.27	

#### 4. Discussion

##### 4.1. A typical benthic fauna

The study of benthic communities in the megatidal Sélune estuary provided essential information on this ecosystem prior to dam removal. Macrobenthic fauna was 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-Saint-Michel. The “Middle estuary sector” appears as transitional between upper Sélune estuary and the bay.

The benthic-demersal fish fauna of the estuary was dominated by four species only: flounder (*Platichthys flesus*), sea bass (*Dicentrarchus labrax*) and two gobies (*Pomatoschistus microps* and *P. minutus*). They are euryhaline benthic-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., 2012; Raffaelli et al., 1990). Between the Sélune estuary and the bay du Mont-Saint-Michel, differences appear in the main benthic-demersal fish species according to the study of Laffaille et al. (2001). Thus, *Gastroteus 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 was 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

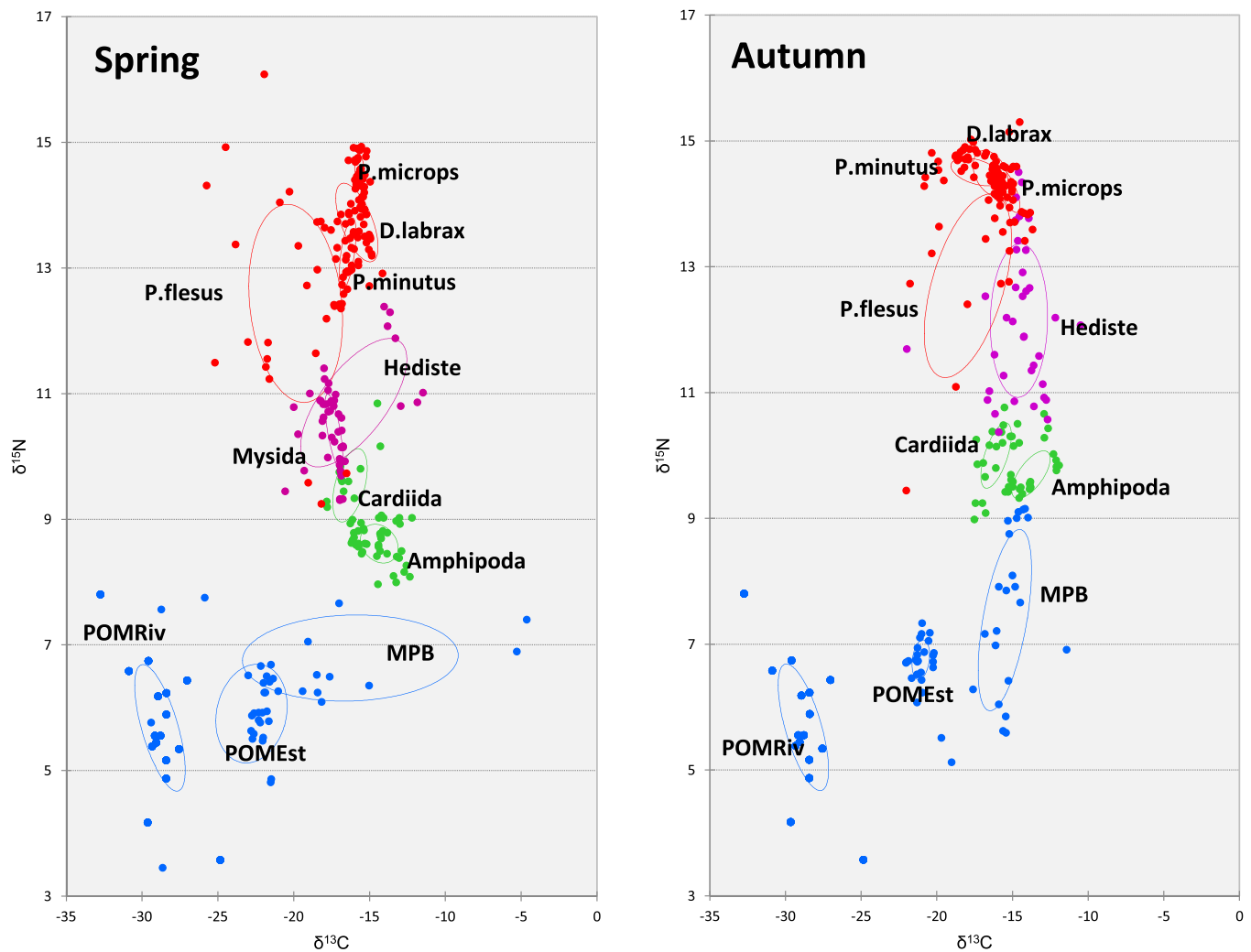
(Whitfield et al., 2012) because of high environmental constraints. The habitat of the Sélune estuary is an alternation of deposit and erosion stages of muddy sands imposed by the strong hydrological constraints, which leads to the frequent relocation of banks and channels visible at low tide (Ehrhold, 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 is responsible for the poor taxonomic richness. It is difficult to compare species richness values between sites since this parameter is dependent of the sampling surface. However, the number of species observed in our study site was low compared these those recorded on the whole intertidal bay of Mont-Saint-Michel (164 species on 175 stations) or on the intertidal flat of bay of Saint-Brieuc (53 and 85 taxa in 2001 and 2019 on 42 stations respectively). Trends characterized in our results are in accordance with conclusions of Ysebaert et al. (2003) on the influence of environmental gradients on estuarine microbenthic communities in the Schelde estuary (based on 3112 samples). Highest diversity and biomass were observed in the intertidal, polyhaline zone (open and middle zones) and decreased with decreasing salinity. As in the Schelde estuary, suspension feeders dominated the polyhaline zone and showed a significant decrease with decreasing salinity.

Abundance of macro-invertebrates showed a maximum in the “middle” sector whatever the period and a minimum in the upstream sectors (“Upper” and “Sée”). Abundance were comparable to those reported by Sturbois et al. (2021) in the bay of Saint-Brieuc in the upper and middle areas, but became lower when the salinity decrease. Most dominant species were common to those observed by Ysebaert et al. (2003) in the Schelde estuary: *Bathyporeia* spp., *Hediste diversicolor* and *Macoma balthica*. Regarding the biomass, highest values were observed in the downstream sectors (“Open” and “Middle”) in spring and became comparable on the whole study site in autumn. Preferential area for feeding juveniles may then vary along the year. Therefore, one can logically wonder whether the Sélune estuary contributes to the nursery function of the bay of Mont-Saint-Michel reported by Kostecki et al. (2012) for the flatfish *Pleuronectes platessa* and *Solea solea*. In our study, we did not collect any individuals of the first species and only two individuals of the second. However, the numerous sea bass juveniles sampled would mean that the Sélune estuary play a role of nursery for this species. Our study alone cannot answer the question of the contribution of the Sélune estuary to the nursery, but completed by a study after the dams have been dismantled and the freshwater flows have been restored, it will allow to follow its trend.

##### 4.2. The importance of microphytobenthos for food web

Stable isotopes were used to model the contribution of organic matter sources to in the Sélune estuary. The food web of the Sélune





**Fig. 8.** Area corrected for standard ellipses (SEAc) of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  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*), *Cardiida* (*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*.

estuary is not very diverse as a consequence of the low taxonomic richness observed. Both *in situ* production of benthic microalgae and terrigenous organic matter entered the food web. This combination of local primary production and freshwater organic matter was already demonstrated to sustain juvenile flatfish on nursery sectors, especially in estuaries (Pasquaud et al., 2008; Vinagre et al., 2008; Kostecki et al., 2010; Dias et al., 2023). However, 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 of Mont-Saint-Michel (Kostecki et al., 2012), but strongly different of the situation reported in the Gironde estuary where intertidal surface and MPB contribution are reduced and POM is the major organic source (Selleslagh et al., 2015). SIAR has already been used to determine basal production sources in fish food webs (Roach et al., 2009). In the bay of Mont-Saint-Michel, Riera (2007) underlined some trophic patterns of the main secondary production: the cultivated (mussels and oysters) and invasive (slipper limpet) shellfish, representing 40 % of the total secondary production in the bay (Arbach Leloup et al., 2008). The diet of these dominant filter feeding molluscs was primarily based on marine plankton while benthic diatoms inhabiting the intertidal flat did not contribute significantly. The present study demonstrated a different

situation for fish juvenile in the Selune estuary (Arbach Leloup et al., 2008), where MPB appears as the main food source. The importance of benthic algae primary production in estuaries and lagoons has already been shown. Quan et al. (2010) characterized the major pathways for energy flow in an artificial lagoon using 4 primary producers. They showed that more than 50 % of organic C in the food chain was derived from epibenthic microalgae, suggesting that the lagoon food web was mostly based on this epibenthic microalgal production. Melville and Connolly (2003) used stable isotope to determine the autotrophic sources supporting production of fish in a tropical estuary. They demonstrated the importance of seagrass, epiphytic algae, and local POM (including phytoplankton), in addition to the organic matter from adjacent mangroves for resident fish species. Our results in the Sélune estuary system tended to confirm the large influence of local primary production on coastal food chain when freshwater inputs of organic matter are limited.

According to the fish digestive content analysis the prey taxa do not only belong to macrobenthos but also to suprabenthos (mysids) and meiobenthos (haracticoids) 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) are clearly primary consumers, regarding 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 *P. minutus* and *P. microps*, 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 digestive tract was *Mesopodopsis slaberryi* 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 in spring in our study (Fig. 8): *Neomysis integer* and *Schistomysis spiritus* (collected in spring by our beam trawl) that are omnivore (Bremer and Vijverberg, 1982; Mauchline, 1967) and logically positioned near the omnivorous polychaete *H. diversicolor*.

The two species of gobies and the sea bass clearly occupy the top of the food chain while the flounder is 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; Leclerc et al., 2013; Pasquaud et al., 2008). 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  $\delta^{15}\text{N}$  (9.24–14.92 ‰ in spring, 9.44–14.16 ‰ 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  $\delta^{13}\text{C}$  (-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. 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).

#### 4.3. Conclusion and perspectives

Despite the freshwater inputs from the Couesnon, the Sée and the Sélune (86 % of the freshwater inputs of the bay of Mont-Saint-Michel, the eastern estuarine bay is dominated by the tide. The high turbidity observed in rivers controls and limits the penetration of light into the water, which thus attenuates phytoplanktonic production and, *de facto*, promote microphytobenthic production (Lefevre et al., 2000). Fig. 9 summarizes circulation of organic matter in the food web, with main ways. The intertidal mudflat support low microphytobenthic production but the high biomass of benthic diatoms makes it one of the key compartments of the food web as demonstrated by Davout et al., 2009). In autumn, harpacticoid copepods (zooplankton) becomes more important.

In the present situation, dams obstruct natural fluxes of water and materials by trapping organic matter, phosphorus and silica in the sediments that decant in their reservoirs (Fovet et al., 2020). With dam removal, rivers can vary widely in the fluctuations and magnitude of flows they experience (Bednarek, 2001). In the Sélune estuary, forecasts suggest that flows should not change after the dams are removed, considering the fact that dams had a low effect at low flow on flow management and no effect beyond a flow of  $30 \text{ m}^3 \cdot \text{s}^{-1}$ . The salinity front should therefore not migrate or migrate very little. The sedimentary dynamics could, however, be modified by the disappearance of retention basins linked to the presence of dams. Biodiversity changes will depend on the balance between (i) the creation of new habitats downstream and (ii) the change in sediment transport.

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

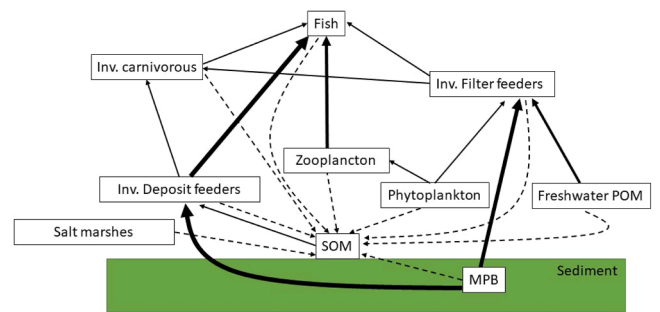


Fig. 9. Simplified diagram of the benthic foodweb in the Sélune estuary. The thickness of the arrow provides information on the intensity of trophic relationships. The dotted arrows represent feces and biodeposits.

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.

#### CRediT authorship contribution statement

**N. Desroy:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **MC Husset:** Writing – review & editing, Software, Resources, Methodology, Formal analysis, Data curation. **L. Goyot:** Writing – review & editing, Visualization, Resources, Methodology, Formal analysis, Data curation. **P. Le Mao:** Writing – review & editing, Visualization, Validation, Resources, Investigation, Funding acquisition, Conceptualization. **L. Soissons:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **JM Roussel:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition. **H. Le Bris:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Funding acquisition, Conceptualization.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgements

This work was funded by the Seine-Normandie Water Agency (Convention AESN / Inra n°1066356). The authors gratefully acknowledge Julien Chev e, Julien Guillaudeau, Manuel Rouquette and Alexandre Robert for their valuable help in field surveys and Alexandre Robert for help in data analysis.

#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104041.

#### Data Availability

Data will be made available on request.

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