
Seasonal dynamic of the benthic food web in subtidal sandbanks

Robert Alexandre ^{1,2,*}, Quillien N ¹, Bacha M ^{1,3}, Cauille C ⁴, Nexer M ¹, Parent B ⁴, Garlan T ⁵,
Carpentier A ⁶, Amara R ³, Desroy Nicolas ¹

¹ France Energies Marines - Environmental Integration R&D Program, 525 Avenue Alexis de Rochon, 29280 Plouzané, France

² IFREMER, Unité Littoral, Laboratoire Environnement et Ressources de Bretagne Nord, CRESCO, 38 rue du Port-Blanc, 35800 Dinard, France

³ Laboratoire d'Océanologie et de Géosciences, UMR 8187 CNRS, Université du Littoral Côte d'Opale, 32 Avenue Foch, 62930 Wimereux, France

⁴ Ocean Zoom, 2 chemin de la Houssinière, 44300 Nantes, France

⁵ Shom (French Hydrographic Office), 13 rue du Chatellier, 29200 Brest, France

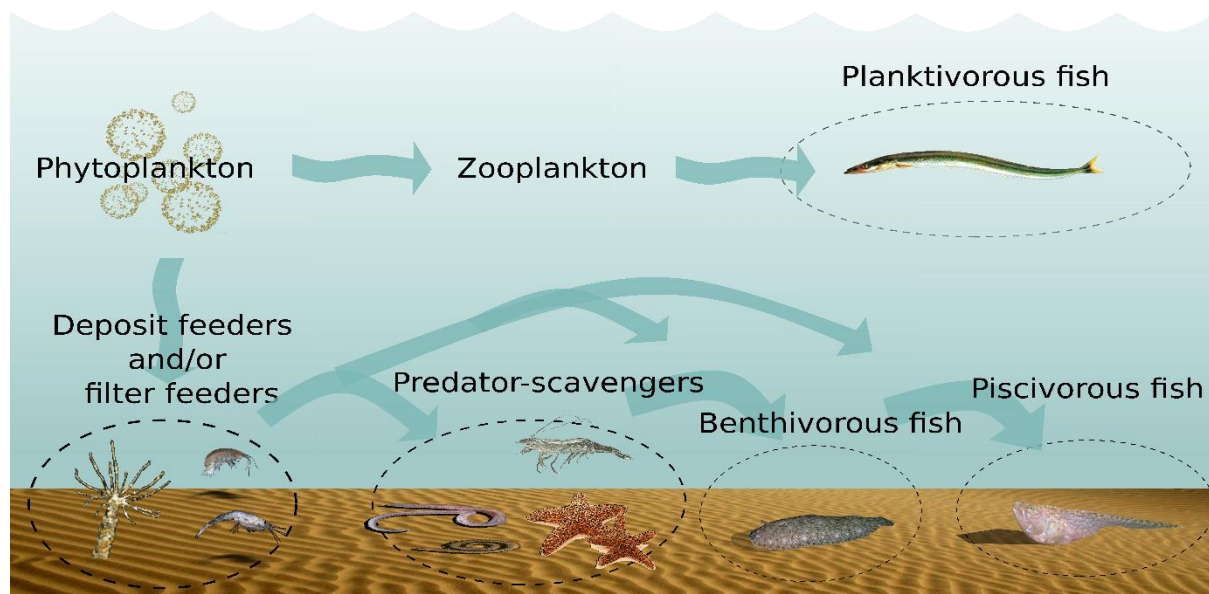
⁶ Université de Rennes, BOREA (Muséum National d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des Antilles), Campus de Beaulieu, 35000 Rennes, France

* Corresponding author : Alexandre Robert, email address : alexandre.robert@ifremer.fr

Abstract :

Submarine sandbanks are prevalent worldwide but, paradoxically, these ecosystems and their dynamics remain largely unknown. As submarine sandbanks are targeted by a large variety of human activities, there is an urgent need for sound scientific knowledge for environmental impact assessments (EIAs) and the appropriate management of biodiversity in these areas. To our knowledge, the present study is the first to investigate the seasonal dynamics of the benthic food web in sandbank areas. We performed a stable isotope analysis in the French part of the southern North Sea. This area is typified by numerous sandbanks and by massive phytoplankton blooms in spring. We found a very simple food web structure that is heavily dependent on organic matter particles in seawater. Primary consumers, i.e. deposit feeders and, to a lesser extent, suspension feeders, dominate the benthic biomass. Small predator-scavengers such as annelids, shrimps and crabs prey upon them. Fish predators such as *Echiichthys vipera* represent a very restricted proportion of the biomass. We observed that the general structure of the food web is relatively well preserved over seasons. We thus propose that the functioning of the ecosystem is resilient to natural disruptions—such as dune migrations—and, probably, to anthropogenic disturbances.

Graphical abstract



Schematic representation of the benthic food web within sandbank areas

Keywords : Macrobenthos, Invertebrates, Fish, Trophic web, Isotopic metrics, Soft sediments, North Sea

1. INTRODUCTION

Submarine sandbanks are widespread worldwide, especially in the southern North Sea, Western-English Channel, in the Iroise Sea and in the Irish Sea. Sandbanks are oriented parallel to the main tidal current and can be ten kilometres long and up to ten metres high. They can also be very stable (Le Bot et al. 2005, Van Lancker et al. 2009) as revealed by studies performed in Belgium where sandbanks position did not change for centuries (De Moor 2002, Aernouts 2005). Nevertheless, sandbanks are covered by smaller bedforms, such as marine dunes/sand waves and ripples, known for their high migration rate (Le Bot 2001). Sandy habitats can thus be dynamic environments at the local scale. Several human activities occur within sandbank areas such as marine aggregate extraction (Poiner & Kennedy 1984, Moolaert et al. 2007, Degrendele et al. 2010) and fishing (ICES 2018). Even under the status of Marine Protected Areas (MPAs), offshore sandbanks are among the most threatened habitats by fishing due to their poor conservation status in European waters (Perry et al. 2022). As sandbanks are suitable habitats for other human activities, such as offshore wind farms, a considerable effort must be paid to increase the knowledge on this ecosystem and its sensitivity.

In the southern North Sea, sandbanks are characterised by a remarkably high phytoplankton production, and by important blooms of *Phaeocystis globosa* (Reigstad & Wassmann 2007, Karasiewicz et al. 2018, Karasiewicz & Lefebvre 2022) but a very low organic matter content (Robert et al. 2021). Despite the fact that high primary production can sustain the benthic ecosystem of sandbanks (Denis & Desroy 2008), the macrobenthic fauna exhibits very low species richness (5 to 12 species per m²) as well as low abundances (100 to 400 individuals per m²), depending on the study and the specific location (Desroy 2002, Van Hoey et al. 2004).

Robert et al. (2021) recently revealed that macrobenthic communities vary depending on (i) the type of bedform (sandbank, barchan dune and transversal dune) and (ii) the season (autumn and spring). However, species composition and diversity (including biological traits diversity) were relatively homogeneous within a given bedform, probably because of the high hydrodynamic activity in their study area. Apart from these studies, the ecosystem functioning of bedform areas remains largely unknown. To our knowledge, the benthic food web of sandbanks has never been investigated so far.

Stable isotope analyses, and especially the light/heavy isotopes ratio of C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$), have been widely used to study marine food webs because they provide temporally integrated information about species' diet and trophic position (from a few days to months; Vander Zanden et al., 2015). A biplot is generally drawn with $\delta^{13}\text{C}$ values as a proxy of food source (Post 2002, Bearhop et al. 2004) and $\delta^{15}\text{N}$ values as a proxy of trophic positions (Post 2002, Hussey et al. 2014). One can consider this biplot as a picture of the isotopic niche (see Newsome et al., 2007), a derivative of the n-dimensional hypervolume that defines the ecological niche *sensu* Hutchinson's (1957). Several univariate metrics have been proposed to describe its shape (Jackson et al. 2011, Layman et al. 2012, Cucherousset & Villéger 2015) and the trophic positions within (Quezada-Romegialli et al. 2018). Mixing models can also be computed to assess the trophic links between food sources and consumers (Govan et al. 2023). All these methods are implemented under the R statistical software (R Core Team 2013) and can be computed using a Bayesian approach which allows for statistical comparisons (Jackson et al. 2011, Quezada-Romegialli et al. 2018, Govan et al. 2023) between groups or communities but also in relation to time and space.

Based on a stable isotope analysis, the present study aims at investigating the benthic food web of sandbanks and its seasonal variations. Three null hypotheses will be tested:

- H1. Sandbanks display a low number of trophic guilds with respect to the poor diversity of both macrobenthic (Desroy 2002, Van Hoey et al. 2004, Breine et al. 2018, Robert et al. 2021) and fish species (Amara 2003, Ellis et al. 2011) found in sandbanks compared to areas without bedforms;
- H2. Seawater Particulate Organic Matter (wPOM) or freshly deposited wPOM are the main source of organic matter in the food web with respect to the remarkably high phytoplankton production in the southern North Sea (Lefebvre et al., 2020) and the very low Sedimentary Organic Matter (sPOM) content (Robert et al. 2021);
- H3. The architecture of the food web, the isotopic composition of the main sources of organic matter, as well as the isotopic composition of the main trophic guilds, vary depending on the season due to a higher contribution of ^{13}C -depleted terrestrially-derived organic matter in autumn/winter. The selective use of heavy isotopes by primary producers, which induces a general ^{15}N -depletion of the trophic web in spring/summer as well as changes of species composition and changes in the relative contribution of the various trophic guilds, could also be responsible for seasonal variations.

2. MATERIALS & METHODS

2.1. Study site

The present study focused on an 80-km² area located on the Flanders banks, offshore the Dunkirk harbour (Figure 1). Because the study area is relatively far from large estuaries, freshwater inputs and terrestrial organic matter inputs are considered negligible and mainly linked to small canals and runoffs from cliffs (Cap-Blanc Nez).

The study area, and more generally the Southern Bight of the North Sea, consist of shallow waters, with a maximum depth of 40 m. It is typified by a wide variety of bedforms such as large sandbanks extending between 8 to 32 km length and with a height of 15 to 20 m. In this area, benthic communities were investigated for the first time by Cabioch & Glaçon (1975) and then revisited by Davoult et al. (1988) and Desroy (2002). A recent paper also described how benthic ecosystem functioning varies with the type of bedform, the season and the position within a bedform (Robert et al. 2021).

2.2. Biological material collection

Macrobenthic organisms (>1 mm) were collected with a Van Veen grab (0.1 m²) via 23 stations distributed between the trough and the crest of three kinds of bedforms: a transversal dune, a barchan dune, and a sandbank. Three stations were also localised in areas without bedforms (see Robert et al., 2021 for details). Three replicates per station were preserved in a 4% buffered formalin solution for abundance and biomass measurements. Two additional replicates were also performed at each station: one for the analysis of the stable isotope composition of the macrobenthic organisms and one for the stable isotope composition of the sediment.

Seawater Particulate organic matter (wPOM) was collected in the water column with a Niskin-bottle, above each kind of dune and in the reference area.

Megabenthic organisms (> 10mm) and fish were collected using a commercial trawl with a “Grande Ouverture Vertical”, equipped with a reduced cod-end mesh of 20 mm, stretched in order to improve the catch of juveniles and small fish. Twenty-six trawl hauls were performed between the trough and the crest of three sandbanks (Figure 1).

Macrofauna, megafauna, fish and water samples dedicated to the analysis of stable isotopes were all frozen at -20°C on-board.

This sampling strategy was set up both in autumn 2019 (October) and spring 2020 (May) in order to assess the seasonal variability of the benthic food web.

2.3. Sample processing and stable isotope analyses

In the laboratory, all the organisms (*i.e.* macrofauna, megafauna and fish) were quickly defrosted to avoid tissue breakdown. They were sorted, identified at species level, counted, and weighed. The abundance and biomass were standardised by the sampling surface. A total of 37 species contributing to more than 90% of the biomass was selected for stable isotopic composition analyses (Table 1). Fish were classified according to their sexual maturity (juveniles vs. adults). Those with a high mobility were not considered as they could have been feeding beyond the location of the sandbank, mostly pelagic species (*Sprattus sprattus* and

Trachurus trachurus) and demersal fish (*Dicentrarchus labrax*). The cephalopod *Loligo vulgaris* was also excluded for the same reasons.

For each season, a maximum of 25 samples per species and size class (fish only) were dissected. Samples consisted of muscle tissue for most of the taxa (*e.g.* fish, crustaceans, echinoderms). For the smallest species such as small annelids, it was often necessary to pool the whole body of several individuals from the same species in order to reach the minimum weight needed for isotope analyses (0.1mg). All samples were finally rinsed with Milli-Q water, freeze-dried for 24h, and powdered manually.

Sediment samples dedicated to the analysis of the stable isotope composition of sPOM were re-suspended in filtered Milli-Q water using an ultrasonic bath. The supernatant was then filtered on pre-combusted (450 °C for 5 h) GF/F filters. Seawater collected for wPOM was also sieved on pre-combusted GF/F filters.

Samples partly composed of calcium carbonate (*e.g.* wPOM, sPOM, small ophiuroids, heart urchins, small crustaceans; see Table 1 for details) were split into two subsamples: one was acidified with 10% HCl for $\delta^{13}\text{C}$ whereas the second remained untreated to avoid $\delta^{15}\text{N}$ enrichment (Pinnegar & Polunin 1999). The $\delta^{13}\text{C}$ values from acidified and the $\delta^{15}\text{N}$ values from untreated subsamples were later combined to obtain valid isotope signatures (*i.e.* undisturbed by CaCO_3 , neither by acidification).

Around 1 mg of powder was weighed for each sample and placed into tin capsules. Samples were analysed for isotopic composition at Cornell University (US) using a Thermo Delta V

isotope mass spectrometer interfaced with a NC2500 elemental analyser. Several in-house standards (CBT, KCRN and Deer) were used to test the instrument measurement variability or long-term drift in the determination of elemental composition (quality control check). Standards were run once every ten samples. All in-house standards were calibrated periodically against international standards to verify their accuracy. Within the runs, isotopic precision for QC standards was 0.2 per mil for nitrogen and carbon. Results from these calibrations are provided in supplementary data 1.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined by weighing the $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ ratios of a sample relative to those of standards (Vienna Pee Dee Belemnite for carbon and N_2 in air for nitrogen):

$$1) \quad \delta^j_E = \frac{[R(^i_E/^j_E)_P - R(^i_E/^j_E)_{std}]}{R(^i_E/^j_E)}$$

with ^iE and ^jE the heavier (higher atomic mass i) and lighter (lower atomic mass j) isotopes of element E . The isotope ^iE in substance P was specified by ^iEP (see the guidelines and recommended terms for expression of stable isotope-ratio and gas-ratio measurement results in Coplen, 2011).

2.4. Data analyses

Potential sources of C & N

Spatio-temporal variations – A Permutational Multivariate Analysis of variance (Permanova, Anderson, 2005) was used to determine whether the stable isotope composition of sPOM and wPOM varied in relation with the season, depth and distance from the coast. The Permanova was computed using 1000 random iterations and Euclidean distance as dissimilarity measure.

Prior to this analysis, the homogeneity of group dispersions was tested thanks to the betadisper function, implemented in the vegan package (Oksanen 2010) of the R statistical software (R Core Team 2013). The mean distance to the centroids in a Principal COordinates Analysis was used for this procedure (Anderson et al. 2006).

Linear models of regressions were also used to provide a deeper insight about how $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of both wPOM and sPOM varied independently with seasons, depth and distance from the coast. A visual inspection of diagnostic plots was done in order to determine whether the conditions of application of the linear models were met.

Basal resources contribution to the diet of primary consumers – A Bayesian Stable Isotope Mixing Model (SIMM) was computed to assess the relative contribution of Sedimentary Organic Matter (sPOM) and water Particulate Organic Matter (wPOM) as food sources for primary consumers (*i.e.* deposit feeders). The *simmr* package (Parnell & Parnell 2019) was used to address this issue. Bayesian priors assumed an equal probability of each food source being consumed to avoid biased statistical inference. The *simmr* package implements mixing models via both Markov Chain Monte Carlo (MCMC) algorithms and faster Fixed Form Variational Bayes (FFVB). Because specific Trophic Discrimination Factors (TDF) between primary consumers and primary producers were unknown, “generic” values provided by the meta-analysis of McCutchan et al. (2003) were employed. The TDF between basal resources (wPOM and sPOM) and primary consumers were set to 1.3 ± 0.3 ‰ for $\delta^{13}\text{C}$ and 2.9 ± 0.32 ‰ for $\delta^{15}\text{N}$.

A diagnostic procedure (see Govan et al., 2023 for details) was used for each of the computed models to check their robustness (not shown). The convergence (values in the diagnostics should all be close to 1; if not, a longer number of chains is recommended) and the posterior correlation between the sources (in general, high correlations -negative or positive- are indicative of the model being unable to determine which food sources are being consumed, though the marginal standard deviations can still be narrow) were particularly considered.

One independent model was run for each season and seasonal differences were assessed by calculating the probability of Bayesian posterior distribution in autumn to be smaller/bigger than in spring. We considered that a tendency occurred when the probability of difference was between 75% and 95%. We considered that the seasonal difference was significant when the probability exceeded 95%.

Invertebrates and fish consumers

Identification of trophic groups – Trophic groups were identified thanks to existing databases such as BIOTIC for invertebrates (<https://www.marlin.ac.uk//biotic/>) and FishBase for fish (<https://fishbase.mnhn.fr/>). When the information was missing, the feeding mode was completed using data from peer-review papers.

The trophic position of each species was also calculated at each season via the Bayesian approach proposed by Quezada-Romegialli et al. (2018) and implemented in the tRrophicPosition package. We used tissues of the suspension feeders *Fabulina fabula*, *Donax vittatus* and *Spisula solida* as baseline to obtain integrated isotopic values of primary producers (isotopic endpoints). We effectively considered that the stable isotope composition of potential sources of carbon and nitrogen (namely wPOM and sPOM) was very variable at a

high frequency (in both space and time) which could mask the effects of the season (Vander Zanden and Rasmussen 1999).

“Generic” values provided by the meta-analysis of McCutchan et al. (2003) were also employed as TDF values in this analysis.

In the Bayesian approach, C and N composition of consumers, baselines and TDFs were modelled as random variables, each having a prior normal distribution on their means and a uniform prior distribution on their standard deviations, while trophic level was treated as random parameter. The model was run independently for each season with 5 parallel chains for the model, 20,000 adaptive iterations (both before and after posterior sampling), and 20,000 iterations discarded as burn in.

Seasonal variations – A Permanova (1000 random permutations, Euclidean distance) was used to assess the variations of the bivariate isotopic composition in relation with (i) the season, (ii) the trophic group and (iii) the interaction between both factors. The betadisper procedure was implemented to verify homogeneity of group dispersions. Three univariate indices of isotopic diversity developed by Layman et al. (2007) were then calculated at the scale of the community but also independently for each trophic group: the $\delta^{15}\text{N}$ Range, the $\delta^{13}\text{C}$ range and the Total Area. The $\delta^{15}\text{N}$ Range (NR) was the distance between the two species with the most enriched and most depleted $\delta^{15}\text{N}$ values (i.e., maximum $\delta^{15}\text{N}$ – minimum $\delta^{15}\text{N}$). The $\delta^{13}\text{C}$ range (CR) was the distance between the two species with the most enriched and most depleted $\delta^{13}\text{C}$ values (i.e., maximum $\delta^{13}\text{C}$ – minimum $\delta^{13}\text{C}$). As suggested by Layman et al. (2007), a higher CR meant that there is a diversification at the basis of the food web with a greater number of food sources. The Total area (TA) was represented by the convex hull area

encompassing all species in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplot. This measure was indicative of the total amount of niche space filled by species. The TA is influenced by species with extreme positions on the $\delta^{13}\text{C}$ and/or the $\delta^{15}\text{N}$ axis. The three univariate indices of Layman et al. (2007) were calculated following the Bayesian approach implemented by Jackson et al. (2011) in the SIBER package. They were calculated with 20,000 iterations from the Markov Chain Monte Carlo (MCMC) simulation. Posterior estimates allow for statistical comparisons between the seasons. We applied the same rule to detect tendencies and statistical differences as we did for the Bayesian Stable Isotope Mixing Model: we considered that a seasonal tendency occurred between 75% and 95% of probability and that a significant difference occurred above 95% probability.

3. RESULTS

3.1. Potential sources of C & N

General characteristics – The isotopic composition of wPOM was, on average, equivalent to $-18.6 \pm 1.8\text{‰}$ (mean \pm standard-deviation) and $5.3 \pm 3.6\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The isotopic composition of sPOM was $-25 \pm 1.5\text{‰}$ and $7.7 \pm 3.4\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Variations depending on the season, depth and distance from the coast – The Permanova analysis revealed a significant effect of the season on the multivariate stable isotope composition of wPOM (p -value=0.003). Conducting a linear regression model showed that a $\delta^{13}\text{C}$ values decreased significantly with increasing distance from the coast (p -value=0.022; Figure 2). Conversely, season (p -value=0.098) had no significant effect on the $\delta^{13}\text{C}$ values. Significantly higher values of $\delta^{15}\text{N}$ were observed in spring compared to autumn with

7.8±3.2‰ in spring and 2.6±1.5‰ in autumn (p-value=0.005) but no effect of distance from coast (p-value=0.403) was observed.

A significant effect of season (Permanova, p-value=0.001) as well as a significant interaction between the factor season and the distance from the coast (Permanova, p-value=0.003) were observed based on the multivariate stable isotope composition of sPOM. The linear regression models revealed a significant reduction of $\delta^{13}\text{C}$ values of sPOM in spring (-25.5±1.5‰) compared to the autumn (-24.5±1.3‰) (p-value=0.016, Figure 2). The distance also had a negative effect on $\delta^{13}\text{C}$ values (p-value=0.011), regardless of the season. Season also negatively influenced the $\delta^{15}\text{N}$ of sPOM with lower values in spring (p-value<0.001): the $\delta^{15}\text{N}$ was equal to 5.1±1.8‰ whereas it was equivalent to 9.8±2.8‰ in autumn. A significant interaction between the factor season and the distance from the coast was also observed via the linear regression model (p-value=0.004). In other words, the $\delta^{15}\text{N}$ of sPOM increased in autumn as the distance from the coast increased whereas it decreased with the distance in spring.

Contribution to the diet of primary consumers – Output of the Bayesian Stable Isotope Mixing Model indicated that wPOM was the main contributor to the diet of Deposit feeders. An overall contribution up to 70% was found for wPOM against less than 30% for sPOM. Nevertheless, seasonal variations occurred (Figure 3). Indeed, the contribution of sPOM declined from 29% to 7% between autumn and spring and the contribution of wPOM increased from 71 to 93% between the two seasons.

3.2. Invertebrates and fish consumers

Characteristics of trophic groups – A total of six trophic groups was defined according to literature data (Figure 5 and Table 1). They differed in their isotopic composition from a multivariate point of view (Permanova, p-value=0.001).

The suspension feeders *Donax vittatus*, *Fabulina fabula* and *Spisula solida* were grouped together and used as baseline for the calculation of trophic position of the other species. They contributed to 5% of the organisms caught during the present study (after standardisation by the sampling surface). The mean $\delta^{13}\text{C}$ of this trophic group was equivalent to $-17.1\pm 0.9\text{‰}$ whereas the mean $\delta^{15}\text{N}$ was $8.8\pm 1.6\text{‰}$.

Deposit feeders contributed to 83% of the biomass. They were comprised of nine species: *Bathyporeia pelagica*, *Echinocardium cordatum*, *Urothoe brevicornis*, *Tellimya ferruginosa*, *Magelona filiformis*, *Lanice conchilega*, *Gastrosaccus spinifer*, *Pontocrates altamarinus* and *Ophelia borealis*. Their average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were $17.5\pm 1.2\text{‰}$ and $9.9\pm 2.1\text{‰}$, respectively. *Bathyporeia pelagica*, *Echinocardium cordatum* showed the lowest trophic positions, around 1, whereas *Tellimya ferruginosa*, *Magelona filiformis*, *Lanice conchilega*, *Gastrosaccus spinifer* and *Pontocrates altamarinus* displayed a trophic position around 1.5. *Ophelia borealis* showed the highest trophic position, above 2, whatever the season.

Predator-scavengers contributed to almost 12% of the biomass and included twelve species: *Pagurus bernhardus*, *Asterias rubens*, *Ophiura ophiura* and *Sigalion mathildae*, *Carcinus maenas*, *Nephtys cirrosa*, *Nephtys hombergii*, *Crangon crangon*, *Liocarcinus holsatus*, *Thia scutellata*, *Palaemon elegans* and *Glycera tridactyla*. Their average isotopic composition was

equivalent to $-16.8 \pm 1.6\text{‰}$ for $\delta^{13}\text{C}$ and $12.9 \pm 1.8\text{‰}$ for $\delta^{15}\text{N}$. Their trophic position varied greatly according to the species. Indeed, *Pagurus bernhardus*, *Asterias rubens*, *Ophiura ophiura* and *Sigalion mathildae* had a trophic position below 2 whereas *Carcinus maenas*, *Nephtys cirrosa*, *Nephtys hombergii*, *Crangon crangon*, *Liocarcinus holsatus*, *Thia scutellata*, *Palaemon elegans* had a trophic position between 2 and 3. Finally, *Glycera tridactyla* exhibited the highest trophic position among predator-scavengers with a value above 3.

Planktivorous fish had a low contribution in the food web with 0.03% of the recorded biomass. They were represented by two sand eels species: *Hyperoplus lanceolatus* (small and big individuals) and *Ammodytes tobianus* (only large individuals have been collected). They showed a mean $\delta^{13}\text{C}$ of $-16.4 \pm 1\text{‰}$ and a mean $\delta^{15}\text{N}$ of $14.9 \pm 0.7\text{‰}$. Their trophic position was equivalent to 3.1.

Benthivorous fish contributed to 0.18% of the biomass and were composed by six species: *Arnoglossus laterna* (only small individuals have been collected), *Pleuronectes platessa* (small and big), *Solea solea* (small and big), *Mullus surmuletus* (only small), *Merlangius merlangus* (small and big) and *Buglossidium luteum* (small and big). Their isotopic composition was $-16.8 \pm 0.9\text{‰}$ for $\delta^{13}\text{C}$ and $13.8 \pm 0.9\text{‰}$ for $\delta^{15}\text{N}$. All the benthivorous fish had a trophic position just below 3.

Piscivorous fish contributed to 0.02% of the biomass and were represented by one single species: *Echiichthys vipera* (big and small individuals). Its $\delta^{13}\text{C}$ mean value was $-16.7 \pm 0.4\text{‰}$.

whereas $\delta^{15}\text{N}$ mean value was equal to $15\pm 0.8\%$. The trophic position of *Echiichthys vipera* was equivalent to 3.1.

1

2 **Seasonal variations** – The biplot (Figure 5) as well as Permanova analysis (not shown) did not
3 reveal any significant seasonal effect at the scale of the community (p -value=0.071) nor at the
4 scale of each trophic group (not shown). From a univariate point of view, a seasonal trend was
5 detected: it was manifested by a decline of the Total Area (TA) between the autumn and
6 spring, at the scale of the community (probability=0.85). This effect was no longer detected
7 when calculating the univariate indices for each trophic group (probability<0.75, whatever the
8 indices and the trophic group).

9

10 Seasonal variations were also relatively low regarding the trophic position of each species
11 (Figure 4). A significant trend (probability=1 for each species hereafter) in the trophic position
12 was detected for *Gastrosaccus spinifer*, *Asterias rubens*, *Ophiura ophiura*, *Nephtys hombergii*,
13 *Crangon crangon*, *Liocarcinus holsatus*, *Arnoglossus laterna* (small), *Merlangius merlangus*
14 (small) and *Echiichthys vipera* (big). Conversely, a significant but small decrease of trophic
15 position was observed for *Bathyporeia pelagica*, *Echinocardium cordatum*, *Magelona*
16 *filiformis*, *Ophelia borealis*, *Nephtys cirrosa*, *Ammodytes tobianus* (big), *Pleuronectes platessa*
17 (small), *Buglossidium luteum* (big) and *Echiichthys vipera* (small).

18

19 4. DISCUSSION

20 The present study represents, to our knowledge, the first investigation about the benthic food
21 web of subtidal sandbanks areas. It is expected that the sound scientific knowledge it provides

22 will be useful for further understanding the ecological functioning of these habitats and to
23 depict changes linked to anthropogenic pressures (including climate change).

24

25 4.1. Phytoplankton blooms are the main source of C and N in the benthic food web

26 **The isotopic composition of food sources varies depending on the season and distance from**
27 **the coast** – Higher $\delta^{13}\text{C}$ values were recorded in autumn relative to spring, both for wPOM
28 and sPOM. Lower $\delta^{15}\text{N}$ values of wPOM were also observed in autumn. It is well known that
29 carbon sources (and especially wPOM) display seasonal variations in their isotopic
30 composition, both in marine, estuarine and freshwater systems. Therefore, results were
31 consistent with those of several other studies (Zohary et al. 1994, France et al. 1997, Bouaziz
32 et al. 2021). The carbon and nitrogen enrichments are generally due to the selective
33 consumption of Dissolved Inorganic Carbon (DIC) and Dissolved Inorganic Nitrogen (DIN)
34 during phytoplankton blooms: the ^{12}C and ^{14}N are primarily consumed while the ^{13}C and ^{15}N
35 accumulate. Some studies also suggest that the increase of $\delta^{13}\text{C}$ results from reduced isotopic
36 fractionation at high cell densities or growth rates, or in relation with day length (Zohary et al.
37 1994, France et al. 1997, Brandenburg et al. 2022). A shift in the species composition can also
38 be responsible for seasonal variations of $\delta^{15}\text{N}$ values, because nitrogen isotope composition
39 can greatly vary between phytoplankton taxa (Vuorio et al. 2006) and because a larger
40 proportion of heterotrophic organisms usually induced higher $\delta^{15}\text{N}$ values of wPOM (Agurto
41 2007, Aberle et al. 2010).

42

43 In general, terrestrial organic matter has depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to marine
44 organic matter (Vizzini et al. 2005) which can induce an increase of the isotopic ratio toward

45 the offshore. Here, both wPOM (in both spring and autumn) and sPOM (in spring only) showed
46 higher values close to the coast compared to offshore stations, which is not in line with this
47 hypothesis. Three processes could be responsible for these results. First, due to particular
48 hydrodynamic conditions in sandbanks areas, water masses with a terrigenous origin can
49 occur in the offshore area whereas the coastal area may exhibit marine characteristics.
50 Secondly, one can hypothesise that the ^{13}C - and ^{15}N -enrichment in the coastal area can result
51 from pollution and contaminants released by the manufacturing industries, primarily
52 metallurgical, chemical, and petrochemical, that surround the Dunkirk city (Dewarumez &
53 Davoult 1997, Desroy 2002). Thirdly, it is possible that the isotopic composition of sPOM varies
54 depending on the substrate, in relation with the biogeochemical process. In the Tagus estuary,
55 Sampaio et al. (2010) revealed that sediment grain size might act as a confounding factor in
56 the analysis of nitrogen. Areas with finer sediments showed the highest $\delta^{15}\text{N}$ values.

57

58 **Importance of the benthic-pelagic coupling** – Outputs of mixing models clearly indicated that
59 wPOM is the main source of carbon and nitrogen in the benthic food web. The southern North
60 Sea is typified by a high phytoplankton production and remarkable blooms between March
61 and June (Schapira et al. 2008). Their intensity and species composition vary from one year to
62 another but the dominant species are generally *Phaeocystis globosa* (Prymnesiophyceae), the
63 diatoms *Chaetoceros* sp., *Thalassionema nitzschioides*, *Paralia marina*, *Guinardia striata*,
64 *Guinardia delicatula*, *Rhizosolenia imbricata* as well as the diatom *Skeletonema costatum*
65 (Lefebvre et al. 2011). During massive *Phaeocystis* blooms, chlorophyll-a concentrations in the
66 water column may reach values up to $50 \mu\text{g.l}^{-1}$ which can even change water viscosity (Seuront
67 et al. 2006). The decline of the bloom is characterised by a massive foam formation that

68 accumulates on the shore. Based on results from the present study and the existing
69 knowledge, one can hypothesise that the wPOM is mainly composed of phytoplankton cells
70 which induce a large injection of carbon and nitrogen into benthic ecosystems (Alderkamp et
71 al. 2007) in this area where other primary producers -macroalgae and microphytobenthos-
72 are considered absent due to high water turbidity. This is in line with the observations by
73 Franco et al. (2008) in permeable and fine grain depositional sediments of the Southern Bight
74 of the North Sea. Results from the present study are also in accordance with those of Kopp et
75 al. (2015) in the eastern English Channel where stronger pelagic–benthic coupling was found
76 in shallow coastal areas mostly due to a reorganisation of the upper consumers relative to two
77 trophic pathways, benthic carbon sources being available to pelagic consumers and,
78 reciprocally, pelagic sources becoming accessible to benthic species.

79

80 The permeable sediments of sandbanks generally display a low organic matter content due to
81 the important transport of organic particles (e.g. detritus and faecal pellets) in the superficial
82 sediments (Volkenborn et al. 2007) by advective pore-water flows (Huettel & Rusch 2000) and
83 other physical process (see the review by Santos et al., 2012). In the studied area, the organic
84 matter content effectively remained below 0.5% and decreased with distance from the coast
85 along with the median grain size (Robert et al. 2021), which probably explains the minor
86 influence of sPOM in the benthic food web. In this context, it is possible that deposit feeders
87 have been selected according to their ability to feed on wPOM rather than sPOM. For this
88 reason, it is difficult to distinguish between suspension and deposit feeders with their stable
89 isotope composition (Kang et al. 2015).

90

91 4.2. A very simplistic food web structure

92 The mass ratio hypothesis suggests that the influence of a species on key ecosystem functions
93 is proportional to its biomass (Garnier et al. 2004, 2007, Vile et al. 2006, Mokany et al. 2008).
94 From this principle, one can hypothesise that the food web of sandbanks is very simple
95 because most of the biomass belonged to three trophic groups only: deposit-feeders,
96 predator-scavengers and suspension feeders. This simple food web also bears similarities with
97 the macrotidal sandy beaches of the Bay of Douarnenez (Brittany, France), described by
98 Quillien et al. (2016). Although the authors did not split species into trophic guilds, the isotopic
99 space occupied by sandy shore species was very similar to that of the present study, with the
100 exception of macroalgae that were not present here. Our results were also consistent with
101 those of Nordström et al. (2009) in a study conducted in sandy bays of the Åland Islands (Baltic
102 sea), where 21 macrobenthic species were found, split in 3 trophic guilds. Sandbanks are
103 covered by marine dunes and megaripples, known to exhibit important migration patterns
104 (Ernstsen et al. 2004, Ferret et al. 2010, Bolle et al. 2013): in the Dunkirk area, dune
105 movements range between 53.40 and 64.45 m.year⁻¹ in the coastal area and between 18.53
106 and 54.58 m.year⁻¹ in the offshore area (Bary et al., *in prep.*). Two recent studies, based on a
107 Biological Traits Analysis (BTA), suggested that such natural disturbance could severely limit
108 the number of ecological niches (Breine et al. 2018, Robert et al. 2021). Our findings
109 corroborate this assumption, showing that only a low number of trophic niches can coexist in
110 such dynamic environments. Due to this very simple food web structure, one can hypothesise
111 that natural or anthropogenic disruptions may strongly affect the ecosystem functioning of
112 sandbank areas (low resistance) because removing one single trophic guild may have
113 cascading effects on the entire ecosystem. In contrast, the ecosystem may have a very high

114 resilience capacity because a low number of trophic guilds has to recover in order to provide
115 a complete recovery of the food web.

116

117 The method by Quezada-Romegialli et al. (2018) provided nuances about food web structure,
118 revealing intra-group variations. It also pointed out some contradictions between the feeding
119 mode and the trophic position of certain species, suggesting that the knowledge on their
120 feeding mode is poorly known or that their diet varies from one habitat to another. Indeed,
121 the polychaete *Ophelia borealis*, considered as a non-selective deposit-feeder, swallowing
122 sediment with its everted proboscis (in Parapar et al., 2021), had a trophic level above 2, such
123 as certain predators. The ecology of *Ophelia borealis* is poorly known but Fauchald & Jumars
124 (1979) believe that the opheliids can, to some extent, select their food sources. Nevertheless,
125 all species have the same general habit, in that all ingest sediment for the contained organic
126 matter. It is thus possible that *Ophelia borealis* focuses on an N-enriched food source but a
127 more in-depth study about its feeding ecology deserves to be performed.

128 *Asterias rubens*, *Ophiura ophiura* and *Pagurus bernhardus* had a trophic position below 2
129 which is not consistent with their predator and/or scavenger behaviour (Allen 1983, Ramsay
130 et al. 1997, Ruiz 2022). Instead, they display a trophic position equivalent to that of deposit-
131 feeders (e.g. *Gastrosaccus spinifer*, *Magelona filiformis*). Although little documented, it seems
132 that, in some cases, *Pagurus bernhardus* could be a filter feeder (Gerlach et al. 1976, Babu
133 1988) and/or a deposit feeder (Orton 1927). Similarly, a review by Ruiz (2022) indicates that
134 the diet of *Ophiura ophiura* may depend on food availability. It can probably feed on detritus
135 such as plant debris and organically enriched sediments when the food is limited. It is thus

136 possible that species with a certain degree of feeding plasticity switch toward organic matter
137 deposits because their preferential food source is very limited on sandbanks.

138 *Glycera tridactyla* had a remarkably high trophic position, equivalent to that of certain fish
139 such as *Echiichthys vipera* and *Hyperoplus lanceolatus*. Only large individuals of *Glycera*
140 *tridactyla* were observed during the present study. They could potentially feed on large preys
141 thanks to their strong jaws connected to venom glands (Böggemann 2002), producing a variety
142 of neurotoxic effects in both vertebrates and invertebrates (von Reumont et al. 2014).

143

144 **Seasonal variations** – Seasonal changes in the isotope composition of higher trophic-level
145 organisms are generally lower than for short-lived autotrophs (Cabana & Rasmussen 1996,
146 Nordström et al. 2009). Low variations have thus been described for benthic invertebrates
147 (Vizzini & Mazzola 2003, Carlier et al. 2007, Nordström et al. 2009) and fish (Sarà et al. 2002,
148 Vizzini & Mazzola 2003, Timmerman et al. 2020). In the Baltic Sea, Cabana & Rasmussen (1996)
149 and Nordström et al. (2009) showed that invertebrates and benthivorous predators had the
150 lowest values of $\delta^{15}\text{N}$ in the middle of the summer, particularly in August. At the La Palme
151 Lagoon (northwestern Mediterranean), Carlier et al. (2007) observed a decrease of the mean
152 $\delta^{13}\text{C}$ values in spring relative to autumn. Our findings suggest that similar seasonal variations
153 occurred on sandbanks. A decline of TA between autumn and spring was at the scale of the
154 community. According to Layman et al. (2007), such response suggests a lower feeding
155 diversity, smaller trophic niches and a lower feeding redundancy. The massive ingestion of
156 phytoplankton material in spring and the higher contribution of wPOM in the diet of primary
157 consumers may explain this result. The lower range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary

158 consumers could then cascade through the food web, affecting the stable isotope composition
159 of the whole community.

160

161 CONCLUSION

162 Sandbanks host a very simple but remarkable food web, largely supported by phytoplankton
163 production. Results indicate that, with the exception of food sources (wPOM and sPOM), the
164 structure of the benthic food web is relatively well-conserved over different seasons. This
165 stability in an area of intense natural disruption suggests that the benthic food web is able to
166 recover quickly after an anthropogenic disruption, for instance during the installation of
167 submarine cables (see Taormina et al., 2018 for a comprehensive review of potential impact
168 of wind farm installation). However, additional investigations on sandbank food web would
169 be necessary to validate this hypothesis. Future studies should now focus on other issues such
170 as the potential role of sandbanks as nursery areas for several fish species. Is food a limiting
171 factor? Are juveniles competing for food and space on sandbanks? Is their growth faster than
172 in other estuarine or coastal nursery grounds?

173

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180

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List of figures

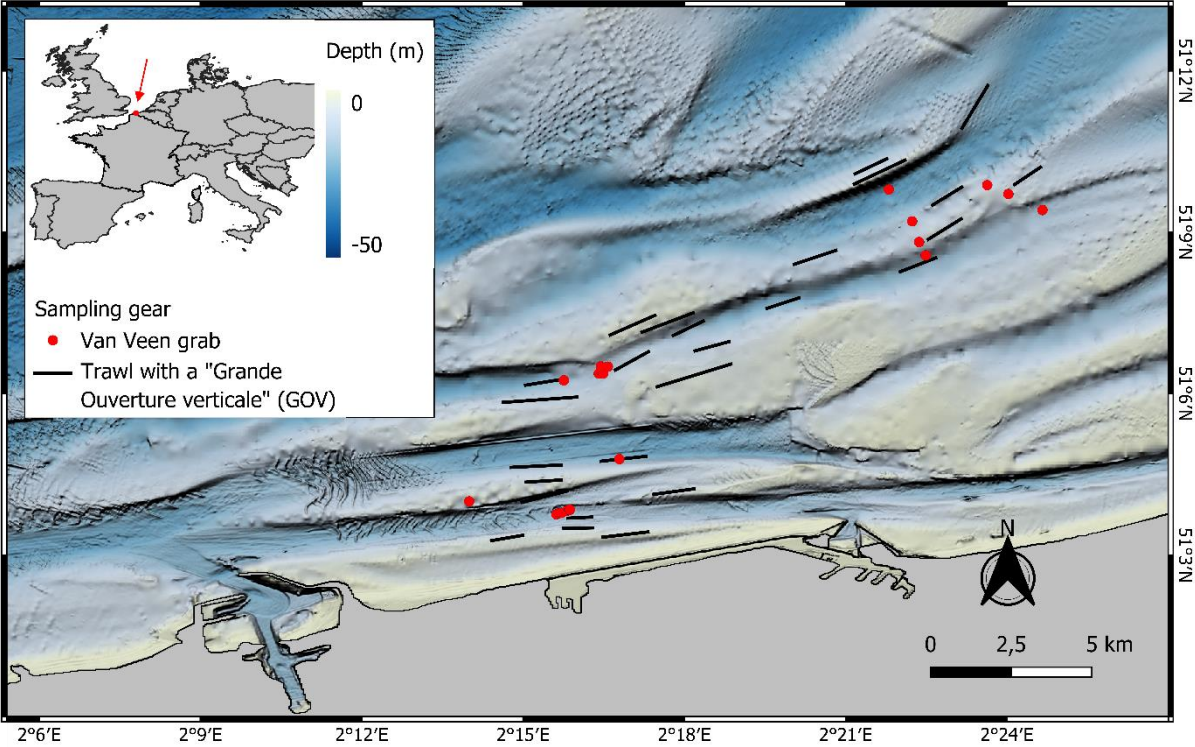


Figure 1 Map of the study area in the North of France. Red dots represent the location of grab samples whereas black lines represent the location of trawl hauls. Depth is shown by a gradient of colours.

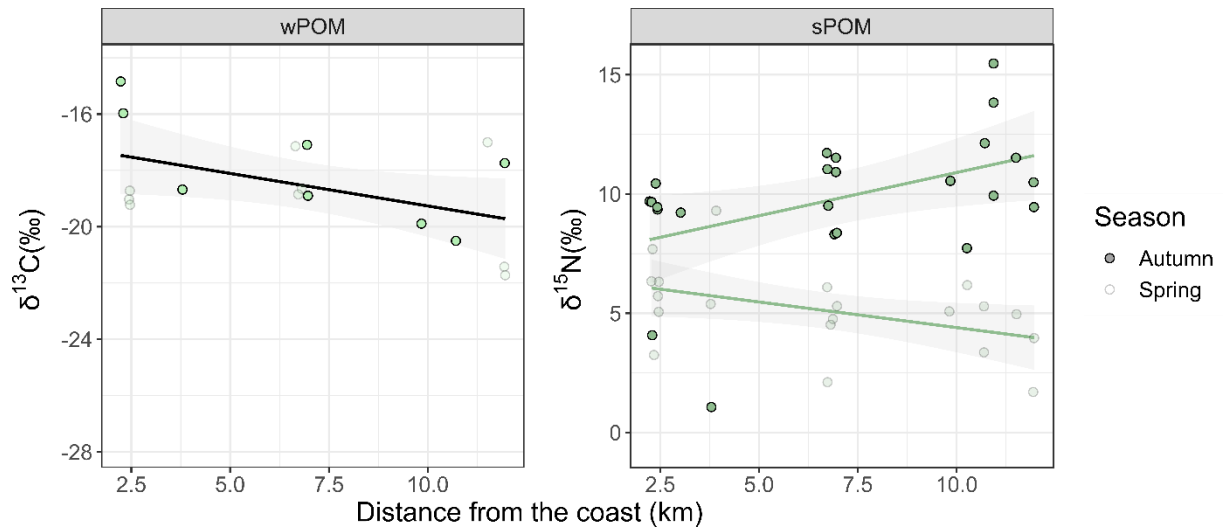


Figure 2 Variations of the $\delta^{13}\text{C}$ values of wPOM and $\delta^{15}\text{N}$ values of sPOM in relation with the distance from the coast. Only significant relationships have been displayed. The black line illustrates a significant effect of the distance on the $\delta^{13}\text{C}$ values of wPOM, whatever the season whereas the green lines illustrate a positive relationship with the distance from the coast in autumn and a negative relationship in spring.

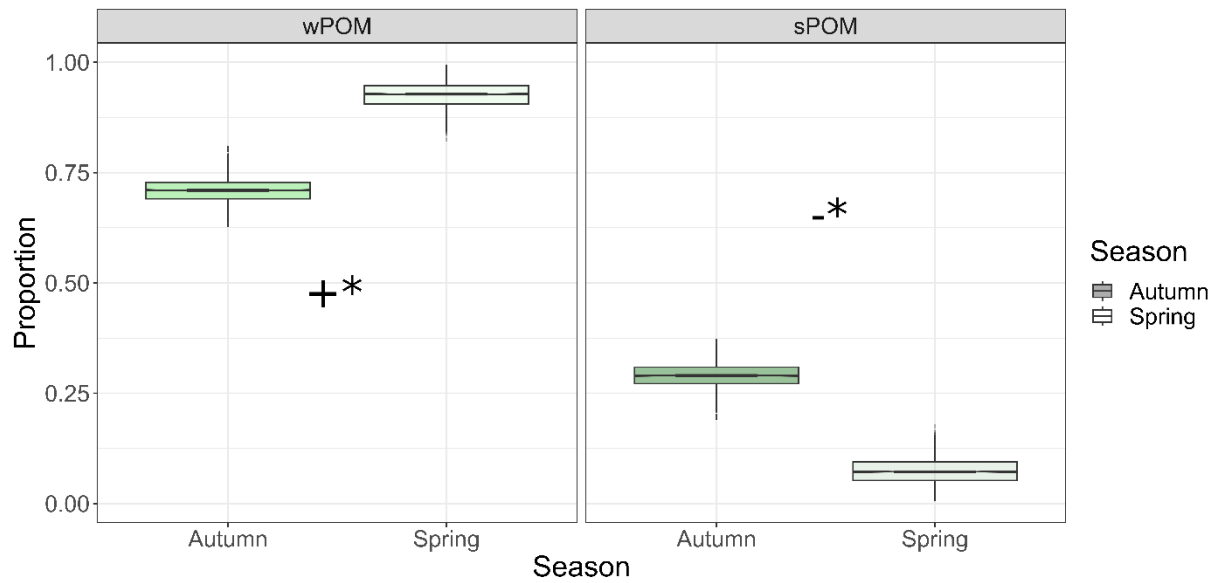


Figure 3 Potential contributions of sPOM and wPOM to the diet of deposit feeders in relation with the season. The contribution of each source has been calculated via a Bayesian Stable Isotope Mixing Model (SIMM). We considered that a seasonal trend (+ or -) occurred when the probability of difference was between 75% and 95%. We considered that seasonal differences were significant (+* or -*) beyond 95% of probability.

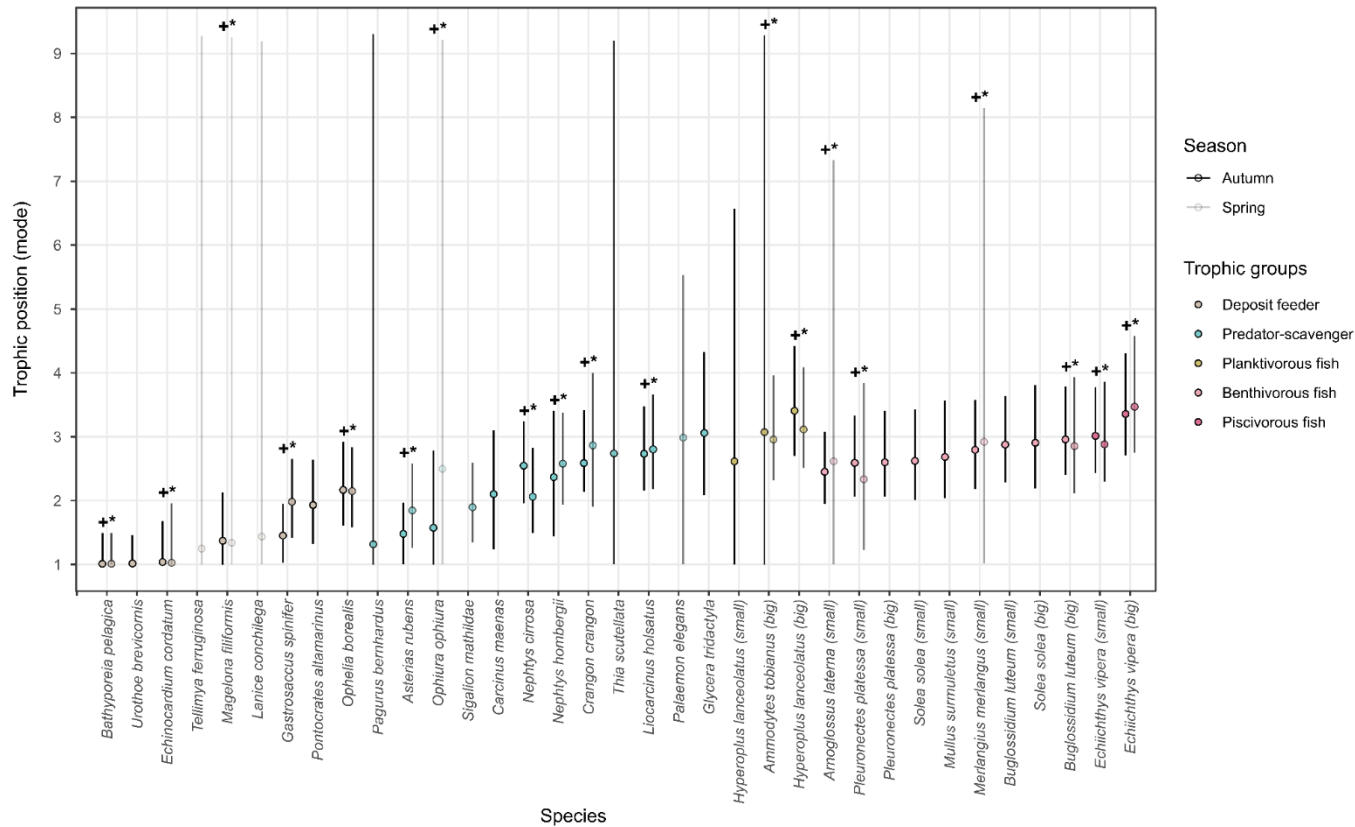


Figure 4 Trophic position of each species, calculated via the Bayesian approach proposed by Quezada-Romegialli et al. (2018). We considered that a seasonal trend (+ or -) occurred when the probability of difference was between 75% and 95%. We considered that seasonal differences were significant (+* or -*) beyond 95% of probability.. Suspension feeders are not included in this graph because their trophic position was unknown (used as baseline to compute the trophic position of the other species).

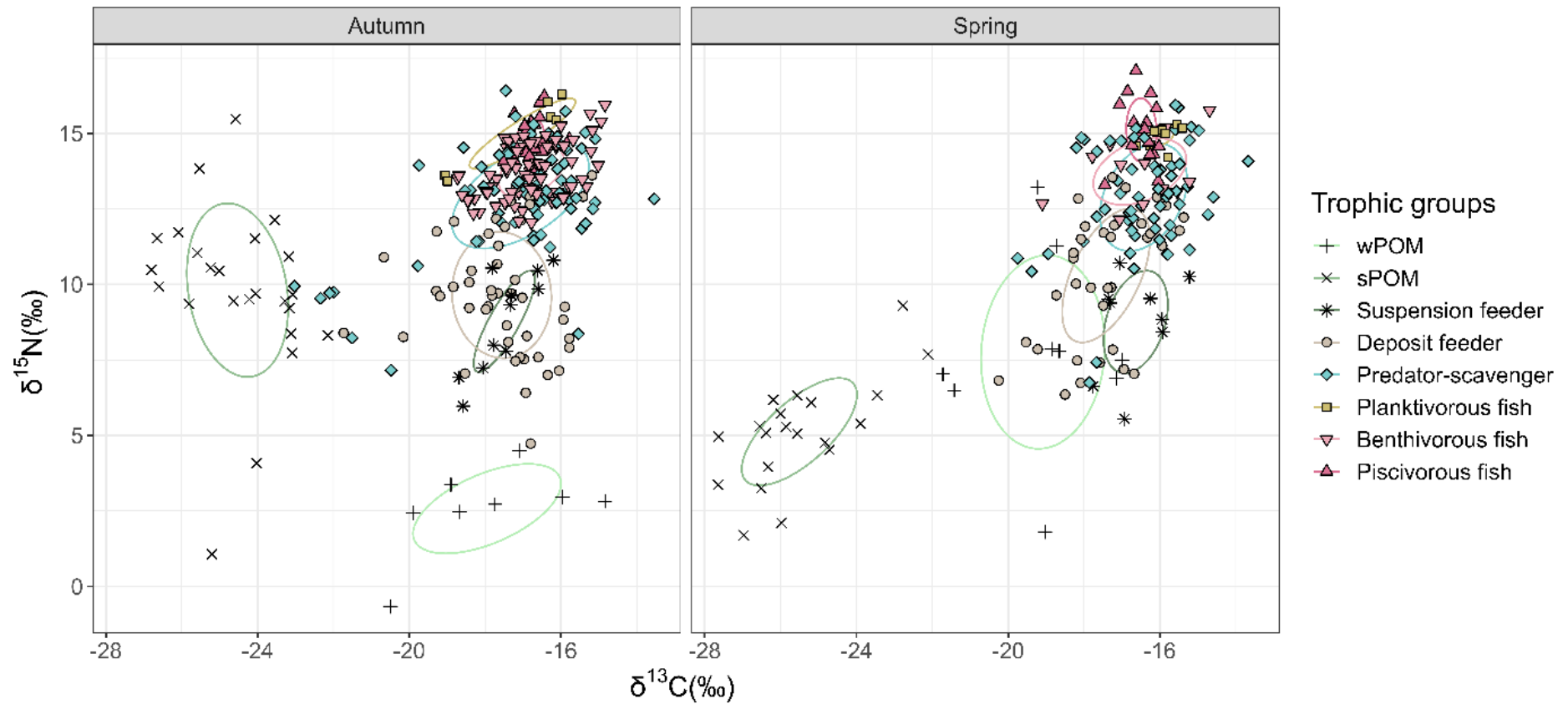


Figure 5 Biplots of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each trophic group, in autumn and spring. Dots correspond to raw data of each sample. Dashed lined circles represent the standard ellipses encompassing 40% of the variability in the isotopic composition of each trophic guild on the biplot.

[List of tables](#)

Table 1 Isotopic composition and characteristics of each species. The mode of the trophic position (TP) as well as the mean (\pm standard-deviation) values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as well as the number of samples per species (n) are provided for each season. An asterisk indicates that the $\delta^{13}\text{C}$ composition is from acidified samples. Colours in the leftmost column show the colour code used for all the figures presented in the present paper, at the exception of Figure 1.

Trophic group	Species	Autumn				Spring			
		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TP	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TP	n
wPOM	wPOM*	-18.0 \pm 1.9	2.6 \pm 1.5	/	8	-19.1 \pm 1.6	7.8 \pm 3.2	/	9
SPOM	SPOM*	-24.5 \pm 1.3	9.8 \pm 2.8	/	24	-25.5 \pm 1.5	5.1 \pm 1.8	/	20
Suspension feeder	<i>Donax vittatus</i>	-18.2 \pm 0.7	7.4 \pm 1.7	NA	3	/	/	/	0
	<i>Fabulina fabula</i>	-17.8 \pm 0.3	7.7 \pm 0.4	NA	3	-16.6 \pm 1.3	7.5 \pm 2.5	NA	3
	<i>Spisula solida</i>	-16.9 \pm 0.6	10.3 \pm 0.5	NA	5	-16.6 \pm 0.7	9.4 \pm 0.8	NA	6
Deposit feeder	<i>Bathyporeia pelagica</i>	-16.8 \pm 0.4	6.8 \pm 1.0	1.01	7	-17.5 \pm 0.6	7.3 \pm 0.4	1.01	6
	<i>Urothoe brevicornis</i>	-16.3 \pm 0.7	8.1 \pm 0.9	1.01	7	/	/	/	0
	<i>Echinocardium cordatum</i> *	-19.3 \pm 1.8	8.4 \pm 1.0	1.02	5	-19 \pm 1.1	7.8 \pm 1.4	1.03	5
	<i>Tellimya ferruginosa</i>	-17.5	9.3	1.29	1	/	/	/	0
	<i>Magelona filiformis</i>	-18.8 \pm 0.4	9.9 \pm 0.2	1.37	3	-18.7	9.6	1.36	1
	<i>Lanice conchilega</i>	-17.4	9.9	1.41	1	/	/	/	0
	<i>Gastrosaccus spinifer</i>	-17.7 \pm 0.4	10.1 \pm 1.3	1.46	15	-16.6 \pm 1.0	11.6 \pm 1.0	1.98	11
	<i>Pontocrates altamarinus</i>	-19.1 \pm 1.2	11.5 \pm 0.5	1.94	4	/	/	/	0
	<i>Ophelia borealis</i>	-16.7 \pm 0.9	12.3 \pm 1.2	2.21	8	-17.4 \pm 0.9	12.1 \pm 0.9	2.14	10
Predator-scavenger	<i>Pagurus bernhardus</i> *	-15.5	8.4	1.27	1	/	/	/	0
	<i>Asterias rubens</i>	-21.2 \pm 1.9	10.2 \pm 0.7	1.50	6	-18.7 \pm 0.9	11.2 \pm 0.7	1.83	5
	<i>Ophiura ophiura</i> *	-17.8 \pm 2.9	10.3 \pm 2.5	1.50	5	-14.6	12.9	2.52	1
	<i>Sigalion mathildae</i>	-15.7 \pm 0.3	11.4 \pm 0.5	1.91	5	/	/	/	0
	<i>Carcinus maenas</i>	-16.6 \pm 1.1	11.9 \pm 0.4	2.07	3	/	/	/	0
	<i>Nephtys hombergii</i>	-16.6 \pm 0.1	12.7 \pm 0.9	2.37	4	-15.8 \pm 1.0	13.4 \pm 0.8	2.56	8
	<i>Nephtys cirrosa</i>	-17.4 \pm 0.7	13.3 \pm 1.3	2.53	20	-16.6 \pm 0.6	11.9 \pm 1.9	2.06	19
	<i>Crangon crangon</i>	-16.0 \pm 0.8	13.6 \pm 0.7	2.65	16	-15.6 \pm 0.4	14.2 \pm 1.3	2.88	5

	<i>Liocarcinus holsatus</i>	-16.2±0.9	13.8±1.0	2.73	15	-16.6±1.1	14.1±1.1	2.81	17
	<i>Thia scutellata*</i>	-19.7	13.9	2.78	1	/	/	/	0
	<i>Palaemon elegans</i>	-15.7±0.8	14.5±1.7	2.99	3	/	/	/	0
	<i>Glycera tridactyla</i>	-16.3±0.6	14.9±1.0	3.08	4	/	/	/	0
Benthivorous fish	<i>Arnoglossus laterna</i> (small)	-16.7±0.6	13.0±0.3	2.43	15	-16.0±0.6	13.5±0.7	2.65	2
	<i>Pleuronectes platessa</i> (small)	-17.2±1.0	13.5±0.9	2.60	22	-16.2±0.9	12.7±0.6	2.33	3
	<i>Pleuronectes platessa</i> (big)	-15.8±0.6	13.5±0.8	2.62	9	/	/	/	0
	<i>Solea solea</i> (small)	-16.7±0.8	13.5±1.0	2.62	7	/	/	/	0
	<i>Mullus surmuletus</i> (small)	-17.0±1.0	13.8±1.1	2.67	7	/	/	/	0
	<i>Merlangius merlangus</i> (small)	-17.3±1.2	14.0±0.9	2.79	9	-15.3±0.9	14.5±1.8	2.91	2
	<i>Buglossidium luteum</i> (small)	-16.7±0.4	14.3±0.4	2.87	22	/	/	/	0
	<i>Solea solea</i> (big)	-15.8±0.4	14.4±0.8	2.92	5	/	/	/	0
	<i>Buglossidium luteum</i> (big)	-17.2±0.3	14.5±0.3	2.95	6	-17.4±1.2	14.1±0.9	2.83	5
Planktivorous fish	<i>Hyperoplus lanceolatus</i> (small)	-19.0±0.1	13.5±0.1	2.61	2	/	/	/	0
	<i>Ammodytes tobianus</i> (big)	-16.3	14.6	3.08	1	-16.2±0.3	14.6±0.4	3.00	4
	<i>Hyperoplus lanceolatus</i> (big)	-16.2±0.2	15.8±0.4	3.40	4	-15.8±0.3	15.1±0.1	3.20	6
Piscivorous fish	<i>Echiichthys vipera</i> (small)	-16.8±0.4	14.7±0.4	2.99	25	-16.4±0.4	14.4±0.6	2.92	9
	<i>Echiichthys vipera</i> (big)	-16.7±0.3	15.7±0.4	3.34	6	-16.6±0.3	16.0±0.6	3.50	7

1

[Supplementary data](#)

[Supplementary data 1](#)

Quality Control Data

std CBT

In-house standards used for normalisation correction

Sample ID	Weight (mg)	N2 Amp	%N	$\delta^{15}\text{N}$ vs. At. Air	CO2 Amp	%C	$\delta^{13}\text{C}$ vs. VPDB
std CBT	1.031	6 044	12.54	17.59	4 340	48.11	-25.61
std CBT	0.985	5 799	12.55	17.58	4 184	48.3	-25.57
std CBT	0.921	5 462	12.6	17.55	3 947	48.5	-25.63
std CBT	1.004	6 003	12.6	17.39	4 338	48.35	-25.55
std CBT	1.047	6 311	12.6	17.39	4 544	48.29	-25.56
std CBT	1.087	6 476	12.48	17.42	4 664	48.03	-25.56
Mean			12.56	17.49		48.26	-25.58
SD			0.05	0.1		0.17	0.03
std KCRN							

In-house standards used for normalisation correction

Sample ID	Weight (mg)	N2 Amp	%N	$\delta^{15}\text{N}$ vs. At. Air	CO2 Amp	%C	$\delta^{13}\text{C}$ vs. VPDB
std KCRN	2.052	2 952	3.08	1.44	6 760	40.62	-13.02
std KCRN	1.992	2 855	3.06	1.51	6 607	40.72	-13.05
std KCRN	1.958	2 812	3.06	1.55	6 569	41.02	-13.02
std KCRN	2.09	3 043	3.02	1.1	7 072	40.88	-13.01
std KCRN	1.994	2 875	3.02	0.95	6 792	40.8	-13.02
std KCRN	1.969	2 909	3.06	1.09	6 792	41.13	-12.96
Mean			3.05	1.27		40.86	-13.01
SD			0.02	0.25		0.19	0.03

std Deer*In-house standard used for precision purposes*

Sample ID	Weight (mg)	N2 Amp	%N	$\delta^{15}\text{N}$ vs. At. Air	CO2 Amp	%C	$\delta^{13}\text{C}$ vs. VPDB
std Deer	0.99	6 637	14.02	6.11	4 280	47.95	-20.02
std Deer	1.081	6 839	13.55	6.07	4 422	46.21	-19.86
std Deer	1.06	6 549	13.4	6.28	4 160	45.47	-19.95
std Deer	1.062	6 560	13.1	6.27	4 248	45.26	-19.96
std Deer	0.997	6 895	14.98	6.33	4 400	50.86	-20.04
	Mean		13.81	6.21		47.15	-19.96
	SD		0.73	0.12		2.33	0.07

Supplementary data 2 C:N ratio per species

Species	C :N ratio				N samples
	min	max	mean	sd	
<i>Ammodytes tobianus</i> (large)	3.2	3.3	3.3	0	5
<i>Arnoglossus laterna</i> (small)	3.1	3.5	3.3	0.1	17
<i>Asterias rubens</i>	4.4	7.9	5.8	1.2	11
<i>Bathyporeia pelagica</i>	4	5.2	4.5	0.4	13
<i>Buglossidium luteum</i> (large)	3.2	3.8	3.3	0.2	11
<i>Buglossidium luteum</i> (small)	3.1	3.4	3.2	0.1	22
<i>Carcinus maenas</i>	3.2	3.5	3.4	0.2	3
<i>Crangon crangon</i>	2.9	3.7	3.2	0.2	21
<i>Dicentrarchus labrax</i> (small)	3.2	3.4	3.3	0.1	4
<i>Donax vittatus</i>	2.9	3.8	3.3	0.4	3
<i>Echiichthys vipera</i> (large)	3.1	3.7	3.3	0.2	13
<i>Echiichthys vipera</i> (small)	3.1	3.4	3.2	0.1	34
<i>Echinocardium cordatum</i>	2.2	8.2	4.9	1.9	10
<i>Fabulina fabula</i>	3.3	4.5	3.8	0.5	6
<i>Gastrosaccus spinifer</i>	3.3	5.6	3.8	0.5	26
<i>Glycera tridactyla</i>	3.2	4.3	3.8	0.5	4
<i>Hyperoplus lanceolatus</i> (large)	3.1	3.5	3.2	0.1	10
<i>Hyperoplus lanceolatus</i> (small)	3.2	3.4	3.3	0.2	2
<i>Lanice conchilega</i>	4.7	4.7	4.7	NA	1
<i>Liocarcinus holsatus</i>	3	3.7	3.2	0.1	32
<i>Loligo vulgaris</i>	3.8	3.8	3.8	NA	1
<i>Magelona filiformis</i>	3.8	3.9	3.8	0.1	4
<i>Merlangius merlangus</i> (small)	3.1	3.3	3.2	0.1	11
<i>Mullus surmuletus</i> (small)	3.1	3.3	3.2	0.1	7
<i>Nephtys cirrosa</i>	2.7	4.5	3.7	0.3	39
<i>Nephtys hombergii</i>	3.1	3.9	3.7	0.2	12
<i>Ophelia borealis</i>	2.7	3.8	3.2	0.3	18
<i>Ophiura ophiura</i>	0.4	6.7	3.8	2.1	6
wPOM	6	13.5	9.8	2.4	17
<i>Pagurus bernhardus</i>	4.9	7.3	5.9	0.9	6
<i>Palaemon elegans</i>	3.3	3.5	3.4	0.1	3
<i>Pleuronectes platessa</i> (large)	3	3.3	3.2	0.1	9
<i>Pleuronectes platessa</i> (small)	3.1	3.4	3.3	0.1	25
<i>Pontocrates altamarinus</i>	3.8	6	4.4	1	4
sPOM	2.6	16	8.5	3	44
<i>Sigalion mathildae</i>	3.5	3.7	3.6	0.1	5
<i>Solea solea</i> (large)	3.1	3.3	3.2	0.1	5
<i>Solea solea</i> (small)	3.2	3.3	3.2	0.1	7
<i>Spisula solida</i>	3.4	4.5	3.8	0.4	11
<i>Sprattus sprattus</i> (small)	3.2	3.5	3.3	0.1	7

<i>Tellimya ferruginosa</i>	3.8	3.8	3.8	NA	1
<i>Thia scutellata</i>	4.7	4.7	4.7	NA	1
<i>Trachurus trachurus</i> (large)	3.1	3.4	3.2	0.1	7
<i>Trachurus trachurus</i> (small)	3	5.3	3.3	0.5	20
<i>Urothoe brevicornis</i>	4.1	6	5.1	0.6	9
