



Seasonal dynamic of the benthic food web in subtidal sandbanks

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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.

KEY WORDS: Macrobenthos · Invertebrates · Fish · Trophic web · Isotopic metrics · Soft sediments · North Sea

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1. INTRODUCTION

Submarine sandbanks are prevalent worldwide and are common in the southern North Sea, western English Channel, Iroise Sea and Irish Sea. Sandbanks are oriented parallel to the main tidal current and can be 10 km long and up to 10 m 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 sandbank 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,

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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 habitats most threatened 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 made to increase the knowledge of this ecosystem and its sensitivity.

In the southern North Sea, sandbanks are characterised by a remarkably high phytoplankton production and by massive 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 m^{-2}) as well as low abundances (100 to 400 individuals m^{-2}), depending on the study and the specific location (Desroy et al. 2003, Van Hoey et al. 2004). Robert et al. (2021) recently revealed that macrobenthic communities vary depending on (1) the type of bedform (sandbank, barchan dune and transversal dune) and (2) the season (autumn and spring). However, species composition and diversity (including biological trait 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, to date, never been investigated.

Stable isotope analyses, and especially the light/heavy isotopes ratio of C ($\delta^{13}C$) and N ($\delta^{15}N$), 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 $\delta^{13}C$ values as a proxy of food source (Post 2002, Bearhop et al. 2004) and $\delta^{15}N$ 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 (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. preprint doi:10.48550/arXiv.2306.07817). All these methods can be performed using 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. preprint doi:10.48550/arXiv.2306.07817) 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 were tested:

H1. Sandbanks display a low number of trophic guilds with respect to the poor diversity of both macrobenthic (Desroy et al. 2003, 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 & Dezécache 2020) and the very low sedimentary particulate 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 AND METHODS

2.1. Study site

The present study focused on an 80 km² area located on the Flanders banks, offshore from Dunkirk harbour (Fig. 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, consists of shallow waters,

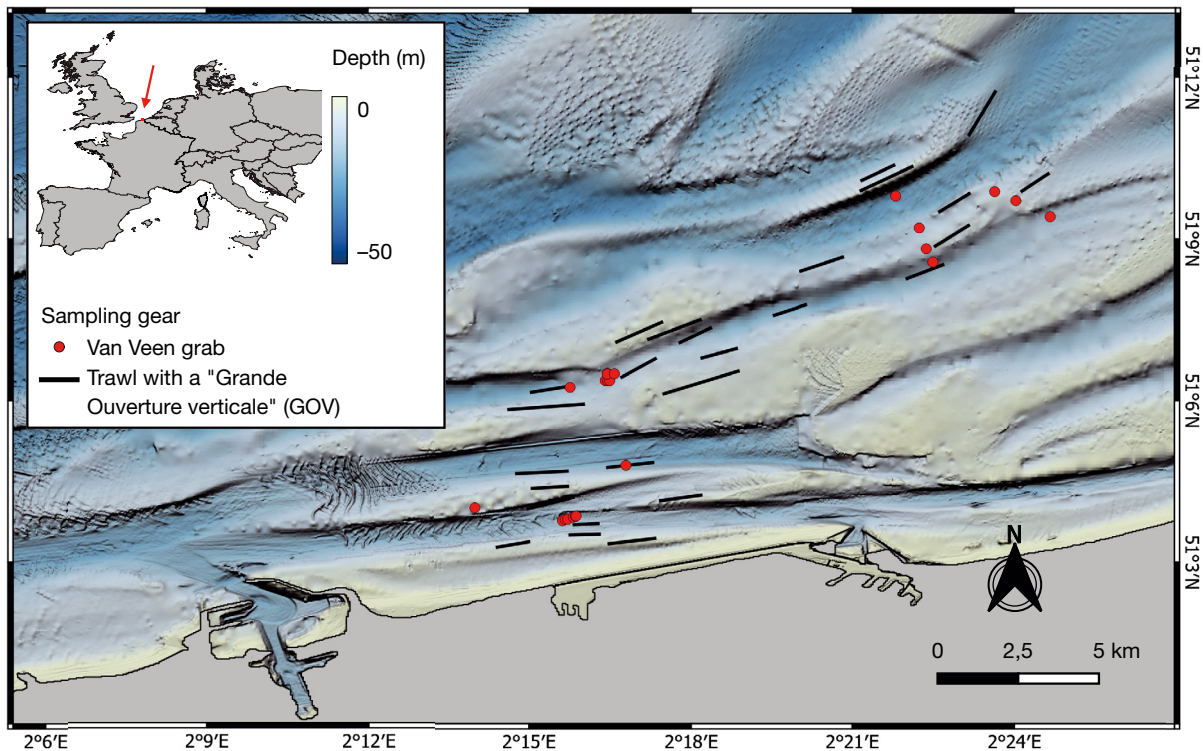


Fig. 1. Study area in the north of France

with a maximum depth of 40 m. It is typified by a wide variety of bedforms, such as large sandbanks extending between 8 and 32 km in 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 et al. (2003). A recent paper also describes 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) at 23 stations distributed between the trough and the crest of 3 kinds of bedform: 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 obtained at each station: 1 for the analysis of the stable isotope composition of the macrobenthic organisms and 1 for the stable isotope composition of the sediment.

wPOM was collected in the water column with a Niskin bottle, above each kind of dune and in the reference area. Megabenthic organisms (>10 mm) and fish were collected using a commercial trawl with a 'Grande Ouverture Verticale', equipped with a reduced cod-end mesh of 20 mm, stretched in order to improve the catch of juveniles and small fish. A total of 26 trawl hauls were performed between the trough and the crest of 3 sandbanks (Fig. 1). Macrofauna, megafauna, fish and water samples for the analysis of stable isotopes were all frozen onboard at -20°C. 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 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 were selected for stable isotopic composition analyses (see 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 (0.1 mg). All samples were finally rinsed with Milli-Q water, freeze-dried for 24 h and powdered manually.

For the analysis of the stable isotope composition of sPOM, sediment samples 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 2 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 samples and the $\delta^{15}\text{N}$ values from untreated subsamples were later combined to obtain valid isotope signatures (i.e. undisturbed by CaCO_3 and acidification). Species that received this treatment are indicated in Table 1.

Around 1 mg of powder was weighed for each sample and placed into tin capsules. Samples were analysed for isotopic composition at Cornell University (USA) 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 10 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 ml^{-1} for nitrogen and carbon. Results from these calibrations are provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m735p027_supp.pdf.

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):

$$\delta^j E = \frac{(^i E/^j E)_P - (^i E/^j E)_{std}}{(^i E/^j E)} \quad (1)$$

where $^i E$ and $^j E$ are the heavier (higher atomic mass i) and lighter (lower atomic mass j) isotopes of element E . The isotope $^i E$ in substance P was specified by $^i EP$ (see the guidelines and recommended terms for expression of stable isotope-ratio and gas-ratio measurement results in Coplen 2011). The C/N ratios are shown in Table S2.

2.4. Data analyses

2.4.1. Potential sources of C and N

Spatio-temporal variations. A permutational multivariate ANOVA (PERMANOVA, Anderson 2005) was used to determine whether the stable isotope composition of sPOM and wPOM varied in relation to 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 using 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 into 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 contributions of sPOM and wPOM as food sources for primary consumers (i.e. deposit feeders). The simmr package (Parnell & Inger 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 (TDFs) between primary consumers and primary producers were unknown, 'generic' values provided by the meta-analysis of McCutchan et al. (2003) were employed. The TDFs between basal resources (wPOM and sPOM)

and primary consumers were set to $1.3 \pm 0.3\%$ for $\delta^{13}\text{C}$ and $2.9 \pm 0.32\%$ for $\delta^{15}\text{N}$.

A diagnostic procedure (see Govan et al. preprint doi:10.48550/arXiv.2306.07817 for details) was used for each of the computed models to check their robustness (not shown). In particular, 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 considered.

One independent model was run for each season and seasonal differences were assessed by calculating the probability of Bayesian posterior distribution in autumn being smaller/larger than in spring. We assumed 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%.

2.4.2. Invertebrates and fish consumers

Identification of trophic groups. Trophic groups were identified using existing databases such as BIOTIC for invertebrates (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-reviewed papers.

The trophic position of each species was also calculated for each season via the Bayesian approach proposed by Quezada-Romegialli et al. (2018) and implemented in the tRophicPosition 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 & 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, the 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 a 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 to (1) the season, (2) the trophic group and (3) 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 (NR), the $\delta^{13}\text{C}$ range (CR) and the TA. NR was the distance between the 2 species with the most enriched and most depleted $\delta^{15}\text{N}$ values (i.e. maximum $\delta^{15}\text{N}$ – minimum $\delta^{15}\text{N}$). CR was the distance between the 2 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 means that there is a diversification at the basis of the food web with a greater number of food sources. The TA is represented by the convex hull area encompassing all species in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplot. This measure is 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 3 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 MCMC simulation. Posterior estimates allowed statistical comparisons between the seasons. We applied the same rule to detect tendencies and statistical differences as we did for the Bayesian SIMM: we assumed that a seasonal tendency occurred at a probability between 75 and 95% and that a significant difference occurred above 95% probability.

3. RESULTS

3.1. Potential sources of C and N

3.1.1. General characteristics

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

3.1.2. Variations depending on the season, depth and distance from the coast

The PERMANOVA analysis revealed a significant effect of season on the multivariate stable isotope composition of wPOM ($p = 0.003$). Conducting a linear regression model showed that $\delta^{13}\text{C}$ values decreased significantly with increasing distance from the coast ($p = 0.022$; Fig. 2). Conversely, season ($p = 0.098$) had no significant effect on the $\delta^{13}\text{C}$ values. Significantly higher values of $\delta^{15}\text{N}$ were observed in spring ($7.8 \pm 3.2\text{‰}$) compared to autumn ($2.6 \pm 1.5\text{‰}$) ($p = 0.005$) but no effect of distance from coast ($p = 0.403$) was observed.

A significant effect of season (PERMANOVA, $p = 0.001$) as well as a significant interaction between the factor season and the distance from the coast (PERMANOVA, $p = 0.003$) 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 ($-25.5 \pm 1.5\text{‰}$) compared to autumn ($-24.5 \pm 1.3\text{‰}$) ($p = 0.016$). The distance also had a negative effect on $\delta^{13}\text{C}$ values ($p = 0.011$), regardless of the season. Season also negatively influenced the $\delta^{15}\text{N}$ of sPOM, with lower values in spring ($p < 0.001$): the $\delta^{15}\text{N}$ was $5.1 \pm 1.8\text{‰}$, whereas it was $9.8 \pm 2.8\text{‰}$ in autumn. A significant interaction between the factor season and the distance from the coast was also observed via the linear regression model ($p = 0.004$). 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 (Fig. 2).

3.1.3. Contribution to the diet of primary consumers

The output of the Bayesian SIMM indicated that wPOM was the main contributor to the diet of deposit feeders. An overall contribution of up to 70% was found for wPOM against less than 30% for sPOM. Nevertheless, seasonal variations occurred (Fig. 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 2 seasons.

3.2. Invertebrates and fish consumers

3.2.1. Characteristics of trophic groups

A total of 6 trophic groups were defined according to literature data in addition to the 2 groups of primary producers (wPOM and sPOM) (Fig. 4, Table 1). They differed in their isotopic composition from a multivariate point of view (PERMANOVA, $p = 0.001$).

The suspension feeders *Donax vittatus*, *Fabulina fabula* and *Spisula solida* were grouped together and used as baseline for the calculation of the trophic

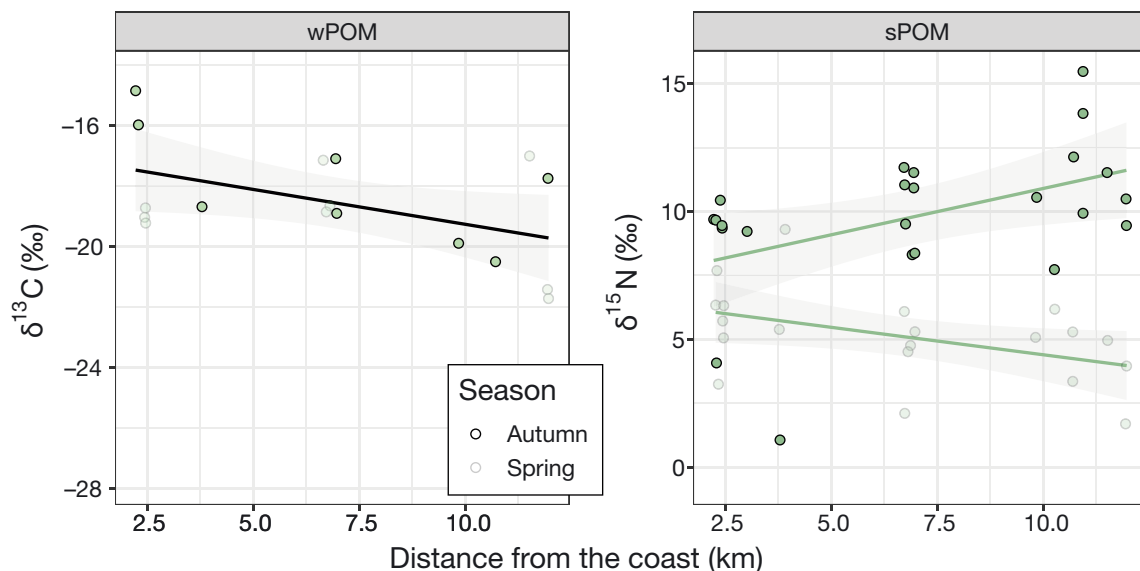


Fig. 2. Variations of the $\delta^{13}\text{C}$ values of seawater particulate organic matter (wPOM) and $\delta^{15}\text{N}$ values of sedimentary POM (sPOM) in relation to distance from the coast. Only significant relationships are displayed. Black line: Significant effect of distance on the $\delta^{13}\text{C}$ values of wPOM, irrespective of season; green lines: positive relationship with the distance from the coast in autumn and a negative relationship in spring

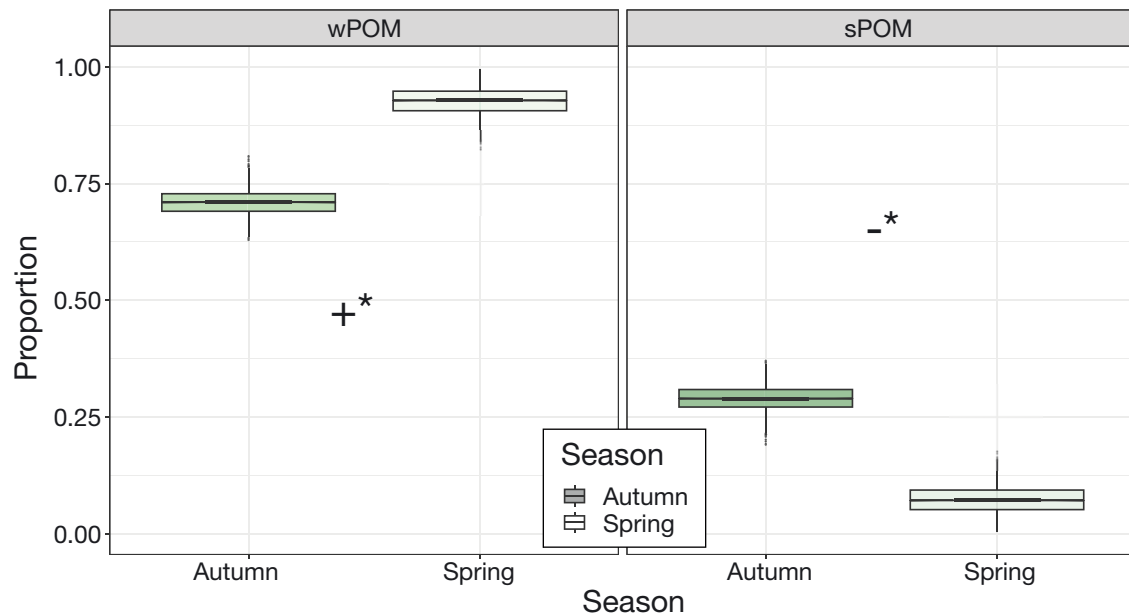


Fig. 3. Potential contributions of sPOM and wPOM to the diet of deposit feeders in relation to season. The contribution of each source was calculated via a Bayesian stable isotope mixing model (SIMM). We assumed that a seasonal trend (+ or –) occurred when the probability of difference was between 75 and 95%. We considered seasonal differences significant (+* or –*) at a probability over 95%

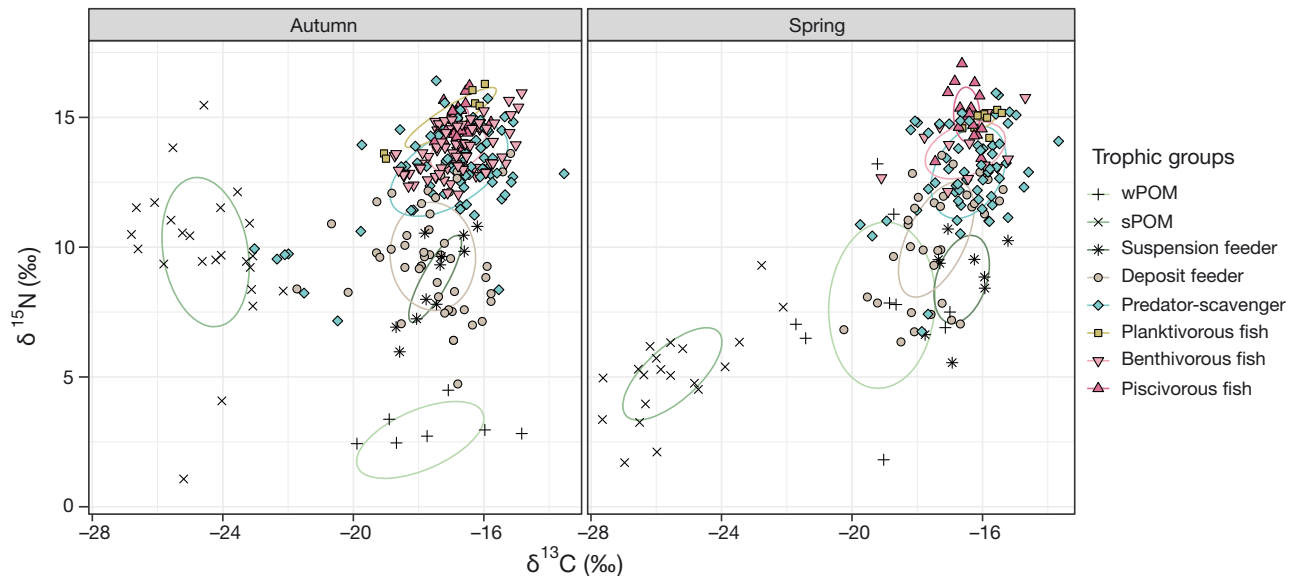


Fig. 4. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each trophic group, in autumn and spring. Dots: data of each sample; ellipses: standard ellipses encompassing 40% of the variability in the isotopic composition of each trophic guild on the biplot

position of the other species. They represented 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 $-17.1 \pm 0.9\text{‰}$ whereas mean $\delta^{15}\text{N}$ was $8.8 \pm 1.6\text{‰}$.

Deposit feeders made up 83% of the biomass. They were comprised of 9 species: *Bathyporeia pelagica*, *Echinocardium cordatum*, *Urothoe brevicornis*, *Telli-*

mya 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. *B. pelagica*, *E. cordatum* and *U. brevicornis* showed the lowest trophic positions, around 1, whereas *T. ferruginosa*, *M. filiformis*, *L. conchilega*, *G. spinifer* and *P. altamarinus* displayed a trophic posi-

Table 1. Isotopic composition and characteristics of each species. The mode of the trophic position (TP) and the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SD), as well as the number of samples per species (n) are provided for each season. na: not applicable

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 ^a	-18.0 \pm 1.9	2.6 \pm 1.5	/	8	-19.1 \pm 1.6	7.8 \pm 3.2	/	9
sPOM	sPOM ^a	-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> ^a	-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> ^a	-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> ^a	-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 \pm 0.9	13.8 \pm 1.0	2.73	15	-16.6 \pm 1.1	14.1 \pm 1.1	2.81	17
	<i>Thia scutellata</i> ^a	-19.7	13.9	2.78	1	/	/	/	0
	<i>Palaemon elegans</i>	-15.7 \pm 0.8	14.5 \pm 1.7	2.99	3	/	/	/	0
	<i>Glycera tridactyla</i>	-16.3 \pm 0.6	14.9 \pm 1.0	3.08	4	/	/	/	0
Benthivorous fish	<i>Arnoglossus laterna</i> (small)	-16.7 \pm 0.6	13.0 \pm 0.3	2.43	15	-16.0 \pm 0.6	13.5 \pm 0.7	2.65	2
	<i>Pleuronectes platessa</i> (small)	-17.2 \pm 1.0	13.5 \pm 0.9	2.60	22	-16.2 \pm 0.9	12.7 \pm 0.6	2.33	3
	<i>Pleuronectes platessa</i> (large)	-15.8 \pm 0.6	13.5 \pm 0.8	2.62	9	/	/	/	0
	<i>Solea solea</i> (small)	-16.7 \pm 0.8	13.5 \pm 1.0	2.62	7	/	/	/	0
	<i>Mullus surmuletus</i> (small)	-17.0 \pm 1.0	13.8 \pm 1.1	2.67	7	/	/	/	0
	<i>Merlangius merlangus</i> (small)	-17.3 \pm 1.2	14.0 \pm 0.9	2.79	9	-15.3 \pm 0.9	14.5 \pm 1.8	2.91	2
	<i>Buglossidium luteum</i> (small)	-16.7 \pm 0.4	14.3 \pm 0.4	2.87	22	/	/	/	0
	<i>Solea solea</i> (large)	-15.8 \pm 0.4	14.4 \pm 0.8	2.92	5	/	/	/	0
	<i>Buglossidium luteum</i> (large)	-17.2 \pm 0.3	14.5 \pm 0.3	2.95	6	-17.4 \pm 1.2	14.1 \pm 0.9	2.83	5
Planktivorous fish	<i>Hyperoplus lanceolatus</i> (small)	-19.0 \pm 0.1	13.5 \pm 0.1	2.61	2	/	/	/	0
	<i>Ammodytes tobianus</i> (large)	-16.3	14.6	3.08	1	-16.2 \pm 0.3	14.6 \pm 0.4	3.00	4
	<i>Hyperoplus lanceolatus</i> (large)	-16.2 \pm 0.2	15.8 \pm 0.4	3.40	4	-15.8 \pm 0.3	15.1 \pm 0.1	3.20	6
Piscivorous fish	<i>Echiichthys vipera</i> (small)	-16.8 \pm 0.4	14.7 \pm 0.4	2.99	25	-16.4 \pm 0.4	14.4 \pm 0.6	2.92	9
	<i>Echiichthys vipera</i> (large)	-16.7 \pm 0.3	15.7 \pm 0.4	3.34	6	-16.6 \pm 0.3	16.0 \pm 0.6	3.50	7

^a $\delta^{13}\text{C}$ composition is from acidified samples

tion of around 1.5. *O. borealis* showed the highest trophic position, above 2, irrespective of season.

Predator-scavengers represented almost 12% of the biomass and included 12 species: *Pagurus bernhardus*, *Asterias rubens*, *Ophiura ophiura*, *Sigalion mathildae*, *Carcinus maenas*, *Nephtys cirrosa*, *N. hombergii*, *Crangon crangon*, *Liocarcinus holsatus*, *Thia scutellata*, *Palaemon elegans* and *Glycera tridactyla*. Their average isotopic composition was $-16.8 \pm 1.6\text{‰}$ 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*, *A. rubens*, *O. ophiura* and *S. mathildae* had a trophic position below 2, whereas *Carcinus maenas*, *N. cirrosa*, *N. hombergii*, *Crangon crangon*, *L. holsatus*, *T. scutellata* and *Palaemon elegans* had a trophic position between 2 and 3. Finally, *G. tridactyla* exhibited the highest trophic position among predator-scavengers with a value above 3.

Planktivorous fish made a low contribution to the food web with 0.03% of the recorded biomass. They

were represented by 2 sand eel species: *Hyperoplus lanceolatus* (small and large individuals) and *Ammodytes tobianus* (only large individuals were 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 represented 0.18% of the biomass and were composed of 6 species: *Arnoglossus laterna* (only small individuals were collected), *Pleuronectes platessa* (small and large), *Solea solea* (small and large), *Mullus surmuletus* (only small), *Merlangius merlangus* (small) and *Buglossidium luteum* (small and large). 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 made up 0.02% of the biomass and were represented by a single species: *Echiichthys vipera* (large and small individuals). Its mean $\delta^{13}\text{C}$ value was $-16.7 \pm 0.4\text{‰}$, whereas the mean $\delta^{15}\text{N}$ value was $15 \pm 0.8\text{‰}$. The trophic position of *Echiichthys vipera* was equivalent to 3.1.

3.2.2. Seasonal variations

The biplot (Fig. 4) and the PERMANOVA analysis (not shown) did not reveal any significant seasonal effect at the scale of the community ($p = 0.071$) nor at the scale of each trophic group (not shown). From a univariate point of view, a seasonal trend was detected: it was manifested by a decrease in the TA between autumn and spring, at the scale of the community (probability = 0.85). This effect was no longer detected when the univariate indices for each trophic group were calculated (probability < 0.75, irrespective of the indices and the trophic group).

Seasonal variations were also relatively low regarding the trophic position of each species (Fig. 5). A significant trend (probability of 1 for each species hereafter) in the trophic position was detected for *Gastrosaccus spinifer*, *Asterias rubens*, *O. ophiura*, *N. hombergii*, *C. crangon*, *L. holsatus*, *Arnoglossus laterna* (small), *M. merlangus* (small) and *E. vipera* (large). Conversely, a significant but small decrease

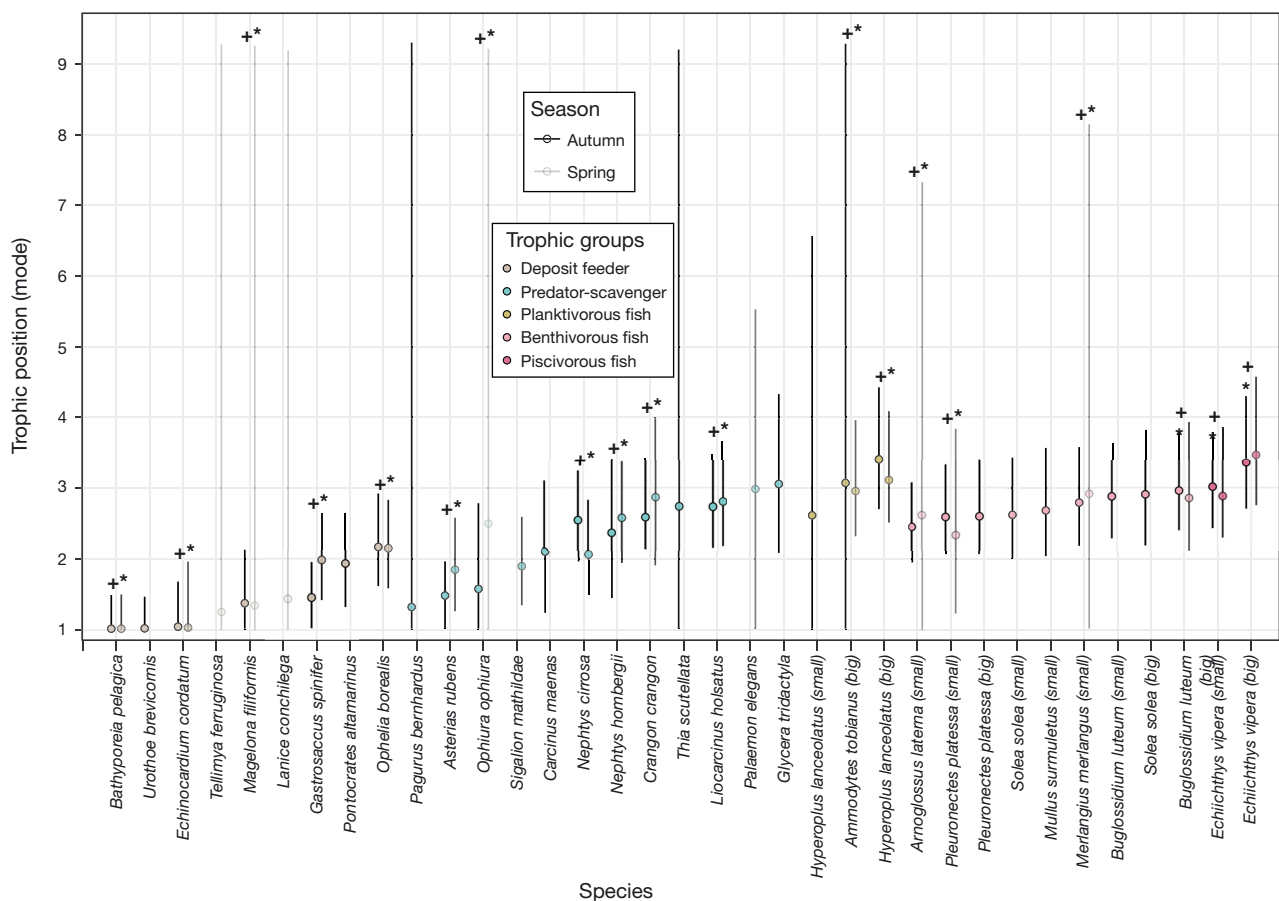


Fig. 5. Trophic position of each species, calculated via the Bayesian approach proposed by Quezada-Romegialli et al. (2018). We assumed that a seasonal trend (+ or -) occurred when the probability of difference was between 75 and 95%. We considered seasonal differences significant (+* or -*) at a probability over 95%. 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)

of trophic position was observed for *Bathyporeia pelagica*, *Echinocardium cordatum*, *Magelona filiformis*, *Ophelia borealis*, *N. cirrosa*, *Ammodytes tobianus* (large), *P. platessa* (small), *B. luteum* (large) and *E. vipera* (small).

4. DISCUSSION

The present study represents, to our knowledge, the first investigation of the benthic food web of subtidal sandbank areas. It is expected that the sound scientific knowledge it provides will be useful for further understanding the ecological functioning of these habitats and depicting changes linked to anthropogenic pressures (including climate change).

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

4.1.1. The isotopic composition of food sources varies depending on the season and distance from the coast

Higher $\delta^{13}\text{C}$ values were recorded in autumn relative to spring, both for wPOM and sPOM. Lower $\delta^{15}\text{N}$ values of wPOM were also observed in autumn. It is well known that carbon sources (and especially wPOM) display seasonal variations in their isotopic composition in marine, estuarine and freshwater systems (e.g. Zohary et al. 1994, France et al. 1997, Bouaziz et al. 2021) so that our results were consistent with those of several other studies. Carbon and nitrogen enrichments are generally due to the selective consumption of dissolved inorganic carbon (DIC) and dissolved inorganic nitrogen (DIN) during phytoplankton blooms: ^{12}C and ^{14}N are primarily consumed while ^{13}C and ^{15}N accumulate. Some studies also suggest that an increase in $\delta^{13}\text{C}$ results from reduced isotopic fractionation at high cell densities or growth rates, or in relation to day length (Zohary et al. 1994, France et al. 1997, Brandenburg et al. 2022). A shift in the species composition can also be responsible for seasonal variations of $\delta^{15}\text{N}$ values, because nitrogen isotope composition can vary greatly among phytoplankton taxa (Vuorio et al. 2006) and because a larger proportion of heterotrophic organisms usually induces higher $\delta^{15}\text{N}$ values of wPOM (Agurto 2007, Aberle et al. 2010).

In general, terrestrial organic matter has lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to marine organic matter (Vizzini et al. 2005), which can induce an increase in

the isotopic ratio toward the offshore. Here, both wPOM (in both spring and autumn) and sPOM (in spring only) showed higher values close to the coast compared to offshore stations, which is a different trend compared to what is usually observed (see Vizzini et al. 2005). Three processes could be responsible for these results. First, due to particular hydrodynamic conditions in sandbank areas, water masses with a terrigenous origin can occur in the offshore area, whereas the coastal area may exhibit marine characteristics. Secondly, it is possible that the ^{13}C - and ^{15}N -enrichment in the coastal area results from pollution and contaminants released by the manufacturing industries, primarily metallurgical, chemical and petrochemical, that surround Dunkirk (Dewarumez & Davoult 1997, Desroy et al. 2003). Thirdly, it is possible that the isotopic composition of sPOM varies depending on the substrate, in relation to the biogeochemical process. In the Tagus estuary, Sampaio et al. (2010) found that sediment grain size might act as a confounding factor in the analysis of nitrogen: areas with finer sediments showed the highest $\delta^{15}\text{N}$ values. Hence, it is possible that fine changes in sediment grain size occur at the scale of our study area and that they induce higher isotopic ratios of sPOM closer to the coast than at the offshore stations.

4.1.2. Importance of benthopelagic coupling

The outputs of the mixing models clearly indicated that wPOM is the main source of carbon and nitrogen in the benthic food web. The southern North Sea is typified by high phytoplankton production and unusually large blooms between March and June (Schapira et al. 2008). Their intensity and species composition vary from one year to another but the dominant species are generally *Phaeocystis globosa* (Prymnesiophyceae) and the diatoms *Chaetoceros* sp., *Thalassionema nitzschioides*, *Paralia marina*, *Guinardia striata*, *G. delicatula* and *Rhizosolenia imbricata*, as well as the diatom *Skeletonema costatum* (Lefebvre et al. 2011). During massive *Phaeocystis* blooms, chlorophyll *a* concentrations in the water column may reach values up to $50 \mu\text{g l}^{-1}$, which can even change water viscosity (Seuront et al. 2006). The decline of the bloom is characterised by massive foam formation that accumulates on the shore. Based on results from the present study and existing knowledge, one can hypothesise that the wPOM is mainly composed of phytoplankton cells that induce a large injection of carbon and nitrogen into benthic ecosystems (Alderkamp et al. 2007) in this area where

other primary producers—macroalgae and micro-phytobenthos—are considered absent due to high water turbidity. This is in line with the observations made by Franco et al. (2008) in permeable and fine grain depositional sediments of the Southern Bight of the North Sea. The results from the present study are also in accordance with those of Kopp et al. (2015) in the eastern English Channel, where stronger benthic–pelagic coupling was found in shallow coastal areas, mostly due to a reorganisation of the upper consumers relative to 2 trophic pathways, benthic carbon sources being available to pelagic consumers and, reciprocally, pelagic sources becoming accessible to benthic species.

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

4.2. A very simplistic food web structure

The mass ratio hypothesis suggests that the influence of a species on key ecosystem functions is proportional to its biomass (Garnier et al. 2004, 2007, Vile et al. 2006, Mokany et al. 2008). From this principle, one can hypothesise that the food web of sandbanks is very simple because most of the biomass belonged to 3 trophic groups only: deposit feeders, predator-scavengers or suspension feeders. This simple food web also bears similarities with the macrotidal sandy beaches of the Bay of Douarnenez (Brittany, France) described by Quillien et al. (2016). Although the authors did not split species into trophic guilds and macroalgae were not present in our study area, their isotopic biplot was very similar to that of the present study. Our results are also consistent with those of Nordström et al. (2009) in a study conducted in sandy bays of the Åland Islands (Baltic Sea), where 21 macrobenthic species were found, split into 3

trophic guilds. Sandbanks are covered by marine dunes and megaripples, known to migrate at a high frequency (Ernstsen et al. 2004, Ferret et al. 2010, Bolle et al. 2013): in the Dunkirk area, dune movements range between 53.40 and 64.45 m yr⁻¹ in the coastal area and between 18.53 and 54.58 m yr⁻¹ in the offshore area (M. Bary pers. comm.). Two recent studies, based on a biological traits analysis (BTA), suggested that such natural disturbance could severely limit the number of ecological niches (Breine et al. 2018, Robert et al. 2021). Our findings corroborate this assumption, showing that only a low number of trophic niches can coexist in such dynamic environments. Due to this very simple food web structure, one can hypothesise that natural or anthropogenic disruptions may strongly affect the ecosystem functioning of sandbank areas (low resistance) because removing a single trophic guild may have cascading effects on the entire ecosystem. In contrast, the ecosystem may have a very high resilience capacity because only a low number of trophic guilds need to recover in order to provide a complete recovery of the food web.

The method of Quezada-Romegialli et al. (2018) revealed intra-group variations in the trophic position of species. It also pointed out some contradictions between the feeding mode and the trophic position of certain species, suggesting that their feeding mode is poorly known or that their diet varies from one habitat to another. Indeed, the polychaete *Ophelia borealis*, considered a non-selective deposit-feeder that swallows sediment with its everted proboscis (Parapar et al. 2021), had a trophic level above 2, equivalent to certain predators. The ecology of *O. borealis* is poorly understood, but Fauchald & Jumars (1979) believe that the opheliids can, to some extent, select their food sources. Nevertheless, all species have the same general habit, in that they all ingest sediment for the contained organic matter. It is thus possible that *O. borealis* focuses on an N-enriched food source, but a more in-depth study of its feeding ecology should be performed.

Asterias rubens, *Ophiura ophiura* and *Pagurus bernhardus* had a trophic position below 2, which is not consistent with their predator and/or scavenger behaviour (Allen 1983, Ramsay et al. 1997, Ruiz 2022). Instead, they display a trophic position equivalent to that of deposit feeders (e.g. *Gastrosaccus spinifer*, *Magelona filiformis*). Although little documented, it seems that, in some cases, *P. bernhardus* could be a filter feeder (Gerlach et al. 1976, Babu 1988) and/or a deposit feeders (Orton 1927). Similarly, a review by Ruiz (2022) indicates that the diet of *O. ophiura* may

depend on food availability. It can probably feed on detritus such as plant debris and organically enriched sediments when food is limited. It is thus possible that species with a certain degree of feeding plasticity switch toward organic matter deposits because their preferential food source is very limited on sandbanks.

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

4.3. Seasonal variations

Seasonal changes in the isotope composition of higher trophic-level organisms are generally smaller than those of short-lived autotrophs (Cabana & Rasmussen 1996, Nordström et al. 2009). Low variation has thus been described for benthic invertebrates (Vizzini & Mazzola 2003, Carlier et al. 2007, Nordström et al. 2009) and fish (Sarà et al. 2002, Vizzini & Mazzola 2003, Timmerman et al. 2020). In the Baltic Sea, Cabana & Rasmussen (1996) and Nordström et al. (2009) showed that the $\delta^{15}\text{N}$ values of invertebrates and benthivorous predators were lowest in the middle of summer, particularly in August. At the La Palme Lagoon (northwestern Mediterranean), Carlier et al. (2007) observed a decrease in mean $\delta^{13}\text{C}$ values in spring relative to autumn. Our findings suggest that similar seasonal variations occur on sandbanks. The decline in TA between autumn and spring was at the community scale. According to Layman et al. (2007), such a response suggests a lower feeding diversity, smaller trophic niches and a lower feeding redundancy. The massive ingestion of phytoplankton material in spring and the higher contribution of wPOM to the diet of primary consumers may explain this result. The lower range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary consumers could then cascade through the food web, affecting the stable isotope composition of the whole community.

5. CONCLUSION

Sandbanks host a very simple particular food web, largely supported by phytoplankton production. Results indicate that, with the exception of food

sources (wPOM and sPOM), the structure of the benthic food web is relatively well conserved over different seasons. This stability in an area of intense natural disruption suggests that the benthic food web is able to recover quickly after an anthropogenic disruption, for instance during the installation of submarine cables (see Taormina et al. 2018 for a comprehensive review of the potential impact of wind farm installation). However, additional investigations of the sandbank food web would be necessary to validate this hypothesis. Future studies should now focus on other issues such as the potential role of sandbanks as nursery areas for several fish species. Among other questions, they need to determine whether food is a limiting factor, if juveniles compete for food and space on sandbank and if they grow faster than in other estuarine or coastal nursery grounds.

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