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Plasticity of trophic interactions in fish assemblages results in temporal stability of benthic-pelagic couplings

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Highlights

- Most fish species displayed trophic plasticity over time
- Trophic resources were used optimally through complementarity
- When considering biomass, dominant species were trophic generalists
- Couplings between benthic and pelagic habitats are a permanent feature of the EEC

Abstract

This study addresses the temporal variability of couplings between pelagic and benthic habitats for fish assemblages at five periods in a shallow epicontinental sea, the Eastern English Channel (EEC). Organic matter fluxes fueling fish assemblages and the relative contribution of their different sources were assessed using stable isotope analysis and associated isotopic functional metrics. Couplings between benthic and pelagic realms appeared to be a permanent feature in the EEC, potentially favored by shallow depth and driven by the combination of two trophic processes. First, trophic interactions exhibited plasticity and revealed resource partitioning. Second, changes in the composition of fish assemblages did not impact benthic-pelagic couplings, as most dominant species were generalists during at least one time period, allowing complete use of available resources. Examining both unweighted and biomass-weighted indices was complementary and permitted a better understanding of trophic interactions and energy fluxes.

Key-words: Food webs, Stable isotopes, Biomass, Isotopic functional indices, Flux

1. Introduction

Identifying and quantifying trophic interactions between organisms is crucial to understand the structure and functioning of food webs (Ings et al., 2009; McCann, 2000). Ecosystems with numerous trophic links are considered more stable and resilient to perturbations (McCann, 2000; Rooney et al., 2006; Rooney and McCann, 2012) and trophic interactions have been proposed as mediators between biodiversity and ecosystem functioning (Hooper et al., 2005; Lynam et al., 2017; Rooney and McCann, 2012; Thompson et al., 2012). Particularly, characterizing spatio-temporal variability of interactions in trophic networks is considered a promising avenue for improving our understanding of the link between biodiversity and ecosystem functioning (Ings et al., 2009; McMeans et al., 2015). However, how this variability is impacted by environmental gradients and anthropogenic pressures has been overlooked so far (Pellissier et al., 2018). Finally, the assessment of trophic interactions and their spatio-temporal dynamics is also essential to sustainably manage marine ecosystems (Seibold et al., 2018), notably for the implementation of the Ecosystem Approach to Fisheries Management (Cresson et al., 2020; Garcia et al., 2003) or for aiming at good environmental status such as recommended in the Marine Strategy Framework Directive in Europe.

Couplings between habitats, defined here as transfers of energy and organic matter between them, have been widely studied both within and between aquatic and terrestrial ecosystems (Darnaude et al., 2004). The existence, strength and variability of coupling fluxes drive food web structure (Post et al., 2000), and functioning and resilience to perturbations (Blanchard et al., 2011; Woodland and Secor, 2013). In particular, couplings can be mediated by foraging when occurring across different habitats (Baustian et al., 2014; McMeans et al., 2015; Quevedo et al., 2009). In marine ecosystems, a major coupling occurs between pelagic and benthic realms, through a bidirectional process: on the one hand, sinking or vertically migrating pelagic organic matter reaches the sea floor (pelagic-benthic coupling (Griffiths et al., 2017)), while on the other hand, benthic organic matter can be feed upon by pelagic species (benthic-pelagic coupling (Gaudron et al., 2016)). Most investigations have focused on pelagic to benthic organic matter fluxes, as plankton sedimentation is considered to be the main source of organic matter for most benthic ecosystems worldwide (Grebmeier and Barry, 1991; Polunin et al., 2001; Stasko et al., 2018; Tecchio et al., 2013). On the contrary, few studies have investigated how benthic organic matter can be integrated in pelagic food webs. Numerous chemical, biological and physical factors can affect couplings between benthic and pelagic habitats (Baustian et al., 2014; Griffiths et al., 2017). These include primary production intensity (Docmac et al., 2017; McMeans et al., 2015; Stasko et al., 2018; Udy et al., 2019; Ying et al., 2020), filtering activity of suspension feeders (Cresson et al., 2016; Gili and Coma, 1998), fish feeding activity (Snickars et al., 2015) or depth (Cresson et al., 2016; Giraldo et al., 2017; Kopp et al., 2015). Despite the potential magnitude of spatial and/or temporal variation of these factors, and of their effects on organic matter fluxes, most studies performed one-off analyses of benthic-pelagic coupling, *i.e.* in one environment or at one season (but see (Cresson et al., 2020; Hayden et al., 2019; McMeans et al., 2015; Silberberger et al., 2018). In shallow waters, the physical proximity between pelagic and benthic habitats and the absence of physical barriers, such as a thermocline, may allow for a strong coupling between these habitats (Duffill Telsnig et al., 2018; Kopp et al., 2015; Woodland and Secor, 2013). Shallow marine ecosystems are thus good case studies to explore benthic-pelagic coupling, its dynamics and its link with ecosystem functioning.

Multiple approaches are available for unraveling spatio-temporal variability in benthic-pelagic coupling, particularly stable isotope analysis and functional diversity. On the one hand, stable isotope analysis is an insightful tool in trophic ecology (Fry, 2006; Layman et al., 2012), suited to quantify contributions of organic matter sources within an ecosystem and to determine factors shaping communities. For instance, community-wide metrics based on stable isotopes were developed by Layman et al. (2007) and by Jackson et al. (2011) and have been widely used to study the isotopic structure of fish assemblages (*e.g.*, Abrantes et al., 2014; Cresson et al., 2016; Hill et al., 2015; Jabot et al., 2017). On the other hand, measuring functional diversity allows for a better understanding of ecosystem functioning and trophic fluxes within biological communities (Cresson et al., 2019). According to Villéger et al. (2008), the functional diversity of a community is the layout of its organisms and of their relative importance (abundance or biomass) in a multi-dimensional functional space. Functional diversity can be split into three components, functional richness (space occupied by species in the functional space), functional divergence or dispersion (variance or degree of clustering of species distribution in the occupied space) and functional evenness (regularity of species distribution in the occupied space). Recently, functional diversity metrics have been merged with stable isotope analysis, where isotopes are used as species traits (Cucherousset and Villéger, 2015; Rigolet et al., 2015), to describe the isotopic diversity of a community. One of the advantages of these new metrics is to deal with the heterogeneous distribution of biomass among species of an assemblage. Accordingly, species with the highest biomass should have the largest contribution to diversity metrics to reflect their expected highest impact on ecosystem functioning (Rigolet et al., 2015). Accounting for species biomass underlines the strength of trophic interactions, energy distributions and fluxes (Rigolet et al., 2015) while ignoring species biomass assumes equitability between species (Cucherousset and Villéger, 2015). Still, isotopic community metrics have drawbacks (Hoeinghaus and Zeug, 2008) and do not necessarily grasp subtle details of food web structure when the number of basal sources is high (Jabot et al., 2017). In particular, two key issues are the failure to account for basal food sources (i.e., the isotopic baseline) and the standardization of isotopic values (Hoeinghaus and Zeug, 2008). One solution is to transform the isotopic niche (in the δ-space, i.e., $\delta^{13}C$ versus $\delta^{15}N$ plot) into a trophic niche (expressed as dietary proportions, i.e., in the p-space) through mixing models (Newsome et al., 2007), but using few basal sources before calculating isotopic metrics to encompass changes both in isotopic baselines and in diet proportions.

According to previous studies conducted in the Eastern English Channel (EEC), a shallow epicontinental temperate sea, benthic-pelagic coupling intensity varies with depth and predators' habitat preferences (Giraldo et al., 2017; Kopp et al., 2015). The present work aims to build upon these initial results to study how benthic-pelagic coupling varies over time, through the determination of the predominant organic matter sources (i.e. benthic *vs* pelagic) fueling fish assemblages in the EEC and how these variations depend on (1) changes in the trophic ecology of species over time and (2) changes in the species composition of the fish assemblage. For this purpose, inferences from isotopic mixing models and functional indices were used at five periods: autumn 2009, 2014, and 2015 and winter 2015 and 2016 to study the topology of energy fluxes (Cucherousset and Villéger, 2015; Rigolet et al., 2015). We used unweighted and biomass-weighted isotopic metrics as a complementary approach to explore trophic interactions and energy fluxes (respectively) within the fish assemblage. We hypothesize that variations in the three complementary facets (i.e. richness, dispersion, and evenness) of trophic and functional diversity occur between periods for fish assemblages because species respond differently to environmental conditions. We also hypothesize that due to the strong benthic-pelagic coupling in this shallow ecosystem (Cresson et al., 2020; Giraldo et al., 2017; Kopp et al., 2015), many species are generalists and can partition their resources through complementarity. The inclusion of biomass will provide more information about the trophic behavior of dominant fish species in the assemblage.

2. Materials and methods

2.1 Study area and sampling

Fish assemblages were sampled during five bottom trawl surveys conducted in the EEC (49.3°N to 51.2°N, 2°W to 2°E, Fig. 1, Table 1). Additionally to providing information on species composition and opportunities to collect fish individuals for further analysis, these surveys also sample or observe most components of the ecosystem, from the abiotic environment to top-predators (Travers-Trolet and Verin, 2014). The CGFS (Channel Ground Fish Survey) occurred on board of R/V Gwen Drez in autumn 2009 (Le Roy, 2009) and on board of the R/V Thalassa in autumn 2015 (Travers-Trolet, 2015). The CAMANOC ("CAMpagne ecosystémique en MANche OCcidentale"- Oct. 2014) and the IBTS surveys (International Bottom Trawl Survey; Jan-Feb 2015 and 2016) were operated on board of the R/V Thalassa (Travers-Trolet and Vérin, 2014; Vérin and Lazard, 2015; Vérin, 2016). A joint dataset between the surveys was generated on the basis of common spatial boundaries, i.e. filtering out data not located in the EEC to avoid any confusion between temporal and spatial variability of the different surveys. The data used for autumn 2009 and winter 2015 were reanalyzed from a previously published dataset (Cresson et al., 2020; Giraldo et al., 2017; Kopp et al., 2015). The complete dataset was published at the following URL address: https://doi.org/10.17882/76378.

Following the standard IBTS protocol (ICES, 2004), fish sampling was performed using a Grande Ouverture Verticale (GOV) bottom trawl towed for 30 minutes during daylight at a constant speed of 4 knots. The sampling scheme is spatially stratified by subdividing the EEC into 1° longitude × 0.5° latitude rectangles. Immediately after trawling, all fish were sorted, identified, weighed, and a subsample was measured for length. At each station, when possible, a minimum of five individuals per species were collected in the modal size-class and frozen onboard. The whole dataset comprises 35 fish species and 1419 individuals (Table S1). Sample size was then reduced to five individuals for each species by random sampling, to limit the influence of some overrepresented species (see afterwards). More than 35 species were encountered during the surveys but only these 35 were collected for further trophic analysis. Therefore, we refer only to these 35 species hereafter when using “fish assemblage”.

Table 1

Details of sampling. For each survey: number (n) and depth (mean ± sd, min – max) of sampling stations used for laboratory analysis. Benthic and pelagic baselines correspond to isotopic values of benthic (*A. opercularis*) and pelagic (copepods) sources used in the mixing model for the five studied periods. Values for baselines were collected concomitantly with fish, with the exception of *A. opercularis* in autumn 2014 (S. Dubois, Ifremer/DYNECO, unpubl. data). Biomass representativeness corresponds to the sum of the biomass of the species sampled for stable isotopes analyses divided by the total biomass of the fish community.

Survey	**Period**	**n station**	**Depth (m)**		**Benthic baseline (‰)**		**Pelagic baseline (‰)**		**Biomass representativeness (%)**
			mean ± sd	**min - max**	**Carbon**	**Nitrogen**	**Carbon**	**Nitrogen**	
CGFS 2009	Autumn 2009	48	37 ± 13	20 - 79	-17.39 ± 0.47	8.74 ± 0.86	-21.07 ± 0.89	10.28 ± 1.70	98
CAMANOC	Autumn 2014	14	46 ± 19	20 - 78	-17.58 ± 0.24	6.93 ± 0.30	-20.95 ± 1.55	7.32 ± 0.94	86
IBTS 2015	Winter 2015	12	43 ± 7	30 - 54	-17.68 ± 0.58	7.30 ± 0.45	-19.77 ± 0.46	6.42 ± 0.89	95
CGFS 2015	Autumn 2015	15	28 ± 9	23 - 53	-17.65 ± 1.00	7.77 ± 1.00	-20.73 ± 0.83	7.77 ± 1.00	92
IBTS 2016	Winter 2016	12	46 ± 11	29 - 61	-17.58 ± 0.69	7.81 ± 0.68	-19.77 ± 0.46	6.42 ± 0.89	82

A suspension feeding bivalve (the queen scallop *Aequipecten opercularis*) and zooplankton (copepods of the calanoid order) were collected to be used as proxies of benthic and pelagic trophic baselines, respectively. *A. opercularis* feeds on a mix of phytoplankton and associated bacterial and detrital material that supports benthic production (Barnes et al. 2009), and displays a $\delta^{13}C$ signature similar to deposit feeders and distinct from zooplankton (Kürten et al., 2013). Following other papers on benthic-pelagic coupling (Cresson et al., 2020; Hayden et al., 2019; Kopp et al., 2015), the use of zooplankton as proxy of pelagic production pathway and bivalves as proxy of benthic production pathway is satisfactory. Without any knowledge about fish diet, the use of these proxies will help determine the relative importance of benthic or pelagic production in the food web to which the different fish species belong (Kiljunen et al., 2020). Bivalves were sampled together with fish with the GOV bottom trawl whereas zooplankton were collected with a WP2 net (200µm mesh size) and frozen for stable isotope analysis. As no copepods were collected in winter 2015, the same isotopic values were used for the pelagic baseline in winter 2016 and 2015. Using primary consumers rather than producers as trophic baselines is advocated (Jennings and van der Molen, 2015; Jennings and Warr, 2003). Isotopic ratios of primary producers are highly variable through time and thus should not be used as isotopic baseline for studies based on muscle tissues, as muscles integrate isotopic signature of individuals' diet over several months. In contrast, primary consumers' tissues integrate primary producers' isotopic signatures on a time scale comparable to that of higher trophic level organisms' muscle, providing a more relevant trophic baseline (Jennings and van der Molen, 2015). In the laboratory, fish were thawed and measured (total length, to the nearest mm), then fish and bivalves were dissected. One sample per individual of white dorsal muscle without skin (fish) or adductor muscle (bivalves) (~ 2g wet mass) was dissected, stored frozen and then freeze-dried for at least 24h. For zooplankton, several individuals were identified to the order or genus level and sorted under a binocular microscope and pooled by sampling station in order to have enough biological material for isotopic ratio analysis. All samples (fish muscle, *A. opercularis* and copepods) were ground into a homogeneous powder (~ 1g dry mass) with a mixer mill for stable isotope analysis.

2.2. Stable isotope analysis

Stable isotopes are largely used as a tool to trace the trophic structure of marine food webs, as they give an integrated view of trophic interactions and organic matter fluxes. Nitrogen isotopic ratios ($\delta^{15}N$) are used to estimate the trophic level of consumers, because consumers are enriched in ^{15}N relative to their prey (Peterson and Fry, 1987; Post, 2002). In contrast, carbon isotopic ratios ($\delta^{13}C$) are used to identify the sources of organic matter fueling trophic pathways since there are little changes of $\delta^{13}C$ values (commonly 1‰) at each trophic level (DeNiro and Epstein, 1978). More specifically, it is an appropriate tracer of couplings, since organic matter of different origin (*e.g.*, benthic or pelagic) exhibit markedly different $\delta^{13}C$ values, and can be followed along food webs.

Isotopic ratios were measured with a Thermo Delta V isotope mass ratio spectrometer, coupled with a Carlo Erba NC 2500 elemental analyzer. Ratios were expressed with the classical δ notation,

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

where X is ^{13}C or ^{15}N respectively, and R the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ respectively. Accuracy of the analyses was checked with different standards for the five surveys, mink (autumn 2014, 2015, winter 2016), acetanilide (winter 2016) and sea bass muscle coupled with bovine liver (autumn 2009). The analytical precision of measures was always ± 0.2 ‰ for both elements.

Since lipids tend to be depleted in ^{13}C compared to proteins, high lipid concentrations in tissues can bias δ^{13}C values (Logan et al., 2008). Using elemental carbon to nitrogen ratios (C:N) as a proxy of lipid content, the mathematical correction for lipids proposed by Post et al. (2007) was applied to all samples with C:N ratios higher than 3.5:

$$\delta^{13}\mathrm{C}_{\mathrm{corrected}} = \delta^{13}\mathrm{C}_{\mathrm{uncorrected}} - 3.32 + 0.99 \times C{:}N \qquad (2)$$

2.3.Trophic level and benthic contribution calculations

For each consumer, the relative trophic contribution of pelagic (copepods) and benthic organic matter (*A. opercularis*) was estimated with a mixing model taking into account the calculation of the benthic contribution and trophic level jointly. Combining the Post equation (Post, 2002) for the trophic level and a two-sources mixing model (Phillips and Gregg, 2003) by correcting for fractionation of δ^{13}C and δ^{15}N, the following system of equations was obtained:

$$\begin{cases} TL_C = TL_{base} + (\delta^{15}N_C - (\alpha\delta^{15}N_B + (1-\alpha)\,\delta^{15}N_P))/\Delta^{15}N \\ \alpha = (\delta^{13}C_C - (TL_C - TL_{base})\Delta^{13}C - \delta^{13}C_P)/(\delta^{13}C_B - \delta^{13}C_P)' \end{cases} \qquad (3)$$

where TL_C is the trophic level of the consumer *C* (fish), TL_{base} is the trophic level of the source ($TL_{base} = 2$ as the sources are primary consumers), α the fraction of the benthic source in fish diet, δ^{15}N and δ^{13}C the nitrogen and carbon isotopic signature respectively, Δ^{15}N and Δ^{13}C the nitrogen (3.4‰) and carbon (1‰) trophic discrimination factor at each trophic level respectively, and *C*, *B* and *P* corresponds to the consumer, the benthic (*A. opercularis*) and pelagic (copepods) organisms respectively.

The following equation was obtained for α by solving the system of equations:

$$\alpha = \frac{\Delta^{15}N\,(\delta^{13}C_P - \delta^{13}C_C) + \Delta^{13}C\,(\delta^{15}N_C - \delta^{15}N_P)}{\Delta^{15}N\,(\delta^{13}C_P - \delta^{13}C_B) + \Delta^{13}C\,(\delta^{15}N_B - \delta^{15}N_P)} \qquad (4)$$

and TL_C was obtained replacing α with its value in (3).

For some individuals, values of benthic contributions lower than zero and higher than one were obtained due to approximations regarding trophic discrimination factors. Trophic discrimination factors values were set to 1‰ and 3.4‰ as suggested by Post (2002). but these values can vary, according to several parameters, such as the species considered (Caut et al., 2009). Furthermore, temporal differences between turnover rates of trophic baselines and fish muscle or other sources of bias potentially unknown can affect values of benthic contributions. Finally, contributions were scaled in order to obtain values strictly between 0 and 1.

$$\%B = \frac{(\alpha - min(\alpha))}{(max(\alpha) - min(\alpha))} \tag{5}$$

Hence, each individual position in the isotopic or δ-space, with coordinates ($\delta^{13}C$,$\delta^{15}N$), was projected in the trophic or p-space, with coordinates ($\%B$,TL_C), while accounting for benthic and pelagic isotopic baselines.

2.4.Trophic interactions and energy fluxes

Assessing fish assemblage functioning from stable isotope analysis classically does not take into account the species unevenness observed in the field, as simultaneous sampling of quantitative (biomass) and qualitative (stable isotopes) data requires a considerable amount of work. However, trophic fluxes in marine ecosystems depend on species relative dominance. Considering species biomass when analyzing stable isotopes might improve our understanding of assemblage functioning particularly in regard to energy fluxes. Thus, for each species, the benthic contribution $\%B$ in its diet was combined with its relative biomass in the fish assemblage, as sampled by the trawl. Trophic structure was partly depicted by isotopic functional indices (IFI), but also by violin plots representing the distribution of consumer biomass across the fraction of contribution of benthic sources for the fish assemblage. We propose to use both unweighted and biomass-weighted IFI and violin plots in an attempt to consider trophic interactions and energy flux within the fish assemblage.

For each survey, species biomass density (B_i, expressed in kg.m^{-2}) was calculated according to the following formula:

$$B_i = \frac{\sum_j B_{i,j}\, S_j}{\sum_{j'} S_{j'}} \qquad (6)$$

with $B_{i,j}$ the average biomass density of species i across stations in stratum j, S_j the surface of stratum j and $\sum_{j'} S_{j'}$ the sum of the stratum surfaces sampled during the survey. Relative species biomass b_i among all fish species captured was then calculated as $b_i = B_i / \sum_{i'=1}^{S_T} B_{i'}$ where S_T is the total number of species captured during the survey. Relative species biomass in the assemblage of 35 species used for isotopic analyses was calculated as $\beta_i = B_i / \sum_{i'=1}^{S_S} B_{i'}$ with $S_S = 35$ the number of species used for isotopic analyses.

In order to account for the fluxes at the assemblage scale, the average benthic contribution weighted by the relative biomasses of the species in the assemblage was calculated as follows:

$$\%B_w = \sum_{i=1}^{S_S} \beta_i \times \%B \qquad (7)$$

Since the number of individuals sampled differed between species, a bootstrap procedure was applied to avoid a possible bias in estimates of $\%B_w$ due to unequal representation. Five individuals per species were sampled with replacement for all species with n>5. Resampling was based on a 100 000 iteration bootstrap procedure, to ensure that the isotopic values for the pseudo individuals are representative of the isotopic variability of the larger initial dataset. Scaled benthic contributions were then computed for each pseudo-individual and their averages across pseudo-individuals are presented as results. After this correction, all individuals had the same importance when biomass is not considered. To keep inter-individual variability in violin plots, pseudo-individual benthic contribution was considered rather than average contribution calculated for species, and one fifth of the species' biomass was applied to each pseudo individual.

The Shannon-Weaver index (Shannon and Weaver, 1963) was used to measure the diversity of the fish assemblage for each survey.

$$H' = -\sum_{i=1}^{S_T} b_i \, log_2(b_i), \quad (8)$$

where b_i is the relative biomass of the species *i* across the S_T species collected in the trawl. *H'* is low when S_T is low and diversity is low (when one species dominate in the assemblage for example). For a given S_T, the maximum diversity (*i.e.* all species are equally common), H_{max}, then equal log_2 (S_T). The ratio between the measured diversity and the maximum theoretical diversity for a given number of species is the Pielou Equitability Index (Pielou, 1976, *J'*), which tends to zero when a species strongly dominates the assemblage or to one when species are evenly distributed.

$$J' = \frac{H'}{H_{max}} \quad (9)$$

2.5. Description of functional indices

Each component of functional diversity (isotopic richness, isotopic dispersion and isotopic evenness) was characterized using one index. These components must be quantified independently to describe functional diversity (Mason et al., 2005; Villéger et al., 2008). As trophic baselines might differ temporally, we followed Quevedo et al. (2009) or Kiljunen et al. (2020) by calculating functional diversity indices in p-space, i.e. using (%B,TL_C), rather than in δ-space (Cucherousset and Villéger, 2015). Average values of (%B,TL_C) per species, i.e. across the five sampled individuals or pseudo-individuals depending on species, were used for these calculations. Both an unweighted and biomass-weighted version of the dispersion and evenness index were calculated for each of the five time-periods, whereas richness can only be unweighted. by definition

2.5.1. Isotopic Richness

Isotopic Functional Richness (IFRic) is similar to the Total Area index developed by Layman et al. (2007) and to the Functional Richness index (FRic) developed by Villéger et al. (2008) but adapted for isotopic data. It represents the trophic diversity of the assemblage. IFRic is the convex hull volume (or surface in a two dimensional space) surrounding species in the trophic space, thus its value is not impacted by biomass consideration. For comparison between time periods, IFRic was standardized by the IFRic value calculated when merging the values of the five time periods ($IFRic_{max}$ hereafter), so that its values were constrained between zero and one (Rigolet et al., 2015). $IFRic_{max}$ represents all values taken by individuals whatever the time-period. By extension, we assume it corresponds to total available trophic space for the assemblage. Then, IFRic represents the trophic resources used at a given period, *i.e.* a subset of the total available trophic resources. When close to one, available resources are efficiently used and/or resource availability is high. When close to zero, resources potentially available to the assemblage are unused and/or resource availability is unusually low.

2.5.2. *Isotopic dispersion*

Isotopic dispersion is an index of isotopic divergence, *i.e.* the variation in the position or the dispersion of species in the isotopic space occupied. Isotopic Functional Dispersion (IFDis) is based on FDis, developed by Laliberté and Legendre (2010). IFDis ranges from zero, when all organisms have the same *%B* and trophic level, to one, when all organisms are far from the center of gravity.

$$IFDis = \frac{\sum_{i=1}^{S_S} w_i \sqrt{\sum_k (x_{i,k} - c_k)^2}}{\max_{i'}(w_{i'} \sqrt{\sum_k (x_{i',k} - c_k)^2})} \tag{9}$$

where w_i is the relative weight of species *i*, with $\sum_{i=1}^{S_S} w_i = 1$ and x_{ik} is the coordinate of species *i* for trait *k*, here *%B* or TL_C. IFDis is thus the weighted mean distance to the weighted center of gravity $\mathbf{c} = (c_k)$ with

$$c_k = \sum_{i=1}^{S_S} w_i x_{i,k}. \tag{10}$$

The unweighted version of this index, denoted IFDis hereafter, assumes an evenly distributed weight across species, i.e. $w_i = \frac{1}{S_S}$, whereas the biomass-weighted version, denoted $\text{IFDis}_{\text{biom}}$ hereafter, takes species relative biomasses as weight, i.e. $w_i = \beta_i$. When $\text{IFDis}_{\text{biom}}$ is close to zero, the assemblage is dominated by generalist species, whereas when it is close to one, it reveals trophic specialization.

2.5.3. *Isotopic evenness*

Isotopic Functional Evenness (IFEve), based on FEve, developed by Villéger et al. (2008) quantifies the uniformity in biomass distribution along the shortest tree that links all species in the trophic space (minimum spanning tree - MST).

$$IFEve = \frac{\sum_{l=1}^{S_S-1} \min\left[\frac{\text{dist}_l(i,j)/(w_i+w_j)}{\sum_{l=1}^{S_S-1} \text{dist}_l(i,j)/(w_i+w_j)}, \frac{1}{S_S-1}\right] - \frac{1}{S_S-1}}{1 - \frac{1}{S_S-1}} \tag{11}$$

where $\text{dist}_l(i,j)$ is the Euclidean distance between species *i* and *j* involved in branch *l* of the MST. As for IFDis, the unweighted version of this index, denoted IFEve hereafter, considers evenly distributed weights w_i across species and the biomass-weighted version, denoted $\text{IFEve}_{\text{biom}}$ hereafter, uses relative biomass as weight. An $\text{IFEve}_{\text{biom}}$ close to zero reveals trophic redundancy and potential competition among species, whereas a value close to one reveals optimal resource use through species complementarity.

All the indices used in this study and their significance were summarized in the Table S2. All analyses and plots were produced using the R software and ggplot2 package (R Core Team, 2019; Wickham, 2016); R scripts developed by Cucherousset and Villéger (2015) and Mouillot et al. (2013) were used for computing isotopic functional indices (see supplementary material in Cucherousset and Villéger (2015) and Mouillot et al. (2013)).

3. Results

3.1. Description of the fish assemblages of the different time periods

The Shannon's index (H') results from a combination of two components, species richness and the equitability of biomass between species. Among the five sampling periods, the H' value in autumn 2009 was the highest (H'= 2.64), resulting from a high number of harvested fish species and a moderate equitability (J'= 0.44, Table 2). The high biomass of *T. trachurus* in autumn 2014 and 2015 (Relative biomass, $b_{T.\ trachurus}$ = 81 and 70% respectively) and the high biomass of *M. merlangus* in winter 2015 and 2016 ($b_{M.\ merlangus}$ = 69.5 and 66% respectively) led to a low diversity (H' between 1.39 and 1.78) and equitability (J' between 0.24 and 0.34). The lowest values of H_{max} were recorded in winter due to the lowest species richness (S_T).

Table 2

Diversity and isotopic functional (unweighted and biomass-weighted) indices. For diversity indices, S_T corresponds to the species richness, H' to the Shannon-Weaver index, H_{max} to the theoretical maximum of diversity and J' to Pielou's equitability index (see Material and methods section for details). For functional indices, S_s corresponds to the number of species subsampled of species for stable isotope analysis, IFRic to the isotopic richness, IFEve, to the isotopic evenness (unweighted, IFEve, and biomass-weighted, $IFEve_{biom}$, respectively), and IFDis to the isotopic dispersion (unweighted, IFDis, and biomass-weighted, $IFDis_{biom}$, respectively).

Periods	**Diversity indices**				**Isotopic functional indices**					
	S_T	**H'**	**H_{max}**	**J'**	**S_s**	**IFRic**	**IFEve**	**$IFEve_{biom}$**	**IFDis**	**$IFDis_{biom}$**
Autumn 2009	62	2.64	5.95	0.44	28	0.34	0.71	0.41	0.38	0.27
Autumn 2014	67	1.45	6.07	0.24	11	0.21	0.79	0.57	0.58	0.23
Winter 2015	42	1.39	5.39	0.26	13	0.34	0.73	0.39	0.45	0.40
Autumn 2015	65	1.57	6.02	0.26	26	0.30	0.81	0.39	0.38	0.22
Winter 2016	39	1.78	5.29	0.34	25	0.37	0.73	0.30	0.38	0.24

The set of species used for isotopic analyses represented between 82% and 98% of the sampled biomass across all periods (Table 1). This subsample of species can thus be considered representative of the fish assemblage captured by the demersal trawl. The assemblage structure differed temporally because species with highest relative biomass b_i differed in time. In autumn 2009, the dominant fish species were *Scyliorhinus canicula*, *Trisopterus luscus* and *Mustelus asterias*, representing 18.5%, 13.5% and 12% of the relative biomass, respectively (Table 3). For the other periods, one species was largely dominant in the assemblage. In autumn 2014 and 2015, *T. trachurus* was clearly the most dominant species (b_i = 81 and 70%, respectively) while in winter 2015 and 2016, the dominant species was *Merlangius merlangus* (b_i = 69.5 and 66%, respectively).

Table 3

The three species with the highest relative biomasses in the ecosystem for each time period, their biomass density (kg.km^{-2}), benthic contribution ($\%B$) and associated trophic level (TL_C).

Periods	**Dominant species in the ecosystem**	**Relative biomass (%)**	**Biomass (× 10^3 kg.km^{-2})**	**Benthic contribution (mean ± sd)**	**Trophic level (mean ± sd)**
Autumn 2009	*Scyliorhinus canicula*	18.5	0.63	0.56 ± 0.20	3.75 ± 0.58
	Trisopterus luscus	13.5	0.46	0.57 ± 0.27	3.71 ± 0.21
	Mustelus asterias	12	0.39	0.65 ± 0.09	3.29 ± 0.33
Autumn 2014	*Trachurus trachurus*	81	3.47	0.24 ± 0.11	3.56 ± 0.24
	Merlangius merlangus	6	0.24	0.56 ± 0.05	4.29 ± 0.10
	Scyliorhinus canicula	4	0.16	0.83 ± 0.08	3.41 ± 0.06
Winter 2015	*Merlangius merlangus*	69.5	4.05	0.56 ± 0.10	5.07 ± 0.13
	Scyliorhinus canicula	10	0.59	0.88 ± 0.08	4.02 ± 0.15
	Limanda limanda	9	0.53	0.78 ± 0.17	4.25 ± 0.16
Autumn 2015	*Trachurus trachurus*	70	8.75	0.14 ± 0.07	3.31 ± 0.19
	Scomber scombrus	9	1.18	0.07 ± 0.07	3.22 ± 0.35
	Merlangius merlangus	4	0.60	0.42 ± 0.07	4.40 ± 0.12
Winter 2016	*Merlangius merlangus*	66	6.03	0.51 ± 0.06	4.27 ± 0.13
	Trachurus trachurus	7	0.63	0.28 ± 0.18	4.73 ± 0.33
	Mustelus asterias	6	0.55	0.78 ± 0.07	3.60 ± 0.35

3.2. Contributions of benthic and pelagic sources

3.2.1. Species scale

Species with pelagic lifestyles had lower *%B* than benthic ones (Table 4). Both *Scomber scombrus* and *T. trachurus* exhibited mean values lower than 30% regardless of the studied period while mean *%B* values were always higher than 82% for benthic species (*e.g. Raja clavata* (Fig. 2A)).

Among the species sampled at least twice, some of them (*Pleuronectes platessa, R. clavata, M. asterias or Microstomus kitt*) always had a stronger benthic contribution (*%B* ≥ 55 ± 5%), whereas others (*T. trachurus*, *Sprattus sprattus*, *Engraulis encrasicolus*, *C. lucerna*) always had a stronger pelagic contribution (*%B* ≤ 45 ± 5% Fig. 2A). Despite some variation and occasional high *%B* values, well-known pelagic species (*e.g. S. scombrus, C. harengus, Spondyliosoma cantharus* or *S. pilchardus*) generally exhibited low *%B* values. However, many species displayed high trophic plasticity, *i.e.* shifted from a stronger benthic to a stronger pelagic contribution depending on the period (Fig. 2A, Table S1). These species were mainly benthic or demersal species (*Callionymus lyra*, *Chelidonichthys cuculus*, *Dicentrarchus labrax, M. merlangus, Mullus surmuletus, Trisopterus* spp.)

The trophic level of most species sampled at least twice also varied among periods (Fig. 2B). For most species sampled in autumn and winter (*e.g. C. lucerna, Gadus morhua, T. trachurus*, *Trisopterus minutus*, *Eutrigla gurnardus*, *Limanda limanda*), their trophic level was generally higher in winter than in autumn. Upper trophic level (>4) species (*e.g. D. labrax*, *G. morhua*, *Zeus faber*, *M. merlangus*) generally displayed trophic plasticity (*i.e.* differed in resource use over time) and generalism (i.e. predated on several trophic levels and/or several food sources within a given period) and exhibited comparable contributions of both benthic and pelagic sources.

Table 4

Results from the mixing model showing the mean contribution of the benthic organic matter source (*A. opercularis*; *%B*) to the community, whether weighing by species biomass or not. Values are reported as quantiles (25% - 50% and 75). The second and third column are expressed at specific scales and represented species with the lowest and highest benthic contribution. For these species, their mean and standard deviation (±sd) but also their minimum and maximum of benthic contribution are reported (See Table S1 for more details).

	Species with the min benthic contribution **mean ± sd.** **[min ; max]**	**Species with the max benthic contribution** **mean ± sd.** **[min ; max]**	**Mean benthic contribution unweighted *%B*** **mean ± sd.** quantiles (25% - 50% - 75%)	**Mean benthic contribution biomass-weighted $\%B_w$** **mean ± sd.** quantiles (25% - 50% - 75%)
Autumn 2009	*S. scombrus* 0.18 ± 0.10 [0.05 ; 0.32]	*R. clavata* 0.85 ± 0.10 [0.71 ; 1.00]	**0.46 ± 0.20** (0.34 - 0.49 - 0.59)	**0.50 ± 0.20** (0.49 - 0.59 - 0.69)
Autumn 2014	*T. trachurus* 0.24 ± 0.11 [0.14 ; 0.42]	*S. canicula* 0.83 ± 0.07 [0.71 ; 0.93]	**0.59 ± 0.22** (0.48 - 0.62 - 0.73)	**0.31 ± 0.20** (0.22 - 0.25 - 0.42)
Winter 2015	*T. trachurus* 0.21 ± 0.13 [0.00 ; 0.35]	*S. canicula* 0.88 ± 0.08 [0.78 ; 0.98]	**0.57 ± 0.23** (0.38 - 0.59 - 0.72)	**0.62 ± 0.17** (0.57 - 0.62 - 0.75)
Autumn 2015	*S. scombrus* 0.07 ± 0.07 [0.00 ; 0.19]	*S. stellaris* 0.82 ± 0.16 [0.63 ; 1.00]	**0.46 ± 0.21** (0.35 - 0.46 - 0.58)	**0.20 ± 0.18** (0.17 - 0.17 - 0.25)
Winter 2016	*T. trachurus* 0.28 ± 0.18 [0.00 ; 0.47]	*R. clavata* 0.89 ± 0.07 [0.81 ; 1.00]	**0.53 ± 0.19** (0.40 - 0.53 - 0.67)	**0.51 ± 0.14** (0.49 - 0.53 - 0.59)

3.2.2. Assemblage scale and energy fluxes

The distribution of *%B* values in the fish assemblages differed between periods and when species relative biomasses were or were not taken into account (Fig. 3).

Regarding trophic interactions (unweighted *%B*), the EEC was fueled by both benthic and pelagic production at around 50% for all periods (mean *%B* values varied from 46 ± 20% in autumn 2009 and 2015 to 59 ± 22% in autumn 2014, Table 4). Regarding energy fluxes (biomass-weighted $\%B_w$), the picture was slightly different. The average benthic contribution in the assemblage dropped by 50% when relative biomasses were included in autumn 2014 and 2015 (*e.g.*, autumn 2014, mean *%B* = 59% and mean $\%B_w$ = 31%, Table 4, Fig. 3). At these periods, the fish assemblages were strongly dominated by pelagic species (*e.g.*, *T. trachurus)* characterized by low *%B* values (24 ± 11% and 14 ± 7% in autumn 2014 and 2015, respectively; Table 3). In contrast, a slight increase of benthic contribution was observed in autumn 2009 and winter 2015 when relative biomasses were included due to the dominance of benthic or demersal species.

3.3. Functional indices

IFRic relies on the subset of total available trophic resources actually used that varies according to the studied periods. IFRic values varied between 0.21 in autumn 2014 to 0.37 in winter 2016 (Fig.4, Table 2). Trophic levels ranged from 2.69 ± 0.61 for *Micromesistius poutassou* to 4.00 ± 0.21 for *M. merlangus* in autumn 2009; from 3.82 ± 0.20 for *C. harengus* to 5.07 ± 0.13 for *M. merlangus* in winter 2015 and from 3.08 ± 0.17 for *R. clavata* to 4.93 ± 0.36 for *C. lucerna* in winter 2016. Autumn 2009, winter 2015 and 2016 were periods with the highest IFRic when the assemblages were composed of species of both low and high trophic level but also of both low and high *%B* values. The assemblages thus exploited a wide range of resources.

In autumn 2009, the polygon was mainly located at the bottom of the whole trophic space. Trophic levels of species were estimated to be lower at this period. On the contrary, in winter 2015 the polygon was mainly located at the top of the whole trophic space, mainly reflecting the highest estimated trophic levels at this period. Lowest ranges of both *%B* and trophic levels were found in autumn 2014, leading to the lowest value of IFRic. At this period, the polygon was located at the center of the whole trophic space. The assemblage was composed of intermediate trophic level species, mainly belonging to both pelagic and benthic-based trophic pathways. Intermediate IFRic values were found in autumn 2015. At this period, the range of *%B* was the highest: from 0.07 ± 0.07 for *S. scombrus* to 0.82 ± 0.16 for *Scyliorhinus stellaris*. This variability reflected that species within the assemblage depended on both benthic and pelagic trophic pathways.

Considering the trophic interactions, despite slight variation between periods, the assemblages' values of the isotopic functional indices were close and no clear seasonal pattern was evidenced. IFDis was moderate and always lower than 0.58, meaning that the assemblages were composed of a mix of generalist and specialist species. IFEve was always high and ranged between 0.71-0.81 (Table 2). Species were evenly distributed in the trophic space and exploited the resources equitably. Considering the energy fluxes, $\text{IFDis}_{\text{biom}}$ and $\text{IFEve}_{\text{biom}}$ were lower than IFDis and IFEve, respectively (Table 2). Thus, the dominant species were rather generalists suggesting a higher trophic redundancy and potential competition between species. However, it should be noted that despite a decrease, $\text{IFEve}_{\text{biom}}$ remained high in autumn 2014 (0.57), while $\text{IFDis}_{\text{biom}}$ (0.23) was low, suggesting resource partitioning.

4. Discussion

Our results indicate a high temporal plasticity in trophic interactions within fish assemblages resulting in variable strengths of benthic-pelagic interactions and energy fluxes in a temperate shallow epicontinental sea. Many species displayed trophic plasticity (*i.e.* may differ in resource use over time) and were generalists (i.e. can predate on several trophic levels and/or several food sources within a given period), supporting strong benthic-pelagic couplings in the EEC. Trophic interactions differed among studied periods but assemblages were always fueled by a mix of benthic and pelagic food sources. Energy fluxes revealed that the contribution of benthic food sources to the assemblages differs according to the relative importance of the different species at each season. Consequently, dominant species usually drove overall fluxes. The shallowness of this ecosystem may allow for these trophic features.

4.1. Fish assemblages differed among studied periods

A number of top-down or bottom-up forces (*e.g.,* resource availability, temperature, fishing pressure) may affect the structure and diversity of fish assemblages (Auber et al., 2017; Lynam et al., 2017; McLean et al., 2018; Thompson et al., 2020). Several studies have demonstrated a positive relationship between diversity and ecosystem functioning (Hooper et al., 2005; Tilman et al., 2014). In our study, autumn 2009 was the period with the highest diversity indices (H’ and J’) which can be explained by the equitability of species biomass in the assemblage. Autumn 2009 and winter 2016 periods were characterized by longer food chains and a greater exploitation of resources. The addition of high trophic level species (*e.g.*, winter 2016) or of intermediate consumers (*e.g.*, autumn 2009) may have lengthened food chains at these periods (Post and Takimoto, 2007).

Higher trophic levels in winter may result from environmental variables such as resource availability. In the EEC, there is an autumnal phytoplanktonic bloom (Breton, 2000). Since phytoplankton is consumed by primary consumers, it results in a higher abundance of zooplankton in autumn than in winter (Eloire et al., 2010). Due to the lower abundance of zooplankton in winter, we can hypothesize that fish feed on higher trophic level preys during this period, which results in the highest overall trophic levels in the fish assemblages.

The composition of fish assemblages varies seasonally with species migration cycles. This is particularly the case for pelagic species such as *T. trachurus*, which is very abundant in the EEC in summer and autumn as observed in autumn 2014 and 2015. During these periods, it migrates from the North Sea to the EEC, probably due to changes in water temperature (Macer, 1977). This is also the case for whiting in winter. During this period, temperature has an strong influence of its spatial distribution (Loots et al., 2011; Zheng et al., 2001), which explains its high biomass in winter 2015.

4.2. Trophic plasticity and trophic resource partitioning strengthen benthic-pelagic couplings

When considering unweighted measures, the average contribution of benthic food sources *%B* to the fish assemblages ranged between 46% and 59% (Table 4). Species were thus always feeding on both benthic and pelagic production as demonstrated for other shallow marine coastal or estuarine ecosystems (Christianen et al., 2017; Griffiths et al., 2017; Kiljunen et al., 2020; Ying et al., 2020). Due to the shallow depth, species can rely on both benthic and pelagic sources due to physical (*e.g.*, resuspension, sedimentation) and/or biological processes (*e.g.*, fish predation) (Baustian et al., 2014; Griffiths et al., 2017).

Many fish species displayed trophic plasticity, relying on benthic or pelagic production depending on the studied period. Such plasticity may originate from changes either in direct predation in relation to environmental variation such as changes in prey abundance or species competition, or in indirect predation such as changes in the diet or trophic level of their prey. This result confirms the hypothesis of Kopp et al. (2015) that species could adapt their foraging strategy in relation to variation of the availability of their trophic subsidies (*i.e*, changes in prey abundance or prey specific composition). These variations may also be due to the variation of organic matter fluxes. An increase of pelagic productivity may result in an increase in pelagic-benthic coupling, whereby benthic species are fueled by pelagic organic matter (Docmac et al., 2017; Hayden et al., 2019). This coupling may be even more pronounced in the EEC due to the shallow depth.

Considering trophic interactions, functional indices (IFRic, IFEve, IFDis) revealed that assemblages were composed of a mix of specialist and generalist species (IFDis between 0.38 and 0.58, Table 2) with little variation over time. In addition, there was low functional redundancy and resources were used optimally through complementarity (IFEve ≥ 0.71, Table 2) between species, thus evidencing niche partitioning. Complementarity between species could result in reduced interspecific competition (Hooper et al., 2005). Following the niche variation hypothesis, species may expand their niches due to a release of interspecific competition (Costa-Pereira et al., 2019; Gajdzik et al., 2018; Van Valen, 1965). Species can partition their resources through a combination of differences in trophic patterns and habitat use. Many species may depend on both benthic and pelagic sources, but can also predate on several trophic levels (i.e., omnivory; Cury et al., 2003, Thompson et al., 2007; Vandermeer, 2006). A shallow depth allows pelagic species to migrate vertically and consume benthic preys (Baustian et al., 2014; Griffiths et al., 2017). Stomach content analyses performed on fish species of the EEC have shown that some benthic preys were found in the diet of some pelagic species. For example, benthic amphipods were found in the stomach contents of clupeidae and benthic fish (*e.g*. callionymidae) in the diet of *S. scombrus* (Cachera, 2013). In this ecosystem, high δ^{13}C values were recorded for pelagic species probably as a result of the consumption of benthic invertebrates. This behavior was observed in other shallow ecosystems like the Seto Sea (mean depth of 37m, (Takai et al., 2002) or the Baltic sea mean (depth of 42m, (Kiljunen et al., 2020)). Similarly, in lakes, pelagic species can derive up to 50-90% of their energy from benthic sources (Schindler et al., 1996; Vander Zanden and Vadeboncoeur, 2002). For benthic species, the shallow depth allows them to adopt an opportunistic behavior by integrating benthic production but also taking advantage of the pelagic production sedimentation via the pelagic-benthic coupling (van Denderen et al., 2018). Thus, depth is one of the main drivers for pelagic-benthic temporal variation in shallow ecosystems, including the EEC (Cresson et al., 2020; Giraldo et al., 2017; Kopp et al., 2015).

4.3. Temporal variation of benthic-pelagic couplings and energy fluxes

When focusing on energy fluxes, the most dominant fish species were generalists ($IFDis_{biom} \leq 0.40$, Table 2). Trophic generalism is common in marine ecosystems (Thompson et al., 2007) and, in our study, it was particularly marked at all periods. In winter, the dominant species was whiting, a high trophic level demersal piscivorous fish. Upper trophic level species are considered as ultimate couplers. Their predatory nature allows them to forage on both benthic and pelagic preys, and to stabilize food webs (Cury et al., 2003, McCann, 2000; Rooney et al., 2006; Rooney and McCann, 2012; Udy et al., 2019).

In autumn 2014, even though the dispersion was similar to other periods (low $IFDis_{biom} \leq 0.40$), evenness was the highest ($IFEve_{biom} = 0.57$, Table 2) suggesting higher optimal resource use in autumn 2014 compared to other periods. According to the resource diversity hypothesis (i.e. ecological opportunity), the diversity of available resources promotes niche expansion and divergence among species of consumers (Araújo et al., 2011; Costa-Pereira et al., 2019). Thus, we can hypothesize that at this period, resources were sufficient to support assemblages leading to niche segregation to reduce competition whereas, for other periods, resources were insufficient leading to some trophic redundancy ($IFEve_{biom} \leq 0.41$, Table 2).

In a similar study on a shallow ecosystem, Ying et al. (2020) suggested that high functional redundancy was caused by the abundance of pelagic fish with similar traits. Our results show that trophic plasticity goes beyond a replacement of dominant species by others with similar traits, and that similar assemblages (in terms of species composition) can respond differently depending on other biotic or abiotic factors (*e.g.*, productivity, competition, niche overlap).

The generalist behavior of dominant species ($IFDis_{biom} \leq 0.40$) may be a way to avoid competition or may also reveal the high abundance of one food source (Lefebvre et al., 2009a). The broadening of resource use may improve ecosystem functioning by allowing a more complete use of all available resources and promote species coexistence (Leduc et al., 2015; Petchey, 2003). However, it should be noted that a generalist species can be either composed of a sum of generalist individuals or a sum of specialist individuals (Bearhop et al., 2004). Additional analyses at the individual level would provide a better understanding of the structure and functioning of this ecosystem (Bolnick et al., 2011, 2003; Clegg et al., 2018; Ingram et al., 2018).

4.4.Strengths and limitations of the study

This study relies on a large temporal sampling plan of a fish assemblage to decipher variability in benthic-pelagic couplings at five different periods. To be comparable and interpretable, isotopic values were standardized to account for the variability of the isotopic baselines (Hoeinghaus and Zeug, 2008) by calculating for each period the benthic contribution ($\%B$) and the trophic level (TL_C) using the same two source mixing model for both metrics. A similar standardization was used by Quevedo et al. (2009) or Kiljunen et al.

(2020) but the originality of our study stands both in the use of the p-space for the determination of the functional isotopic metrics and the use of a common mixing model for both metrics. Another strength is the use of unweighted/biomass-weighted metrics that assess two complementary facets of the trophic relationships in the fish assemblage. However, our approach still relies on strong assumptions regarding isotope mixing models. First, the isotopic values of the sources should reflect the time periods over which the consumer tissues are synthesized (Phillips et al., 2014). Fortunately, isotopic values of the baseline sources in our study stayed quite stable over time with the exception of higher δ^{15}N values for both zooplankton and *A. opercularis* in autumn 2009 that could lead to an underestimation of fish trophic levels at this period. However, we are quite confident in our results since the three autumn periods displayed similar patterns in p-space. Pelagic (zooplankton) and benthic (molluscs such as bivalves or gastropods) baselines are often used in marine studies (e.g. Kiljunen et al., 2020; Kopp et al., 2015). *A. opercularis* is a suspension feeder and the suspended particulate matter it assimilates in the deep layer originates from a mix of reprocessed settling organic matter from the surface and resuspended organic matter from the sediment (Rodil et al., 2020). This explains why isotopic ratios of benthic suspension feeders differ significantly from zooplankton. An alternative to using primary consumers as isotopic baselines would have been to use indicator fish species that rely exclusively on pelagic or benthic subsidies (Duffill Telsnig et al., 2018). In our study, *S. scombrus* and *R. clavata* would be the best candidates. But this approach requires isotopic values at each period and invariable diet of the two fish species, both of which were not the case (Table S2). Second the trophic discrimination factors should be known for each taxon, tissue and diet under study (Phillips et al., 2014). Mixing models are sensitive to the values of trophic discrimination factors for carbon and nitrogen (Bond and Diamond, 2011). However, changing their values identically would have changed the absolute outputs of the mixing model but not their general trend (Lefebvre et al., 2009b). Here, a problem arises if one considers that trophic discrimination factors vary over time. Several studies showed that the trophic discrimination factor of nitrogen in consumer tissues decreased when growth rate increased, both in fish (Gaye-Siessegger et al., 2004) and in invertebrates (Gorokhova, 2018; Lefebvre and Dubois, 2016). More recently, Jacobi et al. (2020) showed that consumer length and season were factors explaining the trophic level of a large river fish beyond δ^{15}N values of its prey. Finally, a starvation period would increase the δ^{15}N values in consumer tissues (Doi et al., 2017). Trophic level values of two fish species stretched the p-space polygons towards higher trophic levels by a value of 0.5 in winter 2015 and 2016. Further, trophic level values of the fish assemblage in winter 2015 were on average higher than for the other periods but still the vast majority of trophic level values remained between 3 and 4.5 whatever the season. Unfortunately, we do not have any evidence to support food and/or growth limitation hypotheses for our fish assemblage and therefore estimations of variable trophic discrimination factors are not possible. In this regard, further developments are obviously needed but in the meantime, we have formulated similar assumptions as previous studies in the field.

Conclusion

Couplings between benthic and pelagic realms are persistent in the EEC where most species display trophic plasticity and can therefore change their food source over time depending on their availability or on potential competition with other species. In addition, dominant species are rather generalist: they can predate on several food sources but also on prey from different trophic levels. These behaviors are permitted by the shallowness of this ecosystem. Finally, accounting for fish biomass in trophic and isotopic functional metrics was complementary and allowed the consideration of energy fluxes within the ecosystem.

List of figures

Fig. 1: Location of sampling stations in the Eastern English Channel (EEC) during the five surveys: CGFS 2009 (green squares), CAMANOC 2014 (orange squares), IBTS 2015 (purple circles), CGFS 2015 (blue squares) and IBTS 2016 (pink circles). Autumn and winter periods were represented by squares and circles, respectively.

Fig. 2: Variation of benthic contributions $\%B$ (A) and trophic level TL_C (B). Green squares: autumn 2009 (CGFS 2009); orange squares: autumn 2014 (CAMANOC); purple circles: winter 2015 (IBTS 2015); blue squares: autumn 2015 (CGFS 2015); pink circles: winter 2016 (IBTS 2016).

Fig. 3: Comparison of violin plots of the scaled benthic contribution unweighted ($\%B$) or weighted by biomass ($\%B_w$). The bottom and top edges of the boxplots represent the first and third quartiles. The horizontal line is the median value. The whiskers' extremities represent 1.5 times the interquartile space (the distance between the first and third quartile). Larger zones of each violin plot represent the benthic contribution values supporting most of the biomass.

Fig 4: Comparison of IFRic among the five studied periods. Each point corresponds to the mean trophic level (TL_C) and benthic contribution ($\%B$) of each species. The black polygon corresponds to the largest IFRic space calculated for the meta-assemblage gathering the 5 studied periods, while the red polygon corresponds to the IFRic of each studied period. The silhouettes represent the three species with the highest relative biomasses in the ecosystem for each studied period. 1: *Scyliorhinus canicula*; 2: *Trisopterus luscus*; 3: *Mustelus asterias*; 4: *Trachurus trachurus*; 5: *Merlangius merlangus*; 6: *Limanda limanda*; 7: *Scomber scombrus.*

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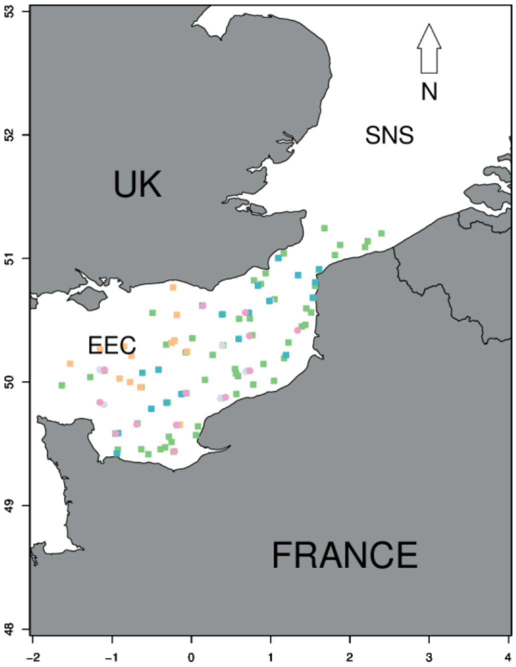
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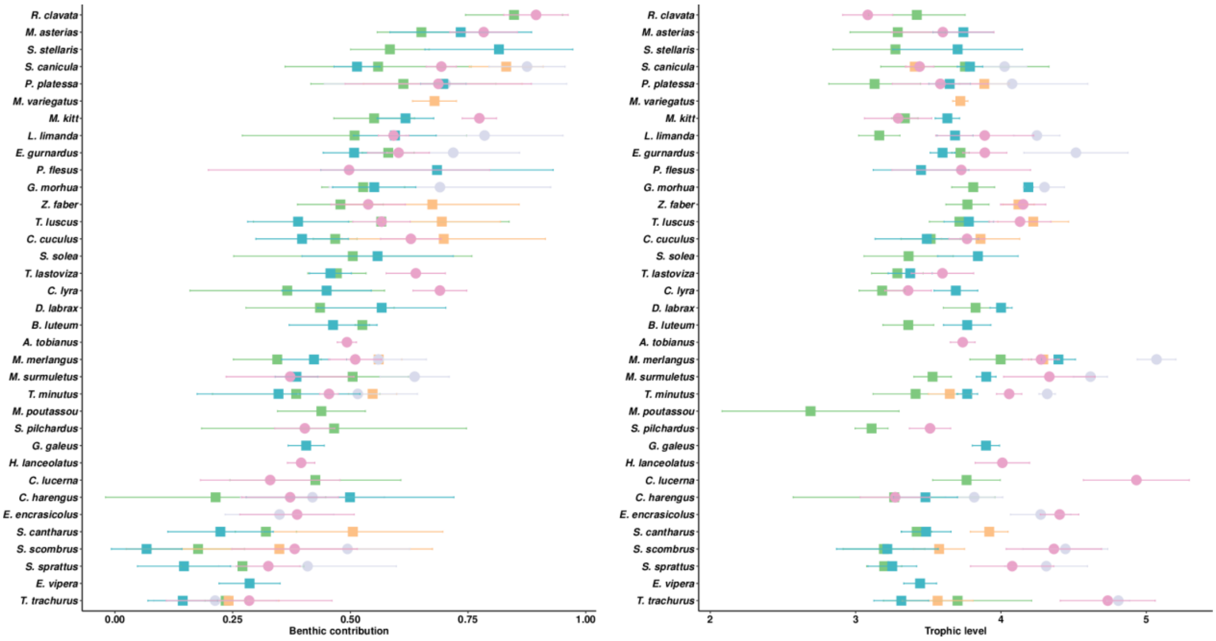
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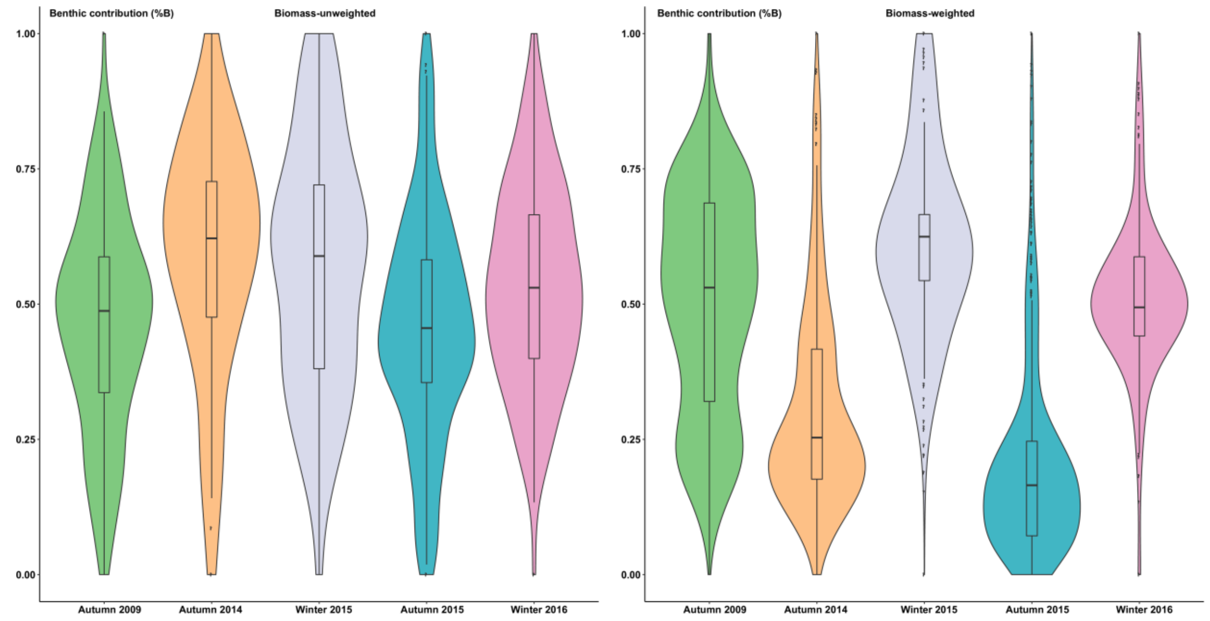
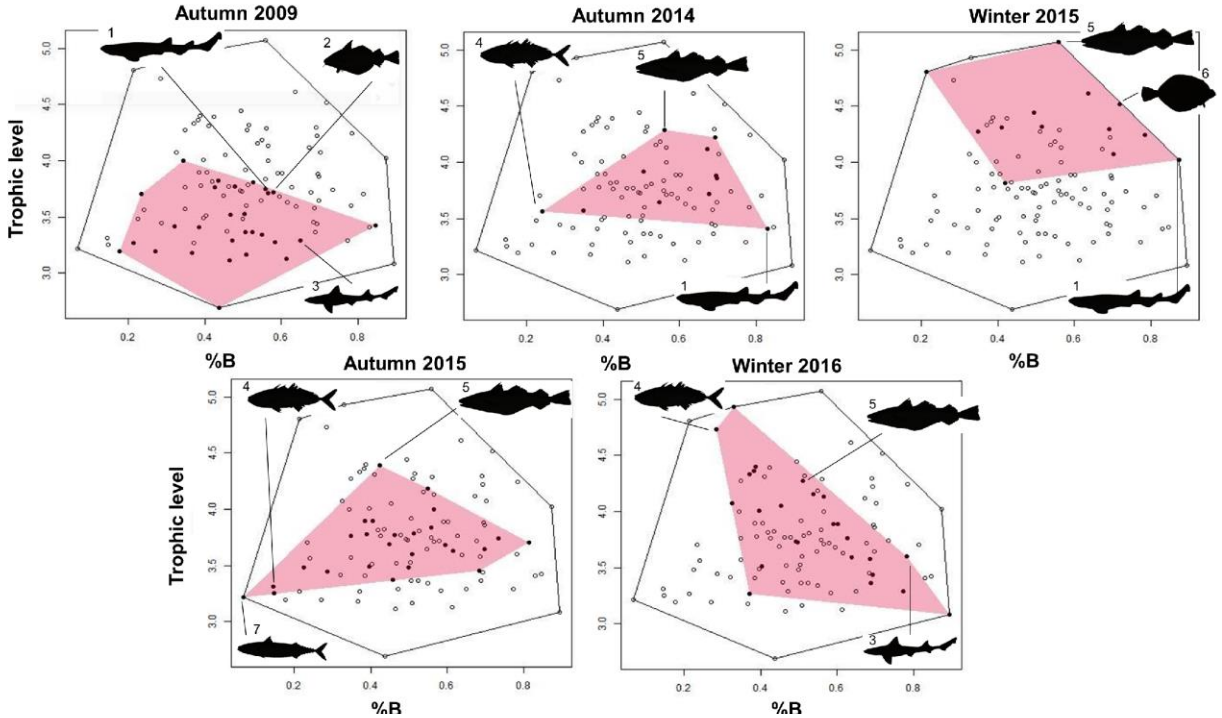
G. morhua
Z. faber
T. luscus
C. cuculus
S. solea
T. lastoviza
C. lyra
D. labrax
B. luteum
A. tobianus
M. merlangus
M. surmuletus
T. minutus
M. poutassou
S. pilchardus
G. galeus
H. lanceolatus
C. lucerna
C. harengus
E. encrasicolus
S. cantharus
S. scombrus
S. sprattus
E. vipera
T. trachurus
0.00
0.25
0.50
0.75
1.00
Benthic contribution
2
3
4
5
Trophic level


Benthic contribution (%B)
Biomass-unweighted
1.00
0.75
0.50
0.25
0.00
Autumn 2009
Autumn 2014
Winter 2015
Autumn 2015
Winter 2016
Benthic contribution (%B)
Biomass-weighted
1.00
0.75
0.50
0.25
0.00
Autumn 2009
Autumn 2014
Winter 2015
Autumn 2015
Winter 2016


Autumn 2009
Autumn 2014
Winter 2015
Autumn 2015
Winter 2016
Trophic level
Trophic level
%B
%B
%B
%B
%B
5.0
4.5
4.0
3.5
3.0
0.2
0.4
0.6
0.8
1
2
3
4
5
1
5
6
1
4
5
7
4
5
3