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Carolina Giraldo, Bruno Ernande, Pierre Cresson, Dorothee Kopp, Marie Cachera, et al.. Depth gradient in the resource use of a fish community from a semi-enclosed sea. *Limnology and Oceanography*, 2017, 62 (5), pp.2213-2226. <10.1002/lno.10561>. <hal-02572875>

HAL Id: hal-02572875

<https://hal.science/hal-02572875v1>

Submitted on 13 May 2020

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Depth gradient on the resource use of a fish community from a semi-enclosed sea

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Abstract :

Depth is one of the environmental variables influencing the structure of marine food webs by directly or indirectly influencing benthic-pelagic coupling and predator-prey relationships. In shallow waters, the high degree of connectivity between pelagic and benthic networks results in complex systems with multiple interactions. Digestive tract (DT) and stable isotope (SI) analyses were used to investigate depth-related changes in feeding patterns for 33 fish species (eastern English Channel [EEC]) collected between 5 m and 80 m depth. Fish species were first arranged into functional groups based upon trophic and habitat similarities. DTs were used to determine the general topology of the food web and SIs were used to estimate the contributions of different sources to fish diets. At the scale of the aggregated EEC food web, the main food sources for all groups were of benthic origin (> 50%). The aggregated food web was then used as a template to explore the influence of depth on resource use by predatory fish. Mixing models including depth as a continuous covariate successfully untangled and identified different feeding strategies among functional groups. In shallow waters, fish species benefited from both pelagic and benthic prey whereas, in deeper waters, they fed predominantly on either benthic or pelagic sources depending on their habitat preferences. Our results support the hypothesis of a stronger benthic-pelagic coupling in shallow waters, notably through fish diet, and highlight the importance of including environmental factors such as depth as proxies of habitat variation to fully understand resource use and food web structure in epicontinental seas.

37 **Introduction**

38 Scientists have long recognized the importance of food web structure and functioning
39 to understand and predict the response of marine ecosystems to environmental change
40 (Woodward et al. 2010). The biotic compartment of marine ecosystems and its trophodynamics
41 respond to variability in the abiotic environment from the individual to the community level
42 (Keyl and Wolff 2008). Consequently, studying how food webs vary along natural gradients
43 from local to regional scales has been recognized as one of the fruitful avenues for future
44 research (Ings et al. 2009). Such environmentally-induced variability can be particularly
45 significant in semi-enclosed shallow seas that present low inertia to global (e.g., climate

change) and/or local variations (e.g., river systems, fisheries) (Mackenzie et al. 2007, Martin et al. 2010). As a result, numerous epi-continental seas (e.g., Baltic Sea, North Sea) are highly dynamic and productive areas fueled by a large number of sources (e.g., freshwater inputs, marine organic matter), characterized by a large number of species and biological interactions, and where commercially important fish are caught every year.

Transfer of energy or matter between benthic and pelagic compartments can be described as a two-way process accounting for the amount of pelagic material that reaches the sea floor (pelagic-benthic coupling) but also for the amount of benthic organic matter that is available and consumed by pelagic species (benthic-pelagic coupling; Gaudron et al. 2016). Studies on pelagic-benthic coupling in polar and temperate regions have successfully identified a close relationship between primary production in the water column and benthic biomass or abundance (Grebmeier 1993, Cresson et al. 2014b). Similarly, deep (> 500 m) benthic trophic webs are largely dependent upon sinking organic matter of pelagic origin (Iken et al. 2001, Cresson et al. 2014a). However, few studies have documented and recognized the importance of benthic production to the whole food web in semi-enclosed shallow marine ecosystems where its contribution is expected to be high due to the proximity between pelagic and benthic species and the virtual absence of physical barriers such as thermoclines. Among the factors influencing benthic-pelagic coupling (e.g., vertical current, primary production, nyctemeral migrations, community composition), depth is one of the main forcing variables (Woodland and Secor 2013) that can be easily measured and is usually available for all studies. Depth is directly or indirectly related to different physical (e.g., water mixing, sinking time of organic matter) and biological processes (e.g., vertical migration of species) (Baustian et al. 2014) and can be used as a proxy of habitat variation to explore benthic-pelagic coupling and its impact on aquatic food webs' structure (Kopp et al. 2015).

70 Energetic links can be studied using fish as integrators of benthic-pelagic coupling (and
71 the other way round pelagic-benthic coupling) by exploring fish trophic interactions and their
72 variation with depth (Romero-Romero et al. 2016). At the community level, fish are
73 characterized by a remarkable diversity of feeding strategies, life-history traits and associated
74 morphologies that are expected to respond differently to environmental variability. Flatfishes
75 (e.g., European plaice), generally characterized as endobenthos-feeders, spend most of their
76 time on the bottom and, for the majority, do not feed by sight (Gibson et al. 2014). Due to the
77 characteristics of such sedentary species, such as swimming short distances and creating
78 moderate disturbances of the bottom to forage (Link et al. 2002), we expect their diet to
79 originate from benthos regardless of depth. Benthic round fish (e.g., Gadoids) share a relatively
80 similar diet with endobenthos-feeders (mainly benthic prey). However, differences in their
81 morphological traits and feeding modes (visual predation) should allow them to take greater
82 advantage of available pelagic prey (e.g., copepods) when moving from deep to shallow
83 feeding grounds (Jönsson et al. 2013). Small forage fish (e.g., sprat, herring) are generally
84 identified as omnivorous pelagic planktivores (Mollmann et al. 2004). Yet, studies show that
85 larger specimens of some species (e.g., herring) can also be nectobenthos-feeders preying on
86 small benthic crustaceans and polychaete worms (Casini et al. 2004). Although the main food
87 sources of this functional group are expected to be of pelagic origin, benthic-derived material
88 may also play a significant role in its diet in shallow environments. Finally, piscivorous round
89 fish (e.g., European seabass) form a broad group that can occupy different habitats (pelagic or
90 demersal) and are among the largest specimens within the fish community. Although they
91 preferentially feed on fish (Juanes et al. 2002) thus occupying higher trophic levels, most
92 piscivores are opportunistic and have flexible diets. Piscivorous round fish are thus likely to
93 consume the most abundant food source regardless of its origin (Post et al. 2000).

In this study, we used data from the eastern English Channel (EEC), a semi-enclosed sea, as a case study to address the following objectives: 1) identify the main trophic interactions and describe the resulting food web structure at the EEC-scale; 2) explore variation in fish resource partitioning with depth; and 3) compare the general structure of trophic interactions within the fish community at the EEC-scale with other shallow semi-enclosed systems. Based on a previous study (Kopp et al. 2015) and common knowledge on species' habitat use and feeding strategy, we hypothesize that benthic-pelagic and pelagic-benthic coupling vary with depth as the latter influences fish diets: pelagic-feeding species benefit from benthic subsidies in shallow waters and the contribution of pelagic sources to their diet increases with increasing depth as the benthic-pelagic coupling weakens; similarly, benthic-feeding species benefit from pelagic subsidies in shallow waters and the contribution of benthic sources to their diets increases with increasing depth as pelagic-benthic coupling weakens.

Diet estimates originating from digestive tract (DT) analysis and stable isotope (SI) analysis provide a snapshot of the current prey sources and integrated information about food resource use over several weeks to months, respectively. DTs of the main fish species (in terms of commercial interest and/or ecological dominance) of the EEC have been reported by Cachera et al. (2017) who studied sources of fish trophic niche variation at the individual level. Additionally, SIs from the different compartments of EEC food web, including the main fish species, were reported by Kopp et al. (2015) who showed an inshore-offshore gradient in the food web structure and concluded that this gradient was related to a weakening of benthic-pelagic and pelagic-benthic couplings towards offshore waters. To further understand the processes underlying this phenomenon, we combined data from DTs and SIs within a Bayesian framework, including depth as an environmental variable (Francis et al. 2011, Semmens et al. 2015). Species of the EEC food web were grouped into functional groups and DTs were used

to define the general topology of the food web whereas SIs were used to calculate proportions of the different prey in the diet of the various functional groups. Lastly, for fish functional groups, variation of diet (based on DTs and SIs) along a depth gradient from 7 to 80m was explored.

Materials and Methods

Data

DT and SI data for fish and the majority of the epifaunal invertebrates ($n = 799$ samples) were collected using a GOV bottom trawl from R. V. “Gwen Drez” during the Channel Ground Fish Survey (October 2009) that covers the whole EEC annually according to a spatially stratified sampling scheme (Le Roy 2009). Additional SI data for zooplankton ($n = 16$) and for benthic suspension feeders ($n = 34$) were respectively collected in January 2010 with a WP2 zooplankton net (International Bottom Trawl Survey; V  rin 2010) and in July 2010 using a French dredge (COMOR survey; Foucher and Quinquis 2010). Finally, particulate organic matter was obtained from water samples collected with Niskin bottles during the French sampling program SOMLIT (October 2009 to June 2010). More details about sampling protocols can be found in Kopp et al. (2015), Cachera et al. (2017) and supplementary tables S1 and S2.

DT data were obtained by identifying prey to the lowest possible taxon in 853 digestive tracts extracted from 16 fish species chosen to represent the main trophic guilds of the EEC fish community (*Chelidonichthys cuculus*, *Chelidonichthys lucerna*, *Clupea harengus*, *Dicentrarchus labrax*, *Gadus morhua*, *Merlangius merlangus*, *Mullus surmuletus*, *Mustelus asterias*, *Pleuronectes platessa*, *Raja clavata*, *Sardina pilchardus*, *Scomber scombrus*, *Scyliorhinus canicula*, *Solea solea*, *Sprattus sprattus*, *Trachurus trachurus*; for more details on digestive tract analysis see Cachera et al. 2017).

Nitrogen and carbon SI ratios, denoted by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, were measured from particulate organic matter, to zooplankton, epifaunal invertebrates, and fish collected from 7 to 80m depth in the EEC. A biplot of the SIs for each fish species arranged in functional groups can be found in Supplementary Figure S1. Specific details on tissue samples analyzed for SI ratios and their preparation can be found in Kopp et al (2015). Briefly, SI data were normalized to account for lipid content based on C:N ratios (Post et al. 2007) and corrected for spatial variation in the isotopic baseline based on SI values of the suspension-feeding bivalve, *Aequipecten opercularis*, taken as the baseline. SI values of the isotopic baseline at sampling sites were obtained by kriging interpolation of published data (Jennings and Warr 2003a, b; Barnes et al. 2009). For both nitrogen and carbon, the isotopic value of each consumer sample was then corrected by subtracting the kriged baseline value at the sampling location and adding the mean kriged baseline value averaged across the entire area (for all sampling sites: $\delta[\text{corrected}] = \delta[\text{consumer}] - \delta[\text{local baseline}] + \delta[\text{mean baseline}]$ with δ the nitrogen $\delta^{15}\text{N}$ or carbon $\delta^{13}\text{C}$ SI ratio). Any further mentioning of SI data in this paper refers to baseline-corrected SI values.

Food web modeling

The topological food web of the EEC was constructed by aggregating qualitatively the 54 species sampled for SI into functional groups based on their taxonomic classification (e.g. fish, cephalopods, bivalves), feeding strategies (e.g., filter feeders, scavengers), trophic guild (e.g., herbivores, piscivores), habitat use (e.g., pelagic, demersal) and morphology (only for fish, i.e., flatfish, round fish) using DT data reported by Cachera et al. (2017) for the main fish species and completed by published data (see Supplementary Table 1 and 2 for references). Aggregation resulted in 15 functional groups from primary producers to piscivorous fish and cephalopods (Table 1). The trophic level (TL) of each species was estimated based on its $\delta^{15}\text{N}$

using the scaled method proposed by Hussey et al. (2014) where the trophic enrichment factor (TEF) of the consumer's $\delta^{15}\text{N}$ is dependent on the $\delta^{15}\text{N}$ value of its prey:

$$TL_{consumer} = \left(\frac{\log(\delta^{15}\text{N}_{lim} - \delta^{15}\text{N}_{base}) - \log(\delta^{15}\text{N}_{lim} - \delta^{15}\text{N}_{TP})}{k} \right) + TL_{base}$$

where $\delta^{15}\text{N}_{lim}$ is the saturating $\delta^{15}\text{N}$ limit as TL increases, $\delta^{15}\text{N}_{base}$ is the $\delta^{15}\text{N}$ value of the isotopic baseline, $\delta^{15}\text{N}_{TP}$ is the consumer's $\delta^{15}\text{N}$ value at a given TL, and k is a rate constant (Hussey et al. 2014). Values for the parameters $\delta^{15}\text{N}_{lim}$, $\delta^{15}\text{N}_{TP}$, and k were taken from Hussey et al. (2014). The bivalve *A. opercularis* was used as isotopic baseline ($TL_{base} = 2$). Trophic level for each functional group was then calculated as the mean value for all individuals within the group (Table 1).

The topological description of the food web consisted of trophic links between functional groups expressed as a binary matrix. A trophic link was established if at least one species of the consumer group fed on one species within the source group according to DT analysis. The relative contributions of each source to consumers' diets were then estimated using the Bayesian isotope mixing model IsoWeb (Kadoya et al. 2012). Isotope mixing models are based on the principle that a consumer's isotopic ratios result from the mixing of the isotopic ratios of its food sources according to their relative contributions to its diet after accounting for TEF (Post 2002). While simple analytical mixing models can only estimate contributions of a few food sources to a single consumer's diet at a time, IsoWeb has the advantage of estimating dietary contributions for all consumers in a food web based on SI data and a topological description of the food web given *a priori*. The model also allows for TEF variation across links assuming that TEFs follow a normal distribution with a mean of 0.8 for carbon and 3.4 for nitrogen (Post 2002, Saigo et al. 2015, Fukumori et al. 2016). The standard

deviations of these normal distributions are assumed to follow a half-Cauchy distribution, for both carbon and nitrogen (see details in Kadoya et al. 2012). Nitrogen TEF values estimated from Hussey's equation (TL calculations) were close to those proposed in IsoWeb (mean value of 3.1). Hussey's equation provides TEF estimates between prey and predator species pairs, while IsoWeb estimates TEF between functional groups (several species) preventing a direct comparison of the estimates obtained by the two methods. The posterior probability densities of TEFs for carbon and nitrogen from this study are provided in the supplementary Figure 2S. The IsoWeb model was run with the following parameters: 10^6 chain length, burn-ins 500.000, and thin number 500 for three parallel MCMC chains. Convergence was assessed using the Gelman-Rubin test (Gelman et al. 2014).

Estimation of predatory fish diet as a function of depth

The resulting EEC-scale food web (referred to as IsoWeb model hereafter) was then used as a template to further explore the effect of depth on food resource use by fish functional groups using the Bayesian isotope mixing model MixSIAR (Stock and Semmens 2013). Compared to IsoWeb, MixSIAR can incorporate continuous covariates as predictors of sources' relative contributions to consumers' diet and multiplicative error structures. In this study, depth was introduced as a continuous covariate affecting sources' contributions to functional groups' diets. Because the model fits a continuous covariate (here depth) as a linear regressor on sources contributions in Isometric Log-Ratio (ILR) transform-space (see Francis et al. 2011; Egozcue and Pawlowsky-Glahn 2003 for details), it can also extrapolate changes in sources' contributions to diet beyond the limits of the observed distribution of the covariate. As results are presented in the space of sources' relative contributions to consumers' after reciprocal transformation from the ILR transform space, depth effect may look non-linear whereas it is linear in the ILR transform space. MixSIAR models were first run for each

functional group keeping the same trophic links, estimated TEFs, and Bayesian model parameters as the ones previously used by IsoWeb. For every MixSIAR dietary estimate, mean contributions and standard deviations are reported.

The “Planktivorous fish” group was excluded from this analysis due to insufficient sample size (40 individuals) to explore diet variation with depth as a continuous covariate. Visual inspection of the final isotopic space (referred to as IsoSpace hereafter) and correlation coefficients between prey sources allowed for the determination of when two sources were indistinguishable. For instance, if two sources presented high overlap in their SI ratios, then, likely solutions could involve one of the two sources but not both at the same time (Inger et al. 2010). Sources were aggregated *a priori* only if the absolute value of the coefficient of correlation was higher than 0.5 and if the combined sources had some functional or ecological significance (e.g., “Benthic decapods-omnivores” and “Benthic decapods-carnivores” combined into “Benthic decapods”) following suggestions by Phillips et al. (2005). Whenever sources were combined, the model was re-run under the same settings (i.e., same MCMC parameters). Convergence was assessed using the default MixSIAR diagnostic Gelman-Rubin and Geweke tests. For each fish functional group, the plot of the IsoSpace and the mean contribution of sources to the diet as a function of depth are reported. The resulting posterior distributions of sources’ contributions to fish functional groups’ diets at the EEC-scale (i.e. without accounting for the influence of depth) and at the minimum and maximum depths are also provided in Supplementary Figure S3 to allow assessing uncertainty in the effect of depth on functional groups’ diets.

Results

EEC-scale food web (IsoWeb model)

The EEC encompassed 5 TLs that, apart from the primary producers, ranged from TL 2 for benthic-suspension feeders (mainly bivalves and gastropods) to almost 5 for cephalopods. Fish TLs varied from 3.17 for planktivorous to 4.4 for demersal piscivorous fish (Table 1). Benthic-suspension feeders were the main food source for endobenthos-feeding fish (30% of the diet) while copepods represented the main food source (27%) for benthos-feeding fish (Table 2). Almost equal contributions of all sources to the diet of piscivorous fish (both demersal and pelagic) and cephalopods suggest generalist diets for the higher TL species. The combined contribution of benthic sources accounted for 54% of the diet of planktivorous fish while pelagic subsidies (copepods and macro-zooplankton) represented 46%. Likewise, benthic and pelagic sources represented 51% and 49%, respectively, of the diet of piscivorous pelagic fish (Table 2). In contrast, the diet of benthos-feeding, endobenthos-feeding and demersal piscivorous fish was largely dominated by benthic subsidies (73%, 100% and 100%, respectively; Table 2). Overall, the contribution of benthic subsidies (i.e., benthic OM, suspension feeders, deposit feeders, benthic predators, and benthic decapods) dominated the diet (51 to 100%) of all fish functional groups, even for those that are commonly reported as pelagic (e.g., planktivorous fish) (Table 2).

Fish diet variation with depth (MixSIAR models)

Using the previous model (IsoWeb) as a template (i.e., same topology and TEF factors), changes in diet with depth, described as a continuous variable, were explored for each fish functional group. Benthos-feeding fish ($n = 237$ individuals) were highly variable in terms of $\delta^{13}\text{C}$ values ($\delta^{13}\text{C}$ range: -15.45‰ to -18.98‰) suggesting that different carbon sources contributed to their diet. An initial MixSIAR model run with the 5 potential sources of this functional group (Figure 1a) showed a large overlap between SI ratios of copepods and deposit

feeders as prey (correlation of -0.90). However, these prey groups were not pooled together to keep pelagic and benthic sources separate. As a result, large standard deviations (hereafter referred to as SD) were observed for estimated sources' contributions to diet due to the difficulty of the model to fully distinguish between the two sources. Overall diet (i.e., integrated across all depths) indicated that individuals fed mainly on copepods ($36.2 \pm 22.7\%$ of their diet) and deposit feeders ($31.3 \pm 19.5\%$) followed by benthic decapods-omnivores prey ($13.5 \pm 5.3\%$). Cephalopods and benthic-suspension feeders were minor dietary items representing less than 10% of individuals' diet each ($8.5 \pm 4.6\%$ and $10.5 \pm 8.3\%$ respectively). Including depth as a continuous covariate of sources' contributions showed that individuals fed primarily on copepods at shallow depths ($< 40\text{m}$) and increased their consumption of deposit feeders with increasing depth (Figure 1b). The contribution of other sources remained low ($<15\%$) and showed little variation with depth. Posterior distributions of sources' contributions (Figure S3, 1st row) show that, despite some uncertainty in sources' contributions at the global scale, there is a clear discrimination between benthic and pelagic sources as depth increases.

A first model for endobenthos-feeding fish ($n = 149$ individuals) showed a large overlap between SI values of benthic predators and deposit feeders as sources (correlation of -0.78). They were combined into a common "benthic predators-worms" group leading to a 4-source mixing model (Figure 1c). Overall, individuals fed mainly on benthic-suspension feeders ($63.8 \pm 5.0\%$) and benthos-feeding fish ($23.8 \pm 6.4\%$). The combined source "benthic predators-worms" and benthic decapods-omnivores appeared as minor dietary sources ($6.2 \pm 6.5\%$ and $6.2 \pm 5.4\%$, respectively). Including depth as a continuous covariate showed that individuals fed mainly on benthic-suspension feeders from shallow waters (7 m) up to 60 m depth. Their contribution decreased substantially in deeper waters (from $\sim 60\%$ at 40 m depth to

~10% at 80 m depth). The contribution of benthos-feeding fish also decreased with increasing depth, whereas the contribution of “benthic predators-worms”, that represented a minor source in shallow waters, increased strongly with depth to become the main source in the deepest waters (Figure 1d). Posterior distributions of sources’ contributions (Figure S3, 2nd row) show the clear shift of main sources as depth increases.

Demersal piscivorous fish ($n = 133$ individuals) were also trophically linked to benthic predators and deposit feeders. Again, the SI ratios of these two sources overlapped largely (correlation of -0.88) and they were thus combined into a “benthic predators-worms” group. Similarly, the SI values of benthic decapods-omnivores overlapped with those of benthic decapods-predators and these groups were combined into a “benthic decapods” group (correlation of -0.52). The same held for benthos-feeding fish and benthic decapods (correlation of -0.91) but these sources were kept separate because of functional difference, which resulted in large SD values for sources’ contributions to diet (Figure 2a). Overall, individuals consumed mainly “benthic predators/worms” ($51.2 \pm 6.4\%$) followed by benthos-feeding fish ($29.2 \pm 12.8\%$) and “benthic decapods” ($19.7 \pm 14.9\%$). Little variation of diet with depth was observed (Figure 2b). “Benthic predators/worms” remained the main food source regardless of the depth, although its contribution decreased slightly (from ~60% to ~40%) with increasing depth, while benthic decapods contribution increased but always remained the lowest one. Posterior distributions of sources’ contributions (Figure S3, 3rd row) show that besides the relative stability of the main sources, uncertainty in their contributions increases with depth.

Pelagic piscivorous fish ($n = 106$ individuals) was the group with the highest number of trophic links (7 sources), which increased uncertainty in the mixing models. As for the

previous group, benthic decapods species were combined into a single source (correlation of -0.55). Similarly, “planktivorous fish” and “macro-zooplankton” were combined into a “planktivores” group (correlation of -0.55). As a result, 5 potential sources instead of 7 were considered (Figure 2c). Individuals were highly dispersed in terms of $\delta^{15}\text{N}$ values ($\delta^{15}\text{N}$ range: from 11.78‰ to 18.29‰) suggesting feeding at different TLs. A large overlap in SI values was still present between “planktivores” and “benthic decapods” (correlation of -0.85). However, these sources were kept separate to distinguish pelagic and benthic sources. Overall, individuals consumed mainly copepods ($37.6 \pm 10.2\%$) followed by “planktivores” ($27.21 \pm 24.1\%$) and “benthic decapods” ($26.5 \pm 16.6\%$). Benthic-suspension feeders and benthic predators were minor sources representing less than 5% of the diet ($3.9 \pm 3.8\%$ and $4.9 \pm 6.1\%$ respectively). When depth was included as a continuous covariate, individuals appeared to feed mainly on a mixture of copepods and “benthic decapods” in shallow waters (~7m depth), but their contribution progressively decreased with depth while the contribution of “planktivores” increased to dominate diet in the deepest waters (Figure 2d). Posterior distributions of sources’ contributions (Figure S3, 4th row) show that, despite some uncertainty in benthic decapods’ contribution at the global scale, there is a clear discrimination between the main food sources, notably of benthic and pelagic origin, along the depth gradient.

Discussion

We present the major trophic pathways towards the main fish species of a semi-enclosed sea and how they vary with depth. Species are not studied in isolation, but instead are positioned within the food web and grouped into functional groups that take into account several biological (taxonomy, feeding strategy, trophic guild, and morphology) and habitat (pelagic, demersal) characteristics that are frequently used in trophic web studies and modeling

approaches. Our results indicate high mixing of pelagic and benthic trophic pathways towards fish in general over a large area (35.000 m²), but also highlight species' ability to forage preferentially on different prey when moving from shallow to deep waters. With increasing depth, benthic-pelagic and pelagic-benthic couplings weaken gradually (and almost linearly) and species' diet more closely reflects their pelagic or benthic affinity (Figure 3). Some fish functional groups related to the bottom, namely endobenthos-feeding fish and demersal piscivorous fish, rely exclusively on benthic sources indicating some dietary specialization. In contrast, benthos-feeding fish and pelagic piscivorous fish integrate both pelagic and benthic sources as part of their diet depending on depth, suggesting a more opportunistic feeding strategy. More precisely, the benthos-feeding group relies partly on pelagic sources at shallow depth whereas they favor benthic subsidies as depth increases. Inversely, pelagic piscivorous fish feed on benthic sources in shallow waters and focus more and more on pelagic subsidies as depth increases. This conclusion was reached thanks to an original approach combining two Bayesian modeling approach: IsoWEB and MixSIAR.

Modeling considerations

The combined use of two different Bayesian mixing models (IsoWeb Kadoya et al., 2012 & MixSIAR Semmens et al. 2015), using DT and SI data simultaneously resulted in better estimates than when used independently and compensated for some of each other's' drawbacks. One of the main advantages of IsoWeb is the use of non-isotopic data, generally DT or stomach contents, to identify main predator-prey relationships that are used to define the general topology of the trophic network. The weaknesses of IsoWeb are the lack of visual outputs to verify that the consumer's SI values lie inside the mixing polygon defined by the sources' positions in the IsoSpace (created by the outer most values of the prey following TEF

adjustments; Phillips et al. 2014) and the lack of a correlation value between prey's SI ratios to determine if sources can be discriminated based on their SI signatures. In this regard, the combined use of IsoWeb with MixSIAR offers several advantages. First, MixSIAR can be built upon IsoWeb calculations (e.g., trophic links, TEF estimates) and provides a simple visual display of the IsoSpace for each node, combining source and TEF uncertainties (Semmens et al. 2015). Second, MixSIAR provides correlation values between sources that can help in making the decision of aggregating prey groups when appropriate. Finally, MixSIAR can include environmental (e.g., depth) or biological variables as covariates affecting sources' contributions to a consumer's diet.

In some cases, natural variability in SI signatures and TEFs of the different sources reduced the discriminative power of the mixing models and resulted in large standard deviations of sources' contribution estimates (see the full posterior distributions of sources' contributions to fish functional groups, Figure S3). Higher uncertainty was especially observed when the mixing model was unable to distinguish between two sources based on their SI values (e.g., copepods and benthic deposit feeders as sources for benthos-feeding fish considered at the EEC-scale). However, for all groups, major and minor dietary sources and dominance of benthic vs. pelagic sources could be identified at the EEC-scale. Interestingly, variation in fish's SI ratios was partly explained by depth. This resulted in a clearer discrimination between food sources and therefore more certain sources' contribution estimates when depth was included as a covariate (Figure S3: middle and right panels versus left panels), thus ultimately providing more relevant and ecologically significant information. Diet estimates from IsoWeb were slightly different from those provided by MixSIAR, which can be explained by two factors. First, IsoWeb allows variation in TEFs that results in larger SD estimates. MixSIAR models were built upon IsoWeb outputs, therefore using the resulting

mean TEFs and SDs calculated for every prey-consumer pair (out of the 10^6 iterations). Values of TEFs used in MixSIAR had therefore narrower variances resulting in narrower SDs in MixSIAR dietary estimates when compared to IsoWeb. Second, prey sources were grouped in MixSIAR models if they overlapped and their grouping had ecological significance (see discussion below). Thus, the number of sources for each predator differed between IsoWeb and MixSIAR models resulting in different dietary estimates.

Benthic-pelagic and pelagic-benthic couplings in shallow semi-enclosed marine ecosystems

Our results at the scale of the entire EEC (IsoWeb model) indicated equally important dietary contributions of benthic and pelagic subsidies for two functional groups of pelagic fish, namely planktivorous and pelagic piscivorous fish, whereas these groups are usually known to feed primarily on zooplankton and small fishes (e.g., Olaso et al. 2005). In parallel, benthos-feeding and endobenthos-feeding fish are known to feed on a variety of bottom animals, but preferentially on crustaceans and polychaete worms, respectively, whereas demersal piscivorous fish also forage on bottom-living fish. For these three functional groups, our results are in agreement with previous studies (Cohen 1990) and confirm that most of their energy is of benthic origin, representing ~73% of their diet (IsoWeb).

Planktivorous fish are important prey for a large number of predators, including larger fish, cephalopods, marine mammals and man (Mackinson and Daskalov 2007). A contribution of benthic sources to their diet suggests that they could be key components of the benthic-pelagic coupling by transferring benthic-derived carbon and energy towards higher trophic levels in shallow semi-enclosed seas, which could potentially differentiate the structure and functioning of their food webs from that of deeper open oceanic ecosystems (Pikitch et al. 2014). In the same vein, piscivores are characterized by generalist diets due to their mobility. This includes a wide variety of prey from invertebrates to fish, of both pelagic and benthic

origin, thereby contributing to benthic-pelagic coupling (Schindler et al. 1996). This is exemplified by the large range of $\delta^{15}\text{N}$ values observed in piscivorous pelagic fish that indicates high dietary plasticity and the consumption of prey from different TL.

Numerous studies in large temperate lakes, with similar characteristics as the EEC (e.g., similar depth range, temperature, presence of benthic and pelagic invertebrates and fish) have found patterns comparable to those of this study. Vander Zanden and Vadeboncoeur (2002), using SI and stomach content data on 16 freshwater fish species (from both littoral and pelagic habitats) showed that benthic-derived energy pathways accounted for more than 50% of total fish energy intake and that this pattern is a general feature common to the large lakes of North America (e.g., Lakes Superior, Michigan and Ontario). Similarly, several studies have emphasized the role of predation and nutrient transfer by mobile predators in benthic-pelagic coupling by showing that benthic invertebrates were the major prey source for pelagic fishes (Stewart and Binkowski 1986, Schindler et al. 1996, Schindler and Scheuerell 2002). Due to the proximity between pelagic and benthic compartments, shallow semi-enclosed seas and large deep lakes ($>20,000 \text{ km}^2$, $\sim 80\text{-}100\text{m}$ depth) share similar physical and biological constraints affecting benthic-pelagic coupling. Moreover, it seems clear that in shallow non-stratified waters, the basis of the benthic and pelagic food webs (i.e., primary producers and primary consumers) are not independent and should be studied as inter-dependent and highly connected units (Boero et al. 1996, Cresson et al. 2014b) to fully understand processes affecting the structure and dynamics of aquatic trophic networks.

Variation of benthic-pelagic and pelagic-benthic couplings along the depth gradient

The use of depth as a continuous variable partly explained the variation in consumers' isotopic ratios and helped untangling complex interactions in the EEC over a large spatial

scale. In shallow waters, pelagic and benthic sources are highly connected and benefit primary and secondary consumers in the two compartments, which are thus difficult to discriminate. It is worth noting that strong links between zooplankton and zoobenthos from both functional (energy fluxes) and structural (life cycle) perspectives (Boero et al. 1996), particularly in coastal marine areas, may indicate even higher proportions of benthic-derived energy for benthos-feeding and pelagic piscivorous fish. For example, the proximity of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of planktivores and benthic decapods rendered their discrimination by the mixing models challenging. This observation highlights the strong connection between compartments, where primary and secondary consumers (i.e., herbivores and omnivores) can have access to both pelagic- and benthic-derived matter. Our results support the hypothesis of a greater consumption of benthic prey by pelagic predators and of pelagic prey by benthic predators in shallow waters. Our results, transposing the initial observations by Kopp et al. (2015) in a depth continuum, suggest stronger benthic-pelagic and pelagic-benthic couplings with decreasing depth through plasticity in fish diet, in addition to already known physical processes (e.g., vertically mixed waters) and ecological features (e.g., vertical migration of zooplankton and epibenthic fauna). In semi-enclosed marine ecosystems, depth is correlated with other environmental and oceanographic variables (e.g., distance to shore, distribution of water masses, currents) making it a suitable variable to account for habitat variation and its potential effect on species diet. The gradual, almost linear, change in the strength of benthic-pelagic and pelagic-benthic couplings along the depth gradient (Figure 3) is probably related to the fact that waters are well-mixed in such ecosystems and the resulting absence of physical barrier in the water column. In open oceanic ecosystems, it is likely that the strength of these couplings shifts more abruptly with depth in relation to physical barriers such as thermoclines or transitions between euphotic, dysphotic and aphotic zones. It is also expected that in such ecosystems

other parameters than depth need to be considered to fully account for the spatial heterogeneity of benthic-pelagic and pelagic-benthic couplings. For example, at a given depth, varying distance to marginal ice zones in the Barents Sea has been proven to influence pelagic-benthic coupling (Tamelander et al. 2006). Similarly, seasonal or inter-annual variations in surface primary and secondary productions modulate the amplitude of primary carbon sources that reaches the bottom and different oceanographic features (e.g., currents, eddies, water column stratification) and ecological features (e.g., structure of the pelagic-food web) can be better proxies than depth to account for variation in the pelagic-benthic coupling (Grebmeier and Barry 1991). Finally, the role of species that perform wide diel vertical migrations (fish and zooplankton) in the pelagic-benthic coupling has also been highlighted in the North Atlantic and Mediterranean seas. Most of these species concentrate at the upper and mid continental slope depths (300-500 m) making them accessible to both, benthic and benthic-pelagic feeders, resulting in relatively strong coupling between benthic and pelagic production (Tecchio et al. 2013, Trueman et al. 2014).

Other sources of dietary variation

Apart from benthic-pelagic and pelagic-benthic couplings, a change in diet with depth is expected due to the mosaic of habitats (i.e., spatial differences in prey abundance or composition due to different sediment types or other abiotic conditions). Endobenthos-feeding fish had no trophic link identified (from previous DT analysis; Cachera et al. 2017) with pelagic prey. Their main prey were all benthic and, due to their sedentary behavior, little variation in diet was expected. However, endobenthos-feeding fish diet varied largely with depth. This pattern could be linked to variation in the abundance of their various benthic prey. Endobenthos-feeding fish fed mainly on benthic-suspension feeders in shallow waters (e.g., 65.5% of their diet at 25m) and switched to benthic-predators and worms in deeper waters

(e.g., 76% at 75m depth). Unfortunately, the benthic-suspension feeders group included bivalves and gastropods that are present in both shallow and deep waters. Similarly, there is no published evidence of a higher abundance of worms in deeper waters in the EEC that could explain the increase of their contribution with increasing depth and no high resolution data on the spatial distribution of polychaetes worms is available for the area. The absence of a known spatial trend in the abundance of both prey sources prevents from being conclusive about the relationship between endobenthos-feeding fish's diet change and prey spatial distribution. However, similar diet variability was found in flatfishes from the Bering Sea. In this area, bivalves dominated flatfishes' diet on the inner shelf (shore to 50m), while polychaetes were the main prey on the middle shelf (~50 to 100m). In this case, diet changes were associated with estimated trends in prey abundance (Yeung and Yang 2014). The authors however emphasized the possible mismatch between diet composition and infauna abundance in regions with high prey availability, where endobenthos-feeding fish preferentially feed on polychaetes even when they are not the dominant prey.

Demersal piscivorous fish had direct trophic links with benthic sources only. Small variations with depth were observed, the diet being composed of benthic predators and worms (~40-50%) followed by bottom-living fish (i.e., Benthos-feeder fish, ~31%) and benthic decapods (15-25%). Our results suggest a more generalist diet than the other functional groups with little intra- and inter-specific variability as shown by the weak dispersion of the consumer's SI ratios. Previous studies have however highlighted high spatial and temporal variability in the diet of species from this group (e.g., Atlantic cod, Daan 1973) that includes a wide variety of prey. This discrepancy might be explained by the fact that we used SI data that integrate diet over longer periods of time than stomach contents. Spatio-temporal diet variability in highly mobile generalist species such as demersal piscivorous fish may integrate

out in terms of SI signature and result in rather similar SI ratios that are unrelated to the sampling depth. Similar patterns have been observed in shelf and lacustrine fish assemblages, where higher TL species integrate coupling of pelagic and benthic pathways, resulting into intermediate $\delta^{13}\text{C}$ values (Woodland and Secor 2013, Schindler and Scheurell 2002). Although the endobenthos-feeding and demersal piscivorous fish had trophic links with benthic prey only, it is worth noting that our approach accounts only for direct predator-prey interactions and that pelagic organic matter might still fuel benthic fish through indirect trophic links (i.e., contribution of pelagic organic matter to the diet of primary consumers), that would then benefit indirectly from pelagic-benthic coupling.

Concluding remarks

The aim of this study was to provide information on the fundamental structure of the trophic network involving fish functional groups in a semi-enclosed sea and over a large spatial scale. The use of Bayesian mixing models integrating both DT and SI data indicated high connection between benthic and pelagic compartments. Including depth as an environmental covariate, the results showed that strong benthic-pelagic and pelagic-benthic couplings in shallow waters result in fish benefiting from both benthic- and pelagic-derived matter as part of their diet. As waters become deeper, these couplings weaken and species consume prey (either benthic or pelagic) progressively more according to their habitat preferences. Future studies in epicontinental seas should include environmental variables such as depth as proxies of habitat variation to untangle consumers' resource use and highlight potentially varying energy pathways structuring food webs. Results from this study enhance our comprehension of trophic interactions sustaining the fish community, which is essential for management and informed decision-making.

516 **Acknowledgments**

517 The post-doctoral position of C. Giraldo was funded by the regional council "Hauts de France"
518 through the project SIMODYN (grant n° 2014_10396). This study is part of the CPER project
519 MARCO (grant n°2016 regional council "Hauts de France" and Préfecture du Nord Pas de
520 Calais). We thank Paul Auchon for his fruitful ideas regarding this study, and Manuel
521 Rouquette and Mickael Baheux (RHBL Ifremer Boulogne sur Mer) for their valuable help in
522 the laboratory. The authors thank Dr. Tracey Loewen from Fisheries and Oceans Canada for
523 proofreading and editing and 2 anonymous reviewers for their valuable feedback that improved
524 the manuscript.

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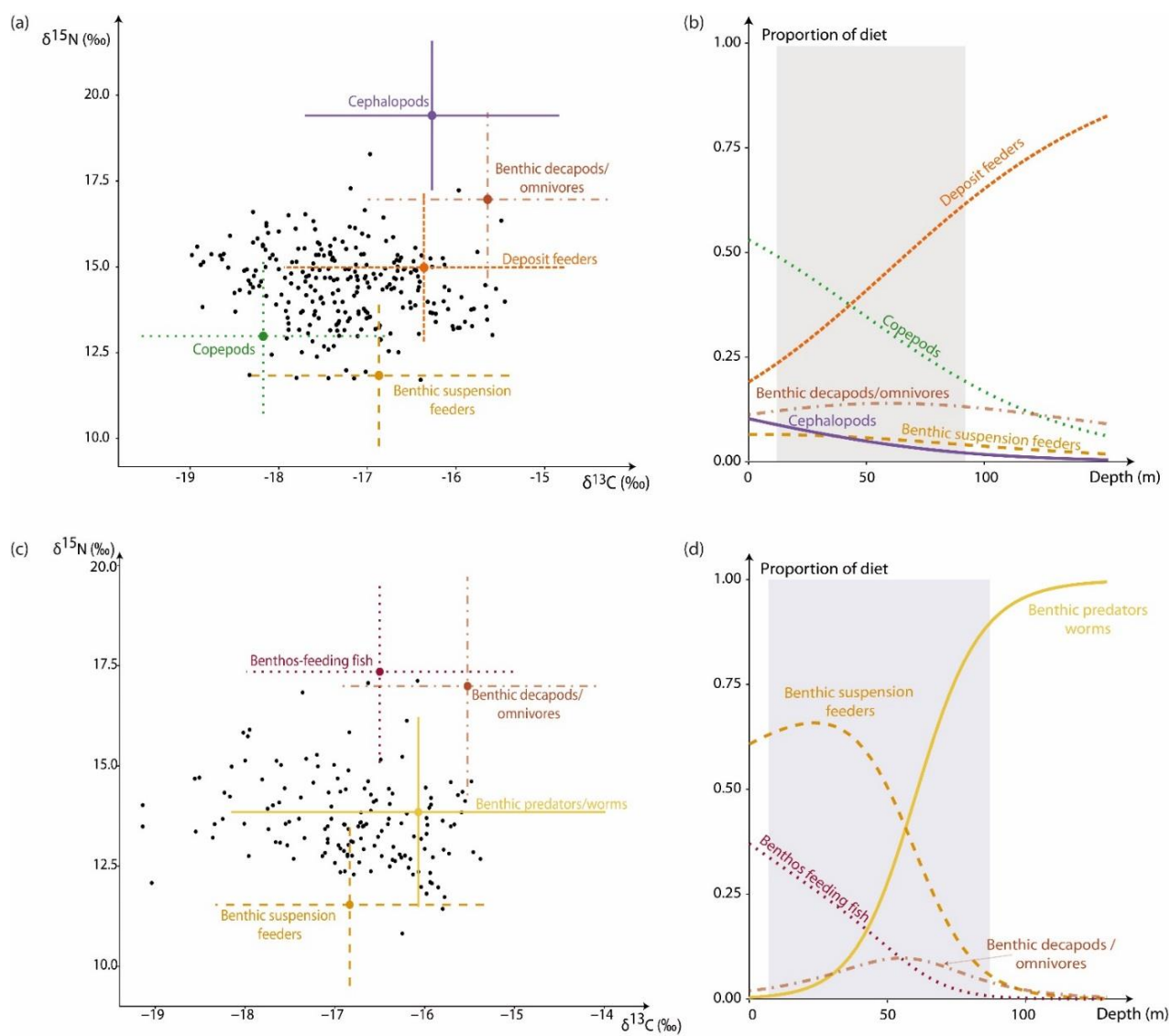
Figure legends

Figure 1: Diet composition of benthos-feeding (a, b) and endobenthos-feeding fish (c, d) as estimated by the MixSIAR mixing model. Iso-Space (a, c) displaying consumer's individual SI values (individual fish black dots) together with sources average SI values (e.g., "Copepods"; colored dots). The latter have been adjusted by TEF means and are associated with error bars indicating ± 1 standard deviation resulting from combined source and discrimination (TEF) uncertainty. Variation in diet as a function of depth is illustrated in panels (b, d). Sampling depth range is illustrated by the grey box and spans from 7-12m to 80m. Extrapolations beyond this depth range were kept for illustration purposes. Figure 2 follows the same conventions as this figure.

Figure 2: Diet composition of demersal (a, b) and pelagic piscivorous fish (c, d) as estimated by the MixSIAR mixing model. Iso-Space (a, c). Variation in diet as a function of depth (b, d).

Figure 3: Variation of the proportional benthic contribution (all benthic sources summed) to the diet of fish functional groups (proportional pelagic contribution is simply obtained as 1-benthic contribution). Blue dashed line: pelagic piscivorous fish; orange dash-dot line: benthos-feeding fish; red continuous line: demersal piscivorous and endobenthos-feeding fish

708 **Figure 1**



709
710

711 **Figure 2**

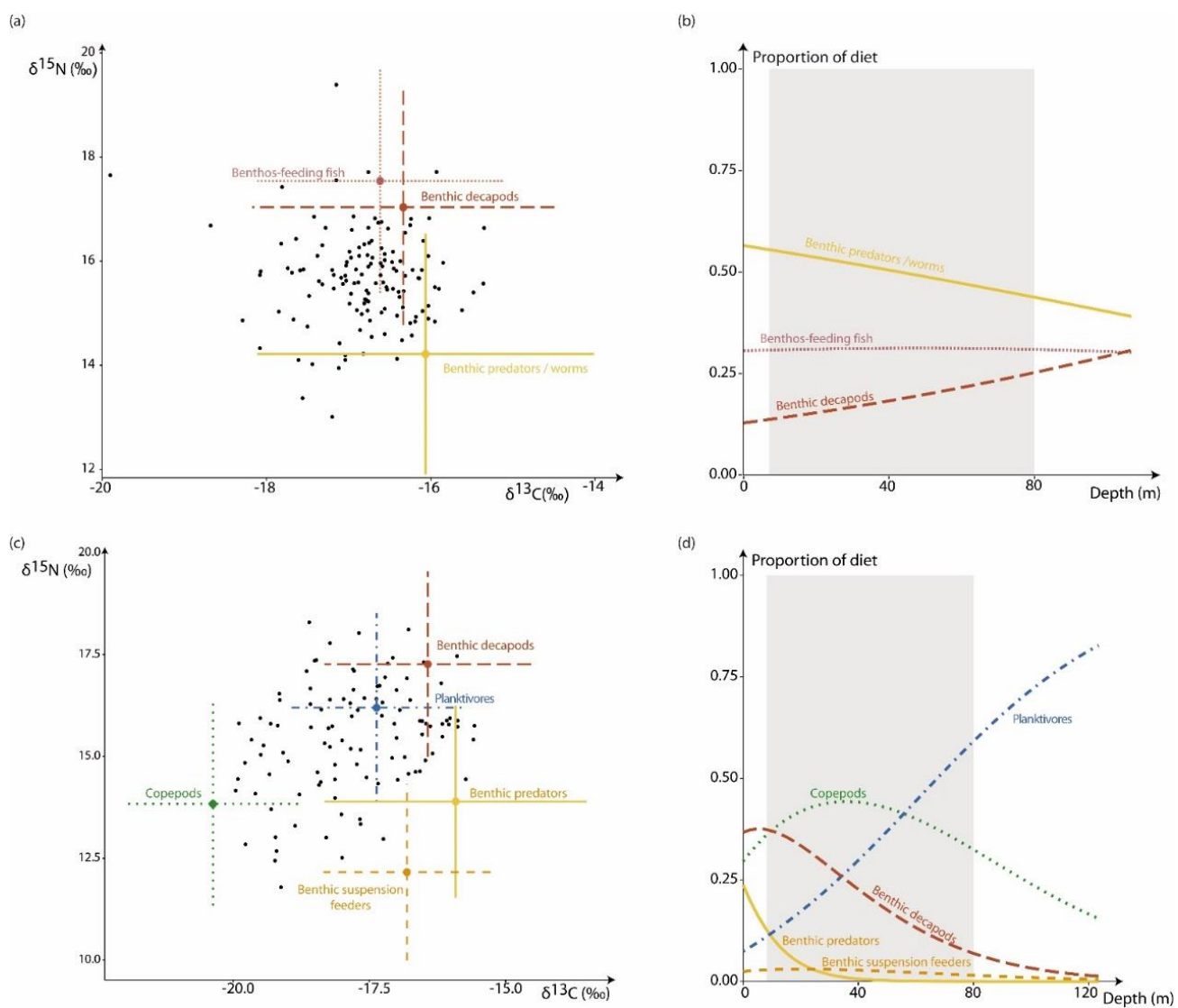
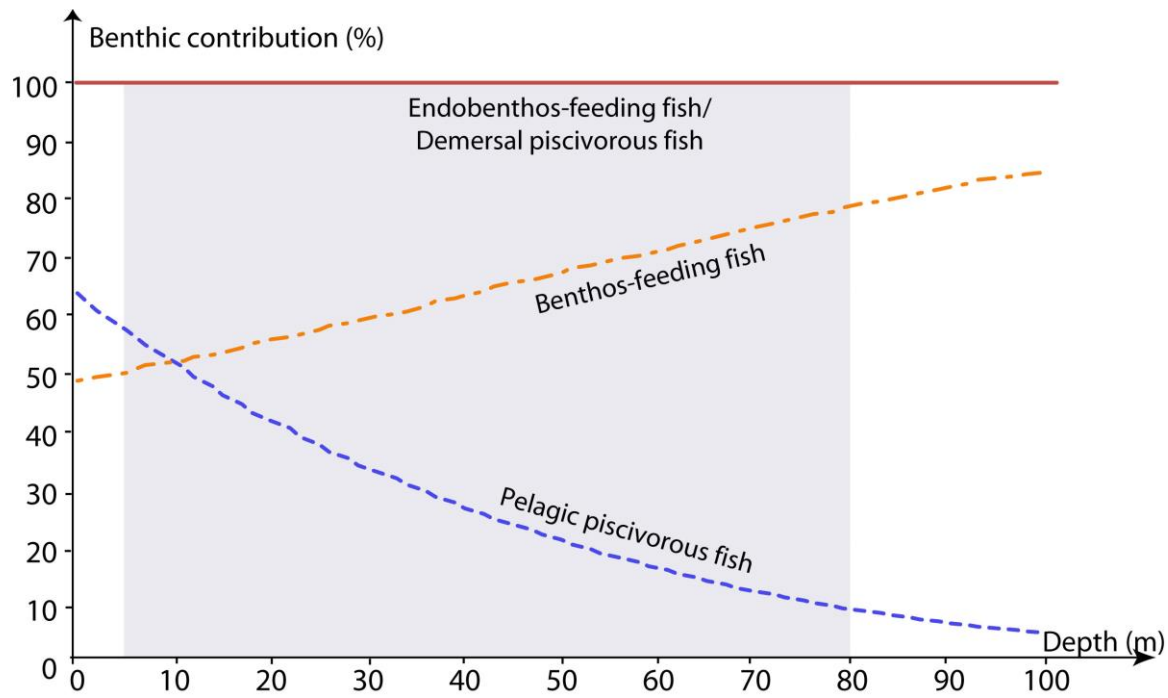


Figure 3



718 **Table 1: Functional groups of the Eastern English Channel food web. Species composition, reported diet and**
719 **mean trophic level (TL) based on SI are given for each functional group. Source data and references are**
720 **available in Supplementary Tables S1 and S2.**

Functional group	Composition	Reported diet	TL
1. Phytoplankton	POM	-	1
2. Benthic OM and detritus	BOM	-	1
3. Copepods	Copepods	Mostly herbivore, although some species are omnivorous/carnivorous or parasites	2.29 ± 0.32
4. Macro-zooplankton	Chaetognaths and fish larvae	Feed on copepods and other zooplankton	3.19 ± 0.03
5. Benthic-suspension feeders	Mainly bivalves and gastropods: <i>Aequipecten opercularis</i> , <i>Glycymeris glycymeris</i> , <i>Laevicardium crassum</i> , <i>Mimachlamys varia</i> , <i>Pecten maximus</i> , <i>Crepidula fornicata</i>	Suspension-feeder, deposit-feeder detritivore, planktivore, bacteria	2.01 ± 0.26
6. Deposit feeders	Mostly <i>Nereis</i> sp (this study) and <i>Aponuphis tubicola</i> , <i>Nephtys caeca</i> , <i>Dasybranchus gajolae</i> , <i>Glycera rouxii</i> (Le Loc'h, Hily, and Grall 2008).	Omnivores feeding on phytoplankton, zooplankton, crustaceans and other worms	2.72 ± 0.15
7. Benthic decapods/ omnivores	Shrimps <i>Palaemon serratus</i> , <i>Processa</i> sp. and Hermit crabs <i>Pagurus bernhardus</i>	Omnivores feeding on algae, crustaceans, gastropods and polychaetes	3.71 ± 0.79
8. Benthic decapods / predators/scavengers	Shrimp <i>Crangon crangon</i> and crabs <i>Liocarcinus holsatus</i> , <i>Maja brachydactyla</i> , <i>Necora puber</i>	Carnivores/scavengers feeding on echinoderms, crustaceans, marine worms, molluscs and dead fishes	3.56 ± 0.39
9. Benthic predators	Mainly echinoderms <i>Psammechinus miliaris</i> and the gastropod <i>Buccinum undatum</i>	Omnivores/scavengers feeding on marine worms, hydroids, small crustaceans, molluscs, diatoms, macroalgae and detritus	2.42 ± 0.37
10. Benthos-feeding fish	Rays <i>Raja clavata</i> , Gobiidae, Triglidae <i>Trigloporus lastoviza</i> , <i>Chelidonichthys lucerna</i> ,	Feed on all kinds of bottom animals, preferably crustaceans	3.83 ± 0.48

	small sharks <i>Scyliorhinus canicula</i> , <i>Scyliorhinus stellaris</i> , <i>Mustelus</i> sp., and small fish <i>Spondyllosoma cantharus</i> , <i>Trisopterus luscus</i> , <i>Trisopterus minutus</i> , <i>Mullus surmuletus</i> , <i>Callionymus lyra</i> , <i>Eutrigla gurnardus</i>		
11. Endobenthos-feeding fish	Flat fishes <i>Buglossidium luteum</i> , <i>Limanda limanda</i> , <i>Microstomus kitt</i> , <i>Platichthys flesus</i> , <i>Pleuronectes platessa</i> , <i>Solea solea</i>	Feed on a wide range of small bottom-living organisms, mainly crustaceans (amphipods, shrimps), also polychaeta worms and bivalve mollusks	3.50 ± 0.44
12. Demersal piscivorous fish	<i>Dicentrarchus labrax</i> , <i>Gadus morhua</i> , <i>Hyperoplus lanceolatus</i> , <i>Merlangius merlangus</i> , <i>Scophthalmus rhombus</i> (flatfish feeding preferentially on fish)	Feeds on fishes and larger crustaceans	4.40 ± 0.49
13. Planktivorous fish	<i>Clupea harengus</i> , <i>Micromesistius poutassou</i> , <i>Sardina pilchardus</i> , <i>Sprattus sprattus</i>	Feeds on planktonic crustaceans	3.17 ± 0.55
14. Pelagic piscivorous fish	<i>Zeus faber</i> , <i>Scomber scombrus</i> , <i>Trachurus trachurus</i>	Feeds on zooplankton and small fish	4.32 ± 0.66
15. Cephalopods	<i>Alloteuthis subulata</i> , <i>Loligo vulgaris</i> , <i>Sepia officinalis</i>	Feed on a wide variety of animals, mainly bony fishes and crustaceans	4.75 ± 0.48

721 **Table 2: Diet matrix showing the contribution of each prey (columns) to the diet of consumers (rows) based on IsoWeb modeling (10⁶ iterations). Values**
722 **are expressed as mean proportions with standard deviations between square brackets. (*) POM. (**) Benthic organic matter. ΣB and ΣP correspond to the**
723 **sum of mean contributions of benthic (B) and pelagic (P) subsidies respectively.**

Consumer	Prey													ΣB	ΣP	Total
	POM	BOM	Copepods	Macro-zooplankton	Benthic suspension feeders	Deposit feeder	Benthic decapods omnivores	Benthic decapods /predators	Benthic predators	Benthos-feeding fish	Planktivorous fish	Pelagic piscivorous fish	Cephalopods			
Copepods	1	-		-	-									-	1	1
Macro-zooplankton	0.37 [0.21]	-	0.63 [0.21]	-	-	-	-	-	-	-	-	-	-	-	1	1
Benthic-suspension feeders	0.35 [0.21]	0.65 [0.21]	-	-	-	-	-	-	-	-	-	-	-	0.65	0.35	1
Deposit feeder	0.37 [0.23]	0.63 [0.23]	-	-	-	-	-	-	-	-	-	-	-	0.63	0.37	1
Benthic decapods /omnivores	0.11 [0.09]	0.17 [0.14]	-	-	0.28 [0.21]	0.44 [0.20]	-	-	-	-	-	-	-	0.89	0.11	1
Benthic decapods /predators	-	0.18 [0.13]	-	-	0.23 [0.17]	0.23 [0.17]	0.17 [0.12]	-	0.19 [0.16]	-	-	-	-	1	-	1
Benthic predators	-	-	-	-	0.72 [0.24]	0.28 [0.24]	-	-	-	-	-	-	-	1	-	1
Benthos-feeding fish	-	-	0.27 [0.17]	-	0.24 [0.16]	0.21 [0.16]	0.15 [0.12]	-	-	-	-	-	0.13 [0.10]	0.73	0.27	1
Endobenthos-feeding fish	-	-	-	-	0.30 [0.18]	0.20 [0.16]	0.14 [0.12]	-	0.22 [0.17]	0.14 [0.11]	-	-	-	1	-	1
Demersal piscivorous fish	-	-	-	-	-	0.21 [0.16]	0.18 [0.14]	0.21 [0.15]	0.21 [0.15]	0.19 [0.15]	-	-	-	1	-	1

Planktivorous fish	-	-	0.30 [0.19]	0.16 [0.14]	0.32 [0.19]	-	0.10 [0.09]	0.12 [0.11]	-	-	-	-	-	0.54	0.46	1
Pelagic piscivorous fish	-	-	0.16 [0.12]	0.17 [0.13]	0.12 [0.10]	-	0.12 [0.10]	0.15 [0.12]	0.12 [0.10]	-	0.16 [0.12]	-	-	0.51	0.49	1
Cephalopods	-	-	-	-	-	-	0.19 [0.15]	0.21 [0.16]	-	0.19 [0.15]	0.23 [0.17]	0.18 [0.14]	-	0.82	0.18	1