

RESEARCH ARTICLE

# Cross-ecosystem trophic structure and benthic–pelagic coupling: Effects of depth, body size, and feeding guild

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## Abstract

Understanding how energy is transferred within and across ecosystems is essential to better understand drivers and future consequences of shifts in energy pathways. We used stable isotope ratios of 1932 fish individuals belonging to the 11 most abundant fish species collected across 300,000 km<sup>2</sup> along the English Channel–Celtic Sea continuum. To examine cross-ecosystem differences in trophic functioning, we assessed the effects of both extrinsic (depth) and intrinsic factors (body size and feeding guild) on resource use and trophic position of fish consumers. Positive relationships between trophic position and body size were observed for zoobenthivore and piscivore fishes, whereas the relationship was negative for benthivore fishes. Body size is thus an important structuring mechanism in the systems. Trophic position decreased with increasing depth for all levels of biological organization. The amplitude of the change between shallow and deep stations was equivalent to more than one trophic level for generalist planktivores and piscivores. In the shallow English Channel, the food web is marked by stronger coupling of benthic and pelagic habitats via diverse pathways, due to the proximity of benthic and pelagic species, whereas in the Celtic Sea, increasing depth leads to a decoupling of benthic and pelagic pathways. For piscivores, a consistent pattern of increasing dependence on benthic subsidies with increasing size and depth highlights the importance of large consumers coupling energy across food web compartments. This study describes the relationship between production and trophic functioning and provides an empirical ecological explanation for cross-ecosystem differences in observed trophic structures.

Understanding how energy and matter is transferred between different parts of the food web (i.e., from primary producers to top predators) within and across ecosystems is essential to better understand the links between trophic complexity and ecosystem functions (Seibold et al. 2018). The transfer of energy through ecosystems, into carbon export and into the production of biomass at higher trophic levels is determined by the availability and incorporation of different kinds of primary producers as sources of basal organic matter to higher trophic levels in food webs (Eddy et al. 2021). Yet,

major research gaps still need to be addressed to quantify the linkages between production and trophic functioning (i.e., the relative availability of basal organic matter sources that support production in food webs) spanning different ecological scales to better understand drivers and future consequences of shifts in energy pathways (Barnes et al. 2018). Examining the drivers that determine the trophic organization of marine communities, and the sources of basal organic matter for the food webs that support those communities is therefore a key research question in marine sciences to better understand the functioning of marine ecosystems (e.g., Udy et al. 2019).

Depth and body size are important structuring mechanisms of marine food webs influencing spatial variability in predator–prey interactions through depth-driven variation of benthic–pelagic coupling (Duffill Telsnig et al. 2019; Ying et al. 2020; Kiljunen et al. 2020) and biologically mediated access to trophic resources (Potapov et al. 2019; Keppeler et al. 2021). Body size, in the context of within- and between-species characteristics, is of paramount importance for several life history and

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ecological processes within and across many levels of biological organization (Peters 1983; Calder 1984), influencing metabolic rates (Kleiber 1932), population density (Reuman et al. 2008), community trophic structure, and matter fluxes (Ings et al. 2009; Potapov et al. 2019). Thus, previous theoretical considerations highlight the importance of considering size-structured food webs that reflect size-based feeding by individuals to model marine ecosystems (Cohen et al. 1993; Trebilco et al. 2013; Blanchard et al. 2017). Notably, pelagic food webs are supposed to be more size-structured, both in terms of trophic level and abundance, than benthic ones (Blanchard et al. 2009; Trebilco et al. 2013). In the pelagic realm, feeding mechanisms are mostly based on active predation, meaning that a predator cannot handle prey larger than its own size. On the contrary, benthic feeders are mostly omnivorous or scavenge on dead organisms, which gives less importance to size as a driver of trophic interactions (Cohen et al. 1993; Ladds et al. 2020).

The coupling between pelagic and benthic systems via diverse pathways results from fluxes in matter, organism movement, and predator–prey interactions (Baustian et al. 2014). These processes actively link the sea floor with the overlying water masses by controlling the amount of pelagic material reaching the sea floor, and also the amount of benthic organic matter available and consumed by organisms in the overlying water masses (Gounand et al. 2018). Consequently, the coupling of fast-energy (phytoplankton) and slower-energy (detrital-based) pathways plays a major role in determining the production, structure, and food web stability in aquatic ecosystems (Griffiths et al. 2017; Cresson et al. 2020; Van Denderen et al. 2021). Depth-driven variability in benthic–pelagic coupling is particularly important in understanding the trophic functioning of highly productive continental shelf ecosystems. The proximity of the shallow seafloor allows a high downward flux in detrital biomass to reach the sediment surface, supporting high benthic secondary production and/or bacterial alteration of organic matter (Moore et al. 2004). In these regions, the inflow of energy at the base of pelagic and benthic food webs determines the dominant feeding strategy of large demersal fish that can easily feed on both pelagic and benthic production pathways (Van Denderen et al. 2018).

Fish exploit their environment in different ways depending on their spatial distributions and feeding strategies making them important integrators of matter fluxes between benthic habitats and the water column, and the different parts of the food web (Vander Zanden and Vadeboncoeur 2002; Woodland and Secor 2013). In a coupled system, a pelagic fish species can exhibit a relatively high benthic contribution (i.e., the inclusion of benthic organic matter). This may be due to the consumption of benthic prey (due to the proximity of the shallow seafloor), or by the consumption of pelagic prey, the production of which is fueled by benthic organic matter, because pelagic prey consume benthic organisms (Petrik et al. 2019; Hayden et al. 2019). Moreover, fish can express three to four ontogenetic niche shifts and grow in mass by five or more orders of magnitude during their life cycle (Werner and

Gilliam 1984). The resulting wide variation in body size they display can be expected to have strong consequences on the trophic organization of fish communities. Sequential use of particular habitats throughout the ontogeny of some marine fish species, from coastal nursery grounds toward offshore adult habitats, may also explain size-related shifts in diet, because of habitat-related changes in trophic pathways (Jennings and van der Molen 2015).

There have been many studies that use traits to explain trophic position–body size relationships (e.g., Keppeler, Montaña, and Winemiller 2020), food web structure (e.g., Brose et al. 2019), and ecosystem functioning (e.g., Mouillot et al. 2021). Functional trait-based approaches (e.g., Endrédi et al. 2021) have important advantages compared to taxonomic ones as they are based on ecological and physiological relationships that are broadly applicable across taxa and regions. Consequently, they have the ability to detect ecologically meaningful cross-ecosystem trends (Muller et al. 2021). Among them trophic functional traits are considered intuitive and efficient to capture ecological interactions (Winemiller et al. 2015; Van Denderen et al. 2018; Cresson et al. 2019), particularly within communities with a large array of traits (McLean et al. 2021; Van Denderen et al. 2021). The species-level functional trait approach links to within-species functional variation due to ontogenetic shifts and size-specific interactions. In addition, as functional traits modulate species differential response to natural or anthropic alteration of the ecosystem, this approach can explain or predict changes in the nature and intensity of matter fluxes at community or ecosystem levels (Cresson et al. 2019, 2020; Hayden et al. 2019). Continental shelf ecosystems, such as the English Channel and the Celtic Sea in the Northeast Atlantic, are home to many pelagic primary producers and benthic secondary consumers. These two shelf ecosystems also receive organic matter from adjacent systems (such as the French and UK coasts and rivers and the English Channel itself for the Celtic Sea) that sustain production of fish biomass at higher trophic levels. However, the relative contribution of these components to fish food webs across this large area of the western European continental shelf (covering about 300,000 km<sup>2</sup>) remains unclear.

The main objective of this study was to elucidate the relative importance of extrinsic (depth) and intrinsic factors (organismal body size and feeding guild) in explaining trophic position and the strength of the benthic–pelagic coupling supporting fish community assemblages across the English Channel–Celtic Sea continuum. Consistent with previous studies and based on our understanding of their relevance to predator habitat use and feeding strategies, we expected depth and body size to be major factors driving the trophic structure and functioning of fish assemblages across the continuum. We expected stronger coupling of benthic and pelagic pathways in shallow waters, sustained through vertically migrating and interacting pelagic and demersal fish, whereas fish more closely reflect their pelagic, benthic, or demersal affinities with increasing depth linked to a decoupling of benthic and pelagic pathways in deeper areas

(Kopp et al. 2015; Giraldo et al. 2017; Cresson et al. 2020; Van Denderen et al. 2021). We also expected that a positive relationship between body size and trophic position could be seen based on increased coupling between benthic and pelagic pathways at larger size (Costa 2009; Arim et al. 2010; Keppeler, Montaña, and Winemiller 2020; Keppeler et al. 2021). For that purpose, we combined information on fish feeding guilds, based on diet and life stage data (Thompson et al. 2020) across the English Channel–Celtic Sea continuum to assess variability in trophic structure of community assemblages, and the relative trophic contribution of organic matter (i.e., pelagic vs. benthic) supporting them. We used stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) to provide evidence of the different production pathways and the relative importance of different organic matter as the base of an ecosystem food web (Fry and Sherr 1989; Vander Zanden and Vadeboncoeur 2002; Christianen et al. 2017), and stable isotope ratios of nitrogen ( $\delta^{15}\text{N}$ ) to provide an indicator of changes in consumer trophic position and nitrogen sources fueling food webs in various ecosystems (Post 2002a).

## Methods

### Study area

We analyzed fish data from the English Channel, a shallow, epi-continental sea located between the United Kingdom and France, and from the Celtic Sea, a broad, gently sloping shelf area that extends from the western English Channel to the Celtic break. In the English Channel, coastal waters are subjected to continental freshwater inputs from the French (Seine and Somme rivers) and UK (Thames estuary and Solent rivers) coasts (Vaz, Carpentier, and Coppin 2007). By contrast, the Celtic Sea shelf area is strongly influenced by oceanic waters that penetrate over the outer shelf (Hill et al. 2008), and inner shelf waters are subjected to intrusions from the English Channel and other inputs from the UK coast, for example, the Bristol Channel and Severn Estuary.

### Data

Fish were sampled from 165 stations across the English Channel–Celtic Sea continuum (Supporting Information Fig. S1) during winter, with a 36/47 Grande Ouverture Verticale demersal trawl with a cod-end of 20-mm stretched mesh. The sampling depth of demersal trawls ranged from 10 to 96 m in the English Channel, and from 68 to 166 m in the Celtic Sea. Sampling was performed during several surveys between 2014 and 2019, including the Évaluation Halieutique Ouest de l'Europe survey in the Celtic Sea (Duhamel, Salaun, and Pawlowski 2014; Leaute, Pawlowski, and Salaun 2015; Leaute, Pawlowski, and Garren 2016; Garren, Laffargue, and Duhamel 2019), and the Channel Ground Fish Survey (Travers-Trolet 2015, 2017), La CAmpanne MANche OCcidentale pluridisciplinaire survey (Travers-Trolet and Verin 2014), and International Bottom Trawl Survey (Verin 2015, 2016, 2018) in the English Channel.

A total of 1932 individuals belonging to the 11 most abundant and shared fish species common across the sampled areas were collected (Table 1; Supporting Information Fig. S1). Fish were sampled randomly along the depth gradient and individuals were selected so as to reflect, as much as possible, the length range observed in catches (Supporting Information Figs. S2, S3). Total fish body length in centimeters was recorded for all individuals and used as a proxy for body size across the study area (Mahé et al. 2018). All fish were frozen on board and processed for analyses in the laboratory.

For each individual fish, a sample of white dorsal muscle tissue was analyzed for stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) composition. Stable isotope ratios were expressed following the classical  $\delta$  notation, as deviation from standards (Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$  and atmospheric  $\text{N}_2$  for  $\delta^{15}\text{N}$ ):  $\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3$ , where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  and the isotopic ratios  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ , respectively. Accuracy of the measurements was checked using internal reference standards (bass muscle, bovine liver, and nicotinamide;  $\text{SD} < 0.2\text{‰}$  for  $\delta^{13}\text{C}$  and  $< 0.1\text{‰}$  for  $\delta^{15}\text{N}$ ). Since lipids are depleted in  $^{13}\text{C}$  relative to other tissue components (DeNiro and Epstein 1978), normalization of  $\delta^{13}\text{C}$  values for samples with a C:N ratio  $> 3.5$  was performed using the equation developed by Post et al. (2007). For details about sampling protocols and stable isotope analysis, see Walters et al. (2021) and Cresson et al. (2020).

### Benthic contribution and trophic positions of fish taxa

Knowledge of the stable isotope baseline (i.e., stable isotope variations at the base of the food web) is required to accurately interpret the isotopic values of a consumer higher in the food web (Layman et al. 2012). In aquatic systems, most primary producers and detrital energy sources have high temporal variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  making it challenging to use as an isotopic baseline reference for secondary consumers that integrate  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  over a longer term. An alternative is to use primary consumers that integrate temporal variability in primary producer stable isotope values over longer time periods, reducing the uncertainty in trophic position estimation of secondary consumers (Cabana and Rasmussen 1996; Vander Zanden et al. 1999; Post 2002b). Suspension feeding bivalves that feed on phytoplankton and mesozooplankton as well as associated bacterial and detrital material (Graf et al. 1982; Billett et al. 1983), and copepods that often comprise the principal biomass of zooplankton assemblages (e.g., Escribano et al. 2007; Figueiredo et al. 2020), are often used to provide a realistic trophic baseline estimate for benthic and pelagic production pathways, respectively (e.g., Olson et al. 2010; Woodland et al. 2012; Hayden et al. 2019). Following the studies conducted in the same ecosystems (Kopp et al. 2015; Cresson et al. 2020; Timmerman et al. 2021; Walters et al. 2021), we used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data of suspension feeding bivalves (the queen scallop, *Aequipecten opercularis*, and the great scallop, *Pecten maximus*) and zooplankton (calanoid copepods) sampled across the study area (Supporting Information Fig. S1 and Table S3) to determine

**Table 1.** Feeding guild information, including species, size class and category (range of actual values), and number of individuals (*N*) for fish sampled across the English Channel–Celtic Sea continuum following the guild classification by Thompson et al. (2020).\*

Species	Size class	Size category (cm)	<i>N</i>	Feeding guild
Plaice ( <i>Pleuronectes platessa</i> )	Overall		257	
	Js	3–12 (10.9–11.5)	2	Benthivore
	Jm	12–25 (12.7–25.0)	87	Benthivore
	M	25–39 (25.2–38.8)	146	Benthivore
Sole ( <i>Solea solea</i> )	Overall		134	
	Jm	10–19 (10.2–19.0)	44	Benthivore
	M	19–28 (19.3–27.9)	69	Benthivore
	L	28+ (28.9–49.0)	21	Benthivore
Thickback sole ( <i>Microchirus variegatus</i> )	Overall		34	
	Jm	7–13 (10.6–12.5)	6	Zoobenthivore
	M	13–17 (13.9–17.0)	28	Zoobenthivore
Poor cod ( <i>Trisopterus minutus</i> )	Overall		129	
	Jm	7–14 (8.0–14.0)	42	Zoobenthivore
	M	14–19 (14.1–19.0)	81	Zoobenthivore
	L	19+ (19.1–21.0)	6	Zoobenthivore
Grey gurnard ( <i>Eutrigla gurnardus</i> )	Overall		51	
	Jm	12–24 (14.5–24.0)	38	Piscivore
	M	24–31 (24.3–30.5)	12	Piscivore
	L	31+ (35.5)	1	Piscivore
Cod ( <i>Gadus morhua</i> )	Overall		65	
	Js	3–23 (15.5)	1	Piscivore
	Jm	23–45 (28.6–45.0)	27	Piscivore
	M	45–75 (45.9–73.0)	28	Piscivore
Lesser spotted dogfish ( <i>Scyliorhinus canicula</i> )	Overall		63	
	Jm	24–47 (38.9–43.9)	3	Piscivore
	M	47–62 (48.2–62.0)	46	Piscivore
	L	62+ (62.1–77.0)	14	Piscivore
John Dory ( <i>Zeus faber</i> )	Overall		53	
	Js	3–17 (10.7–14.7)	10	Piscivore
	Jm	17–34 (18.0–33.5)	19	Piscivore
	M	34–44 (35.0–44.0)	14	Piscivore
Whiting ( <i>Merlangius merlangus</i> )	Overall		472	
	Js	3–12 (10.6–12.0)	7	Generalist planktivore
	Jm	12–24 (12.1–24.0)	163	Piscivore
	M	24–34 (24.1–34.0)	248	Piscivore
Horse mackerel ( <i>Trachurus trachurus</i> )	Overall		305	
	Js	3–10 (6.1–9.9)	20	Generalist planktivore
	Jm	10–20 (10.1–19.9)	113	Generalist planktivore
	M	20–30 (20.0–29.9)	146	Piscivore
Mackerel ( <i>Scomber scombrus</i> )	Overall		369	
	Jm	14–29 (15.8–29.0)	176	Generalist planktivore
	M	29–35 (29.1–34.9)	132	Generalist planktivore
	L	35+ (35.2–47.5)	61	Generalist planktivore

Jm, juvenile-medium fish from half of length at maturity to length at maturity; Js, small juvenile fish of 3 cm to half of length at maturity; L, large fish above half-length at infinity; M, medium fish from length at maturity to half-length at infinity.

\*Taxa were ordered according to feeding guild. In this study, all size classes of plaice and sole were pooled to create one generic “Benthivore” guild, whereas they are classified as either “Coastal benthivores” or “Specialized benthivores” in Thompson et al. (2020) and Js horse mackerel were classified as “General planktivores,” whereas they are classified as “Zooplanktivores” in Thompson et al. (2020).



the relative contribution of benthic and pelagic organic matter for each fish consumer. In the English Channel, *A. opercularis* and calanoid copepod individuals were collected simultaneously with fish during the La CAMPagne MANche OCCidentale pluridisciplinaire survey in 2014 (Travers-Trolet and Verin 2014). Calanoid copepods were also collected during the Channel Ground Fish Survey in 2015 (Travers-Trolet 2015) and the International Bottom Trawl Survey in 2016 (Verin 2016). In the Celtic Sea, *P. maximus* individuals were collected simultaneously with fish during Évaluation Halieutique Ouest de l'Europe surveys in 2015 and 2016 (Leaute, Pawlowski, and Salaun 2015; Laute, Pawlowski, and Garren 2016) and from commercial fishing operations in 2015, and calanoid copepods during the Évaluation Halieutique Ouest de l'Europe survey in 2014 (Duhamel, Salaun, and Pawlowski 2014).

For each individual fish consumer, the relative contribution of pelagic (copepods) and benthic (*A. opercularis* and *P. maximus*) organic matter and trophic position was estimated with a mixing model taking into account the calculation of the benthic contribution and trophic position jointly using the formula proposed by Timmerman et al. (2021).

$$\alpha_i = \frac{\Delta^{15}\text{N} (\delta^{13}\text{C}_P - \delta^{13}\text{C}_F) + \Delta^{13}\text{C} (\delta^{15}\text{N}_F - \delta^{15}\text{N}_P)}{\Delta^{15}\text{N} (\delta^{13}\text{C}_P - \delta^{13}\text{C}_B) + \Delta^{13}\text{C} (\delta^{15}\text{N}_B - \delta^{15}\text{N}_P)}$$

This equation results from a combination of the equation used to calculate trophic level adapted to a two-source system (Post 2002b):

$$\text{TL}_{C,i} = \frac{\delta^{15}\text{N}_F - (\alpha\delta^{15}\text{N}_B + (1-\alpha)\delta^{15}\text{N}_P)}{\Delta^{15}\text{N}} + \text{TL}_{\text{baseline}}$$

and of a two-source mixing model equation (Phillips and Gregg 2003):

$$\begin{cases} \delta^{13}\text{C}_F = \alpha(\delta^{13}\text{C}_B + \Delta^{13}\text{C}) + (1-\alpha)(\delta^{13}\text{C}_P + \Delta^{13}\text{C}) \\ \delta^{15}\text{N}_F = \alpha(\delta^{15}\text{N}_B + \Delta^{15}\text{N}) + (1-\alpha)(\delta^{15}\text{N}_P + \Delta^{15}\text{N}) \end{cases}$$

Trophic level is then calculated by replacing  $\alpha$  by its value in the previous formula.

$\alpha_i$  is the fraction of the benthic source (i.e., benthic contribution), which varies from 0 (supported only by pelagic sources) to 1 (supported only by benthic sources), and  $\text{TL}_{C,i}$  is the combined trophic level for the individual fish consumer  $i$ ,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  the nitrogen or carbon isotopic composition, respectively, with subscript F, B, and P referring to the fish, and the benthic (*A. opercularis* and *P. maximus*) and pelagic (copepods) sources, respectively.  $\Delta^{13}\text{C}$  and  $\Delta^{15}\text{N}$  are the isotopic fractionation factor, which represents the enrichment in the heavier isotope ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) with each trophic level (i.e., the theoretical isotopic difference between a fish and its diet). The magnitude of this per trophic-step isotope fractionation ( $\Delta^{13}\text{C}$  and  $\Delta^{15}\text{N}$ ) has been set to the most classical

values, that is, 1‰ for carbon, and 3.2‰ for teleosts and 2.3‰ for chondrichthyans for nitrogen (Sweeting, Polunin, and Jennings 2006; Hussey, MacNeil, and Fisk 2010), as to cope with differential nitrogen assimilation between these groups (Chouvelon et al. 2012).  $\text{TL}_{\text{base}}$  is the baseline trophic level, here assumed to be 2 as the sources are primary consumers. To account for spatial variations in stable isotopic values, several isotopic baselines (i.e.,  $\delta^{15}\text{N}_B$  and  $\delta^{13}\text{C}_B$ ,  $\delta^{15}\text{N}_P$  and  $\delta^{13}\text{C}_P$ ) were considered by sampling different individuals of *A. opercularis* and *P. maximus* and copepods across the study area, that is, at the scale of the shallow, epi-continental English Channel to the deeper and stronger oceanic influence of the Celtic Sea (Supporting Information Fig. S1 and Table S3). This formula was aimed at tackling the methodological issue that  $\alpha$  and trophic level are linked: accurate calculation of trophic level requires knowledge of the actual contribution of each pathway to determine the best isotopic baseline, while estimating the baseline requires knowledge of the trophic level, to determine the fractionation factor value to apply (i.e.,  $\Delta\text{N} \times \text{TL}$ ). Recent Bayesian mixing models (e.g., tRophicPosition; Quezada-Romegialli et al. 2018) perform these calculations simultaneously, but produce outputs that are a distribution of  $\alpha$  and trophic level for a group of individuals, and not individual values, as required in this study. Nevertheless, recent analysis confirmed that results of both methods provide comparable results (Cresson et al. 2023).

Our analysis was performed at the functional group level rather than at the taxonomic level. To assess the strength of the benthic–pelagic coupling and the trophic structure of fish assemblages in relation to extrinsic (depth) and extrinsic factors (body size and feeding guild) across the English Channel–Celtic Sea continuum, we fitted community level and feeding guild-specific generalized linear models (GLMs). Individual fish were assigned to one of six feeding guilds (“Generalist planktivore,” “Zooplanktivore,” “Coastal benthivore,” “Specialist benthivore,” “Zoobenthivore,” and “Piscivore”). Guilds were defined by previous modeling and statistical analysis of the fish community composition in the North Sea by Thompson et al. (2020) based on extensive species diet and life stage data. Specifically, a guild was defined as a group of predators whose prey differentiates it from other predator guilds (Thompson et al. 2020). Following Thompson et al. (2020), each fish species was grouped into five size class categories (< 3 cm considered larvae [Lv]; small juvenile fish [Js] of 3 cm to half of length at maturity; juvenile-medium fish [Jm] from half of length at maturity to length at maturity; medium fish [M] from length at maturity to half-length at infinity and large fish [L] above half-length at infinity) to classify into the different feeding guilds (see specific details of feeding guild classification and diet differences between guilds in the supporting material of Thompson et al. 2020). Thompson et al. (2020) pooled data in this way for several reasons: (1) stomach contents analysis captures only a snapshot of a predator’s diet; (2) predators are typically gape-limited; (3) the developmental stage of fish is important for stock assessment; and (4) fishing is known to disproportionately remove large fish

from high trophic levels. In this study, the “Coastal benthivore” and the “Specialist benthivore” guilds ( $n = 44$  and  $n = 345$  individuals in this study, respectively) were pooled to create one generic “Benthivore” guild, and the “Zooplanktivore” guild ( $n = 20$ ) was included in the “Generalist planktivore” guild. This resulted in four feeding guilds identified: “Generalist planktivore,” “Piscivore,” “Zoobenthivore,” and “Benthivore” (Table 1). The “Zoobenthivore” guild consumed relatively high proportions of benthic dwelling shrimp and crabs (73.2%), but also fish (15%) and planktonic prey (11.7%), thus differentiating this guild from the “Benthivore” guild, which consumed high proportions of benthic prey (> 76.8%; see supplementary material of Thompson et al. 2020). The “Piscivore” group occurred in 119 stations, while the “Benthivore” (74 stations), “Generalist planktivore” (60 stations), and “Zoobenthivore” (23 stations) guilds represented a smaller fraction of the observations. Spatial distribution of observations and density plot of fish length for each species is given in Supporting Information Fig. S2.

The GLMs with a beta distribution (Cribari-Neto and Zeileis 2010) were fitted to the benthic contribution and GLMs with a Gaussian distribution and identity link function were fitted on trophic position. For all GLMs, body size and depth values were tested as the two continuous predictor variables, and the interaction between body size and depth was also tested as an interaction term in the models to account for potential variation in the slope of the relationship. For numerical stability, predictors were scaled and centered. Model selection was determined by manually running different combinations of covariates in a stepwise process starting from a full model including all the variables listed above including the interaction term to the null model. We tested the influence of within and between species variation (i.e., within guild differences) by running the GLMs at the community level with just feeding guild as the covariate. Significant differences were detected between guilds ( $p < 0.001$ ), indicating that variation between guilds was much greater than within guilds (see details in Supporting Information Table S4). Model parameters were estimated by maximization of the model likelihood. Models were ranked according to Akaike’s information criterion, which balances the goodness of fit by the number of parameters to favor model parsimony. Differences in Akaike’s information criterion less than 2 were considered not significant and the simpler model was selected to favor model parsimony. Assumptions of homoscedasticity and of normal distribution of residuals were confirmed with visual examination of residuals vs. fitted and Q–Q plots. The performance of the best fitted model was evaluated by examining spatial patterns in model residuals with correlograms, residual maps, and Moran’s  $I$ -test for spatial autocorrelation (Bivand and Wong 2018; Bjornstad 2022). Residual spatial autocorrelation was not observed ( $p > 0.05$  for every model). To explore how minimum and maximum benthic contribution and trophic position values increase with depth and body size, we used quantile regression procedures (Koenker 2024). In order to

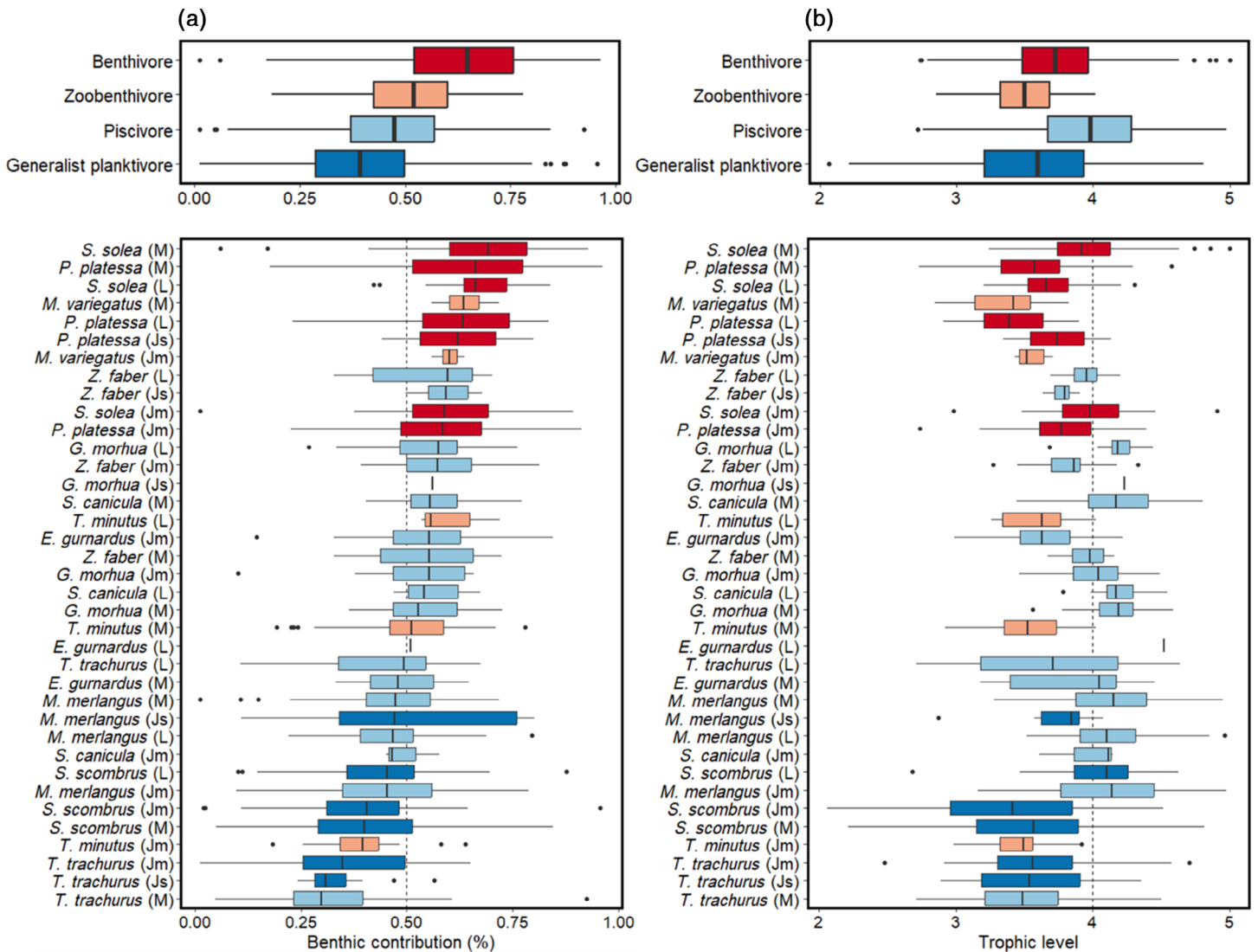
encompass a broad range, we used 5<sup>th</sup> and 95<sup>th</sup> quantiles for the lower and upper boundaries, respectively, similar to that used in comparable studies (e.g., Scharf, Juanes, and Rountree 2000; Costa 2009; Kopp et al. 2015). All data preparation and statistical analyses were conducted in the R programming environment (R Core Team 2022).

## Results

Benthic contribution was highest in the benthivore guild (Fig. 1a), with a median benthic contribution of 64.6% (including more than 50% for all *Pleuronectes platessa* and *Solea solea* size classes), indicating dependence on the benthic pathway as expected. The generalist planktivore guild belonged to the pelagic pathway with a median benthic contribution of 39.2%. Benthic contribution was lower than 50% for all size classes of *Scomber scombrus*, and smaller size classes of *Trachurus trachurus* and *Merlangius merlangus*. By contrast, zoobenthivore and piscivore guilds depended on both benthic and pelagic pathways with a median benthic contribution centered around 50% for both groups (51.9% and 47.2%, respectively).

The highest median trophic position values, that is, higher than trophic level 4, were mostly among piscivorous consumers (median trophic position of 4.0) that depended on both pathways (e.g., *Eutrigla gurnardus*, *Gadus morhua*, *Scyliorhinus canicula*, and medium- and large-size classes of *M. merlangus*; Fig. 1b; Table 1). Most fish consumers in the benthivore, zoobenthivore, and generalist planktivore guilds were centered at mid-trophic levels (median trophic position of 3.7, 3.5, and 3.6, respectively).

At the community level, the best model explaining benthic contribution included body size and depth (Supporting Information Table S1). Benthic contribution is rather constant with depth (even if the slope is statistically significant, the estimated slope value is very low = 0.0346,  $p < 0.05$ ; Fig. 2a). However, the observed range of values (as evidenced by the difference between the 5% and 95% quantiles in Fig. 2a) decreased with depth, resulting in smaller variations in benthic contribution with increasing depth. A significant positive increase in benthic contribution with increasing body size was found (slope = 0.0899,  $p < 0.001$ ; Fig. 2b). The range of values of the benthic contribution was larger for small fish than for larger individuals. The best model explaining trophic level in the fish community included body size, depth, and the interaction between body size and depth (Supporting Information Table S2). The trophic level of consumers significantly decreased with increasing depth (slope =  $-0.1806$ ,  $p < 0.001$ ; Fig. 2c). Observed change in trophic position (between shallower and deeper stations) was equivalent to one trophic level. The range of values decreased constantly with depth, with consumers with the highest average trophic level values (TL = 4.0) observed at shallow depths (< 20 m), and mid (TL = 3.5) and lower trophic level consumers (TL < 3.5) at deeper depths (> 120-m depth). The trophic level in the fish community increased significantly with increasing body size (slope = 0.1105,  $p < 0.001$ ; Fig. 2d).

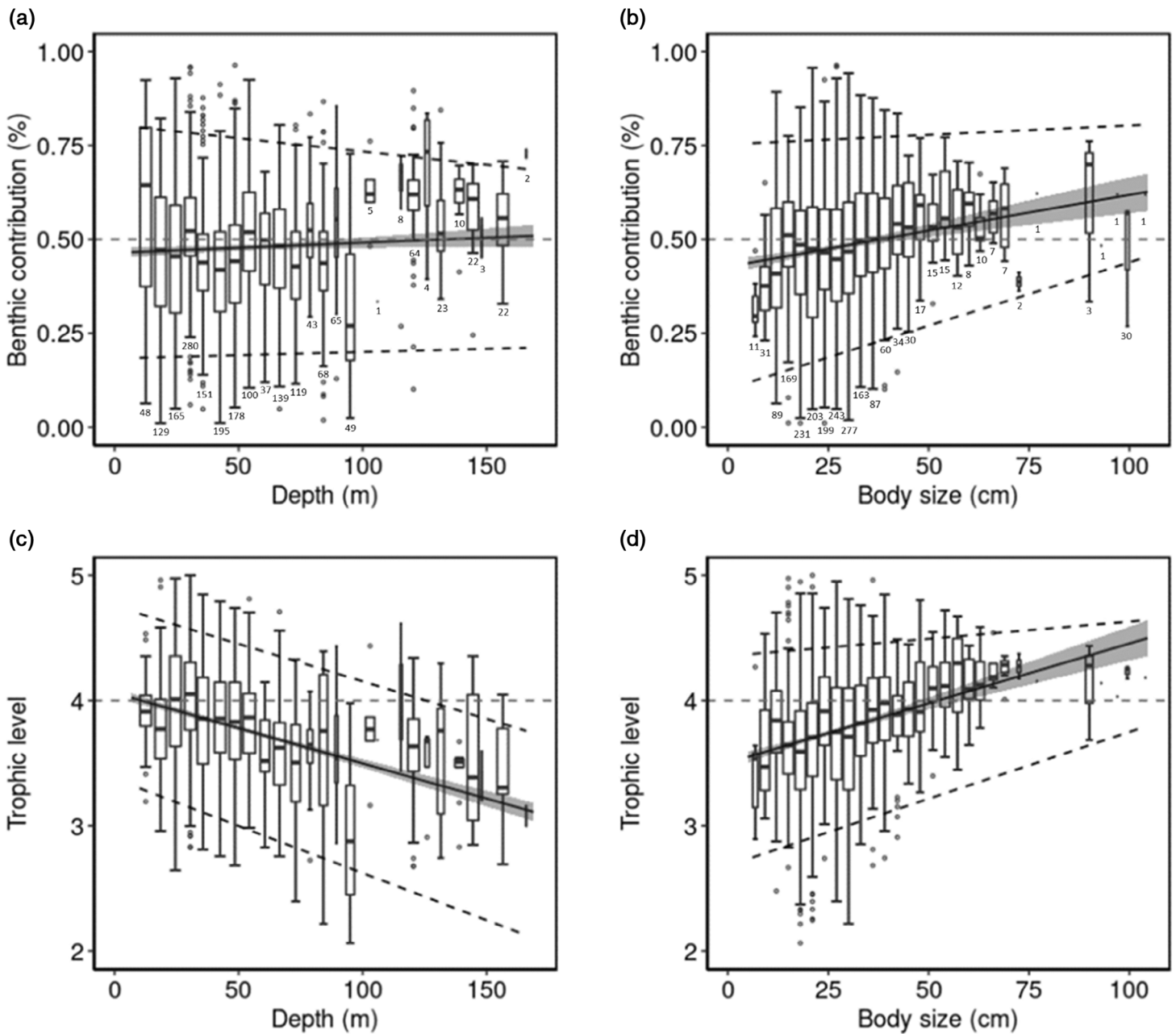


**Fig. 1.** Contribution of benthic source (a) and trophic levels (b) for the four fish feeding guilds (upper panels) and fish consumers (lower panels). Js, small juvenile fish of 3 cm to half of length at maturity; Jm, juvenile-medium fish from half of length at maturity to length at maturity; M, medium fish from length at maturity to half-length at infinity; L, large fish above half-length at infinity. Vertical gray dashed lines indicate equal contribution of pelagic and benthic pathways (a), and calculated trophic level of 4 (b).

Observed change in trophic position was equivalent to one trophic level (from approximately 3.5 at 10 cm to 4.5 at 100 cm). The width of the trophic spectrum, as evidenced by the variability in trophic level values, reduced for larger individuals compared to smaller sized fish.

Considering feeding guilds separately, benthic contribution increased significantly with increasing depth for piscivore fishes (slope = 0.0840,  $p < 0.001$ ; Fig. 3a), with values indicating reliance on both pathways at shallower depths (as evidenced by the difference between the 5% and 95% quantiles), but greater reliance on the benthic pathway (> 50% benthic contribution) at deeper depths (corresponding to > 100-m depth; Figs. 3a, 4). Generalist planktivore fish confirmed their pelagic affinity by staying in the pelagic pathway

(< 50% benthic contribution) even at shallower depths, while benthivore fish relied primarily on the benthic pathway whatever the depth stratum (> 50% benthic contribution; Fig. 4). Benthic contribution significantly increased with increasing body size for all feeding guilds (Fig. 3b; Supporting Information Table S1). For generalist planktivores, average benthic contribution ranged from 33% at 6.1 cm to 46% at 47.5 cm, corresponding to individuals at small and large size largely relying on the pelagic pathway. Piscivore fishes showed large variations in benthic contribution at smaller size (between 10.7 and 38.5 cm) mainly with values indicating reliance on the pelagic pathway (between 39% and 48% benthic contribution). Conversely, the observed range of the benthic contribution was smaller with increasing size, with values

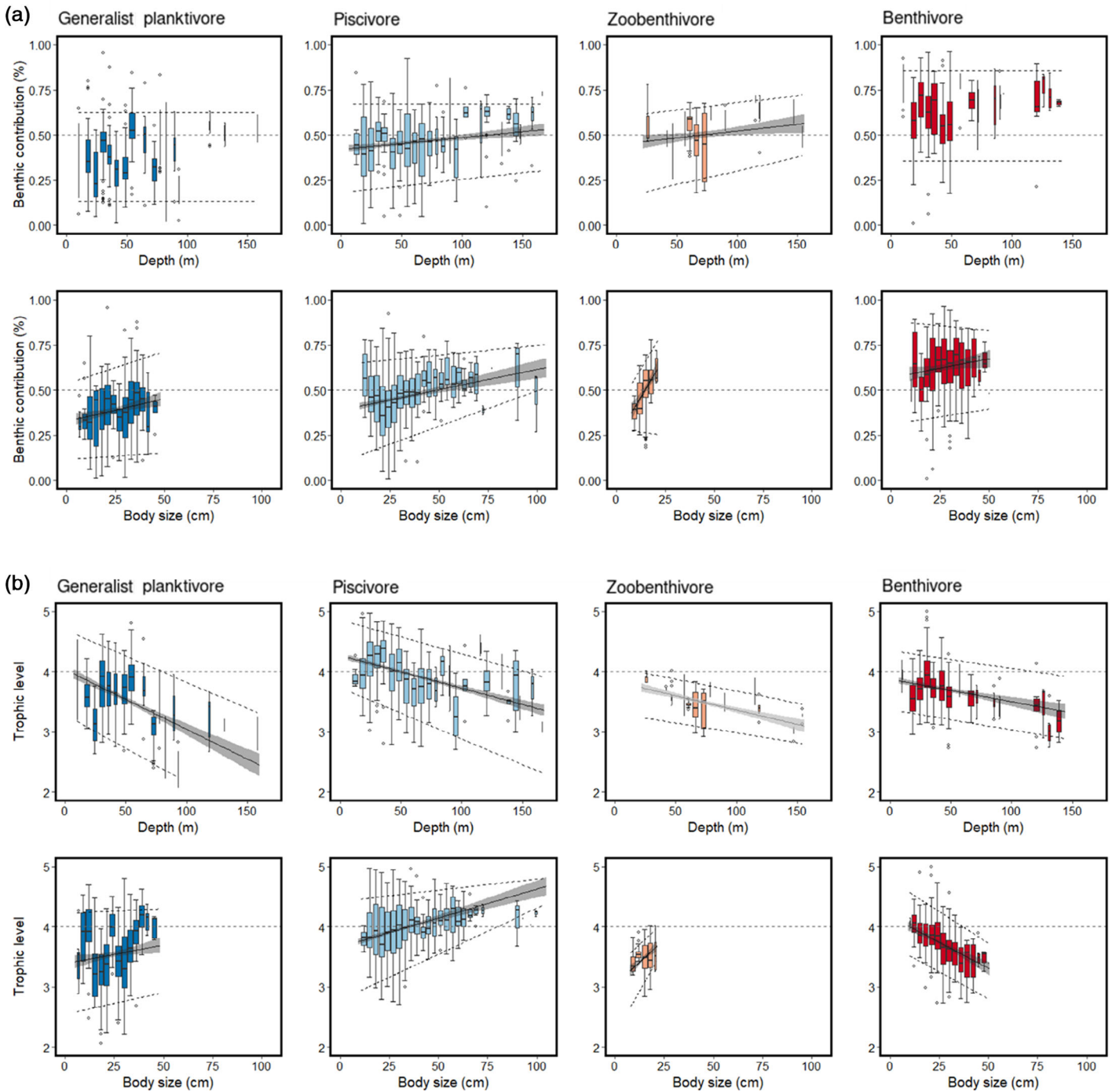


**Fig. 2.** Relationships between (a) benthic contribution and depth, (b) benthic contribution and body size, (c) trophic level and depth, and (d) trophic level and body size in the sampled fish community. Solid lines are prediction of the GLMs (see Supporting Information Tables S1 and S2) and shading around trend lines represents 95% confidence interval. The boxplots show the benthic contribution and trophic level for individuals in bins of 6-m depth and in bins of 3 cm body size, the midline of the box shows the median of the data, the limits of the box show the interquartile range, and the whiskers extend to a maximum of 1.5 times the interquartile range. Numbers represent the number of observations per bin (a, b). The black dashed lines represent the 5% and 95% quantiles of the observed distribution. Horizontal gray dashed lines indicate equal contribution of pelagic and benthic pathways (a, b), and calculated trophic level of 4 (c, d).

indicating reliance on both pathways at intermediate size, whereas larger individuals predominantly relied on the benthic pathway. Zoobenthivores displayed a strong change in average benthic contribution from small to larger size (from 40% at 8.0 cm to 60% at 21.0 cm). The interaction between body size and depth accounted for significant variation in the

slope of the relationship (slope =  $-0.3631$ ,  $p < 0.05$ ), which most likely resulted from the limited size range for this guild. For benthivore fish, average benthic contribution did not vary much with increasing size (from 59% at 10.2 cm to 67% at 50.1 cm), highlighting the importance of the benthic pathway for consumers closely related to the bottom.

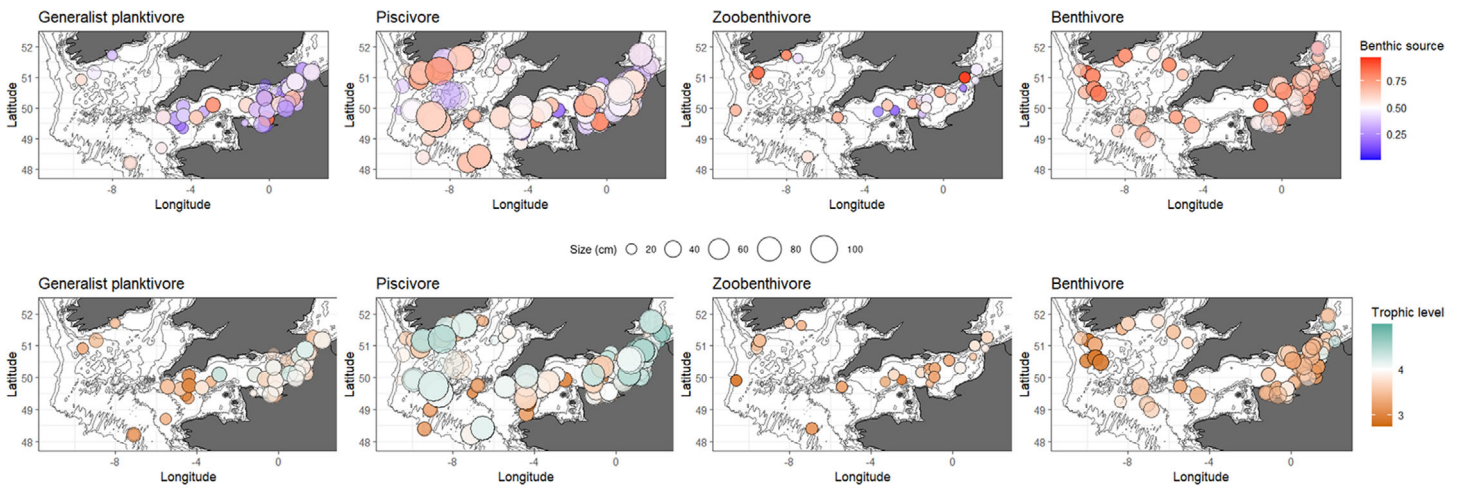




**Fig. 3.** Effect of depth and body size on estimated benthic contribution (**a**) and trophic level (**b**) in each of the four fish feeding guilds. Black solid lines indicate linear relationships predicted by the selected GLMs (see Supporting Information Tables S1 and S2). Shading indicates 95% confidence interval. The boxplots show the benthic contribution and trophic level for groups in bins of 6-m depth and in bins of 3 cm body size, the midline of the box shows the median of the data, the limits of the box show the interquartile range, and the whiskers extend to a maximum of 1.5 times the interquartile range. The black dashed lines represent the 5% and 95% quantiles of the observed distribution. Horizontal gray dashed lines indicate equal contribution of pelagic and benthic pathways (**a**), and calculated trophic level of 4 (**b**).

For trophic level, the best model for each feeding guild included body size and depth, and the interaction between body size and depth was also significant for the generalist

planktivore guild (Supporting Information Table S2). Trophic level was significantly higher at shallower depths compared to deeper depths for all feeding guilds as observed at the community



**Fig. 4.** Spatial distribution of benthic sources and trophic level by fish feeding guild across the English Channel–Celtic Sea Shelf continuum. Point sizes are proportional to the average total fish body length per station. Isobaths (black lines) are shown at 10-, 20-, 40-, 80-, 100-, 120-, 160-, and 200-m depth.

level (Figs. 2c, 3b). The amplitude of the change in average trophic position with depth was around one trophic level for generalist planktivore and piscivore fishes. Average trophic level decreased less with depth for zoobenthivores, and even to a lesser extent for benthivores (Figs. 3b, 4). The observed relationships between trophic level and body size are positive for piscivore and zoobenthivore, whereas benthivore fishes tended to have negative relationships. No significant change in average trophic level was detected for generalist planktivore fish. The interaction between size and depth accounted for significant variation in the slope of the relationship, with body size increasing slightly with increasing depth for this guild. The amplitude of the change in average trophic position with size was almost one trophic level for piscivore fishes (0.9 levels), but less for benthivore (0.7 levels) and other fishes (0.5 and 0.2 levels for zoobenthivores and generalist planktivores, respectively).

## Discussion

This study is based on more than 1900 fish individuals collected over 300,000 km<sup>2</sup>. Our analysis revealed that the relationship between trophic position and body size in fish communities greatly differs according to the level of biological organization (i.e., feeding guild). Indeed, consistent positive body size–trophic position relationships are not expected for all kinds of communities or taxa (Keppeler, Montaña, and Winemiller 2020). Trophic position increased significantly with body size in the whole community, consistent with the expectation that predator–prey relationships lead to powerful size-based trophic structuring (Trebilco et al. 2013). The most frequent pattern for feeding guilds was an increase in trophic position with increasing body size. However, the slope of the relationship was steeper in guilds supported by both pelagic and benthic pathways (piscivore and zoobenthivore guilds) than in those supported by the pelagic pathway (generalist planktivores).

The less steep slope of generalist planktivores may be related to species, such as forage fish and early life stages of taxa, that are not plastic, that is, always belonging to a pelagic-based pathway whatever the level of pelagic production. This is also consistent with stomach content analysis, with, for example, both mackerel (*S. scombrus*) and horse mackerel (*T. trachurus*) feeding on high proportions of krill and other zooplankton (Euphausiidae, Calanidae, and Temoridae) whatever the area (Thompson et al. 2020; Cresson et al. 2023), and exhibiting an overall opportunistic feeding strategy depending on the availability of prey (Kvaavik et al. 2020). The steeper relationships between trophic position and body size in piscivores and zoobenthivores was often more pronounced for the smaller size classes (as illustrated by the zoobenthivore guild at 10 cm length). This may be linked to ontogenetic changes in diet composition, including prey size and taxonomic identity, to meet energy requirements. Mouth gape limitation is an important element here, that is, as the predator grows, it will add larger prey to its diet to maximize energy demands (e.g., Keppeler, Montaña, and Winemiller 2020). In such cases, the bottom-up control exerted by the most abundant and easily accessible prey types should be much weaker as predatory fish are more selective about food resources (Petrik et al. 2019). The ontogenetic dietary shift should thus translate into a change of trophic level with body size. Stomach content studies confirm this hypothesis, with for example cod feeding on benthic prey whatever the body size, but shifting from amphipod and decapod larvae to fish and crustaceans as it grows (Fritsch 2005; Rault et al. 2017). The same is observed for whiting (*M. merlangus*) whose diet shifts from amphipods and mysids to fish with increasing predator size (Timmerman et al. 2020).

In contrast to the other three feeding guilds in this study, a decrease in trophic position with increasing body size was observed for benthivore fishes. These results confirm

negative or blurred relationships observed in ecosystem models between body size and trophic level of benthic species (Travers-Trolet et al. 2019). Contrary to predators with a more pelagic lifestyle, the patterns observed in bottom-orientated consumers may be linked to variation in the types and sizes of prey occupying benthic habitats. For example, species such as sole (*S. solea*) and plaice (*P. platessa*), whose diets consist of an abundance of disproportionately large benthic prey including invertebrate crustaceans as well as fish species such as sand lance (via opportunistic predation/scavenging of carrion/living organisms) often present disproportionately low predator–prey mass ratios (Scharf, Juanes, and Rountree 2000; Rijnsdorp and Vingerhoed 2001). An ontogenetic dietary shift could thus result in an inconclusive change in trophic position with size or decreasing trophic position with size. In their individual-based model, Travers-Trolet et al. (2019) showed that this emerging pattern in benthic fish varies spatially and is both explained by the spatial variability of prey availability and by the independence of trophic and size structures of benthic invertebrates. Thus, spatial heterogeneity and structurally complex benthic habitats may be linked to higher trophic specialization, further weakening the dependence of trophic position on body size in the benthic pathway.

Another interesting pattern to notice is a decreasing trophic niche breadth with increasing body size for piscivore fishes, such as cod starting at around 50 cm length (size class category from 45 to 75 cm, medium fish from length at maturity to half-length at infinity; Table 1), which appears to be a common phenomenon in large top predators (Scharf, Juanes, and Rountree 2000). This observed trend is consistent with theoretical expectations based on predator–prey mass ratios (i.e., a slower increase in predator–prey mass ratio with predator size leads to a slower rate of increase in trophic level with body size and a lower efficiency of trophic transfer at higher trophic levels and larger body sizes; Barnes et al. 2010), but different from other empirical studies (Costa 2009) and theoretical expectations based on fish metabolism, locomotion, and prey encounter (Arim et al. 2010; Keppeler and Winemiller 2020).

Cross-ecosystem differences in the supply of organic matter have been detected and related to fish assemblage structure and productivity (e.g., Udy et al. 2019). In this study, we considered depth as a proxy of the continuum between English Channel and Celtic Sea ecosystems. The highest variabilities in benthic contribution and higher trophic positions were observed in fish sampled in the English Channel. In contrast, smaller variations in benthic contribution and lower trophic positions were observed in the deeper areas of the Celtic Sea, notably with rather low trophic position values (< 3.5) for fish consumers located in deeper areas (> 100-m depth). High variance in benthic contribution and higher trophic positions in the consumer community at shallow depths is consistent with the hypothesis of stronger benthic–pelagic and pelagic–benthic couplings in coastal areas through plasticity in fish diet (Kopp et al. 2015; Giraldo et al. 2017; Timmerman

et al. 2021). Smaller variations in benthic contribution and lower trophic positions with increasing depth can be linked to a decoupling of benthic and pelagic pathways in deeper areas, corroborating previous studies that show depth is a major factor driving the degree of connectivity between pelagic and benthic systems from coastal to offshore areas (Kopp et al. 2015; Giraldo et al. 2017; Duffill Telsnig et al. 2019; Van Denderen et al. 2021). However, it is interesting to note the observed range of values with increasing depth, as evidenced by a decline in the 95% quantile whereas the 5% quantile remained relatively flat (Fig. 2a). The latter is unexpected since the benthic contribution should be higher at deeper depths. This unexpected pattern may be related to low production at deeper depths and higher contribution of pelagic sources via downward matter (i.e., debris) as observed in other systems (Hayden et al. 2019; Ying et al. 2020). In the Celtic Sea and neighboring shelf and slope systems, pelagic production has been shown to be the main source of organic matter fueling fish assemblages (Trueman et al. 2014; Silberberger et al. 2018; Day et al. 2019; Duffill Telsnig et al. 2019; Walters et al. 2021), whereas both benthic and pelagic production have similar importance to the whole food web in the semi-closed, shallow (< 80-m depth) English Channel ecosystem. This is due to upper consumers, mostly fishes, able to access and use both benthic and pelagic carbon sources regardless of their water column preference and the virtual absence of physical barriers (e.g., thermoclines), resulting in stronger pelagic–benthic coupling (Kopp et al. 2015; Giraldo et al. 2017; Cresson et al. 2020; Timmerman et al. 2021). In deeper areas of the Celtic Sea (> 100-m depth), the system is more structured by trophic level due to size-dependent predation (e.g., Day et al. 2019). In this study, fish more closely reflected their pelagic, benthic or demersal affinities with increasing depth linked to a decoupling of benthic and pelagic pathways in deeper areas. The results are consistent with a decrease in diet diversity of fish from shallow to deep areas in the Celtic Sea previously reported and related to changes in prey abundance and composition due to different habitats, as well as other abiotic conditions (Day et al. 2019; Walters et al. 2021).

We found that differences in basal food resources across the continuum do exist, as supported by the patterns observed for the different feeding guilds. In coastal areas, piscivores and zoobenthivores relied partly on pelagic sources at shallower depths whereas they focus more on benthic sources as depth increases. In contrast, depth was not identified as a factor influencing basal resource use in generalist planktivores and benthivorous fishes, confirming their dependency on pelagic and benthic pathways, respectively, whatever the depth stratum. Considering trophic level, piscivorous fishes had the highest average trophic positions throughout the depth continuum, and showed a consistent pattern of increasing dependence on benthic subsidies with increasing size and depth. They thus occur at the convergence of both benthic and pelagic pathways in shallow areas (high variability in benthic



contribution), while they largely rely on benthic pathways in decoupled deeper stations. This is consistent with stomach content analyses that showed large individuals of piscivorous fishes, namely cod, consume large quantities of benthic prey, such as malacostracans, in the deeper areas (> 120-m depth) of the Celtic Sea, indicating dependence mainly on the benthic pathway (Day et al. 2019). Large cod also prey on demersal (e.g., *Trisopterus esmarkii*, *Merluccius merluccius*, and *Micromesistius poutassou*) and pelagic (e.g., *T. trachurus*) fish species (Rault et al. 2017) that can consume benthic prey (Petrik et al. 2019; Cresson et al. 2023), which also explains the high benthic contribution (i.e., integration of benthic organic matter) in large piscivorous fishes. These predators can be expected to be important stabilizers across spatially heterogeneous landscapes, such as the English Channel–Celtic Sea continuum, by responding rapidly to fluctuations in resource abundance and coupling different habitats and food web compartments in space (McCann, Rasmussen, and Umbanhowar 2005; Rooney, McCann, and Moore 2008; Petrik et al. 2019). They lead to an integration of trophic levels/food web compartments, and hence produce an average and blur the differences between the pelagic and benthic pathways when moving up the food web, resulting in significant pelagic–benthic coupling across regions. Interestingly, zoobenthivore fishes had rather low median trophic positions (3.5) over much of the study area. This group contained small-sized benthic-demersal species (thickback sole and poor cod) that are constrained to feed on prey according to gape dimensions (Scharf, Juanes, and Rountree 2000), limiting their prey field to small bottom-dwelling organisms (Thompson et al. 2020).

The high variability in trophic positions observed in this study highlights foraging behavior on prey covering a wide trophic spectrum. However, median trophic position values for all feeding guilds differed by only 0.5 levels (trophic position of 3.5–4.0). Similarly, for the Bay of Biscay continental shelf, fishes were organized into functional/trophic groups comparable to those reported in this study (Lassalle et al. 2014): piscivorous demersal fish, piscivorous and benthivorous demersal fish, suprabenthivorous demersal fish, benthivorous demersal fish, and five groups of pelagic feeders (mean trophic position of 3.5–4.2). This kind of fish trophic structure was also observed in the neighboring Irish Sea and North Sea (Jennings and van der Molen 2015; Silberberger et al. 2018) and more broadly in other temperate continental shelf ecosystems (e.g., Woodland and Secor 2013).

While we observed significant relationships between resource use and trophic position values, they are highly dependent on the accuracy of the baseline isotope predictions derived from the two-source mixing model and the theoretical isotopic difference between a fish and its diet (i.e., the isotopic fractionation factor) used in this study. Moreover, calanoid copepods, which are used as a baseline for purely herbivorous feeding in this study could theoretically represent different trophic levels in themselves, if some omnivorous species are included (e.g., Chen et al. 2018). Additionally, in some areas where

baseline isotope data were scarce, such as in the western English Channel and southern extent of the Celtic Sea (Supporting Information Fig. S1), we know that our baseline correction may not be efficient enough and may have led to overestimates in the contribution of pelagic/benthic organic matter to fish food webs. At such a large spatial scale, it is of course also difficult to balance sampling effort across space and species. Inferences about the emerging patterns in relation to depth, body size, and feeding guild at the community and feeding guild level are therefore tentative due to small sample sizes, particularly for species in the zoobenthivore guild that were under represented in our sampling. Moreover, because fish samples were collected in winter across multiple years we were not able to assess temporal shifts in baseline isotope values. More readily available baseline data, and increased understanding of how energy and matter is transferred between different parts of the food web, from primary producers to top predators, within and across ecosystems, will enable greater capacity to map and predict estimates of resource use and trophic positions, while also accounting for variability in environmental conditions at particular spatial scales.

Finally, allocations to the different feeding guilds (Table 1) were directly taken from Thompson et al. (2020). However, some deviations from certain species' feeding behavior, as it has been documented in other studies, need to be highlighted as possible sources of bias. One example is the classification of all size classes of grey gurnard (*E. gurnardus*) to the piscivore guild. Yet, in this species ontogenetic shifts from a more invertebrate-based to a fish diet have been previously reported (e.g., Floeter and Temming 2005). Such a shift in grey gurnard prey composition has been observed from shallow to deep regions in the central North Sea (Weinert et al. 2010), which is particularly relevant for this current study. Another point is the classification of plaice and sole into one generic benthivore guild, whereas they are classified as either “coastal benthivores” or “specialized benthivores” in Thompson et al. (2020). Both species have quite different prey spectra, particularly in the adult stage. This can be inferred from previous studies presenting stomach content analyses, from both species' morphology or from general descriptions of the two species (Heessen, Daan, and Ellis 2023). Nevertheless, the results of this study highlight the need of using a common and comprehensive data source such as that provided by Thompson et al. (2020).

## Conclusion

Over a large spatial continuum of marine ecosystems, we showed here the relative importance of depth and body size as factors driving the trophic structure of marine fish communities, considering either all species jointly or separating feeding guilds. As depth controls the ability of fish to access trophic subsidies, it drives the intensity of benthic–pelagic coupling. Size controls the ability of fish to access prey, but was less important in benthic areas, consistent with the more size-



structured pelagic realm. Finally, biological differences between feeding guilds explained changes in matter fluxes and trophic structure at the community level, and confirms the efficiency of functional approaches to understand ecological mechanisms at fine scale.

### Author Contributions

Andrea Walters: Contributed substantially to the study's conception, data analysis, drafting the manuscript, and approved the final submitted manuscript. Dorothee Kopp: Contributed substantially to the study's conception, data acquisition and analysis, drafting the manuscript, and approved the final submitted manuscript. Pierre Cresson: Contributed substantially to the study's conception, drafting the manuscript, data acquisition and analysis, and approved the final submitted manuscript. Marianne Robert: Contributed substantially to the study's conception, data acquisition and analysis, drafting the manuscript, and approved the final submitted manuscript.

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### Conflicts of Interest

None declared.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article.

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