Title: Benthic food resources and the condition of bentho-demersal fish: spatial trends and relationships in the northern shelf of the Bay of Biscay.

Authors: Thomas Outrequin[1], Hubert du Pontavice [2], Jérôme Guitton[1], Pauline Boët[1], Jacques Grall[3], Pascal Laffargue[1], Hervé Le Bris[1]

Affiliation:

1. DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, IFREMER, Rennes, Nantes, France

2. IFREMER, HMMN, Laboratoire Ressources Halieutiques, F-14520 Port en Bessin, France

3. OSU UAR 313 IUEM, Univ Brest, CNRS, IRD, 29280 Plouzané, France

The authors made the following contributions. Thomas Outrequin: Conceptualization, Writing - Original Draft, Writing - Review and Editing; Hubert Du Pontavice: Conceptualization and Investigation; Jérôme Guitton: Methodology and Resources; Pauline Boët: Investigation and Resources; Jacques Grall: Writing - Review and Editing, Supervision; Pascal Laffargue: Writing - Review and Editing, Supervision; Hervé Le Bris: Writing - Review and Editing, Supervision.

Correspondence concerning this article should be addressed to Thomas Outrequin.

Postal address: 65 rue de Saint-Brieuc, Rennes, 35000, France

E-mail: thomas.outrequin@institut-agro.fr

Abstract:

To understand the trophic functioning of continental shelves, it is necessary to evaluate the factors that drive production at different levels. For bentho-demersal fish, one such factor is spatial variability in the biomass of their macrobenthic prey. In this study, we investigated the distribution of the macrobenthos in the northern part of the continental shelf of the Bay of Biscay in order to determine how variability in these prey resources might affect the bentho-demersal fish that feed on them. Due to the scarcity of available field data, an empirical graph model and a biochemical model were used to produce different indices of macrobenthic biomass, which were then used to generate three maps illustrating the distribution of this biomass in the Bay of Biscay. In general, values from these maps showed high Spearman correlations with the limited data available, but also discrepancies at greater depths where field data are quite poor. Globally, a pronounced decline in macrobenthic biomass was observed from the coast to offshore, but with particularly high values in deeper muddy sediments. Among eight fish species analyzed, the four most known for their strongly benthivorous diet demonstrated positive relationships between body condition and the macrobenthic biomass indices, with the strongest associations detected for smaller-sized fish. This suggests that biomass index maps may be i) indicative of the availability of benthic prey at the level of the continental shelf along a major coastal-offshore gradient, and ii) useful for studying spatial variability in the transfer of energy or matter along the food chain within this ecosystem. However, there is a clear need for macrobenthic data from field surveys at the shelf scale, notably in deep circalittoral areas, to confirm or improve the accuracy of the spatial biomass trends estimated by models.

Highlights:

- Estimates of macrobenthic biomass exhibited coastal-to-offshore trend on the shelf.
- The sparse field data macrobenthic biomass correlated with data from models.
- In deeper areas, muddy sediments contained the greatest macrobenthic biomass.
- Body condition of benthivorous fish improved with increased macrobenthic biomass.
- Diet literature suggests biomass maps reflect food resources beyond macrofauna.

Key words: Macrobenthic biomass, fish, body condition, continental shelf, food resource, Bay of Biscay

Introduction

The northwest Atlantic shelf is a vast area whose location between the continent and the ocean creates strong environmental gradients that influence ecological processes such as matter production and transfer (Hall, 2002). Within this ecosystem, benthic invertebrates play a preeminent role as a link between primary producers and top predators (Chen et al., 2021), particularly bentho-demersal fish. From the coast to the shelf break, strong declining gradients are typically observed in levels of nutrients, organic matter, and primary production, and it is generally assumed that the biomass and/or production of benthic invertebrates follow the same trend (Hall, 2002; Wei et al., 2010). Given the role of these invertebrates as prey for bentho-demersal fish (Amezcua et al., 2003; Armstrong, 1982; Day et al., 2019), it is likely that such spatial trends in food resources will have repercussions for fish populations across the continental shelf.

The northern part of the continental shelf of the Bay of Biscay offers an ideal location to study spatial trends in these prey resources--particularly in the macrobenthic component--and the consequences for the bentho-demersal fish that depend on them for food (*e.g.,* Lagardère, 1987; Le Loc'h and Hily, 2005). In this area, there is a strong terrigenous influence from the numerous small coastal rivers that flow onto the coastal fringe as well as two larger rivers, the Vilaine and the Loire (Borja et al., 2019). Given this, it is logical to expect a coastal-to-offshore gradient in the production or biomass of benthic invertebrates. However, to confirm this kind of trend, it would be necessary to have data covering the entire study area, as was done in the North Sea by Reiss et al. (2010). Unfortunately, the available data on macrobenthic biomass in the Bay of Biscay are scattered in time and mainly restricted to coastal areas or to specific shelf habitats (*e.g.,* mid-shelf fishing grounds) (Kopp et al., 2015; Le Loc'h et al., 2008; Rigolet et al., 2014; Robert, 2017). In such a case, though, it may be possible to estimate biomass using established models, such as the empirical model developed by Chassé and Glémarec (1976) based on depth and sedimentary substrates. More recently, mechanistic models like ERSEM (Kay et al., 2018) have also shown promise for predicting the spatial variability of macrobenthic biomass (*e.g.,* Timmermann et al., 2012).

Higher-quality habitats, such as those offering more food resources, are generally associated with improved body condition among predators (Engelhard et al., 2013; Liao et al., 1995). Therefore, it may be that patterns of abundance or scarcity of macrofaunal food resources across the shelf could translate

into spatial variability in the body condition of bentho-demersal fish predators. Within the Bay of Biscay, bentho-demersal fish communities have been well described (Souissi et al., 2001), and the diets of most species are known (*e.g.,* Rault et al., 2017; Day et al., 2020). With this information, it is possible to characterize the extent to which each species might be dependent on macrobenthic invertebrates. Moreover, thanks to the EVHOE sampling surveys (Laffargue et al., 2020), biometric data are available for multiple bentho-demersal fish species across several years. By analyzing patterns in macrobenthic biomass and the body condition of bentho-demersal fish—and taking into account the diet plasticity of these fish with respect to benthic macrofauna—it might be possible to detect the influence of spatial trends in benthic food resources on higher trophic levels. Such information can then be used to shed light on the broader trophic functioning of continental shelves.

The work presented here aimed to (1) describe spatial variability in macrobenthic biomass at the shelf scale in the Bay of Biscay based on data from models, (2) compare these data to the limited field data available, and (3) assess whether macrofaunal biomass data generated by such models exhibit a relationship with the body condition of bentho-demersal fish, and might thus be representative of the underlying availability of food resources.

2. Materials and Methods

2.1. Macrobenthic biomass indices

2.1.1. From an empirical biomass model (Chassé and Glémarec, 1976)

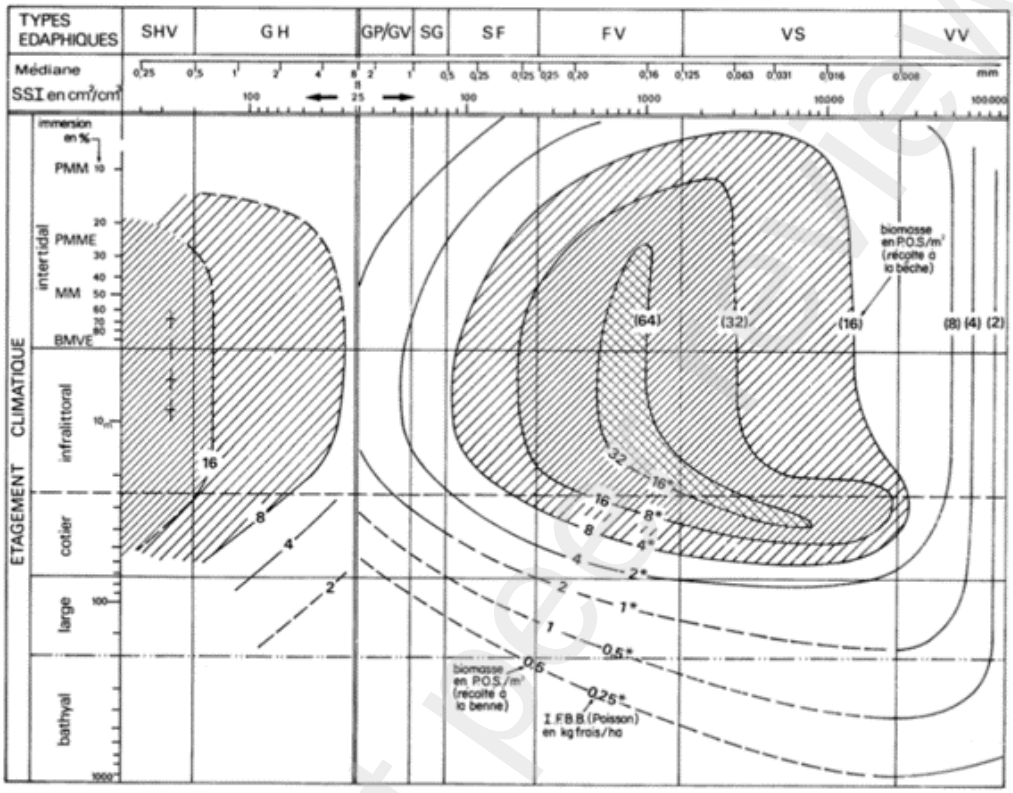


Figure 1: Graph model from Chassé and Glémarec (1976). Y-axis corresponds to logged bathymetric depth, and x-axis to granulometry divided into broad substrate categories.

The first model used to generate macrobenthic biomass indices was based on a graph of biomass isopleths created from grab samples in the Bay of Biscay (Chassé and Glémarec, 1976) (Figure 1). Depth data came from depth maps (GEBCO Bathymetric Compilation Group, 2023). This model is subsequently referred to as the “graph” model.

Biomass values were digitized from this graph (Figure 1) for each substrate category (silted heterogeneous sand (SHV), heterogeneous gravel (GH), clean/muddy gravel (GP/GV), coarse sand (SG), fine sand (SF), muddy fine sand (FV), sandy mud (VS), and pure mud (VV)), and for each bathymetric stratum (with a step of 10 m between 0 and 100 m depth, then from 100 to 200 m). Once rasterized, each cell was assigned a biomass value (in $g.m^{-2}$ dry weight (DW)) corresponding to the lower-bound isopleth. The maximal cell value was 32 $g.m^{-2}$ DW, associated with shallow muddy fine

sand (FV). Finally, macrobenthic biomass values were assigned to each sub-section (substrate category and bathymetric stratum), corresponding to the averaged biomass value over the proportion of cells. This process provided an average value of macrobenthic biomass for each substrate category and bathymetric stratum.

The first substrate map used was the 'Atlas du littoral français: Atlas des fonds meubles du plateau continental du Golfe de Gascogne [Atlas of the French coastline: Atlas of the soft bottoms of the continental shelf of the Bay of Biscay]' obtained from the same study as the graph model described above (Chassé and Glémarec, 1976). The map of biomass indices resulting from this first substrate map is hereafter referred to as the 'Biomass$_{1976}$ map'. The second substrate map used is more recent than the first (Vasquez et al., 2023) and is based on a more-extensive dataset describing the nature of the seabed. We adapted the substrate categories in this map to correspond to those of the biomass graph model based on a comparative analysis of the two substrate maps (results are in Supplementary Materials 1). The second map of biomass indices is subsequently referred to as the 'Biomass$_{2023}$ map'.

Some approximations were necessary for certain areas (5% of the shelf surface for Biomass$_{1976}$ and Biomass$_{2023}$ maps) where the substrate x bathymetry intersection was not represented in the graph model, and biomass data were not available. These areas were approximated by another substrate with similar levels of macrobenthic biomass and similar trends along the depth gradient. For the Atlas substrate maps, biomass values for muddy/clean gravel (GP/GV) were approximated by biomass from coarse sand (SG) below 80 meters depth, and biomass values from muddy heterogeneous sand (SHV) were approximated by biomass from muddy fine sand (FV) below 50 meters depth. For the more-recent substrate maps, biomass values of gravel and coarse sand from the graph model were averaged (GP/GV and SG) for the "coarse substrate" category. Descriptions of the substrate categories of the graph model and the two substrate maps are available in Supplementary Materials 2.

2.1.2. From a biogeochemical model (POLCOMS-ERSEM)

The second set of modeled data used to generate a macrobenthic biomass index came from a mechanistic biogeochemical model. The data originated from the outputs of the POLCOMS-ERSEM model, a regional high-resolution coupled hydrodynamic-ecosystem model for low trophic levels, driven by a reanalysis of data from the period 2000–2015 (Kay et al., 2018). POLCOMS-ERSEM links a general ocean circulation model, POLCOMS (the Proudman Oceanographic Laboratory Coastal Ocean

Modelling System) and a marine ecosystem model, ERSEM (European Regional Seas Ecosystem Model; Butenschön et al., 2016). It covers the European shelf seas, with a horizontal resolution of 0.1° (around 11 km). As we are interested in the biological part of the model, we will refer to it subsequently as the ERSEM model. In this model, three groups represent the bulk of macrobenthic biomass, and they were initially calibrated using data estimated by Bryant *et al.* (1995) based on macrobenthic biomass values in the North Sea. We selected deposit- and suspension-feeding groups as the macrobenthic components of interest (the only other group, 'meiobenthos', was not considered).

Biomass values were summed from all suspension and deposit feeders in ERSEM to create a macrobenthic biomass index. Macrobenthic biomasses were averaged over the last 10 years (2006–2015) to minimize potential yearly effects. The macrobenthic biomass index from ERSEM was expressed in gC/m² and the map of these values is referred to here as the "$Biomass_{ERSEM}$ map".

2. 2. Biological field data

2.2.1. Biomass of macrobenthic invertebrates

Macrobenthic biomass indices from the three biomass maps described above were compared to field data collected in the circalittoral area (*i.e.,* less than 15 m depth) of the northern part of the shelf of the Bay of Biscay. Table 1 provides a summary of the various surveys from which data on macrobenthic biomass were obtained; the spatial distribution of sampled stations (from 2 to 5 grabs per station) is presented in Figure 2. As seen in this figure, these data are very sparse over both time and space, and no single survey covers the full extent of the continental shelf.

Table 1: Summary of different macrobenthic surveys in which biomass data were collected, with the gear used, the time of the year, the year sampled, the average bathymetry (and its range), and the number of stations for each.

Survey	Sampling gear	Time	Bathymetry	N	Reference
RetroB	Van Veen grab	March (2008)	20.1 (15-25.6)	17	(Le Bris, 2008)
Nurse2008	Van Veen grab	August - September (2008)	21.8 (16.3-35.3)	20	(Brind'Amour, 2008)
PLOOPS 1	Van Veen grab	July (2009)	27.6 (23-35)	18	(Dubois, 2010a)
PLOOPS 2	Van Veen grab	February - November (2010)	25.5 (21.3-32.8)	24	(Dubois, 2010b)
Isobaie 2	Van Veen grab	June (2010)	77.3 (18.9-154)	11	(Le Bris, 2010)
FEBBE 1	Day grab	May - August (2013)	101.3 (78-113)	18	(Laffargue, 2013a)
FEBBE 2	Day grab	August (2013)	101.9 (91-113)	23	(Laffargue, 2013b)
APPEAL1	Hamon grab	May (2018)	60.7 (53-74)	15	(Le Loc'h and Grall, 2018a)
APPEAL 2	Hamon grab	August (2018)	59.2 (52-73)	15	(Le Loc'h and Grall, 2018b)
APPEAL 4	Hamon grab	September (2019)	109.5 (98.4-125.1)	12	(Le Loc'h and Grall, 2019)

RetroB and Nurse2008 were two surveys performed in a coastal bay (Bay of Vilaine) (Brind'Amour, 2008; Le Bris, 2008), in a shallow circalittoral area under the terrigenous influence. PLOOPS 1 and 2 surveyed a coastal area in the Bay of Concarneau (Dubois, 2010a; Dubois, 2010b), which, although it also features a shallow circalittoral fringe, has less terrigenous influence compared to the Bay of Vilaine. APPEAL 1 and 2 focused on the deeper limit of the shallow circalittoral fringe, to the south of the island of Groix (Le Loc'h and Grall, 2018a; Le Loc'h and Grall, 2018b). APPEAL 4 and FEBBE 1 and 2 surveyed a deep circalittoral muddy bank, the so-called "Grande Vasière" (Laffargue, 2013a; Laffargue, 2013b; Le Loc'h and Grall, 2019). Finally, Isobaie 2 covered an coastal-to-offshore transect from the Loire estuary and Bay of Vilaine towards the shelf break (Le Bris, 2010).

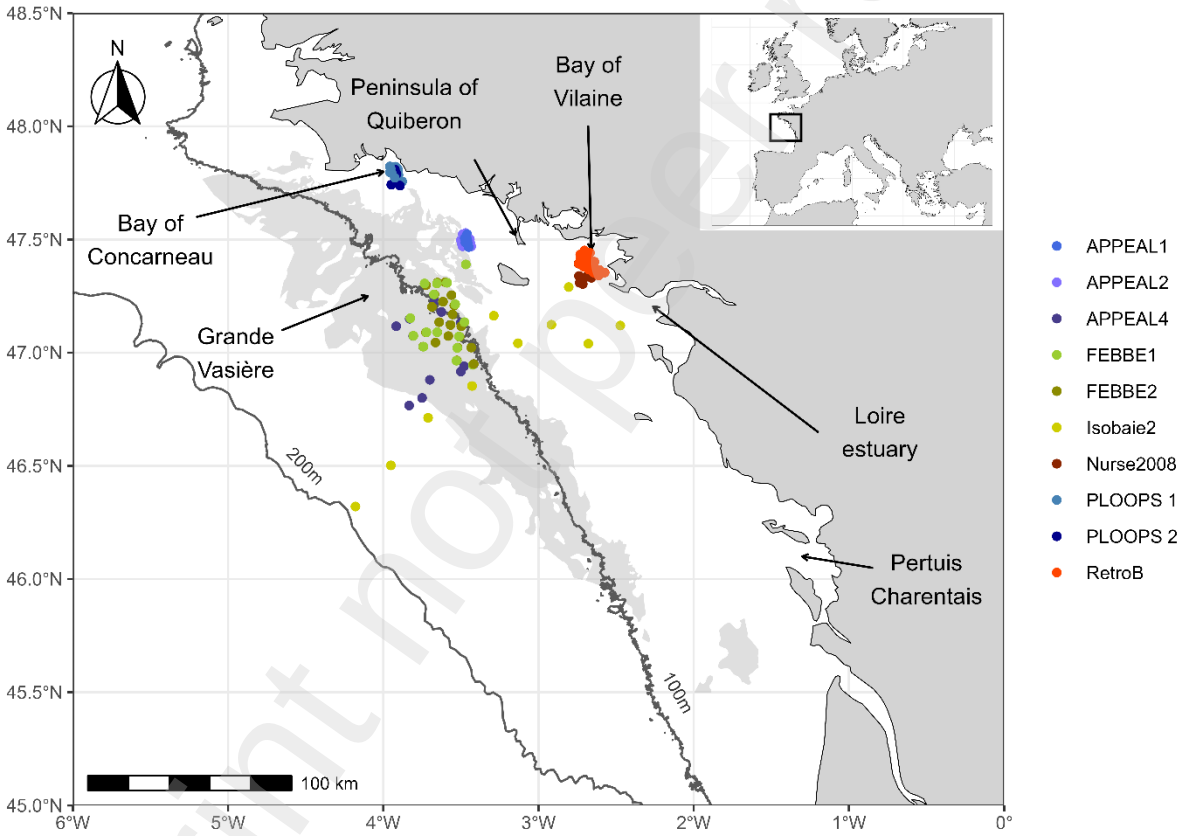


Figure 2: Locations of macrobenthic field observation stations on the northern shelf of the Bay of Biscay. Different surveys are represented with different colors. The light gray shaded area is the mid-shelf mud belt known as the "Grande Vasière".

Each survey counted taxa down to the lowest taxonomic level, and biomass was measured for most of the taxa, sampled stations, and studies. When individual mass was not available, it was approximated using values from the closest phylogenetic relative from the same station or from a neighboring station of the same survey. Biomass values in wet weight were converted into ash-free dry

weight using Brey's conversion factors (www.thomas-brey.de/science/virtualhandbook). For each station, observed macrobenthic biomass was the average of the values obtained from two to five replicates.

2.2.2. Data on individual bentho-demersal fish

Individual biometric data (total length and mass) from autumnal EVHOE surveys (between 2008 and 2022, onboard Thalassa R/V) were used to assess the body condition of a limited selection of bentho-demersal fish species. Body condition is ultimately a reflection of a fish's habitat quality, and consequently also of food resource availability (Cavraro et al., 2019; Karlson et al., 2018; Liao et al., 1995; Schloesser and Fabrizio, 2019). We examined most of the benthivorous species for which sufficient data were available across the continental shelf (Supplementary Materials Figure SM4 and SM5). Four demersal species were considered: whiting (*Merlangius merlangus*), striped red mullet (*Mullus surmuletus*), poor cod (*Trisopterus minutus*), and pout (*Trisopterus luscus*). Four benthic taxa were also considered: scaldfish (*Arnoglossus* spp.), small-spotted catshark (*Scyliorhinus canicula*), common sole (*Solea solea*), and thickback sole (*Microchirus variegatus*). *Arnoglossus* spp. includes both *A. laterna* and *A. imperialis*, which are assumed to have a similar diet (Castro et al., 2013), and the combination of the two made it possible to cover a wide coastal-to-offshore gradient.

2.3. Data analysis

2.3.1. Comparison of macrobenthic biomass indices from models

Once we had generated the maps of the three macrobenthic biomass indices, we compared the spatial patterns presented. Each map was standardized and gridded with the 0.1° x 0.1° ERSEM grid, and each grid cell was assigned an average biomass index value (weighted by the surface area of each biomass value within the grid cell). $Biomass_{ERSEM}$, $Biomass_{1976}$, and $Biomass_{2023}$ were then compared using Spearman correlations. Specifically, for a given cell, a buffer area of 5 cells was considered (resulting in a 25-cell window) and Spearman correlations were computed for the values of each biomass map in this window, allowing us to highlight potential differences in spatial trends between the different maps. Negative values meant that the two maps in question depicted opposite trends in macrobenthic biomass. All analyses were conducted using R 4.3.1 (R core team, 2023); maps were processed using the raster and sf packages (Hijmans, 2023; Pebesma, 2018).

206 **2.3.2. Comparison between field data on macrobenthic biomass and biomass indices**
207 **from models**

208 Macrobenthic biomass indices from the three maps generated here were compared to values
209 of macrobenthic biomass from field datasets. For this, the nearest macrobenthic biomass values from
210 each of the three maps were assigned to each field station sampled, and these values were averaged
211 within a 500-m buffer surrounding the station. Values from biomass index maps and field values were
212 log-transformed and normalized so that the final data ranged between 0 and 1. Then, Spearman
213 correlations were calculated between macrobenthic biomass values from field data and indices from
214 models.

215 **2.3.3. Relationship between body condition and macrobenthic biomass indices**

216 Fish body condition was assessed using the body condition factor developed by Le Cren (1951),
217 which represents 'the deviation of an individual from the average weight for length' in a given population.
218 Le Cren's condition factor, K_n, compensates for allometric changes, enabling comparisons of body
219 condition between small and large individuals. Indeed, the response of body condition to macrobenthic
220 resource availability may vary in a size-dependent manner due to trophic shifts and diet plasticity.

221 For each species, log length-mass relationships (LMR) were fitted using individual biometric
222 data. Observations with a Cook's distance greater than 4/n (n = number of observations) were
223 considered outliers and removed (Altman and Krzywinski, 2016). For each species, homogeneity of
224 variance and the normal distribution of residuals were checked visually.

225 K_n is the observed individual mass divided by the predicted mass according to each species'
226 LMR. To take into account ontogenic variations, individuals were split into two size groups, to reflect the
227 trophic size thresholds reported in the literature for six of the fish species (Table 2).

228 Finally, we created mixed-effect linear models to assess the relationship between the body
229 condition factor and the macrobenthic biomass indices. One model was computed for each of the eight
230 fish taxa and the three macrobenthic biomass index maps ($Biomass_{1976}$, $Biomass_{2023}$, and
231 $Biomass_{ERSEM}$), and fitted using the lme4 R package (Bates et al., 2015). Models were computed with
232 station as a random effect to account for intra-station correlations (Zuur et al., 2009) and also included
233 a size category effect (*i.e.,* Small or Large), with the exception of the models for *Arnoglossus* spp. and

Microchirus variegatus. Each station was assigned the average value of macrobenthic biomass within a 5000-m buffer around its location. The sensitivity of results to this buffer was explored, and no major differences were observed when comparing results from 1-km to 50-km buffers. Macrobenthic biomass indices were scaled to allow the comparison of their respective effects on K_n. Chi-squared tests were used to evaluate these results against the null hypothesis (*i.e.,* a model without a biomass effect). During model evaluation, mixed-effect linear models were refitted using maximum likelihood, and only significant models (p-value < 0.05) were kept. Additionally, the variance explained by selected mixed-effect linear models was computed using conditional R-squared and marginal R-squared values; conditional R-squared included random and fixed effects of the model, while marginal R-squared corresponded to the variance explained only by the fixed effect (Zuur et al., 2009).

Since the spatial extent of the biomass maps varied, the amount of data per species and size class available for the mixed-effect linear models also differed. The quantity of data used for each mixed-effect linear model and each macrobenthic biomass model is provided in Table SM6.

Table 2: Size thresholds used to account for ontogenic shifts in different fish species.

Species	Size shift	Trophic shift	Reference
Arnoglossus spp.	-		(Schückel et al., 2011)
Merlangius merlangus	20	Shift from benthic invertebrates to fish.	(Hislop et al., 1991)
Microchirus variegatus	-		(Amezcua et al., 2003)
Mullus surmuletus	18	Shift from benthic invertebrates to shrimp, ophiurids, and polychaetes.	(Bautista-Vega et al., 2008)
Scyliorhinus canicula	22	Shift from small invertebrates to larger decapods, cephalopods, and fish.	(Šantić et al., 2012)
Solea solea	30	Shift toward epibenthic decapods and higher trophic level.	(Fanelli et al., 2022)
Trisopterus luscus	25	Shift from benthic invertebrates towards shrimp and fish.	(Armstrong, 1982)
Trisopterus minutus	17	Shift from small crustaceans to larger decapods and fish.	(Armstrong, 1982)

3. Results

3.1. Maps of macrobenthic biomass indices

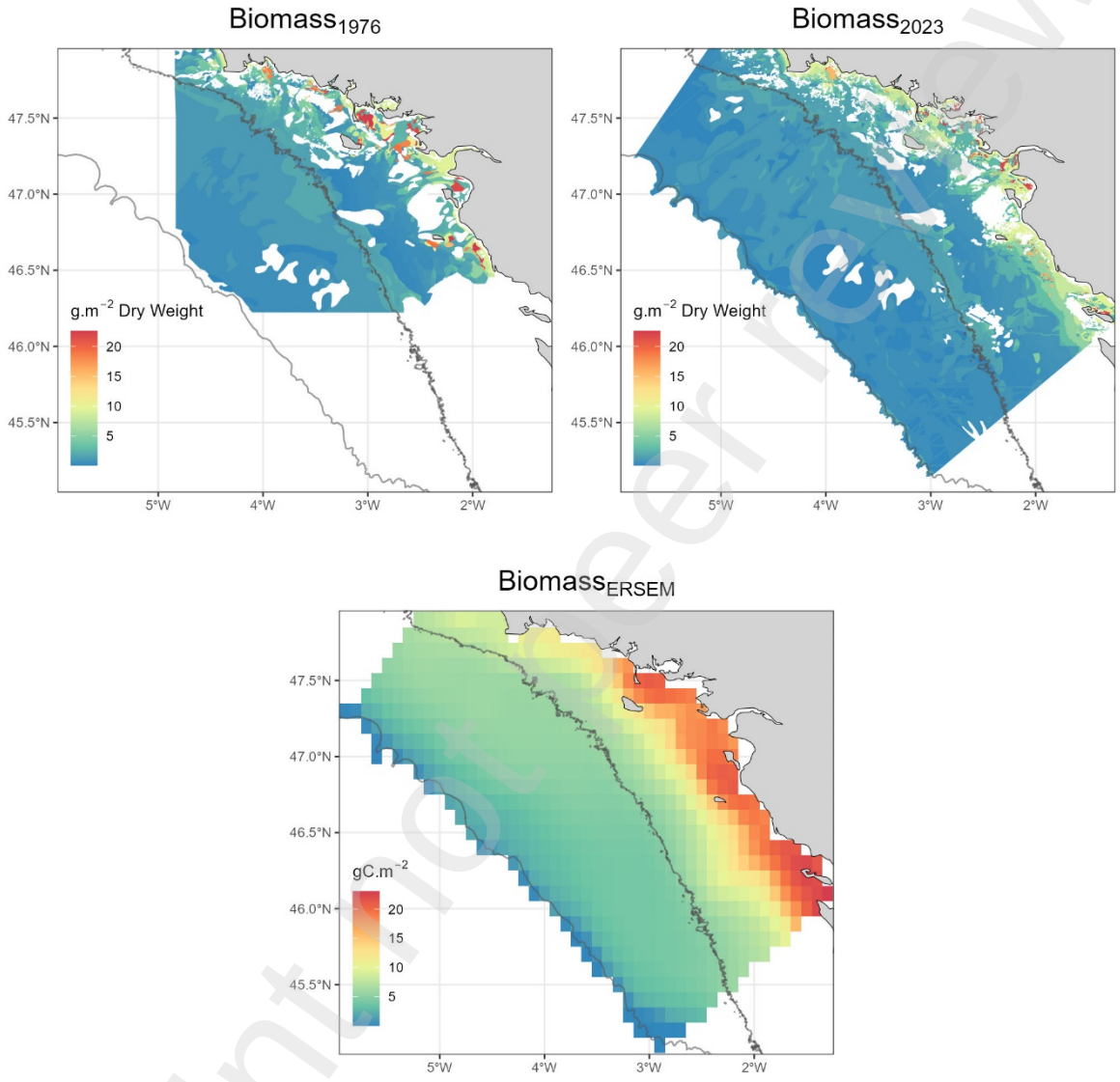


Figure 3: Maps of macrobenthic biomass indices obtained from the graph and ERSEM models. White areas in the Biomass$_{1976}$ and Biomass$_{2023}$ maps correspond to hard bottom substrate, where soft bottom macrobenthic biomass could not be assessed. Gray lines represent the 100- and 200-meter isobaths.

The Biomass$_{1976}$ and Biomass$_{2023}$ maps highlighted high values of macrobenthic biomass along the coast, in concentrated areas characterized by shallow patches of mud, sandy mud, and muddy sand

substrate. Instead, index values from the $Biomass_{ERSEM}$ map were higher along a coastal fringe ranging from the Pertuis-Charentais to the peninsula of Quiberon (Figure 3).

The $Biomass_{ERSEM}$ map depicts a decreasing gradient in biomass towards the shelf break, inversely related to water depth, while the $Biomass_{1976}$ and $Biomass_{2023}$ maps highlight patches of substrate at moderate depths that support higher macrobenthic biomass. Overall, the $Biomass_{1976}$ and $Biomass_{2023}$ maps were highly correlated (Spearman correlation = 83.09%), while the $Biomass_{ERSEM}$ map exhibited a weaker correlation with the two others (49.82% and 62.84%, respectively). The most substantial differences were noted between the $Biomass_{1976}$ and $Biomass_{ERSEM}$ maps; patches corresponding to certain habitats (*e.g.,* the large mud belt in the central part of the shelf, or at the edge of the continental shelf) exhibited opposing trends in macrobenthic biomass between these two maps (Figure 4).

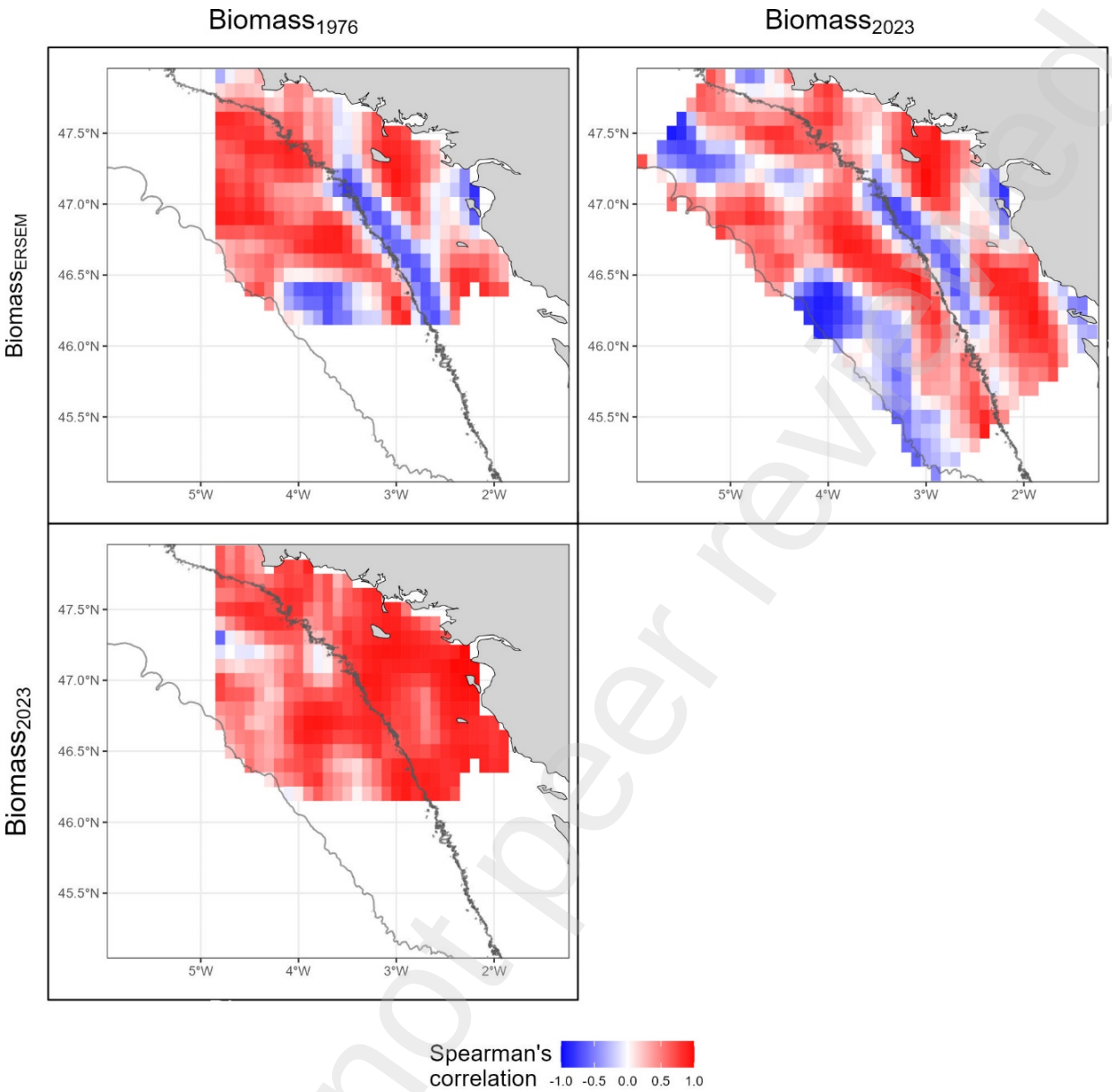


Figure 4: Maps of local Spearman correlations, with blue representing negative correlations and red positive correlations. Gray lines represent the 100- and 200-meter isobaths.

3.2. Biomass indices from models *versus* field biomass data

Despite differences in absolute trends, positive Spearman correlations were detected between the three indices of macrobenthic biomass and field data on macrobenthic biomass (60.4%, 66.9%, and 77.5% for $Biomass_{1976}$, $Biomass_{2023}$, and $Biomass_{ERSEM}$, respectively; Figure 5). Based on the ERSEM model, the highest level of biomass was predicted for stations located at 15–20 m depth. Instead, the graph model ($Biomass_{1976}$ and $Biomass_{2023}$) estimated the highest levels of biomass at a depth of 20-50

m, and similar, lower, levels between stations at 15–20 m and 50–75 m. Most of the stations that were estimated to have high biomass levels (from $Biomass_{1976}$ and $Biomass_{2023}$) were sampled as part of the PLOOPS surveys (Figure SM7). The bathymetric gradient previously noted in the $Biomass_{ERSEM}$ index is also evident in Figure 5, as stations tended to aggregate along the y-axis according to their bathymetry. This pattern was less marked for the $Biomass_{1976}$ and $Biomass_{2023}$ indices, which generated similar estimates of biomass at depths of 50–75 m and 75–100 m.

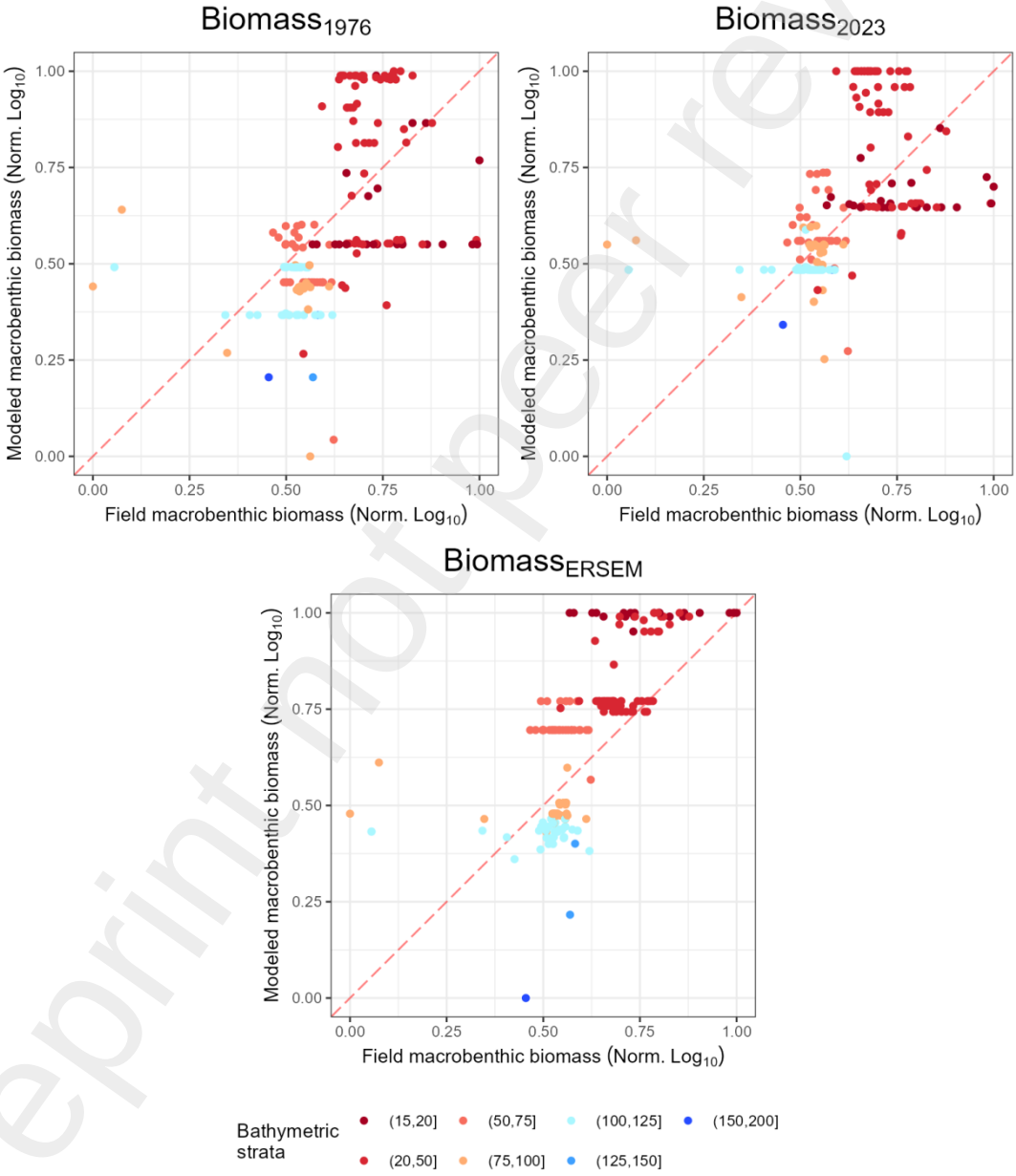


Figure 5: Modeled macrobenthic biomass indices versus *field data on macrobenthic biomass. Stations are colored according to their bathymetric range, with red shades for shallower depths and blue for deeper ones. The red dashed line corresponds to the isoline.*

3.3. Relationship between body condition and macrobenthic biomass indices

Of the numerous mixed-effect linear models we constructed to test the effect of the macrobenthic biomass indices as predictors of body condition in various fish species, 15 detected significant effects, *i.e.*, a macrobenthic biomass index explained significantly more variance than the null model (Table 3). No such models were found for *Trisopterus minutus* and *Scyliorhinus canicula*, and only one significant model was obtained for *Microchirus variegatus* and for *Merlangius merlangus*. Instead, significant positive relationships were found between the three macrobenthic biomass indices and body condition factors for the species *Arnoglossus spp.*, *Mullus surmuletus*, *Solea solea*, and *Trisopterus luscus*. The level of variance explained remained globally low, with the maximum observed for the relationship between body condition in *Mullus surmuletus* and the $Biomass_{1976}$ index (14.7%) (Table 3). On average, *Mullus surmuletus* and *Arnoglossus* spp. were the two taxa with the highest amount of variance explained by macrobenthic biomass indices.

Table 3: Summary of mixed-effect linear models that identified a significant relationship between macrobenthic biomass indices and body condition factors of fish. Chi2 and p-value correspond to the test of the model against a null model including only an intercept and the random effect of station. R2m is the marginal R-squared value and R2c is the conditional R-squared value.

Macrobenthic index	Species	R2m	R2c	Chi2	p-value
$Biomass_{1976}$	*Arnoglossus spp.*	0.143	0.419	5.4	2.01e-02
	Mullus surmuletus	0.147	0.327	14.94	1.87e-03
	Solea solea	0.038	0.197	18.46	3.53e-04
	Trisopterus luscus	0.066	0.183	8.11	4.38e-02
$Biomass_{2023}$	*Arnoglossus spp.*	0.073	0.383	4.01	4.52e-02
	Merlangius merlangus	0.014	0.183	9.22	2.65e-02
	Mullus surmuletus	0.085	0.313	15.54	1.41e-03
	Solea solea	0.034	0.18	19.84	1.83e-04
	Trisopterus luscus	0.072	0.229	20.18	1.56e-04
$Biomass_{ERSEM}$	*Arnoglossus spp.*	0.126	0.43	5.87	1.54e-02
	Microchirus variegatus	0.131	0.464	5.33	2.10e-02
	Mullus surmuletus	0.1	0.301	23.67	2.93e-05

Solea solea	0.038	0.184	20.22	1.53e-04
Trisopterus luscus	0.085	0.238	22.64	4.80e-05

In all taxa in which a significant relationship was detected between body condition and macrobenthic biomass, the relationship was positive; the only exception to this was found in *M. merlangus*. Additionally, these relationships were stronger (steeper slope) for smaller-sized individuals, although this pattern was identified for large individuals of *Mullus surmuletus* as well.

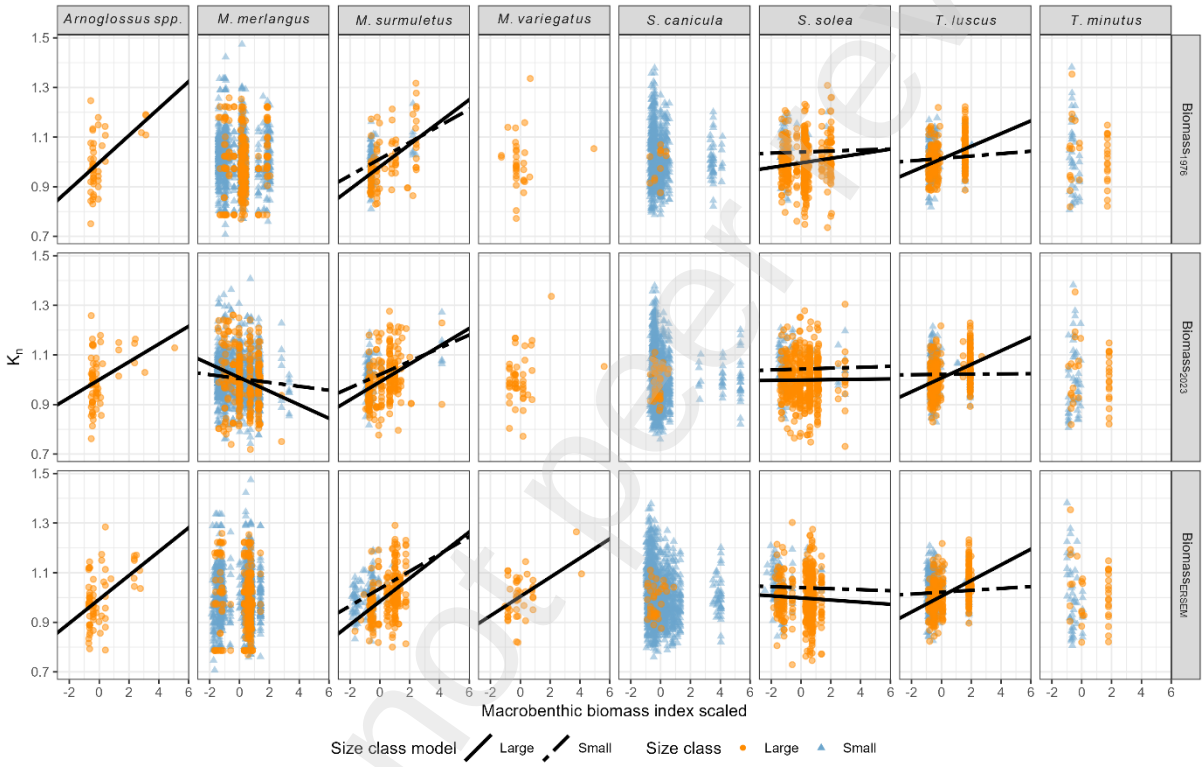


Figure 6: Significant linear mixed-effect models selected. Data used to fit models are shown here; orange dots correspond to small individuals and blue triangles to larger ones.

The only species for which K_n exhibited a steep negative relationship with macrobenthic biomass was *Merlangius merlangus*. For *Solea solea,* instead, larger individuals seemed to show higher values of K_n, with only a very weak (positive or negative depending on the biomass index) relationship with macrobenthic biomass indices.

4. Discussion

The northern part of the shelf of the Bay of Biscay is a particularly productive ecosystem, supporting both pelagic and benthic trophic pathways (Cresson et al., 2020) that provide essential resources for fish species. One such resource is the macrobenthos; these organisms are a key food source for bentho-demersal fish, which tend to be opportunists that will eat whatever benthic prey is available (Day et al., 2019; Rault et al., 2017). However, spatial variability in macrobenthic biomass on this shelf remains largely unexplored. To date, quantitative data on macrobenthic biomass in the Bay of Biscay are limited to very coastal areas (*e.g.,* Dutertre et al., 2013) or specific habitats (*e.g.,* muddy areas like the Grande Vasière; (Le Loc'h et al., 2008). The benthic characteristics of these areas have been extrapolated to the entire shelf through ecosystem modeling (Lassalle et al., 2011). The present study aims to fill this gap by analyzing the spatial distribution of macrobenthic biomass over the whole northern shelf of the Bay of Biscay and evaluating the relationship between variations in this biomass and the fish that feed (to a greater or lesser degree) on the macrobenthos. The lack of field data on macrofaunal biomass in much of the study area prompted us to explore and use existing models, of which two were particularly relevant to our objective and the marine region we were studying.

The empirical "graph model" from Chassé and Glémarec (1976) is based on depth and sediment typology, with the assumption that hydro-sedimentary characteristics drive ecological processes and features of macrobenthic communities (Glémarec, 1969; McArthur et al., 2010; Reiss et al., 2015). The graph model was defined on the basis of a limited number of sediment classes, reflecting the substrate distribution presented in the "Atlas des fonds meubles du plateau continental Nord Gascogne" [Atlas of the French coastline: Atlas of the soft bottoms of the continental shelf of the Bay of Biscay] (Chassé and Glémarec, 1976). This modeling strategy is comparable to the habitat suitability modeling framework adopted by Degraer et al. (2008), since the map involved an initial biophysical dataset and spatial interpolation from this dataset with physical data maps.

In the ERSEM model, which is part of the POLCOMS-ERSEM biophysical model, macrobenthic biomass of suspension and deposit feeders is the direct result of flows from ecological processes (primary production, organic matter sedimentation) that supply the seafloor. Bentho-pelagic coupling models like the ERSEM model have already demonstrated their ability to accurately represent macrobenthic biomass at a small scale (Ehrnsten et al., 2019). This model also incorporates other

processes, such as organic matter ingestion or bioturbation (Butenschön et al., 2016)—but not the remobilization of buried organic matter (Butenschön et al., 2016)—that could boost macrobenthic biomass (Qin et al., 2010) and benefit the benthos during periods of low input (Zhang et al., 2019). However, the ERSEM model is only based on muddy sediments and, unlike the graph model, does not account for spatial variability in substrate types, despite the critical role these characteristics play in the modeled processes and in determining benthic invertebrate biomass. Indeed, the nature of a substrate reflects numerous features and processes (*e.g.,* permeability, deposition, resuspension, organic content, among others) (Chen et al., 2018; Idier et al., 2010; Pace et al., 2021) that can influence macrobenthic characteristics and biomass (Ehrnsten et al., 2019; Pearson and Rosenberg, 1978).

The graph and ERSEM models reproduced biomass gradients that were largely similar to each other, particularly in the overall decrease from the coast to the shelf break and the presence of heterogeneous coastal zones with high biomass. This gradient is indicative of a significant terrigenous influence, one whose intensity increases with proximity to river outlets (Loire and Vilaine estuaries), particularly in the southeastern region of the study area. However, there were substantial differences between the two types of models. The two maps derived from the graph model showed discontinuities in this biomass gradient, with distinct patches of high biomass values, particularly in the muddiest zone (the Grande Vasière). With the graph model, the use of the most recent substrate map only marginally changed the distribution of biomass; this was unsurprising given that these maps largely reproduce substrate data from previous versions and retain high local uncertainties due to their extremely heterogeneous spatial sampling coverage and limited sedimentary field data (Kaskela et al., 2019; Pierrejean et al., 2022). Instead, the biomass distribution provided by the ERSEM model was much less patchy, illustrating the more continuous nature of the spatial distribution of the variables used to estimate biomass, especially because this model does not take into account sedimentary substrate features.

Based on an exhaustive census of surveys and research projects carried out over the last decade, we gathered all available field data on spatial variability in macrobenthic biomass in the study area. A preliminary analysis of the data highlighted not only spatial gaps (especially between 120 and 200 m) but also heterogeneity in the sampling gear used (3 types) and in the years (10 years from 2008 to 2019) and months/seasons (from March to November) in which samples were collected. Keeping in mind these limitations, when these data were standardized and examined at a broad scale, they seemed to describe a depth gradient roughly comparable to those we estimated from models (Spearman

correlations ranging from 60% to 80%). Even the limited amount of field data we were able to find is useful in understanding the strengths or deficiencies of the models. For example, when comparing coastal areas, the ERSEM model seemed to better reflect the reality of the observed biomass difference, which was lower in the Bay of Concarneau (PLOOPS surveys) than in the Bay of Vilaine (RetroB and Nurse2008 surveys). This difference was reversed in the graph model, which seemed to underestimate macrobenthic biomass in pure muddy substrates such as those found in the Bay of Vilaine (Le Bris and Glémarec, 1995). This may reflect the fact that terrigenous influences, which are known to increase benthic biomass (Deubel et al., 2003; Escobar-Briones and Soto, 1997; Zuschin and Stachowitsch, 2009), were not taken into account in the graph model, which only considered depth and sediment type. This point was discussed by Dutertre *et al.* (2013), who explained that in the shallow part of the Bay of Biscay, although 26% of macrobenthic diversity patterns could be explained by substrate, hydrodynamics, and depth, the inclusion of parameters quantifying riverine influence (Vilaine and Loire) made it possible to explain an additional 16%.

For both types of models, there is a notable deficiency at the continental shelf edge. The absence of a peak in macrobenthic biomass at the shelf edge seems to indicate that the two models ignore the hydrological context of the shelf break, where biological production is stimulated by upwelling (Simpson and Sharples, 2012; Vandromme et al., 2014). Although limited field data were available in this area, some of the deepest field observations could indicate the presence of a peak; such a pattern would be consistent with estimates made by Le Loc'h *et al.* (2008) at three sampling stations in the slope area, which they compared to the highly productive mud zone in the middle of the continental shelf.

By analyzing the relationship between fish body condition and macrobenthic biomass indices, our aim was to explore the impact of the distribution of food resources on the shelf as indicated indirectly by the macrobenthic component. In our study, the relationship between macrobenthic biomass indices and body condition factor (K_n) was significant and positive for four of the eight bentho-demersal fish species tested. These relationships were similar for all models of macrobenthic biomass and for most of the fish species examined, which emphasizes the importance of the coastal-to-offshore gradient in the spatial distribution of macrobenthic food resources. It also suggests bottom-up processes in which food availability may be a determining factor, as seen in other contexts (Brosset et al., 2015; Laurel et al., 2001; Porath and Peters, 1997).

In many cases, the presence or absence of significant relationships can be explained by the trophic or life-history characteristics of the species analyzed. Among the different species studied, whiting (*Merlangius merlangus*), poor cod *(Trisopterus minutus*), and small-spotted catshark (*Scyliorhinus canicula*) exhibited a negative or non-existent relationship between body condition and biomass indices. For whiting, this could be explained by the fact that the diet of small individuals (less than 22 cm) is both pelagic and benthic, while that of larger individuals is also based on pelagic and demersal fishes (Day et al., 2019). This feeding characteristic is shared by the poor cod, which has a very generalist diet featuring macrobenthic, suprabenthic, and pelagic prey, including fish at larger sizes (Armstrong, 1982). The small-spotted catshark is also thought to feed on pelagic resources such as euphausiids (Rodríguez-Cabello et al., 2007), which are often found near the continental slope of the Bay of Biscay (Peña et al., 2019), where the fish in our study were mainly found. For these species, the absence of significant relationships with macrobenthic biomass may reflect dietary compensation with pelagic prey when benthic food resources are less available.

Compared to the other flatfish studied, the common sole (*Solea solea*) did not exhibit a strong positive relationship between body condition and macrobenthic biomass indices, even though it is mostly benthivorous (Lagardère, 1987; Rault et al., 2017). For small sole individuals, whose distribution is more coastal than that of large individuals, it is difficult to find an explanation for this weak relationship. For large individuals, which are mainly found further offshore (Figure SM5), the relatively high body condition scores in an area of poorer macrobenthic biomass may be related to the fact that these individuals have accumulated reserves in more coastal areas during the summer period (Rijnsdorp, 1990), before migrating offshore in the autumn (where they were sampled) to reproduce a few months later (Le Bec, 1983). This may not be the case for the other fish that did show a relationship between their body condition and macrobenthic biomass, such as *Arnoglossus* spp. and *M. surmuletus,* which are known to reproduce later than the common sole (Gibson and Ezzi, 1980; N'Da and Déniel, 1993).

In the case of pout (*Trisopterus luscus*), only the smaller individuals demonstrated a strong positive relationship between body condition and macrobenthic biomass. The small individuals of this species are known to feed mainly on macrobenthic and suprabenthic invertebrates (Castro et al., 2013), while the diet of larger individuals includes fish (Armstrong, 1982). Scaldfishes (*Arnoglossus* spp.) and the two age classes of striped red mullet (*M. surmuletus*) also exhibited strong relationships between body condition and macrobenthic biomass indices. Scaldfishes feed mainly on suprabenthic

invertebrates (Castro et al., 2013), but also on macrofauna and even benthic fish (Déniel, 1981). Striped red mullet feed on epibenthic crustaceans (*e.g.,* Galatheidae and Portunidae) but mainly rely on more infaunal prey such as bivalves or polychaetes (Pavičić et al., 2018; Serrano et al., 2003). Unlike these other species, thickback sole (*M. variegatus*) demonstrated a relationship only between its body condition and the macrobenthic biomass index from the ERSEM map. Its diet relies heavily on benthic macroinvertebrates (Amezcua et al., 2003; King and Fives, 1990) and it is difficult to explain why the relationship was not established using the data from the other two maps.

With the diets of these species in mind, it seems justifiable to assume that the macrobenthic biomass maps also represent a wider range of benthic prey, such as suprabenthic prey which are less effectively sampled by grabs (Sorbe, 1981). The various relationships observed between fish body condition and biomass maps illustrate both differences among fish species in their dependence on benthic resources as well as variability in the availability of such resources. Certain areas (*e.g.,* coastal habitats or mudflats like the Grande Vasière) offer better feeding conditions for benthic-feeding fishes. In such areas, competition between benthic feeders is reduced through processes such as individual specialization (Sánchez-Hernández et al., 2021). Areas with scarcer benthic resources, such as deeper zones (*e.g.,* in the vicinity of the shelf edge), may instead experience heightened intra- and interspecies competition (Holbrook and Schmitt, 1989). This could drive adaptive strategies such as shifts to (i) prey with lower energy content, with consequences for fish growth and body condition (Cormon et al., 2016; Hiddink et al., 2016; Kamimura et al., 2021) and/or (ii) prey at higher trophic levels as suggested by the isotope study of Schaal et al. (2016). This highlights the trophic plasticity of fish with respect to conditions of resource availability or competition (Pelage et al., 2022). Our study supports the idea that demersal fishes generally depend on trophic resources at spatial scales that are smaller than that of the continental shelf, a hypothesis that has already been corroborated by different approaches (*e.g.,* Chouvelon et al., 2012). Our body condition results are also consistent with the trends reported by Schaal et al. (2016) regarding the trophic levels of demersal fishes along the coastal-to-offshore isotopic gradient, which were characterized by a trophic shift that those authors hypothesized to be due to lower prey abundance offshore.

5. Conclusion

By providing visual representations of the spatial distribution of benthic resource availability, the macrobenthic biomass maps analyzed here could be valuable tools in the study of spatial variability in trophic networks, bentho-pelagic coupling, and matter fluxes on the continental shelf. The two models we used to estimate macrobenthic biomass had different strengths and limitations based on the different modeling assumptions employed. Nevertheless, both models, which are based on different ecological hypotheses, revealed similar coastal-to-offshore distribution trends, with notable differences in the mid-shelf and near-coastal areas. Unfortunately, few of Europe's continental shelves (*e.g.,* in the North Sea; Reiss et al., 2010) have been sampled thoroughly enough to effectively reveal benthic biomass gradients on a large spatial scale. These data are crucial for understanding certain processes affecting marine populations or, more recently, for the development of ecosystem models (*e.g.,* Lassalle et al., 2011; Corrales et al., 2022; Lopez De Gamiz-Zearra et al., 2023), especially in deeper areas where macrobenthic samples are limited (*e.g.,* beyond the Grande Vasière in the Bay of Biscay).

To better understand the functioning and status of fish populations, our study highlighted the importance of recognizing spatial variability in the macrobenthic resources on which these fish depend. The coastal-to-offshore gradient in macrobenthic biomass, and its relationship with body condition in certain bentho-demersal fish, raises an important question about the viability of deeper populations. This question is all the more crucial in the context of climate change: for example, deepening mechanisms have been clearly demonstrated in bentho-demersal fish on the continental shelves of the northeast Atlantic (*e.g.,* Dulvy et al., 2008) and their impact on the populations of the species concerned has yet to be fully assessed.

Acknowledgements:

The authors wish to thank the crew of each survey, as well as the technicians involved in the sampling at sea during surveys and in the laboratory. The authors also wish to thank Stanislas Dubois, François Le Loc'h, and Anik Brind'Amour for providing access to the data from the surveys they directed. We thank Plymouth Marine Laboratory and Susan Kay for providing the POLCOMS-ERSEM projections. This work was supported by a PhD grant from the project Bentroph, which was co-funded by the Brittany region and IFREMER.

References

Altman, N., Krzywinski, M., 2016. Analyzing outliers: influential or nuisance? Nature Methods 13, 281–282. https://doi.org/10.1038/nmeth.3812

Amezcua, F., Nash, R., Veale, L., 2003. Feeding habits of the Order Pleuronectiformes and its relation to the sediment type in the north Irish Sea. Journal of the Marine Biological Association of the UK 83, 593–601. https://doi.org/10.1017/S0025315403007525h

Armstrong, M.J., 1982. The predator-prey relationships of Irish Sea poor-cod (Trisopterus minutus L.), pouting (Trisopterus luscus L.) and cod (Gadus morhua L.). ICES Journal of Marine Science 40, 135–152. https://doi.org/10.1093/icesjms/40.2.135

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Soft. 67. https://doi.org/10.18637/jss.v067.i01

Bautista-Vega, A.A., Letourneur, Y., Harmelin-Vivien, M., Salen-Picard, C., 2008. Difference in diet and size-related trophic level in two sympatric fish species, the red mullets Mullus barbatus and Mullus surmuletus, in the Gulf of Lions (north-west Mediterranean Sea). Journal of Fish Biology 73, 2402–2420. https://doi.org/10.1111/j.1095-8649.2008.02093.x

Borja, A., Amouroux, D., Anschutz, P., Gómez-Gesteira, M., Uyarra, M.C., Valdés, L., 2019. The bay of biscay, in: World Seas: An Environmental Evaluation. Elsevier, pp. 113–152. https://doi.org/10.1016/B978-0-12-805068-2.00006-1

Brind'Amour, A., 2008. NURSE 2008 cruise,Gwen Drez R/V. https://doi.org/10.17600/8050080

Brosset, P., Ménard, F., Fromentin, J.-M., Bonhommeau, S., Ulses, C., Bourdeix, J.-H., Bigot, J.-L., Beveren, E.V., Roos, D., Saraux, C., 2015. Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. Marine Ecology Progress Series 529, 219–231. https://doi.org/10.3354/meps11275

Bryant, A.D., Heath, M.R., Broekhuizen, N., Ollason, J.G., Gurney, W.S.C., Greenstreet, S.P.R., 1995. Modelling the predation, growth and population dynamics of fish within a spatially-resolved shelf-sea ecosystem model. Netherlands Journal of Sea Research 33, 407–421. https://doi.org/10.1016/0077-7579(95)90055-1

Butenschön, M., Clark, J., Aldridge, J.N., Allen, J.I., Artioli, Y., Blackford, J., Bruggeman, J., Cazenave, P., Ciavatta, S., Kay, S., Lessin, G., van Leeuwen, S., van der Molen, J., de Mora, L., Polimene, L., Sailley, S., Stephens, N., Torres, R., 2016. ERSEM 15.06: a generic model for marine biogeochemistry and the ecosystem dynamics of the lower trophic levels. Geosci. Model Dev. 9, 1293–1339. https://doi.org/10.5194/gmd-9-1293-2016

Castro, N., Costa, J.L., Domingos, I., Angélico, M.M., 2013. Trophic ecology of a coastal fish assemblage in Portuguese waters. Journal of the Marine Biological Association of the United Kingdom 93, 1151–1161. https://doi.org/10.1017/S0025315412001853

Cavraro, F., Bettoso, N., Zucchetta, M., D'Aietti, A., Faresi, L., Franzoi, P., 2019. Body condition in fish as a tool to detect the effects of anthropogenic pressures in transitional waters. Aquat Ecol 53, 21–35. https://doi.org/10.1007/s10452-018-09670-4

Chassé, C., Glémarec, M., 1976. Atlas du littoral français : Atlas des fonds meubles du plateau continental Du Golfe de Gascogne. Cartes biosédimentaires 28.

Chen, D., Wang, Y., Melville, B., Huang, H., Zhang, W., 2018. Unified Formula for Critical Shear Stress for Erosion of Sand, Mud, and Sand–Mud Mixtures. Journal of Hydraulic Engineering 144. https://doi.org/10.1061/(ASCE)HY.1943-7900.0001489

Chen, Y.-Y., Edgar, G.J., Fox, R.J., 2021. The Nature and Ecological Significance of Epifaunal Communities within Marine Ecosystems, in: Oceanography and Marine Biology. CRC Press, Boca Raton, pp. 585–719. https://doi.org/10.1201/9781003138846-9

Chouvelon, T., Spitz, J., Caurant, F., Mèndez-Fernandez, P., Chappuis, A., Laugier, F., Le Goff, E., Bustamante, P., 2012. Revisiting the use of δ15N in meso-scale studies of marine food webs by considering spatio-temporal variations in stable isotopic signatures – The case of an open ecosystem: The Bay of Biscay (North-East Atlantic). Progress in Oceanography 101, 92–105. https://doi.org/10.1016/j.pocean.2012.01.004

Cormon, X., Ernande, B., Kempf, A., Vermard, Y., Marchal, P., 2016. North Sea saithe Pollachius virens growth in relation to food availability, density dependence and temperature. Marine Ecology Progress Series 542, 141–151. https://doi.org/10.3354/meps11559

Corrales, X., Preciado, I., Gascuel, D., Lopez de Gamiz-Zearra, A., Hernvann, P.-Y., Mugerza, E., Louzao, M., Velasco, F., Doray, M., López-López, L., Carrera, P., Cotano, U., Andonegi, E., 2022. Structure and functioning of the Bay of Biscay ecosystem: A trophic modelling approach. Estuarine, Coastal and Shelf Science 264, 107658. https://doi.org/10.1016/j.ecss.2021.107658

Cresson, P., Chouvelon, T., Bustamante, P., Bănaru, D., Baudrier, J., Le Loc'h, F., Mauffret, A., Mialet, B., Spitz, J., Wessel, N., Briand, M.J., Denamiel, M., Doray, M., Guillou, G., Jadaud, A., Lazard, C., Prieur, S., Rouquette, M., Saraux, C., Serre, S., Timmerman, C.-A., Verin, Y., Harmelin-Vivien, M., 2020. Primary production and depth drive different trophic structure and functioning of fish assemblages in French marine ecosystems. Progress in Oceanography 186, 102343. https://doi.org/10.1016/j.pocean.2020.102343

Day, L., Kopp, D., Robert, M., Le Bris, H., 2019. Trophic ecology of large gadiforms in the food web of a continental shelf ecosystem. Progress in Oceanography 175, 105–114. https://doi.org/10.1016/j.pocean.2019.03.007

Day, L., Le Bris, H., Saulnier, E., Pinsivy, L., Brind'Amour, A., 2020. Benthic prey production index estimated from trawl survey supports the food limitation hypothesis in coastal fish nurseries. Estuarine, Coastal and Shelf Science 235, 106594. https://doi.org/10.1016/j.ecss.2020.106594

Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Vincx, M., Van Lancker, V., 2008. Habitat suitability modelling as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea. Continental Shelf Research 28, 369–379. https://doi.org/10.1016/j.csr.2007.09.001

Déniel, C., 1981. Les Poissons plats (Téléostéens, Pleuronectiformes) en baie de Douarnenez: reproduction, croissance et migration des Bothidae, Scophthalmidae, Pleuronectidae et Soleidae. Université de Bretagne occidentale - Brest.

Deubel, H., Engel, M., Fetzer, I., Gagayev, S., Hirche, H.-J., Klages, M., Larionov, V., Lubin, P., Lubina, O., Nöthig, E.-M., Okolodkov, Y., Rachor, E., 2003. The Kara Sea ecosystem: phytoplankton, zooplankton and benthos communities influenced by river run-off. Proceedings in Marine Sciences no. 6, Elsevier, pp. 237–266.

Dubois, S., 2010a. PLOOPS 1 cruise,Thalia R/V. https://doi.org/10.17600/10070020
Dubois, S., 2010b. PLOOPS 2 cruise,Thalia R/V. https://doi.org/10.17600/10070090
Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., Skjoldal, H.R., 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology 45, 1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x
Dutertre, M., Hamon, D., Chevalier, C., Ehrhold, A., 2013. The use of the relationships between environmental factors and benthic macrofaunal distribution in the establishment of a baseline for coastal management. ICES Journal of Marine Science 70, 294–308. https://doi.org/10.1093/icesjms/fss170
Ehrnsten, E., Norkko, A., Timmermann, K., Gustafsson, B.G., 2019. Benthic-pelagic coupling in coastal seas – Modelling macrofaunal biomass and carbon processing in response to organic matter supply. Journal of Marine Systems 196, 36–47. https://doi.org/10.1016/j.jmarsys.2019.04.003
Engelhard, G.H., Blanchard, J.L., Pinnegar, J.K., van der Kooij, J., Bell, E.D., Mackinson, S., Righton, D.A., 2013. Body condition of predatory fishes linked to the availability of sandeels. Mar Biol 160, 299–308. https://doi.org/10.1007/s00227-012-2088-1
Escobar-Briones, E.G., Soto, L.A., 1997. Continental shelf benthic biomass in the western Gulf of Mexico. Continental Shelf Research 17, 585–604. https://doi.org/10.1016/S0278-4343(96)00047-7
Fanelli, E., Principato, E., Monfardini, E., Da Ros, Z., Scarcella, G., Santojanni, A., Colella, S., 2022. Seasonal Trophic Ecology and Diet Shift in the Common Sole Solea solea in the Central Adriatic Sea. Animals 12, 3369. https://doi.org/10.3390/ani12233369
GEBCO Bathymetric Compilation Group, 2023. GEBCO 2023 Grid. https://doi.org/10.5285/F98B053B-0CBC-6C23-E053-6C86ABC0AF7B
Gibson, R.N., Ezzi, I.A., 1980. The biology of the scaldfish, Arnoglossus laterna (Walbaum) on the west coast of Scotland. Journal of Fish Biology 17, 565–575. https://doi.org/10.1111/j.1095-8649.1980.tb02788.x
Glémarec, M., 1969. Les Peuplements benthiques du plateau continental nord-Gascogne. Atelier offset de la Faculté des sciences, Brest, France.
Hall, S.J., 2002. The continental shelf benthic ecosystem: current status, agents for change and future prospects. Envir. Conserv. 29, 350–374. https://doi.org/10.1017/S0376892902000243
Hiddink, J.G., Moranta, J., Balestrini, S., Sciberras, M., Cendrier, M., Bowyer, R., Kaiser, M.J., Sköld, M., Jonsson, P., Bastardie, F., Hinz, H., 2016. Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. Journal of Applied Ecology 53, 1500–1510. https://doi.org/10.1111/1365-2664.12697
Hijmans, R.J., 2023. raster: Geographic Data Analysis and Modeling.
Hislop, J.R.G., Robb, A.P., Bell, M.A., Armstrong, D.W., 1991. The diet and food consumption of whiting (Merlangius merlangus) in the North Sea. ICES Journal of Marine Science 48, 139–156. https://doi.org/10.1093/icesjms/48.2.139
Holbrook, S.J., Schmitt, R.J., 1989. Resource Overlap, Prey Dynamics, and The Strength of Competition. Ecology 70, 1943–1953. https://doi.org/10.2307/1938124
Idier, D., Romieu, E., Pedreros, R., Oliveros, C., 2010. A simple method to analyse non-cohesive sediment mobility in coastal environment. Continental Shelf Research 30, 365–377. https://doi.org/10.1016/j.csr.2009.12.006

Kamimura, Y., Taga, M., Yukami, R., Watanabe, C., Furuichi, S., 2021. Intra- and inter-specific density dependence of body condition, growth, and habitat temperature in chub mackerel (Scomber japonicus). ICES Journal of Marine Science 78, 3254–3264. https://doi.org/10.1093/icesjms/fsab191

Karlson, A., Reutgard, M., Garbaras, A., Gorokhova, E., 2018. Isotopic niche reflects stress-induced variability in physiological status. Royal Society Open Science 5, 171398. https://doi.org/10.1098/rsos.171398

Kaskela, A.M., Kotilainen, A.T., Alanen, U., Cooper, R., Green, S., Guinan, J., van Heteren, S., Kihlman, S., Van Lancker, V., Stevenson, A., the EMODnet Geology Partners, 2019. Picking Up the Pieces—Harmonising and Collating Seabed Substrate Data for European Maritime Areas. Geosciences 9, 84. https://doi.org/10.3390/geosciences9020084

Kay, S., Andersson, H., Eilola, K., Wehde, H., Ramirez-Romero, E., Jordà, G., Catalan, I., 2018. Climate change and European aquatic resources (CERES) deliverable D1.3 projections of physical and biogeochemical parameters and habitat indicators for European seas, including synthesis of sea level rise and storminess., CERES report.

King, P.A., Fives, J.M., 1990. Littoral and Benthic Investigations on the West Coast of Ireland: XXIII. A Contribution to the Biology of the Thick-Back Sole Microchirus variegatus (Donovan, 1808) in the Galway Bay Area. Proceedings of the Royal Irish Academy. Section B: Biological, Geological, and Chemical Science 90B, 23–31.

Kopp, D., Lefebvre, S., Cachera, M., Villanueva, M.C., Ernande, B., 2015. Reorganization of a marine trophic network along an inshore–offshore gradient due to stronger pelagic–benthic coupling in coastal areas. Progress in Oceanography 130, 157–171. https://doi.org/10.1016/j.pocean.2014.11.001

Laffargue, P., 2013a. FEBBE 1 cruise,Gwen Drez R/V. https://doi.org/10.17600/13050040

Laffargue, P., 2013b. FEBBE 2 cruise,Gwen Drez R/V. https://doi.org/10.17600/13050050

Laffargue, P., Garren, F., Duhamel, E., 2020. EVHOE 2020 cruise. https://doi.org/10.17600/18000661

Lagardère, J.P., 1987. Feeding ecology and daily food consumption of common sole, Solea vulgaris Quensel, juveniles on the French Atlantic coast. Journal of Fish Biology 30, 91–104. https://doi.org/10.1111/j.1095-8649.1987.tb05735.x

Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., Hily, C., Labry, C., Le Pape, O., Marquis, E., Petitgas, P., Pusineri, C., Ridoux, V., Spitz, J., Niquil, N., 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management. Progress in Oceanography 91, 561–575. https://doi.org/10.1016/j.pocean.2011.09.002

Laurel, B. j., Brown, J.A., Anderson, R., 2001. Behaviour, growth and survival of redfish larvae in relation to prey availability. Journal of Fish Biology 59, 884–901. https://doi.org/10.1111/j.1095-8649.2001.tb00159.x

Le Bec, C., 1983. Cycle sexuel et fécondité de la sole Solea vulgaris (Quensel, 1806) du Golfe de Gascogne. Revue des Travaux de l'Institut des Pêches Maritimes 47, 179–189.

Le Bris, H., 2010. ISOBAIE 2 cruise,Gwen Drez R/V. https://doi.org/10.17600/10050050

Le Bris, H., 2008. RETROB cruise,Gwen Drez R/V. https://doi.org/10.17600/8050020

Le Bris, H., Glémarec, M., 1995. Macrozoobenthic communities of an oxygen under-saturated coastal ecosystem: The Bay of Vilaine (southern Brittany). Oceanologica Acta 18, 573–581.
Le Cren, E.D., 1951. The Length-Weight Relationship and Seasonal Cycle in Gonad Weight and Condition in the Perch (Perca fluviatilis). The Journal of Animal Ecology 20, 201. https://doi.org/10.2307/1540
Le Loc'h, F., Grall, J., 2019. APPEAL ATL 19-2 cruise,Côtes De La Manche R/V. https://doi.org/10.17600/18001062
Le Loc'h, F., Grall, J., 2018a. APPEAL ATL 18-1 cruise,Côtes De La Manche R/V. https://doi.org/10.17600/18001061
Le Loc'h, F., Grall, J., 2018b. APPEAL ATL 18-2 cruise,Côtes De La Manche R/V. https://doi.org/10.17600/18000466
Le Loc'h, F., Hily, C., 2005. Stable carbon and nitrogen isotope analysis of Nephrops norvegicus / Merluccius merluccius fishing grounds in the Bay of Biscay (Northeast Atlantic). Can. J. Fish. Aquat. Sci. 62, 123–132. https://doi.org/10.1139/f04-242
Le Loc'h, F., Hily, C., Grall, J., 2008. Benthic community and food web structure on the continental shelf of the Bay of Biscay (North Eastern Atlantic) revealed by stable isotopes analysis. Journal of Marine Systems 72, 17–34. https://doi.org/10.1016/j.jmarsys.2007.05.011
Liao, H., Pierce, C.L., Wahl, D.H., Rasmussen, J.B., Leggett, W.C., 1995. Relative Weight (W) as a Field Assessment Tool: Relationships with Growth, Prey Biomass, and Environmental Conditions. Transactions of the American Fisheries Society 124, 387–400. https://doi.org/10.1577/1548-8659(1995)124<0387:RWWRAA>2.3.CO;2
Lopez De Gamiz-Zearra, A., Hansen, C., Corrales, X., Quincoces, I., Preciado, I., Andonegi, E., 2023. Parameterization and tuning of the Bay of Biscay Atlantis model v1. https://doi.org/10.5194/egusphere-2023-1368
McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D., Radke, L.C., 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuarine, Coastal and Shelf Science 88, 21–32. https://doi.org/10.1016/j.ecss.2010.03.003
N'Da, K., Déniel, C., 1993. Sexual cycle and seasonal changes in the ovary of the red mullet, Mullus surmuletus, from the southern coast of Brittany. Journal of Fish Biology 43, 229–244. https://doi.org/10.1111/j.1095-8649.1993.tb00425.x
Pace, M.C., Bailey, D.M., Donnan, D.W., Narayanaswamy, B.E., Smith, H.J., Speirs, D.C., Turrell, W.R., Heath, M.R., 2021. Modelling seabed sediment physical properties and organic matter content in the Firth of Clyde. https://doi.org/10.5194/essd-2021-23
Pavičić, M., Šiljić, J., Jurica, D.B., Matić-Skoko, S., 2018. Feeding habits of the striped red mullet, Mullus surmuletus in the eastern Adriatic Sea. Acta Adriatica 59, 123–136. https://doi.org/10.32582/aa.59.1.10
Pearson, T., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology 16, 229–311.
Pebesma, E., 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10, 439. https://doi.org/10.32614/RJ-2018-009
Pelage, L., Lucena-Frédou, F., Eduardo, L.N., Le Loc'h, F., Bertrand, A., Lira, A.S., Frédou, T., 2022. Competing with each other: Fish isotopic niche in two

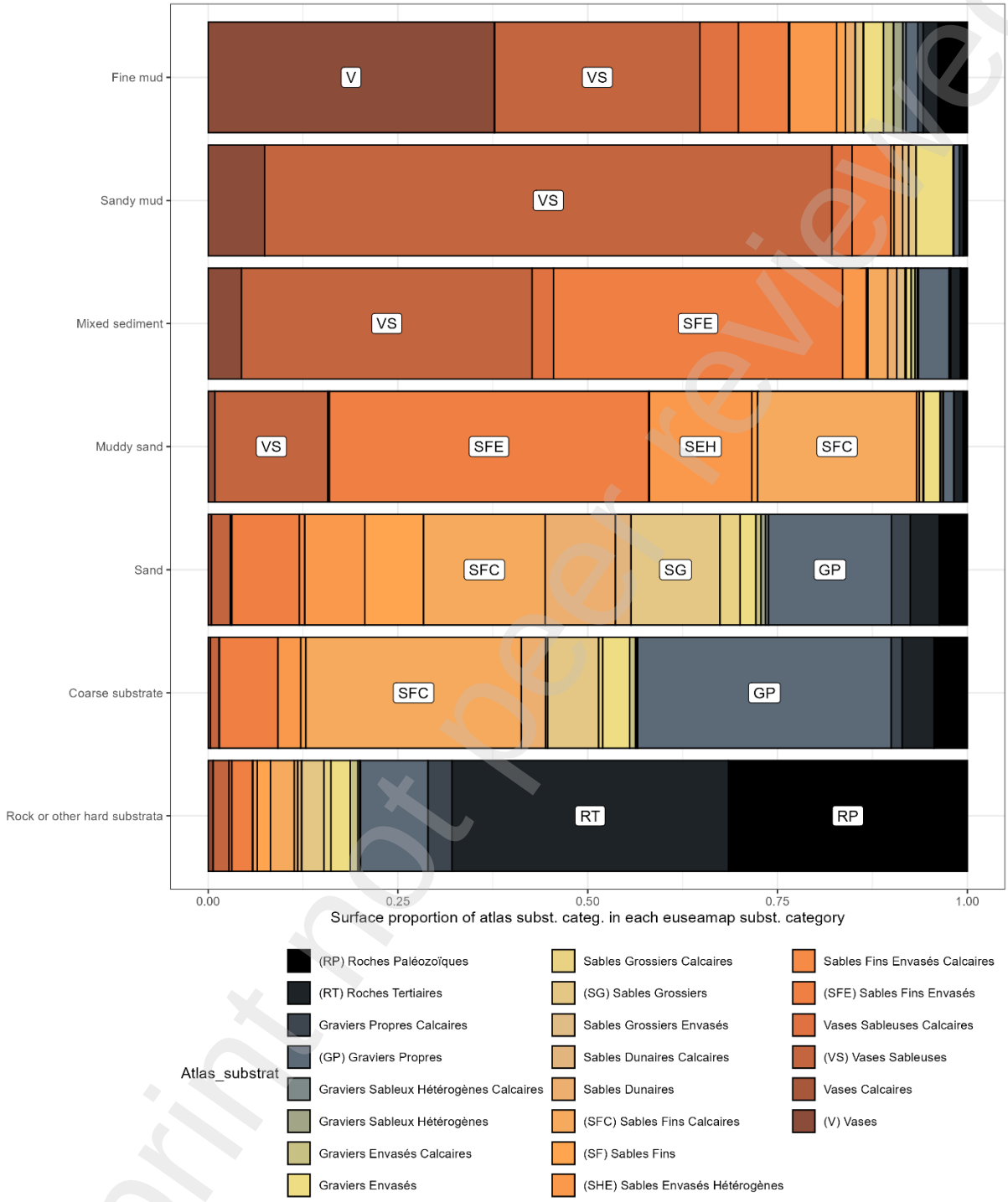
resource availability contexts. Front. Mar. Sci. 9. https://doi.org/10.3389/fmars.2022.975091
Peña, M., González-Quirós, R., Munuera-Fernández, I., González, F., Romero-Romero, S., Nogueira, E., 2019. Vertical distribution and aggregation patterns of krill (Crustacea: Euphausiacea) in the Bay of Biscay: interannual and seasonal variability. Can. J. Zool. 97, 619–630. https://doi.org/10.1139/cjz-2018-0119
Pierrejean, M., Laffargue, P., Desroy, N., 2022. Test de déploiement des suivis du compartiment de la macrofaune benthique sur les fonds meubles du plateau via les campagnes halieutiques de l'Ifremer, au titre de la DCSMM. Ifremer. https://doi.org/10.13155/92737
Porath, M.T., Peters, E.J., 1997. Use of Walleye Relative Weights (W) to Assess Prey Availability. North American Journal of Fisheries Management 17, 628–637. https://doi.org/10.1577/1548-8675(1997)017<0628:UOWRWW>2.3.CO;2
Qin, X.-B., Sun, H.-W., Wu, J.-Z., Wang, R.-N., Sun, T.-H., 2010. Bioturbation of macrobenthos on estuarine sediment. Ying Yong Sheng Tai Xue Bao 21, 458–463.
R core team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [WWW Document]. URL https://www.r-project.org/ (accessed 12.20.22).
Rault, J., Le Bris, H., Robert, M., Pawlowski, L., Denamiel, M., Kopp, D., 2017. Diets and trophic niches of the main commercial fish species from the Celtic Sea. Journal of Fish Biology 91, 1449–1474. https://doi.org/10.1111/jfb.13470
Reiss, H., Birchenough, S., Borja, A., Buhl-Mortensen, L., Craeymeersch, J., Dannheim, J., Darr, A., Galparsoro, I., Gogina, M., Neumann, H., Populus, J., Rengstorf, A.M., Valle, M., van Hoey, G., Zettler, M.L., Degraer, S., 2015. Benthos distribution modelling and its relevance for marine ecosystem management. ICES Journal of Marine Science 72, 297–315. https://doi.org/10.1093/icesjms/fsu107
Reiss, H., Degraer, S., Duineveld, G.C.A., Kröncke, I., Aldridge, J., Craeymeersch, J.A., Eggleton, J.D., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Pohlmann, T., Rachor, E., Robertson, M., Vanden Berghe, E., van Hoey, G., Rees, H.L., 2010. Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. ICES Journal of Marine Science 67, 278–293. https://doi.org/10.1093/icesjms/fsp253
Rigolet, C., Dubois, S.F., Thiébaut, E., 2014. Benthic control freaks: Effects of the tubiculous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities. Journal of Sea Research 85, 413–427. https://doi.org/10.1016/j.seares.2013.07.013
Rijnsdorp, A.D., 1990. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, Pleuronectes platessa L. Netherlands Journal of Sea Research 25, 279–289. https://doi.org/10.1016/0077-7579(90)90027-E
Robert, A., 2017. Effets combinés des facteurs naturels et anthropiques sur la diversité fonctionnellle des vasières à langoustines (Nephrops norvegicus) du golfe de Gascogne (phdthesis). Agrocampus Ouest.
Rodríguez-Cabello, C., Sánchez, F., Olaso, I., 2007. Distribution patterns and sexual segregations of Scyliorhinus canicula (L.) in the Cantabrian Sea. Journal of Fish Biology 70, 1568–1586. https://doi.org/10.1111/j.1095-8649.2007.01444.x

794 Sánchez-Hernández, J., Hayden, B., Harrod, C., Kahilainen, K.K., 2021. Population
795 niche breadth and individual trophic specialisation of fish along a climate-
796 productivity gradient. Rev Fish Biol Fisheries 31, 1025–1043.
797 https://doi.org/10.1007/s11160-021-09687-3
798 Šantić, M., Rađa, B., Pallaoro, A., 2012. Feeding habits of small-spotted catshark
799 (Scyliorhinus canicula Linnaeus, 1758) from the eastern central Adriatic Sea.
800 Marine Biology Research 8, 1003–1011.
801 https://doi.org/10.1080/17451000.2012.702912
802 Schloesser, R.W., Fabrizio, M.C., 2019. Nursery Habitat Quality Assessed by the
803 Condition of Juvenile Fishes: Not All Estuarine Areas Are Equal. Estuaries and
804 Coasts 42, 548–566. https://doi.org/10.1007/s12237-018-0468-6
805 Schückel, S., Sell, A., Kröncke, I., Reiss, H., 2011. Diet composition and resource
806 partitioning in two small flatfish species in the German Bight. Journal of Sea
807 Research 66, 195–204. https://doi.org/10.1016/j.seares.2011.06.003
808 Serrano, A., Velasco, F., Olaso, I., Sánchez, F., 2003. Macrobenthic crustaceans in
809 the diet of demersal fish in the Bay of Biscay in relation to abundance in the
810 environment. Sarsia 88, 36–48. https://doi.org/10.1080/00364820308469
811 Simpson, J.H., Sharples, J. (Eds.), 2012. The shelf edge system, in: Introduction to the
812 Physical and Biological Oceanography of Shelf Seas. Cambridge University
813 Press, Cambridge, pp. 304–351.
814 https://doi.org/10.1017/CBO9781139034098.013
815 Sorbe, J.C., 1981. Rôle du bentos dans le régime alimentaire des poissons démersaux
816 du secteur Sud Gascogne. Kieler Meeresforschungen - Sonderheft 5, 479–489.
817 Souissi, S., Ibanez, F., Hamadou, R.B., Boucher, J., Cathelineau, A.C., Blanchard, F.,
818 Poulard, J.-C., 2001. A new multivariate mapping method for studying species
819 assemblages and their habitats: Example using bottom trawl surveys in the Bay
820 of Biscay (France). Sarsia 86, 527–542.
821 https://doi.org/10.1080/00364827.2001.10420491
822 Timmermann, K., Norkko, J., Janas, U., Norkko, A., Gustafsson, B.G., Bonsdorff, E.,
823 2012. Modelling macrofaunal biomass in relation to hypoxia and nutrient
824 loading. Journal of Marine Systems 105–108, 60–69.
825 https://doi.org/10.1016/j.jmarsys.2012.06.001
826 Vandromme, P., Nogueira, E., Huret, M., Lopez-Urrutia, Á., González-
827 Nuevo González, G., Sourisseau, M., Petitgas, P., 2014. Springtime
828 zooplankton size structure over the continental shelf of the Bay of Biscay. Ocean
829 Sci. 10, 821–835. https://doi.org/10.5194/os-10-821-2014
830 Wei, C.-L., Rowe, G.T., Escobar-Briones, E., Boetius, A., Soltwedel, T., Caley, M.J.,
831 Soliman, Y., Huettmann, F., Qu, F., Yu, Z., Pitcher, C.R., Haedrich, R.L.,
832 Wicksten, M.K., Rex, M.A., Baguley, J.G., Sharma, J., Danovaro, R.,
833 MacDonald, I.R., Nunnally, C.C., Deming, J.W., Montagna, P., Lévesque, M.,
834 Weslawski, J.M., Wlodarska-Kowalczuk, M., Ingole, B.S., Bett, B.J., Billett,
835 D.S.M., Yool, A., Bluhm, B.A., Iken, K., Narayanaswamy, B.E., 2010. Global
836 Patterns and Predictions of Seafloor Biomass Using Random Forests. PLoS
837 ONE 5, e15323. https://doi.org/10.1371/journal.pone.0015323
838 Zhang, Y., Cheng, L., Li, K., Zhang, L., Cai, Y., Wang, X., Heino, J., 2019. Nutrient
839 enrichment homogenizes taxonomic and functional diversity of benthic
840 macroinvertebrate assemblages in shallow lakes. Limnology and
841 Oceanography 64, 1047–1058. https://doi.org/10.1002/lno.11096

Zuschin, M., Stachowitsch, M., 2009. Epifauna-dominated benthic shelf assemblages: lessons from the modern adriatic sea. PALAIOS 24, 211–221. https://doi.org/10.2110/palo.2008.p08-062r

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, Statistics for Biology and Health. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-87458-6

850 **Supplementary material**



851

852 *Figure SM1: Relative proportion of the area of each Atlas map substrate polygon contained in each*
853 *Euseamap substrate polygon.*

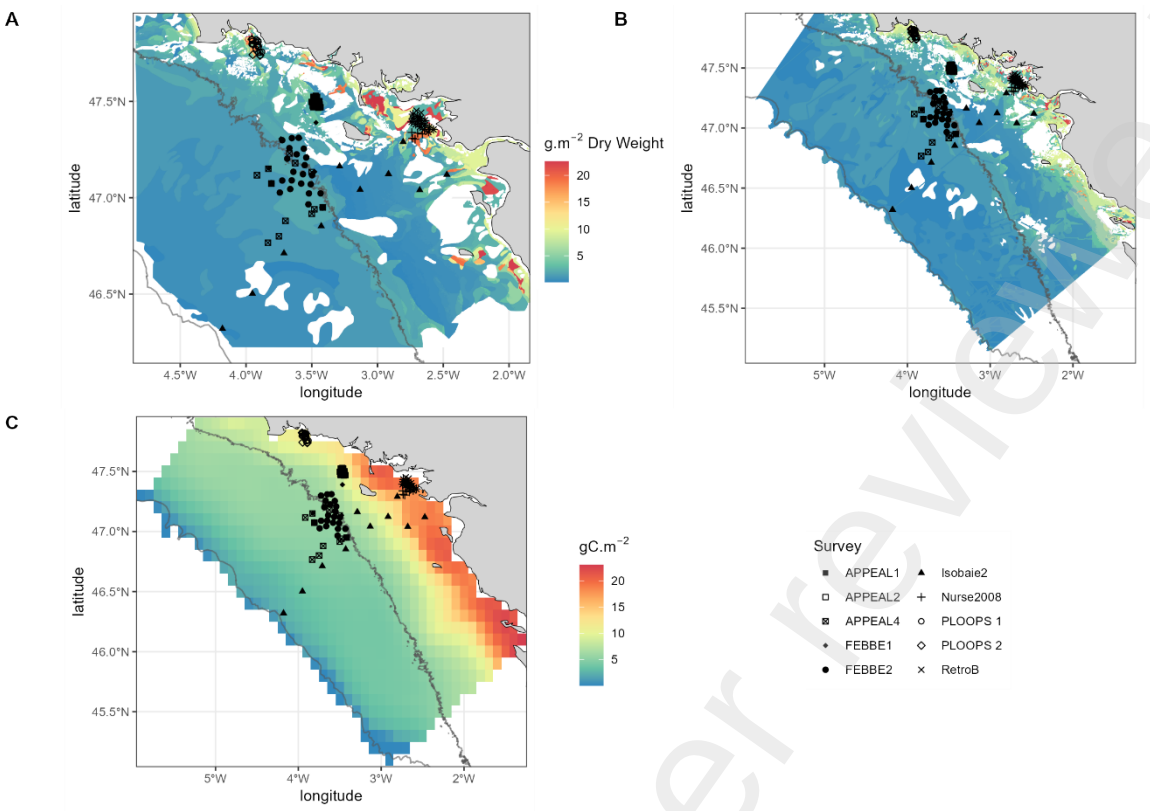
854

855 Table SM2: Different substrate categories of different substrate maps and the correspondence between
856 them and the graph model.

Graph model substrate categories	Atlas biosedimentary substrate categories	Euseamap substrate categories
	Roches Paléozoïques ; Roches Tertiaires	Rock or other hard substrata; Seabed; Worm reefs
GP-GV	Graviers Envasés ; Graviers Envasés Calcaires ; Graviers Propres ; Graviers Propres Calcaires	Coarse substrate
GH	Graviers Sableux Hétérogènes ; Graviers Sableux Hétérogènes Calcaires	
SG	Sables Grossiers ; Sables Grossiers Calcaires	Coarse substrate
SF	Sables Dunaires ; Sables Dunaires Calcaires ; Sables Fins ; Sables Fins Calcaires	Sand
SHV	Sables Envasés Hétérogènes ; Sables Grossiers Envasés	
FV	Sables Fins Envasés ; Sables Fins Envasés Calcaires	Muddy sand
VS	Vases Sableuses ; Vases Sableuses Calcaires	Mixed sediment Sandy mud
VV	Vases ; Vases Calcaires	Fine mud

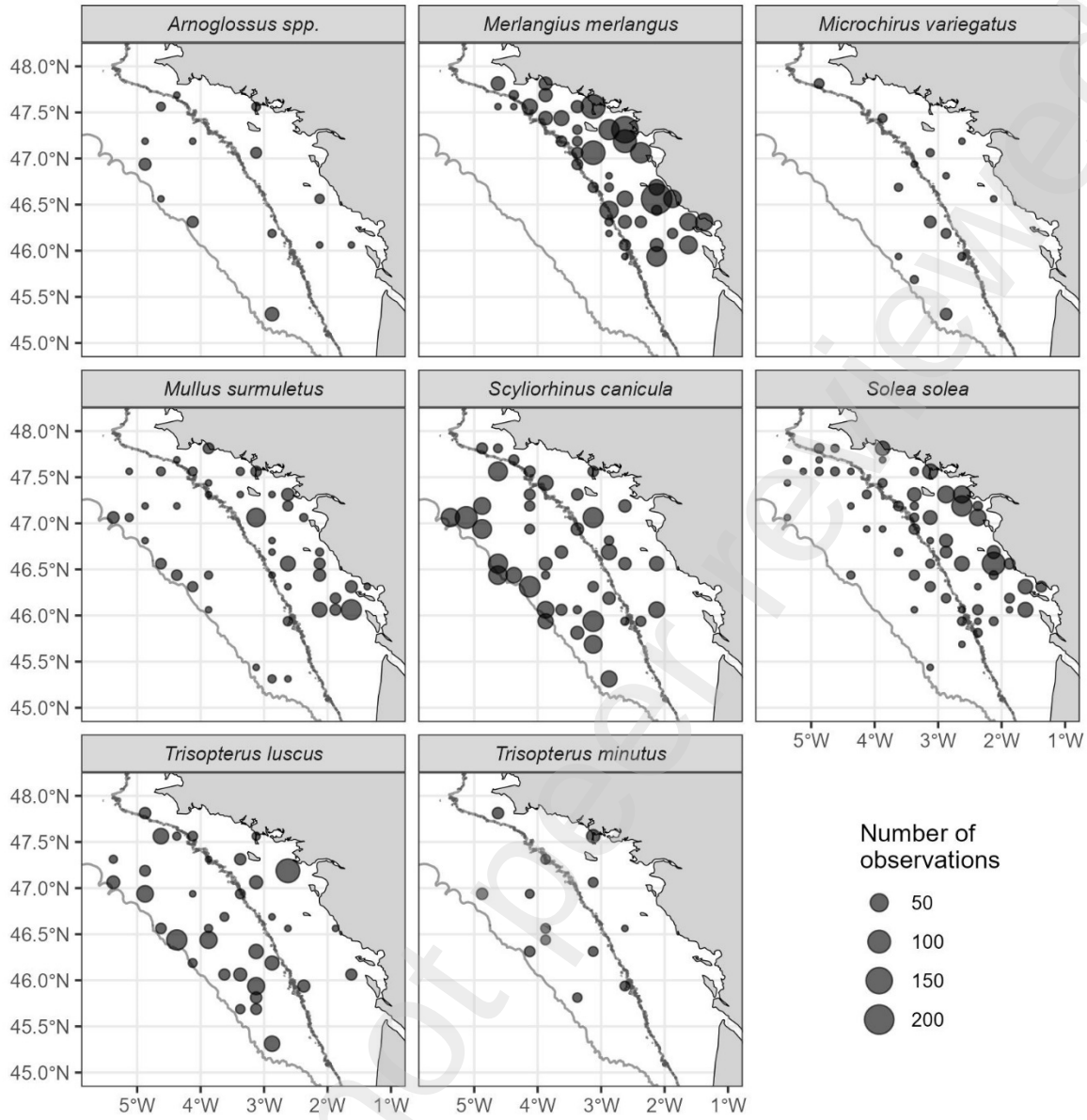
857

858



859

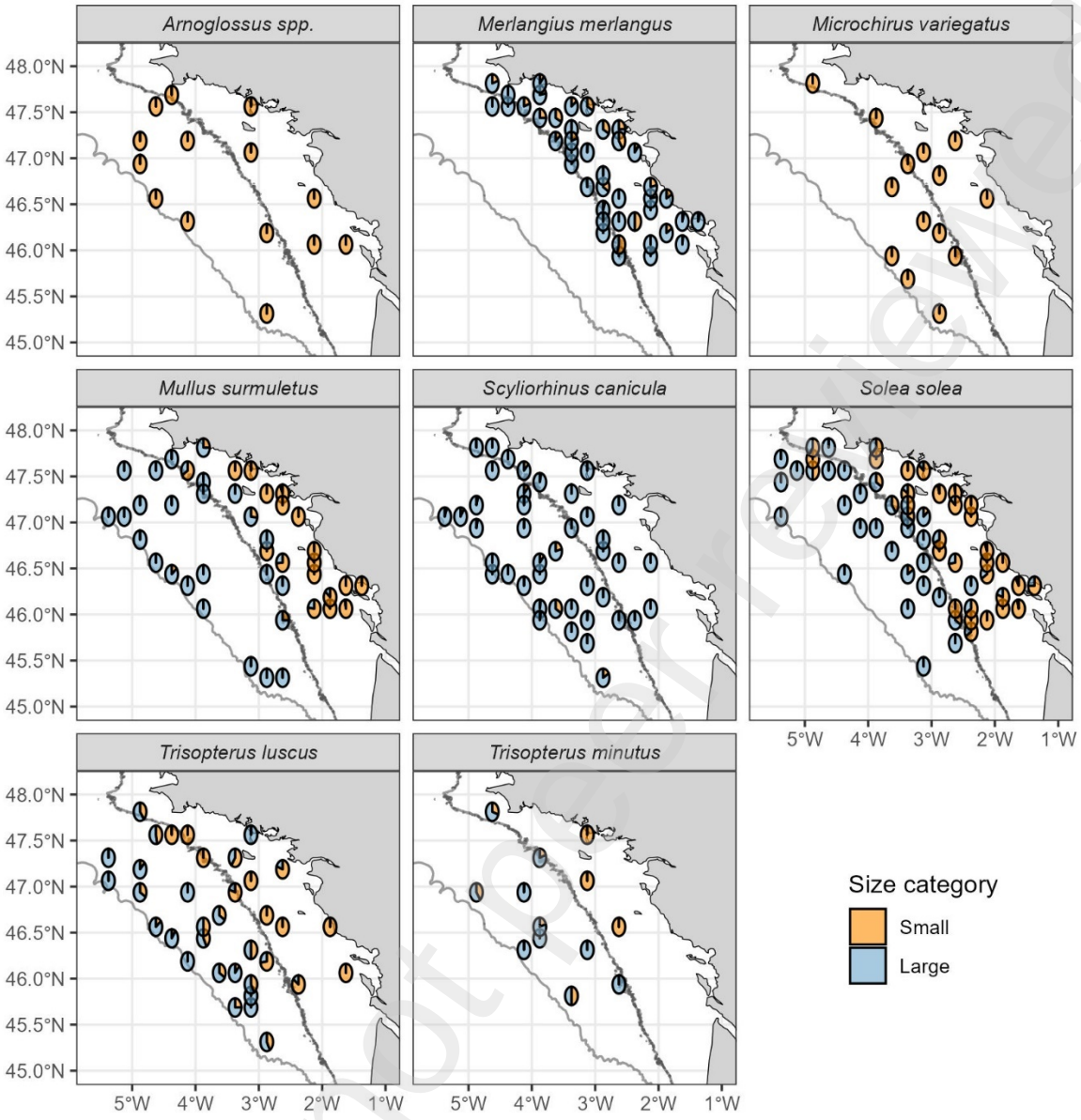
860 *Figure SM3: The location of sampling stations from various surveys along the continental shelf of the*
861 *Bay of Biscay. Panel A depicts values of the macrobenthic biomass index obtained from the graph model*
862 *based on 'Atlas' substrate maps, B shows values from the graph model based on a recent substrate*
863 *map, and C is the average biomass of suspension and deposit feeders estimated by the POLCOMS-*
864 *ERSEM model between 2006–2015. Gray lines represent the 100- and 200-meter isobaths.*



865

866 *Figure SM4: Spatial distribution of available data on bentho-demersal fish condition. Gray lines*
867 *represent the 100- and 200-meter isobaths.*

868



869

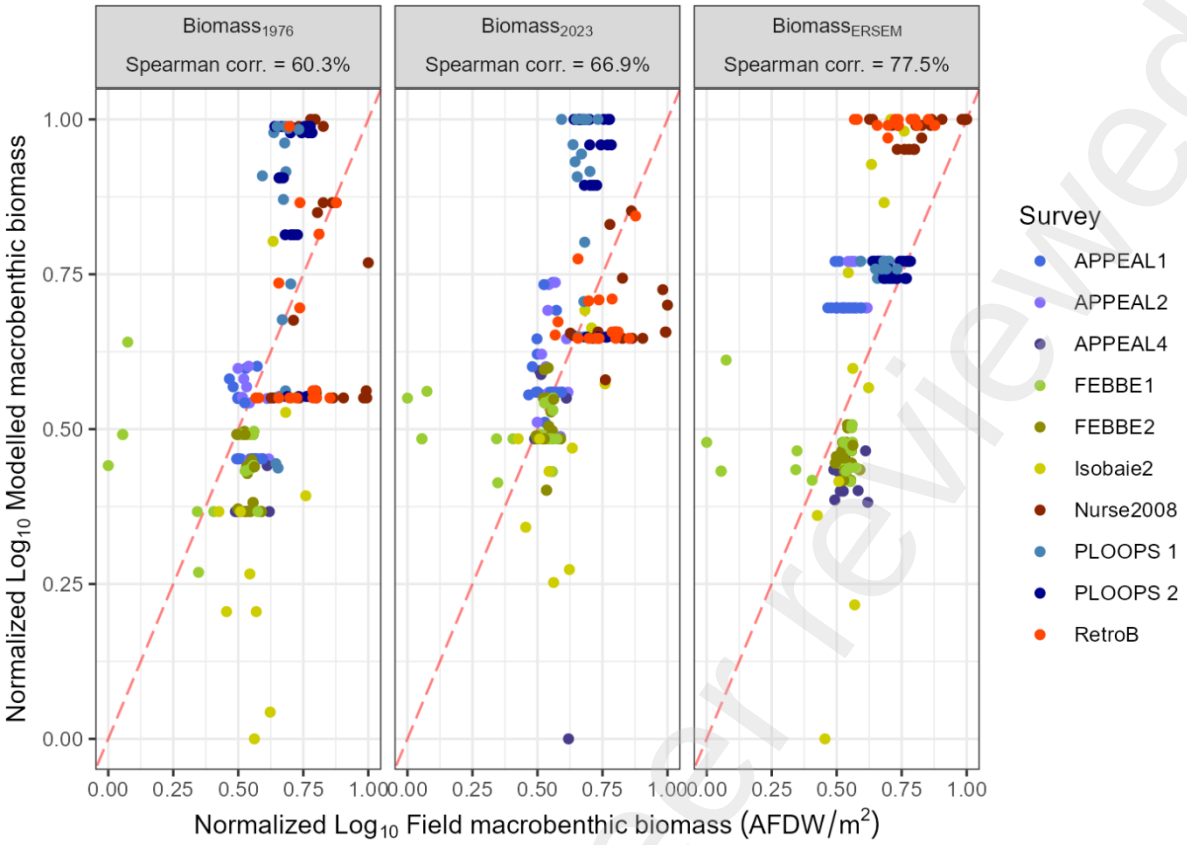
870 *Figure SM5: Relative proportion of 'Small' and 'Large' size-class categories in the available data on*
871 *bentho-demersal fish condition. Gray lines represent the 100- and 200-meter isobaths.*

872

873 Table SM6: Number of samples included in the analysis, based on the biomass model used—"graph
874 model" ($Biomass_{1976}$, $Biomass_{2023}$) or ERSEM model ($Biomass_{ERSEM}$)—and the fish size categories,
875 small (S) or large (L).

Species	Number of individuals
Arnoglossus spp.	$Biomass_{1976}$: 45
	$Biomass_{2023}$: 67
	$Biomass_{ERSEM}$: 67
Merlangius merlangus	$Biomass_{1976}$: 253 (S) & 975 (L)
	$Biomass_{2023}$: 268 (S) & 1192 (L)
	$Biomass_{ERSEM}$: 268 (S) & 1192 (L)
Microchirus variegatus	$Biomass_{1976}$: 32
	$Biomass_{2023}$: 48
	$Biomass_{ERSEM}$: 48
Mullus surmuletus	$Biomass_{1976}$: 95 (S) & 91 (L)
	$Biomass_{2023}$: 211 (S) & 123 (L)
	$Biomass_{ERSEM}$: 211 (S) & 123 (L)
Scyliorhinus canicula	$Biomass_{1976:}$ 12 (S) & 683 (L)
	$Biomass_{2023}$: 35 (S) & 1094 (L)
	$Biomass_{ERSEM}$: 35 (S) & 1098 (L)
Solea solea	$Biomass_{1976}$: 418 (S) & 121 (L)
	$Biomass_{2023:}$ 490 (S) & 140 (L)
	$Biomass_{ERSEM}$: 490 (S) & 140 (L)
Trisopterus luscus	$Biomass_{1976}$: 217 (S) & 204 (L)
	$Biomass_{2023}$: 274 (S) & 309 (L)
	$Biomass_{ERSEM}$: 274 (S) & 310 (L)

876



877

878 Figure SM7 Biplot of modeled macrobenthic biomass compared to observed macrobenthic biomass.
879 Stations are colored according to their respective survey.

880