FOOD WEB STRUCTURE IN RELATION TO ENVIRONMENTAL DRIVERS ACROSS A CONTINENTAL SHELF ECOSYSTEM

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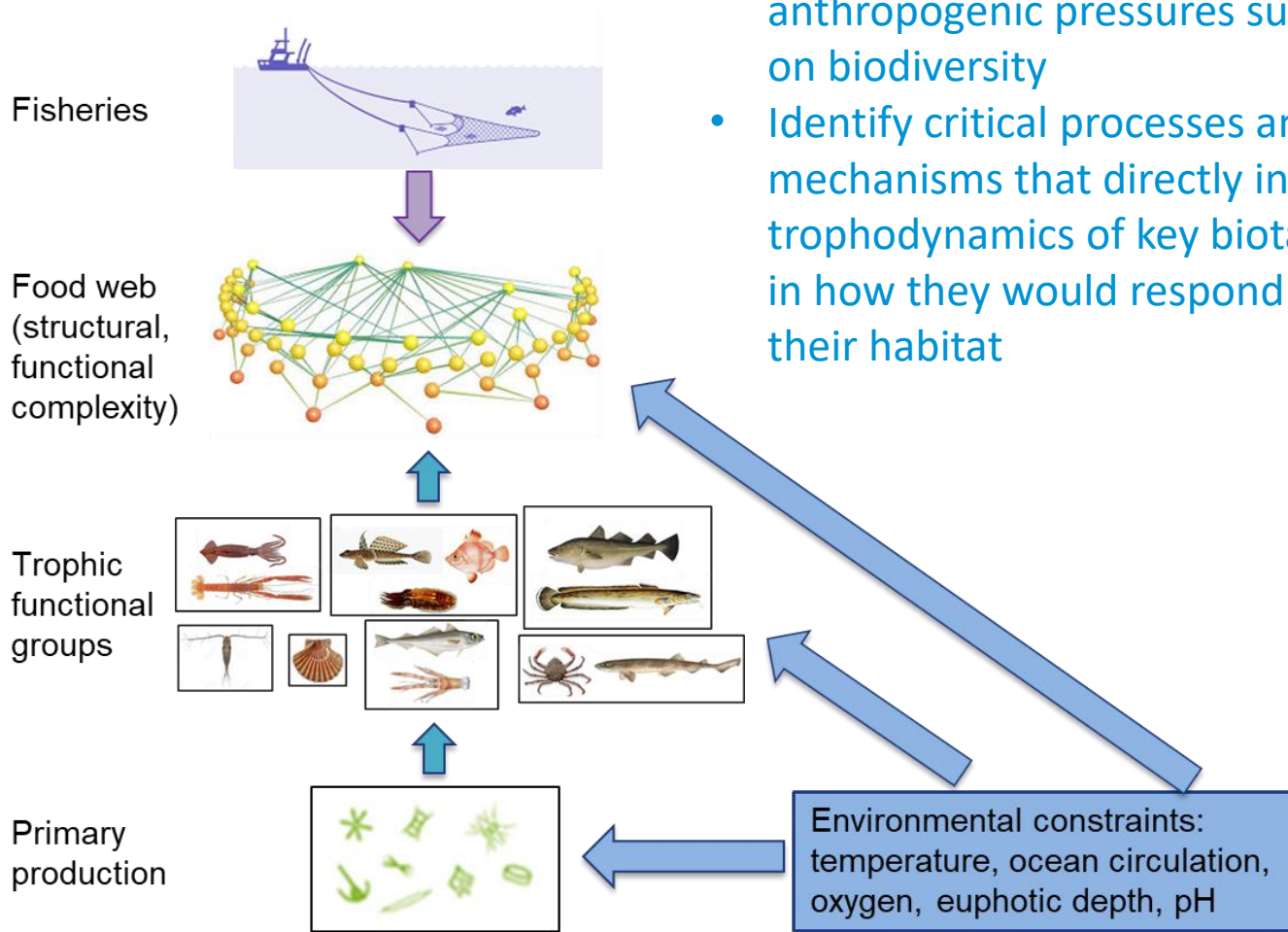[2] Ifremer, Channel and North Sea Fisheries Research Unit, RH, Boulogne-sur-Mer.

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Context

Understand the biological and physical drivers that influence the spatial structuring of food webs

Major gaps in current understanding
- Predict the response of ecosystems to the effects of global change, including anthropogenic pressures such as fishing on biodiversity
- Identify critical processes and mechanisms that directly influence the trophodynamics of key biota, particularly in how they would respond to changes in their habitat

Fisheries

Food web (structural, functional complexity)

Trophic functional groups

Primary production

Environmental constraints: temperature, ocean circulation, oxygen, euphotic depth, pH

Context

Ecosystem models are an important tool to understand the effects of climate change and other anthropogenic activities across all trophic levels
- Food web/ecosystem models require trophic level estimates

Trophic food web (stable isotope analysis)
- Nitrogen (δ^{15}N) give an indication of the trophic level occupied by a consumer, and
- Carbon (δ^{13}C) the food sources underpinning the food web

Isotope data is limited by baseline variability
- Now have ways to correct for baselines/circumvent this issue
- Use these estimates in ecosystem models, but there are a few studies that do this

Aims

Within this context, the main objective was to examine the physical and biological factors that influence the spatial structuring of the CSS food web

- Deciphering the effects of spatial gradients on trophic functioning has previously been referred to as a promising, but overlooked, area of research (Ings et al. 2009)

Identified relationships between $\delta^{13}C$ and $\delta^{15}N$ baseline values and the environment to produce reliable estimates of trophic baseline to support robust comparisons of consumer trophic ecology across the CSS

- Invertebrates and fishes spanning a large trophic range from sites sampled across the spatial domain of the CSS were then used to assess spatial trends in $\delta^{13}C$ and $\delta^{15}N$ of organisms at higher trophic levels within the food web

The specific aims were to:
(i)   Characterise the food web structure at the scale of the whole sampling area (regional scale)
- Hierarchical cluster analysis
- Biomass-weighted isotopic diversity metrics (Cucherousset and Villéger 2015) as a proxy for functional diversity
(ii)   Identify biological and physical variables driving the trophic functional groups and the wider trophic network structure to highlight the spatial structure of the food web
- Two sets of statistical models, one set at the regional scale and the other for each trophic group
(iii)   Compare functioning of trophic groups based on spatial areas identified in trophic group models to identify underlying species assembly processes at different spatial scales
- Isotopic overlap (similarity and nestedness) metrics (Cucherousset and Villéger 2015)

Methods

Sample collection for stable isotope analysis

- EVHOE surveys 2014, 2015 and 2016

- GOV (Grande Ouverture Verticale) demersal trawl

- 975 epifaunal invertebrates, zooplankton, fish and cephalopods (63 species)

- Water depths 57-306 m
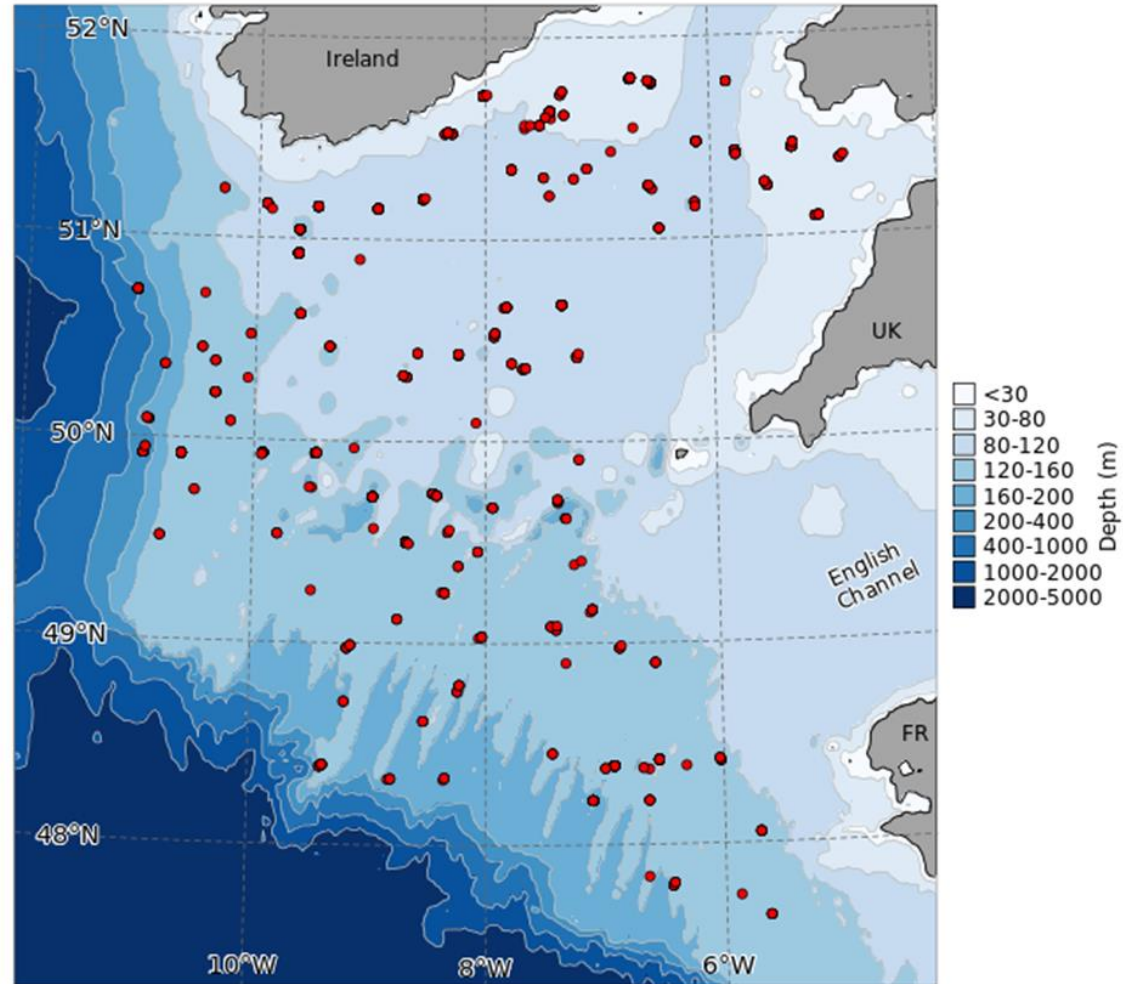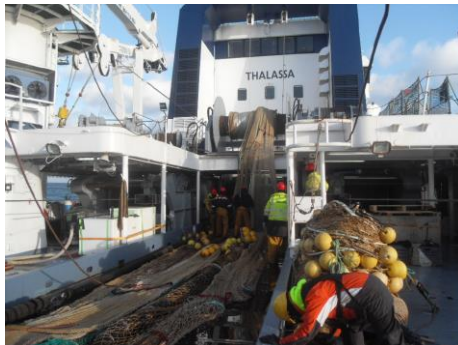
Methods

Trophic baseline

- The great scallop (*Pecten maximus*)
- Assess spatial variation in baseline $\delta^{13}C$ and $\delta^{15}N$, based on environmental data (Barnes et al. 2009; Jennings and Van Der Molen 2015)
- Predicted baseline $\delta^{13}C$ and $\delta^{15}N$ as follows:

$$\delta^{13}C_{base,i} = 0.322T_i - 20.347$$
$$\delta^{15}N_{base,i} = b_0 + b_1 T_i + b_2 S_i + b_3 S_{min,i} + b_4 T_i S_i + \varepsilon_i$$

where T and S are annual mean bottom temperature and salinity, respectively, S_{min} is minimum monthly salinity, and b_0, b_1, b_2, b_3, b_4 are the fit statistics used to simulate uncertainty in $\delta^{15}N_{base}$

Trophic levels (TLs) of taxa

- Method established by Post (2002) to estimate TLs for taxa:

$$TL_i = \lambda_{base} + [(\delta^{15}N_i - \delta^{15}N_{base})/\Delta^{15}N]$$

where λ_{base} is the corresponding base TL, assumed here to be 2, $\delta^{15}N_i$ is the corrected $\delta^{15}N$ value for the individual i, $\delta^{15}N_{base}$ is the mean of all *P. maximus* corrected $\delta^{15}N$ values, fractionation factor ($\Delta^{15}N$) of 3.4‰ (Post 2002) as the average ^{15}N enrichment between the muscle tissue of fishes and invertebrates, and *P. maximus* as the base TL

- The TL for a species was then calculated by averaging the individual TLs

Methods

Characterisation of food web and trophic groups of species

- Hierarchical clustering (via Euclidean distances and the Ward method)
  - Distinguish clusters of species according to their $\delta^{13}C$ and $\delta^{15}N$ values
  - Boot-strapped matrix of distances between species

- Show ranges of isotopic ratios expected for trophic transfer of pelagic and benthic organic matter, respectively

  (Darnaude et al. 2004)
  - Trophic increases of +1‰ in $\delta^{13}C$ and +4.5‰ in $\delta^{15}N$ and of +2‰ in $\delta^{13}C$ and +2.5‰ in $\delta^{15}N$
  - Pelagic (copepods) and benthic primary consumers (*P. maximus*) used as starting point for the pelagic and benthic pathway, respectively

Methods

Quantifying isotopic diversity metrics for the CSS food web

Four diversity metrics (Cucherousset and Villéger 2015) applied to provide information on how the isotopic functional space (i.e. total area of the convex hull) is filled by species

- Species represented by points and their positions (weighted by biomass) in a scaled multidimensional space (0-1) correspond to their $\delta^{13}C$ and $\delta^{15}N$ values

(a) Isotopic Divergence index degree to which species distribution in the isotopic space maximizes the trophic divergence within the food web

Low IDiv (i.e. closer to 0) relative biomasses are dominated by more generalist species, i.e. species closer to the centre of gravity of the convex hull

High IDiv (i.e. closer to 1) species with the highest biomass occupy the isotopic space more densely on the edges of the convex hull, revealing a trophic specialization and thus a high degree of niche differentiation in the food web

(b) Isotopic Dispersion index average trophic diversity in the food web

Low IDis species have the same isotope values

High IDis most of the points (or their weight) are far from the centre of gravity of the group of points

(c) Isotopic Evenness index regularity in species distribution and the density in species packing in the occupied isotopic space

Low IEve food web is composed of clusters of species (i.e. packed species) and implies trophic redundancy and competition for food

High IEve species and relative biomasses are evenly distributed in the isotope space, resulting in higher functional regularity and allowing optimal resource use through niche partitioning

(d) Isotopic Uniqueness index is the inverse of the average isotopic redundancy. Isotopic redundancy reflects the average closeness of species in the isotope space

Low IUni each species has at least one species with the same position in the isotope space (i.e. clustering of species with similar diets) and implies trophic redundancy

High IUni most species (or species with the highest biomass) are isolated in the isotope space

Spatial isotopic trends in relation to the environment

Generalised Additive Models (GAMs)

- Predict isotopic composition as a function of environmental variables

- Biologically meaningful environmental variables

    (a) bathymetry

    (b) seabed habitat

    (c) bottom temperature

    (d) chlorophyll a

- Fitted regional scale- and trophic group-specific GAMs separately on $\delta^{13}C$ and $\delta^{15}N$ data
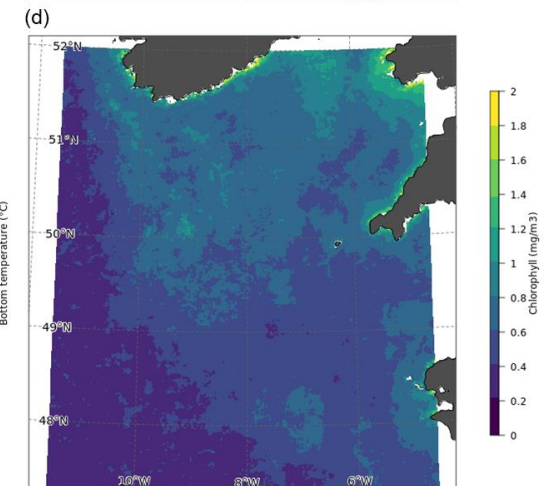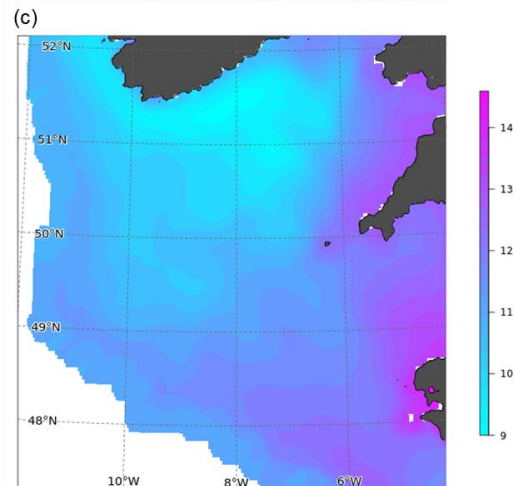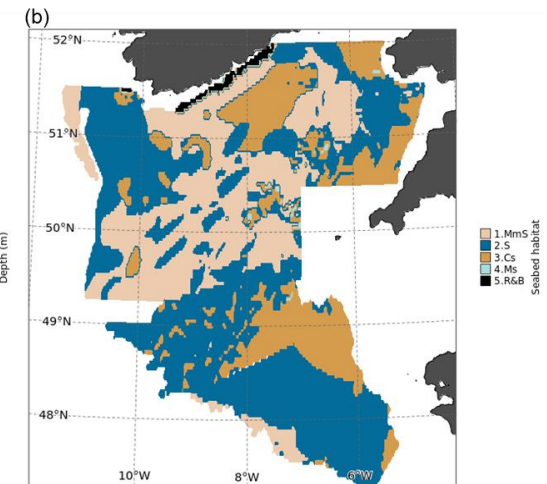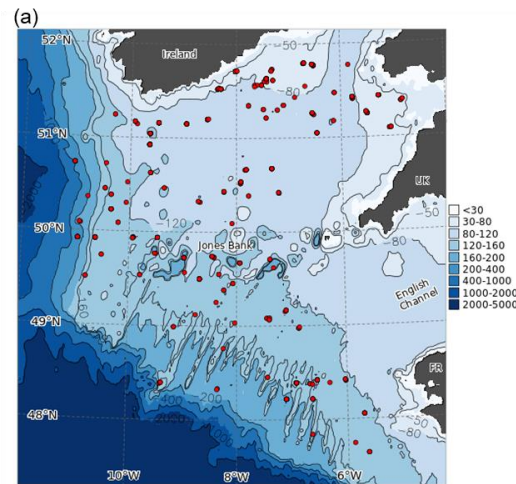
Methods

Overlap indices of trophic groups based on areas identified using GAMs

To better infer the spatial effect of environmental conditions on the functioning of trophic groups

- Compared the position and overlap in the isotopic space (i.e. size of the isotopic niche) among trophic groups associated with key predictor variables across the CSS

- Overlap indices **Isotopic Similarity** and **Isotopic Nestedness** (Cucherousset and Villéger 2015) were quantified based on spatial areas identified from trophic group models.

For selected trophic groups

- Extracted the δ^{13}C and δ^{15}N data for each species at each station across the spatial areas identified to create trophic groups per spatial area

- Biomass indices for each species at each station was raised to the spatial area surface (instead of the whole CSS domain) to create species biomass indices per spatial area

- Isotopic overlap metrics were quantified using the total convex hull areas of two groups and the volume of isotopic space they shared (i.e. volume of their intersection)

Hierarchical cluster analysis identified 8 functional groups

- Group 1, Pelagic primary consumers
- Group 2, Benthic primary consumers
- Group 3, Demersal/benthic fish & benthic cephalopods
- Group 4, Pelagic/demersal/ benthic fish, demersal cephalopods & macrobenthos carnivores
- Group 5, Demersal/benthic fish, demersal cephalopods & macrobenthos carnivores
  - positioned at the same TL as group 4, but is less ^{13}C depleted, marking the benthic pathway
  - group 4 is positioned more on the pelagic pathway
- Group 6, Pelagic/demersal fish & demersal squid
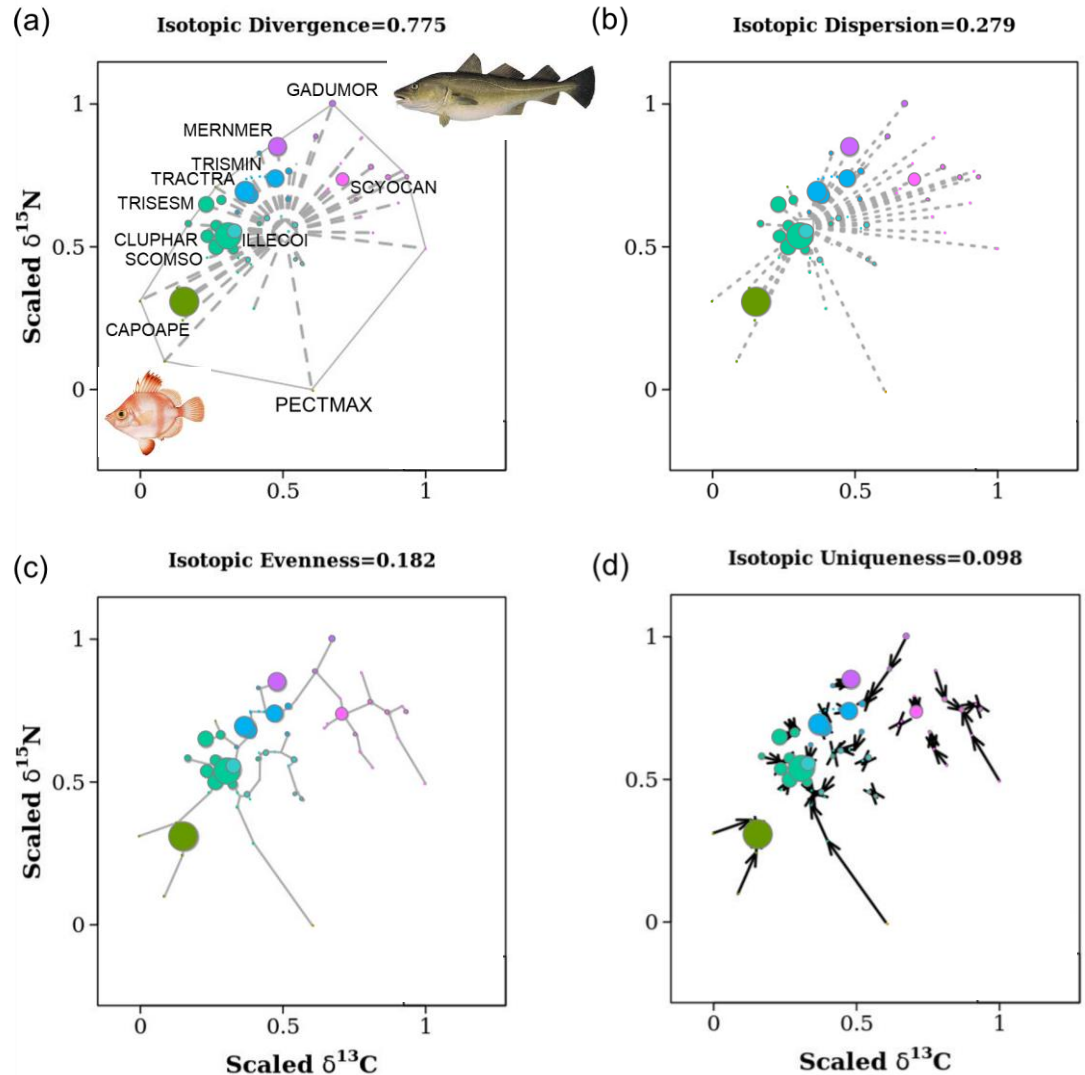- Group 7, Demersal predatory fish
- Group 8, Demersal/benthic fish & macrobenthos carnivores

Mean δ^{15}N values ranged from 6.84‰ to 14.95‰

- Mean trophic level (TL) estimates spanned three TLs
- The δ^{13}C values varied greatly among primary consumers

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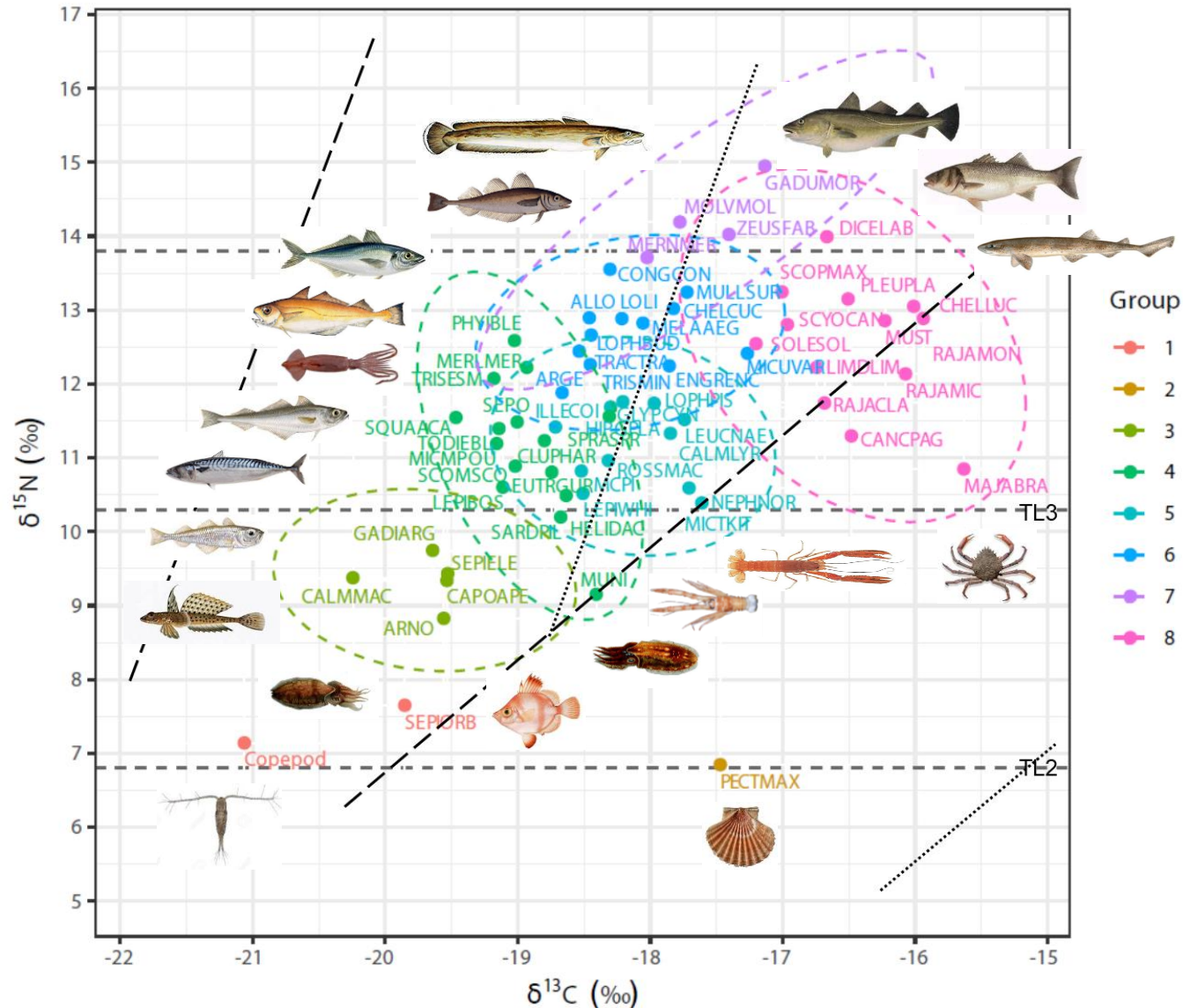
Results : Regional scale structure of the CSS food web

Biomass-weighted values influenced distribution of points within the convex hull

- High Isotopic Divergence (0.76)

- High biomass species occupied the isotopic space more densely on the edges of the convex hull

- Trophic specialization and high degree of niche differentiation in the food web

- Low Isotopic Dispersion (0.28)

- Average trophic diversity in the food web was low

- Low Isotopic Evenness (0.18)

- Food web composed of clusters of species

- Trophic redundancy and competition for food

- Low Isotopic Uniqueness (0.10)

- Distance between points (size of the arrows) was smaller among groups 4-8 compared to group 3. Clustering of species with similar diets.

- Implies high trophic redundancy within TL3

(a) Isotopic Divergence=0.775

(b) Isotopic Dispersion=0.279

(c) Isotopic Evenness=0.182

(d) Isotopic Uniqueness=0.098

Scaled δ^{15}N

Scaled δ^{13}C

GADUMOR, MERNMER, TRISMIN, TRACTRA, SCYOCAN, TRISESM, CLUPHAR, SCOMSO, ILLECOI, CAPOAPE, PECTMAX

Results : Spatial variability in isotopes in relation to the environment

Table 2. Summary of generalized additive models (GAMs) of the relationship between the most explanatory environmental variables and $\delta^{13}C$ and $\delta^{15}N$ for (a) regional scale models and (b-g) trophic group models. BotTemp = bottom temperature, CHLa = chlorophyll *a* concentrations, DEPTH = water depth, seaHab = seabed habitat, (lon,lat) = spatial auto-correlation term.

	Model formula	N. terms	% dev	r^2
1. Carbon ($\delta^{13}C$)				
(a) Regional scale	$\delta^{13}C \sim CHLa + DEPTH + (lon,lat)$	2	43.7	0.425
(b) Benthic primary consumers (G2)	$\delta^{13}C \sim BotTemp + (lon,lat)$	1	88.6	0.866
(c) Pelagic/demersal/benthic fish, demersal cephalopods & macrobenthos carnivores (G4)	$\delta^{13}C \sim CHLa + (lon,lat)$	1	37.1	0.336
(d) Demersal/benthic fish, demersal cephalopods & macrobenthos carnivores (G5)	$\delta^{13}C \sim seaHab + (lon,lat)$	1	58.3	0.563
(e) Pelagic/demersal fish & demersal cephalopods (G6)	$\delta^{13}C \sim CHLa + DEPTH + (lon,lat)$	2	68.6	0.667
(f) Demersal predatory fish (G7)	$\delta^{13}C \sim CHLa + (lon,lat)$	1	35.0	0.287
(g) Demersal/benthic fish & macrobenthos carnivores (G8)	$\delta^{13}C \sim DEPTH + (lon,lat)$	1	60.1	0.555
2. Nitrogen ($\delta^{15}N$)				
(a) Regional scale	$\delta^{15}N \sim CHLa + BotTemp + (lon,lat)$	2	42.3	0.409
(b) Benthic primary consumers (G2)	$\delta^{15}N \sim seaHab + (lon,lat)$	1	90.6	0.888
(c) Pelagic/demersal/benthic fish, demersal cephalopods & macrobenthos carnivores (G4)	$\delta^{15}N \sim CHLa + (lon,lat)$	1	60.5	0.567
(d) Demersal/benthic fish, demersal cephalopods & macrobenthos carnivores (G5)	$\delta^{15}N \sim seaHab + (lon,lat)$	1	64.1	0.604
(e) Pelagic/demersal fish & demersal cephalopods (G6)	$\delta^{15}N \sim CHLa + DEPTH + BotTemp + (lon,lat)$	3	82.0	0.796
(f) Demersal predatory fish (G7)	$\delta^{15}N \sim CHLa + (lon,lat)$	1	49.0	0.427
(g) Demersal/benthic fish & macrobenthos carnivores (G8)	$\delta^{15}N \sim BotTemp + seaHab + (lon,lat)$	2	61.6	0.566

N. terms, number of terms; % dev, per cent deviance explained by model.

Results : Overlap indices of trophic groups in relation to the environment

To explore species assembly processes at different spatial scales, we compared two spatial areas based on:

- Low and high chlorophyll *a* conditions

- Little structuring effect on niche space among group 4

- Important in groups 6 and 7

- Shallow and deep waters

- Strong structuring effect on niche size in benthic feeding species
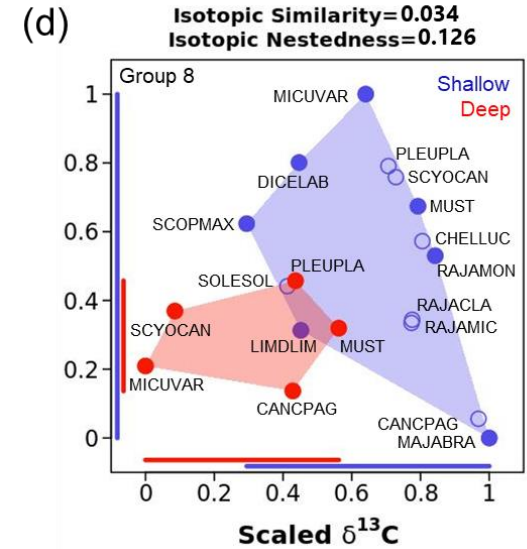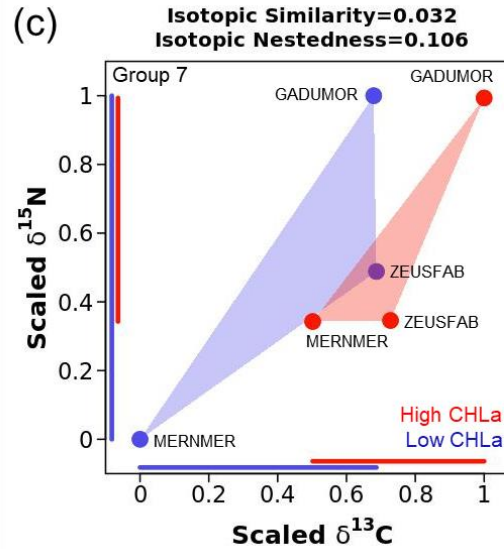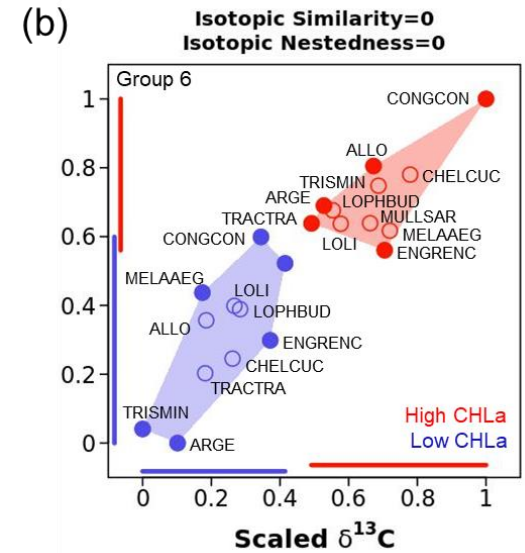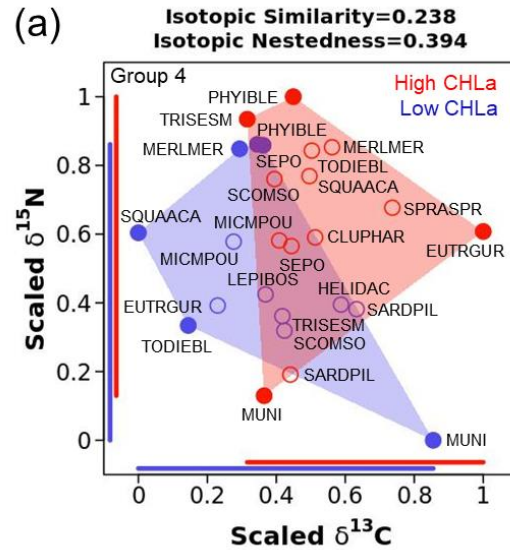
Summary of main findings

Food web structure in the regional Celtic Sea

Identified 8 groups that could be interpreted with trophic and habitat information

Two energy pathways based on pelagic (primary producer based) and benthic (detrital-based) organisms, respectively, exist and are coupled by upper TLs in the CSS

Weighted abundance diversity indices provided several ecological indicators on the status of the ecosystem

- Relatively complex food web
- High trophic redundancy at high TLs suggesting resilience to disturbances

Results highlight the necessity of controlling resource extraction and monitoring of the abundance of the main functional groups of the ecosystem, especially predatory fishes in order to keep the functioning of the system under multiple pressures (Moullec et al. 2017; Dolder et al. 2018; Hernvann and Gascuel 2020)

Biological and physical drivers of trophic variability

Environmental conditions influenced the stable isotope values of consumers

- Trophic response varied across trophic groups, suggesting a high degree of niche differentiation in the food web, whereby consumers couple resources that are also compartmentalised in space
- In agreement with mosaic of different seabed habitats that provide complex microhabitat structures for epibenthic assemblages in the CSS (Ellis et al. 2013)

The majority of variation in food web complexity (compositional, taxonomic and functional diversity) was explained by a pronounced spatial gradient

- Distinct trophic assemblages associated with chlorophyll *a* concentrations, water depth and bottom temperature, resulting in different trophic niche shapes

Overall, results contribute to our understanding of the underlying ecological processes structuring local trophic assemblages and the wider CSS ecosystem

- Provide improved depictions of trophic links and biomass flows for ecosystem models, effective tools to evaluate climate and fishing effects on exploited ecosystems

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d e s   r é s e A u x
T r o p h i q u e s   à   l a
g e s t i o n   d e s   s t o c k s
e n   M E r   c e l t i q u e

Acknowledgements