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# Effects of life-history traits and network topological characteristics on the robustness of marine food webs

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ABSTRACT

Management targets for biodiversity preservation are shifting from individual species to an ecosystem-wide focus. Indeed, the perturbation analysis of interaction networks, such as food webs, better captures the response of biodiversity to environmental pressures than single-species considerations. Here we propose a framework that examines food web robustness to a given perturbation based on life history traits and the topology of the food web, at different scales: local (species), intermediate (species directly linked together by a trophic interaction), and global (food web). Applying this framework to the Celtic Sea, a historically exploited fishing ground, we showed that the species sensitive to fishing were not the most central (i.e. with many interaction links, estimated based on eigenvector centrality) and that there is no both highly sensitive and exposed species to fishing. We then investigated how the loss of central, sensitive and exposed species to fishing could impact the robustness of the food web. We showed that the food web was the least robust to the simulated loss of species with many predators (i.e. forage species) and most exposed to fishing pressure, indicating that conservation priority could be focused on these species. Estimating species' sensitivity to fishing was insufficient to predict food web robustness since the simulated removal of the most sensitive species led to a robustness level similar to that of a random removal sequence. Unlike what is often documented, the network appeared relatively robust to the simulated loss of the most central species, due notably to their implication in redundant trophic interactions and the fact that their disappearance increases modularity. This suggests that species-level metrics such as centrality should be completed by analysis at the scale of the whole food web to prioritize species conservation.

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## 1. Introduction

A shift in focus from species to ecological networks of interactions has recently been proposed as a necessary step in the adaptation of conservation from species centered goals to the maintenance of ecosystem integrity and the services ecosystems underpinned (Scotti and Jordán, 2010; Legagneux et al., 2014; Harvey et al., 2017; Pecl et al., 2017; Chase et al., 2020). Ecological networks, and in particular food webs, provide a powerful unified framework to jointly address biodiversity and ecosystem functioning (Thompson et al., 2012), and guide the management of complex ecosystems (McDonald-Madden et al., 2016). Indeed, the food web concept encapsulates in a single framework cascading effects due to fluctuations in species' abundances, predator-prey dynamics, and emergent properties of direct and indirect trophic links at the scale of the whole network (Jordán et al., 2006; Wallach et al., 2017). The network structure is a major determinant of a food web capacity to withstand the spread of a perturbation (Albert et al., 2000; Solé and Montoya, 2001; Dunne et al., 2002b) and hence affects the robustness of ecosystems (Dunne et al., 2002b, 2004; Tylianakis et al., 2007; Stouffer and Bascompte, 2011; Hattab et al., 2016; Robinson and Strauss, 2020).

The robustness of a food web facing a perturbation can be evaluated based on its capacity to withstand the cascading effects generated by the removal of species (Dunne et al., 2002b, 2004; Dunne and Williams, 2009; Jacob et al., 2011; Jonsson et al., 2015). Human impact on marine ecosystems is intensifying and has already caused numerous declines and even local extinction of marine species (Brooker et al., 2014; Duarte et al., 2020). As ecosystems are being degraded at an unprecedented rate, the need to understand which perturbation sequences are expected to disturb the most ecosystem stability is pressing (Jonsson et al., 2015) and should be easily applicable to all ecosystems (i.e. not being challenging to parametrize nor requiring large computational resources). The importance of species in the robustness of the food web can be tested by removing species one by one according to different sequences (Solé and Montoya, 2001; Dunne et al., 2002b). The decline of well-connected species was reported to have a disproportionate impact on their ecosystems relative to their biomass (Jordán, 2009; Klemm et al., 2012; Worm and Paine, 2016). Indeed, central species with many interactions, are likely to influence numerous species and have thus been defined as food web hubs that should be prioritized for conservation (Solé and Montoya, 2001; Curtsdotter et al., 2011). Measures of centrality accounting for direct and indirect trophic links help to assess a species' importance in mediating the spread of perturbations across the food web (Estrada, 2007a; Jordán, 2009). However, common indices of species importance in the food web have been criticized as not the best suited to select the species to manage to conserve the largest number of species in food webs (McDonald-Madden et al., 2016).

We propose here that to evaluate the potential of a species to spread perturbation across the food web, its topological importance into the food web should be assessed alongside its vulnerability. Vulnerability to a given pressure can be defined as the combination of sensitivity and exposure (IPCC, 2001). Sensitivity (also called intrinsic vulnerability) has been computed based on life history and biological traits that determine the tolerance of a species to environmental conditions and the way it uses the resource (Cheung et al., 2005; Vasconcelos et al., 2017a; Foden et al., 2019). Computation of a sensitivity index can be done by identifying values of one trait corresponding to a level of sensitivity to pressure (e.g. low, medium, high), based on published bibliography and expert knowledge, then compute a total sensitivity score based on the sensitivity score of each trait (Cheung et al., 2005, 2018; Halpern et al., 2007; Vasconcelos et al., 2017b). However, this type of computation implies an arbitrary definition of the threshold values of sensitivity. This can be circumvented by computing the sensitivity to a given pressure based on the multivariate space of the traits (McLean et al., 2019). On the other hand, exposure to one pressure could be evaluated as the amount of impacted biomass of one species, or the spatial extent of the impact (Halpern et al., 2008; Cheung et al., 2018). The amount of catch for instance can be used as an exposure index to fishing pressure (Cheung et al., 2018). A species can be sensitive and exposed to a given pressure but not central, or it may be central but not sensitive nor exposed. In both cases, the species would not spread a perturbation across the food web. In that sense, one can ask whether the robustness of the food web to the spread of a perturbation can be inferred from the sensitivity of its components. To answer this question and shift the sensitivity assessment focus from species to ecological network, we propose a framework that examines food web robustness to a given perturbation at the local (species), intermediate (species directly linked together by a trophic interaction), and global (food web) level, based on species traits and the topology of the food web. Specifically, we investigated the impact on food web robustness of the loss of the sensitive species, the exposed species, and the central species.

We applied the above robustness assessment framework to a food web exposed to fishing pressure in a historically exploited fishing ground, the Celtic Sea. Fishing impacts on the ecosystems are numerous, from decreased species abundance and depletion of higher trophic levels (Pauly and Palomares, 2005) to altered food webs as fishing pressure increases (Gilarranz et al., 2016). At the species level, life-history traits (e.g. maximum length, longevity, or age at maturity) are good proxies of species' demographic characteristics and enable us to characterize fish and benthic invertebrates sensitivity to fishing by ranking them along a "slow-fast" continuum of life-history strategies (Pianka, 1970; Le Quesne and Jennings, 2012; Beukhof et al., 2019b). Fishing tends to favor small-sized, short-lived species that mature early and have a better capacity to recover after a fishing perturbation (Jennings et al., 1998; Le Quesne and Jennings, 2012; Wiedmann et al., 2014). In the Celtic Sea, the intense development of fishing in the area during the second half of the 20th century until its peak in the late 1980s, altered the ecosystem structure through the depletion of large demersal predators, e.g. cod *Gadus morhua*, whiting *Merlangius merlangus* and hake *Merluccius merluccius*, (Guénette and Gascuel, 2012; Hernvann and Gascuel, 2020). Based on traits and food web topology for 69 species (including bony fishes, elasmobranches, cephalopods, bivalves, and crustaceans), we assessed the vulnerability to fishing of both species and the food web. We investigated whether the food web is still threatened by fishing pressure and which species would most likely spread a perturbation to the whole food web. Specifically, (i) at the species' level we assessed (i-a) the sensitivity of the species to fishing pressure, (i-b) whether the most sensitive species to fishing are the most central, (i-c) whether the most vulnerable (sensitive crossed exposed) species are the most central, and (i-d) what is the topological role of species in spreading a perturbation. Then (ii) at the level of groups of interlinked species, we measure whether stabilizing patterns were more numerous than non-stabilizing ones. Finally, (iii) at the level of the food web, we

evaluated whether it is the loss of sensitive, exposed, central species or with a large biomass that is the most detrimental for the food web robustness. For a better understanding of the processes at play, the importance of the number of predators and prey was assessed to distinguish which species' characteristics affect ecosystem-level properties.

## 2. Materials and methods

### 2.1. Study area

The Celtic Sea is a shelf ecosystem (range depth 57–340 m) located in Northwestern Europe. It is characterized by a gradient of sediments from sand to mud habitats. It harbors a larger species richness than the surrounding area due to its position at the biogeographical border between warm water Lusitanian species and cold water Boreal ones (ICES, 2018a). For decades, the Celtic Sea has been an important fishing ground for European countries and fishing has been shaping its ecosystem (Hernvann and Gascuel, 2020). The importance of fishing driving the ecosystems has decreased after 2009 (Mérillet et al., 2020) but remains high, with around 4 million tons landed per year on average over 2000–2015 (Hernvann and Gascuel, 2020).

### 2.2. Food web data

In this study, we represent the upper part of the Celtic Sea food web (i.e., starting at the level of primary consumers and detritivores) by drawing the network of trophic relationships connecting the 69 taxa most frequently observed during the bentho-demersal EVHOE survey (Garren et al., 2019; more than 5% of the sampling sites over 2000–2016). Most of these taxa are specified at the species level whereas some are at the genus level for simplicity, we hereafter used the term "species" for referring to all taxa. The EVHOE survey samples bentho-demersal communities annually and includes species from five classes: Actinopterygii, Bivalvia, Cephalopoda, Elasmobranchii, and Malacostraca (Mérillet et al., 2020).

The trophic links between species were established from the literature review conducted by Hernvann et al. (2020). For each taxon, this review gathers information about species' diets (including cannibalism when documented) for at least three bibliographical references, as geographically close to the Celtic Sea as possible. Conversely to this study where trophic data was then aggregated into functional groups, the information was kept at the species' level to investigate the sensitivity to fishing pressure at the species level and the consequences of each species loss on the food web.

As part of the EATME program, isotopic measurements were conducted on individuals collected in the Celtic Sea for the 69 species. We used the $\delta^{15}N$ and $\delta^{13}C$ to compute the trophic position of species in the food web and get a qualitative insight on benthic/pelagic influence in their food web sources, respectively. These analyses were made after performing a lipid correction (when the ratio between C and N concentrations exceeded 3.5; Sweeting, Polunin, and Jennings, 2006). A baseline correction was also applied to account for the isotopic variability that may result from the spatial heterogeneity in the food web based resource signatures. This correction used relationships established between the isotopic signatures of *Aequipecten opercularis* and environmental data (Barnes et al., 2009; Jennings and van der Molen, 2015; see Appendix Fig. S5).

Trophic levels TL of species *i* were computed from Post (2002) equation (Eq. (1)):

$$TL_i = \frac{\delta^{15}N_i - \delta^{15}N_{base}}{3.4} + TL_{base} \quad (1)$$

where $\delta^{15}N_i$ is the corrected $\delta^{15}N$ value for the species *i* and $\delta^{15}N_{base}$ is the mean of the $\delta^{15}N_{base}$ values of primary consumers (bivalves, $TL_{base} = 2$; see Table S1). There might be a mismatch between the trophic position and the trophic links (from bibliography) of some species: species feeding on a species at a slightly higher trophic level. However, this study is mostly based on indices and analysis using the structure of the food web, so this mismatch does not affect our conclusions.

### 2.3. Vulnerability index of species: sensitivity and exposure to fishing

The vulnerability of a species to fishing was defined as a combination of its sensitivity and its exposure, according to the definition of the IPCC (IPCC, 2001) that was largely followed in the literature (Smit and Wandel, 2006; Williams et al., 2008; Cheung et al., 2018; Foden et al., 2019). Sensitivity is the degree to which a species is affected by a perturbation while exposure is the magnitude of the perturbation (IPCC, 2001; Foden et al., 2019) but there is still no consensus on the exact definition (Wheatley et al., 2017). Adaptive capacity, defined as the degree to which a species can adjust, moderate or take advantage of a perturbation, is sometimes subtracted to the combination of the sensitivity and exposure (IPCC, 2001). Here, the adaptive capacity of a species to endure fishing pressure was considered as already accounted for in the computation of the sensitivity score, following Foden et al. (2019).

To quantify a taxon's sensitivity to fishing, we selected six traits widely used to characterize the life-history strategies of marine species and their sensitivity to perturbation: longevity, maximum length, reproductive guild, fecundity, age at maturity, and size of the offspring (Winemiller and Rose, 1992; Jennings et al., 1998; Le Quesne and Jennings, 2012; Wiedmann et al., 2014). Most of these traits came from the PANGAEA database (Beukhof et al., 2019a) but were completed by literature (see Table S2). We applied a Hill-Smith analysis (Hill and Smith, 1976), a centered and normed factorial analysis, used here to investigate the life-history and sensitivity characteristics of our set of marine species and summarize these characteristics in a score that reflects the sensitivity to fishing (Kleyer et al., 2012; Dray et al., 2014; Spitz et al., 2014; Mouton et al., 2019). This analysis has the advantage to give the same

weight to quantitative and qualitative traits (without regard to the number of modalities of qualitative traits). It is thus adapted to the analysis of datasets with both quantitative and qualitative traits and no missing values (while the widely used Gower dissimilarity enables to deal with missing values). The first axis of the Hill-Smith analysis represents the strongest linear correlation between the traits (captures most of the variance in the trait data) and therefore the best reduction of the information driven by the considered set of traits on a single linear axis. As we considered six traits characterizing life-history strategies and sensitivity to perturbation, the scores of species on this first axis were used as a sensitivity index. The well-founded of using the first axis for sensitivity scores was assessed based on whether the loadings of the traits along this axis made ecological sense.

The most direct impact of fishing at the species level consists of the loss of a proportion of the population. Thus, we considered that the exposure to fishing pressure should describe the magnitude of the mortality induced by fishing. Therefore, we defined exposure to fishing as the proportion of biomass of a population that is exploited by fishing (i.e. fishing mortality). This metric was preferred to the fishing effort since some heavily fished species might have a large population and be slightly affected by fishing while some lightly fished species might have a larger proportion of their population removed by fisheries. This definition makes the Exposure independent of any notion of species productivity that may be linked to Sensitivity, hence preventing potential redundancies between our two indicators of interest. We expressed the exposure of a species $i$ as:

$$Exposure_i = \frac{C_i}{B_{tot,i}} \quad (2)$$

where $C_i$ is the biomass of the species $i$ landed (i.e. catches) and discarded and $B_{tot,i}$ is the total biomass present in the Celtic Sea (area 7e-j) in 2016. For species whose stocks are assessed and have a spatial distribution relevant to our study area (i.e. 17 species out of the 69 considered in this study), total biomass and catch were directly available from the International Council for the Exploration of the Sea (ICES) working groups' reports (ICES, 2020). For species without stock assessment (i.e. the remaining 42 species), exposure was computed using the fishing mortality rates estimated for the corresponding functional groups by the Ecopath with Ecosim (EwE) Celtic Sea model (Hernvann et al., 2020). These rates are issued from the ratio of on-shelf catches in ICES divisions 7e-j (official landings from STATLANT, (ICES, 2019) elevated by discard rates from the DISCARDLESS project, http://www.discardless.eu/) and biomass estimated for the corresponding area from the EwE mass balance equations. As EwE functional groups can gather several species with

**Table 1**
Summary of food web metrics used in this study, their definition and known implication for food web robustness.

| Level of the robustness indicator | Metric | Definition | Relation to food web robustness | Ref. |
|---|---|---|---|---|
| Species level | Eigenvalue centrality | Quantify how densely a species is linked to highly connected species | Measure the relative importance of each species in what is akin to a flow simulation in which each species influences all its partners simultaneously. Species with high centrality are expected to facilitate the spread of perturbations to the food web. | (Delmas et al., 2019; Bonacich, 1987) |
| Species level | Number of prey | Number incoming links | The highest number of prey, the more generalist. | (Dunne and Williams, 2009) |
| Species level | Number of predators | Number of out-coming links | The highest number of predators, the more vulnerable to predation. | (Dunne and Williams, 2009) |
| Species level | Average shortest path length | Mean minimum number of interactions from one species to another | Species with shorter chains are likely to spread a perturbation faster in the ecological network ( Dunne et al., 2004; Hattab et al., 2016). | (Williams et al., 2002) |
| Species level | Topological role | Characterize how much a taxon is connected to species within its own module compared to species in other modules | Described species as either (1) peripheral, (2) connectors, (3) module connectors or (4) network connectors (Kortsch et al., 2015). The species in (3) and (4) are the most connected and the more prone to spread a perturbation. | (Guimerà and Nunes Amaral, 2005) |
| Level of group of interlinked species | Motifs | Three nodes configurations that tend to be over-represented in a food web | The tritrophic chain, direct competition, and apparent competition are stabilizing motifs ( Borrelli, 2015). See Fig. 5 for motif schema. | (Milo et al., 2002) |
| Food web level | Connectance | Proportion of directed links realized out of the maximum number of possible links | It characterizes food web robustness to the loss of species (Estrada, 2007b). It is a good estimate of community sensitivity to a perturbation, and large values of connectance characterize food webs in which a perturbation can easily spread ( Martinez, 1992; Delmas et al., 2019). | (May, 1973; Dunne et al., 2002a) |
| Food web level | Modularity | Measure the degree of compartmentalization | Expected to be positively associated with robustness since the spread of a perturbation will be lessened in a modular network (perturbation tends to stay in the modules) (Thébault and Fontaine, 2010; Grilli et al., 2016). | (Stouffer and Bascompte, 2011) |
| Food web level | Nestedness | Indicates the level to which the diet of specialist species is a subset of the diet of generalist species | Nested food web would be more robust to the loss of species than less nested ones (Thébault and Fontaine, 2010). | (Almeida-Neto et al., 2007) |

similar biological characteristics and trophic ecology, the same exposure was attributed to our food web's species when matching the EwE functional group. The term exposed species was used for species with exposure values above the median value (Fig. 4).

The vulnerability was graphically determined in a two-dimensional space formed by sensitivity and exposure. The vulnerability was categorized as high, medium, and low according to the position of each species in one of the 4 rectangles which were partitioned based on the median values of sensitivity and exposure. The vulnerability was high for species for which both sensitivity and exposure values were above the median value. The medium vulnerability occurs when either one value was above the median and the other below. Finally, species vulnerability was low when both sensitivity and exposure values were below the median value.

### 2.4. Computation of a proxy of the spread of a perturbation across a food web: the eigenvector centrality

The more connected a species is to other species, the more a perturbation affecting that species is likely to spread across the whole food web (Dunne et al., 2002b; Delmas et al., 2019). To account for the potential for a perturbation affecting a species to spread to other species, we calculated the average shortest path length per species as the mean minimum number of interactions from one species to another (Dunne et al., 2004; Hattab et al., 2016). Further, to quantify the degree to which a species is connected to other highly connected species, we used the eigenvector centrality metric, which is akin to a simulation of flow across a food web (Bonacich, 1987; Delmas et al., 2019) and better identifies the fastest route to collapse than the other centrality measures (such as degree centrality, clothedness centrality, betweenness centrality; Allesina and Pascual, 2009; Delmas et al., 2019). Species heavily connected to other highly connected species hence get higher scores of eigenvector centrality (hereafter coined "centrality" for simplicity; Table 1), computed as:

$$CE_i = \frac{1}{\lambda}\sum_j A_{ij} CE_j$$

where λ is a constant, A is the adjacency matrix so $A_{ij}$ is 1 if species I interact with j and 0 otherwise. This can be rewritten and solved as an eigen equation:

$$Ac = \lambda c$$

where c is the vector of all the eigen centrality values of all the species in the food web. A summary of the food web metrics used here is provided Table 1.

### 2.5. Different roles of species in spreading a perturbation: species topological roles

All species will not have the same role spreading a perturbation according to the way they interact with species within their module or in other modules (Blanchet et al., 2019). Species topological role can characterize how much a taxon is connected to species within its own module compared to species in other modules. This allows discriminating between generalist species that are hub connectors and more peripheral species, only linked to species in their own module. Species topological role relies on module identification, computed here based on a spin glass algorithm. Topological roles are described by (1) the standardized within-module degree z and (2) the among-module connectivity participation coefficient PC (Guimerà and Nunes Amaral, 2005). The within-module degree z described how well a species is connected within its own module, relatively to the other species in its module. It is computed as follows:

$$z = \frac{k_{is} - \overline{k}}{SD_k}$$

where $k_{is}$ is the number of links from species $i$ to other species within its own module $s$, $\overline{k}$ and $SD_k$ are the mean and the standard deviation of $k_{is}$ over all the species in module $s$. The topological role of a species is also described by the among-module connectivity PC that evaluates how well connected to other modules a species is. It is defined as follows:

$$PC = 1 - \sum_{s=1}^{N}\left(\frac{k_{is}}{k_i}\right)^2$$

where $k_i$ is the number of links to or from species $i$, $k_{is}$ is the number of links from species $i$ to species in module $s$, and $N$ the total number of modules. Since the within-module degree z and the among-module connectivity PC rely on the module membership, which is a stochastic metric, the mean and 95% CI of 1000 iterations of each of these 2 metrics were computed, following Kortsch et al. (2015).

The z-PC space was divided in areas, characteristic of a role, following the threshold used by (Kortsch et al., 2015 modified from Guimerà and Nunes Amaral, 2005): $z = 2.5$ and $PC = 0.625$. Species with $z \geq 2.5$ are classified as module hubs and as non-hubs for $z < 2.5$. The PC threshold corresponds to a species that has at least 60% of its links within its own module. Species with $z < 2.5$ and $PC < 0.625$ are peripherals, those with $z < 2.5$ and $PC \geq 0.625$ are connectors, those with $z \geq 2.5$ and $PC < 0.625$ are modules connectors and those with $z \geq 2.5$ and $PC \geq 0.625$ are network connectors.

### 2.6. Analysis of the frequency of groups of interlinked species: network motifs

In complex networks, some patterns of interconnection between nodes happen at a frequency above random. Those are named network motifs (Milo et al., 2002). The preferred elimination of unstable patterns of interconnections can explain the motif dominance. The most represented motifs are thus the ones bringing stability to the network (Stouffer and Bascompte, 2010; Borrelli, 2015). Despite there is no direct one to one relationship between the relative persistence of modules in isolation and their effect on the persistence of the food web (Stouffer and Bascompte, 2010), certain motifs confer stability to the whole food web: tritrophic chain, omnivory, direct competition and apparent competition (Stouffer and Bascompte, 2010; Borrelli, 2015). The frequency of the 16 possible types of thee-node connected group of interlinked species (Davis and Leinhardt, 1967) was investigated in this food web.

### 2.7. Comparing the robustness of the food web for different perturbation sequences

To evaluate the robustness of the food web to a perturbation, we simulated primary extinctions of species (i.e., removal of species from the food web) according to various removal sequences. One species was considered extinct when all its prey has been removed (Solé and Montoya, 2001). This approach has two limitations: (1) it does not allow for the adaptive rewiring of the trophic interactions (e.g. diet shift to other preys) induced by species removal, which happens in natural communities (Staniczenko et al., 2010; Thierry et al., 2011); (2) a species extinction occurs only when all its preys went extinct as well, which is a stringent condition that is less likely to be observed in real ecosystems. In our study, rewiring could not be accounted for since the food web topology reconstructed here integrates data from trophic studies covering a long-time span and informs separately each trophic link. To circumvent the second limitation, secondary extinction of a species was computed for two different extinction thresholds: a species was removed when 50% of its incoming links remained (threshold 50%) or when 0% of its incoming links remained (threshold 0%). The results for the threshold 0% are presented in Fig. 6 while the threshold 50% gave similar results and were analyzed in supplementary (Fig. S2).

We monitored accumulated secondary extinctions (i.e. the extinction caused by the removal of all the prey of one species) and several metrics of food-web structure that were widely used to study the fragility of ecological networks (i.e. connectance, modularity, and nestedness) (Gaiarsa and Guimarães, 2019). Secondary extinctions inform on the robustness of the food web and are negatively correlated with it (Dunne et al., 2002b). The connectance ($L/S^2$) is computed from the number of links (L) and the number of species (S) and gives information on how densely connected is the food web (see Table 1 for information on the relationship with robustness). The values of connectance were tracked to illustrate if the food web, following the removal of one species, was getting more prone to spread a perturbation (Cordone et al., 2018). Modularity informs the degree of compartmentalization of the food web. This metric was computed using a spin glass algorithm and simulated annealing, following Newman and Girvan (2004) (see Table 1). In the case of community structure, modularity values range from 0 (no modules) to 1 (strong community structure) (modularity for any kind of networks ranges from −1 to 1, Cherifi and Santucci, 2013). Finally, nestedness indicates the level of sharing of interaction partners among species (Thébault and Fontaine, 2010) (see Table 1). This metric was computed with the NODF ("nestedness metric based on overlap and decreasing fill") (Almeida-Neto et al., 2008). High values of nestedness occur when the diet of specialists consumers is a subset of the diet of generalists consumers (Nordstrom et al., 2015), with 0 indicating full complementarity of trophic links between species and 100 completely nested links.

These simulations of extinctions were done by removing species in six different orders to characterize the effect of different species traits and network characteristics on the food web robustness: (1) Sensitivity, from the highest to the lowest sensitivity score, (2) Centrality, from species with the highest to the lowest eigenvector centrality values, (3) Exposure, from species with the highest to the lowest exposure to fishing pressure, (4) Biomass, from the highest to the lowest biomass, (5) Prey, from species with the highest to the lowest number of predators and (6) Predator, from species with the highest to the lowest number of prey. The connectance and accumulated secondary extinctions generated in each of these six removal scenarios were compared to a null model in which species are randomly selected and removed from the food web. This random removal was iterated 500 times and confidence intervals were computed (mean $\pm$ standard deviation).

To compare the robustness of this food web with others, we computed the R50, defined as the proportion of species that have to be removed to result in a total species' loss $\geq$ 50% of the species in the original web (Dunne and Williams, 2009). The larger the R50 is (maximum value of 50%), the less the removal of a species (primary removal) leads to secondary extinction and the more robust the food web is.

### 2.8. Supplementary data and analyses for the interpretation of vulnerability and robustness patterns

The biomass of each species from the EVHOE data in 2016 (Evaluation des resources Halieutiques de l'Ouest de l'Europe, Garren et al., 2019) was elevated to the depth-sediment strata, to account for the irregular sampling within a stratum. This biomass was used in the biomass removal sequence. In addition, to provide an order of magnitude of the proportion of the biomass that is sensitive or vulnerable to fishing pressure and understand its potential implications in the sequential extinctions, the proportion of each species relative to the total biomass of all species in our dataset was computed. To investigate the potential relationships between the different metrics used to characterize the system (i.e., $\delta^{13}C$, $\delta^{15}N$, TL, number of prey, number of predators, sensitivity, centrality, and exposure) as well as the existence of a pattern of sensitivity and centrality across trophic levels and trophic pathways, a correlation analysis was performed between those metrics (Fig. S1). Since all metrics were not normally distributed, Spearman correlation was used.

All analyses were conducted in R 4.0.2 (R Core Team, 2020). The average shortest path length was computed for all the species to another with shortest.path function from the R package 'igraph'. The centrality and modularity were calculated using the same

'igraph' package, while nestedness was computed using the package 'RInSp'. The frequency of each group of interlinked species was computed using the *triad.census* function ('igraph' package). The secondary extinction analysis was performed with modified functions from the R package 'NetworkExtinction' (Corcoran-Barrios et al., 2019). P-values of the correlation tests were displayed using the *chart.Correlation* function from the R package 'PerformanceAnalytics' (Peterson et al., 2020).

## 3. Results

### 3.1. Robustness of the network studied from species-level metrics

#### 3.1.1. Sensitivity of the species to fishing pressure

The bentho-demersal species in the Celtic Sea can be characterized by a "slow-fast" continuum of life history, from small, short-lived species producing small offspring (Fig. 1, axis 1 left-hand side) to large, long-lived species with large offspring (Fig. 1, axis 1 right-hand side). This first axis accounts for the larger share of the variability of the dataset (37.24%) and was used as a sensitivity score, with species having the highest sensitivity to fishing toward the right of the first axis (Fig. 1). Indeed, large, long-lived species with low reproductive output are typically the most sensitive to fishing pressure. The second axis accounts for 16.69% of the variability and mostly characterizes a gradient from highly fecund and non-guarder species to low fecund species that bear their offspring. The species most sensitive to fishing in the Celtic Sea are mostly elasmobranchs: sharks, spurdog *Squalus acanthias*, tope shark *Galeorhinus galeus* and smooth-hound *Mustelus sp.* followed by rays, cuckoo ray *Leucoraja naevus*, thornback ray *Raja clavata*, blonde ray *Raja brachyura* and small-eyed ray *Raja microocellata*. Some large fishes also show high values of sensitivity such as European conger *Conger conger* and ling *Molva molva* (Fig. 1, axis 1).

#### 3.1.2. Sensitivity and centrality

Highly connected species (i.e. with largest values of centrality) are large piscivorous fishes, namely whiting, megrim *Lepidorhombus whiffiagonis*, cod, hake, turbot *Scophthalmus maximus*, and squid *Loligo sp.*. The most central species are not the most sensitive to fishing (Fig. 2). We observed some weak but significant relationships: the species most sensitive to fishing tend to be at high trophic levels (Fig. S1, correlation test=0.43, p-value<0.001), to have a wide range of preys (Fig. S1, correlation test=0.53, p-value<0.001) and to

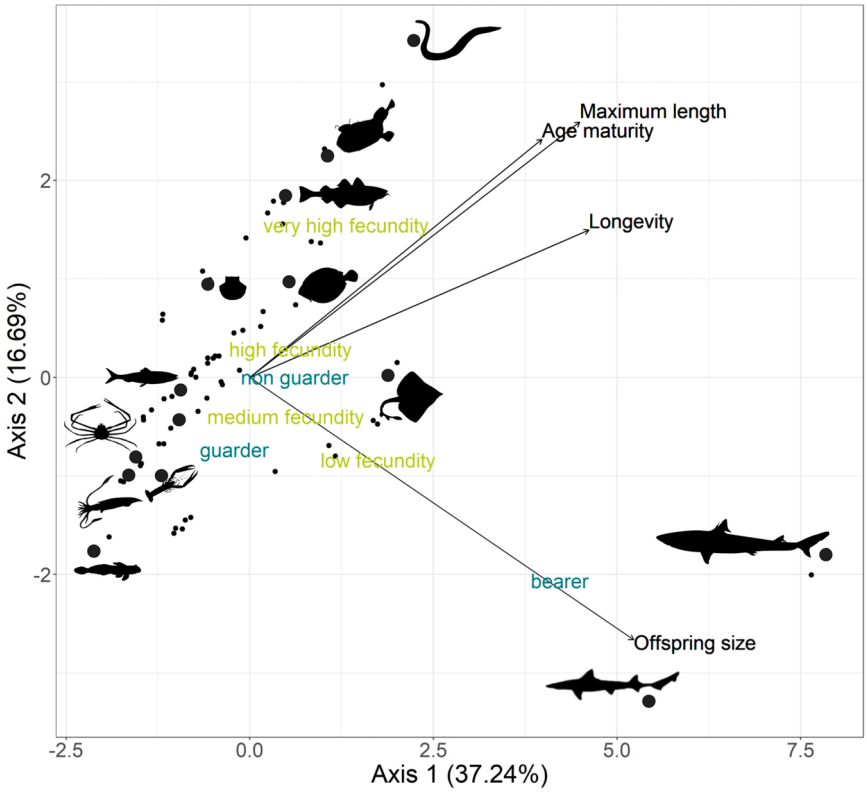



**Fig. 1.** Factorial map of Hill Smith analysis on six functional traits related to a slow-fast gradient of life-history strategies: maximum length, longevity, offspring size, age at maturity, reproductive guild (modalities in blue), and fecundity (modalities in yellow-green). Points represent the 69 species. Species names are given in Table S1. Silhouettes depict the distribution of some selected species in the factorial space (large black dots). The most sensitive species to fishing (right part) are characterized by high values of maximum length, longevity, age at maturity, and offspring size and tend to bear their offspring.

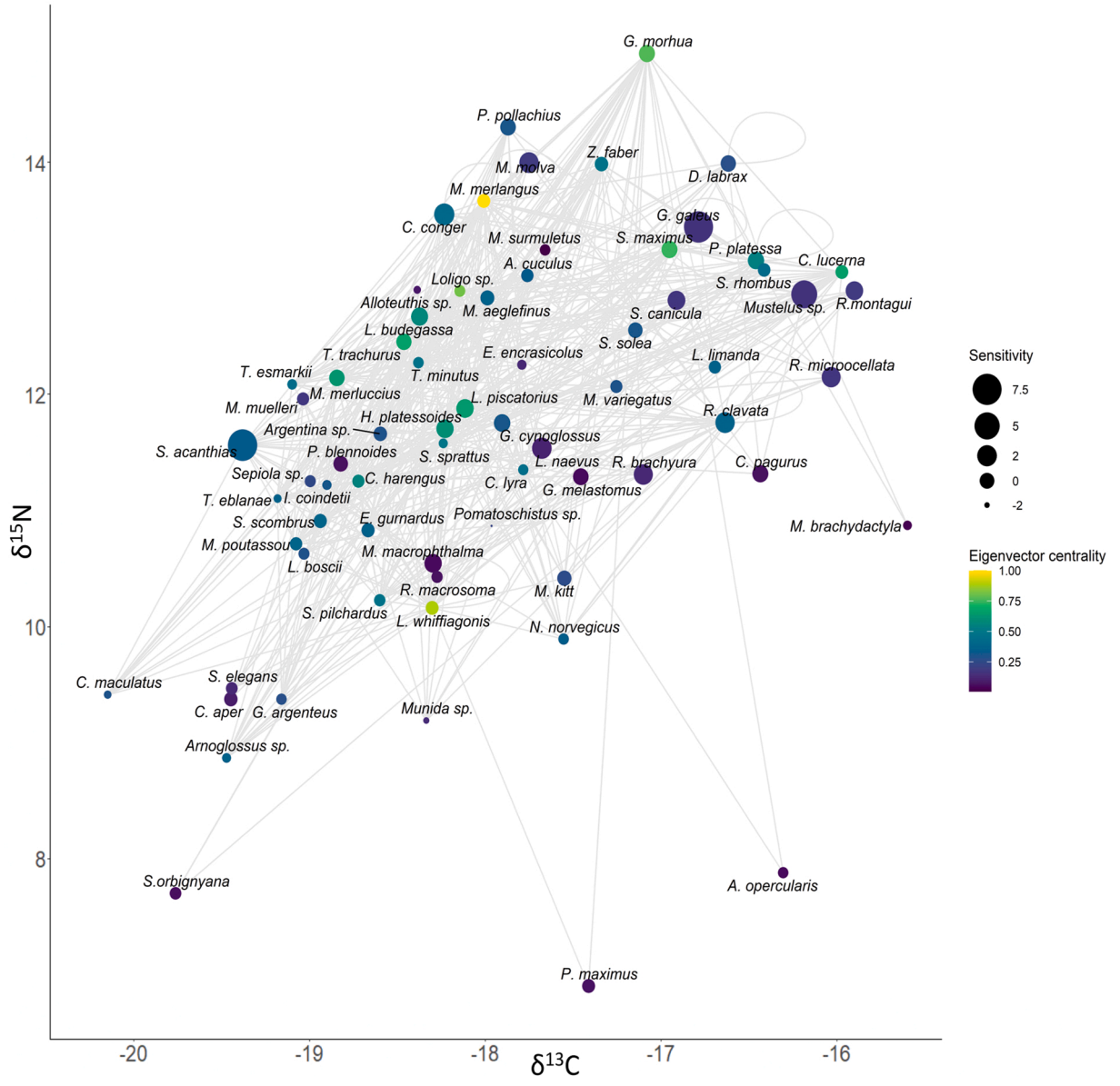



**Fig. 2.** Representation of the Celtic Sea food web in the isotopic space with sensitivity to fishing (size of the dots) and centrality (color scale from dark blue to light green). The isotopic space is defined by the isotopic ratio of carbon 13 C ($\delta^{13}C$) and nitrogen 15 N ($\delta^{15}N$). The nitrogen axis is consistent with species trophic level while the carbon axis discriminates pelagic (more negative) from benthic (less negative) pathways.

feed on the benthic food path, i.e. with the highest values of $\delta^{13}C$ (Fig. S1, correlation test=0.38, p-value<0.01). Exposure also tends to be higher for species feeding on the benthic than on the pelagic food path (Fig. S1, correlation test=0.52, p-value<0.001).

### *3.1.3. Vulnerability (sensitivity crossed with exposure) and centrality*

Vulnerable species are defined as both sensitive and exposed to fishing. In the Celtic Sea, there are no species with very high vulnerability values, i.e. no species in the top right corner (Fig. 3). However, twenty-four species have high values of vulnerability (i.e. both sensitivity and exposure values above the median). Among those species, the most vulnerable are cod, edible crab *Cancer pagurus*, smooth-hound, and to a lesser extent hake, anglerfish *Lophius piscatorius*, blackbellied anglerfish *Lophius budegassa*, European conger, European plaice *Pleuronectes platessa*, and ling (Fig. 3). In addition, three of these vulnerable species (cod, hake, and anglerfish) have high values of centrality. These species, despite being central, are not accounting for a large proportion of the total biomass (Fig. 3), which suggests that if these species become affected by an external factor (i.e. environmental conditions or human pressures), they would have a low impact on the total biomass of the Celtic Sea in a first instance (yet for more precise prediction, productivity should be accounted for). However, considering their centrality values, meaning the potentiality for spread perturbation, they might have a

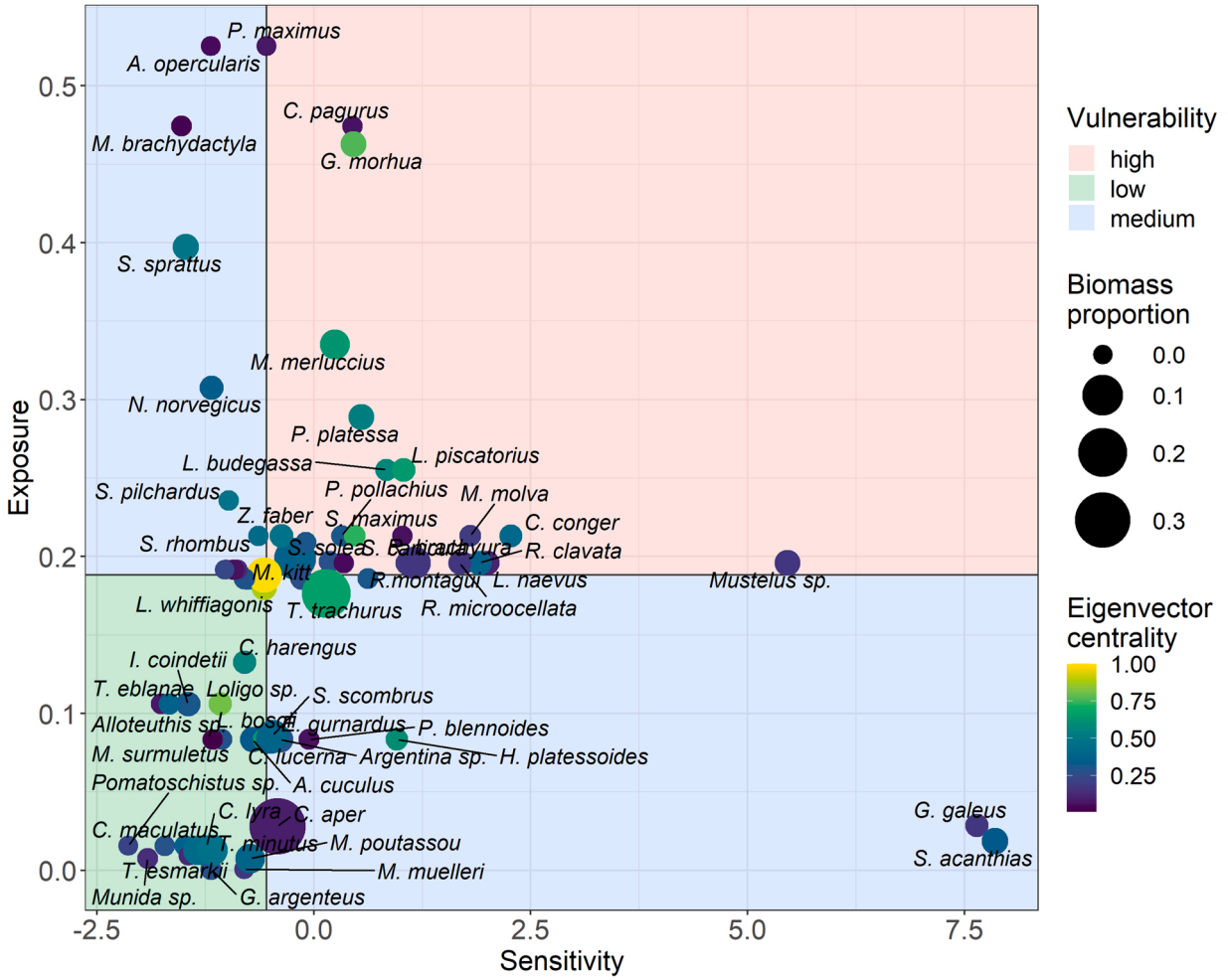



**Fig. 3.** Summary plot of the vulnerability of species (sensitivity combined with exposure), species biomass, and the potentiality for the perturbation at the species-level to spread (eigenvector centrality). Solid lines depict median values of sensitivity and exposure. Species relative biomass (each species biomass is divided by the total biomass of the 69 studied species) is given as a proxy of their importance in trophic flux. Proportions lower than 0.1 are in the 0 category in the graph legend. Vulnerability is determined graphically accounting for the position of the median values of sensitivity (median=0.55) and exposure (median=0.19).

large impact on the food web. Twenty-two species are ranked as intermediately vulnerable. Among them, tope shark and spurdog are highly sensitive species that have low values of exposure. Conversely, queen scallop, European spider crab *Maja brachydactyla,* and sprat have low sensitivity values but are highly fished. Twenty-three species have a low vulnerability to fishing, with the lowest vulnerability encountered for squat lobster *Munida sp.* and gobies *Pomatoschistus sp.*

### *3.1.4. Topological role of the species*

The Celtic Sea food web studied here has 3 modules. Topological analysis showed that no species are module connectors, nor network connectors. Twenty-seven species are network connectors and 42 are peripheral (Table S1). Whiting was the connector species with the highest values of within-module degree z and is also the species with the lowest value of average shortest path length (Fig. 4). Herring *Clupea harengus* has the largest value of within-module degree z. Among the most vulnerable species, both anglerfish species and smooth hound are connector species with quite high values of within-module degree z. Cod is categorized as a peripheral species, but at the limit with connector species and with high values of within-module connectivity (Fig. 4). Conversely, queen scallop *Aequipecten opercularis*, king scallop *Pecten maximus* and striped red mullet *Mullus surmuletus* are very peripheral species, having only few links and only with species within their module.

## *3.2. Group of interlinked species*

The most common motifs are the basic components of any network, i.e. the empty graph (no links between 3 species) and the single directed edge (one link between two of the three species), which are not informative on the function realized. More informatively,

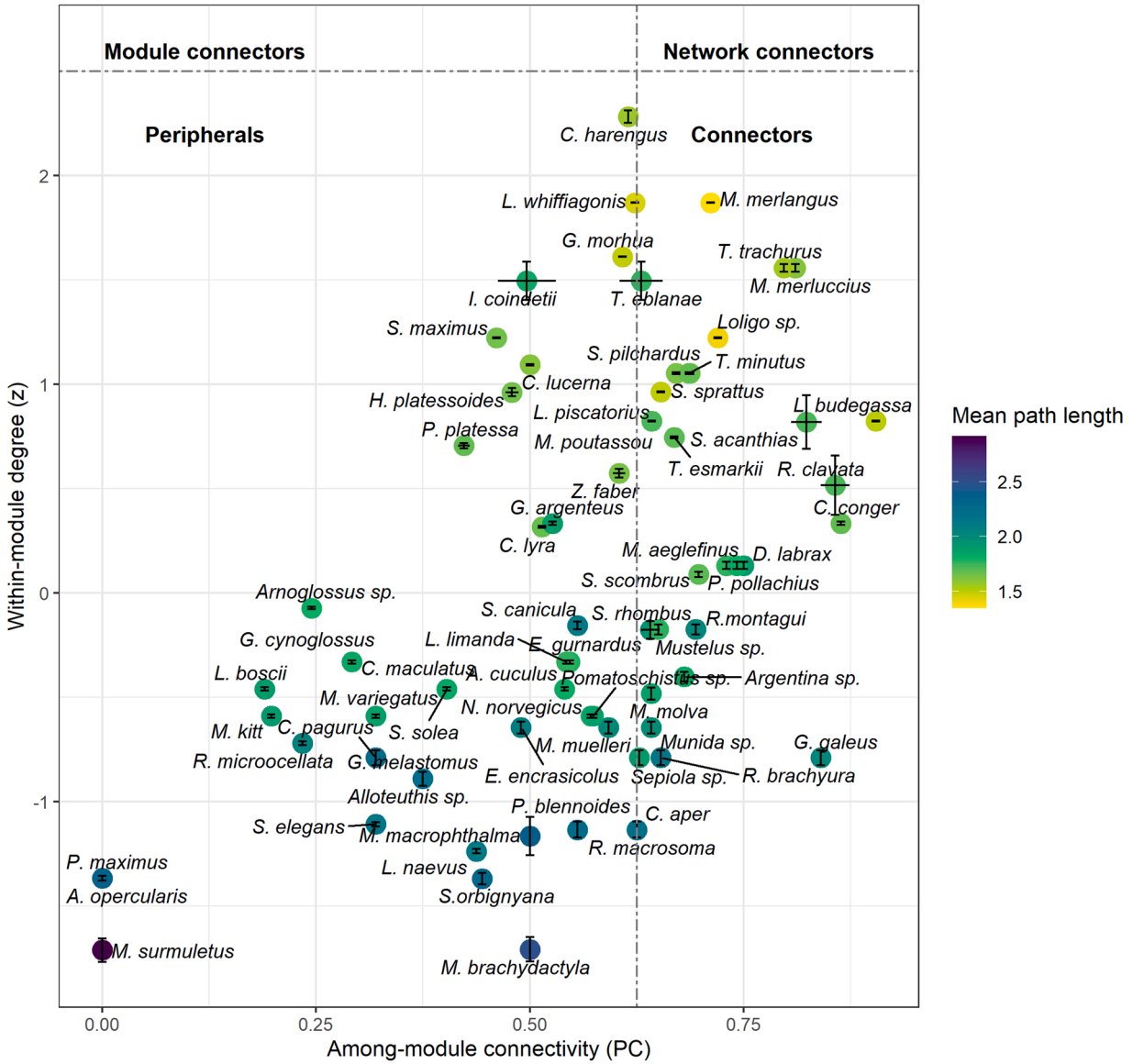



**Fig. 4.** Topological role of species based on their module membership. The dots are the mean values of 1000 within-module degree z and 1000 among-module connectivity PC computation. The brackets are the 95%CI. Four topological roles are defined: peripheral (lower-left), connectors (lower-right), module connectors (upper-left) and network connector (upper-right).

apparent competition is the most common motifs in the food web, followed by direct competition, tritrophic chain and three species trophic loop. The motif 111D (similar to apparent competition but with one of the prey species preying on the predator) is also quite common, while the intra-guild predation is considered as stable but not common here (Fig. 5).

### 3.3. *Large scale patterns: food web metrics and secondary extinction*

We computed several metrics informing on the large scale emergent structural properties of the food web. Our food web of 69 species and 559 links has a value of connectance of 0.12 and a value of nestedness of 45.31.

The removal of the first 7% of the most exposed species to fishing causes the largest number of secondary extinctions (Exposure removal sequence, Fig. 6A) and increase in connectance, with values significantly higher than the random model (Fig. 6B).

Then, after the removal of 19% of the species, the simulated extinctions of species with the largest number of predators lead to the highest and fastest rate of secondary extinctions, significantly higher than the null model (Prey removal sequence, Fig. 6A). Removing species from the most to the least central produces secondary extinctions comparable to the random removal sequence (Centrality removal sequence, Fig. 6A). Regarding connectance, the most significant reduction occurs when removing species according to their

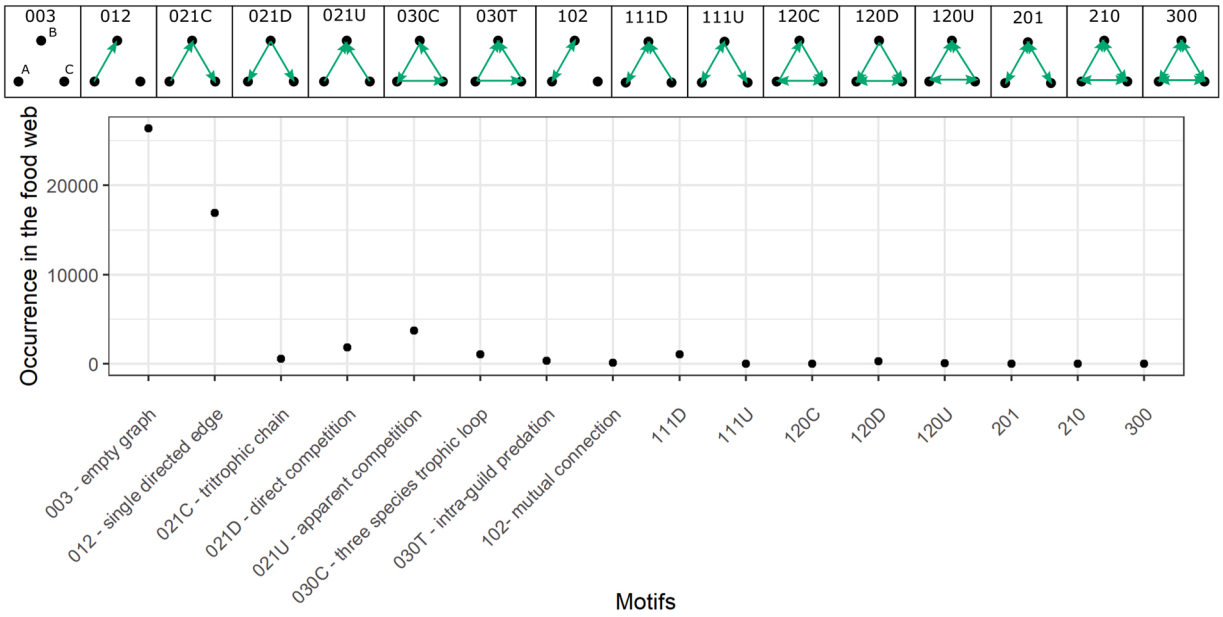



**Fig. 5.** Occurrence of the 16 possible 3 nodes connected graphs in the food web and graphical representation of their configuration. When available, the name of the motif was given.

number of prey (Predators removal sequence) but also their influence (Centrality removal sequence) and lead to a food web with a significantly lower connectance than with a random sequence (Fig. 6B). For these two removal sequences, values of modularity show the largest increase (Fig. 6C) and values of nestedness the largest decrease (Fig. 6D), significantly different from the random sequence.

Removing species with the highest biomass led to a number of secondary extinction lower than the random model for the first 35% of the species and similar to the random model after (Fig. 6A).

Finally, removing the species according to the largest number of prey (Predators removal sequence) and the most sensitive species (Sensitivity removal sequence) leads to the lowest number of accumulated secondary extinctions, even lower than the null model (Fig. 6A). The Sensitivity removal sequence does not lead to variations in connectance different from the random model (Fig. 6B). Nestedness increases with the Sensitivity removal sequence and is significantly higher than the random removal sequence from 4% to 73% of the species removed (Fig. 6D).

Globally, the Sensitivity and Predator removal sequences lead to the most robust food web (R50 = 50%), followed by the Biomass removal sequence (49%), the random model (46%), the Centrality removal sequence (46%), the Exposure removal sequence (45%), and the Prey removal sequence (39%).

## 4. Discussion

Our analyses allowed to assess how fishing pressure applied at the species' level could influence food web robustness. From the characterization of the sensitivity and vulnerability of a species to fishing pressure, we studied the potential spread of that perturbation at different levels: at the species' level, with the centrality values and topological role, at the level of the group of interlinked species, with motifs analysis, and the level of the whole network with secondary extinctions simulations. Based on large scale emergent structural properties, this food web appears to have medium robustness to the spread of perturbation, when compared to other food webs: its connectance (0.12) correspond to medium values (0.026–0.351, Dunne et al., 2002a; 0.05–0.17, Woodward et al., 2010; 0.174–0.285, Angelini and Vaz-Velho, 2011; 0.13, Kéfi et al., 2015; 0.04, Marina et al., 2018), its modularity (0.20) is medium-low (0.22–0.49, Newman and Girvan, 2004; 0.27–0.35, Kortsch et al., 2015, 0.01–0.5, Montoya et al., 2015, all computed with the M modularity metric and spin glass algorithm), and it has medium values of nestedness (45.31) (40–70, Almeida-Neto et al., 2008; computed with NODF). In addition, motifs with the highest occurrence (i.e. apparent competition, direct competition, tritrophic chain) are known to be stable (i.e. following a small perturbation from equilibrium, the system will return to the original equilibrium state), and to contribute to the food web stability (Borrelli, 2015). This stability of the food web is also confirmed by the very large values of R50 for all removal sequences (except Prey removal sequence), indicating that very few secondary extinctions occur.

Our findings highlighted that the robustness of the Celtic Sea ecosystem to fishing is not closely related to the sensitivity of its species to this pressure. The most sensitive species were medium size elasmobranchs, which have intermediate trophic levels (circa TL=3.5 here). Species positioned on intermediate trophic levels often have high structural importance, with the largest values of centrality (Scotti and Jordán, 2010). However, we showed that this is not the case in the Celtic Sea, where these most sensitive species are not the most central and are thus, if targeted, unlikely to spread a perturbation to the food web. Yet, spurdog is a sensitive species that has a connector role between modules. It could thus propagate a perturbation if more fished. Conversely, the food web has low

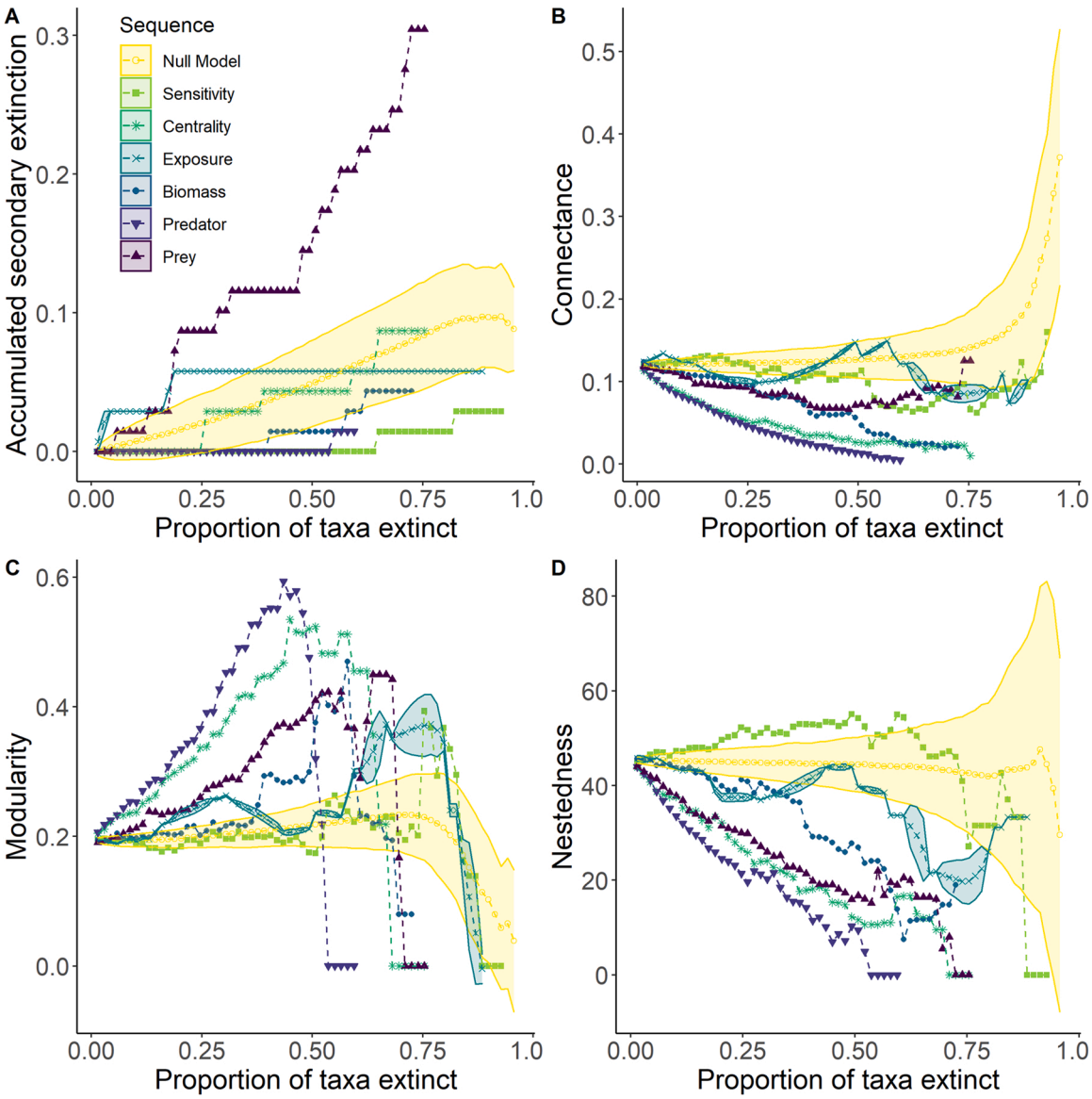



**Fig. 6.** Accumulated secondary extinctions for threshold 0% (A), connectance (B), modularity (C), and nestedness (D) in response to the primary removal of species according to five different removal sequences: sensitivity = decreasing sensitivity to fishing, centrality = decreasing eigenvector centrality values, exposure = decreasing exposure to fishing, prey = decreasing number of predators, predators = decreasing number of prey. The shaded area represents the random model (500 iterations) and its confidence interval. Some species have the same exposure score, so their order was randomly drawn (500 iterations), leading to a confidence interval (shaded area) on the exposure curve.

robustness to the removal of the most exposed species at an early stage of perturbation (i.e. when removing 7% of the most exposed species). These highly exploited species are queen scallop, king scallop, edible crab, European spider crab, sprat, hake and cod. The observed increase in connectance when removing these species originates from a faster decrease in the number of potential interactions than in the realized ones and is due to these removed species having in general fewer feeding links than the average in the food web. Interestingly, these species are respectively the ones with the lowest and highest TL of our food web, pointing toward robustness of the food web to the exploitation of intermediate TL. This raised one of the limitations of food web reconstruction since the species considered were sampled with a bottom trawl, which is not adapted to sample the basal components (phyto and zooplankton are missing while benthos is underrepresented), as well as the top predators. The use of subsets of food webs to assess the state of the whole ecosystem is discouraged (De Jonge et al., 2019). However, this was not the case in this study, which accounts for a large trophic span (i.e. from TL 2–4.38), including the most frequently observed megafauna (fish, elasmobranchs, crustacean, bivalves and cephalopods, observed at more than 5% of the EVHOE sampling sites over 2000–2016). These species are thus considered to provide a representative picture of the Celtic Sea ecosystem.

We showed that none of the species considered in this study is very highly vulnerable to fishing, i.e. both very highly sensitive and exposed. This could be linked to the long history of exploitation of the area (Guénette and Gascuel, 2012) that depleted large demersal predators and let remaining populations that are very rarely caught by bottom trawl scientific sampling (e.g. angel sharks *Squatina sp.* (Shephard et al., 2019). The most vulnerable species include smooth-hound, a sensitive and moderately exposed species, which is also a connector species between modules, susceptible to spread a perturbation. Other vulnerable species are large piscivorous species (cod, hake, anglerfishes, plaice, conger and ling) that are not very sensitive but are highly fished. Amongst these large piscivorous species, cod, anglerfishes, hake and conger are central species and are likely to propagate a perturbation to the whole food web through top-down control. This potential to propagate perturbation is confirmed by their topological role as hake, both anglerfishes and conger are connector species and cod has many links within its own module and is nearly classified as a connector species. These species are important commercial stocks under quotas in the area, whose decrease should lead to significant cascading impacts in the food web. This would be one factor that favored catastrophic regime shifts in the ecosystem when fishing drastically reduced the abundance of these species over 1950–1970 (Hernvann and Gascuel, 2020).

The robustness of the Celtic Sea food web to the removal of species with many preys and highly connected species was relatively high. Body size was positively correlated with the number of prey (Fig. S3, correlation test = 0.72, p-value<0.001). This result is in line with what was observed in a similar secondary extinction study (Jacob et al., 2011), which noticed that the loss of small-bodied species was more critical for food web robustness than the loss of large ones. This finding is probably influenced by the fact that the secondary extinction analysis does not account for top-down control and thereby tends to emphasize the bottom-up effects of small size, low TL species (Jacob et al., 2011). This limitation has been overcome here by complementing the secondary extinction analyses with food web metrics (i.e. connectance, modularity, nestedness) that enable to characterize the food web structure and propose mechanisms. By removing species with many preys and highly connected species, we observed that connectance decreases before the food web collapses, making in the first instance the propagation of a perturbation less likely and the food web more robust. This finding contradicts the documented low robustness of the food web when removing its most connected species (Dunne and Williams, 2009; Staniczenko et al., 2010; Curtsdotter et al., 2011; De Visser et al., 2011; Cordone et al., 2018) but see Allesina and Pascual (2009). These results can be explained by a particular structure of the food web, in which pelagic and benthic pathways are substantially coupled. Indeed, increased modularity indicates increased compartmentalization, which can promote stability by restricting the spread of the perturbation outside the module (Thébault and Fontaine, 2010). On the other hand, a decrease in nestedness implies the removal of redundant trophic interactions (Nordstrom et al., 2015), which translates here into the removal of whiting, megrim, and squid that are preyed upon by generalist species. Species with many preys and high values of centrality are thus hubs between different modules and are implicated in redundant trophic interactions. This is confirmed by the topological role of these species (whiting, megrim and squid) that are connectors between modules, which could explain the special behavior of the Celtic Sea food web facing the removal of those species. This relatively high robustness of the food web to the removal of species with many preys could be one of the stabilizing factors of the more pelagic-dominated state of the ecosystem after the depletion of high trophic levels before 1980 (Hernvann and Gascuel, 2020).

Forage species are crucial for food web stability as their predators are both benthic and pelagic and allow the coupling between these two compartments, which has been shown to participate in food web stability and resilience (Blanchard et al., 2011). In the Celtic Sea, the lowest robustness is obtained by removing species with the largest number of predators, namely herring, sprat, sardine *Sardina pilchardus*, dragonet *Callionymus lyra*, horse mackerel *Trachurus trachurus* and the two pouts species *Trisopterus esmarkii* and *Trisopterus minutus*. Among these species, horse mackerel, sardine, sprat and pouts are connector species, while herring is very close to the limit of connector species and is highly linked to species in its own module. This is in line with Moullec et al. (2017) that showed that, if well manage, these species could spread a benefitable increase in biomass through the food web of the Celtic Sea and help rebuild the biomass of higher trophic levels. These species belong to intermediate trophic levels (between 3 and 3.5) and account for a large proportion of the biomass of the species considered in this study but also a large proportion in the catches (ICES, 2018b; Hernvann and Gascuel, 2020). Since the removal sequence from the highest to the lowest biomass is one of the removal sequence leading to the highest robustness, it is probably more the number of predators (structure of the network) than the biomass that drives the lowest robustness in the Celtic Sea. This conclusion is subjected to the condition that structure of network is determined, at least in part, by biomass flux, which was reported by several authors (Barnes et al., 2018; Danet et al., 2021; Hashemi et al., 2021). Nevertheless, harvesting forage species does not always destabilize high trophic level piscivore fish, as Soudijn et al. (2021) showed that when piscivore fishing mortality is high, they benefit from the harvest of their forage species preys. Indeed, they showed that when piscivore abundance is low, the harvest of forage fish makes them produce more juvenile forage fish that are then preyed upon by piscivores. Unlike Soudijn et al., we did not consider the fluxes of biomass between species, which might influence the spread of a perturbation, with a larger spread between species linked by a large flux of biomass. However, we were able here to partition out the effect of every species on network robustness. Similarly, rewiring was not investigated here and each trophic link was reconstructed separately from trophic studies covering a long-time span. This makes the response of the food web to removal-scenarios interpretable regarding the time covered by the bibliographical studies. Nonetheless, rewiring is important to account for in the context of the effect of climate change on species distributions and could be distinguished between topological rewiring (i.e. addition or loss of connections due to the arrival or local extinction of species) and interaction strength rewiring (i.e. reroute flux between existing connections and altered interactions strength) (Bartley et al., 2019). This study focuses on an area and a period (Celtic Sea 2000–2016) where no incoming species or local extinction was recorded, thereby topological food web rewiring could be not considered. Our study does not aim to model biomass flows among species, hence making it impossible to account for interactions strength rewiring. However, by construction from various bibliographical studies including areas neighboring the Celtic Sea, the diet matrix likely covers most of the possible trophic links, including some that might not happen in the Celtic Sea but could be issued of rewiring between species already

present in this ecosystem. Further, taking trophic links from bibliographical studies covering North-East Atlantic makes the results more easily transferable to other ecosystems.

Network theory has been identified as a helpful tool to support ecosystem-based fisheries management (Gaichas and Francis, 2008; Dee et al., 2017). Extinction simulations as used here are not an attempt to predict precisely how an ecosystem would collapse as this could be explored through an ecosystem model representing biomass flows through the compartments of the ecosystem. Here, we compare the characteristics of the species that would lead to the lowest robust food web if threatened by a perturbation. We worked at the resolution of the species that are usually grouped into the same compartment of ecosystem models. This framework represents a widely applicable approach to account for the importance of species to the robustness of a food web since it only requires a topological network as input and could help with prioritizing management or conservation for understudied species in a data limited context. Exposure and trait-based sensitivity metrics relative to fishing brought here complementary information to the network analysis. Indeed, our study, similarly to McDonald-Madden et al. (2016), suggests that widely used mesoscale metrics such as centrality were not always adapted to prioritize species conservation to maintain the structure and the functioning of the food web. On the contrary, our exposure metric highlighted that in some cases, the current fishing exploitation pressure should prevail on topology-based metrics, while sensitivity must be considered as it implies different abilities of species to tolerate various exposure levels. Such metrics could be relevant in the context of exploring potential new fishing management strategies. In particular, integrating the sensitivity to fishing could provide an idea of the risk of exploiting new species in the context of implementing balanced harvest (Zhou et al., 2019).

Studying fishing perturbation, we showed that estimating the sensitivity to fishing at the level of the 69 species of the food web was insufficient to predict potential alteration at the level of the ecosystem since the simulated removal of the most sensitive species led to a robustness level similar to the one of the random removal sequence. This highlights the importance of basing conservation strategies on both a study of sensitivity/vulnerability at the species level but also the ecosystem level. Overall, the Celtic Sea food web appears robust to the loss of species sensitive to fishing. Yet, the food web robustness is the lowest when the species the most exposed to fishing pressure are removed first, highlighting that cautious management should remain. This study focused on fishing since this variable has a documented impact on species' biomass in the Celtic Sea, due to its long history of exploitation (Hernvann and Gascuel, 2020). However, climate change will likely become the main driver of this ecosystem in the coming years. The framework proposed in this work could easily be adapted to assess species sensitivity to temperature or pH tolerance by selecting relevant traits, helping to identify sensitive species that may impact food web robustness. It could also unravel early warnings about the loss of certain species that could jeopardize a food web more than their sensitivity at the species' level could suggest.

## CRediT authorship contribution statement

L.M., M.R., S.P., M.M., R.P. and D.K. conceived and designed the study; L.M conducted the analyses; L.M. and P.-Y. H. analyzed the trophic network; and L.M., all co-authors commented on the results and contributed to write the paper.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02048.

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