Species's traits and network topology drive the robustness of a marine food web to species removal

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Abstract

The analysis of the dynamics of interaction networks (i.e. trophic webs) better capture the state of ecosystem facing a perturbation than individual species dynamics could. We propose a framework that examines network robustness to a given perturbation at the local (species), mesoscale (species directly linked together) and global (network) level, based on traits and the topology of the network. Using the Celtic Sea as an example, we showed that the network was the least robust to the simulated loss of forage taxa and the most exposed taxa to fishing pressure, indicating conservation priority could be focused on these taxa. However estimating the sensitivity to fishing at the taxa 'level was insufficient to predict the robustness of the network. The network appeared relatively robust to the simulated loss of the most central taxa, suggesting that mesoscale metrics such as centrality, although widely used, are not always adapted to prioritize species conservation.

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 goals to the maintenance of ecosystem integrity and the services ecosystems underpin (Scotti & Jordán 2010; Harvey *et al.* 2017; Pecl *et al.* 2017). Ecological network enables to evaluate the vulnerability of ecosystems to a perturbation through the study of the changes in the structure of the network (Tylianakis*et al.* 2007; Stouffer & Bascompte 2011; Hattab *et al.*2016; Robinson & Strauss 2020). Its use to assess ecosystem state has increased in the recent years as it allows considering in a single framework the effects of fluctuation in species' abundance and their preys and predators, but also on indirectly linked species and the whole network itself (Jordán *et al.* 2006; Wallach *et al.* 2017).

The risk of network collapse can be characterized by its robustness to species extinction, namely its capacity to withstand the cascading perturbation generated by the removal of species (Dunne *et al.*2004; Dunne & Williams 2009; Jonsson *et al.* 2015). Human impact on ecosystems is intensifying and has already caused numerous collapses of species (Duarte *et al.* 2020). As ecosystems are being degraded at an unprecedented rate, the need to understand which perturbation sequences are expected to be more devastating than others has become pressing (Jonsson *et al.* 2015). The collapse of some well-connected species is expected to have a disproportionate impact on their ecosystems relatively to their biomass, and these species have to be identified (Jordán 2009; Klemm *et al.* 2012; Worm & Paine 2016). Central species with a large number of interactions, are likely to influence numerous species and thus have been defined as network hubs that should be prioritized for conservation (Curtsdotter *et al.*2011). To identify these central species, mesoscale

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measures (i.e. intermediate level between the species (local) and the entire network (global)), such as eigenvector centrality, betweenness centrality or closeness centrality have proven to be particularly suited for the assessment of species importance in the spread of a perturbation across the network (Estrada 2007; Jordán 2009).

Sensitivity and vulnerability assessment of species (defined as sensitivity added to exposure (IPCC 2001)) have largely been conducted based on species traits (Tillin *et al.* 2010; Le Quesne & Jennings 2012; van Treeck *et al.* 2020). However, to evaluate properly the potential of a species to spread perturbation across the network, its centrality should be assessed alongside its sensitivity and exposure to a given pressure. Indeed, a species can be sensitive and vulnerable but not central, or it may be central but not sensitive nor vulnerable. In both cases, the species would not spread a perturbation across the network. In that sense, one can ask whether the robustness of the trophic network 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 network robustness to a given perturbation at the local (species), mesoscale and global (network) level, based on species traits and on the topology of the network. Specifically, we investigated the impact on the robustness of the network of the loss of the sensitive species, the exposed species and the central species.

We applied this framework to fishing pressure robustness of a trophic network from 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 & Palomares 2005) to altered trophic networks 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 to characterize their sensitivity to fishing by ranking them along a "slow-fast" continuum of life history strategies (Le Quesne & Jennings 2012). Fishing tends to favour 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 & 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 climax in the late 1980's, deeply altered the ecosystem structure through the depletion of large demersal predators, i.e. cod, whiting, hake and sole (Guénette & Gascuel 2012; Hernvann & Gascuel 2020). Based on literature and isotopic measurements for 69 taxa (including fishes, elasmobranches, cephalopods, bivalves, and crustaceans), we assessed the vulnerability to fishing of both taxa and the trophic network structure. Specifically, we investigate whether (i) the most sensitive and the most exposed taxa to fishing are the most central; and whether (ii) the loss of sensitive, exposed or central taxa is the most detrimental for the network robustness. For a better understanding of the processes at play, we tested the robustness of the network against different species 'removal sequences, and notably assessed the importance of the number of predators and preys.

Materials and Methods

Study area

The Celtic Sea is a shelf ecosystem (range depth 57-340m) located in Northwestern Europe. It is characterized by a gradient of sediments from shallow 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 & Gascuel 2020). Importance of fishing driving the ecosystems have decreased after 2009 (Mérillet *et al.* 2020) but remains high, around 4000 thousand tons landed per years over 2000-2015 (Hernvann & Gascuel 2020).

Food-web data

We studied the trophic network corresponding to the upper part of the Celtic Sea trophic network (TL>=2), defined at genus or species resolution and restricted to interactions between most abundant and common

taxa observed during the scientific survey EVHOE (see Mérillet et al., 2020). Trophic links between taxa were taken from the literature review conducted in Hernvann et al. (2020), keeping the information at the taxon's level. We collected isotopic measurements for 69 taxa of the most commonly found in bottom trawls in the Celtic Sea (EATME project). We applied a lipid correction for the taxa with a C/N >3.5, following Sweeting, Polunin, & Jennings (2006). We then applied a baseline correction based on isotopic signatures of *Aequipecten opercularis* , using bottom temperature for δ13C (Barnes *et al.* 2009) and using bottom temperature and salinity correction for δ15N (Jennings & van der Molen 2015). The performance of the correction was then checked by looking at the correlation between real and corrected values for other bivalves (i.e. *Pecten maximus* , *Aequipecten opercularis* , *Pseudamussium peslutrae* and *Pseudamussium clavatum*). Trophic levels TL of taxa i were computed from Post (2002) equation, as follows:

$$\text{TL}_i = \frac{\delta 15 N_i - \delta 15 N_{\text{base}}}{3.4} + \text{TL}_{\text{base}}$$

with δ15Ni the corrected δ15N value for the taxa i and δ15Nbase the mean of the δ15N base values of bivalves (TLbase = 2).

We computed several metrics informing on the structural properties of the network. Connectance (L/S2), computed from the number of links (L) and the number of species (S), gives information on how densely connected is trophic network. Our network of 69 species and 559 links has average values of connectance (0.12), with connectance ranging from 0 to 1, with 0 indicating the least possible number of interactions (Delmas *et al.* 2019). For a complete description of these metrics see Delmas et al. (2019) and Kortsch et al. (2018).

Vulnerability index of taxa: sensitivity and exposure to fishing

To quantify a taxon's sensitivity to fishing, we selected six traits widely used to characterize the life-history strategies of marine taxa: longevity, maximum length, reproductive guild, fecundity, age at maturity and size of the offspring (Winemiller & Rose 1992; Jennings *et al.* 1998; Le Quesne & Jennings 2012). Most of these traits came from PANGAEA database (Beukhof *et al.* 2019a), but were completed by literature. We applied a Hill-Smith analysis (Hill & Smith 1976), a multivariate analysis that enables to use both qualitative and quantitative traits, and gives the same weight to quantitative and qualitative traits (independently of the number of levels for a qualitative trait).

We used the proportion of biomass of a population that is exploited by fishing, to reflect the exposure to fishing. We expressed the exposure of a taxon i as the ratio between its removal by fisheries and its stock biomass in the study-area:

$$\text{Exposure}_i = \frac{C_i}{B_{\text{tot},i}}$$

With C_i the biomass of the taxon i landed (i.e. catches) and discarded and $B_{\text{tot},i}$ the total biomass present in the Celtic Sea (area 7e-j) in 2016. This ratio was directly available from the International Council for the Exploration of the Sea (ICES) working groups' reports for species whose stocks are assessed and have a spatial distribution relevant with our study area (ICES 2020). For species without stock assessment, 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 onshelf 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 similar biological characteristics and trophic ecology, the same exposure was attributed to our network's taxa when matching the EwE functional group.

Vulnerability of a taxon to fishing was defined as sensitivity added to exposure, following the simplified definition of the IPCC (IPCC 2001). Finally, the proportion of each taxon relatively to the total biomass of all taxa in our dataset was computed to provide an order of magnitude of the proportion of the biomass that

is sensitive or vulnerable to fishing pressure. To compute proportion of the total biomass represented by each taxon, we used EVHOE data in 2016 (Evaluation des ressources Halieutiques de l'Ouest de l'Europe,(Garren *et al.* 2019)). The biomass of each taxon was elevated to the depth-sediment strata, to account for the irregular sampling within a stratum, before computing the proportion.

Computation of a proxy of the flow of a perturbation across a network: the eigenvector centrality

The more connected a taxon is to the rest of the network, the more a perturbation affecting that taxon is likely to spread across the whole network (Dunne *et al.* 2002; Delmas *et al.* 2019). To quantify the degree to which a taxon is connected to other highly connected species, we used the eigenvector centrality metric, which is akin to a simulation of flow across a network (Bonacich 1987; Delmas *et al.* 2019). Taxa heavily connected to other highly connected taxa hence get higher scores of eigenvector centrality. Finally, to investigate whether there is a pattern of sensitivity and centrality across trophic pathways (pelagic for the lowest values of δ13C and benthic for the highest values) and trophic levels, a linear regression between sensitivity or eigenvector centrality and corrected values of δ13C or δ15N was realised (Fig. S1).

Quantifying the robustness of the food web to a perturbation

To evaluate the robustness of the network to taxa's extinction, we simulated primary extinctions of taxa (i.e. removal of taxa from the network) according to various removal sequences and monitored the values of connectance and accumulated secondary extinctions (i.e. the extinction caused by the removal of all the prey of one taxon). Connectance is a good estimate of community sensitivity to a perturbation, and large values of connectance favour the spread of a perturbation (Martinez 1992; Delmas *et al.* 2019). On the other hand, secondary extinctions inform on robustness of the network, and is negatively correlated with it (Dunne *et al.* 2002). These simulations of extinctions were done by removing taxa in five different orders: (1) Sensitivity, from the highest to the lowest sensitivity score, (2) Centrality, from taxa with the highest to the lowest eigenvector centrality values, (3) Exposure, from taxa with the highest to the lowest exposure to fishing pressure, (4) Prey, from taxa with the highest to the lowest number of prey and (5) Predator, from taxa with the highest to the lowest number of predators. The connectance and accumulated secondary extinctions generated in each of these 5 removal scenarios were compared to a random mode in which taxa are randomly selected and removed from the network. This random removal was iterated 500 times. We followed the same procedure for modularity and nestedness (Fig. S3). To compare the robustness of this network with other networks, we computed the R50, defined as the proportion of taxa that have to be removed to result in a total taxa's loss [?]50% of the species in the original web (Dunne *et al.* 2004).

All analyses were conducted in R 4.0.2 (R Core Team 2020). The secondary extinction analysis was performed with modified functions from the NetworkExtinction package (Corcoran-Barrios *et al.* 2019).

Results

The Celtic Sea is characterized by a "slow-fast" continuum of life history, from small, short-lived taxa producing small offspring to large, long-lived taxa with large offspring (Pianka 1970; Beukhof *et al.* 2019b). Large, long-lived species with low reproductive output are typically the most sensitive to fishing pressure (Winemiller & Rose 1992; Le Quesne & Jennings 2012; Wiedmann *et al.* 2014). The most sensitive taxa to fishing 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).

Highest values of eigenvector centrality (hereafter called centrality for simplicity) characterize highly connected taxa linked to taxa that are themselves highly connected. In the Celtic Sea, these are large piscivorous fishes, namely whiting *Merlangius merlangus* , megrim *Lepidorhombus whiffiagonis* , cod *Gadus morhua* , hake *Merluccius merluccius* , turbot *Scophthalmus maximus* , and squid *Loligo sp.* . In our case, the most central species are not the most sensitive (Fig. 2). Notwithstanding this observation, taxa at high trophic levels tend to be more sensitive to fishing and more central than other species. Indeed, sensitivity tends to

increase toward the top of the network (higher values of δ15N) and centrality increases with trophic levels (Appendix, Fig. S1).

Vulnerable taxa are defined as both sensitive and exposed to fishing. In the Celtic Sea, we found no highly vulnerable taxon, i.e. no taxa in the top right corner (Fig. 3). However, some taxa had medium-high values of vulnerability: cod, edible crab *Cancer pagurus*, smooth-hound, and to a lesser extent hake, anglerfish *Lophius piscatorius*, European conger, European plaice *Pleuronectes platessa*, blackbellied anglerfish *Lophius budegassa* and ling (Fig. 3). In addition, three of these vulnerable taxa (cod, hake and anglerfish) have high values of centrality. These taxa, despite being central, are not accounting for a large proportion of the total biomass (Fig. 3), which suggests that whether these taxa are affected or favored by an external factor (i.e. environmental conditions or human pressures), it would have a low impact on the total biomass of the Celtic Sea.

Simulating scenarios of species extinction sequences, we found that connectance (defined as the number of realized interactions in the network divided by the potential ones) is decreasing the fastest when the taxa are sequentially removed according to their number of preys (Preys removal sequence) and their influence (Centrality removal sequence) (Fig. 4A.). These removal scenarios are also responsible for the fastest collapse of the network (the remaining taxa are not linked together) after simulating the extinction of respectively 60% and 75% of the taxa of the network. These scenarios of taxa extinctions lead to a network with a lower connectance than if the taxa were deleted following a random sequence (Fig. 4A.). For these two removal sequences, values of modularity show the largest increase and values of nestedness the largest decrease (Fig. S2). Sequentially removing taxa with the highest number of predators (Predators removal sequence) provokes a less steady decrease of the connectance, but still with values lower than the model of random extinctions. The network collapses after the removal of 75% of the taxa. Conversely, the removal of only the 7% of the taxa that are the most exposed to fishing (Exposure removal sequence) leads to an increase in connectance, with values higher than the random model. Removing the taxa most sensitive to fishing (Sensitivity removal sequence) does not lead to variations in connectance different from the random model and causes the later collapse of the network, after removing 93% of the taxa (Fig. 4A.).

The removal of the first 7% of the most exposed taxa to fishing (Exposure removal sequence) causes the largest number of secondary extinctions (Fig. 4B.). Then, the simulated extinctions of taxa with the largest number of predators (Predators removal sequence) leads to the highest and fastest rate of secondary extinctions, higher than the null model, after the removal of 19% of the taxa. Removing taxa from the most to the least central (Centrality removal sequence) produces secondary extinctions comparable to the random model (Fig. 4B.). Finally, removing the taxa with the largest number of preys (Preys removal sequence) and the most sensitive taxa (Sensitivity removal sequence) leads to the lowest number of accumulated secondary extinctions, even lower than the null model (Fig. 4B.).

A network is the most robust to node loss when the removal of taxa (primary removal) does not lead to secondary extinctions. The R50 robustness (Dunne *et al.* 2004) is defined as the proportion of taxa that has to be removed to reach the loss of [?]50% of the taxa in the original network. The larger the R50 is (maximum value of 50%), the more robust the network is. Here, the Sensitivity and Preys removal sequences lead to the most robust network (R50=50%), followed by the random model (46%), the Centrality removal sequence (46%), the exposure removal sequence (45%) and the Predator removal sequence (39%).

Discussion

Since the ecological role of taxa heavily depends on their position in the trophic network, we were interested in identifying whether the sensitivity and exposure of taxa to fishing pressure (i.e. vulnerability), completed by taxa's centrality, could have consequences on the robustness of the trophic network.

The secondary extinction analysis conducted here highlighted that the robustness of the Celtic Sea to fishing is not closely related to the sensitivity of its taxa to this pressure. This behaviour of the network results from the respective characteristics and feeding ecology of the taxa. Indeed, in the Celtic Sea, the most sensitive taxa are medium size elasmobranchs which are not top predators and have medium trophic levels (circa

TL=3). Medium trophic levels taxa often have a high structural importance, with usually the largest values of centrality (Scotti & Jordán 2010). However, we showed that this is not the case in the Celtic Sea were the most sensitive taxa are not the most central and are thus, if targeted, unlikely to spread a perturbation to the whole network. Considering both the sensitivity and the exposure to fishing pressure, we showed that none of the taxa considered in this study is highly vulnerable to fishing, which could be linked to the long history of exploitation of the area (Guénette & Gascuel 2012). The most vulnerable taxa include smooth hound, a sensitive and moderately exposed taxon, as well as large piscivorous taxa (cod, hake, anglerfishes, plaice, conger, ling) that are not very sensitive but are highly fished. Amongst these large piscivorous taxa, cod, anglerfish and hake are central taxa and are likely to propagate a perturbation to the whole network through top-down control. These species are important commercial stocks under quotas in the area, whose decrease should lead to significant cascading impacts in the trophic network.

The robustness of the Celtic Sea network to the removal of taxa with many preys and highly connected taxa was relatively high. The removal of taxa with many preys leads to the fastest collapse of the network, but only happens after removing 60% of the taxa, which is far from realistic conditions. Connectance decreases before the network collapses, making in a first instance the propagation of a perturbation less likely and the network more robust. Likewise, the network seems relatively robust to the removal of the most central taxa (decrease in connectance and a number of secondary extinctions similar to the one expected by chance). This finding contradicts the expected low robustness of a network facing the removal of its most connected taxa (Dunne & Williams 2009; Staniczenko *et al.* 2010; Curtsdotter*et al.* 2011; De Visser *et al.* 2011) but see (Allesina & Pascual 2009). Nevertheless, the robustness of the network facing these two removal sequences is in line with the observed increase in modularity and decrease in nestedness (Fig. S2). Indeed, the increased modularity indicates an increased compartmentalization, which is known to promote stability by restricting the spread of the perturbation outside the module (Thébault & Fontaine 2010). On the other hand, a decrease in nestedness implies the removal of the redundant trophic interactions first (Nordstrom *et al.* 2015), which translates here into the removal of whiting *Merlangus merlangius* , megrim and squid *loligo sp.* that are preyed upon by generalist taxa.

The removal of taxa with many predators leads to the lowest robustness of the trophic network. Taxa with the largest number of predators here belong to intermediate trophic levels (between 3 and 3.5) namely herring*Clupea harengus* , sprat *Sprattus sprattus* , sardine *Sardina pilchardus* , dragonet *Callionymus lyra* , pouts*Trisopterus esmarkii* and *Trisopterus minutus* and horse mackerel *Trachurus trachurus* (Table S1). These forage species account for a large proportion of the biomass of the taxa considered in this study but also a large proportion in the catches (ICES 2018b; Hernvann & Gascuel 2020). These species are crucial for the network stability as their predators display medium to high trophic levels and are both benthic and pelagic. Hence, forage species allow the coupling between these two pathways, which has been shown to participate to trophic network stability and resilience (Blanchard *et al.* 2011). In addition, if affected by a perturbation, these taxa heavily destabilize the network of the Celtic Sea (Moullec *et al.* 2017).

The food-web topology reconstructed here integrates data from trophic studies covering a long time-span. Thus, the restructuration of the network due to changes in diets could not be investigated. Nonetheless, this makes the response of the network to removal-scenarios interpretable regarding the long-term history of the ecosystem. The relatively high robustness of the network to the removal of taxa with many preys could be one of the stability factors (with predation control of benthopelagic predator larvae by pelagic fish, Baum & Worm, 2009) of the more pelagic-dominated state of the ecosystem after the depletion of high trophic levels before 1980 (Hernvann & Gascuel 2020).

Finally, the network has low robustness to the removal of the most exposed taxa at early stage of perturbation (i.e. when removing the 7% of the most exposed taxa). These highly exploited taxa are queen scallop*Aequipecten opercularis* , king scallop *Pecten maximus* , edible crab, European spider crab *Maja brachydactyla* , cod, sprat and hake. This increase in connectance originates from a faster decrease in the number of potential interactions than in the realized ones and is due to these removed taxa having in general fewer feeding links than the averaged species in the network. This raised one of the limitations of network recon-

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struction, since the taxa considered were sampled with a bottom trawl that is not adapted to sample the basal components of the network (phyto and zooplankton are missing while benthos is underrepresented), as well as the top predators. Nevertheless, taxa included here are megafauna with the highest occurrence and account for most part of the network, enabling notably the survival of commercial taxa. These taxa are thus considered to provide a representative picture of the Celtic Sea ecosystems. Trophic levels were computed from local isotopic data collected in the Celtic Sea whereas the trophic links were taken from the literature. Thus, there might be a mismatch between the trophic position and the trophic links of some taxa with taxon feeding on taxon at slightly higher trophic level. However, because the computation the centrality score of one taxon is not based on data specific to our study area, it could be applied to other North-East Atlantic studies. In addition, we did not consider the fluxes of biomass between taxa, which could modulate our findings. Indeed, it might influence the spread of a perturbation, with a larger spread between taxa linked by a large flux of biomass.

Network theory has been identified as a helpful tool to support ecosystem-based fisheries management (Gaichas & Francis 2008; Dee*et al.* 2017). Exposure and trait-based sensitivity metrics relative to fishing brought here a complementary information to the network analysis. Indeed, our study 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 network. 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 are particularly promising in the context of exploring potential new fishing management strategies. In particular, integrating the sensitivity to fishing, they could be used to investigate the risk of exploiting new species regarding to their own productivity potential (Zhou *et al.* 2019).

Studying fishing perturbation, we showed that the trophic network of the Celtic Sea was the least robust to the simulated loss of taxa with many predators (i.e. forage taxa) and of the 7% taxa the most exposed to fishing pressure. Estimating the sensitivity to fishing of the 69 taxa of the network was insufficient to predict its robustness since the simulated removal of the taxa most sensitive led to a robustness level similar as that of a random removal sequence. This study focused on fishing since this variable has a documented impact on taxa's biomass in the Celtic Sea, due to the long history of exploitation of this ecosystem (Hernvann & 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 traits known to respond to these pressures. Ultimately, such a framework could be used in complement of management tools to indicate which taxon could impair ecological network structure and ecosystem functioning under increasing global change. It could also unravel early warnings about the loss of certain taxa that could jeopardize a trophic network more than their sensitivity at the taxon's level could suggest.

Acknowledgments

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**Figures and Tables**

Figure 1.
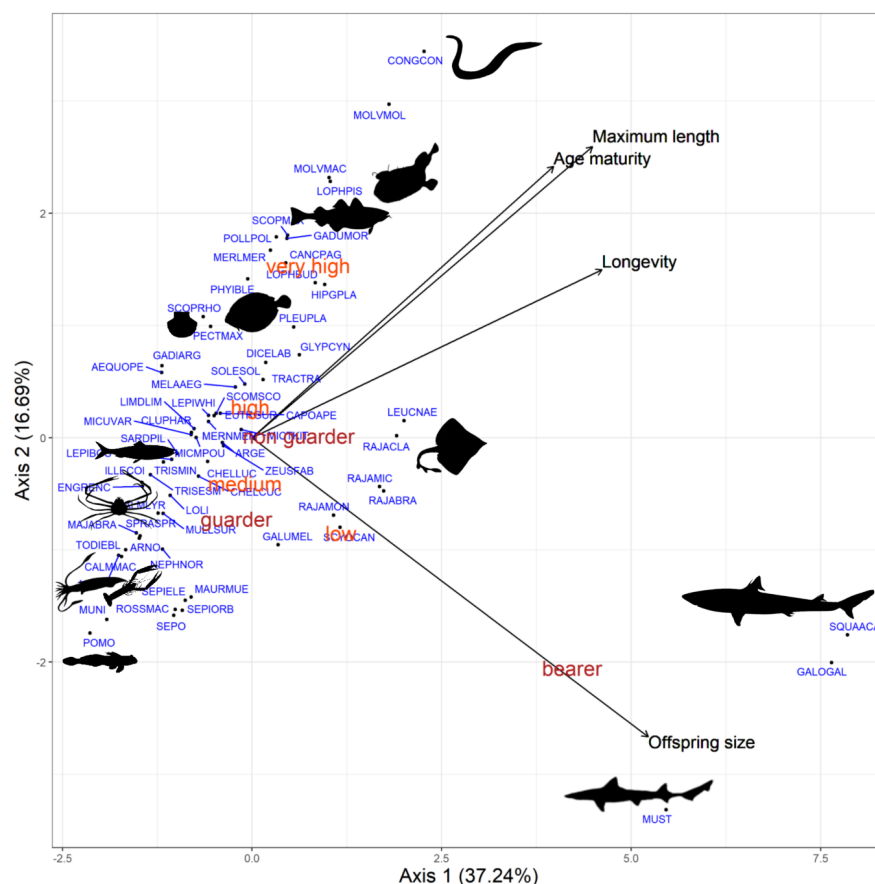
Factorial map of Hill Smith analysis on six functional traits related to a slow-fast gradient of life strategies: maximum length, longevity, offspring size, age at maturity, reproductive guild (modalities in deep red) and fecundity (modalities in orange). The most sensitive taxa (right part) are characterized by high values of maximum length, longevity, age at maturity and offspring size and tend to bear their offspring. Full names of the taxa are given in Table S1.

Figure 2.
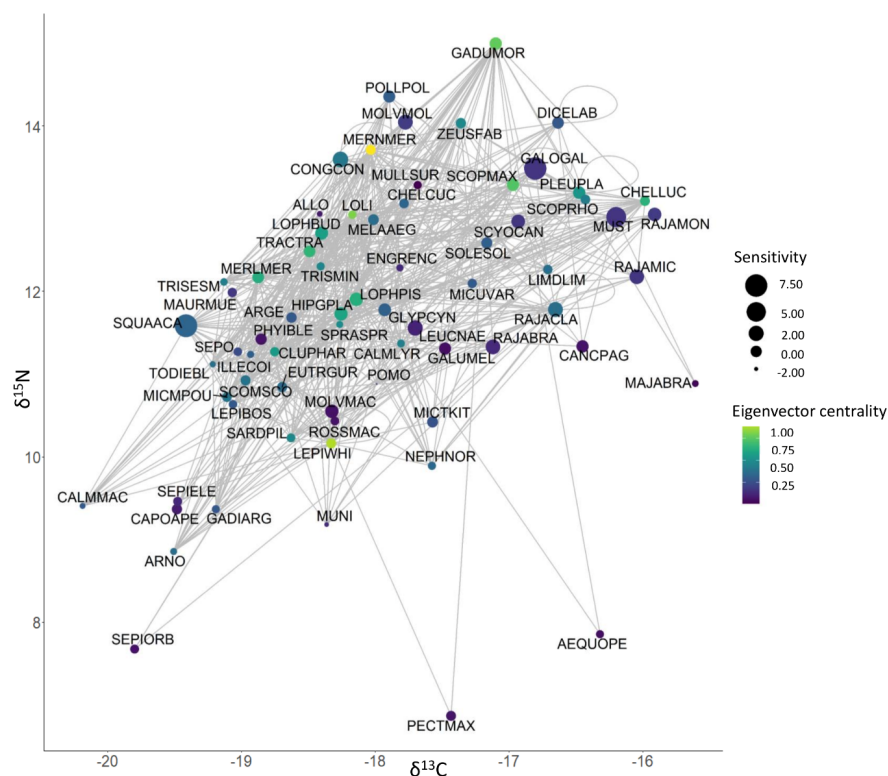
Representation of the trophic network of the Celtic Sea in the isotopic space with sensitivity to fishing (size of the dots) and centrality (color scale from dark blue to light green). The isotopic space is defined by isotopic ratio of carbon 13C and nitrogen 15N. The nitrogen axis is consistent with species trophic level while the carbon axis discriminates pelagic (more negative) from benthic (less negative) pathways. Full names of the taxa are given in Table S1.

Figure 3.
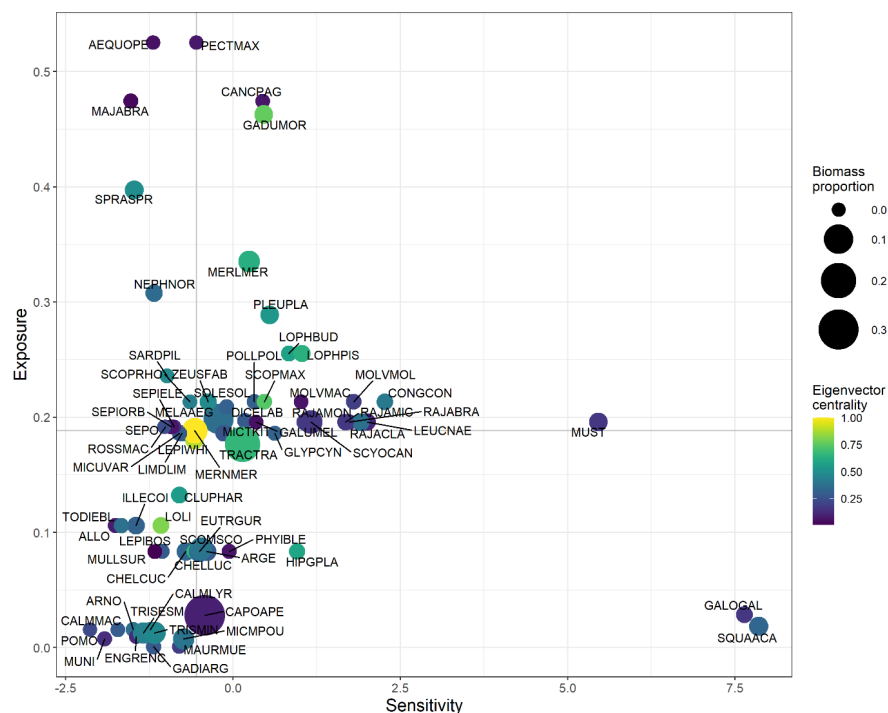
Summary plot of the vulnerability of taxa (sensitivity added to exposure), taxa biomass and the potentiality for the perturbation at the taxa's level to spread (eigenvector centrality). Solid lines depict median values of sensitivity and exposure. Taxa's relative biomass (each taxon's biomass is divided by the total biomass of the 69 studied taxa) is given as a proxy of their importance in trophic flux. Proportion lower than 0.1 are in the 0 category in the graph legend.

Figure 4.
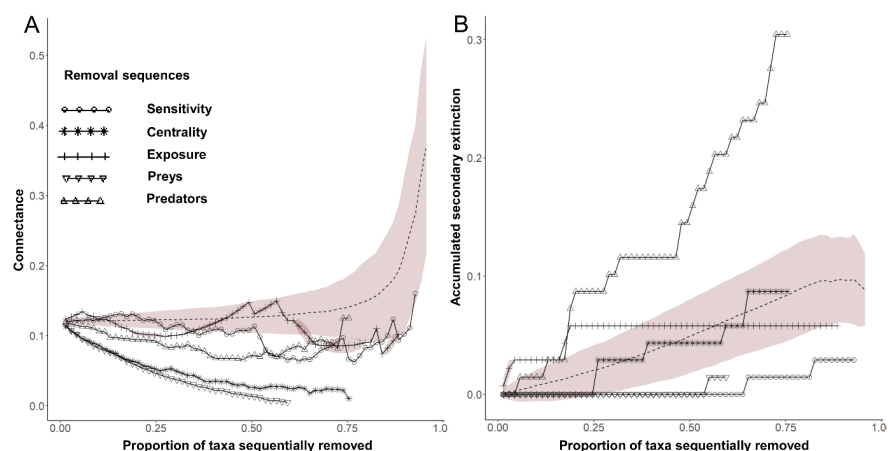
Connectance (A) and accumulated secondary extinctions (B) in response to the primary removal of taxa according to five different removal sequences: sensitivity = decreasing sensitivity to fishing, centrality = decreasing eigenvector centrality values, exposure = decreasing exposure to fishing, preys = decreasing number of prey, predators = decreasing number of predators. The shaded area represents the random model (500 iterations). Some taxa have the same exposure score, so their order was randomly drawn (500

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iterations), leading to a confidence interval (shaded area) on the exposure curve.

Supplementary materials

Table S1: Trophic network metrics for each taxon: Isotopic position (corrected values of δ15N and δ13C), trophic level, number of prey, number of predators, sensitivity to fishing estimated from life history traits, eigenvector centrality and exposure to fishing pressure.

Taxa	Latin names	$\delta^{15}N_{corr}$	$\delta^{13}C_{corr}$	TL	Number of preys	Number of predato
AEQUOPE	*Aequipecten opercularis*	7.83	-16.35	2.285	0	2
ALLO	*Alloteuthis* sp	12.90	-18.46	3.775	0	4
ARGE	*Argentina* sp.	11.64	-18.67	3.407	1	12
ARNO	*Arnoglossus* sp.	8.83	-19.56	2.578	2	12
CALMLYR	*Callionymus lyra*	11.33	-17.85	3.315	1	22
CALMMAC	*Callionymus maculatus*	9.38	-20.24	2.74	0	12
CANCPAG	*Cancer pagurus*	11.30	-16.48	3.305	0	5
CAPOAPE	*Capros aper*	9.34	-19.53	2.729	0	4
CHELCUC	*Chelidonichthys cuculus*	13.02	-17.83	3.812	3	11
CHELLUC	*Chelidonichthys lucerna*	13.05	-16.01	3.821	20	10
CLUPHAR	*Clupea harengus*	11.23	-18.80	3.286	2	26
CONGCON	*Conger conger*	13.55	-18.30	3.968	19	3
DICELAB	*Dicentrarchus labrax*	13.99	-16.67	4.098	14	0
ENGRENC	*Engraulis encrasicolus*	12.24	-17.86	3.584	0	7
EUTRGUR	*Eutrigla gurnardus*	10.81	-18.74	3.161	4	12
GADIARG	*Gadiculus argenteus*	9.34	-19.24	2.728	2	11
GADUMOR	*Gadus morhua*	14.95	-17.14	4.379	34	6
GALOGAL	*Galeorhinus galeus*	13.44	-16.84	3.936	10	0
GALUMEL	*Galeus melastomus*	11.27	-17.52	3.297	3	1
GLYPCYN	*Glyptocephalus cynoglossus*	11.74	-17.97	3.435	1	11
HIPGPLA	*Hippoglossoides platessoides*	11.69	-18.30	3.42	16	12
ILLECOI	*Illex coindetii*	11.20	-18.98	3.276	16	2
LEPIBOS	*Lepidorhombus boscii*	10.60	-19.11	3.1	1	9
LEPIWHI	*Lepidorhombus whiffiagonis*	10.13	-18.37	2.962	34	10
LEUCNAE	*Leucoraja naevus*	11.52	-17.74	3.37	3	1
LIMDLIM	*Limanda limanda*	12.22	-16.74	3.578	0	16
LOLI	*Loligo* sp.	12.89	-18.21	3.772	35	7
LOPHBUD	*Lophius budegassa*	12.66	-18.45	3.707	29	4
LOPHPIS	*Lophius piscatorius*	11.86	-18.18	3.472	33	1
MAJABRA	*Maja sp.*	10.85	-15.63	3.173	0	2
MAURMUE	*Maurolicus muelleri*	11.95	-19.12	3.496	0	7
MELAAEG	*Melanogrammus aeglefinus*	12.82	-18.06	3.754	7	10
MERLMER	*Merluccius merluccius*	12.13	-18.92	3.55	20	11
MERNMER	*Merlangius merlangus*	13.67	-18.08	4.003	35	16
MICMPOU	*Micromesistius poutassou*	10.69	-19.16	3.126	4	15
MICTKIT	*Microstomus kitt*	10.39	-17.61	3.038	0	9
MICUVAR	*Microchirus variegatus*	12.06	-17.31	3.528	0	10
MOLVMAC	*Molva macrophthalma*	10.52	-18.37	3.076	0	4
MOLVMOL	*Molva molva*	14.00	-17.82	4.1	5	4
MULLSUR	*Mullus surmuletus*	13.24	-17.72	3.877	0	1
MUNI	*Munida* sp.	9.15	-18.41	2.674	0	9
MUST	*Mustelus* sp.	12.86	-16.23	3.764	10	0
NEPHNOR	*Nephrops norvegicus*	9.86	-17.62	2.882	0	14

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| Taxa	Latin names	$\delta^{15}N_{copp}$	$\delta^{13}n_{copp}$	TL	Number of preys	Number of predato
PECTMAX	*Pecten maximus*	6.85	-17.48	1.996	0	2
PHYIBLE	*Phycis blennoides*	11.38	-18.90	3.33	2	1
PLEUPLA	*Pleuronectes platessa*	13.15	-16.51	3.85	12	12
POLLPOL	*Pollachius pollachius*	14.31	-17.94	4.191	11	4
POMO	*Pomatoschistus* sp.	10.84	-18.03	3.172	0	13
RAJABRA	*Raja brachyura*	11.29	-17.16	3.303	6	1
RAJACLA	*Raja clavata*	11.74	-16.69	3.436	21	1
RAJAMIC	*Raja microocellata*	12.14	-16.07	3.552	7	1
RAJAMON	*Raja montagui*	12.89	-15.94	3.773	10	1
ROSSMAC	*Rossia macrosoma*	10.40	-18.35	3.041	0	4
SARDPIL	*Sardina pilchardus*	10.20	-18.68	2.982	0	23
SCOMSCO	*Scomber scombrus*	10.89	-19.02	3.184	4	16
SCOPMAX	*Psetta maxima*	13.25	-17.01	3.878	21	9
SCOPRHO	*Scophthalmus rhombus*	13.07	-16.46	3.826	7	10
SCYOCAN	*Scyliorhinus canicula*	12.80	-16.97	3.748	9	0
SEPIELE	*Sepia elegans*	9.43	-19.53	2.756	0	5
SEPIORB	*Sepia orbignyana*	7.65	-19.85	2.232	0	3
SEPO	*Sepiola sp.*	11.23	-19.08	3.286	0	11
SOLESOL	*Solea solea*	12.55	-17.20	3.672	0	12
SPRASPR	*Sprattus sprattus*	11.56	-18.31	3.383	0	24
SQUAACA	*Squalus acanthias*	11.55	-19.47	3.378	22	0
TODIEBL	*Todaropsis eblanae*	11.08	-19.27	3.241	18	3
TRACTRA	*Trachurus trachurus*	12.44	-18.54	3.642	16	17
TRISESM	*Trisopterus esmarkii*	12.07	-19.18	3.533	0	21
TRISMIN	*Trisopterus minutus*	12.26	-18.45	3.589	2	20
ZEUSFAB	*Zeus faber*	13.99	-17.40	4.096	27	0

Figure S1: Linear regression of the sensitivity over corrected values of $\delta^{13}C$ (A.) and $\delta^{15}N$ (B.) and eigenvector centrality over corrected values of $\delta^{13}C$ (C.) and $\delta^{15}N$ (D.).
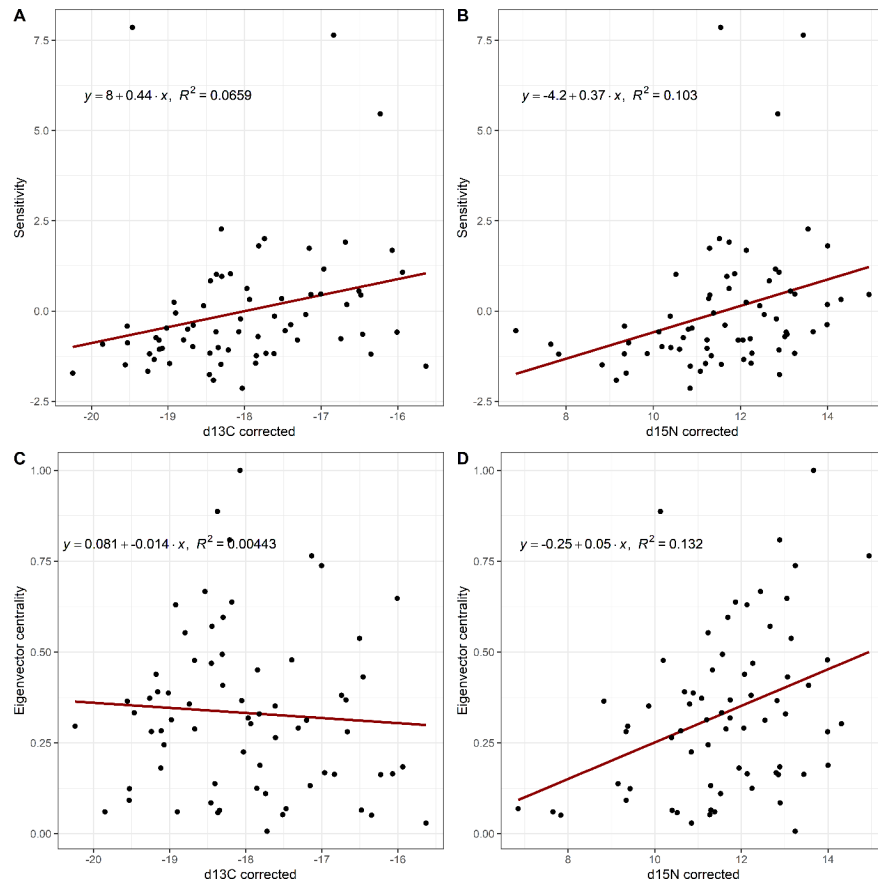
Figure S2: Modularity and nestedness trends in response to the primary removal of taxa according to five different removal sequences: *Sensitivity* = decreasing sensitivity to fishing, *Centrality*= decreasing eigenvector centrality values, *Exposure* = decreasing exposure to fishing, *Preys* = decreasing number of prey, *Predators* = decreasing number of predators

Modularity is positively associated with robustness, with perturbation spread hindered by the modules. Modularity of the Celtic Sea trophic network has low values (0.20) with modularity ranging from 0 (no modules) to 1 (strong community structure) with typical values usually spanning from 0.3 to 0.7 (Newman & Girvan 2004). Finally, nestedness occurs when the diet of specialist is a subset of generalists. It has medium values in the Celtic Sea (45.31) with 0 indicating full complementarity of trophic links between taxa and 100 completely nested links (Almeida-Neto *et al.* 2008).
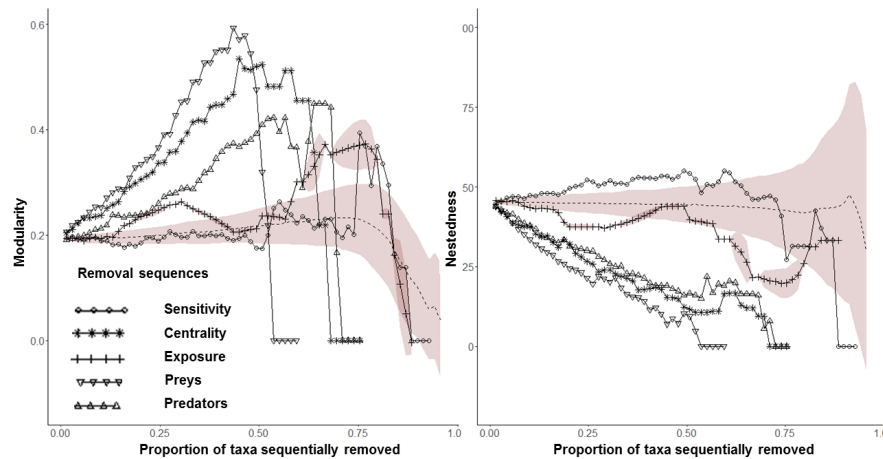
Values of modularity are negative when the number of links between taxa in a module is lower than expected by chance.

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Figure S3: Correlation plots between trophic position characteristics and the metrics whose link with network robustness is investigated. The strength of the correlation is given by Spearman's correlation coefficients and supported by the level of significance (*** for p-value<0.001, ** for p-value<0.01, * for p-value<0.1). Taxa with the largest number of preys tend to have large values of centrality.