



## Loop analysis quantifying important species in a marine food web

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### ABSTRACT

Improving the predictive power of food web analysis is a major challenge. Identifying the relationships that link topological and dynamical features may help. We used the predictions of loop analysis about the effect of perturbations targeted to the components of Barents sea food web to quantify their sensitivity and community impact, that we summarized in two new indices, *NI* and *NS*. Using a multivariate analysis we interpreted the meaning of these indices in a benchmarking exercise using several well recognized indices of species topological (positional) importance. Our findings suggest that the information the two indices proposed here provides does not overlap with that of more diffused topological indices of positional importance (i.e. centrality indices). The former express the dynamic consequences of the topology in which species are embedded, whereas for the latter such dynamical consequences are mostly hypothesized on a topological base. The indices of loop analysis are based on the effective role a species plays in passing the impacts to other species (*NI*) and their role as sinks of the perturbations entering anywhere in the system (*NS*). These two indices, in the end, reveal how the topology of the network affects the response of the species to perturbations and thus emphasize the interaction between topology and dynamics. Based on our results, the question related to conservation is whether to prioritize sensitive species, that can be more strongly influenced when others are perturbed, or species of high impact, that can more strongly influence the rest of the community if perturbed.

### 1. Introduction

In the era of global change, predicting the consequences of perturbations in ecological communities is increasingly necessary but also more extremely challenging (Beauchesne et al., 2021). This is because the multiplicity of direct and indirect interaction pathways and their associated feedback often confounds causes and effects of stressors (Bodini et al., 2024). In the last decade several works have emphasized the importance of non-trophic interactions in affecting community dynamics (Kéfi et al., 2015; Miele et al., 2019; Salinas et al., 2023). Still, food web (who eats whom models) analysis occupies a relevant position as a tool that helps predicting the response of species to perturbations: it frames ecological communities in a holistic perspective, through which complex dynamics can be captured and their implications for ecosystem management unveiled (Schoener, 1993; Montoya et al., 2006; Beauchesne et al., 2021). In this framework, focusing on key components is a way to manage complexity as they allow studying the whole system but

simplifying the results.

One way to do this is to target important species in the food web (). Beyond anecdotic, intuitive and experimental knowledge (Paine, 1966, 1969; Mills et al., 1993; Power et al., 1996), species' importance can be identified from their position in the food web (e.g. Allesina and Bodini, 2004; Estrada, 2007; Jordán, 2009; Scotti and Jordán, 2010; Gouveia et al., 2021; Borzone Mas et al., 2022; Mérillet et al., 2022).

The most classical indices of positional importance are the centrality indices (Boguna et al., 2009; Jordán, 2009). They provide specific features that are important in the communication between network nodes and, accordingly, in the spreading of perturbation through the food webs (for an overview on centrality indices in ecology see Gouveia et al., 2021). Other topological measures have been developed and used to predict the consequences of perturbation causing species removal on whole network properties such as resilience and robustness (e.g. Allesina and Bodini 2004; Marina et al., 2024).

The topological approach offers a way to quantifying the roles and

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functions of the nodes in a food web, with potential for predictions (Cirtwill et al., 2018; Lai et al., 2021). However, the predictive capability of food web positional indices to forecast effects of perturbations needs to be improved, and metrics that incorporate dynamics should be developed (Yodzis, 2000, 2001; Dambacher et al., 2002, 2003; Wine-miller and Layman, 2005; Dambacher and Ramos-Jiliberto, 2007). Without this improvement food web research would remain theoretically excellent, but practically challenging to effectively exploit the potential of holistic approach, as management programs like the Ecosystem Based Management for fisheries call for (Pikitch et al., 2004; Dambacher et al., 2015).

One possibility is thinking of indices that capture the species' response to perturbations as a function of the position they occupy in the network. This requires considering the whole suite of paths that connect any given species to the others and the overall effect that such paths produce in spreading the perturbations from one species to another. In this way the dynamic (i.e. each species' response to impacts) would emerge as the consequence of the position a species occupies in the web of connections, given that each position has a characteristic linkage pattern.

In this paper we address this issue. Because quantitative analyses of food web networks are often constrained by the availability and/or quality of data, several studies on the positional importance of species privileged qualitative investigations (Kortsch et al., 2015; Lopez-lopez et al., 2022; Marina et al., 2024). Qualitative techniques have been used to develop metrics that incorporate dynamics in a topological framework (Kok, 2009; Lane, 2008), and in this work we exploited the potential of loop analysis (Puccia and Levins, 1985) due to the possibility it offers to forecasting the species' response to press perturbations (Bodini, 2000; Ortiz et al., 2013; Martone et al., 2017) by identifying paths that propagate their effects and feedback that modulate them.

The main output of loop analysis is a table of predictions, that summarizes the responses of each and all the components of a network as induced by press perturbations entering the system (see Methods). Such responses are signs for the expected direction of change for the abundance of the variables: + for an increase; - for a decrease. Also, null elements may appear in the matrix whenever a given species is predicted not to vary. The table of predictions thus may be used as a diagnostic tool in that it identifies species that are i) most resistant to perturbations (e.g. those showing a high fraction of null responses to perturbations); ii) most sensitive to perturbations (e.g. those without null responses to perturbations entering anywhere in the network) and iii) which has weak or strong effect on the other species.

Accordingly, in this work, we suggest two novel measures of positional importance in food web networks, based on how the linkage pattern of the species in a food web network mediates the response to external perturbations. One of these metrics measures the fraction of nodes in a network that can be affected when a perturbation enters a given node (index of impact). The other metric counts the number of nodes from which effects of perturbations can reach any given node (index of sensitivity). We discuss the relevance of the introduced metrics using several topological indices as benchmarks. We used the Barents Sea food web network as a case study.

## 2. Data

### 2.1. The Barents Sea

The Barents Sea is a relatively shallow, continental shelf sea connected to the Arctic Ocean (average depth is 230 m, maximum depth is 500 m), with a surface of 1,6 million km<sup>2</sup>. It is in the focus of intense research, because it is the target of intense fisheries and because it is heavily influenced by atlantification, the northward expansion of several fish stocks from the Atlantic Ocean, that is the consequence of climate change and warming sea temperature (Fossheim et al., 2015).

### 2.2. The food web and its aggregated counterpart

The Barents Sea food web count as many as 239 tropho-species with 2461 feeding links ( $C = 0,043$ ) and it was shaped exploiting the 2004–2016 Russian-Norwegian Ecosystem Survey (Planque et al., 2014; Pecuchet et al., 2020). Details about species composition and presence-absence for pelagic (Pecuchet et al., 2022) and benthic (Kortsch et al., 2015, 2019) species helped shaping the web in its final form. For the purposes of this study, it would have been too computationally complicated studying the whole food web as it was constructed, so one of the authors (Capelli, 2022) revised it to reduce its dimensionality. Capelli (2022) collapsed the original structure in a more tractable 21-node network. Aggregation proceeded along with the information provided in Pedersen et al. (2021).

The species were first divided in 6 large groups: phytoplankton, zooplankton, benthos, fish, seabird, and mammals. Detritus was added as a bridge component between benthic and pelagic organisms. A finer resolution was adopted for zooplankton, benthos, fish and mammal to capture as much detail as possible in the framework of analytical tractability.

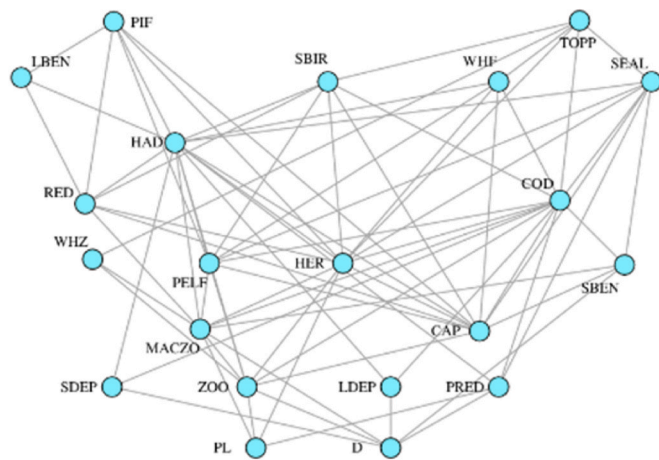
Mammals comprised whales, and seal (SEA). The former counted top predators (TOPP, i.e. *Orcinus orca*), fish-feeding whale (toothed whale, *Odontocetes*, WHF) and zooplankton-feeding whale (baleen whale, *Mysticetes*, WHZ). The polar bear, *Ursus maritimus*, was not included because of its limited presence, confined to marginal areas near dry land. Fish species comprised the most commercially important species, which were maintained as single nodes in the aggregated network. They are cod (*Gadus morhua*, COD), haddock (*Melanogrammus aeglefinus*, HAD), capelin (*Mallotus villosus*, CAP), herring (*Clupea harengus*, HER). Also red fish (species of the genus *Sebastes*, RED) another commercially important group, was included as a node. The other species were clustered according to their feeding habits and size, to obtain the following components: piscivorous fish (PIF), pelagic planktivorous fish (PELF), small benthivorous fish (SBEN) and large benthivorous fish (LBEN). Nodes representing benthic species included predatory feeding invertebrates (PRED), large deposit suspension feeding invertebrates (LDEP) and small deposit suspension feeding invertebrates (SDEP). Zooplankton is divided into macrozooplankton (MACZO) and zooplankton (ZO). Phytoplankton (PL) and detritus (D) at the bottom of the food chain and seabirds (SBIR) at the top of the food web complete the network. Table A1 in appendix describes in detail the species composition of the 21 selected compartments. Fig. 1 depicts the network.

## 3. Methods

### 3.1. Network topology and positional importance

The positional importance of food web nodes was characterized by several indices that are summarized in Table 1. They are: degree (D, Wassermann and Faust, 1994), in-degree ( $D_{in}$ , Wassermann and Faust, 1994), out-degree ( $D_{out}$ , Wassermann and Faust, 1994), closeness centrality (CC, Wassermann and Faust, 1994), betweenness centrality (BC, Wassermann and Faust, 1994), eigenvector centrality (EC, Wassermann and Faust, 1994), the keystone index (K, Jordán et al., 1999) and the topological importance index for various step numbers ( $TI^1, TI^2, TI^3, TI^4, TI^5$ , Jordán, 2009).

We characterized the network position of nodes also by their trophic level (TL, i.e. trophic height (see Luczkovich et al., 2003), defined as 1 plus the average distance from producers (for producers,  $TL = 1$ ). While the importance of weighting ecological interactions has often been outlined (Scotti et al., 2007; Gouveia et al., 2021), there are cases where information on weights is not available and only binary network data are at disposal. These latter may be analysed qualitatively however, and loop analysis (Puccia and Levins, 1985) offers an opportunity to testing a new approach that is presented in what follows.



**Fig. 1.** The food web of the Barents Sea ecosystem as collapsed into a 21 compartment network. Functional groups are CAP: capelin, COD: cod, D: detritus, HAD: haddock, HER: herring, LBN: large benthivorous fish, LDEP: large deposit suspension feeding invertebrate, MACZO: macrozooplankton, PELF: pelagic planktivorous fish, PIF: piscivorous fish, PL: plankton, PRED: predatory feeding invertebrate, RED: redfish, SBEN: small benthivorous fish, SBIR: seabirds, SDEP: small deposit suspension feeding invertebrate, SEAL: seals, TOPP: top predators, WHF: fish eater whales, WHZ: zooplankton eater whales, ZOO: zooplankton. All arrows point upwards, from prey to predator, even if arrowheads are not shown for simplicity. Note that TL is not accurately shown. The minimum (TL = 1 for D) and maximum (TL = 4.78 for TOPP) values are clear, but PIF has a lower value (TL = 4.61) than its prey LBN (TL = 4.72). This is possible because PIF also has several low-TL preys. To avoid confusion, we decided to illustrate the food web in a way that does not necessarily show TL but all arrows point upwards. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 3.2. Loop analysis and positional importance

Loop analysis is a simple but robust mathematical methodology (Puccia and Levins, 1985; Bodini, 2000) that has become increasingly attractive to applications in ecology, especially for analysing socio-ecological systems (Ortiz et al., 2013; Rodriguez et al., 2021; Fábian et al., 2022). In loop analysis, the interactions between nodes are represented only by the signs of the relationships. Nodes themselves are not expressed quantitatively, and only the sign of the variation of their level is considered: it could be biomass or number of individuals, but it is not specified, as it is uninteresting for making predictions, which are only given as direction of variation: increase, decrease or no change (Puccia and Levins 1985). The scripts that compose the software tool for the loop analysis algorithm and the simulations are available at Pereira et al. (2023). For the analysis any network turns into a community matrix (Levins, 1968) in which only three types of coefficients are possible: +1 identifies a positive effect exerted by the row variable over the rate of change of the column variable; -1 indicates that the row variable has a negative effect over the rate of change of the column variable; a null coefficient stands for no interaction. Coefficients along the main diagonal indicate self-effects (how a variable affects its own rate of change). We converted food web data of the Barents Sea into a community matrix (Jacobian matrix) by transforming trophic links (from prey to predators) as bidirectional dynamical effects: positive (+) from prey (resource) to predator (consumer) and negative (-) from the latter to the former. Also, we set each coefficient along the main diagonal equal to -1, thus assuming self-regulation of nodes, considering intraguild regulative processes (within the functional group represented by the graph node, see Puccia and Levins, 1985). By manipulating the community matrix one can predict the direction of change (increase, decrease, or no effect) of any variable in response to perturbations that alter parameters

**Table 1**

List of the studied indices, their abbreviation, definition and ecological interpretation (references also provided).

index	abbr.	definition	ecological significance	reference
in-degree	$D_{in}$	the number of incoming links	the number of prey species (resources)	Wassermann and Faust (1994)
out-degree	$D_{out}$	the number of outgoing links	the number of predators (consumers)	Wassermann and Faust (1994)
degree centrality	DC	the normalized number of links	the sum of prey and predatory species, related to the size of the network	Wassermann and Faust (1994)
closeness centrality	CC	the sum of the length of shortest paths from a given node to all others	trophic position close to the middle of the food web	Wassermann and Faust (1994)
betweenness centrality	BC	the frequency of the considered node on the shortest paths connecting all pairs of other nodes	maintenance of unique trophic pathways	Wassermann and Faust (1994)
eigenvector centrality	EC	quantifies how densely a species is linked to highly connected species	being a trophic generalist with generalist resources and consumers	Wassermann and Faust (1994)
keystone index	K	the topological importance in maintaining vertical flows	maintenance of non-redundant bottom-up and top-down flows	Jordán et al. (1999)
topological importance	$TI^n$	the topological importance of species $i$ when effects up to $n$ steps are considered	being a trophic generalist with generalist neighbours within a distance of $n$ steps	Jordán (2009)
node impact	NI	the simulated effect going to other nodes in the network	population size generating response in many other species	here
node sensitivity	NS	the simulated effect coming from other nodes in the network	population size of other species generating response in focal species	here
trophic level	TL	the distance from producers in a food web plus one	average vertical position along trophic chains	Luczkovich et al. (2003)

governing the rate of change of any other component (i.e., press perturbations: Bender et al., 1984). The net effect (the sum of the direct effect plus all the individual indirect effects) on species  $i$  resulting from a perturbation on species  $j$  is given by the element of the inverse community matrix.

Figure B2 in the Supplementary material summarizes these concepts showing a signed digraph (Figure B2a), its corresponding community matrix in its general form (Figure B2b) and its numeric counterpart (Figure B2c). Inverting the community matrix one obtains the net effect of species  $j$  on species  $i$  due to the direct interaction and all possible indirect interactions through which species  $i$  and  $j$  are connected via all intermediate  $k$  species. The elements  $(-a_{ij}^{-1})$  of this inverted matrix indicate the effect that a press perturbation (Bender et al., 1984; Puccia and Levins, 1985) on species  $j$  extend over species  $i$ . The inverted matrix  $A^{-1}$  is given in Figure B2d. This procedure has a graphical counterpart

(Puccia and Levins, 1985) that shows how predictions derive from the topology of the network. The foundations of this method are given in the Supplementary material, Appendix C.

To overcome the problems posed by the qualitative nature of the interactions, predictions about the response of variables' level to press perturbations were obtained on a probabilistic base applying a numerical simulation. The routine randomly assigned numerical values to the coefficients of the community matrix (i.e. the coefficients of the links in the signed digraph). This procedure was executed  $n \times 1000$  times, where  $n$  is the number of nodes in the model (for  $n = 21$ , 21.000 matrices, out of which 7605 were stable). At each run, the community matrix that is formed is accepted if and only if it satisfies the asymptotic Lyapunov criteria (Logofet 1993). The  $z$  stable community matrices among the  $n \times 1000$  that we simulated were accepted and inverted. Thus, each model in the simulation yields  $z$  stable community matrices, and each of them rendered a table of predictions. An overall table of predictions is then obtained combining these tables on a percentage of sign base. For a given prediction, if all the  $z$  matrices (100% of the cases) yield the same sign (+ or -), the direction of change (i.e. the prediction) is easily assigned (+ or -). However, when multiple paths with different sign connect the same two components, cases emerge in which a certain quota of the matrices yields a given sign (e.g. +), but some other matrices render the opposite sign (-) for a given prediction. Overall, this prediction, whether it is a + or a -, depends on the percentage of matrices that return a sign in respect to those that yield the opposite sign, according to the rules of selection that can be summarized as follows: if the percentage of matrices that yield a positive prediction lies in the interval 75–100% then the prediction is said to be a plus. If this percentage is between 60% and 75% the + sign is accompanied by a question mark (?+), indicating a tendency to be positive. If the percentage of matrices yielding a (+) for a given prediction lies between 40% and 60% then the prediction is said to be statistically null (0\*). If the percentage of matrices yielding a + sign for a given prediction lies between 25% and 40% the sign is negative with a question mark, and finally if the percentage of matrices is lower than 25% the prediction is negative. The 0\* is a neutral result due to a more or less equal number of matrices yielding the negative and the positive sign for a given prediction. Accordingly, it can be considered a statistically null prediction indicating a quasi-compensation between positive and negative effects.

Based on the change between initial stability and local stability after perturbation, Ortiz et al. (2013, 2017) suggested a measure of keystone species based on loop analysis ( $KQ_{iLA1}$ ). It is transformed to another measure that is sensitive to the biomass/effect ratio as well ( $KQ_{iLA2}$ ). Node  $i$  is considered a keystone species if its  $KQ_i$  values (especially  $KQ_{iLA2}$ ) are higher. Here we suggest another, complementary definition of important species based on loop analysis, and it exploits the information in the table of predictions. We define Node Sensitivity ( $NS$ ) as

$$NS = 1 - \frac{\sum_i X_{ij}}{n} \quad (1)$$

where  $X_{ij} = 1$  if the prediction is 0\* or 0; whereas  $X_{ij} = 0$  when a given sign (+, +?, -, -?) occurs. Thus,  $X_{ij}$  is the number of 0\* or 0 incoming effects to node  $j$ . Node  $j$  can be considered a sensitive species if its  $NS$ -value is high. On the contrary a low  $NS$  value indicates a rather inert species, which is resistant to perturbations entering the system. Independently of the size (strength) of the effects, this defines the proportion of other network nodes with some (less than 40% or more than 60%) effect on node  $j$ , either positive or negative. Nodes that are very sensitive to perturbations affecting other species, that is those with a high  $NS$  coefficient, not necessarily exert a strong influence over the others when they become the target of perturbations (e.g. perturbations entering through these nodes propagate some effect to a high fraction of the other components). So, symmetrically, we are interested in their impact on the other species. Accordingly, we can define an index of Node Impact ( $NI$ )

as:

$$NI = 1 - \frac{\sum_j X_{ij}}{n} \quad (2)$$

This is the proportion of non-zero out-going effects to nodes  $j$ , so the higher the  $NI$ -value is, the more impacting node  $i$  can be considered.

### 3.3. Statistical analysis

Index values were pre-treated in two steps in order to ensure comparability. First, because some topological indices exhibited a moderately right-skewed distribution we applied the most straightforward transformation computing the square root of the data. No transformation was needed for  $NS$ ,  $NI$  and  $TL$ . Second, variables were normalized (by subtracting the mean and dividing by the standard deviation) to have commensurable scale. Subsequently, Principal Component Analysis (PCA) was performed in PRIMER v7 software (Clarke and Gorley, 2015) to obtain the ordination of objects (functional groups) and variables (topological indices).

## 4. Results

The table of predictions for the Barents Sea network (Table 2), allows computing the indices  $NS$  and  $NI$  for every component.

As it was explained in the Methods, these indices are based on the proportion of 0\* and 0 predictions in rows and columns of the table. The values for the two indices are listed in Table 3, which summarizes all network indices values for each of the 21 trophic groups: 12 centrality indices, 2 indices based on loop analysis, (columns  $NS$  and  $NI$ ) and the trophic level. Also, Fig. 2 visualizes the values of  $NI$  and  $NS$  for each node.

Considering  $NS$ , the species that ranks highest are haddock and seal ( $NS = 0.67$ ). To have a perception of how this index is computed one must look at their columns in the table (Table 2, columns HAD and SEAL): both contain as many as 7 null (0\*)-values. HAD and SEAL share the highest sensitivity to perturbations as they respond to perturbation targeting 14 out of 21 nodes, the highest fraction among all the network's components. On the other hand, small benthivorous fish (SBEN) and detritus (D) rank the highest as for index  $NI$  ( $NI = 0.71$ ). In this case one must look at the rows labelled SBEN and D in Table 2 to discover that only 6 0\* values are present. This means that perturbations that propagate from SBEN and D affect the highest proportion of network nodes in comparison with any other node. The lowest positions in the  $NS$  rank are occupied by zooplankton ZOO,  $NS = 0.29$ , Table 3), capelin (CAP,  $NS = 0.38$ ) and herring (HER,  $NS = 0.43$ ). This latter shows also the lowest performance in terms of impact on network nodes (HER,  $NI = 0.33$ ), predatory feeding invertebrates (PRED,  $NI = 0.38$ ) have also low impact as well as fish eating whales (WHF,  $NI = 0.38$ ). Herring combines low sensitivity to perturbation with low impact on the rest of the network (Table 3).

Consider pairwise correlations of the indices (Table 4, Fig. 3). While indices of positional importance positively correlate each other with few exceptions, the behaviour of  $NS$  and  $NI$  is different because i) they are weakly correlated with the other indices, and ii) they show opposite tendency as  $NS$  positively correlate with most of the indices whereas  $NI$  show a tendency to be negatively correlated. Likely the indices used as benchmarks contain redundant information about the positional importance of the nodes, whereas  $NS$  and  $NI$  likely carry different information. The only relevant correlation involving the new indices associate positively  $NI$  to  $K$  and  $NS$  mostly correlates with  $EC$  ( $-0.26$ , Table 4).

The indices  $NI$  and  $NS$  are negatively correlated with one another, but their association is weak ( $-0.20$ ). High sensitivity weakly reflects on high impact on other nodes. The general relationships among the indices are shown in the PCA plots (Fig. 4).

**Table 2**  
The table of predictions for the Barents Sea food web, obtained applying the algorithm of loop analysis. The table reads row by column: every row indicate the component that undergoes a press perturbation; the response of all the network nodes can be read column by column along the rows.

	TOPP	SEAL	WHF	WHZ	SBIR	PIF	COD	HAD	RED	PELF	CAP	HER	LBEN	SBEN	PRED	LDEP	SDEP	MACZO	ZOO	PL	D
TOPP	+	0*	?	-	?	?	0*	?	0*	?	0*	?	?	?	0*	?	?	?	0*	0*	0*
SEAL	0*	+	?	?	?	0*	?	0*	?	0*	0*	0*	?	?	?	?	?	?	0*	?	0*
WHF	0*	?	+	?	?	0*	?	0*	?	0*	0*	?	0*	?	?	?	?	?	0*	0*	-
WHZ	+	0*	?	+	?	0*	?	?	?	0*	?	0*	?	?	?	?	?	?	0*	?	?
SBIR	?	?	?	?	+	?	?	?	?	?	?	?	?	?	?	?	?	?	0*	?	?
PIF	0*	?	0*	?	?	+	?	?	?	?	?	?	?	?	?	?	?	?	0*	?	?
COD	?	0*	0*	?	0*	?	+	?	?	?	?	?	?	?	?	?	?	?	0*	?	+
HAD	0*	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0*	?	?
RED	?	0*	?	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0*	?	?
PELF	0*	?	?	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0*
CAP	+	?	?	?	?	+	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
HER	0*	?	0*	-	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
LBEN	0*	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SBEN	0*	?	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
PRED	0*	+	0*	0*	0*	0*	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?
LDEP	0*	?	0*	0*	0*	0*	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?
SDEP	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
MACZO	?	0*	?	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ZOO	+	0*	?	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
PL	?	0*	?	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
D	?	?	0*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Chart4a illustrates how the network nodes distribute along the two principal components in relation to their value for the 15 indices that we considered. Fig. 4b does the same for the 3rd and the 4th principal components. The correlation of individual indices with the PCs is given in Table 5.

The first four axes explain a cumulative 93,50% of variation (Fig. 4, caption). However, the greatest part of the variability pertains to the first two components, with a cumulative 78% of the variance explained. Nonetheless, Table 5 tells that none of the two indices computed from the table of predictions contribute significantly to the first two principal components (correlation near 0). This points out the difference between NI/ NS and the other indices, as already signaled by the correlation coefficients (Table 4 and Fig. 3). The fact that neither NS nor NI correlate with PC1 indicates that each node's linkage richness is not determinant for these two metrics. The same holds for PC2, which correlates in opposite ways with in-degree (positive correlation) and out-degree (negative correlation) centrality. Also, trophic level (TL) contributes significantly to this component. Indices from loop analysis play a role only in respect to PC3 and PC4. Considering the former, a major contribution comes from NI and K, from NS, but with a lower correlation (see Table 5); all the other indices play a marginal role. PC4 shows a strong correlation only with index SN, which, thus, define the meaning of this component. In the discussion we provide a more in-depth analysis of these results.

The PCA shows also the relationships among the functional groups of the Barents ecosystem, not only among the indices. Haddock (HAD) is nicely separated along PC1 and PC4. Fish-eater and zooplankton-eater whales (WHF and WHZ) are quite close to each other along PC2, PC3 and PC4, they are mostly separated along PC1. Detritus (D) and plankton (PL) are close on PC2 and PC3 but somewhat separated along PC1 and PC4. Redfish (RED) is always very close to the middle of the plots.

**5. Discussion**

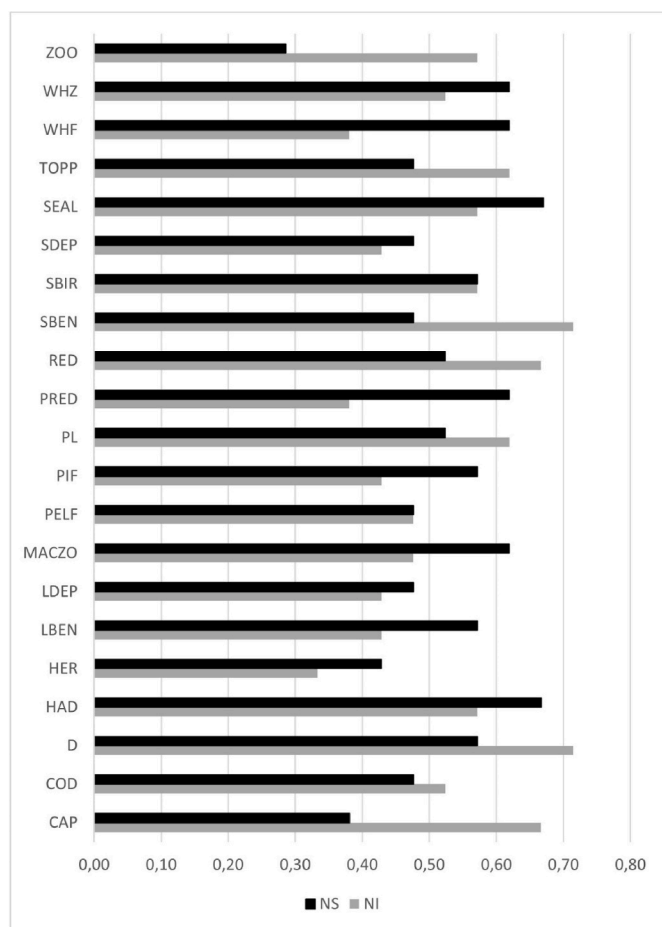
To understand what the two indices presented here may contribute to food web analysis one needs to expand from the information they carry. For each node in the network, SN and IN are defined by the fraction of null predictions along, respectively, its column and row of the table of predictions. The less 0\* along its column the less resistant the species in question is to perturbations entering the system through the various nodes. In other words, when a higher fraction of the network's nodes are perturbed, effects percolate to that species and only in a few cases it remains unaffected (high sensitivity, low resistance). On the contrary, a high fraction of 0\* defines a species that is generally resistant to perturbations. Index IN quantifies the impact of every node over the network in terms of the number of nodes it affects when targeted by perturbations. A high number of 0\* along a node's row in the table of predictions tells that it exerts a moderate impact on the network.

These outcomes depend on the structure of the network, because effects of perturbations are transported from one node to the others by pathways that the arrangement of interaction links forms. Consider NS: its value depends on the paths ending in each node and that come from any other component; Index NI on the other hand, accounts for the pathways that leave a given node toward the others (to propagate the impacts to them). A 0\* in a node's row/column means that paths with opposite effects (positive and negative) balance each other out. This outcome does not depend on the absolute number of paths: it can be 2 or many but a 0\* appears in the table of predictions as long as they carry different effects (positive/negative) that compensate each other. This explains why the two indices do not correlate with in-degree (D<sub>in</sub>) and out-degree (D<sub>out</sub>) centrality (Table 4, Fig. 4), which do instead depend on the number of direct incoming and outgoing connections.

Also, the two indices do not correlate with closeness centrality (CC, Table 4, Fig. 4) The spreading of the perturbations, in fact, depends not only on the shortest paths, although they are often the strongest in magnitude. A 0\* prediction, for example, as well as a given defined

**Table 3**  
Values of node-level network indices for 21 trophic groups.

	$D_{in}$	$D_{out}$	DC	CC	BC	EC	K	$TI^1$	$TI^2$	$TI^3$	$TI^4$	$TI^5$	NI	NS	TL
CAP	0.50	0.05	0.55	0.69	0.05	0.32	4.13	1.40	1.43	1.46	1.48	1.49	0.67	0.38	3.00
COD	0.20	0.45	0.65	0.71	0.12	0.32	4.20	2.16	1.89	1.91	1.87	1.87	0.52	0.48	3.55
D	0.30	0.00	0.30	0.51	0.03	0.11	10.79	1.28	1.02	1.01	0.95	0.94	0.71	0.57	1.00
HAD	0.25	0.45	0.70	0.77	0.19	0.34	4.42	2.44	2.10	2.10	2.04	2.04	0.57	0.67	3.63
HER	0.40	0.20	0.60	0.71	0.08	0.33	2.92	1.61	1.63	1.64	1.65	1.65	0.33	0.43	3.08
LBEN	0.05	0.10	0.15	0.47	0.00	0.09	1.38	0.38	0.42	0.41	0.42	0.41	0.43	0.57	4.72
LDEP	0.10	0.05	0.15	0.51	0.01	0.09	0.62	0.32	0.43	0.42	0.43	0.42	0.43	0.48	2.00
MACZO	0.35	0.15	0.50	0.67	0.09	0.26	4.37	1.55	1.50	1.46	1.45	1.44	0.48	0.62	2.33
PELF	0.30	0.15	0.45	0.65	0.02	0.28	1.77	1.05	1.14	1.18	1.20	1.21	0.48	0.48	3.44
PIF	0.00	0.30	0.30	0.56	0.01	0.18	4.02	0.83	0.83	0.83	0.83	0.83	0.43	0.57	4.61
PL	0.20	0.00	0.20	0.51	0.01	0.12	8.21	0.49	0.53	0.55	0.55	0.56	0.62	0.52	1.00
PRED	0.15	0.10	0.25	0.56	0.02	0.13	1.04	0.69	0.75	0.72	0.72	0.72	0.38	0.62	2.00
RED	0.20	0.15	0.35	0.61	0.02	0.21	1.78	0.99	0.98	0.98	0.97	0.97	0.67	0.52	3.81
SBEN	0.10	0.15	0.25	0.56	0.01	0.15	0.88	0.56	0.67	0.67	0.69	0.69	0.71	0.48	3.11
SBIR	0.05	0.30	0.35	0.59	0.01	0.23	3.09	0.74	0.88	0.89	0.92	0.93	0.57	0.57	4.42
SDEP	0.10	0.05	0.15	0.51	0.01	0.09	0.62	0.32	0.43	0.42	0.43	0.42	0.43	0.48	2.00
SEAL	0.05	0.35	0.40	0.63	0.02	0.24	3.93	1.00	1.06	1.08	1.09	1.09	0.57	0.67	4.12
TOPP	0.00	0.30	0.30	0.56	0.03	0.17	14.98	0.93	0.84	0.84	0.84	0.84	0.62	0.48	4.78
WHF	0.05	0.25	0.30	0.57	0.01	0.21	2.69	0.60	0.74	0.75	0.78	0.79	0.38	0.62	4.34
WHZ	0.05	0.10	0.15	0.48	0.00	0.08	0.60	0.38	0.41	0.42	0.42	0.42	0.52	0.62	3.17
ZOO	0.35	0.10	0.45	0.65	0.06	0.25	9.48	1.28	1.31	1.28	1.29	1.28	0.57	0.29	2.00



**Fig. 2.** Diagram showing the NS and NI values for the 21 trophic groups. Data in Table 2.

prediction (+/-) may come about because numerous long pathways balance or overcome few, more intense paths with opposite effect. The lack of correlation with the betweenness centrality (BC, Table 4, Fig. 4) becomes clear considering that nodes are always starting or ending points of the paths that spread the effects of the perturbations;

accordingly, how frequently a node is on the shortest paths between any two nodes does not contribute to define NS and NI.

The two indices from loop analysis showed low association also with the indices of topological importance ( $TI^1$ ,  $TI^2$ ,  $TI^3$ ,  $TI^4$ , and  $TI^5$ , Table 4, Fig. 4). Such indices quantify the role of network nodes in propagating effects either directly ( $TI^1$ ) or indirectly ( $TI^2$ ,  $TI^3$ ,  $TI^4$ , and  $TI^5$ ) but they do not do it in a functional perspective (i.e. they do not consider the sign or the magnitude of the interaction links) but only in topological terms as function of the degree centrality that any node exhibits (Jordán et al., 2006; Jordán, 2009).

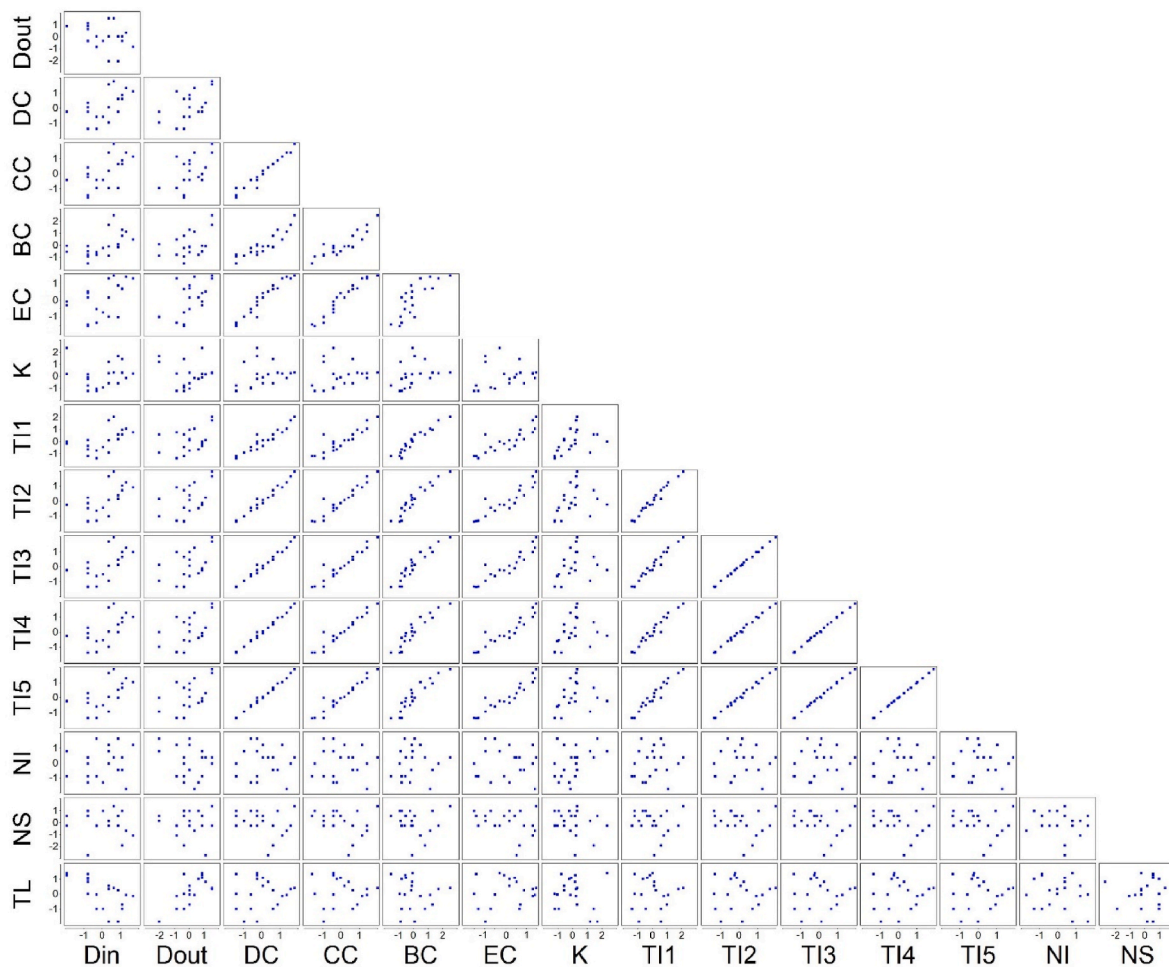
TI indices exploit the reciprocal of the degree centrality to define the topological relevance of a species over another. For example, if, say, species A is a direct neighbour of B (a direct link from A to B exists) and B has several other direct neighbours, then the link A-B is rather unimportant for B as this latter establishes many other direct connections; thus, the topological importance of A on B is weak. If, instead, A is the only direct neighbour of B, the former plays an important role on the latter, as it is the only topological constraints that B possesses. This topological importance emerges also along indirect longer chains:  $TI^5$ , for example, considers chain of 5 links from A to B and at each step the inverse degree centrality of any intermediate node is multiplied to obtain the indirect topological importance that A has on B. If two or more 5-step paths connects A to B one obtains the overall topological importance of A on B through 5-steps pathways.

Because the degree centrality is not associated to any of the two indices computed using the tables of predictions it is not surprising that these latter do not correlate with the TI. PC1 is strongly determined by most of the indices of topological importance, namely DC, CC, BC, EC, and the indices of topological importance  $TI^2$ ,  $TI^3$ ,  $TI^4$ , and  $TI^5$ . In synthesis, the PC1 can be thought of as a dimension of interaction richness. In particular, the negative correlation that exists between the centrality indices and the PC1 suggests that this latter represents a dimension of “low connectivity”, which translates into a degree of linearity of food webs (Hall and Raffaelli, 1993; Raffaelli and Hall, 1996).

NS and NI do not correlate with the PC2, which is mostly determined by in-degree, out-degree and the trophic level, thus an axis of vertical food web position. PC3 and PC4 together account for only about 15% of the variance (Fig. 4, caption; 9.10% for PC3 and 6.40% for PC4). Nevertheless, they cannot be neglected here because these are the only components in which the indices from the table of predictions show high correlation: NI correlates high with PC3 (Table 5) and NS with PC4. Considering this latter, NS is the only index that show high correlation; thus PC4 can be considered a sensitivity axis.

**Table 4**  
Pairwise correlations among the 15 indices calculated for network nodes.

	D <sub>in</sub>	D <sub>out</sub>	DC	CC	BC	EC	K	TI <sup>1</sup>	TI <sup>2</sup>	TI <sup>3</sup>	TI <sup>4</sup>	TI <sup>5</sup>	NI	NS
D <sub>out</sub>	-0.34													
DC	0.55	0.52												
CC	0.56	0.54	0.97											
BC	0.56	0.43	0.9	0.9										
EC	0.48	0.58	0.97	0.97	0.79									
K	0.07	-0.02	0.35	0.21	0.35	0.26								
TI <sup>1</sup>	0.54	0.44	0.96	0.89	0.95	0.85	0.46							
TI <sup>2</sup>	0.57	0.48	0.99	0.95	0.95	0.92	0.38	0.99						
TI <sup>3</sup>	0.57	0.48	0.99	0.95	0.94	0.93	0.38	0.98	1					
TI <sup>4</sup>	0.57	0.49	1	0.96	0.93	0.94	0.37	0.98	1	1				
TI <sup>5</sup>	0.56	0.5	1	0.96	0.93	0.95	0.37	0.97	1	1	1			
NI	0.15	-0.2	0.11	0.03	0.1	0.04	0.44	0.19	0.13	0.14	0.12	0.12		
NS	-0.16	-0.02	-0.19	-0.23	-0.06	-0.26	-0.2	-0.09	-0.15	-0.16	-0.17	-0.17	-0.2	
TL	-0.57	0.78	0.16	0.14	-0.06	0.27	-0.08	0.06	0.08	0.09	0.11	0.11	-0.13	0.03

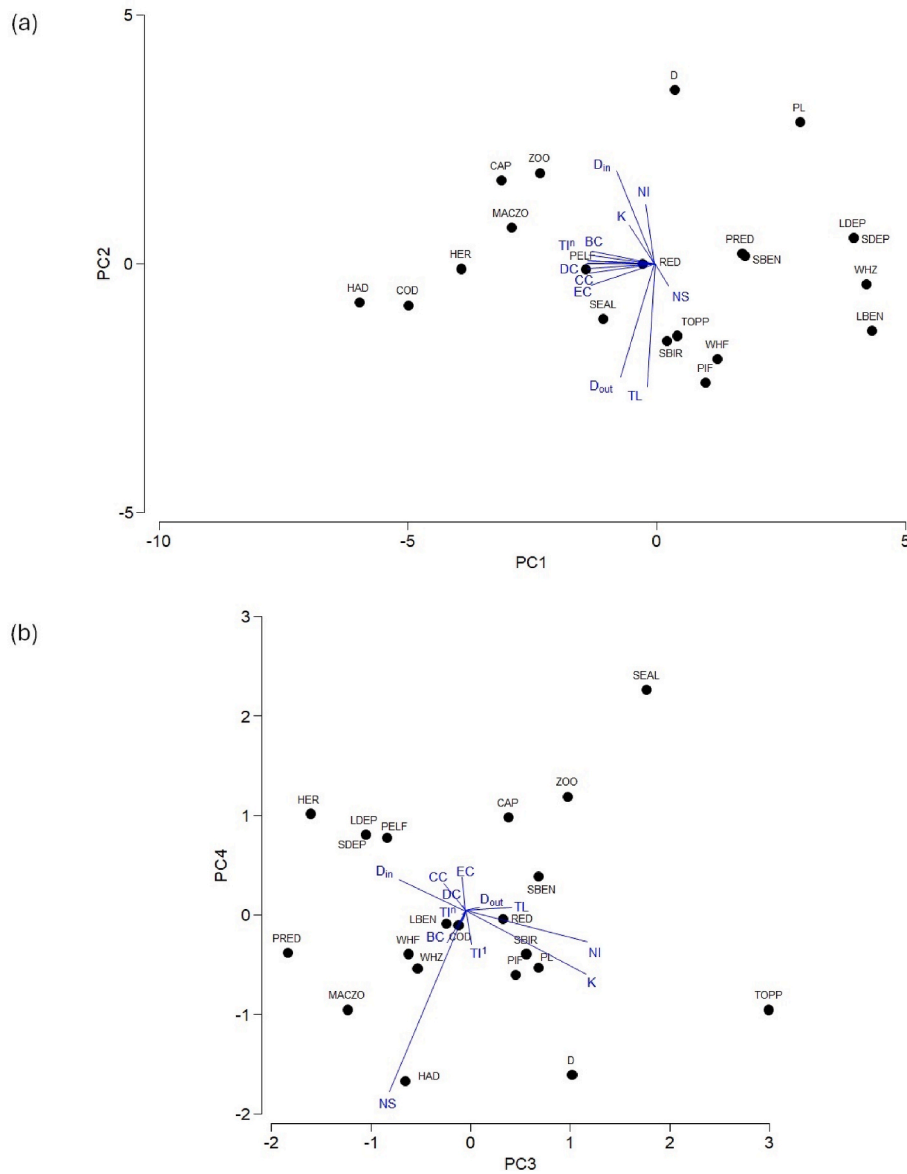


**Fig. 3.** Cross-correlations among all of the 15 studied network indices (12 centralities, trophic level, and 2 indices based on loop analysis). Self-correlations (e.g. TL-TL) are not shown.

PC3 shows high correlation with the index of impact *NI* and with *K*, the keystone index. These two indices contribute equally to this component. Their relationship is visualized also in [Table 4](#) and [Fig. 3](#), which show the two indices as positively associated one another. Although a relationship between these two indices is not straightforward, their correlation can be interpreted considering that index *NI* assigns a node a level of importance as controlling factor over the network's nodes; index *K* on the other hand emphasizes the role a species plays in the bottom-up and top-down control ([Jordán, 2009](#)). Further analysis would be needed to dig in the details of this relationship to

make it clearer and formally understandable. According to the meaning of these two indices it can be hypothesized that the PC3 represents an axis of topological control.

Considering the relationships between the indices as we described above it can be posited that the two indices proposed in this paper differ from other topological indices essentially because they are based on dynamical consequences of their position within the structure of the interactions. Betweenness centrality, for example, measures the extent to which a node lies on paths connecting other nodes in the food web ([Jordán et al., 1999](#); [Jordán, 2009](#)). Species or trophic guilds with high



**Fig. 4.** The first 4 axes of the Principal Component Analysis. Figure (a) shows PC1 and PC2, whereas (b) shows PC3 and PC4. For the 4 axes, the Eigenvalues equal 9,4 (PC1), 2,3 (PC2), 1,37 (PC3) and 0,9 (PC4). The percentage of variance values are 62,7% (PC1), 15,3% (PC2), 9,1% (PC3) and 6,4% (PC4). Cumulative variance increases as 62,7% (PC1), 78% (PC2), 87,1% (PC3) and 93,5% (PC4).

**Table 5**  
PC axes and their contribution to explaining variation.

	PC1	PC2	PC3	PC4
D <sub>in</sub>	-0.182	<b>0.449</b>	-0.318	0.152
D <sub>out</sub>	-0.165	<b>-0.546</b>	0.07	0.015
DC	<b>-0.325</b>	-0.025	-0.015	0.026
CC	<b>-0.316</b>	-0.045	-0.103	0.134
BC	<b>-0.305</b>	0.061	-0.092	-0.152
EC	<b>-0.309</b>	-0.104	-0.014	0.164
K	-0.124	0.186	<b>0.581</b>	-0.308
TI <sup>1</sup>	<b>-0.317</b>	0.04	0.027	-0.165
TI <sup>2</sup>	<b>-0.325</b>	0.017	-0.022	-0.053
TI <sup>3</sup>	<b>-0.325</b>	0.014	-0.013	-0.045
TI <sup>4</sup>	<b>-0.326</b>	0.003	-0.017	-0.018
TI <sup>5</sup>	<b>-0.326</b>	0.001	-0.014	-0.019
NI	-0.043	0.284	<b>0.591</b>	-0.154
NS	0.064	-0.106	-0.366	<b>-0.87</b>
TL	-0.037	<b>-0.596</b>	0.226	0.016

value for this index are supposed to exert much control over information (impacts) passing along the web. However, the real expression of this control is only hypothetical. The indices of loop analysis are based on the effective role a species plays in passing the impacts to other species (*NI*) and their role as sinks of the perturbations entering anywhere in the system (*NS*). These two indices, in the end, reveal how the topology of the network affects the response of the species to perturbations and thus emphasize the interaction between topology and dynamics. High *NI* identifies species that exert a strong control over the others whereas high *NS* indicates species that are particularly sensitive to perturbations. Nevertheless, it should be pointed out that these features depend on the overall topology of the network (see Supplementary material, [Appendix C](#)). Also, simply considering the total number of null responses in a table of predictions one may have a clue about the overall resistance of a system to perturbations. This can have practical application in management related questions, more specifically in the field of environmental impact assessment, in which knowing how resistant an ecosystem can be to perturbations may guide decisions about a certain project.



For conservation management, importance is a hard concept. Based on our results, the question related to conservation is whether to prioritize sensitive species (that can be more strongly influenced when others are perturbed, potentially being subject of secondary extinctions) or species of high impact (that can more strongly influence the rest of the community if perturbed, potentially generating more secondary extinctions). As for this latter attribute Table 3 indicates that redfish and capelin rank very high and their impact on the community may be relevant. But they are also commercially important species; so the fishing practice, inducing a systematic perturbation on it, may extend impacts to a large array of other species of the Barents ecosystem. This may not be so for herring, which rank low for *NI*.

The node sensitivity index (*NS*) clearly identifies Haddock as a sensitive species. This same species was signaled relevant because it was a high generalist also by other studies, based on trophic generality (i.e. high generalist, Pecuchet et al., 2020). This is also a candidate species for wasp-waist control, exerting both bottom-up and top-down effects (Jordán et al., 2024) and ultimately contributing to the wasp-waist dynamics of the community (Fauchald et al., 2011). The other derived index (*NI*) suggests that herring (HER) can be the least important to influencing other trophic groups, according to our model. These results may be valuable for maximum sustainable yield assessment (if confirmed by additional empirical data or models), as sustainability may be increased by reducing the catch on fish with extreme community roles (either highly sensitive or highly important).

The predictive power of food web research essentially depends on how to understand the relationship between structure (food web position) and dynamics (effects of perturbation). For this, various ecological functions can be mapped onto different network properties. These include, for example, nodes governing energy flows (e.g. dominators, Allesina and Bodini, 2004) and species exerting strong control over others through trophic cascades (e.g. sea otters, Nicholson et al., 2024). Loop analysis, based on quantifying the effects of perturbations, is a particular approach, somewhere between topological analysis and real dynamical simulations. Similarly, to node removal experiments (Dunne et al., 2002; Dunne and Williams, 2009; Bellingeri and Bodini, 2013), loop analysis quantifies the effects of change, without explicitly considering effects such as prey switching, extensively studied for vertebrates (Rennie et al., 2009), invertebrates (Ladygina et al., 2008) and also in models (Archibald et al., 2023) as well as food web rewiring (Bartley et al., 2019; D'Alelio et al., 2019; Polazzo et al., 2022).

### 5.1. Limitations and future perspectives

Although in the present paper we addressed the question of how to predict functionality in food webs by structural analyses, indicators may also be quantified at the level of the whole community (ecosystem), focusing on global, system-level properties (see a classical approach in Finn, 1976 and more recent studies on the Barents Sea in Kortsch et al., 2019; Jordán et al., 2024).

While predicting the effects in multi-species food webs is increasingly possible, some models also address the additivity of effects in the case of multiple perturbations (May et al., 1979; Legovic and Gecek, 2010; Mórèh et al., 2021, 2024). This research direction (already established in loop analysis and implemented in software) might also be better explored in future research focusing on additivity (e.g. double exposure). Considering weighted trophic networks provides more realistic results (Scotti et al., 2007; Gouveia et al., 2021), in general, so testing and developing the present approach might be desirable on (several) weighted networks.

We suggest that applying loop analysis to quantifying the role and function of organisms (functional groups) in ecological communities is a promising perspective, yet to be enriched by weighted data, multiple perturbations and experimental tests, but possibly offering simple, transparent, quantitative and communicable indicators for conservation management.

Indices *NI* and *NS* provide a complementary information to conservationists, from a systems-based perspective. The former indicates which species should be protected against perturbations to avoid major consequences at the whole ecosystem level (e.g. reducing fishing pressure on capelin may benefit other species, included itself). The latter highlights which species requires attention for its own conservation. The two indices provide also valuable information about the effects of the multiple stress that affects the ecosystem and that are now extremely diffuse and whose relevance for ecosystem management is prominent (Birk, 2019; Bodini et al., 2024). We suggest that these indices, being quantitative, transparent and simple, might be developed and used as indicators in the future.

### CRedit authorship contribution statement

**Ferenc Jordán:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Katalin Patonai:** Writing – review & editing, Visualization, Investigation, Formal analysis. **Greta Capelli:** Writing – review & editing, Investigation, Data curation. **Raul Primicerio:** Writing – review & editing, Supervision, Investigation, Data curation. **Antonio Bodini:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

### 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.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.indic.2024.100500>.

### Data availability

Data will be made available on request.

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