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The effect of fish life-history structures on the topologies of aquatic food webs

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ABSTRACT

Biological organisms can vastly change their ecological functionality due to changes in body size and diet across their life. Consequently, it has been increasingly recognized that to attain sufficient biological realism, food webs may need to include life-history structures. The objective of the work is to study theoretically whether and how the inclusion of life-history structures affects the food web topology. Topological research was done by applying network theory metrics for three different food web types with two different sizes that were generated by using the niche-model. The dynamical modeling was performed by using an allometric trophic network modeling approach. The different types included food webs with and without the life-history structure for top predators (three fish species). Each of the generated random food webs analyzed reached dynamical equilibrium conditions with respect to the biomass densities of the species prior to the network analysis. Our results suggest that food web topologies are not largely affected by the inclusion of age- or stage-structure. In addition to the topological study, the relationship between the metrics used in this work was investigated by using Pearson correlation. Results suggested that only a few pairs of metrics had a strong positive correlation and most of the correlations did not change with food web size or type.

1. Introduction

Network theory plays an important role in many areas of science, including biology (Newman, 2010), where it has been applied to represent the patterns of interactions between different functional elements. Biochemical and metabolic networks (e.g., protein-protein networks) have been studied by molecular biologists whereas neuroscientists use network analysis to study the interactions between brain cells. Ecologists use network analysis tools to study the interactions between different functional groups, e.g. between predators and their prey species (Newman, 2010; Pavlopoulos et al., 2011; Hahn and Kern, 2005; Koschützki and Schreiber, 2008). In ecology, an increasing amount of attention have been focused on food webs during the past decade as network analysis has become a popular tool to examine the role of species in ecological communities (Allesina and Pascual, 2009; Jordán et al., 2006).

Food web models offer insight into the dynamics of natural populations and species and, in particular, the processes driving the dynamics (Pimm, 1991). Traditionally, food webs have been approached from two different points of view. Lindeman presented the energetic view that describes food webs as pathways for energy flow (Belgrano et al., 2005). The other approach, initiated by May (1973), emphasizes the dynamical factors that are formed from interactions between species. The latter study initialized a discussion on the effect of growing complexity on instability in food webs (reviewed e.g. by Dunne et al., 2005). Together these points of view have led to topological research on the structure of food webs (Jordán et al., 2006; Montoya et al., 2006; Williams and Martinez, 2000).

The studies on food web structures have usually focused on properties that describe their internal structure, e.g. connectance, the size of the web and the number of trophic links between species. These variables are of importance when trying to obtain a deeper understanding of the dynamic properties of the system in the presence of internal forcing, e.g. predation and energy transfer. Furthermore, recent advances in ecosystem network analysis have shown that a new synthesis coupling ecosystem dynamics and network analysis is needed to gain new insight about available theory and methodology transferrable to biological systems (Williams and Martinez, 2000; Endrédi et al., 2018). When network theory is combined with different, more traditional approaches, e.g., dynamic, and static bioenergetics models, a deeper understanding

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of the community structure and functioning could be achieved.

Traditionally, food webs have been structured by species or functional groups consisting of one or several species with the same or similar range of predators, prey, and metabolic properties (McCann, 2012). However, since the discovery of the fundamental role of body size on the stability of food web dynamics (Brose et al., 2006), it has become questionable, whether species' ecological functionality can be sufficiently approximated through the species average adult body size alone. Deviations from this assumption may be particularly large among indeterminately growing organisms, whose body size changes by several orders of magnitude across their lifetime, such as fishes (Wootton, 1998). To this end, the general niche model for describing the structure of food webs originally presented by Williams and Martinez (2000) has been recently extended to include the life-history structure of fishes (Bland et al., 2019). In this extension, fish life-histories are split into discrete life-history stages among which biomass transfers from lower to higher stages through aging. While it is straightforward to calculate how the addition of the life-history structure affects simple network properties, such as the number of nodes and links, the questions related to the broader impacts on the topology and structure of food webs require further study.

In the present work, we delve into the structural and topological properties of life-history structured food webs by utilizing network theory tools combined with dynamical modeling. We utilize the newly extended niche model by Bland et al. (2019) to randomly generated food webs characteristic of northern hemisphere aquatic ecosystems and which include fish life-history structuring. Although network analysis has been utilized many times to study the topology of food webs (both theoretical and empirical) in previous studies (for example, see Rocchi et al., 2017), it has not been used to study the topology of food webs that include life-history structuring which is the aim of this work. The generated food webs will be simulated to allow them to reach biologically meaningful equilibrium with respect to the community structure and species' biomasses (hereafter called as stable food webs).

The dynamic modeling is performed by using allometric trophic network model (ATN model; Brose et al., 2006). Detailed network analysis will then focus on the generated, stable food webs to investigate how the inclusion of the life-history structuring of fishes affects key network properties of the food webs. The network analysis tools as well as the statistical analysis performed for the networks include centrality metrics describing direct or indirect effects of the links of the nodes (degree, clustering coefficient, eigenvalue – based metrics and nestedness (Unipartite Nestedness based on Overlap and Decreasing Fill, UNODF – algorithm)).

2. Materials & methods

In the following sections, we first review tools provided by network theory to analyze the topology of the stable food webs, followed by the investigation of our key study question of how addition of the fish life-history structures alters the structural properties of aquatic food webs.

2.1. Adjacency matrix

The structure of the food web and the properties of the ecosystem are most likely connected via the flow of energy. Thus, the topological position of the species (or nodes) in the network affects the functions of the other nodes (Rocchi et al., 2017; Jordán et al., 2006). In the present study food webs are directed graphs (digraphs) which means that the energy (biomass) flow has a direction, moving from the lower trophic levels to the upper ones. The direction of the energy flow can also occur in reverse direction e.g. in the case of fishes' breeding (Bland et al., 2019). The random food webs in the present study are directed networks and therefore, both incoming and outgoing connections for several metrics are considered.

For the analyses of the food web topology, a central property of the food web is its adjacency matrix which has a size of $N \times N$, N describing the number of species. In adjacency matrix, a generic element $a_{ij} = 1$ if there is a connecting link between nodes i and j (0 otherwise). i.e., species i is feeding on species j (see e.g. Pavlopoulos et al., 2011). The flow of energy within the ecosystem is represented by the links that point from prey to predator. If the links point from predator to prey, they present feeding links as in the present work.

2.2. Node degree

A key property of each node is its degree that gives the number of links it has to its neighboring nodes. Therefore, it is an index that indicates the topographical local importance of the node (Jordán et al., 2006). For directed networks, we must separate incoming and outgoing links. In general, the total degree for the node i is (Newman, 2010):

$$DEG_i = inDEG_i + outDEG_i \tag{1}$$

The out-degree of a node i is therefore a row-wise sum of the elements of the adjacency matrix and the in-degree is the column-wise sum of the elements. In this work, we neglect cannibalism, i.e., here we neglect the links $i \rightarrow i$. However, this is not strictly true: if an age structure is added, the fish species can still eat younger individuals of the same species. In the present work, $inDEG_i$ of a node describes the number of predators of the species i whereas $outDEG_i$ the number of prey species of i.

2.3. Clustering coefficient

Many real-world networks display properties that are typical for networks that are known as small worlds (Watts and Strogatz, 1998). These networks can be recognized by two features: their diameters (i.e., the maximum of the shortest paths between all pair of nodes in the network) increase logarithmically with the number of nodes. In addition, the nodes in the networks tend to form clusters, i.e., two randomly chosen neighbor nodes of a node are more probably also neighbors than in purely random network. This property has been studied by using the concept of clustering coefficient that gives a measure of how node's neighbor nodes are connected: it measures the link density in the neighborhood of the chosen node. Generally, the default approach to quantify the clustering coefficient in terms of the elements of the adjacency matrix is by studying the links between the neighborhood nodes of a chosen node i.

The proportion of connected pairs to the number of all possible pairs can be expressed as.

$$CLU_i = \frac{\sum_{j \neq i} \sum_{h \neq (i,j)} a_{ij} a_{ih} a_{jh}}{D_i(D_i - 1)} = \frac{\left(A^3\right)_{ii}}{D_i(D_i - 1)} \tag{2}$$

where $(A^3)_{ii}$ is the ith element of the main diagonal of the matrix product AAA which, in fact, is the total number of three-step paths from a node i to itself.

As described by Fagiolo (2007), each product of $a_{ij}a_{ih}a_{jh}$is meant to count if there exists a triangle (a "triplet") between nodes i, j and h. Therefore, Eq. (2) describes the relative number of "triplets" formed between the node i and two of its interconnected neighbors with respect to the total possible number of triplets.

However, ecological networks show nonmutual relationships which leads to asymmetric adjacency matrices, and thus the definition for clustering coefficient is also different. Fagiolo (2007) presented a more specific formulation for other network types (weighted undirected/directed networks and binary directed networks). The motivation for the work was the observation that the direction of the links between the nodes has a major effect on quantifying clustering coefficient as different network motifs are formed (Milo et al., 2002). Here we apply the approach of Fagiolo and the clustering coefficient for binary directed network is presented as the net sum of the clustering coefficients

calculated for different triangle patterns (cycle, middleman, in and out) in terms of adjacency matrix as

$$CLU_i = \frac{\left(A + A^T\right)^3_{ii}}{2T_i} \tag{3}$$

where the variable T_i in the denominator is the maximum number of "triangles" that can be formed for different patterns (for example: species i is eaten by species j which also eats species k but which it eaten by species i). The numerator corresponds to the *i*th element of the main diagonal of the matrix product, representing the number of connections that are realized. Above, T_i depends on the total degree of a node *i* but also the total number of false triplets for different triangle patterns is taken into account. The overall clustering coefficient is defined as the average of the clustering coefficients over the network. In general, a perturbation affecting one single species will propagate fast across the whole cluster of species in the food web (Gilarranz et al., 2012). However, several studies disagree whether food webs show "small world" properties (Dunne et al., 2002).

2.4. Closeness and betweenness

In general, indicators of centrality contain information with respect to energy transfer in the network and therefore they offer information to identify the keystone species of the food web (Jordán et al., 2006). These indicators include closeness and betweenness centralities that are both associated with the concept of path length (Freeman, 1977, 1978). Closeness centrality describes the position of the node *i* with respect to other (reachable) nodes in the food web. It is defined as the inverse sum of the distance from a node to all the other nodes, so for node *i* it is (for incoming links)

$$CLO_i = \frac{1}{\sum_s d(i,j)} \tag{4}$$

In Eq. (4), *d(i,j)* describes the distance from node *i* to node *j* (geodesic path) and *s* denotes all nodes $j \neq i$ in the network. The index is calculated for outgoing connections correspondingly. If there is no path between two nodes *i* and *j*, the measure is not defined and therefore, it cannot be used for isolated nodes. However, as we are using Mathwork's Matlab version of the metric, if no nodes are reachable from node *i*, then closeness score will be zero for *i*. Also, a scaling factor is used.

Betweenness centrality was originally introduced in the field of social sciences (Freeman, 1978). The more commonly a node occurs on a randomly chosen shortest path between two arbitrary nodes *j* and *h*, the higher a score node *i* will obtain. Therefore, betweenness centrality quantifies how often each node acts as a connecting node along the shortest path between two other nodes in the digraph. Since there can be several shortest paths between two nodes, betweenness is usually normalized as

$$BET_i = \sum_{j \neq i} \sum_{h \neq i} \frac{n_{jh}(i)}{\mathrm{N}_{jh}} \tag{5}$$

Here, $n_{jh}(i)$ is the total number of shortest paths between *j* and *h* that include *i* and N_{jh} is the total number of shortest paths between *j* and *h*. Therefore, BET describes the probability that a randomly selected geodesic path includes node *i*. The built-in presumption here is that energy flows through geodesic paths (not necessarily the case). As food webs are directed networks, the shortest path from *j* to h might be different from the shortest path from *h* to *j* as the reverse path does not exist very likely. Eq. (5) still takes this into account (Newman, 2010).

2.5. Assortativity

A well-known measure for diversity is assortativity by degree, often referred to as assortativity (Foster et al., 2010). This measure describes the nodes' tendency to link to other nodes with respect to a chosen measure (Newman, 2002, 2003). In general, the assortativity of the network is determined for the degree of the nodes, although other metrics could be applied as well. If the network shows assortative mixing, then the nodes with high degree (or nodes with low degree) have a tendency to connect to other nodes with high degree (or nodes with low degree). The networks of this type are called assortative. On the other hand, the network is disassortative if nodes with high degree are connected to nodes with low degree or vice versa. Ecological importance of assortative food webs is clear as they are resilient to network failure: a removal of a species does not fragment the food web too much. On the other hand, different toxins can spread efficiently in assortative food webs via different processes (bioconcentration, bioaccumulation and biomagnification, see e.g., Lavoie et al., 2013).

The assortativity coefficient is defined as the Pearson correlation coefficient of degree between a pair of mutually linked nodes. By definition, the assortativity coefficient can obtain values between [−1,1]: if the network shows perfect assortative mixing, then a value of 1 is obtained. For the value of 0 the network is non-assortative, whereas the value of −1 shows the network to be fully disassortative. For directed networks, we follow the presentation by Foster et al. (2010). In their work, four different combinations of in-degree and out-degree were presented: $r(in,in)$, $r(in,out)$, $r(out,in)$ and $r(out,out)$. They defined Pearson correlation coefficient as

$$r(\alpha,\beta) = \frac{\sum_s \left[\left(j_i^\alpha - \overline{j^\alpha}\right)\left(k_i^\beta - \overline{k^\beta}\right)\right]}{E\sigma^\alpha\sigma^\beta} \tag{6}$$

where *E* is the total number of links in the network, α and β describe the degree type (either in or out) and *s* denotes all links. The variables j_i^α and k_i^β are the α-degree of the source node and the β-degree of the target node for link *i*, respectively. The terms $\overline{j^\alpha}$ and $\overline{k^\beta}$ are the averages across the nodes for both degree types, and σ^α and σ^β are the standard deviations for both degree types. As an example of the interpretation of the pairwise correlation: if a food web shows disassortative behavior in the *r (out, in)* measure, it means that species with many preys eat more frequently species that do not have many predators.

2.6. Nestedness

In ecological networks, species are typically densely linked to each other, and nested substructures can be formed. These structural patterns are known generally as nestedness and it has been found to emerge and be present both in bipartite and unipartite networks (Mariani et al., 2019). In the review paper by Mariani et al. (2019), nestedness is described as "a hierarchical organization where the set of neighbors of a node is a subset (superset) of the neighbors of lower (larger) degree". In other words, the nodes with fewer links tend to interact with subsets of the neighboring nodes of the nodes with higher degree. An ecological example could be a situation where the diet of the most specialized species is a subset of the diet of a less specialized species. Usually, nestedness is based on degree but as for many metrics, different properties could be used. The fundamental interpretation of nestedness behavior patterns varies widely in the literature, however (Cantor et al., 2017; Montoya et al., 2006).

Different methods to calculate the metric and to quantify the pattern of nestedness has been categorized by Ulrich et al. (2009) and Mariani et al. (2019). These categories include gap-counting metrics, overlap metrics, distance metrics and eigenvalue-based metrics which all have been initially built on bipartite networks. However, new versions for unipartite and directed networks have been developed already and, for example, Almeida-Neto et al. (2008) proposed a new metric for quantifying nestedness. This approach was developed further by Lee et al. (2012) and Cantor et al. (2017), leading for a presentation for directed unipartite networks, as the nested overlap and decreasing fill – approach

(NODF) basically depends on studying the pairwise comparisons of the indices of the adjacency matrix (incidence matrix for bipartite networks). In terms of the elements of the adjacency matrix,

$$NES = \frac{2}{N(N-1)}\sum_{i}\sum_{j,i<j}\frac{\sum_{l\neq i,j}\left(1-\delta_{k_i,k_j}\right)a_{il}a_{jl}}{min\left(k_i,k_j\right)} \tag{7}$$

where $\delta_{k_i,\,k_j}$ is the Kronecker delta (obtaining value of 1 if $k_i = k_j$ and 0 in other case) and either rows or columns are investigated. Therefore, k is either outdegree (rows) or indegree (columns). NES will obtain values close to 1 only when the adjacency matrix is highly nested (neglecting self-interactions). If the network is completely non-nested, then NES will obtain value of 0. Due to directedness of the food webs, the metric will have two different values as nestedness among rows measures the diet overlap among the predators and nestedness among columns describes the level at which the prey are sharing predators. In general, the metric offers a different view on the network with respect to local, single-node analysis. One of the questions related to it in the food webs is to understand how species share their energy resources and recently, UNODF – algorithm was developed to tackle this question quantitatively. Nestedness has been studied especially in mutualistic networks but as Cantor et al. (2017) have shown, it can be found in multiple biological scales although the processes generating it in each system might be different. This acts as a motivation to study nestedness in this work. Aggregation is also of importance here: the strong modules are aggregated, producing high nestedness. These modules can be presented effectively as a single node in the food web (Jordán et al., 2018). The carrying idea is that positional similarity of the species provides information about their functional overlap: the species with similar traits (for example, by size values) can form an aggregate that can be presented as one single functional group (node).

2.7. Eigenvector-based metrics

Several metrics used in this work are based on the properties of eigenvectors of matrices constructed from the adjacency matrix of the network. As for many measures, they have been first introduced in the analysis of social networks and used elsewhere than in the field of biology (Bonacich, 1987). The technique is based on the idea that the more important neighboring nodes a node has, the more important the node itself is. The Eigenvector centrality (ECE) is calculated for each node by solving

$$ECE_i = \frac{1}{\lambda}\sum_{S} ECE_s \tag{8}$$

Above S means all nodes that have a directed link to node i and λ denotes the largest eigenvalue of the adjacency matrix A. Eq. (8) can be therefore written as

$$Ax = \lambda x \tag{9}$$

where x is the Eigenvector centrality of all the nodes.

Both LeaderRank (Lü et al., 2011) and Pagerank (Brin and Page, 1998) centralities are variants of the eigenvector centrality measure that aim at overcoming the problems reported for it (Newman, 2010). They consider only incoming connections and the score for each node is proportional to the sum of the scores of its neighbors. In mathematical terms PageRank, which is used by Google to rank web pages, is defined as

$$PGR_i = \alpha\sum_{j} a_{ij}\frac{PGR_j}{outDEG_j} + \beta \tag{10}$$

where j marks the nodes that point to node i and both α and β are positive constants of which α is called a damping factor and β is a constant extra term (a small amount of "centrality") that is added to each node to avoid problems associated with Eigenvector centrality: the problem arises if a node that does not have incoming links (top predator in our simulated food webs) points to a node that have only this incoming link: such a node will have a score of zero as it is pointed by a node with a score of zero. This can continue as long there are more nodes with only incoming link originated from a node with score of zero. In addition, to avoid division by zero, an outdegree score of 1 is given for the nodes that initially have outdegree of score zero.

Kleinberg (1999) contributed to the discussion by presenting another centrality algorithm called "hubs and authorities", also known as HITS, which was developed originally for finding authorities in a hyperlinked environment on the WWW. It also applies eigenvectors but instead of using inward links only (as PageRank and LeaderRank), it uses node's outward connections: a node has a high "hubs" centrality if it points to other nodes with high "authority" centrality. This opens a possibility for quantifying "hubs" and "authorities": a hub is a node that (most probably) points to a node that contains more information than the hub itself i.e. hubs are the nodes that point to the authorities (they may also refer to the same node). For this reason, HITS is used only for directed networks as there is no distinction in the direction of the interaction in undirected networks. In ecological terms, the nodes that are eaten by many species (are pointed to by many) are authorities and the species that prey on "authority" species are hubs.

The straightforward application of eigenvector-based measures to food webs is not possible as the food webs are reducible: a path (a finite sequence of directed links that form a route between two distinct nodes) between every possible node does not exist. Therefore, additional changes to the adjacency matrix must be performed. We follow here the approach by Allesina and Pascual (2009) and connect the primary producers of the food webs to every other species at the upper trophic levels (consumers and predators). Their motivation was that "species that are central mediate the interaction among those that are more peripheral and therefore should be considered the most important species". This acts as the motivation in this work, as well. Furthermore, the Leaderrank algorithm has a similar built-in property than in Allesina and Pascual's modification: a ground node with a bidirectional link between it and every other node is added and the network becomes strongly connected. In general, eigenvector-based measures can be used to identify keystone species i.e. species that have either a large number of predators (important energy source for many species) or that are eaten by a species with a large number of links in the food web. The difference between degree centrality is that the score of prey species is proportional to the sum of the scores of its predators, not just the number of the predators.

2.8. Leverage

The last measure presented here is known as leverage centrality (LEV). It is similar to the concept of eigenvector centrality as it ranks higher the nodes that have neighbor nodes with higher degree. The more important the node is for its neighboring nodes, the higher leverage centrality it has, i.e., the node is in central position if its immediate neighbors rely on the node in some respect. Contrary to eigenvector centralities, leverage can bring information that cannot be reached by using e.g., degree or betweenness. It also captures the local assortative or disassortative behavior of the network as it is quantified by the degree of the node with respect to its immediate neighbors. By definition, a node with a high degree has a low leverage centrality if all its closest nodes also have a high degree and therefore leverage centrality might be used for identifying group of nodes that have a high degree centrality (acting as generalists in the food webs) with respect to the other local nodes. For a node i with total degree DEG_i it is defined as

$$LEV(i) = \frac{1}{DEG_i}\sum_{j\in S_i}\frac{DEG_i - DEG_j}{DEG_i + DEG_j} \tag{11}$$

where each node j belongs to the neighborhood S_i of the node i. By

definition, a node with negative value of LEV is influenced by its neighborhood nodes, as they have larger number of connections. In addition, a node with positive leverage affects the neighborhood nodes because they tend to have fewer links. In general, leverage could be applied to locate modules i.e., communities inside food webs. These substructures are also known as motifs (Milo et al., 2002; McCann, 2012) and they have been studied to understand the dynamics of higher-order sets of interactions instead of pairwise interactions (consumer-resource).

2.9. The computational tools

The metrics and the software/toolboxes/libraries used in this work are listed in Table 1. The abbreviations are used throughout the work. For each metric presented above and for each food web size and type, we plot the kernel density estimates (KDE) that are calculated by using Mathwork's Matlab function 'ksdensity' (statistics and machine learning toolbox). For each KDE, the bandwidth of the KDE was set by trial-and-error to obtain the plotted curve. From the "pool" of simulated food webs, we chose randomly 1000 webs for each size and type for further investigation.

2.10. The random web generation, filtering and the statistical analysis

This work applies the food web generating Niche model (Williams and Martinez, 2000) expanded to include fish life-history structures in the context of aquatic food webs (Bland et al., 2019). The original niche model itself is based on the cascade model by Cohen et al. (1985): in the cascade model, each species is assigned a random value between the interval [0,1] and it has a specific probability of consuming species that have lesser value. Similarly, in niche model a random niche value is drawn for each species but the prey species of each consumer are constrained to have a lower value (or a range of values which has a center value less than the consumer's niche value) than the consumer itself. On the other hand, the niche range of each consumer can also exceed niche value of themselves, enabling niche overlapping. The species with the smallest niche value has a range of 0 so there is also at least one basal species.

In the study by Bland et al. (2019), the original niche model (Williams and Martinez, 2000) was extended by incorporating life-history structure for fishes. The type of the species was determined by using the trophic level that was estimated by using the average of the shortest paths to basals and the prey-averaged trophic position. The three species with the highest trophic levels were fish species (for simplicity) but the generation of the life-history stages added fish species to lower trophic levels as well. If an age-structure was created, the adjacency matrix was updated and Leslie matrix created to describe the biomass transfer between age classes. The weights for the three youngest life-history stages were generated using von Bertalanffy isometric growth curve and the metabolic rates of different species were estimated using the body weight as a proxy. The differential equation describing the biomass-transfer from the lowest trophic levels to the top of the food web are described in Online Resource 6 (Eqs. A1-A4).

The generation, modeling and the statistical analysis of the stable food webs is presented schematically in Fig. 1. The generation is described in Bland et al. (2019) and the dynamical modeling is performed by using ATN model (Brose et al., 2006). During Niche-web generation, a food web is discarded if certain conditions are not met. These conditions include: a) no isolated species or disconnected groups, b) connectance value high enough, c) all species are connected to basal species and d) no cyclic eating patterns (e.g., A eats B that eats A). For the food webs that fulfill the requirements, other parameters (metabolic rates, trophic levels, etc.) are determined before age-structure determination.

In ATN model, the simulation time span is set to 100 years and the interactions between different species were simulated for 90 days each year. In this work, random food webs have two different sizes (30 and 35 species) and for each size, three different types of webs are generated. Type A food web includes three functional groups (nodes) for fishes, i.e. no age classes within species. Therefore, there are 27 and 32 producers and consumers in total for sizes 30 and 35, correspondingly. Age-structure approach is applied for food web types B and C, and the difference between types B and C is in the adjacency matrix presentation: for type B, the biomass transfer between age groups is included in the adjacency matrix and extra directed links are genererated between consequent age classes whereas for type C, extra directed links are genererated also due to breeding of the fishes in addition to type B links. Age classes are 0, 1, 2 and 3+ years in the work. The mark "+" denotes the accumulation of the biomass in the final age class. For types B and C, as each fish species node is split into three additional nodes, the total

Table 1
The list of the metrics used in the work. The column "Classification" is used to classify the measure: distance refers to the paths between nodes (typically the shortest paths), connection refers to the links between the nodes and eigenvector refers to the eigenvalues of the adjacency matrix. The abbreviation for each measure as well as the used software/library/toolbox are marked. In the fourth column, BCT stands for "Brain connectivity toolbox", developed by Rubinov and Sporns (2010) for Matlab environment. UNODF is a package developed by Cantor et al. (2017).

Classification	Measure	Abbreviation	Software or library
Distance	Betweenness	BET	Matlab
	Closeness	inCLO, outCLO	Matlab
Connection	Clustering coefficient	CLU	BCT (Matlab)
	Assortativity	r	BCT (Matlab)
	Nestedness	NES	UNODF (R)
	Leverage	LEV	iGraph (R)
	Degree	inDEG, outDEG	Matlab
Eigenvector	Hubs and authorities	HUBS, AUTH	Matlab
	Leaderrank	LDR	iGraph
	Pagerank	PGR	Matlab

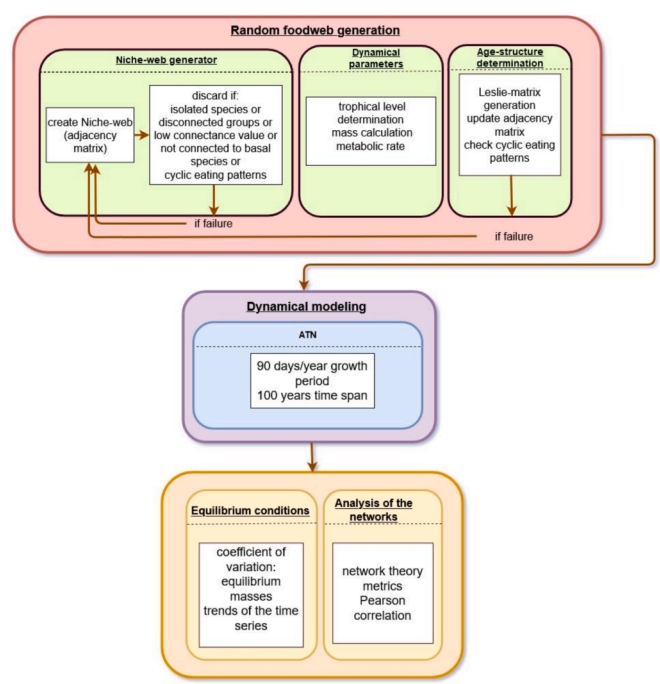

Fig. 1. A schematic presentation of the web generation and the modeling work. The work consists of three separate phases of which the first phase consists of random foodweb generation following Niche-model and age-structure determination. The second phase includes the dynamical modeling by using ATN model and the last phase filtering of the networks and their network theory – based analysis.

number of consumers and producers equals 18 and 23 for food web sizes 30 and 35, correspondingly.

A generated food web is chosen for network analysis if the biomass density of each species has reached its dynamic equilibrium state. This is checked by using the coefficient of variation (CV) which was used in two ways to filter the (suitable) stable food webs from all the generated ones. Firstly, the CV was calculated for each species with respect to their simulated biomass densities for the last 20 years of the simulation. Secondly, the slopes of each biomass density time series were calculated for the last 20 years of the simulation by using a linear fit and the CV of the slopes was calculated. If the mean values for the both CVs were 0.1 or less, the generated random food web was saved for further study. The CVs were used to study the fluctuation (the biomasses should not fluctuate or the fluctuation should be constrained with respect to time at the end of the simulation) or the trends of the biomasses during the simulations. If the food web met these two conditions, it was accepted for further analysis. This trial-and-error procedure was continued for each size and type until the desired number of stable food webs for each type was achieved (1000 in this study). These food webs for each class are picked for a more detailed analysis (Fig. 1). In general, successful food webs consisted of ca. 2–20% of the total number of randomly generated webs after the filtering process.

The centrality measures for each food web are calculated separately, as well as the average of the measures. Table 1 lists the network measures used in the present study and their abbreviations as well as the computational tools used to quantify the metrics. Finally, the Pearson correlation coefficient between different variables is calculated if possible.

2.11. Pearson correlation coefficient matrix

The correlation coefficients between the chosen pairs of measures are calculated for all network types and both sizes, and the results are presented in Fig. 6 (see next section). The upper part of the Fig. 6 provides correlation coefficients for pairs of variables that were calculated for the whole network: assortativity (four measures) and nestedness. The bottom part of the Fig. 6 includes the correlations for measures that were calculated nodewise (inDEG, outDEG, inCLO, outCLO, BET, LEV, CLU) and the correlation coefficients were calculated for the whole simulated data. The eigenvector-based metrics were not presented here to maintain the readability of Fig. 6 but their correlations and the correlations between the measures shown at the bottom part of Fig. 6 were nevertheless studied.

3. Results

Since nodes in directed networks have both incoming and outgoing links, the analysis for assortativity produces four different combinations. These combinations are plotted for each food web type A-C and both sizes in Fig. 2. In each subplot, KDEs are presented for the corresponding data set. Additional statistical data is presented in Online Resource 1, including mean values for the data set.

As observed in Online Resource 1, all combinations have a mean value in negative range, thus showing disassortative behavior patterns. However, r(in, in) has the largest means (closest to zero) and ca. 20–30% of the simulated food webs show assortative behavior. Only one other case showed similar behavior (r(in, out)/30 species food web/TYPE C). For r(in, out) and r(out, in) metrics, the modes of type A curve differ the most when compared to the modes of the other types (Fig. 2) which is the case for mean values as well. Over 70% of data show disassortative behavior, in general.

By using data offered by Online Resource 1, one could estimate the frequentist probability that a randomly picked stable food web produced by the Niche model shows disassortative behavior with respect to all measures: for example, for food web type A / 30 species it is ca. 67%. This estimate varies between 56 and 67% across all types and sizes. If

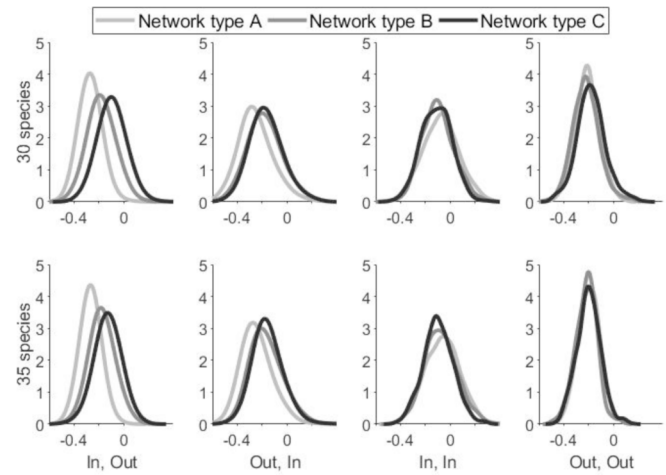

Fig. 2. The assortativity of the simulated data set. A kernel density estimates (KDE) is presented for each network size and type. For further details, see methods section 2.10.

presuming that disassortativity describes the food web properties correctly, the results of Fig. 2 can be interpreted as follows (from the leftmost pair to the rightmost pair): a) species with many predators prefer not to eat generalists (or they feed more likely on specialists), b) generalists prefer not to eat species with many predators, c) species that have many predators do not prefer to eat other species with similar number of predators and d) generalists do not prefer to eat other generalists. As mentioned by Foster et al. (2010), the general "spindle" shape of food webs might explain some of the patterns: there are fewer species at the higher and lower trophic levels of the food webs and on the other hand, the ones at the same or similar trophic level tend to have similar out- and indegrees.

The KDE plots for indegree (inDEG), outdegree (outDEG), incloseness (inCLO) and outcloseness (outCLO) are presented in Fig. 3 and additional statistical data is presented in Online Resource 2. Approximately 20% of the species are eaten only by one predator, whereas ca. 30% of the species prey only on one species. The portion of species that have 10 or more predators is negligible, whereas the portion of species that has a diet of 10 or more other species is between 5 and 16%, type A food webs having the largest values. Type A food webs have a higher mean for both indegree and outdegree and both sizes: the distributions peak at lower values than distributions of B and C, but a type A food webs have more nodes with higher number of incoming or outgoing links. This can be explained at least partially by the connectance (the

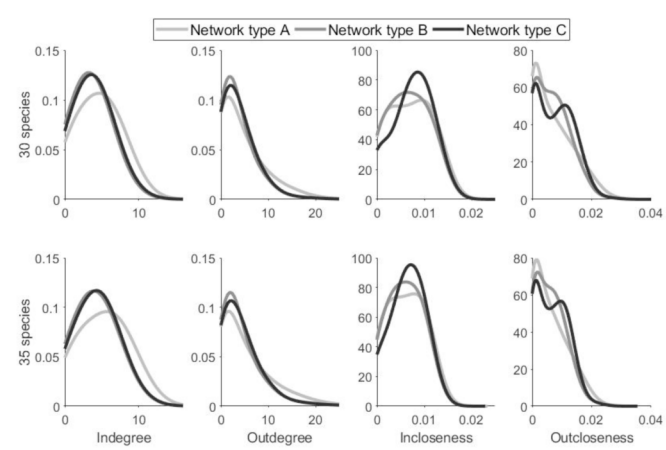

Fig. 3. The in- and outdegree as well as in- and outcloseness of the simulated data set. A kernel density estimates (KDE) is presented for each network size and type. For further details, see methods section 2.10.

number of realized links with respect to all possible links in the food web) that has a lower value after age-structure addition: for type A is has a value of ca. 15% whereas for types B and C, it is ca. 12%. This means that newly added fish species has fewer links compared to the removes species.

The simulated data for clonesess shows almost identical mean values between different stable food webs. KDEs for outCLO shows also slight bimodality, the distributions peaking at 0 (or close to it) as there are many nodes with zero or few outgoing links on the edge of the food webs. The modes of type C for inCLO show also shifting to right. According to Table 1 in Online Resource 2, for a major portion of nodes, incloseness is between 0 and 0.015 and outcloseness between 0 and 0.020.

The means for clustering coefficient (CLU), leverage (LEV), betweenness (BET) and nestedness (NEST) are presented in Online Resource 3 Table 1 and KDEs in Fig. 4. CLU means change between types A-C 10–20%, whereas means of LEV show similar results across all stable food webs. The mean of BET shows an increase of ca. 157–158% from type A to type C (opposite to the mean values of NEST that decrease ca. 25% from type A to type C). The mean values for CLU are close to the empirical values reported by Dunne et al. (2002).

The location of the modes for NEST (rows) KDEs show also similar behavior (30/35 species): type A (0.24/0.24) differs clearly with types B (0.15/0.18) and C (0.18/0.18). Similarly, the modes for NEST (columns) differ between type A (0.30/0.30) and types B (0.20/0.21) and C (0.22/0.20). The CLU for 90–94% of nodes has a score between 0 and 0.4, whereas LEV has both negative (two thirds) and positive (one third) values across all food webs. In fact, the mean of LEV has a value of ca. -0.12, indicating that, on the average nearly half of the nodes (ca. 48%) are connected to nodes with higher (total) degree. A large portion of nodes has a BET score between 0 and 0.1 and the increase in BET values with type B and C food webs indicate that the total number of different shortest paths between two (arbitrary) distinct nodes in types B and C is lower than with type A: node *i* appear more frequently on that path. The eigenvector-based measures reveal very similar shapes for all KDEs for each data set (Fig. 5) (additional statistical data is presented in Table 1 in Online Resource 4). Bimodality can be observed with HUBS and AUTH data but in general, there is no clear difference between data set of different sizes for HUBS whereas the number of nodes obtaining AUTH score of 0.04 (or larger) drops noticeable for larger size as expected. The percentage of nodes obtaining a score smaller than the mean for types A, B and C (30/35 species) showed similar results for PGR between sizes

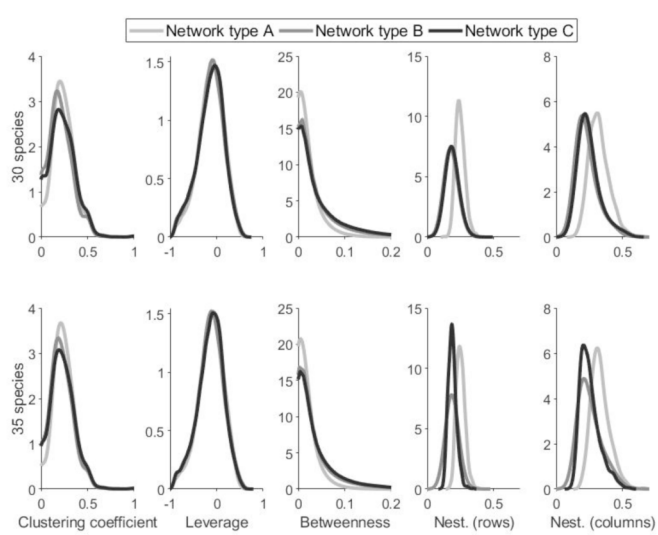

Fig. 4. The clustering coefficient, leverage, betweenness and nestedness of the simulated data set. A kernel density estimates (KDE) is presented for each network size and type. For further details, see methods section 2.10.

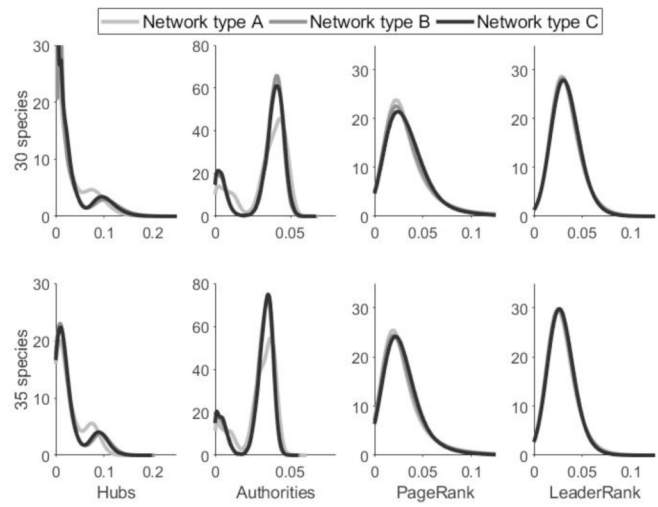

Fig. 5. The hubs, authorities, PageRank and LeaderRank of the simulated data set. A kernel density estimates (KDE) is presented for each network size and type. For further details, see methods section 2.10.

but decreased with type: 65/67, 63/63 and 59/60, and 62/63, 60/60, 56/57 for LDR. The corresponding values for HUBS also showed a slight increase with type: 64/64, 71/71 and 70/71 whereas for AUTH, an opposite trend was observed: 34/36, 27/30, 28/29.

The portion of nodes obtaining a PGR score of 0.01 or larger shows a slight decreasing trend with size which can be seen more clearly with corresponding LDR results. However, there is no observable difference with different types for PGR and LDR. These results can be explained by the definition of the metrics: the sum over the network equals 1 and as network size increases, the average score per node decreases together with the probability of a node to obtain a high score.

The calculated Pearson correlation coefficients between the chosen pair of measures for types A, B and C are presented in Fig. 6. The matrices located at the upper part of Fig. 6 contain correlations between measures that are calculated network-wise whereas the lower part of table includes correlations for measures calculated node-wise. The

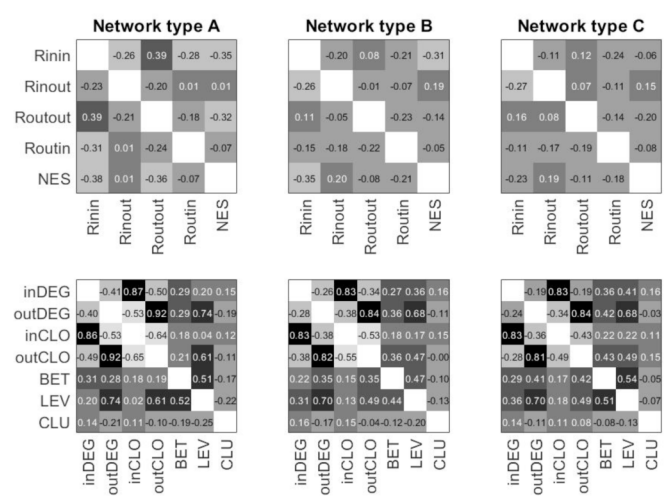

Fig. 6. The Pearson correlation coefficient matrices presented for network types A, B and C (both network sizes. The color scale of the elements is between white (−1) and black (+1). The numerical values of the correlations are also marked inside each cell. In each plot, lower triangular matrix describes a network with 35 species and the upper triangular matrix a network with 30 species, correspondingly. The diagonal elements are left blank as they have no interpretation (for example, the correlation between inDEG metrics of two different network sizes).

correlations for node-wise measures are obtained by using the whole data set (1000 × 30 or 1000 × 35 data points for each metric). In each matrix plot, the cells located at the lower triangular matrix are the correlations calculated for the food web of size 35 species, whereas the cells located at the upper triangular matrix are the corresponding values for the network of size 30 species.

A weak positive correlation was found only between r(out, out) – r (in, in) which was not found after age-structure activation in food web types B and C (Fig. 6 upper row). A weak negative correlation was found between several measures (light color) for all types (not necessarily for the same pairs), but on the average, the correlations decrease from type A to C.

The node-wise correlations coefficients show noticeable higher absolute values (Fig. 6 lower row) that stay as moderate or strong positive correlations across all types. A strong positive correlation was found for several pairs of measures: inDEG–inCLO, outDEG-outCLO and outDEG-LEV. A moderate positive (or near) correlation was found for pairs: outCLO-LEV and BET-LEV. A moderate or a weak negative correlation for all types and sizes was found for pairs: outDEG-inCLO and inCLO-outCLO. In general, several pairs of measures showed very similar behavior patterns irrespective of the food web type or size.

The correlations between Eigenvector-based metrics and nodewise metrics (inDEG, outDEG, inCLO, outCLO, BET, LEV, CLU) were not presented in Fig. 6 but there were no clear differences across all types and sizes. PGR was in a moderate or strong positive correlation between inDEG and inCLO, otherwise the correlation remained weak or had a (weak) negative correlation for outDEG and outCLO. LDR showed identical correlation compared to PGR. Otherwise, no correlation with the other metrics was observed. In addition to HUBS, AUTH showed weak or moderate correlation between several metrics (outDEG, outCLO, BET, LEV).

The correlation between different Eigenvector-based measured showed a strong negative correlation between HUBS and AUTH across all sizes and types, as expected. A weak positive (negative) correlation was observed between HUBS (AUTH) and PGR and LDR. The correlation was studied in detail by plotting the data points (Fig. 1–3 in Online Resource 5) which reveals non-linear dependency between HUBS and the other metrics, AUTH and the other metrics, PGR-HUBS and PGR-AUTH, LDR-HUBS, LDR-AUTH, and a strong linear correlation between LDR and PGR. The behavior did not depend on food web type or size. Except for LDR-PGR pair, a linear correlation could therefore most probably fail to capture the essential relationship between these metrics if the whole data is applied: for example, a correlation between PGR and HUBS would show negative dependency with HUBS $<$ ca. 0.06 but positive dependency after the limit (Fig. 1-3 in Online Resource 5) although there is a weak positive correlation when studied across the whole data. The limit values are equal to local minima for KDEs of HUBS and AUTH, indicating that HITS divides the nodes of the food webs in two separate groups. In general, HUBS showed a strong negative correlation with AUTH and vice versa if the correlation was studied across whole data which is expected as the metrics are exclusive properties.

4. Discussion

Results suggests that few pairs of measures have a strong positive correlation between them (and only for a specific node-wise metrics). Most of the correlation coefficients do not change with the food web size or type, i.e. age-structure does not affect the results. The Pagerank (as well as Leaderrank) metrics showed a moderate or strong positive correlation between indegree and incloseness. The correlation between eigenvector-based metrics revealed non-linear dependencies that were not analyzed by using linear correlation, the LeaderRank and PageRank being the exceptions (a strong positive correlation). In addition, none of the pairs showed strong negative correlations except the correlation between HUBS and AUTH which is due to their exclusive definitions. In general, weak correlations between different pairs indicate that the chosen metrics capture different aspects of the stable food webs. The number of sampled food webs is 1000 and consequently, the observed correlations might be at least partly due to natural statistical variation. However, the results were checked for a group of 300 random food webs and the differences were marginal. In addition, Cantor et al. (2017) did not find correlation between different centrality metrics and nestedness, whereas in the study by Capocefalo et al. (2018) both distance-related metrics and average degree showed significant correlations between nestedness in empirical networks.

According to the previous studies (Foster et al., 2010 and references therein), food webs show disassortative patterns for r(out, in) and r(in, out) measures, similarly to our simulations. They also noted that the behavior patterns changed to assortative for other pairs (r(out, out) and r(in, in)) in empirical food webs which holds true only partly in this study: ca 20–30% of the stable food webs showed assortativity for r(in, in). According to Newman (2003), the correlation was found to be negative (disassortative) for many biological network types (neural networks, marine food webs and freshwater food webs) and according to the author, in a case of different node types a random mixing will pair unlike nodes and the correlation should be closer to perfectly disassortative network ($r = -1$). The random networks in the present work were generated by using Niche model which could explain the differences at least partly.

In nature, disassortative properties of the food webs can be beneficial against network failures and there is a connection between nestedness, assortativity and clustering coefficient: exceedingly disassortative empirical networks tend to show nested behavior and vice versa (Jonhson et al., 2013). They also concluded that nested food webs increase the number of coexisting species and make the network more resistant to fragmentation i.e. random extinctions. The research by Cantor et al. (2017) showed that the estimates for nestedness produced by UNODF algorithm for a set of diverse empirical biological networks has a positive linear relationship with connectance (proportion of realized links in relation to possible links) of the network and nestedness does not increase with the network size. Our food webs have connectance of ca. 0.15 and nestedness of between 0.15 and 0.3: when comparing these values to the values in the work by Cantor, it can be seen that the results here parallel well with the empirical data presented and the values obtained from the linear regression fit in their work.

Another tested metrics (HITS) gives two separate ratings for a node (hub and authority scores). The plotted data in Online Resource 5 showed also that a single node could not have a high score for both measures simultaneously (even though some nodes could reach relative high scores for both metrics, acting as a generalist and a species eaten by many) We did not we investigate the multinode centrality i.e. the effect of sets of nodes to the topology (Capocefalo et al., 2018) nor the concept of keystone species. Quantitative approach for the set-subset relationships would offer another and very interesting view on the simulations performed here as well.

In conclusion, the extended model by Bland et al. (2019) produces food webs that are not largely affected by the inclusion of life-history of the fishes with respect to the chosen network theory measures studied in the present work. This gives at least partly an indication that the measures describe the properties of the stable food webs. On the average, our network-wise topological properties indicated that the stable random food webs generated are both dissassortative and nested. In addition, nestedness decreased as new life-history stages were introduced. The topological (distance- and connection-based) node-wise properties showed two-fold results: a few metrics showed changes in results as new life-history stages were introduced (in-and outdegree, in- and out-betweenness), whereas no noticeable differences were observed for clustering coefficient, leverage and closeness which was also the case for the eigenvector-based measures. Interestingly, degree-measures did not correlate with betweenness although they showed changes after life-stage addition. A network-wise correlation study showed only weak negative or positive correlation which indicates that the chosen

measures capture different properties of the stable food webs. Instead, the distance- and connection-based measures that correlate strongly probably monitor similar changes in topology. This information could be used to find measures that capture versatile properties for the similar studies in the future. The sizes of the food webs can also play a role in the effect of topology to the dynamics and larger size could improve the resolution of the results. Furthermore, a recent study has shown a very interesting connection between the mobility and the species importance at different network scale (Olmo Gilabert et al., 2019). A variety of network metrics was modelled as a function of different traits and it was found that the size and mobility are the best predictors for species importance at local, meso- and global scale.

We did not consider weighted links as we lack precise empirical data on the weights, especially concerning life-history pathways, but it is recognized that the results can differ if weighted links are applied. Similarly, added life-history structures could be used for other species and traits as well but their inclusion for fishes is particularly important as fish body sizes and diets change radically with aging, changing their ecological positioning. Ontogenic diet shifts as well as several evolutionary applications, such as fishing-induced evolution, typically warrant for the inclusion of fish life-histories into the food web. Finally, the results of the present work do not rule out the possibility that the dynamics of the generated food webs might still differ (Bland et al., 2019), for example, with respect to their oscillatory properties before and after the life-history inclusion. This, however, is beyond the scope of the present work.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2021.e00213.

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