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## Summary

Present changing environment calls for improvements of our knowledge of natural systems structure and function through a holistic view. Such a whole system perspective might help to better understand responses of ecosystems to perturbations. Models of ecological networks have proven to be very useful tools for understanding structure, and dynamics of ecosystems (Petchey et al. 1999, 2008, Carey et al. 2013). In this thesis I am presenting two modelling approaches to deal with the whole system approach: topological food web analysis (chapter 2) and loop analysis (chapter 3 and 4). Both these studies privilege the qualitative analysis over the quantitative one, to overcome the lack of data, but also to show what insights can be obtained by qualitative analysis.

In chapter 2 the topology of the food web is considered to study the functioning of the Baja California Sur ecosystem. I identified through centrality indices key node species and analyzed system resilience to the removal of the most vulnerable fish species based on a previous classification of high, medium and low risk species. Effects are evaluated by using global indices. Results highlight the structural resilience of the web to removals, but also that removals of highly vulnerable species result in significant changes in system attributes compared to random removal.

In chapter 3 the evolution of the Black Sea ecosystem during the period 1960-1990 is evaluated through qualitative models (i.e. loop analysis). These models reconstruct the linkage structure of the whole community. I validated the outcomes of loop analysis with statistical investigation of biomass time series. This helped to understand how the structure of the interactions can explain variations in the biomass level of the variables and what hypotheses about drivers and mechanisms responsible for the changes could be shaped accordingly.

In chapter 4 a database of real and random food webs was taken into account. I studied these food webs through loop analysis to unveil how positive input on basal and top species affects top and basal species, respectively. The aim was to identify possible differences in the propagation of indirect impacts in response to positive perturbations that occur at the extreme of the food webs (i.e. either targeting basal or top species). I compared real systems (i.e. marine, terrestrial and freshwater food webs) with random networks. I found an overrepresentation of positive predictions (i.e. the species are predicted to increase their abundance) and an underrepresentation of negative predictions for the top species when basal species are perturbed. This occurs in both real and random systems. Considering the latter the same trend (i.e. overrepresentation of positives signs and underrepresentation of negative ones) was found when predicting the responses of basal species following perturbations on top species. I showed that these findings are due to the topological structure of the food webs (e.g. number and length of trophic paths) rather than depending on the patterning of interactions strengths. Thus, the responses of top species following

perturbations on basal species are predictable, while the same trend does not hold when studying the responses of basal species after perturbations targeted on top species. These results are particularly relevant and interesting considering the importance of basal and top species as target for many anthropogenic impacts (e.g. overfishing, eutrophication).

This thesis contributes to unfold a path toward: 1) the understanding of the effect of disturbance on ecological communities and ecosystems; 2) an improved comprehension of the interplay between top-down and bottom-up control; 3) the capability to deal with uncertainty in assessing the response of communities and ecosystems in the face of disturbance. I used relatively simple methodologies (i.e. topological food web and loop analysis) that focus on the qualitative arrangement of trophic interactions. This may seem a limitation because anxiety for interaction strength quantification often precludes the exploration of cases in which data are lacking. However, I show there are cases for which even the study of qualitative data can be of crucial importance in terms of management, especially in the framework of ecosystem-based management (EBM).

## General introduction

Human activities alter biological communities by influencing species diversity, abundance and genetic composition. It has been shown that in most cases anthropogenic pressures are targeted either at the bottom or at the top of the food webs (Wollrab et al. 2012). Land-based activities (e.g. fertilization) spread pollutants and nutrients into soils, streams, lakes, coastal waters and oceans. Such contaminations have pervasive consequences on primary producers (Asner et al. 1997, Behrenfeld et al. 2006, Haberl et al. 2007) and can create conditions for algal blooms (i.e. eutrophication; see Abell et al. 2012). Apex predators, on the other hand, are strongly affected by fishing, hunting, bioaccumulation of toxicants and habitat loss (Connell 1990, Laliberte and Ripple 2004, Schipper et al. 2008, Lotze and Worm 2009). Direct perturbations can propagate and have community-wide consequences. These impacts affect the abundance of species that are not directly influenced by human activities and can erode the robustness of food webs (i.e. their ability to persist in the future and maintain their functions; see Gilarranz et al. 2016). For example, during the late 20th century the loss of favorable habitats and the reduction of food availability due agricultural intensification led to the collapse of European farmland bird populations (Fuller et al. 1995, Donald et al. 2001). Landscape fragmentation in coastal southern California cause the local extinction of coyotes, thus determining the absence of the apex predator from some patches (Crooks and Soulé 1999); this releases the pressure on mesopredators and triggers a cascade effect that ends with the disappearance of avian prey from landscape fragments. Also, overfishing of apex consumers has produced deep consequences in the structure and functioning of marine systems. Sandin et al. 2008 showed the degradation due to fishing pressure from a reef dominated by top predators and corals to a reef dominated by small planktivorous fishes and algae (i.e. densities reduction of longer-lived, larger-bodied individuals). Overfishing was one of the factors that caused system-wide trophic cascades that led to regime shifts in the Black Sea (Daskalov et al. 2007, Oguz et al. 2007): by altering predation and herbivory, the overfishing of pelagic top predators in the 1970s and of planktivorous fish in the 1990s caused changes in the abundance of the zooplankton, jellyfish, and phytoplankton, as well as in surface oxygen and phosphate concentrations.

Investigating and understanding ecosystem responses to perturbations is crucial. The indirect food web propagation of impacts targeting single species was investigated by both experimental (Pace et al. 1999, Duffy et al. 2015) and modeling (Ebenman et al. 2004) approaches. Studying natural

ecosystems through a holistic view (i.e. by taking into account the whole food web topology or considering biomass flow in ecological networks) has increased the knowledge of their relationships and properties (e.g. key/central species). The generation of plausible explanations and testable hypotheses pertaining to community structure and dynamics (Montoya et al. 2006, Thompson et al. 2012, Borrett et al. 2014), and the formulation of predictions regarding their responses to natural and anthropogenic perturbations (Yodzis 2001, Clark et al. 2001) are key points of this thesis. The importance of ecological knowledge for management policies has increased markedly with the advent of approaches like ecosystem-based management (EBM; see Field and Francis 2006). Quantitative and qualitative ecosystem models are essential tools for understanding how human activities and environmental change influence ecosystems. They can be used to forecast how entire ecosystems respond to alternative management actions or changes in climatic conditions. The best hope for greater sustainability of ecosystems is to reduce uncertainty through a comprehensive ecosystem view (Borsford et al. 1997). In this thesis, models based on species interactions were studied through two different methodologies (topological food web and loop analysis). This helped to describe ecosystem-wide effects of anthropogenic perturbations such as overfishing (chapters 2-4), eutrophication (chapters 2-4) and introduction of alien species (chapter 3).

## Ecological disturbance:

### the effect of species removal on food webs, a topological study

#### 2.1 Key species and impact of fishery through food web analysis

<sup>1</sup>Marine ecosystems are undergoing major changes through overexploitation, habitat loss, pollution, species introduction, ocean acidification and warming (Halpern et al. 2008a, Hoegh-Guldberg and Bruno 2010, Burrows et al. 2011, Doney et al. 2012). Fisheries management, once focused primarily on large-scale industrial fisheries, is now addressing also on Small-Scale Fisheries (SSFs) and their dependent human communities (Allison et al. 2001, Jacquet et al. 2008, Chuenpagdee 2011, Kolding et al. 2014). SSFs are ubiquitous and of great importance (Finkbeiner 2015). Small- and large-scale fisheries each contributes to approximately half of global fisheries capture, but SSFs employ over 96% of the world's fishers (Chuenpagdee et al. 2006).

Given the complexity of the issues and failure of traditional fisheries management efforts (Botsford et al. 1997, Hilborn et al. 2007), new management strategies have been called for. In particular, there has been a shift in focus from single species or sectors to the whole ecosystem as the unit of management. This view has produced a framework called "Ecosystem-Based Management" (EBM, Long et al. 2015). EBM is increasingly taking hold as demonstrated by the ever greater effort devoted to its application worldwide (Pew 2003, USCOP 2004, Lester et al. 2010, Link 2010). EBM is a cross-sectorial, holistic approach (Link 2002a, Ruckelshaus et al. 2008, Halpern et al. 2008b, Francis et al. 2011, Link et al. 2012) that is expected to prevent the overexploitation of resources, support ecosystem restoration, maintain ecosystem health, and therefore promote human well-being (Long et al. 2015). One of the fifteen principles that constitute the pillars of EBM posits that ecosystem connections are central to understand system behavior and to design effective management strategies (Long et al. 2015). Connections functionally link different parts of a system and allow impacts to spread from one part to the others. Although the attention focuses on connections that link variables of sub-domains of the socio-ecological systems, i.e. how changes in

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<sup>1</sup> Published chapter: Rocchi, M., Scotti, M., Micheli, F., and Bodini, A. (2017). Key species and impact of fishery through food web analysis: A case study from Baja California Sur, Mexico. *Journal of Marine Systems*, 165, 92-102.

societal priorities or regulative framework may affect the dynamics of species (Long et al. 2015), connections can be central also within the ecological domain of this enlarged ecosystem. Understanding linkages between species, in particular, can improve our knowledge about how the ecological community may respond to environmental or anthropogenic stress and can thus provide valuable indications of possible impacts on ecosystems of management regulation and policies (Carey et al. 2013).

The interest in structural features of food webs is justified on the grounds of the potential relationship that links food web structure and ecosystem functions (Petchey et al. 1999, 2008). In particular, centrality indices can provide information about the transmission of control (top-down vs. bottom-up) and the flow of energy in ecosystems (Jordán et al. 2006, 2009), and overall structural metrics can give indications about the integrity of the food web upon which ecosystem functions depend (Miehls et al. 2009, Bondavalli and Bodini 2014).

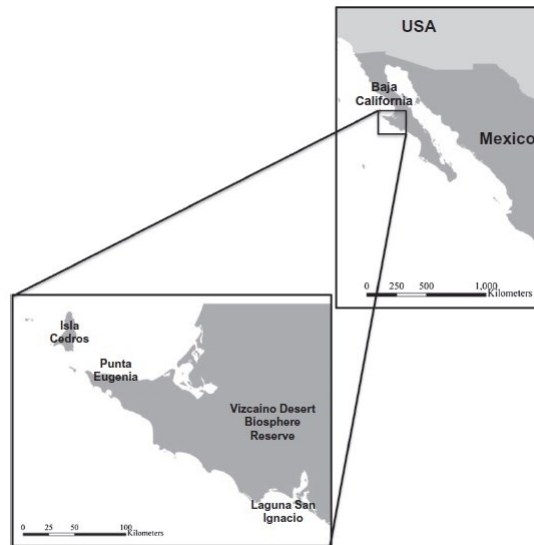
In this study I reconstructed the linkage structure of the coastal marine ecosystem of the North Pacific region of Baja California Sur, Mexico, which is exploited by local SSFs. I produced a qualitative food web that I then used to simulate the disappearance of vulnerable species (Micheli et al. 2014) due to excessive fishing pressure. I studied this food web to reveal: (1) which species are the most central (i.e. functionally important; Jordán and Sheuring 2002) in the community; (2) whether these central species are also the most vulnerable considering their productivity and the cumulative effects of multiple fisheries (Micheli et al. 2014); (3) if centrality analysis can contribute to integrate the list of species at risk introduced by Micheli et al. (2014); (4) how species centrality changes after the removal of one or more species; (5) how the structural features of the community as a whole change when central species disappear or when species are instead removed at random. In addition I investigated which species loss could induce the largest impacts in terms of secondary extinctions through the method of the dominator tree (Allesina and Bodini 2004). Results of these analyses have implications for our understanding of food web structure, fishing impacts, and ecosystem-based fisheries management.

## **2.2 Methods**

### **2.2.1 Study Area**

I performed my investigation on the coastal marine ecosystem located along the coast of the Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico (Figure 2.1). This ecosystem supports local fishing communities that are organized in fishing cooperatives (McCay et al. 2014). The North Pacific region can be defined as temperate to subtropical, with sea surface temperatures ranging from 12° to 27° C throughout the year. This region is characterized by a mosaic of rocky reef and sandy subtidal ecosystems that encompass the southern edge of the range of giant kelp (*Macrocystis pyrifera*) where a zone of persistent upwelling maintains high biological productivity (Martone 2009).





**Figure 2.1** – Map of the study area located along the coast of the Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico (reproduced from Micheli et al. 2014, with permission).

The fishing cooperatives of the central Baja California region belong to FEDECOOP (Federacion Regional de Sociedades Cooperativas de la Industria Pesquera de Baja California), which acts as a co-management agency with the national and regional fisheries agencies to monitor resources and develop management plans. The fishing cooperatives of the North Pacific date back to the late 1930s, as a manifestation of the Mexican cooperative movement that was mainstreamed into national fisheries development policies (Ponce-Diaz et al. 2009, McCay et al. 2014). SSFs represent 99% of registered fishing vessels on the Baja California and Baja California Sur peninsula (INEGI 2008<sup>2</sup>). Cooperatives have renewable 20-year concessions for different species, including red spiny lobster (*Panulirus spp.*), abalone (*Haliotis fulgens* and *H. corrugata*), wavy turban snail (*Megastrea undosa*), sea cucumber (*Parastichopus parvimensis*), red sea urchin (*Mesocentrotus franciscanus*), and the red alga *Gelidium robustum*. Fishers also catch many species of finfish but, in contrast with benthic invertebrates and algae, do not hold territorial rights for them (i.e. fishing cooperatives do not have exclusive access to finfish within a geographically defined area; see Afflerbach et al. 2014). Within the food web, species are subjected to different fishing pressure and risks, applied through a variety of fishing methods (Micheli et al. 2014). Therefore, fisheries have different kinds of concessions (i.e. fishing permits), and harvest species that vary greatly in their commercial value. This permits structure imposes disincentives for switching to different fishing targets when one is depleted, in some cases leading to further depletion.

<sup>2</sup> <http://www.inegi.org.mx/> [last accessed on February 9, 2016].

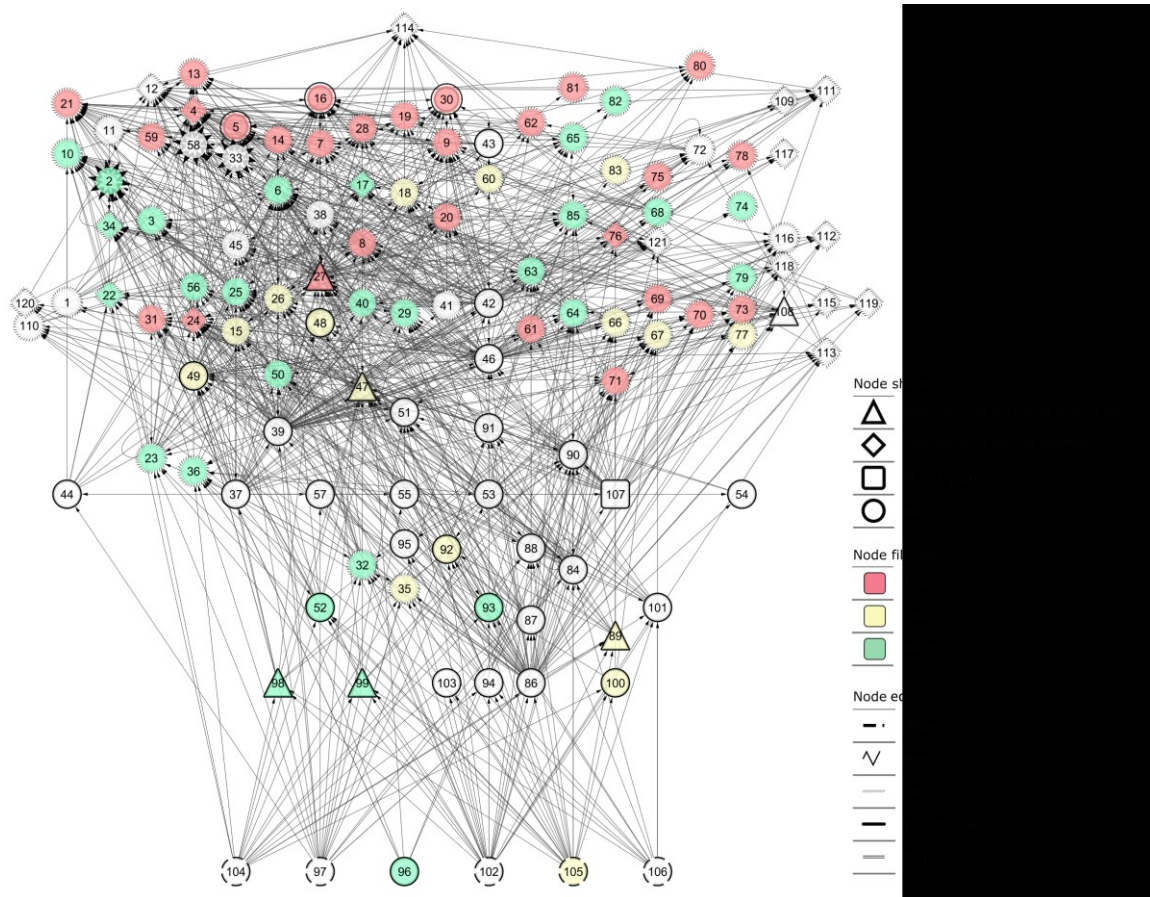
### 2.2.2 Food web construction and trophic structure

I constructed an adjacency matrix that reports presence/absence of trophic interactions (i.e. who eats whom) among species or species groups within the food web. Rows represent prey species and columns represent predator species. Each coefficient  $a_{ij}$  is 1 if the row species  $i$  is a prey of the column species  $j$  and 0 elsewhere (May 1973, Hannon 1973, Šiljak 1975, Cohen 1978, Dunne et al. 2002a, Abarca-Arenas et al. 2007, Gaichas and Francis 2008, Navia et al. 2010, 2012). I constructed an unweighted food web (i.e. all trophic interactions are set to 1) because no information about link strength (i.e. amount of biomass flowing from prey to predators) was available. Community composition and trophic resolution level were based on active collaboration with experts. Starting from species considered in Micheli et al. (2014), I added appropriate nodes for a better representation of a coastal marine food web. All subtidal pelagic and benthic coastal environments and associated species (from rocky reefs, kelp forests, seagrass beds, and sandy bottoms) are well represented. Intertidal habitats, where target species do not occur, and estuaries, which in the study area are not directly adjacent to the fishing grounds, are not included, though some species occasionally use these habitats for foraging or as juveniles. Data on trophic interactions were obtained from the Kelpforest Database (Beas-Luna et al. 2014), literature and general online sources such as FishBase (Froese and Pauly 2015), Encyclopedia of Life<sup>3</sup>, Discover Life<sup>4</sup> and Animal Diversity Web<sup>5</sup> (see Table 2.5 in Appendix 2.5.1 for a detailed description of diet sources for each node). When dietary information was unavailable for some species in the study area, data from similar ecosystems were used to complete the food web. Thus, the food web is mainly literature based due to the lack of local data (e.g. gut content or stable isotopes analysis) that characterized the study area. The prey set of each node, identified from the literature (i.e. diet composition), was checked by expert marine biologists working in Baja California (Table 2.5). The adjacency matrix that summarizes all trophic interactions of the Baja California Sur food web can be retrieved from the following link: <http://www.sciencedirect.com/science/article/pii/S0924796316303190> [Last accessed: January 30, 2017]. The resulting food web of the North Pacific region of Baja California Sur is visualized in Figure 2.2. The food web is composed of 121 nodes ( $S = 121$ ) and 979 trophic interactions ( $I = 979$ ). In the graph, each node stands for a species or a trophospecies (i.e. a group of species with equivalent feeding habits and preyed upon by the same set of predators), while directed edges indicate the presence of trophic interactions. Nodes represent 100 species and 21 trophospecies: 3 birds, 3 marine mammals, 75 fish, 34 invertebrates, 4 algae, zooplankton and phytoplankton.

<sup>3</sup> <http://www.eol.org> [last accessed on February 9, 2016].

<sup>4</sup> <http://www.discoverlife.org/> [last accessed on February 9, 2016].

<sup>5</sup> <http://animaldiversity.org/> [last accessed on February 9, 2016].



**Figure 2.2** – Food web diagram representing trophic interactions in the area located along the coast of the Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico. Each node represents either a species or a trophospecies (see Table 2.5 in Appendix 2.5.1 for a detailed description of each node). The edges connecting the nodes stand for trophic interactions (each arrowhead edge leaves the prey and enters the predator). Species’ vertical position reflects the trophic level. The color of the nodes indicates different levels of vulnerability (V), the type of the edge specifies taxonomic groups, and the shape displays fishing permits. The food web diagram was visualized with Cytoscape (Shannon et al. 2003).

I used network analysis to investigate the food web structure of the Baja California Sur marine system. I identified key (i.e. most central) species through centrality indices and explored the resilience of the system by evaluating the changes in both global structural indices and species’ centrality indices due to the local extinction of vulnerable species (as defined by Micheli et al. 2014).

## 2.2.3 Topological analysis

### 2.2.3.1 Global structural indices

There are many structural indices that describe global features of food webs. These global structural indices can be related to various aspects of food web functioning such as energy delivery (Allesina and Bodini 2004), stability (Rooney et al. 2006), and robustness (Dunne et al. 2002b). Table 2.1 summarizes the indices I computed to assess the consequences of species' removals on the whole food web structure. I selected the most commonly used indices for which ecological interpretation is associated to changes in their values (see the last column in Table 2.1).

Indices	Explanation	Interpretation
<b>Assortativity coefficient (AC)</b>	Correlation between the degree (i.e. the number of connections) of two neighboring nodes (Newman 2002, Sokhn et al. 2013).	$AC < 0$ , the network is disassortative (i.e. high degree nodes are connected to low degree nodes). $AC > 0$ , the network is assortative (i.e. high degree nodes are connected to high degree nodes). $AC = 0$ , the connections between nodes do not depend by their degree.
<b>Clustering coefficient (CC)</b>	Measured as the ratio between the number of edges involving the neighbors of a node $i$ , and the maximum number of edges that could exist. The clustering coefficient of the food web is the average of the clustering coefficients of all nodes. If the food web is fully connected, the clustering coefficient is then equal to 1.	An increase in the values of this index indicates that species tend to compete with other species in more clustered groups (Sokhn et al. 2013).
<b>Modularity (MD)</b>	Qualitative measure for food web clustering. MD ranges from 0 to 1: if MD approaches 1, this indicates strong modular structure; if the number of intra-modular edges is no more than what could be expected from random networks, then $MD = 0$ (Sokhn et al. 2013).	When this index increases the food web becomes more fragmented and therefore more vulnerable.
<b>Betweenness centrality equal to 0 (BC0)</b>	Betweenness centrality of a node $i$ is the fraction of shortest paths in a food web that passes through $i$ . The global index derived from this centrality quantifies the number of nodes with betweenness centrality equal to zero.	If the number of species with a betweenness centrality equal to 0 increases, then more species compete with only one particular group of species and hence belong to a unique subnetwork; instead, if there is a decrease this indicates that less species compete (Sokhn et al. 2013).
<b>Directed connectance (C)</b>	Computed as the ratio between existing and all possible trophic interactions (i.e. $C = I/S^2$ , Martinez 1992).	Lower directed connectance value can reveal a decrease in food web robustness (Dunne et al. 2002b).
<b>Linkage density (LD)</b>	The average number of feeding links per species.	It is more sensitive to data aggregation than C (Dunne et al. 2006). Lower link density values can reveal a decrease in food web robustness (Dunne et al. 2002b).
<b>Average path length (APL)</b>	The average distance between any two nodes in the undirected network.	A decrease in this index can be an indicator of faster spread of disturbance in the whole food web.
<b>Diameter (DM)</b>	The shortest undirected path (number of trophic interactions) between the two most distant nodes in the network.	This can be an indicator of how fast disturbance can spread in the whole food web.

**Table 2.1** – Global structural indices. A brief description for each index is provided (Explanation) together with the meaning as a function of the values computed (Interpretation).

### 2.2.3.2 Trophic levels and local centrality indices

To characterize the food web structure I calculated species' trophic level with the cheddar library in the R environment (Hudson et al. 2013). There are different methods for measuring trophic levels of species and trophospecies in food webs (e.g. see Williams and Martinez 2004, Scotti et al. 2006). I used the prey-averaged trophic level that returns for each predator 1 plus the mean trophic level of its prey, using the matrix inversion method of Levine (1980).

Besides the trophic level, I quantified the structural roles of species by computing centrality indices. Such indices were developed in social network analysis and can be used as an approximation of species' functional importance (e.g. see Jordán and Sheuring 2002, Jordán et al. 2006, Abarca-Arenas et al. 2007, Jordán 2009, Navia et al. 2010). I considered some of the most commonly applied indices: degree centrality, betweenness centrality, and closeness centrality. Table 2.2 provides a synthetic description of the indices.

Indices	Explanation	Interpretation
<b>In-degree (<math>D_{in,i}</math>)</b>	The total number of a node's prey.	High value for $D_{in,i}$ are characteristic of species that show generalist trophic habits.
<b>Out-degree (<math>D_{out,i}</math>)</b>	The total number of a node's predators.	Species that exhibit a high value for $D_{out,i}$ are vulnerable species (i.e. species undergoing high predatory pressure).
<b>Degree (<math>D_i</math>)</b>	The degree of node $i$ ( $D_i$ ) is obtained summing together the total number of all its prey (in-degree, $D_{in,i}$ ) and its predators (out-degree, $D_{out,i}$ ).	Species that show a high value for $D_i$ are hubs (i.e. they locally interact with many other species).
<b>Betweenness centrality (<math>BC_i</math>)</b>	Counts how many times a target node $i$ lies on the shortest paths connecting every other pair of species $j$ and $k$ in the food web. It considers shortest paths with a strict bottom-up perspective (i.e. tracing biomass flow from primary producers to consumers).	It measures how central a given node is in terms of being included in many shortest paths in the network, thus describing how crucial (i.e. high index values) a species is in mediating the diffusion of indirect effects throughout the whole food web in a bottom-up perspective.
<b>Undirected betweenness centrality (und<math>BC_i</math>)</b>	The count is the same as for $BC_i$ but the undirected version accounts for the spread of both bottom-up and top-down effects (i.e. without being constrained by the direction of biomass flow).	The interpretation is the same for $BC_i$ but considering a top-down and bottom-up perspective.
<b>Undirected closeness centrality (<math>CL_i</math>)</b>	Measures the length of the shortest paths from a given species $i$ to all other species in the food web.	It measures how close a node is to the others and quantifies how rapidly an effect that generates from species $i$ can spread in the food web both from top-down and bottom-up perspective (i.e. it is not constrained by biomass flow direction in the food web and does not implement a strict bottom-up perspective).

**Table 2.2** – Centrality indices. Degree centralities are divided into: in-degree ( $D_{in,i}$ ), out-degree ( $D_{out,i}$ ) and degree ( $D_i$ ). Betweenness centralities are separated into the directed ( $BC_i$ ) and undirected (und $BC_i$ ) version, while for the closeness centrality I considered the undirected version ( $CL_i$ ).

Species that show a high value for  $D_i$  (degree centrality; Table 2.2) are hubs (i.e. they locally interact with many other species). When  $BC_i$  (betweenness centrality) is high the node  $i$  plays an important role in mediating indirect effects. High  $CL_i$  (closeness centrality) values identify nodes that, when disturbed (e.g. decline of their population size), spread the impact to other food web nodes more rapidly.

I used centralities indices to integrate the list of species "at risk" elaborated by Micheli et al. (2014). I suggested centralities indices as an approximation of species' importance and considered clustering patterns (i.e. sub-group of species with similar values). The hypothesis was that if high risk species are grouped all (or most) together, the other species in the same cluster (but not classified as high risk) could be thought as of potentially at risk. Centrality indices were computed with Cytoscape (Shannon et al. 2003) and using the igraph library in the R environment (Csárdi and Nepusz 2006). See the Appendix 2.5.1 for the algorithms of centrality indices.

#### **2.2.4 Removal analysis**

Removal analysis was conducted to mimic the effects of a possible collapse of certain species due to overfishing (Hamre 1994, Dolgov 2002). Frequently, species may become functionally extinct as a result of excessive fishing pressure (Dayton et al. 1998, Jackson et al. 2001), where their densities are too low to play their ecological role as consumers or resources within the food web. Functional extinctions are relatively common, and would result in a particular node, or species, to no longer be part of a network, functionally. I simulated this scenario here. Species to be removed were selected using the risk-based approach introduced by Micheli et al. (2014). Micheli et al. extended Productivity-Susceptibility Analysis (PSA) to assess the cumulative risk posed by multiple fisheries to the species of the North Pacific marine food web. PSA defines species vulnerability ( $V$ ) as a function of productivity ( $P$ ) and aggregated susceptibility ( $AS$ ):  $V = \sqrt{P^2 + AS^2}$ . Productivity is calculated by using information on species life history such as age and size at maturity, fecundity, reproductive strategy, and trophic level (Hobday et al. 2007). Two or more fisheries may affect a single species and it is assumed that their cumulative potential impact may be larger (e.g. additive or multiplicative) than that generated by the single fishery with the greatest impact (Halpern et al. 2008b). Aggregated susceptibility accounts for possible cumulative effects of multiple overlapping fishing activities and is assessed on the basis of several attributes (e.g. the selectivity of fishing gears and post-capture mortality of discarded bycatch; see Micheli et al. 2014). To investigate how fishing can modify the structure of the food web I considered the vulnerability of species that takes into account the cumulative risk due to multiple fisheries (Micheli et al. 2014). According to the values of these vulnerability scores I classified species as at high, medium and low risk (Table 2.6 in Appendix 2.5.2). The first group (i.e. high risk) included 28 species: 3 mammals, 24 fish, and 1 invertebrate; medium risk species comprised 28 species: 1 bird, 22 fish, and 5 invertebrates; the latter group (i.e. low risk) was composed of 16 species: 9 fish, 6 invertebrates and 1 algae (Table 2.6). I explored the impacts of single species removals or

different combinations of high/medium/low risk species removals (i.e. by removing combinations of two, three or four nodes at the same time) and considered the effects on the entire food web structure. The impacts on single species were investigated only for the removal of different combinations of high risk species. The number of all possible combinations ( $N$ ) was determined by:  $N = \frac{n!}{r!(n-r)!}$ , where  $n$  is the number of high/medium/low risk species taken  $r$  at a time ( $r = 1, 2, 3$ , or 4) without repetition. Removal scenarios were targeted first to the 28 high risk species, which were all removed one at a time. Second, all possible pairs of high risk species were removed. Then I removed all possible combinations of three and four high risk species. I repeated the same procedure by considering the medium and low risk species. In summary, for single species removals I had 28 different scenarios for high and medium risk species, and 16 scenarios for low risk species. Two species removals yielded 378 combinations for both high and medium risk species, and 120 scenarios for low risk species. For three species removals, both high and medium risk species generated 3,276 different combinations, whereas 560 scenarios were obtained with the subset of low risk species. Combinations of four species were 20,475 for high and medium risk species, and 1,820 for low risk species. I did not consider scenarios in which removals targeted mixed combinations of high, medium and low risk species although this is not unrealistic.

The influence of species removals on the whole food web was assessed using global structural indices (Table 2.1) and visualized through frequency histograms of assortativity coefficient (AC), clustering coefficient (CC), modularity (MD), directed connectance (C), linkage density (LD), diameter (DM), average path length (APL) and number of nodes with betweenness centrality equal to 0 (BC0). The impact of removals on single species was assessed on the basis of changes in their centrality indices. For degree centrality, to quantify the effects of species' removals ( $remD_i$ ) I considered the ratio between the values with ( $D_i^{rem}$ ) and without removals (i.e. in the original food web;  $D_i$ ):  $remD_i = D_i^{rem}/D_i$ . Hence, a value equal to 1 means no change in degree centrality, while values  $< 1$  identify those species whose total degree centrality decreased after removals. To assess the changes in betweenness and closeness centralities (indices for which I used the normalized versions that bring all values into the range [0, 1]; see Appendix 2.5.1), the values computed for each removal experiment ( $BC_i^{rem}$  and  $CL_i^{rem}$ ) were subtracted from their counterparts computed in the original food web ( $BC_i$  and  $CL_i$ ):  $remBC_i = BC_i - BC_i^{rem}$ ;  $remCL_i = CL_i - CL_i^{rem}$ . Therefore, a null value means no change, a positive value stands for a decrease and a negative value indicates an increase in the centrality score. The impacts of high risk species removals on centrality indices of all other species in the food web were visualized by heat maps.

To further investigate whether species at risk (according to the definition provided by Micheli et al. 2014) occupy most central structural positions in the food web I compared the consequences of their removal with those produced by random removals of the food web species, independently of their vulnerability score. I considered single species removals as well as combination of up to four species selected at random. Thus, I had respectively 121, 7,260, 287,980 and 8,495,410 possible removal scenarios to be compared with the ones based on targeted removals (i.e. these latter

scenarios follow the vulnerability index criteria). The presence of a significant difference between the effect of targeted and random deletions indicates that the species that are most vulnerable to fishing pressure are also important from a structural point of view (i.e. this is for testing whether targeted removals have more consistent negative effects on food web topology compared to random deletions). This would imply that the disappearance of vulnerable species has consequences on the community structure and possibly function. This analysis evaluates whether the vulnerability ranking proposed by Micheli et al. (2014) also reflects species' structural importance.

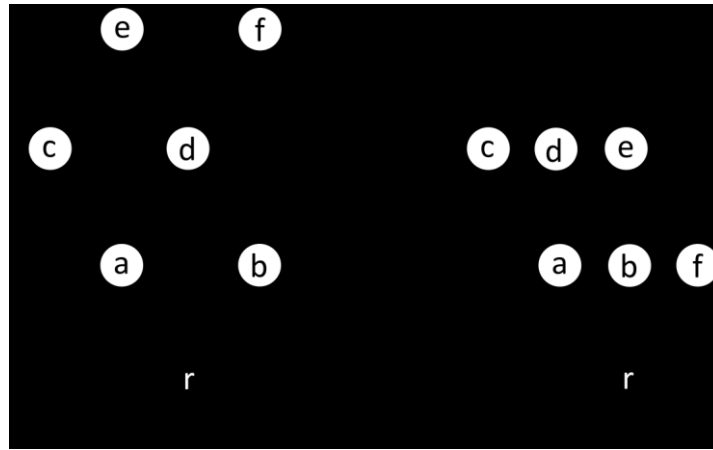
### 2.2.5 Statistical analysis

To investigate a possible aggregation bias (i.e. the presence of significant differences in the centrality indices of species vs. trophospecies) in the original food web (i.e. in absence of any removal) I applied the Kolmogorov-Smirnov test (KS-test). To compare index values obtained after targeted removals (i.e. risk-based) with those obtained from random deletions I performed the Mann-Whitney-Wilcoxon test. All statistical analyses were performed in R.

### 2.2.6 Dominator tree

I constructed the dominator tree for the North Pacific region of Baja California Sur, Mexico. Dominator tree is useful to predict secondary losses caused by single species removal and to identify which nodes are likely to cause the greatest impacts if removed. Dominator trees are topological structures in which nodes are sequentially connected based on their dominance relations. They make visible those pathways that are essential for energy delivery in food webs (i.e. strict bottom-up perspective). Using the dominator tree, one can easily see which species act as bottlenecks for energy distribution to other species. Such bottlenecks are called dominators because their removal precludes energy from reaching the nodes that follow them in the chain from producers to consumers. By applying the dominator tree Allesina and Bodini (2004) showed how the intricacy of real food webs could be unfolded to simpler structures that make apparent which nodes are likely to cause the greatest impact if removed. An example of a simple food web and its dominator tree is given in Figure 2.3. Species  $f$  receives energy along the pathways  $r \rightarrow a \rightarrow d \rightarrow f$  and  $r \rightarrow b \rightarrow f$ . Figure 2.3B shows that only the root dominates  $f$ , because it is the only node in common between the two paths. When either  $a$  or  $d$  become extinct, species  $f$  may survive because at least one pathway remains at its disposal. All the energy available to  $e$  passes through  $r$  and  $a$ ; so that both are dominators of this node, and  $a$  is its immediate dominator.





**Figure 2.3** - Hypothetical network rooted in r (left side) and the corresponding dominator tree (right side). The node r represents the external environment, the ultimate source of energy for all the species.

## 2.3 Results

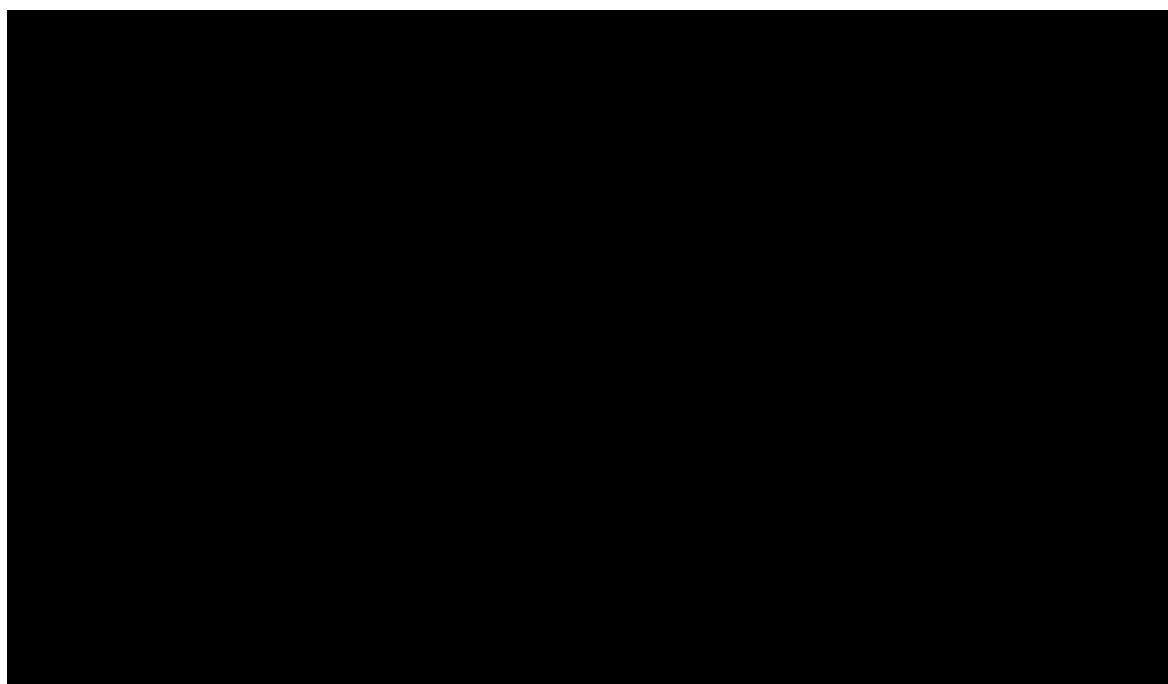
### 2.3.1 Topological analysis

The food web is depicted in Figure 2.2. The directed connectance is 0.07 and the network is disassortative ( $R = -0.34$ ): high degree nodes (i.e. nodes with many connections) are connected to low degree nodes (i.e. nodes with few connections). All centrality indices differ significantly between species and trophospecies ( $D_{in,species} > D_{in,trophospecies}$ ,  $p < 0.001$ ;  $D_{out,species} < D_{out,trophospecies}$ ,  $p < 0.001$ ;  $D_{species} < D_{trophospecies}$ ,  $p = 0.003$ ;  $undBC_{species} < undBC_{trophospecies}$ ,  $p < 0.001$ ;  $BC_{species} < BC_{trophospecies}$ ,  $p = 0.024$ ;  $CL_{species} < CL_{trophospecies}$ ,  $p = 0.010$ , see Table 2.2 for the description of all indices). This result confirms that the level of aggregation (species vs. trophospecies) can bias the analyses. Trophospecies have a significantly higher number of trophic interactions than single species ( $D_{species} < D_{trophospecies}$ ,  $p = 0.003$ ). This implies that trophospecies may be involved in a higher number of pathways and influence betweenness and closeness values. Thus, I restricted the analysis to individual species (100 nodes) and excluded trophospecies. The values for the indices are reported in Table 2.6 of Appendix 2.5.2. Twelve species occupy the most central positions in the trophic network, based on degree, betweenness, and closeness centralities (Table 2.3).

ID code	Species	Category	$D_{in}$	$D_{out}$	D	BC	undBC	CL
6	<i>Paralabrax clathratus</i>	Fish	37(1st)		47(2nd)	0.089(2nd)	0.036(2nd)	0.603(2nd)
4	<i>Paralichthys californicus</i>	Fish	30(2nd)		40(3rd)	0.071(3rd)	0.021(4th)	0.577(3rd)
27	<i>Octopus</i> sp.	Invertebrate		37(1st)	58(1st)	0.111(1st)	0.089(1st)	0.635(1st)
24	<i>Semicossyphus pulcher</i>	Fish	24(4th)		32(5th)		0.027(3rd)	0.569(4th)
47	<i>Panulirus interruptus</i>	Invertebrate			36(4th)		0.020(5th)	0.569(5th)
21	<i>Stereolepis gigas</i>	Fish	28(3rd)			0.030(4th)		
16	<i>Zalophus californianus</i>	Mammal	24(5th)					
84	<i>Pugettia producta</i>	Invertebrate		25(3rd)				
41	<i>Clupeids</i>	Fish		30(2nd)				
105	<i>Eisenia arborea</i>	Algae		21(4th)				
49	<i>Cancer anthonyi</i>	Invertebrate		19(5th)				
19	<i>Sphyræna argentea</i>	Fish				0.016(5th)		

**Table 2.3** – The 12 most central species in the Baja California coastal food web. For each index, I consider the species that occupy the top five positions. For each species and index, I show centrality values and ranking position (1st to 5th).

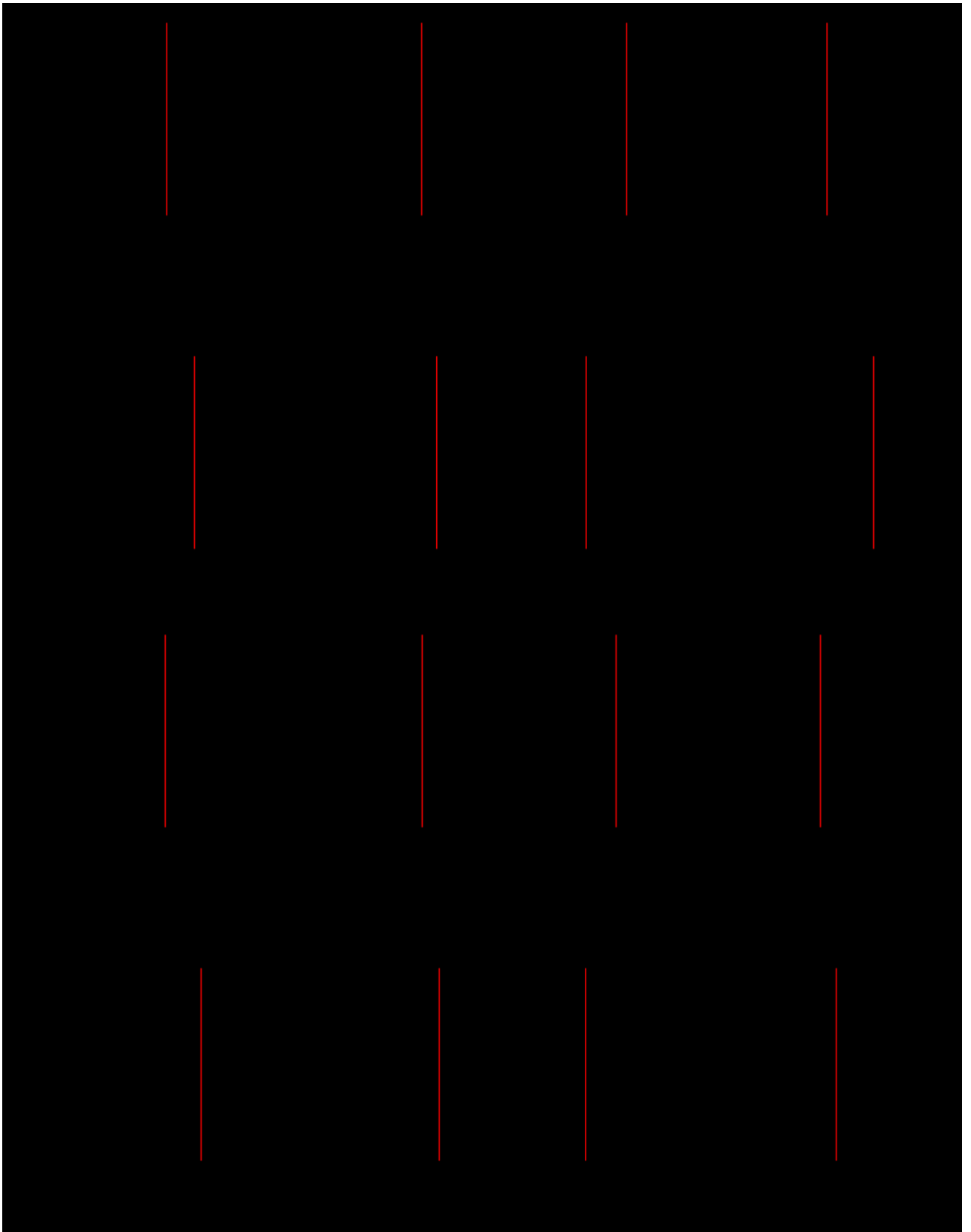
To reveal species' cluster (i.e. sub-group of species with similar centralities value) I considered three sets with: (I) six indices ( $D_{in}$ ,  $D_{out}$ , D, BC, undBC, CL); (II) two sets of three indices that differ for the presence of either directed (D, BC, CL) or undirected (D, undBC, CL) betweenness. The mCLUST R library was used to estimate the optimal number of clusters. Such number was 7, 5 and 7, respectively (Figure 2.4). High risk species are distributed in all cluster.



**Figure 2.4** - Percentage of species at high risk in three different scenarios.

### **2.3.2 Removal analysis**

The food webs generated by the removal experiments (i.e. the food webs constructed using different scenarios of either targeted or random species deletion; see Figure 2.5) did not show significantly different values of global structural indices when compared with the values computed in the original food web (i.e. see the red line in Figure 2.5). This holds true for the global structural indices AC, CC, MD, C, BC0, APL and DM. Link density shows a progressive increase in the difference between the value in the original web and the ones obtained through species removals (Figure 2.5). I found similar patterns of global structural indices for random and selective removals (i.e. when one to four species are removed) across risk levels (i.e. medium and low risk species deletions; see Figures 2.8-2.12 in Appendix 2.5.2).



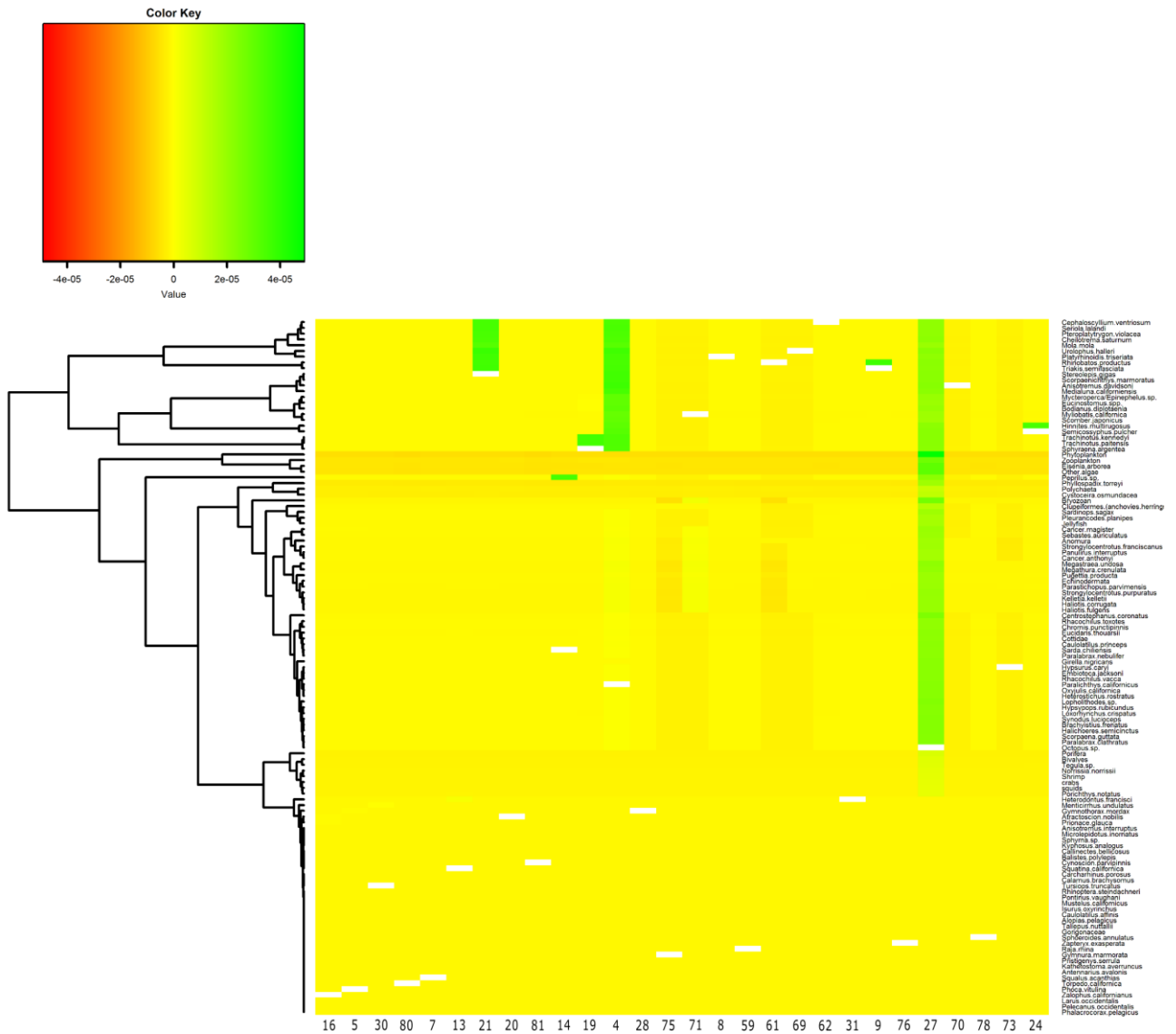
**Figure 2.5** – Frequency histograms for global structural indices following removals of four species (20,475 combinations): high risk species removal (A) and random removals (B). In each chart the red line shows the value of the index for the food web with no removals.

There is no significant difference between selective and random removals in the case of CC (Mann-Whitney-Wilcoxon test; Table 2.4). Significant differences emerged, instead, for AC, MD and APL, under removal scenarios from two to four species removed (Table 2.4). Indices MD and APL were significantly higher when the food web was exposed to targeted removals (Table 2.4). Different values for C and LD occurred when three and four species were removed (Table 2.4). Different values for BC0 emerged only when four species were removed (Table 2.4).

Species removed	AC	CC	MD	BC0	C	LD	APL	DM
1	0.980	0.774	0.787	0.656	0.394	0.394	0.712	NA
2	0.010	0.500	<0.001	0.903	0.715	0.715	< 0.005	NA
	ASH < R		ASH > R				ASH > R	
3	<< 0.001	0.472	<< 0.001	0.145	< 0.004	< 0.004	<< 0.001	NA
	ASH < R		ASH > R		ASH > R	ASH > R	ASH > R	
4	<< 0.001	0.641	<< 0.001	<< 0.001	<< 0.001	<< 0.001	<< 0.001	0.180
	ASH < R		ASH > R	ASH > R	ASH > R	ASH > R	ASH > R	

**Table 2.4** – Mann-Whitney-Wilcoxon test for the comparison of global structural indices computed after either targeted (i.e. high risk) or random removals. The scenarios comprise single removals and multiple removals of all possible combinations up to four species (see the different rows of the table). ASH key labels targeted removals of species at risk; R key identifies random extinctions. Numbers indicate the p-values of the Mann-Whitney-Wilcoxon test. ASH > R indicates that the index is significantly higher for targeted removals than for random removals, while ASH < R stands for significantly lower values in case of targeted removals if compared to random deletions.

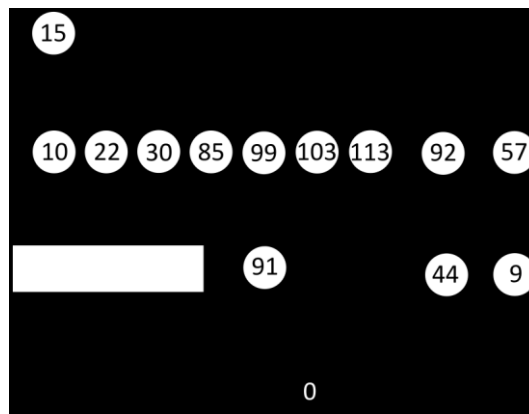
One example of the impact of removals on single species, assessed by computing centrality indices, is given in Figure 2.6 (all the others cases are reported in Appendix 2.5.2). *Octopus* sp. is the species that, if removed (either individually or in combination with other species), determines the greatest impact (based on centrality index D; see also Figures 2.13-2.15 in Appendix 2.5.2). The most impacted species are all fish: the pelagic thresher shark *Alopias pelagicus*, the shirtfin weakfish *Cynoscion parvipinnis* and the smooth stargazer *Kathetostoma avertuncus*. Two invertebrate species are also affected when some combinations of two to four species are removed: the scallop *Hinnites multirugosus* and the sea cucumber *Parastichopus parvimensis*. Considering index BC, the kelp bass *Paralabrax clathratus*, *Octopus* sp., the halibut *Paralichthys californicus* and the Pacific barracuda *Sphyrnaea argentea* (three fish and one invertebrate) are the most impacted species in all the removal scenarios (i.e. their value decreases; Figures 2.13-2.15 in Appendix 2.5.2). When *Octopus* sp. is the target of removal, both as single species and in combination with others, more than 50% of the remaining species shows a decrease in closeness (Figures 2.4 and 2.13-2.15 in Appendix 2.5.2). The removal of *Paralichthys californicus* and the giant seabass *Stereolepis gigas* also induces a decrease in this index. Phytoplankton, zooplankton, the kelp *Eisenia arborea* and other algae increase their closeness for all combinations of species except for the deletion of *Octopus* sp. (i.e. both as single species or in combination with others), for which their values decrease.



**Figure 2.6** – Changes in closeness centrality due to the targeted removal of one species at high risk (i.e. 28 different scenarios). On the x axis the identification codes of single species removed (16, *Zalophus californianus*; 5, *Phoca vitulina*; 30, *Tursiops truncatus*; 80, *Torpedo californica*; 7, *Squalus acanthias*; 13, *Squatina californica*; 21, *Stereolepis gigas*; 20, *Atractoscion nobilis*; 81, *Cynoscion parvipinnis*; 14, *Sarda chiliensis*; 19, *Sphyrna argentea*; 4, *Paralichthys californicus*; 28, *Gymnothorax mordax*; 75, *Gymnura marmorata*; 71, *Myliobatis californica*; 8, *Platyrrhinoidis triseriata*; 59, *Raja rhina*; 61, *Rhinobatos productus*; 69, *Urolophus halleri*; 62, *Cephaloscyllium ventriosum*; 31, *Heterodontus francisci*; 9, *Triakis semifasciata*; 76, *Zapteryx exasperata*; 27, *Octopus* sp.; 70, *Anisotremus davidsoni*; 78, *Spherooides annulatus*; 73, *Hypsurus caryi*; 24, *Semicossyphus pulcher*; I followed the order of species' deletion shown in the heat map). The species removed are indicated by white boxes in each scenario. Along the column are visualized the changes in closeness centrality (i.e. in response to targeted removals) for each species listed on the right side of the heat map. The order along the y axis depends on the clustering method (i.e. complete linkage method with Euclidean distance measure that finds similar clusters). In the upper left corner the color scale used for visualization and the corresponding numerical range for the index. According to this scale, green boxes indicate lowest closeness values after removals.

### 2.3.3 Dominator tree

The dominator tree is depicted in Figure 2.7. I found a topology that is very close to the star-like architecture, one of the extreme configurations for dominator trees (Allesina and Bodini 2004). There are four main features that deserve attention: (I) the dominance of *Cynoscion parvipinnis* (57) by *Octopus sp.* (9); (II) the control of *Pristigenys serrula* (92) by crabs (44); (III) the fact that phytoplankton (91) dominates eight species: Zooplankton (10), Clupeiformes - anchovies, herrings (15), Bivalves (22), *Pleurancodes planipes* (30), Bryozoan (85), *Hinnites multirugosus* (99), Porifera (103), and Gorigonaceae (113); (IV) that evidence that zooplankton (10) dominates Clupeiformes - anchovies, herrings (15).



**Figure 2.7** – Dominator tree diagram of the area located along the coast of the Vizcaino Desert Biosphere Reserve in the North Pacific region of Baja California Sur, Mexico. Nodes are connected based on their dominance relations. Each node represents either a species or a trophospecies. Nodes not explicitly shown in the figure fall in the rectangular compartment and are exclusively dominated by the root node. 9, *Octopus sp.*; 10, Zooplankton; 15, Clupeiformes (anchovies, herrings); 22, Bivalves; 30, *Pleurancodes planipes*; 44, crabs; 57, *Cynoscion parvipinnis*; 85, Bryozoan; 91, Phytoplankton; 92, *Pristigenys serrula*; 99, *Hinnites multirugosus*; 103, Porifera; 113, Gorigonaceae.

## 2.4 Discussion

I identified 12 species as the most central (i.e. topologically and therefore possibly functionally important) in the food web of Baja California (Table 2.3). Five of these 12 species are the most central for at least three indices and could be thought of as key players in the community. They are: the kelp bass *Paralabrax clathratus*, the California halibut *Paralichthys californicus*, *Octopus sp.*, the California sheephead *Semicossyphus pulcher* and the spiny lobster *Panulirus interruptus*. All of them are evaluated as at risk for the cumulative effects of multiple fisheries according to Micheli's vulnerability index (Micheli et al. 2014). Of these five species, three are high risk species, one medium, and one low (see Table 2.3 and Figure 2.2).

Our results show that removing up to four target species (i.e. at risk; see Micheli et al. 2014) does not alter the overall structural attributes of the food web. Thus, the network appears to be structurally resilient: it tends to maintain its integrity in the face of several simulated extinction

events. Link density is the only structural index that shows a significant difference between the original web and those obtained after removals. This result indicates that, as the number of removed species increases, the average number of feeding links per species decreases. This effect may have consequences on ecological function and food web resilience to additional species loss because it reduces the diet breadth of species and the number of pathways through which materials and energy move through the web, and thus the functional redundancy of the assemblage (e.g. Micheli and Halpern 2005). The sensitivity of link density to changes in food web structure has been already reported in the literature, with a previous study showing how link density is more sensitive to data aggregation than connectance (Dunne et al. 2006). Thus, the result of a significant change of link density with species removals is not surprising. In contrast, all other indices were unaffected by removals.

Food web structure is differentially affected in selective (i.e. targeted to high risk species) and random removals depending on the indices considered and the number of species removed (Table 2.4). The significant differences between target (i.e. risk based) and random removals assume high relevance because the analysis was conducted in a conservative way (i.e. species at risk are also included in random removals). Modularity (MD) was significantly higher when removals targeted to high risk species were compared to random extinctions. Thus, removing species at high risk can create a more fragmented food web. This is due to the central position that some of the high risk species occupy in the network of trophic interactions. Their loss may render the whole network more fragile and thus possibly more vulnerable to further extinction events. Directed connectance (C) increases significantly when high risk species are removed. It has been shown previously that connectance is related to the relative importance of functional and redundant links in food webs; in particular, when C increases the number of redundant links becomes greater than that of functional links (Bondavalli and Bodini 2014). Allesina et al. (2009) showed that functional connections affect food web robustness, whereas redundant links are neutral. Targeted removals, by significantly increasing connectance (and thus the fraction of redundant links) in comparison with random removals, would make the food web less robust than its original counterpart as the number of independent pathways (i.e. those composed by functional connections and that are fundamental for energy delivery) likely decreases (but see Dunne et al. 2002). In summary, the presence of some significant differences (e.g. MD and C) between the effect of targeted and random deletions confirms that species at high risk of depletion from fishing are important from a structural point of view.

The analysis of species centrality expands in a functional perspective the concept of structural connectedness (Jordán et al. 2006, Jordán 2009). *Octopus* sp. ranked highest for all the centrality indices. Closeness centrality indicates how close a species is to the others; results of this index suggest that *Octopus* sp. plays an important role in the spread of both direct and indirect effects being responsible for their diffusion in the ecosystem via shortest paths. Because the bulk of energy travels through food webs along pathways that tend to be short (Bellingeri and Bodini 2015),



*Octopus* sp. may enter several main routes for energy delivery from primary producers to top species. This hypothesis needs to be tested with empirical measurements and experiments, as the ecological role of *Octopus* sp. in this food web is unknown. Empirical and theoretical studies quantifying the main pathways for energy delivery and the strength of these routes would elucidate the role *Octopus* sp. and other species with high values of closeness centrality play in energy delivery, and whether these species may act as bottlenecks for energy distribution to other species in the food web (Allesina and Bodini 2004). The high value of closeness for this species (calculated as undirected index) suggests that *Octopus* sp. might be involved in spreading top-down control, e.g., it may be part of a trophic cascade from its predators to its prey. Control by high level consumers upon lower trophic levels can be possible through several paths in a food web. However, the fast spreading of the indirect effects is expected to spread through the shortest paths. Such shortest paths become the dominant routes through which top predators exert their control. The highest value of closeness, combined with the highest value of betweenness centrality, suggests that *Octopus* sp. might enter in several of these dominant routes through which cascading trophic interactions may manifest (Hodgson 2005). Network position in itself, however, does not guarantee a prominent role in top-down regulations. This hypothesis, as highlighted above, remains to be tested.

*Octopus* sp. is the species that, if removed, determines the greatest change on other species' centralities. I found that more than 50% of the remaining species showed a decrease in their closeness centrality values after the removal of *Octopus* sp. This result suggests that decline or loss of *Octopus* sp. might cause a substantial reorganization of the energy flow in the food web. This is because the reduced closeness for a high proportion of species imposes that pathways for energy delivery would elongate, with potential loss of efficiency. However, this hypothesis arises from a static analysis of the food web. In real, dynamic food webs, species would actively respond to species loss through mechanisms such as diet switching (Barnum et al. 2015), which would buffer the effects of species loss. Nevertheless, a reorganization of the energy flows within the ecosystem might still occur, with potential impacts on the amount of energy that reaches the top species and possibly the fisheries. Gaichas et al. (2008) have proposed that protecting highly connected species in the network, also called hub species, is crucial for preventing potential impacts of fishing activities on the whole ecosystem structure. The central role that *Octopus* sp. might play, as suggested by the centrality indices, supports the correctness of the present regulative framework, which limits the catch to this species to fishing cooperatives that hold exclusive fishing permits. This regulative framework (i.e. exclusive access to cooperatives) applies also to the spiny lobster *Panulirus interruptus*, another species that plays a major role in the economy of the fishing cooperatives and that is also central in the food web, based on the present analysis (Figure 2.2). These conclusions that emphasize the role of *Octopus* sp. must be taken with circumspection, however, and further scrutiny on the role this species plays in Baja California is needed. Results obtained in this study strongly depend on the assumptions made about the position that *Octopus* sp.

occupies within the food web (i.e. as defined by the adjacency matrix compiled). Nevertheless, it has been pointed out that these predators are voracious and adaptable, and they impact many prey species, including commercially valuable fish and invertebrates (Doubleday et al. 2016). Also, several marine predators rely on this species for food. This confirms that the positional importance of *Octopus* sp. as a hub with many incoming and outgoing connections consists of a reasonable assumption. The dominator tree highlights the potential importance of *Octopus* sp., whose disappearance could bring *Cynoscion parvipinnis* to secondary extinction. However, the dominator tree also shows that the dominance of *Octopus* sp. does not cascade over a larger group of species. The loss of other dominators (i.e. phytoplankton, zooplankton and crabs), which dominate larger ensemble of species, is unrealistic because these variables group a huge variety of species (i.e. they are trophospecies).

*In silico* removals conducted in this study provide suggestions about how exploitation of vulnerable species through multiple fisheries could expose the marine community to cascading effects that can lead to modification of structural integrity of the Baja California coastal food web. In general, the North Pacific Baja California food web shows an intrinsic resilience to species loss. This study highlights the potential of the whole system approach in fisheries management. The local extinction of a central species might cause a restructuring of the energetic backbone of the ecosystem through which energy travels from primary producers to top consumers (Bellingeri and Bodini 2016). This ultimately may affect the entire fishing sector as fish production is supported by the energetic contribution from lower levels.

By applying a network approach to the coastal food web of Baja California, I found that many of the species at high risk from multiple fisheries are also the most central in the network. Their reduction or loss may reduce food web robustness, possibly making the community more prone to secondary extinctions. Another consequence that I hypothesize is that patterns of energy transfer may be altered with consequences toward the top of the food chain where, in general, commercially and ecologically important species are found. This study shows the potential of a food web approach for examining possible ecosystem-wide effects of fishing in data-poor contexts, and produces hypotheses to be tested in further research. However, this approach presents some limitations. First, structural food web analyses are based on a static view of network that precludes assessing dynamical aspects. For example, top-down and bottom-up regulative mechanisms are certainly linked to the centrality of species. Most central species are likely to enter the formation of the shortest pathways and are intermediate to many pathways through which top-down (or bottom-up) control is spread; nonetheless, a static food web does not provide any information on how this positional importance affects population dynamics (Scotti and Jordán 2015). Second, quantitative information about link strength is lacking. This information is essential for relating the positional importance of the species within the energetic budget of the entire community and the pathways for energy delivery that support fisheries (Bellingeri and Bodini 2016). In particular, food webs are sensitive to the lack of information concerning link strength. Considering unweighted and weighted

versions of a food web, it has been shown that weighting could affect ranking (i.e. node ordering) of topological indices (Scotti et al. 2007). Local indices ( $D_i$ ) are affected by weighting very seriously, instead BC and CL (that consider indirect effects) are less impacted. Despite these limitations, a network approach is a promising starting point for bridging the gap between EBM theory (i.e. based on the development and improvement of key principles; see Long et al. 2015) and practice (i.e. how can we deal with the complexity associated to whole systems, in particular in the case of data-poor systems?) and strive to manage ecosystems in a more sustainable way.

## 2.5 Appendix

### 2.5.1 Methods

The structural position of species was characterized by analysis of centrality indices (Wasserman and Faust 1994). These are used as an approximation of functional importance: species were ranked as a function of their local (i.e. degree centrality,  $D_i$ ) or global (i.e. betweenness,  $BC_i$  and undBC $_i$  and closeness centrality,  $CL_i$ ) position.

(I) The degree of a species  $i$  is the sum of its total neighbors ( $D_i$ ); numbers of prey and predators make the in-degree ( $D_{in,i}$ ) and the out-degree ( $D_{out,i}$ ) index, respectively (1).

$$D_i = D_{in,i} + D_{out,i} \quad (1)$$

(II) Directed betweenness centrality ( $BC_i$ ) and undirected betweenness centrality (undBC $_i$ ) are used to count how many times a target node  $i$  lies on the geodesics (i.e. shortest paths) connecting every other pair of species  $j$  and  $k$  in the food web. Normalized betweenness for species  $i$  is computed using the following equation:

$$BC_i = \frac{\sum_{j,k=1}^S \frac{d_{jk}(n_i)}{d_{jk}}}{\left[ \frac{(S-1)(S-2)}{2} \right]} \quad (3)$$

where  $d_{jk}(n_i)$  is the number of geodesics between nodes  $j$  and  $k$  that pass through species  $i$ ;  $d_{jk}$  stands for the total number of geodesics between nodes  $j$  and  $k$ ,  $S$  is the total number of species in the food web (i.e. the denominator represents the number of pairs of species not including the species  $i$ ). The undirected form of this index (undBC $_i$ ) accounts for the spread of both bottom-up and top-down effects; instead, directed betweenness centrality ( $BC_i$ ) considers shortest paths within a strict bottom-up perspective (i.e. tracing biomass flows from primary producers to consumers).

(III) Closeness centrality ( $CL_i$ ) measures how short the geodesics from a given species  $i$  to all other species that can be reached in the food web are. In its normalized form is computed using the following equation:

$$CL_i = \frac{S-1}{\sum_{j=1}^S d_{ij}} \quad (2)$$

where  $S$  represents the total number of species in the food web, and  $d_{ij}$  is the length of the shortest path from species  $i$  to  $j$ .

Species that show a high value for  $D_i$  are hubs (i.e. they are connected with many other species). When  $BC_i$  is high the node  $i$  plays an important role in mediating indirect effects throughout the food web. High  $CL_i$  values identify nodes that, when disturbed (e.g. decline of their population size), more rapidly spread the impact to other nodes.

ID_code	Node	Diet sources			
		Kelpforest Database	Literature	Online datasets	Experts
1	Cottidae			<a href="#">Animal Diversity Web</a> <a href="#">Walla Walla University</a>	yes
2	<i>Phalacrocorax pelagicus</i>	yes	Ainley et al. 1981	<a href="#">Encyclopedia of Life</a>	yes
3	<i>Scorpaenichthys marmoratus</i>	yes	O'Connell (1953)	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Birch Aquarium at Scripps</a>	yes
4	<i>Paralichthys californicus</i>	yes		<a href="#">Encyclopedia of Life</a>	yes
5	<i>Phoca vitulina</i>	yes	Brown et al. 1983	<a href="#">Encyclopedia of Life</a> <a href="#">The Marine Mammal Center</a> <a href="#">Cabrillo Marine Aquarium</a>	yes
6	<i>Paralabrax clathratus</i>	yes		<a href="#">Encyclopedia of Life</a> <a href="#">Cabrillo Marine Aquarium</a>	yes
7	<i>Squalus acanthias</i>		Wilga et al. 1998 Laptikovskiy et al. 2001 Alonso et al. 2002 Shark Trust 2010	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
8	<i>Platyrrhinoidis triseriata</i>			<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Discover Life</a> <a href="#">Aquarium of the Pacific</a>	yes
9	<i>Triakis semifasciata</i>		Ferry-Graham 1998 Kao 2000	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Monterey Bay Aquarium</a>	yes
10	<i>Scorpaena guttata</i>	yes		<a href="#">Encyclopedia of Life</a>	yes
11	<i>Peprilus</i> sp.				yes
12	<i>Sphyrna</i> sp.		Torres-Rojas et al. 2006 Shark 2011		yes
13	<i>Squatina californica</i>	yes	Escobar-Sánchez et al. 2006	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">FAO</a>	yes
14	<i>Sarda chiliensis</i>		Bernard et al. 1985	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
15	<i>Sardinops sagax</i>	yes		<a href="#">FishBase</a>	yes

16	<i>Zalophus californianus</i>	yes	Schultze 1983 Francis et al. 1991 Lowry et al. 1999 Fish et al. 2003 Porras-Peters et al. 2008 Pope et al. 2010	<a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a>	yes
17	<i>Seriola lalandi</i>	yes		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Birch Aquarium at Scripps</a>	yes
18	<i>Scomber japonicus</i>		Bayhan et al. 2007	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
19	<i>Sphyaena argentea</i>	yes	Schultze 1983 Arizmendi-Rodriguez et al. 2014	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">IUCN</a> <a href="#">MarineBio</a>	yes
20	<i>Atractoscion nobilis</i>		Donohoe 1997	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
21	<i>Stereolepis gigas</i>	yes		<a href="#">Encyclopedia of Life</a> <a href="#">Birch Aquarium at Scripps</a>	yes
22	<i>Caulolatilus princeps</i>	yes		<a href="#">Encyclopedia of Life</a> <a href="#">Discover Life</a> <a href="#">Birch Aquarium at Scripps</a>	yes
23	<i>Chromis punctipinnis</i>	yes		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">IUCN</a>	yes
24	<i>Semicossyphus pulcher</i>	yes	Turner et al. 1969 Topping et al. 2005	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a>	yes
25	<i>Oxyjulis californica</i>	yes	Tegner 1989	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Monterey Bay Aquarium</a>	yes
26	<i>Hypsypops rubicundus</i>	yes		<a href="#">FishBase</a> <a href="#">Monterey Bay Aquarium</a> <a href="#">Aquarium of the Pacific</a>	yes
27	<i>Octopus</i> sp.	yes	Carroll et al. 1989	<a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a> <a href="#">Walla Walla University</a>	yes

28	<i>Gymnothorax mordax</i>	yes		<a href="#">FishBase</a>	yes
29	<i>Embiotoca jacksoni</i>	yes		<a href="#">Encyclopedia of Life</a>	yes
30	<i>Tursiops truncatus</i>		Hanson et al. 1993 Barros et al. 2000 Segura et al. 2006	<a href="#">Encyclopedia of Life</a> <a href="#">The Marine Mammal Center</a>	yes
31	<i>Heterodontus francisci</i>	yes	Turner et al. 1969 Summers et al. 2004 Huber et al. 2005 Zacharias et al. 2006	<a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a> <a href="#">FAO</a> <a href="#">Birch Aquarium at Scripps</a>	yes
32	<i>Girella nigricans</i>	yes		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Discover Life</a>	yes
33	<i>Pelecanus occidentalis</i>		Anderson et al. 1980	<a href="#">Encyclopedia of Life</a> <a href="#">MarineBio</a>	yes
34	<i>Paralabrax nebulifer</i>	yes	Roberts et al. 1984	<a href="#">Encyclopedia of Life</a>	yes
35	<i>Kyphosus analogus</i>			<a href="#">FishBase</a>	yes
36	<i>Medialuna californiensis</i>	yes	Boerger 2011	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Birch Aquarium at Scripps</a>	yes
37	Zooplankton	yes			yes
38	<i>Sebastes auriculatus</i>	yes		<a href="#">Encyclopedia of Life</a> <a href="#">Birch Aquarium at Scripps</a>	yes
39	Shrimp				yes
40	<i>Porichthys notatus</i>	yes		<a href="#">Encyclopedia of Life</a>	yes
41	Clupeids (anchovies, herrings)				yes
42	Squids				yes
43	Jellyfish		Sapsis et al. 2011		yes
44	<i>Pleurancodes planipes</i>				yes
45	<i>Mola mola</i>		Pope et al. 2010	<a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a> <a href="#">Monterey Bay Aquarium</a> <a href="#">Thys 2016</a>	yes
46	Crabs				yes
47	<i>Panulirus interruptus</i>	yes	Castañeda-Fernández-de-Lara et al. 2005 Zacharias et al. 2006	<a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a>	yes

			Morales-Zárate et al. 2011	
48	<i>Callinectes bellicosus</i>		Millikin et al. 1984 Díaz-Tenorio et al. 2006	yes
49	<i>Cancer anthonyi</i>		Tegner 1989 Carroll et al. 1989	<a href="#">Encyclopedia of Life</a> yes
50	<i>Brachyistius frenatus</i>	yes		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Encyclopedia of Life</a> yes
51	<i>Loxorhynchus crispatus</i>			<a href="#">Animal Diversity Web</a> <a href="#">Monterey Bay Aquarium</a> <a href="#">Cabrillo Marine Aquarium</a> yes
52	<i>Mesocentrotus franciscanus</i>			yes
53	Bryozoan			yes
54	<i>Hinnites multirugosus</i>			yes
55	Porifera			
56	<i>Microlepidotus inornatus</i>			<a href="#">FishBase</a> <a href="#">Discover Life</a> yes
57	Gorigonaceae			yes
58	<i>Larus occidentalis</i>	yes	Hunt et al. 1980	<a href="#">Walla Walla University</a> yes
59	<i>Raja rhina</i>		Robinson et al. 2007	yes
60	<i>Synodus lucioceps</i>			yes
61	<i>Rhinobatos productus</i>		Farrugia et al. 2011	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Birch Aquarium at Scripps</a> yes
62	<i>Cephaloscyllium ventriosum</i>			<a href="#">Encyclopedia of Life</a> yes
63	<i>Rhacochilus toxotes</i>	yes	Feder et al. 1974	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> yes
64	<i>Rhacochilus vacca</i>	yes	Wares 1968	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> yes
65	<i>Pteroplatytrygon violacea</i>		Camhi et al. 2009 Véras et al. 2009 Vaske et al. 2012	<a href="#">Encyclopedia of Life</a> yes
66	<i>Halichoeres semicinctus</i>	yes	Hobson 1976 Adreani et al. 2008	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Discover Life</a> yes



67	<i>Balistes polylepis</i>	yes		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Discover Life</a>	yes
68	<i>Cheilotrema saturnum</i>			<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a>	yes
69	<i>Urolophus halleri</i>		Babel 1967	<a href="#">FishBase</a>	yes
70	<i>Anisotremus davidsoni</i>	yes	Hubbs 1968	<a href="#">Encyclopedia of Life</a> <a href="#">Cabrillo Marine Aquarium</a>	yes
71	<i>Myliobatis californica</i>	yes	Gray et al. 1997 Zacharias et al. 2006	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
72	<i>Mycteroperca/Epinephelus</i> sp.		Arizmendi-Rodriguez et al. 2014		yes
73	<i>Hypsurus caryi</i>	yes		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
74	<i>Antennarius avalonis</i>			<a href="#">FishBase</a> <a href="#">Discover Life</a>	yes
75	<i>Gymnura marmorata</i>			<a href="#">Encyclopedia of Life</a> <a href="#">IUCN</a>	yes
76	<i>Zapteryx exasperata</i>		Espinoza et al. 2013	<a href="#">FishBase</a> <a href="#">Discover Life</a>	yes
77	<i>Anisotremus interruptus</i>			<a href="#">Encyclopedia of Life</a>	yes
78	<i>Sphoeroides annulatus</i>		Arizmendi-Rodriguez et al. 2014	<a href="#">FishBase</a> <a href="#">Discover Life</a>	yes
79	<i>Calamus brachysomus</i>			<a href="#">FishBase</a> <a href="#">Discover Life</a>	yes
80	<i>Torpedo californica</i>	yes	Fowler 2005		yes
81	<i>Cynoscion parvipinnis</i>		Rowell et al. 2010		yes
82	<i>Kathetostoma averruncus</i>			<a href="#">FishBase</a> <a href="#">Discover Life</a>	yes
83	<i>Pristigenys serrula</i>			<a href="#">FishBase</a>	yes
84	<i>Pugettia producta</i>			<a href="#">Encyclopedia of Life</a> <a href="#">Walla Walla University</a>	yes
85	<i>Heterostichus rostratus</i>	yes		<a href="#">Encyclopedia of Life</a> <a href="#">Cabrillo Marine Aquarium</a>	yes
86	Polychaeta		Morales-Zárate et al. 2011	<a href="#">Encyclopedia of Life</a>	yes
87	Anomura		Morales-Zárate et al. 2011		yes

88	<i>Centrostephanus coronatus</i>		Vance 1979		yes
89	<i>Megastraea undosa</i>	yes	Zacharias et al. 2006 Morales-Zárate et al. 2011	<a href="#">Encyclopedia of Life</a>	yes
90	Echinodermata		Morales-Zárate et al. 2011	<a href="#">Encyclopedia of Life</a>	yes
91	<i>Kelletia kelletii</i>			<a href="#">Encyclopedia of Life</a>	yes
92	<i>Megathura crenulata</i>	yes	Morales-Zárate et al. 2011 Mazariegos-Villarreal et al. 2013	<a href="#">Encyclopedia of Life</a>	yes
93	<i>Strongylocentrotus purpuratus</i>		Kato et al. 1985 Tegner 1989	<a href="#">Encyclopedia of Life</a> <a href="#">Animal Diversity Web</a>	yes
94	<i>Norrissia norrissii</i>	yes			yes
95	<i>Lopholithodes</i> sp.			<a href="#">Encyclopedia of Life</a>	yes
96	<i>Parastichopus parvimensis</i>				yes
97	Phytoplankton				yes
98	<i>Haliotis fulgens</i>	yes	Tutschulte et al. 1988 Guzman del Proo et al. 2003		yes
99	<i>Haliotis corrugata</i>		Tutschulte et al. 1988 Guzman del Proo et al. 2003 Morales-Zárate et al. 2011	<a href="#">Encyclopedia of Life</a>	yes
100	<i>Eucidaris thouarsii</i>				yes
101	<i>Tegula</i> sp.			<a href="#">Encyclopedia of Life</a> <a href="#">California State University</a>	yes
102	Other algae				yes
103	<i>Taliepus nuttallii</i>				yes
104	<i>Phyllospadix torreyi</i>				yes
105	<i>Eisenia arborea</i>				yes
106	<i>Cystoceira osmundacea</i>				yes
107	Bivalves				yes
108	<i>Cancer magister</i>	yes		<a href="#">Encyclopedia of Life</a>	yes
109	<i>Alopias pelagicus</i>			<a href="#">Encyclopedia of Life</a>	yes
110	<i>Bodianus diplotaenia</i>			<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
111	<i>Carcharhinus porosus</i>		Lessa et al. 1997	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">IUCN</a>	yes

112	<i>Caulolatilus affinis</i>		<a href="#">Encyclopedia of Life</a>	yes
113	<i>Eucinostomus spp.</i>	Arizmendi-Rodriguez et al. 2014		yes
114	<i>Isurus oxyrinchus</i>		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">IUCN</a>	yes
115	<i>Menticirrhus undulatus</i>		<a href="#">Encyclopedia of Life</a>	yes
116	<i>Mustelus californicus</i>		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
117	<i>Pontinus vaughani</i>		<a href="#">Encyclopedia of Life</a>	yes
118	<i>Rhinoptera steindachneri</i>	Navarro-González et al. 2012	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes
119	<i>Trachinotus kennedyi</i>		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">IUCN</a>	yes
120	<i>Trachinotus paitensis</i>		<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a> <a href="#">IUCN</a>	yes
121	<i>Prionace glauca</i>	yes	<a href="#">FishBase</a> <a href="#">Encyclopedia of Life</a>	yes

**Table 2.5** - Sources of diet data (i.e. trophic interactions) for each node. They are organized based on identification code (ID\_code; increasing order). The sources are split up into: Kelpforest Database (Beas-Luna et al. 2014), literature, online datasets (for which I reported hyperlink connections) and knowledge of experts.

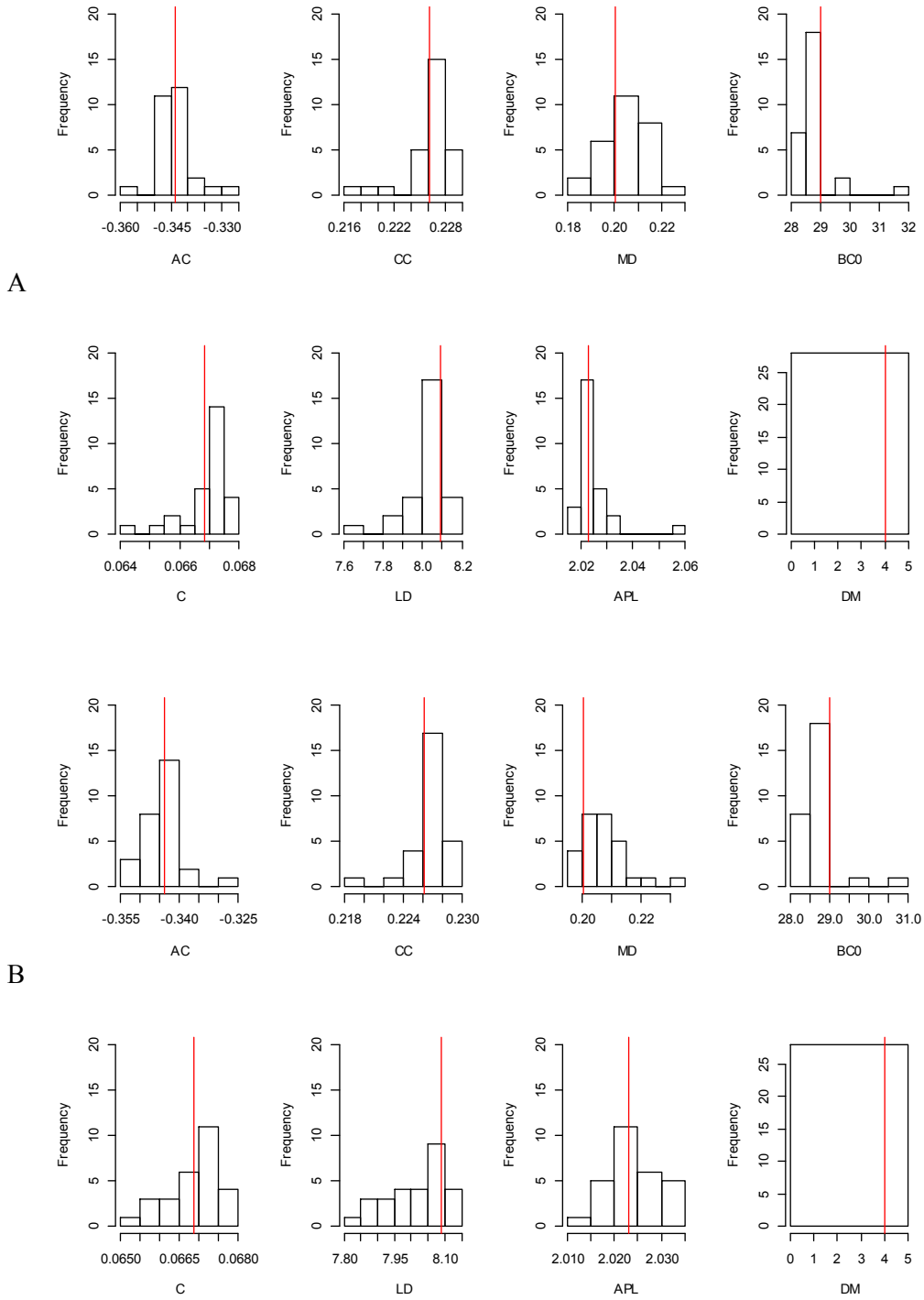
## 2.5.2 Results

Node	Degree			Betweenness		Closeness		ID_code	Res	V
	TL	D <sub>i</sub>	D <sub>in</sub>	D <sub>out</sub>	BC <sub>i</sub>	undBC <sub>i</sub>	undCC <sub>i</sub>			
Phytoplankton	1.000	20	0	20	0.00000	0.01237	0.52174	97		
Other algae	1.000	27	0	27	0.00000	0.02670	0.54054	102		
<i>Phyllospadix torreyi</i>	1.000	16	0	16	0.00000	0.00487	0.44610	104	*	
<i>Eisenia arborea</i>	1.000	21	0	21	0.00000	0.01340	0.49587	105	*	Low
<i>Cystoceira osmundacea</i>	1.000	11	0	11	0.00000	0.00163	0.42403	106	*	
<i>Parastichopus parvimensis</i>	1.000	6	0	6	0.00000	0.00028	0.41522	96	*	Med
Polychaeta	2.000	55	3	52	0.00385	0.07207	0.64171	86		
<i>Norrissia norrissii</i>	2.000	14	4	10	0.00280	0.00401	0.51502	94	*	
<i>Haliotis fulgens</i>	2.000	10	3	7	0.00046	0.00106	0.47244	98	*	Med
<i>Haliotis corrugata</i>	2.000	10	4	6	0.00098	0.00167	0.47059	99	*	Med
<i>Eucidaris thourarsii</i>	2.000	6	3	3	0.00023	0.00065	0.39088	100	*	Low
<i>Taliepus nuttallii</i>	2.000	2	2	0	0.00000	0.00001	0.35398	103	*	
<i>Megastraea undosa</i>	2.250	13	4	9	0.00056	0.00164	0.49793	89	*	Low
Anomura	2.333	19	3	16	0.00088	0.00856	0.51064	87		
<i>Mesocentrotus franciscanus</i>	2.400	13	5	8	0.00055	0.00228	0.47619	52	*	Med
<i>Strongylocentrotus purpuratus</i>	2.400	13	5	8	0.00079	0.00236	0.44610	93	*	Med
<i>Tegula</i> sp.	2.400	13	5	8	0.00461	0.00403	0.49587	101		
<i>Kyphosus analogus</i>	2.500	8	6	2	0.00016	0.00141	0.45627	35	*	Low
<i>Pugettia producta</i>	2.600	31	6	25	0.00424	0.01680	0.53097	84	*	
<i>Girella nigricans</i>	2.625	16	8	8	0.00138	0.00653	0.50209	32	*	Med
<i>Megathura crenulata</i>	2.708	12	6	6	0.00095	0.00172	0.49180	92	*	Low
<i>Centrostephanus coronatus</i>	2.714	12	7	5	0.00044	0.00216	0.47619	88	*	
<i>Lopholithodes</i> sp.	2.737	5	3	2	0.00009	0.00025	0.45455	95		
Zooplankton	3.000	43	2	41	0.00061	0.05226	0.59701	37		
<i>Pleurancodes planipes</i>	3.000	10	2	8	0.00016	0.00113	0.43478	44	*	
Bryozoan	3.000	21	2	19	0.00071	0.00533	0.50000	53		
<i>Hinnites multirugosus</i>	3.000	4	2	2	0.00004	0.00015	0.41237	54	*	
Porifera	3.000	12	2	10	0.00047	0.00246	0.45455	55		
Gorigonaceae	3.000	2	2	0	0.00000	0.00000	0.37855	57		
Bivalves	3.000	33	2	31	0.00090	0.02216	0.56872	107		
<i>Medialuna californiensis</i>	3.122	15	11	4	0.00075	0.00612	0.52632	36	*	Med
<i>Chromis punctipinnis</i>	3.192	27	8	19	0.00214	0.01046	0.55556	23	*	Med
Echinodermata	3.210	32	12	20	0.01140	0.02170	0.54054	90		
Shrimp	3.333	70	4	66	0.00303	0.12018	0.69364	39		
<i>Kelletia kelletii</i>	3.352	14	5	9	0.00200	0.00185	0.49793	91	*	
<i>Loxorhynchus crispatus</i>	3.435	16	10	6	0.00395	0.00572	0.52632	51	*	
<i>Panulirus interruptus</i>	3.571	36	19	17	0.01250	0.01958	0.56872	47	*	Low
<i>Myliobatis californica</i>	3.602	15	13	2	0.00185	0.00489	0.50420	71	*	High
<i>Cancer anthonyi</i>	3.627	30	11	19	0.00940	0.01213	0.56604	49	*	Low
<i>Brachyistius frenatus</i>	3.636	13	7	6	0.00034	0.00146	0.51282	50	*	Med
Crabs	3.718	69	9	60	0.02364	0.12610	0.68966	46		
<i>Eucinostomus</i> spp.	3.752	10	7	3	0.00053	0.00163	0.50420	113		
<i>Balistes polylepis</i>	3.844	13	12	1	0.00027	0.00582	0.51064	67	*	Low

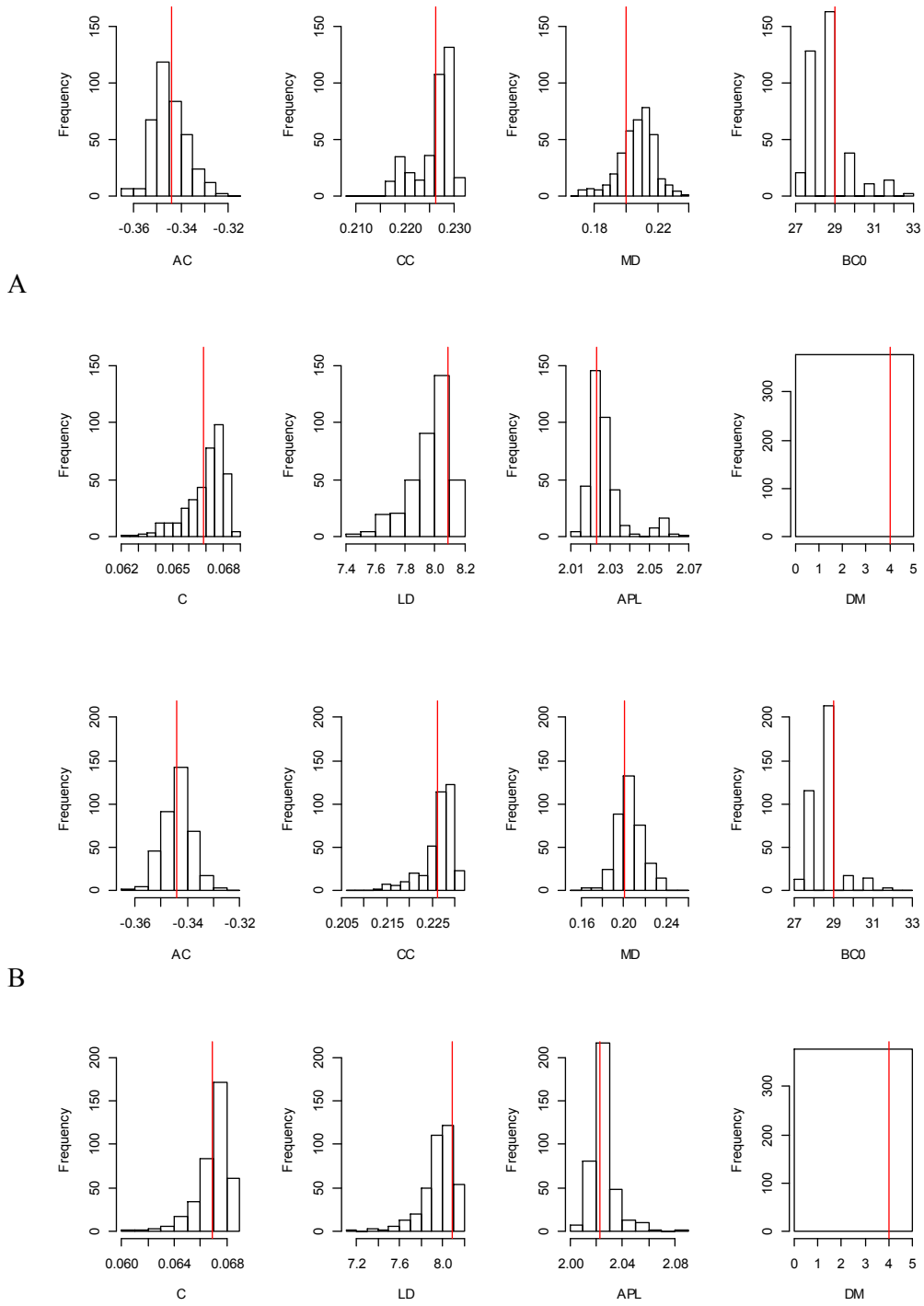
<i>Anisotremus interruptus</i>	3.846	6	4	2	0.00009	0.00036	0.46154	77	*	Low
<i>Sardinops sagax</i>	3.865	20	6	14	0.00164	0.00522	0.52632	15	*	Low
<i>Rhinobatos productus</i>	3.877	7	5	2	0.00009	0.00041	0.47431	61	*	High
<i>Bodianus diplotaenia</i>	3.895	10	7	3	0.00095	0.00388	0.50209	110	*	
<i>Callinectes bellicosus</i>	3.909	8	6	2	0.00019	0.00083	0.48387	48	*	Low
<i>Halichoeres semicinctus</i>	3.911	14	9	5	0.00308	0.00529	0.51948	66	*	Low
<i>Semicossyphus pulcher</i>	3.922	32	24	8	0.00796	0.02670	0.56872	24	*	High
<i>Heterodontus francisci</i>	3.929	16	15	1	0.00057	0.00780	0.52174	31	*	High
<i>Anisotremus davidsoni</i>	3.952	10	8	2	0.00012	0.00076	0.49587	70	*	High
<i>Embiotoca jacksoni</i>	3.961	22	12	10	0.00203	0.00579	0.52632	29	*	Med
<i>Rhacochilus vacca</i>	3.962	19	12	7	0.00132	0.00492	0.52174	64	*	Med
<i>Cancer magister</i>	3.969	16	7	9	0.00177	0.00166	0.51724	108	*	
<i>Hypsurus caryi</i>	3.980	12	7	5	0.00021	0.00083	0.50209	73	*	High
Clupeids (anchovies, herrings)	4.000	31	1	30	0.00026	0.01882	0.52174	41	*	
<i>Porichthys notatus</i>	4.013	18	5	13	0.00260	0.00415	0.51282	40	*	Med
Squids	4.013	49	5	44	0.00337	0.04859	0.61538	42		
<i>Trachinotus kennedyi</i>	4.013	6	4	2	0.00009	0.00021	0.47431	119	*	
<i>Trachinotus paitensis</i>	4.013	6	4	2	0.00009	0.00021	0.47431	120	*	
<i>Menticirrhus undulatus</i>	4.017	4	3	1	0.00002	0.00005	0.45627	115	*	
Cottidae	4.017	11	2	9	0.00031	0.00105	0.44610	1	*	
<i>Urolophus halleri</i>	4.037	7	6	1	0.00004	0.00028	0.48193	69	*	High
<i>Hypsypops rubicundus</i>	4.038	22	12	10	0.00219	0.00519	0.53097	26	*	Low
<i>Caulolatilus princeps</i>	4.055	14	10	4	0.00220	0.00411	0.52402	22	*	Med
<i>Oxyjulis californica</i>	4.073	25	15	10	0.00503	0.00997	0.55300	25	*	Med
<i>Microlepidotus inornatus</i>	4.099	8	6	2	0.00019	0.00081	0.48980	56	*	Med
<i>Calamus brachysomus</i>	4.149	5	4	1	0.00005	0.00031	0.46154	79	*	Med
<i>Octopus</i> sp.	4.156	58	21	37	0.11120	0.08949	0.63492	27	*	High
<i>Rhacochilus toxotes</i>	4.183	15	9	6	0.00046	0.00193	0.51724	63	*	Med
<i>Rhinoptera steindachneri</i>	4.210	6	6	0	0.00000	0.00034	0.48000	118	*	
<i>Mola mola</i>	4.321	11	8	3	0.00034	0.00235	0.51502	45	*	
<i>Platyrrhinoidis triseriata</i>	4.332	14	13	1	0.00011	0.00365	0.51724	8	*	High
<i>Prionace glauca</i>	4.338	14	12	2	0.00035	0.00457	0.52174	121	*	
<i>Mustelus californicus</i>	4.358	9	9	0	0.00000	0.00132	0.48387	116	*	
<i>Zapteryx exasperata</i>	4.370	6	6	0	0.00000	0.00004	0.48193	76	*	High
<i>Caulolatilus affinis</i>	4.370	6	6	0	0.00000	0.00004	0.48193	112	*	
<i>Paralabrax nebulifer</i>	4.423	21	17	4	0.00054	0.00491	0.53812	34	*	Med
<i>Scorpaenichthys marmoratus</i>	4.451	20	18	2	0.00305	0.00668	0.53097	3	*	Med
<i>Atractoscion nobilis</i>	4.469	12	11	1	0.00002	0.00121	0.50847	20	*	High
<i>Heterostichus rostratus</i>	4.479	18	12	6	0.00901	0.00167	0.48387	85	*	Med
<i>Sebastes auriculatus</i>	4.483	17	8	9	0.00369	0.00328	0.52863	38	*	
<i>Cheilotrema saturnum</i>	4.495	8	3	5	0.00019	0.00053	0.46693	68	*	Med
<i>Antennarius avalonis</i>	4.526	2	2	0	0.00000	0.00000	0.43321	74	*	Med
<i>Scomber japonicus</i>	4.599	20	9	11	0.00341	0.00410	0.53097	18	*	Low
<i>Paralabrax clathratus</i>	4.612	47	37	10	0.08884	0.03625	0.60302	6	*	Med
<i>Seriola lalandi</i>	4.641	13	10	3	0.00024	0.00181	0.50420	17	*	Med
<i>Phalacrocorax pelagicus</i>	4.661	13	13	0	0.00000	0.00355	0.48980	2	*	Med
<i>Synodus lucioceps</i>	4.673	7	2	5	0.00002	0.00020	0.47244	60	*	Low
<i>Gymnura marmorata</i>	4.684	3	3	0	0.00000	0.00005	0.44610	75	*	High

<i>Pristigenys serrula</i>	4.718	1	1	0	0.00000	0.00000	0.40956	83	*	Low
<i>Pelecanus occidentalis</i>	4.783	5	5	0	0.00000	0.00020	0.47809	33	*	
<i>Sphoeroides annulatus</i>	4.794	5	5	0	0.00000	0.00012	0.46875	78	*	High
<i>Pontinus vaughani</i>	4.805	4	4	0	0.00000	0.00000	0.46693	117	*	
<i>Scorpaena guttata</i>	4.805	20	18	2	0.01052	0.00311	0.52863	10	*	Med
<i>Mycteroperca/Epinephelus</i> sp.	4.826	15	10	5	0.00717	0.00310	0.50209	72		
<i>Larus occidentalis</i>	4.853	7	7	0	0.00000	0.00055	0.45455	58	*	
<i>Squalus acanthias</i>	4.858	14	13	1	0.00000	0.00258	0.50209	7	*	High
Jellyfish	4.859	13	3	10	0.00163	0.00254	0.48583	43		
<i>Triakis semifasciata</i>	4.865	22	20	2	0.00401	0.00484	0.53333	9	*	High
<i>Sarda chiliensis</i>	4.879	9	7	2	0.00377	0.00233	0.49587	14	*	High
<i>Pteroplatytrygon violacea</i>	4.889	11	9	2	0.00284	0.00076	0.49793	65	*	Med
<i>Raja rhina</i>	4.895	8	8	0	0.00000	0.00067	0.47431	59	*	High
<i>Peprilus</i> sp.	4.930	7	2	5	0.00025	0.00085	0.41379	11		
<i>Gymnothorax mordax</i>	4.940	12	11	1	0.00076	0.00056	0.51282	28	*	High
<i>Phoca vitulina</i>	4.948	19	19	0	0.00000	0.00486	0.52863	5	*	High
<i>Cephaloscyllium ventriosum</i>	4.970	7	4	3	0.00015	0.00024	0.46154	62	*	High
<i>Sphyrna argentea</i>	5.004	16	11	5	0.01610	0.00346	0.49793	19	*	High
<i>Paralichthys californicus</i>	5.034	40	30	10	0.07083	0.02142	0.57692	4	*	High
<i>Stereolepis gigas</i>	5.072	30	28	2	0.02952	0.01337	0.55814	21	*	High
<i>Kathetostoma averruncus</i>	5.084	2	2	0	0.00000	0.00000	0.40816	82	*	Med
<i>Alopias pelagicus</i>	5.084	2	2	0	0.00000	0.00000	0.40816	109	*	
<i>Tursiops truncatus</i>	5.094	14	13	1	0.00057	0.00259	0.50633	30	*	High
<i>Zalophus californianus</i>	5.100	24	24	0	0.00000	0.00893	0.51948	16	*	High
<i>Carcharhinus porosus</i>	5.140	12	11	1	0.00020	0.00331	0.49180	111	*	
<i>Sphyrna</i> sp.	5.151	25	23	2	0.00386	0.01892	0.54545	12		
<i>Cynoscion parvipinnis</i>	5.156	2	1	1	0.00000	0.00000	0.41379	81	*	High
<i>Squatina californica</i>	5.230	14	13	1	0.00042	0.00333	0.51502	13	*	High
<i>Torpedo californica</i>	5.272	7	7	0	0.00000	0.00025	0.45113	80	*	High
<i>Isurus oxyrinchus</i>	5.473	15	15	0	0.00000	0.00369	0.50000	114	*	

**Table 2.6** - Centrality indices of the 121 species in the Baja California Sur food web. Species are ordered based on trophic level (TL; increasing order). See index names in text and equations in Appendix 2.5.1. The asterisk (Res column, standing for the node resolution) indicates whether the node identifies a single species (i.e. absence of the asterisk stands for nodes that represent trophospecies). The last column (V) specifies how nodes are considered (i.e. low/medium/high risk) according to vulnerability score (Micheli et al. 2014).

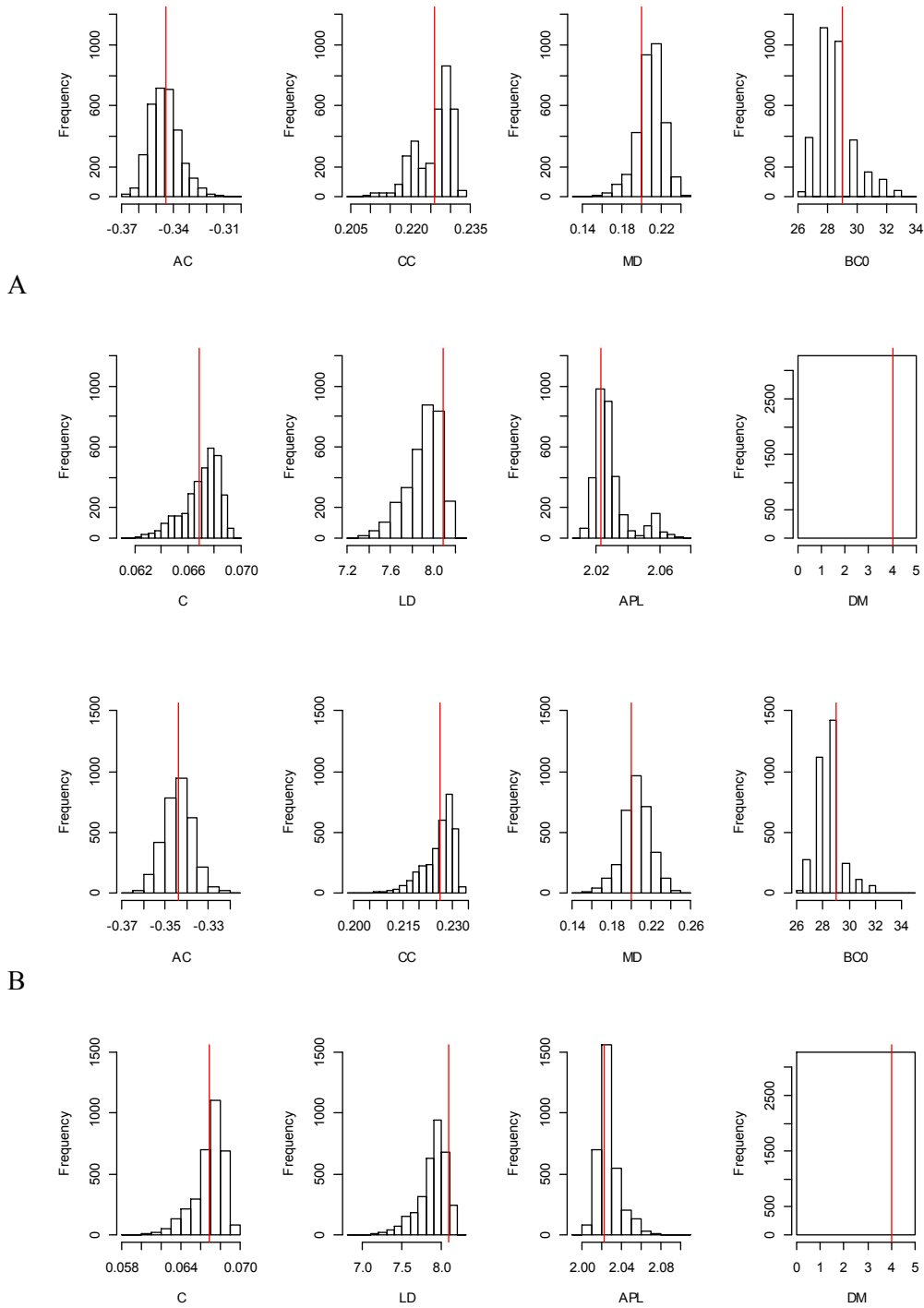


**Figure 2.8** – Frequency histograms for global structural indices following removal of one species (28 combinations): high risk species removal (A) and random removals (B). In each chart the red line shows the value of the given index for the food web with no removals.



**Figure 2.9** – Frequency histograms for global structural indices following removals of two species (378 combinations): high risk species removal (A) and random removals (B). In each chart the red line shows the value of the given index for the food web with no removals.

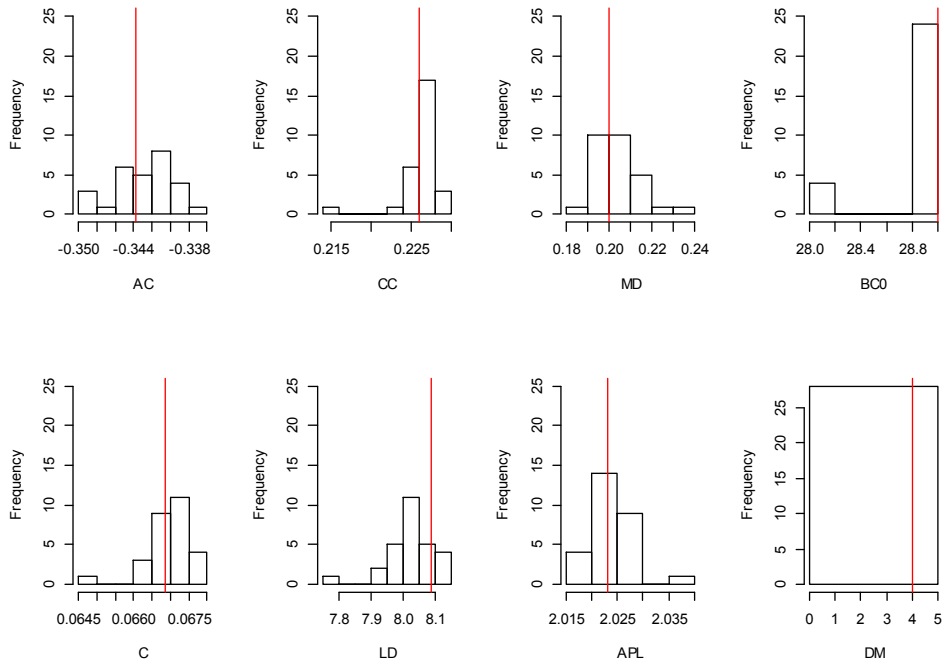




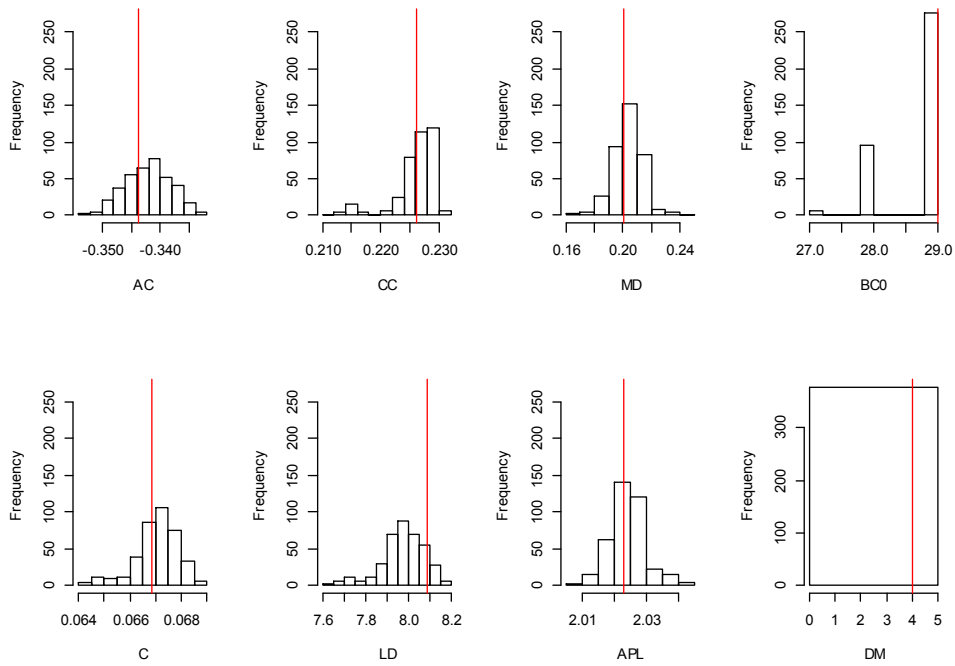
**Figure 2.10** – Frequency histograms for global structural indices following removal of three species (3,276 combinations): high risk species removal (A) and random removals (B). In each chart the red line shows the value of the given index for the food web with no removals.

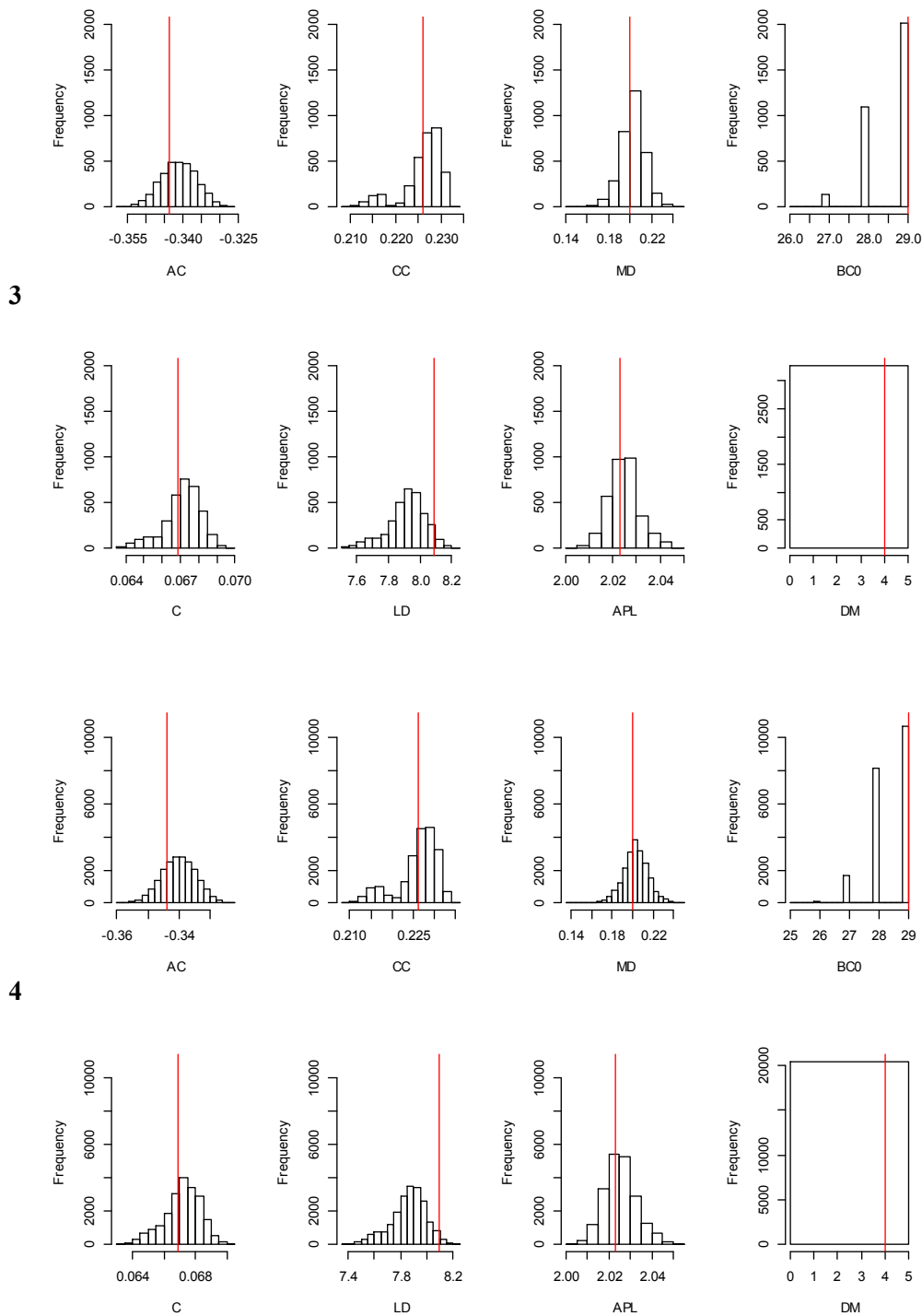
# Species removed

1



2

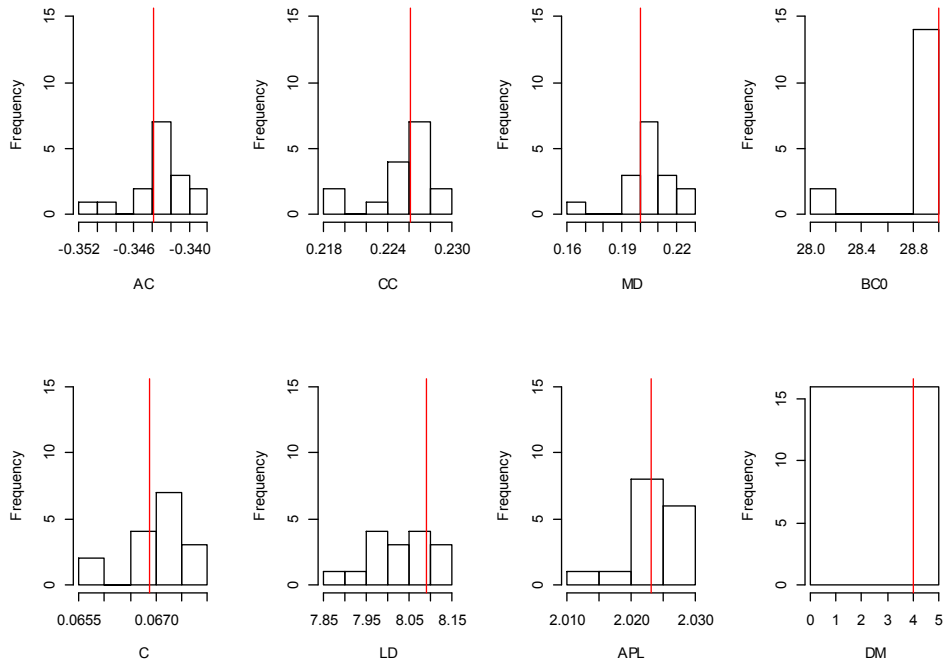




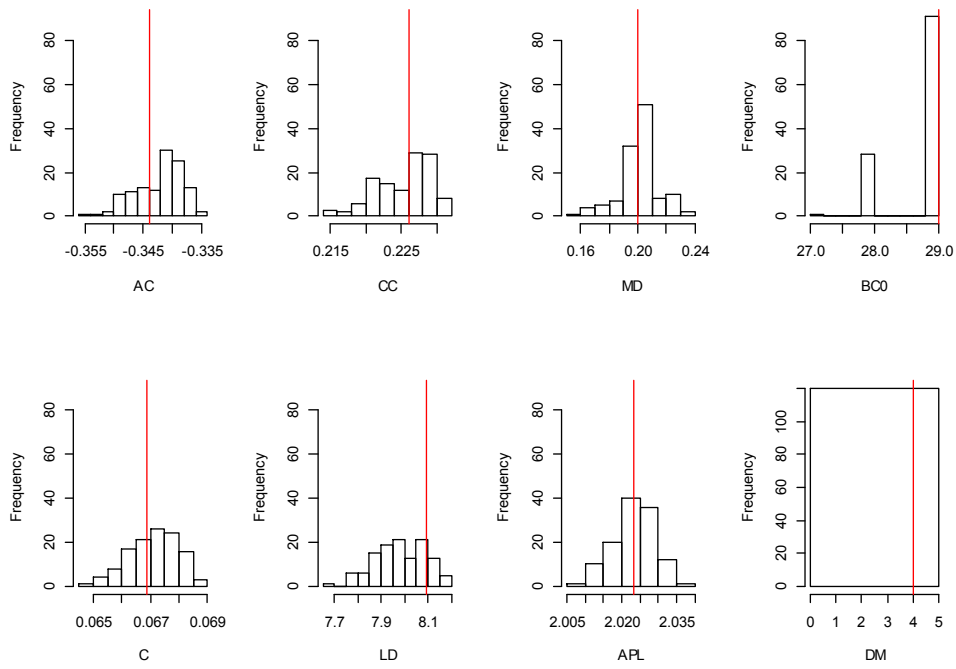
**Figure 2.11** – Frequency histograms for global structural indices in case of medium risk species removals. They refer to results obtained under different scenarios of species removals (Species removed). In each chart the red line shows the value of the given index for the food web with no removals. I omitted the comparison with random removals scenarios because they have already been illustrated in the Figure 2.8 – 2.10 that included the removal scenarios with high risk species.

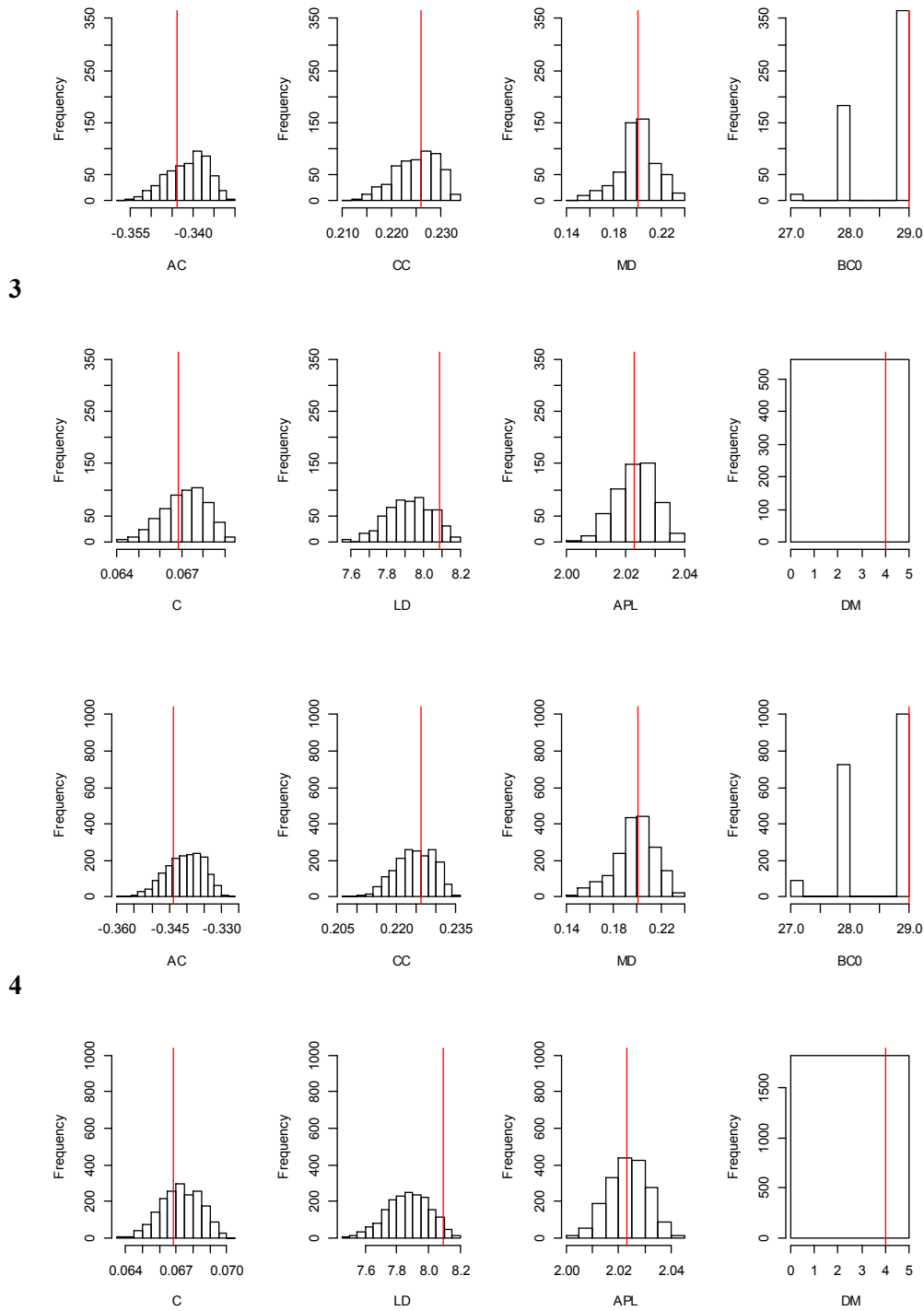
# Species removed

1



2





**Figure 2.12** – Frequency histograms for global structural indices in case of low risk species removals. They refer to results obtained under different scenarios of species removals (Species removed). In each chart the red line shows the value of the given index for the food web with no removals. I omitted the comparison with random removals scenarios because they have already been illustrated in the Figure 2.8 – 2.10 that included the removal scenarios with high risk species.





























## **Ecological disturbance:**

### **exploring causal drivers of ecological change by qualitative modelling**

#### **3.1 Insights into the ecology of the Black Sea**

<sup>6</sup>During the period 1960-2000 the Black Sea ecosystem underwent deep modifications. Overfishing (Prodanov et al. 1997; Daskalov 2002; Gucu 2002), excess nutrient loading (Mee 1992; Zaitsev 1992) and the presence of invasive species (Shiganova 1998; Kideys and Romanova 2001; Kideys 2002) have been indicated as major drivers for community reorganization. These triggered a series of processes that culminated in the shift from a planktonic food chain, whose backbone was the zooplankton-planktivores-piscivores grazing chain, to a web in which the main flow of energy was diverted to jellyfish (Shushkina and Musayeva 1990; Mills 1995). In particular, such transition has been highlighted by the outburst of the comb jellyfish *Mnemiopsis leidyi* and the contemporary collapse of the planktivorous (mainly anchovy) stock (Oguz et al. 2008a,b). Ecologists directed their efforts toward disentangling causative mechanisms of these transformations with emphasis on the relative importance and balancing of bottom-up forcing and top-down cascades (Bănanu et al. 2010). The bulk of the investigations converged to indicate overfishing as the main driver of community reorganization (Daskalov 2002; Oguz and Gilbert 2007; Llope et al. 2011). Alternative views included climate, eutrophication, and invasive species as possible causes of change. One question of interest is how the interplay between these drivers determined the observed changes in the Black Sea (Daskalov 2002; Oguz and Gilbert 2007). Such interplay is problematic to unravel because the reticulate of connections between species in the community makes causal linkages inherently difficult to grasp. Most research conducted on regime shift in the Black Sea ecosystem exploited the information contained in the time series of species biomasses (Daskalov et al. 2007; Oguz and Velikova 2010). To explore the causality behind the changes in consumer/resource populations, the relationships between adjacent trophic levels were investigated (Daskalov et al. 2007). Annual averages of each trophic level biomass were used as

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<sup>6</sup> Submitted chapter: Bodini, A., Rocchi, M., Scotti, M. Insights into the ecology of the Black Sea through the qualitative loop analysis of the community structure. *Limnology and Oceanography*.

the response variable and regressed against other trophic levels and environmental variables (Daskalov et al. 2007). All these data handlings were conducted in the framework of bottom-up vs. top-down control as reference scheme for interpretation. Models have been also introduced in support of these analyses. Mass-balance models (Daskalov 2002; Akoglu et al. 2014), energy flow networks (Gucu 2002; Vasas et al. 2007), and dynamical models (Oguz et al. 2001; Oguz et al. 2008b; Llope et al. 2011) were developed to substantiate in terms of interaction mechanisms the evidence from the statistical models.

In this research I did not explore shifts in population levels of one species accompanying the population changes in another to find subsets of causative chains that fit into reference models for interpretation (i.e. the bottom-up or top-down control perspectives). Instead, I focused on the possible propagation of impacts due to drivers from target variables to the rest of the community. Impact propagation occurs through pathways of interactions that emerge from the linkage structure of the community. In this study the whole structure of the interactions becomes the major focus of investigation as possible locus of explanation for the changes that were observed in the biomass trends of relevant variables (e.g. jellyfish, planktivorous, and piscivorous fish). I analyzed the interactive network of the Black Sea ecosystem by applying the qualitative algorithm of loop analysis (Levins 1974, Puccia and Levins 1985). Such algorithm identifies direct and indirect pathways through which impacts can propagate, and allows predicting expected changes in the level of all the system variables under the effect of press perturbations on target variables. I compared model predictions with observed variations (i.e. field data) in the biomass level of the variables. The overall aim of this effort is to shed light on mechanisms responsible for changes in the Black Sea ecosystem. Loop analysis in fact offers the opportunity to connect in a causal perspective the sources of change (i.e. the drivers), the structure of the linkages between the variables, and their patterns of variation (Dambacher and Ramos-Jiliberto 2007). Also, loop analysis predicts changes observed in populations as a function of the whole network of variables rather than referring to pre-defined chains of effects that combine dynamical features of one-link relationships (e.g. phytoplankton-zooplankton, zooplankton-planktivores, or piscivores-planktivores). With this case study I show how loop analysis can be applied for testing hypotheses on the set of interactions responsible for the spreading of perturbations in marine ecosystems.

## **3.2 Methods**

### **3.2.1 Loop analysis**

Loop analysis is a qualitative technique that uses signed digraphs to represent networks of interacting variables (Levins 1974; Puccia and Levins 1985). Variables may represent the abundance or biomass of single species (e.g. *Noctiluca scintillans* or *M. leidy*) as well as groups of species (e.g. edible zooplankton or planktivorous fish). Loop analysis predicts changes in the abundance or biomass of system variables in response to parameter changes targeted to specific

variables (i.e. press perturbations; see Bender et al. 1984; Bodini 2000). An example is a stressor that increases the mortality rate of a species. This increased mortality reduces the growth rate of the target species and this is called negative input. As a result of this input the biomass level of the species can change. Furthermore, such input may propagate its effects to the other species that are connected by the network to the target variable. Variable responses can be calculated by a routine that summarizes in a matrix implementation the algorithm of loop analysis. Main features of the loop analysis algorithm are provided in the Supplemental Information (SI, henceforth; see Appendix A1). The predictions obtained with loop analysis indicate the direction of change for the level of the variables in response to press perturbation on target variables; the responses are expressed as increase (+), decrease (-) or no change (0). These outcomes can be arranged in a table of predictions (SI, Appendix A2). One example of table of predictions is given in Figure 3.1b for the associated model (Figure 3.1a). The entries of any table of predictions denote variations expected in the level (e.g. biomass) of all column variables in response to positive parameter inputs (i.e. perturbations that increase the rate of change of target variables) affecting any row variable. Conventionally, the calculation considers positive inputs; consequences of negative inputs can be obtained by simply reversing the signs in the table. In models with few variables and/or a limited number of connections, expected changes for the variables can be tracked through the graph anatomy (Bodini 1998, 2000). However, when variables and connections increase multiple pathways of interactions are likely to exist. If such pathways have opposite signs, the model yields ambiguous predictions about the response of the variable that is connected to the source of change through these paths. In these cases, a numerical simulation might help. I used a routine that randomly assigns (from a uniform distribution) numerical values in the interval (0,1] to coefficients of the community matrix (i.e. the coefficients of the links in the signed digraph). This procedure and the code for the R statistical environment (R Core Team 2014) are described in the SI, Appendix A3.

### **3.2.2 Model construction**

Signed digraphs were built upon knowledge concerning main trophic interactions (i.e. who eats whom) that characterized the pelagic community of the Black Sea. This knowledge was provided by the vast literature about the ecology of the system. Particular attention was given to what presented in modelling exercises, which included conceptual models (Daskalov et al. 2007; Oguz and Gilbert 2007; Oguz et al. 2008a), dynamic models (Oguz et al. 2001; Oguz et al. 2008b), and mass-balance models (Daskalov 2002; Gucu 2002; Vasas et al. 2007; Akoglu et al. 2014). The presence/absence of certain players led us to identify two phases as for community structure and models: (1) the pre-invasion phase in which *M. leidy* was not present; (2) the post-invasion phase in which *M. leidy* became established as local population after invasion. The structure of the community changed from one period to the next. Also, I could not identify a unique representation of the system within each period. Therefore, alternative graphs (built upon a core model) were

constructed for the different phases (the whole array of alternative graphs is shown in the SI, Appendix B1-B2). All the graphs are equally plausible, on the basis of the ecological information at my disposal. In the models, some variables represent single species (i.e. *N. scintillans* or *M. leidy*), while others lump together many populations (e.g. edible phytoplankton or planktivorous fish). This uneven resolution is justified by the structure of the database. For several groups in fact data were aggregated and considering resolution at the species level could not be possible. Hence, the architecture of the various models came out as a reasonable compromise between the need to describe the system in its complexity and the possibility to use field data to verify model predictions.

### **3.2.3 Data series and statistical analyses**

Oguz and Gilbert (2007) divided the ecological history of the Black Sea in four periods called pre-eutrophication (1960-1970), eutrophication (1970-1980), iper-eutrophication (1980-1990) and post-eutrophication (1990-2000). This partitioning reflected the succession of events that occurred in the ecosystem with reference to its trophic state. Considering the data at my disposal, I focused on the 1960-1990 as main period of investigation. I used annual time series of the groups that entered as variables in my models. Time series for edible phytoplankton and edible zooplankton biomasses were collected from Prodanov et al. (1997). The periods covered are: 1960-1989 for phytoplankton and 1964-1992 for zooplankton. Biomasses of *N. scintillans* (1960-1988) and jellyfish (1960-1988) were obtained from Simonov et al. (1992); in the case of jellyfish the data refer to ctenophores. For planktivorous fish and piscivorous fish, biomass data on both stocks and catches were available. These data were obtained from Prodanov et al. (1997). The time series for planktivorous stock spans from 1967 to 1993. Catch data for this group cover a longer period: from 1950 to 1999. Stock data of piscivorous fish covered the period from 1971 to 1988 and catch data were obtained for the period 1950-1992. The post-eutrophication phase (see Oguz and Gilbert 2007) was not completely covered by my data set. Nonetheless, my time series refer to periods that encompass the main transformations that occurred in the Black Sea, from the eutrophication to the bloom of *M. leidy* in late 1980s.

In the literature it has been shown that a convenient partitioning of the time series to catch significant variations in the abundance of trophic groups considers decadal periods (Gucu 2002; Daskalov et al. 2007; Oguz and Gilbert 2007; Oguz et al. 2012). This is corroborated by the observation that pelagic fish stocks showed marked decadal-scale fluctuations (Daskalov 2003; Oguz et al. 2006; Daskalov et al. 2007). This perfectly matches the main subdivision operated by Oguz and Gilbert (2007) to distinguish different phases determined by the trophic status of the water body. To use proficiently my data set I considered decadal periods but found useful to further partition the time series into periods of 5 years. This helped to grasp significant variations in fish stock time series from 1971 to 1989. Variables such as phytoplankton and zooplankton showed variations that seem to reproduce decadal trends as well (Daskalov 2003; Oguz 2007; Oguz and

Gilbert 2007). In any case, periods of 5 and 10 years seem a reliable timing to identify long term variations in the biomass trends, as required for applying loop analysis (Bodini 1998, 2000). For each and every group of pelagic populations I compared biomass data between consecutive periods in search for significant differences from one period to the next. All statistical comparisons were based on empirical data and performed using the Mann-Whitney  $U$  test in the R statistical environment (R Core Team 2014). Differences along the time series were expected to confirm the classification proposed by Oguz and Gilbert (2007). The outcomes of these comparisons were used as a benchmark for model predictions.

### **3.2.4 Biomass trends and model predictions**

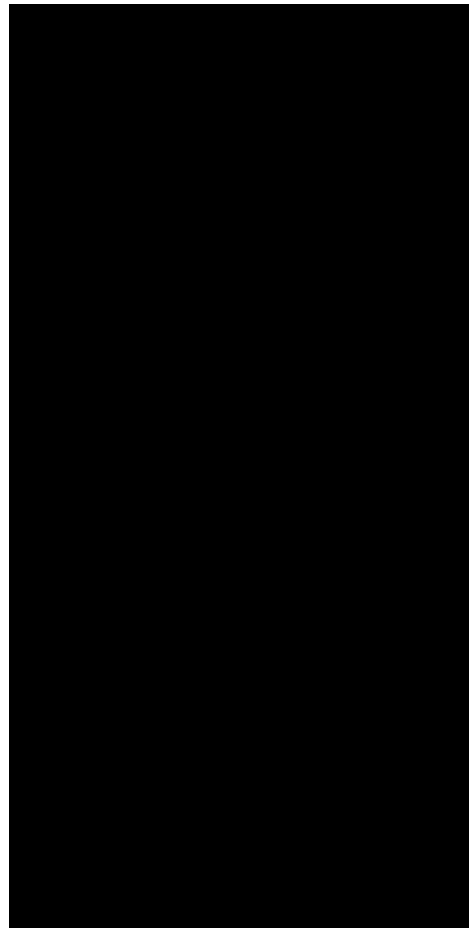
Model predictions were scrutinized in respect to biomass variations between successive periods as detected by the statistical analysis. The statistical analysis identified the variations for the levels of the variables in the empirical dataset. Such variations were compared with the expected direction of change for the variables in response to a parameter change (i.e. as predicted by the model). In ecology it is often the case that the entry point of a parameter change is not known. In the case of the Black Sea, however, several literature sources agree in identifying certain types of perturbations that affected the system and the period in which they occurred (e.g. see Oguz and Gilbert 2007). Therefore, I simulated these perturbations as inputs to specific variables to obtain the expected variations in the biomass of all the variables in the model. Reliable predictions are those that meet statistically significant variations observed in the time series. The non-significant difference in the biomass levels of a variable between successive periods corresponds to a null prediction (i.e. no variation expected for a variable in response to a certain input) (Puccia and Levins 1985). Thus, my approach consists of two steps: (1) using loop analysis to predict the variation expected in the level of all variables following inputs affecting specific target variables, according to the literature; (2) examining the soundness of model predictions with respect to statistically significant variations in the time series data.

## **3.3 Results**

### **3.3.1 Pre-invasion period (1960-1980)**

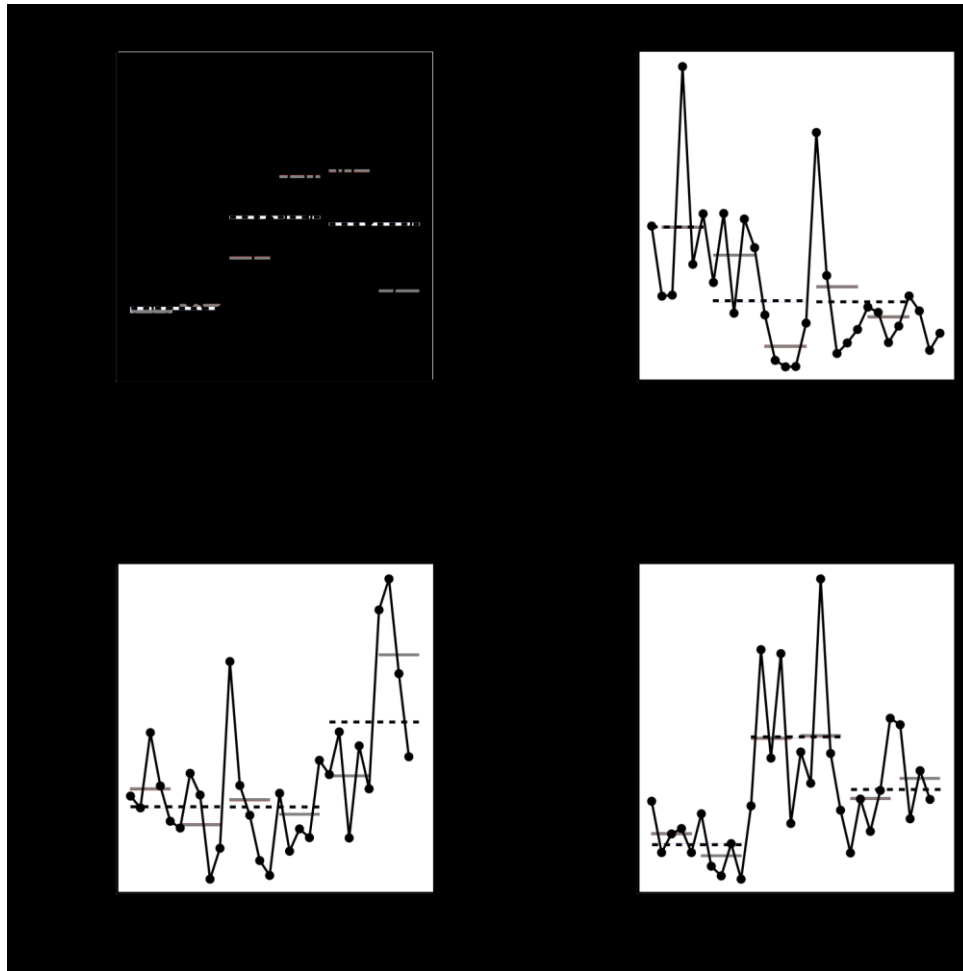
The signed digraph in Figure 3.1a depicts the structure of the trophic interactions of the Black Sea in the pre-invasion period (i.e. before *M. leidy* settled in the Black Sea). This model was selected from a suite of community structure graphs that were investigated for their capability to qualitatively predict changes observed in the biomass trends of the trophic groups. The entire suite of models is reported in the Appendix B1 of SI. The graph in Figure 3.1a corresponds to the 5th model of the pre-invasion period in the Appendix B1. The trophic interactions that make up the community have been constructed on the base of the literature at disposal. With the exception of *N. scintillans*, all variables represent trophic groups. The reason for this choice is that previous

researches on the Black Sea exploited data sets that were organized around groups of pelagic populations (Daskalov et al. 2007; Oguz and Gilbert 2007). *N. scintillans* was reported as a significant component of the trophic web so that data for the single species were collected and made available (Simonov et al. 1992). The fundamental backbone around which the model is constructed is the grazing chain from inorganic nutrients to top predators. Phytoplankton has been divided in two variables: edible and inedible phytoplankton. To this scheme I added also edible zooplankton, and gelatinous organisms such as *N. scintillans* and jellyfish (e.g. *Aurelia aurita*). Planktivores enter the model with two variables: adults and juvenile stages (larvae). This choice can help to detect the possible importance that the larvae of planktivores played in sustaining the bloom of the invader *M. leidy* starting from the 1980s (Oguz et al. 2008a,b). Piscivorous fish, whose main prey is planktivorous fish, are depicted also as feeding upon zooplankton. This takes into account the presence in this group of demersal fish that were described as zooplankton eaters (Gucu 2002).



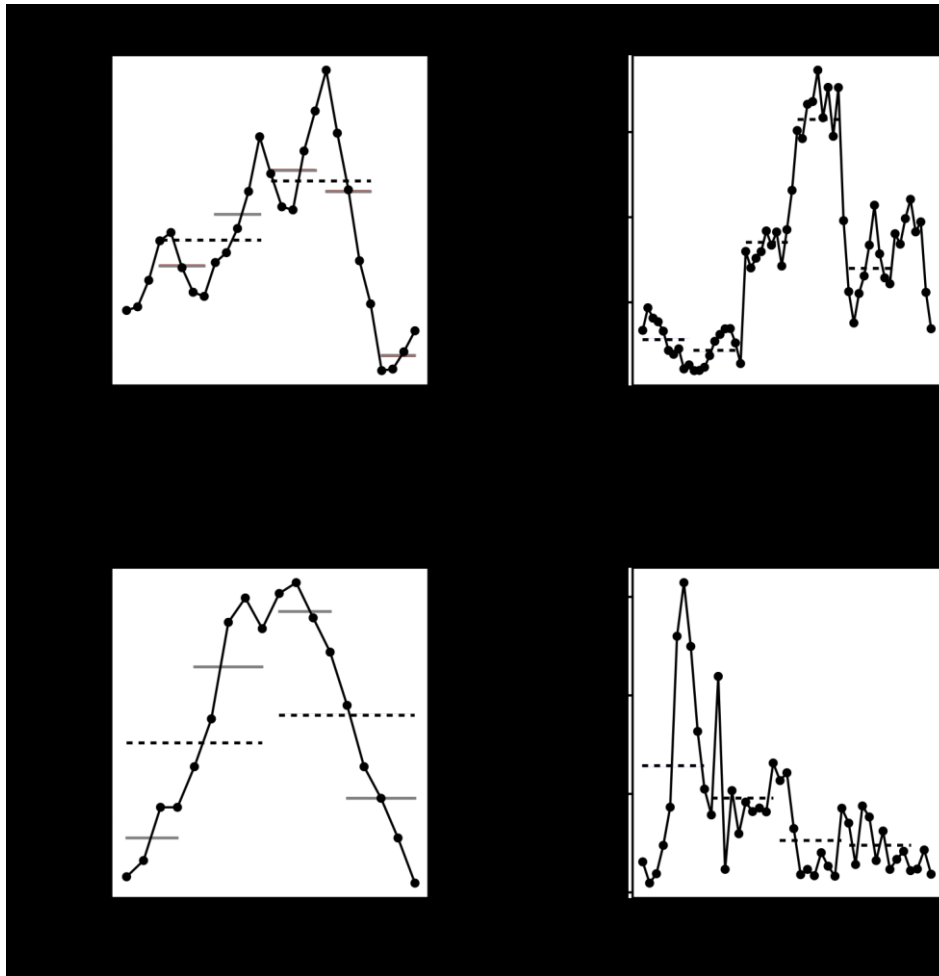
**Figure 3.1** - Signed digraph describing the community structure for the pre-invasion period (a) and its table of predictions (b). All interactions refer to trophic relationships or consumption of resources (i.e. see the connection from nutrients to phytoplankton) except for the mutual (positive) connection between planktivorous fish and their larvae (i.e. such connection describes reproduction and ontogenetic development). Keys for nodes are: inorganic nutrients (N), inedible phytoplankton (IP), edible phytoplankton (EP), *N. scintillans* (NC), edible zooplankton (EZ), jellyfish (J), planktivorous fish (PZ), larvae of planktivorous fish (LPZ), and piscivorous fish (TP).

Figures 3.2 and 3.3 illustrate the data sets for most of the trophic groups that enter as variables in the models. Data availability limited the number of variables for which biomass trends could be reported; in particular, no trends for inorganic nutrients are presented. Figure 3.2 describes the biomass trends for phytoplankton, zooplankton, *N. scintillans*, and jellyfish. The charts in Figure 3.3 show the trends for stocks and catches of planktivorous fish and piscivorous fish. Solid grey lines and dotted black lines in the charts identify average values calculated over periods of 5 and 10 years, respectively. The whole data set is reported in the SI (Appendix C2).



**Figure 3.2** - Biomass time series of phytoplankton (a), zooplankton (b), *N. scintillans* (c), and jellyfish (d). Source data are available in the SI, Appendix C1. Average biomass over periods of 5 and 10 years is visualized with solid gray lines and dotted black lines, respectively.





**Figure 3.3** - Stock and catch time series of planktivorous fish (3a, stock; 3b, catch) and piscivorous fish (3c, stock; 3d, catch). Stocks and catches are expressed as 1,000 tons. Source data are in the SI, Appendix C1. Average biomass over periods of 5 and 10 years is visualized with solid gray lines and dotted black lines, respectively. In the case of catches, for the sake of clarity only average values over periods of 10 years are shown.

Biomasses (which refer to stocks and catches in the case of fish) in the different periods were compared with the Mann-Whitney  $U$  test. Results are reported in Tables 3.1 (plankton groups) and 3.2 (fish).

Group	Data set	10 years			5 years				
		Period	W	p	Period	W	p		
Phytoplankton	1960-1989	<b>1960-69 &lt; 1970-79</b>	<b>16</b>	<b>0.004</b>	**	1960-64 > 1965-69	14	0.421	
						1965-69 < 1970-74	10	0.214	
		1970-79 > 1980-89	49	0.544		<b>1970-74 &lt; 1975-79</b>	<b>5</b>	<b>0.041</b>	*
						1975-79 < 1980-84	11	0.421	
Zooplankton	1964-1992	<b>1964-69 &gt; 1970-79</b>	<b>46</b>	<b>0.047</b>	*	1965-69 > 1970-74	13	0.500	
						<b>1970-74 &gt; 1975-79</b>	<b>25</b>	<b>0.004</b>	**
		1970-79 > 1980-89	50	0.515		1975-79 < 1980-84	6	0.111	
						1980-84 > 1985-89	11	0.655	
<i>Noctiluca scintillans</i>	1960-1988	1960-69 > 1970-79	55	0.370		1960-64 > 1965-69	18	0.155	
						1965-69 < 1970-74	11	0.421	
		<b>1970-79 &lt; 1980-88</b>	<b>16</b>	<b>0.009</b>	**	1970-74 > 1975-79	12	0.579	
						1975-79 < 1980-84	6	0.111	
Jellyfish	1960-1988	<b>1960-69 &lt; 1970-79</b>	<b>4</b>	<b>&lt; 0.001</b>	***	<b>1980-84 &lt; 1985-88</b>	<b>2</b>	<b>0.032</b>	*
						1960-64 > 1965-69	19	0.104	
						<b>1965-69 &lt; 1970-74</b>	<b>1</b>	<b>0.008</b>	**
		1970-79 > 1980-88	62	0.089	.	1970-74 < 1975-79	11	0.421	
				1975-79 > 1980-84	19	0.111			
				1980-84 < 1985-88	7.5	0.311			

**Table 3.1** - Changes in the biomass of planktonic groups in the period 1960-1992. Results of the Mann-Whitney *U* test applied to biomass data of phytoplankton, zooplankton, *N. scintillans*, and jellyfish. Differences refer to periods of either 5 or 10 years. Significant differences in bold.

Group	Data set	10 years			5 years				
		Period	W	p	Period	W	p		
Planktivorous fish (stock)	1967-1993	<b>1970-79 &lt; 1980-89</b>	<b>23</b>	<b>0.022</b>	*	<b>1970-74 &lt; 1975-79</b>	<b>4</b>	<b>0.048</b>	*
						1975-79 < 1980-84	6	0.111	
						1980-84 > 1985-89	14	0.421	
						<b>1985-89 &gt; 1990-93</b>	<b>20</b>	<b>0.008</b>	**
Planktivorous fish (catch)	1950-1999	1950-59 > 1960-69	66	0.124		<b>1950-54 &gt; 1955-59</b>	<b>25</b>	<b>0.004</b>	**
						1955-59 > 1960-64	17	0.210	
		<b>1960-69 &lt; 1970-79</b>	<b>0</b>	<b>&lt; 0.001</b>	***	<b>1960-64 &lt; 1965-69</b>	<b>3</b>	<b>0.028</b>	*
						<b>1965-69 &lt; 1970-74</b>	<b>0</b>	<b>0.004</b>	**
						1970-74 < 1975-79	6	0.111	
		<b>1970-79 &lt; 1980-89</b>	<b>1</b>	<b>&lt; 0.001</b>	***	<b>1975-79 &lt; 1980-84</b>	<b>0</b>	<b>0.004</b>	**
				1980-84 > 1985-89	14	0.421			
				<b>1985-89 &gt; 1990-94</b>	<b>25</b>	<b>0.004</b>	**		
				1990-94 < 1995-99	5	0.075	.		
Piscivorous fish (stock)	1971-1988	1971-79 < 1980-88	32.5	0.254		<b>1971-74 &lt; 1975-79</b>	<b>0</b>	<b>0.010</b>	*
						1975-79 < 1980-84	4	0.095	.
						<b>1980-84 &gt; 1985-88</b>	<b>20</b>	<b>0.008</b>	**
Piscivorous fish (catch)	1950-1992	1950-59 > 1960-69	55	0.370		<b>1950-54 &lt; 1955-59</b>	<b>0</b>	<b>0.004</b>	**
						<b>1955-59 &gt; 1960-64</b>	<b>23</b>	<b>0.016</b>	*
						1960-64 < 1965-69	9	0.273	
		<b>1960-69 &gt; 1970-79</b>	<b>75</b>	<b>0.031</b>	*	1965-69 > 1970-74	17	0.201	
						1970-74 > 1975-79	18	0.155	
		1970-79 > 1980-89	44	0.685		1975-79 < 1980-84	6	0.111	
				1980-84 > 1985-89	19	0.111			

**Table 3.2** - Changes in stock and catch of fish groups in the period 1950-1999. Results of the Mann-Whitney *U* test applied to data about planktivorous and piscivorous fish. Both stocks and catches are measured in terms of biomass. Differences refer to periods of either 5 or 10 years. Significant differences in bold.

Figure 3.1b shows the table of predictions below the community structure graph (Figure 3.1a). This table provides expectations about the direction of change for the level of the column-variables (i.e. the biomass) following positive parameter inputs on the row-variables. Predictions were obtained with a simulation routine based on quantification of interaction coefficients (i.e. link intensities).

Values of link intensities were assigned randomly in the uniform interval (0,1]. The results of the simulations and the predictions for the complete set of models are given in the SI (Appendix B1). The direction of change that the model predicts for each variable following specific input is contrasted with variations in their biomass trends in the period 1960-1980.

(1) *Piscivorous fish*. Although my data set was far from complete, I observed that after 1970 the stock of piscivorous fish increased (Figure 3.3c): it resulted significantly higher in the period 1975-1979 than in 1971-1974 ( $W = 0$ ,  $p = 0.010$ ; Table 3.2). No stock data prior 1970 were available, but I observed that piscivores catch decreased significantly between the 1960s and the 1970s ( $W = 75$ ,  $p = 0.031$ ; Table 3.2). These trends suggest that in the 1970s a release in the fishing pressure could have been beneficial for this group, which started to recover (Daskalov 2002, 2003). The release from fishing pressure can be interpreted as a positive input to piscivorous fish. In the model of Figure 3.1a this positive input is expected to increase the level of piscivorous fish (entry corresponding to last row, last column in the table of predictions; see Figure 3.1b), a prediction that matches with what the stock trend for this group indicates (Table 3.2).

(2) *Planktivorous fish*. The reduced catch of piscivorous fish might have forced fishing activity to switch to planktivorous fish. The significant increase in planktivores catch between the 1960s and the 1970s corroborates this scenario ( $W = 0$ ,  $p < 0.001$ ; Table 3.2). However, Daskalov et al. (2011) did not document any increased mortality for planktivores in the 1970s and no input on planktivores should be considered as due to the increased catch. On the other hand the positive input on piscivorous fish is expected to reduce the level of planktivores, a result that is not coherent with the significant increase that this group showed in the 1970s. The stock of this group in fact augmented significantly from the period 1970-1974 to 1975-1979 ( $W = 4$ ,  $p = 0.048$ ; Table 3.2). The lack of agreement between the model and the data suggests that other causes might have come into play. One such cause is nutrient load. Strong addition of inorganic nutrients (nitrogen and phosphorous) commenced between late 1960s and early 1970s (Oguz and Gilbert 2007). It seems plausible that nutrient load acted as an additional press perturbation on the Black Sea. The increased nutrient supply enters the model as a positive input on the variable N. Predicted effects of this input on fish variables (Figure 3.1b, first row of the table of predictions) are that planktivores increase and piscivores diminish. In the case of piscivores, however, the positive input on nutrients yields a minus sign with a question mark. This result comes from the simulations (SI, Appendix B1; see the 5th model of the pre-invasion period), which yielded 64% of the matrices with a negative prediction and 36% with a positive sign. Thus, the effect of an increased nutrient load percolates up to piscivores through both positive pathways and negative pathways. The prevalence of the negative sign tells us that the tendency for piscivores to decrease is prevailing, but also that the magnitude of this change can be mitigated by the effect of opposite pathways. It is not unrealistic to hypothesize that the overall effect of the two inputs (i.e. reduced catch and increased nutrient load) on piscivores is of an increase, in agreement with their stock trend. The two inputs have opposite effects on the level of planktivores. For predictions to be in agreement with stock

trend the contribution of the positive input on nutrients must predominate over the negative effect due to the reduced mortality of piscivores. A quantitative assessment would be necessary to resolve this uncertainty but this requires that the intensity of interaction links is known. Nevertheless, predictions suggest that the increase in the level of planktivores stock is a plausible scenario although it requires that conditions over the strength of the paths and consequently on links are met. If the effect of the positive input on nutrients prevails over that induced by the positive input on the piscivores, still the overall effect on the piscivores can remain positive. The question mark that appears in the predictions about the level of piscivores for input on nutrients reveals that a counterbalance between opposite pathways is at work. This counterbalance may reduce noticeably the magnitude of the resulting negative effect. Thus, it is reasonable expecting that the negative effect due to nutrient overload may be compensated by the positive input on piscivores in determining the biomass level of this latter component.

Besides effects on fish stocks, the combined action of the two inputs must have reflected on the other variables as well. Figure 3.2 shows biomass trends for groups other than fish.

(3) *Jellyfish*. The biomass of jellyfish increased significantly between late 1960s and early 1970s ( $W = 1$ ,  $p = 0.008$ ; Table 3.1). In particular, this increase occurred between 1969 and 1971, when the biomass of jellyfish peaked (despite fluctuations, the biomass of jellyfish remained high for all the 1970s). The two inputs produce opposite predictions on this variable and matching predictions with data is possible only by assuming that the effect of the increased nutrient load prevails.

(4) *N. scintillans*. The biomass of *N. scintillans* fluctuated widely. Averages taken over periods of 5 and 10 years between 1960 and 1980 did not show any significant variation (see Figure 3.2c and Table 3.1). This component is predicted to increase by the model: the lack of variation shown by the biomass trend does not accommodate at all in this predictive framework.

(5) *Zooplankton*. The biomass of this group declined during the period 1970-1980 (Figure 3.2b). Its decrease began in late 1960s and continued for the successive 10 years. In particular, I observed a significant decrease in zooplankton biomass from the period 1970-1974 to the period 1975-1979 ( $W = 25$ ,  $p = 0.004$ ; Table 3.1), to reach the lowest biomass in 1978. The positive input to inorganic nutrients is predicted to decrease the level of the zooplankton, but the positive input on piscivores tends to increase this component. However, the question mark accompanying this latter prediction (Figure 3.1b, last row of the table of predictions) shows that opposite effects are carried by pathways connecting zooplankton to the piscivores, the source of change. This may result in the compensation between positive and negative effects, so that the overall increase that emerged from the simulation could be not too strong in magnitude. Thus, it is reasonable expecting this component to decrease following the two inputs. Indeed, an agreement between model predictions and biomass trend can be possible by considering the effect of the positive input to nutrients greater in magnitude than that produced by the positive input on piscivores.

(6) *Phytoplankton*. The biomass of phytoplankton increased during the 1970s. Its levels in the period 1970-1974 were lower than the levels measured in 1975-1979 ( $W = 5$ ,  $p = 0.041$ ; Table 3.1).

The analysis conducted over decadal periods (1960-1969 and 1970-1979) also reveals a significant increase for this component ( $W = 16$ ,  $p = 0.004$ ; Table 3.1). This might confirm that eutrophication began in late 1960s and continued in the following decade, during which phytoplankton biomass increased continuously (Oguz and Gilbert 2007). Model predictions are compatible with these trends. However, this increase seems to be due exclusively to the increased nutrient load. Indeed, the cascade trophic effect from piscivores due to the positive input on this variable does not affect phytoplankton (0\* prediction).

### 3.3.2 Post-invasion period, with low *M. leidy* biomass (1980-1989)

A second period characterized by strong changes began in the 1980s when the presence of *M. leidy* was detected. Its abundance remained low until the end of the decade (Oguz et al. 2008a); only in 1989 a noticeable increase of this population was reported in the Black Sea (Gucu 2002; Oguz et al. 2008a). A concomitant collapse of planktivorous fish (mainly anchovies) was detected (Oguz et al. 2008a). Since in the first part of the 1980s the presence of *M. leidy* was considered negligible, I decided to use the community structure of Figure 3.1a to analyze the events that took place in that period. Here I compare the main changes predicted by the model with the differences in biomass tested over the period 1980-1989.

(1) *Piscivorous fish and planktivorous fish*. Catch over planktivorous fish increased further between the end of 1970s and early 1980s ( $W = 0$ ,  $p = 0.004$ ; Table 3.2). This was accompanied by an increase in the mortality of the group (Daskalov et al. 2011). However, overfishing does not seem having triggered any effect since no significant changes were detected for the stock of this group between 1980-1984 and 1985-1989 (Table 3.2). On the contrary, the model predicts a reduction in the level of planktivores if their mortality increased (negative input on PZ). In the period 1980-1985 nutrient enrichment of anthropogenic origin reached its highest levels (Daskalov 2003; Oguz and Gilbert 2007). Also, strong nitrate supply into the surface productive layer occurred, due to the enhanced vertical mixing that was induced by lower winter temperatures (Oguz and Gilbert 2007). Therefore, an additional input of nutrients occurred and the model can predict the system response to it if I assume a further positive parameter change in the dynamics of variable N. The model predicts that the response of planktivores to this input is of an increase. Increased mortality and higher resource availability exerted on this group opposite effects, whose compensation may be the reason of the observed lack of variation in their stock. Both inputs are predicted to decrease the level of piscivorous fish. Biomass trend (Figure 3.3c) showed that the stock decreased significantly between 1980-1984 and 1985-1988 ( $W = 20$ ,  $p = 0.008$ ; Table 3.2); in this case the model explains correctly the behavior of the group.

(2) *Jellyfish and N. scintillans*. *N. scintillans* increased in biomass between the 1970s and the 1980s ( $W = 16$ ,  $p = 0.009$ ; Table 3.1). In particular, this difference is due to the strong increase that was observed between 1980-1984 and 1985-1988 ( $W = 2$ ,  $p = 0.032$ ; Table 3.1). Overfishing of planktivorous fish and nutrient overload that occurred during the 1980s must have favored the

growth of this organism and such scenario is reproduced by model predictions; in fact, both inputs are predicted to augment the level of *N. scintillans*. However, I observed discrepancies between model predictions and biomass trends of jellyfish. The data show that the biomass of this group did not change significantly between early 1980s and late 1980s (see Figure 3.2d and Table 3.1) whereas expectations from the model are that both inputs increase jellyfish biomass.

(3) *Zooplankton*. This group did not change significantly neither between decades (1970s vs. 1980s) nor within the 1980s (Table 3.1). The two inputs (positive on nutrients and negative on planktivores) are predicted to change the level of this component in opposite directions; compensation of effects may be the explanation for the lack of significant variations in the level of zooplankton biomass.

(4) *Phytoplankton*. My data set indicates that the period in which phytoplankton increased most noticeably was in the 1970s and its biomass remained high until early 1980s, when it started to decline. Table 3.1 shows that a significant decrease characterized this component in the 1980s: biomass in 1980-1984 was significantly higher than in 1985-1989 ( $W = 22$ ,  $p = 0.028$ ; Table 3.1). This contradicts previous evidence of literature that indicated the 1980s as the period of maximum eutrophication (i.e. a period during which phytoplankton biomass should have increased markedly - intense eutrophication period; Oguz and Gilbert 2007). The model predicts an increase in the level of phytoplankton groups (both edible and inedible) as due to the positive input of inorganic nutrients; the negative input on planktivores increases inedible phytoplankton and decreases edible algae. Overall, model predictions about phytoplankton are not in agreement with the observed trend of its biomass.

### 3.3.3 Post-invasion period, with high *M. leidyi* biomass (1989-1994)

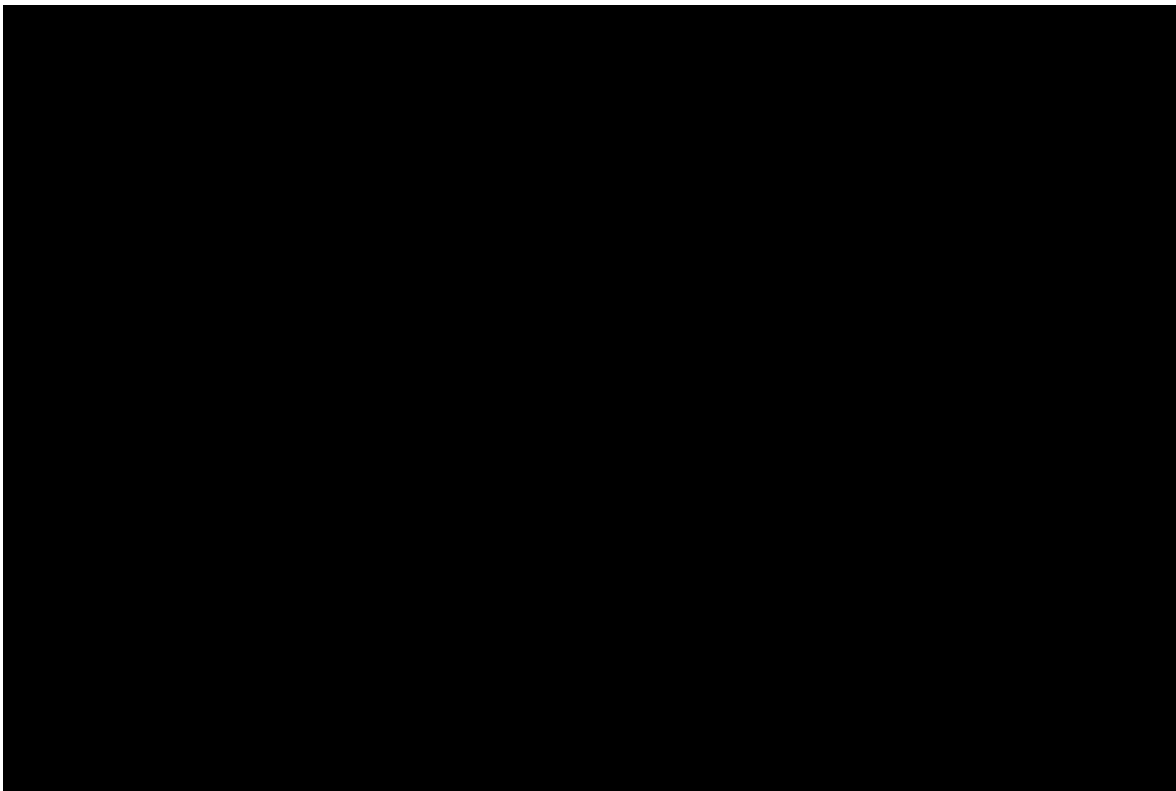
To further investigate the ecosystem response to perturbations in the post-invasion period I added the comb jelly *M. leidyi* as an additional variable. I considered the predatory activity of *M. leidyi* as mainly directed to zooplankton and larvae of planktivorous fish (Gucu 2002; Oguz et al. 2008a,b). In Figure 3.4 I present three graphs that reconstruct the structure of the community with *M. leidyi*. They essentially add this invader to the community represented in Figure 3.1a. Three different scenarios are presented: (1) *M. leidyi* that feeds upon both planktivorous larvae and zooplankton (Figure 3.4a); (2) the invader that preys upon zooplankton only (Figure 3.4b); (3) the comb jelly that consumes fish larvae only (Figure 3.4c). According to the literature, the period in which *M. leidyi* markedly increased goes from 1989 to 1993 (Shiganova 1998; Oguz and Gilbert 2007; Oguz et al. 2008a). My biomass database does not cover that period except for planktivorous fish. The stock of this latter group markedly declined in the period 1986-1993 (Figure 3.3a; see Oguz and Gilbert 2007; Oguz et al. 2008a; Daskalov et al. 2011) and I found a significant decrease between 1985-1989 and 1990-1993 ( $W = 20$ ,  $p = 0.008$ ; Table 3.2). The literature causally connects the outburst of *M. leidyi* and the decline of planktivores (mainly anchovies) identifying overfishing as the main cause for both these phenomena (Prodanov et al. 1997; Gucu 2002; Daskalov et al. 2011).

The three graphs of Figure 3.4 predict that an increased mortality for planktivores (negative input on variable PZ) reduces the level of this component. But the response of *M. leidy* is not so straightforward. Here I discuss how the predictions about the response of *M. leidy* change according to its feeding habits.

(1) *M. leidy* feeding on both planktivorous larvae and zooplankton. Model 3.4a predicts no change for the comb jelly population: overfishing of planktivores does not affect its biomass. However, this prediction does not reflect a true null response to overfishing. Rather, it stems from the compensation between opposite effects that spread via multiple pathways connecting planktivores to *M. leidy*. Models 3.4b and 3.4c help unraveling the mechanisms that may link overfishing to *M. leidy* bloom.

(2) *M. leidy* feeding on zooplankton only. In model 3.4b a negative input on planktivores is expected to increase the biomass of *M. leidy*. This is in agreement with the hypothesis that overfishing might have triggered the bloom of *M. leidy*.

(3) *M. leidy* feeding upon planktivorous larvae only. Model 3.4c predicts that the biomass of the invader decreases following overfishing of planktivores.



**Figure 3.4** - Signed digraphs describing the community structure of the post-invasion period and their tables of predictions. Post-invasion refers to the period after the establishment and the outburst of *M. leidy*. Keys for nodes are the same as in Figure 3.1 and MN indicates *M. leidy* population. The three graphs describe different scenarios for the feeding preferences of *M. leidy*: (a) the invader preys upon both edible zooplankton and larvae of planktivorous fish; (b) the comb jelly feeds preferentially on edible zooplankton; (c) the invader consumes mainly larvae of planktivorous fish.

One can combine the outcomes of the three models in Figure 3.4 and conclude that the response of *M. leidy* to overfishing may depend on whether it feeds preferentially on zooplankton or on planktivorous larvae. Therefore, the hypothesis that overfishing might have triggered also the bloom of *M. leidy* seems to hold only if this population fed preferentially on zooplankton rather than on larvae of planktivorous fish.

Oguz and Gilbert (2007) and Oguz et al. (2008a) proposed that the climate played a key role in the bloom of *M. leidy*. Severe winter conditions affected the Black Sea from 1979-81 to 1985-87 and kept the population of the invader in check. Warmer temperatures characterized the period 1988-90 and these new conditions were favorable to the growth of *M. leidy*. Potential consequences of warmer temperatures can be predicted by assuming a positive input to *M. leidy* in the model. Given the structure of the graph 3.4a, such positive input is expected to result in an increase of *M. leidy* biomass. Moreover, this version of the graph predicts that both planktivores and their larvae diminish following this positive input, a result that may explain the concomitant collapse of planktivores and the outburst of *M. leidy*. These outcomes indicate that climate conditions that favored *M. leidy* contributed also to reduce planktivores stock in addition to the loss due to harvesting. In the literature it has been reported that the increased predation of *M. leidy* over planktivores larvae might have conspired with overfishing to further reduce the stock of planktivores (Oguz and Gilbert 2007; Oguz et al. 2008a,b). Models 3.4b and 3.4c display different behavior with respect to this hypothesis. In model 3.4b, where the invader feeds on zooplankton only, the positive input due to warmer temperatures maintains the level of planktivores unchanged, while that of their larvae is expected to increase. Predictions from model 3.4c, where the feeding preference of *M. leidy* is on larvae of planktivores, indicate that the positive input on *M. leidy* decreases both planktivores and their larvae. So, the hypothesis that climate change favored *M. leidy* growth but even contributed to further reduce the population of planktivores holds only if the comb jelly invader gets its food mainly from the larvae of planktivorous fish.

### **3.4 Discussion**

The database considered in this study covers the period from late 1960s to late 1980s. A comparison between model predictions and biomass trends (tested with statistical analysis) was thus possible for the pre-invasion period only (i.e. with reference to *M. leidy* invasion). This allowed validating a basic scheme for the community structure that I used also in the post-invasion period. Scholars who focused on the Black Sea worked with data from different regions (i.e. western coast and interior basin, Oguz and Gilbert 2007; northwestern part, Oguz and Velikova 2010). Other studies targeted the whole basin by combining data from various regions that were presented in different studies (Daskalov 2002; Daskalov et al. 2007). Difficulties associated to the use of Black Sea data were highlighted by Myroshnychenko et al. (2014). The heterogeneity of the data makes difficult to compare results in a meaningful way. Here I followed the whole basin



approach and combined data from different regions to obtain average values for the biomass of the main pelagic groups. However, my database displays some differences if compared to those presented in the above-cited studies. The sources of data I used in this investigation are all described in the SI (Appendix C1).

According to the literature on the Black Sea, overfishing of top predators (i.e. piscivorous fish) has ignited a trophic cascade mechanism (Daskalov et al. 2007; Daskalov et al. 2011). During the 1970s, such trophic cascade stabilized the ecosystem and resulted in lower stock of piscivorous fish, higher stock of planktivores, lower zooplankton biomass, and higher phytoplankton biomass. My data set, however, does not indicate that in 1970s the hypothesized trophic cascade occurred. Stock trends show that both piscivorous fish and planktivores increased (see Figure 3.3 and Table 3.2: piscivorous fish stock 1971-74 < 1975-79,  $W = 0$ ,  $p = 0.010$ ; planktivorous fish stock 1970-74 < 1975-79,  $W = 4$ ,  $p = 0.048$ ). Trends of biomass stocks lead to think that in the 1970s pelagic predators increased in response to a positive effect on their growth rate associated to the reduced catch (Table 3.2: piscivorous fish catch 1960-69 > 1970-79,  $W = 75$ ,  $p = 0.031$ ). Thus, I assumed that a positive input on piscivorous fish must have entered the system. The model predicts that the level of top predators increases and that of the planktivorous fish declines. Since this latter component shows an increasing trend for its stock, to reconcile biomass trends and model predictions I considered an additional input given by the increased nutrient load. The combined action of the two inputs may explain the variation observed in the stock of the fish groups. The predictive scenario that the model offers for the other trophic groups is compatible with their biomass trends, but under certain conditions. The input on nutrients is predicted to increase both phytoplankton groups, whereas the input on pelagic predators would have no effect on their biomass. Overall, phytoplankton is expected to increase, a result that is in agreement with its biomass trend for the 1970s (Figure 3.2a, Table 3.1). Both zooplankton and jellyfish show opposite responses to the inputs on nutrients and piscivorous fish. The condition that needs to be met for matching predictions with biomass trends (i.e. zooplankton decreasing and jellyfish increasing; see Figure 3.2b,d and Table 3.1) is that the consequences of the positive input on nutrients prevail over the effects of the positive input on piscivorous fish. Only in this case jellyfish would be increasing and zooplankton would be decreasing. Although a quantitative analysis is needed to test these assumptions, which requires that information on link strength is at disposal, the interesting conclusion is that nutrient load must have driven ecosystem dynamics in this period. This finding challenges the dominant role of the trophic cascade associated to the overfishing of top predators, a perspective commonly accepted in the literature (Prodanov et al. 1997; Gucu 2002; Daskalov et al. 2007; Oguz 2007; Daskalov et al. 2011). I present this conclusion as a hypothesis to be further explored rather than a definitive statement. The commonly accepted view is that in the 1970s the first regime shift was driven by the overfishing of pelagic predators whose effects percolated down to the phytoplankton (Daskalov et al. 2011). What emerges from my investigation is that such top-down cascade cannot explain by itself what occurred in the decade 1970-1980. First, my database

shows that the stock of piscivorous fish did not decline. It increased instead, and this indicates that the 1970s coincided with a recovery phase for this group (possibly due to a drop in the catch). Nonetheless, if the trophic cascade mechanism dominated the dynamics of the community one would expect the biomass of the other trophic groups to change accordingly (i.e. with alternate correlations between adjacent trophic levels). The positive input to piscivorous fish would yield more piscivores, less planktivores, more zooplankton, and a decline of phytoplankton. However, the observed biomass trends for the other trophic groups do not match with this pattern. They can be predicted by the model only under the assumption that the increased nutrient load acted as additional input to the system. Therefore, I suggest that the effects of the nutrient load dominated over the consequences of the reduced fishing pressure on piscivorous fish. Moreover, the model predicts that any impact on piscivorous fish may not percolate down to phytoplankton. The resistance of phytoplankton to perturbations that affect piscivores derives from a compensative balance between positive and negative pathways that connect the latter component to phytoplankton. Considering the response of phytoplankton groups to a positive input on piscivorous fish, the simulation returns about 50% of the matrices with positive prediction and another 50% with negative sign (SI, Appendix B1; see the 5th model of the pre-invasion period). This highlights the presence of pathways with opposite effects that tend to compensate each other. Although this outcome requires to be corroborated through further studies, it is in agreement with previous finding based on experimental research (Micheli 1999). Indeed, the spreading of effects attenuates through marine pelagic food webs, resulting in a weak coupling between phytoplankton and herbivores. Model predictions about *N. scintillans* are inconsistent with its biomass trend. The model in Figure 3.1a predicts an increase for this species (both inputs tend to augment it), but its biomass shows no significant variations between 1960s and 1970s (see Figure 3.2c, Table 3.1). Several authors (see Oguz and Gilbert 2007 and references therein) documented that the abundance of this species increased in the 1970s. One possible reason for the discrepancy between model predictions and biomass trend can be attributed to the incompleteness of the data set. Despite this divergence, the model in Figure 3.1a seems to be sufficiently reliable in describing the structure of the community. Most predictions are consistent with the changes that trophic groups showed in the pre-invasion period, as portrayed by their biomass trends. This consistency depends on certain conditions that emerge as hypotheses about the drivers that governed the dynamics of the system. Our data set does not include biomass trends for the post-invasion period, with the exception of the stock of planktivorous fish. Model predictions can only be used to discuss hypotheses about the mechanisms proposed as causes of the outburst of *M. leidy* and the concomitant crash of planktivores. The shift in dominance between planktivorous fish and *M. leidy* was explained by “two major and contrasting hypotheses” (Oguz et al. 2008a): (1) overfishing of planktivorous fish (Prodanov et al. 1997; Gucu 2002; Daskalov et al. 2007); (2) excessive food competition and predation by *M. leidy* on larvae of planktivorous fish (Vinogradov et al. 1989; Kideys et al. 2000; Purcell et al. 2001; Shiganova et al. 2001). My models can help disentangling the interplay between

mechanisms and add to the debate around main drivers of fish collapse and invader outburst. This possibility is offered by the three scenarios about *M. leidyi* feeding behavior that the graphs in Figure 3.4 present. The hypothesis that overfishing caused the collapse of planktivores and the concomitant outburst of the gelatinous invader seems to hold in the case of *M. leidyi* feeding only (or preferentially) on zooplankton (model 3.4b). However, the predation/competition hypothesis grounds both on the more efficient exploitation of resources (i.e. zooplankton) that *M. leidyi* shares with planktivores and on the strong pressure it exerted over their larvae (Vinogradov et al. 1989; Kideys et al. 2000; Purcell et al. 2001; Shiganova et al. 2001). Changes in the winter temperature regimes governed the outburst of *M. leidyi* (Shiganova et al. 2001). The comb jelly abundance remained negligible when constrained by lower winter temperatures in the 1980s, while an abrupt explosion was observed in correspondence of higher winter temperatures in late 1980s and early 1990s. I considered that climatic conditions of late 1980s must have favored the growth of this species, which thus began to interfere with planktivorous fish through competition and predation. Such scenario combines the predation/competition hypothesis and the climatic factor hypothesis that Oguz et al. (2008a) discussed as separate mechanisms. This is coherent with the fact that, although *M. leidyi* was present in the Black Sea since early 1980s, its abundance remained extremely low until the end of the decade. Thus, conditions must have changed so that the growth rate of *M. leidyi* was favored. Some authors pointed out that these changing conditions could be attributed to increased winter temperatures during late 1980s (Oguz and Gilbert 2007; Oguz et al. 2008a). In models 3.4a and 3.4c, the positive input to *M. leidyi* yields a reduced biomass for both planktivores and their larvae, whereas *M. leidyi* itself would be increasing. In model 3.4b, the same input does not affect the planktivorous fish, but their larvae are predicted to increase. According to these outcomes, the concurrent effect of food competition and predation on fish larvae may explain both the collapse of the planktivorous fish and the outbreak of *M. leidyi*. The causative chain of effects triggered by more favorable climatic conditions for the explosion of *M. leidyi* is a plausible explanation, should it resists quantitative assessments. The interplay between the inputs (i.e. overfishing and climatic variation) and the interactions between *M. leidyi* and planktivores deserves further attention. The models in Figure 3.4 present three scenarios: one (model 3.4a) in which the invader interacts with planktivores through both competition and predation; another in which *M. leidyi* competes through the exploitation of the common resource (i.e. zooplankton, model 3.4b); and the third (model 3.4c) in which *M. leidyi* inhibits planktivores through predation on their larvae. Although the models provide qualitative indications that collapse of planktivores and outburst of *M. leidyi* can be concomitant because of a single driver (either overfishing or climatic variation), I have to consider that both inputs affected the Black Sea and their combined effect must be accounted for. If competition for zooplankton and predation on larvae were both at work in the system (model 3.4a), the outburst of *M. leidyi* likely would be caused by the increased growth rate due to climate variation; overfishing, in fact, is expected not to change significantly the level of the invader. The effect of climate variation on the growth of *M. leidyi* would reduce further the

abundance of planktivores besides overfishing, thus contributing to the collapse of this group. If *M. leidy* fed preferentially on zooplankton, so that competition would be the major force at work (model 3.4b), overfishing would explain the collapse of planktivores and also the outburst of *M. leidy*. However, the climatic conditions favorable to *M. leidy* would not contribute to the collapse of the fish stock. If the invader inhibited the planktivores only through predation (model 3.4c), then the effect of climatic variation would conspire with overfishing to make conditions for planktivores worse. To create conditions for the outburst of the comb jelly, the climatic effect on *M. leidy* would have to be strong enough to overcome the negative impact produced by overfishing. Both inputs must have concurred to create the observed scenario at the end of the 1980s, a picture that matches with what Oguz et al. (2008a) posited. My conclusion, however, comes out from the much simpler structural analysis of paths and feedbacks that loop analysis provides. In the absence of any quantitative analysis, model results help to identify whether the predicted direction of change for the variables can be compatible with the observed phenomena (i.e. outburst of *M. leidy* and collapse of planktivores) and generate hypotheses about potential causative mechanisms affecting the dynamics of the ecosystem.

### **3.5 Conclusions**

In this chapter I focused on the transformations that occurred in the Black Sea during the period 1960-1990. I assumed that constructing and analyzing the trophic structure of its community could contribute to identify which mechanisms produced the observed patterns of change. Qualitative models can be useful in this respect. This is because mapping out interactions between relevant variables can help understanding how the links of recognized direct effects also determine indirect effects. However, it is clear that the structure of the trophic interactions does not fully explain ecosystem dynamics. Important factors such as physiological responses to changing conditions, complex life cycles, and seasonality play a key role. My analysis shows how the trophic structure may propagate the effects of changing conditions within the community. It helps to ascertain whether the resulting effects (i.e. predicted changes in the level of variables) are compatible with observed patterns of biomass change, possibly suggesting further interpretation in terms of ecological mechanisms.

Other issues deserve to be discussed to frame my analysis in a correct perspective. (1) According to the methodology of loop analysis, I translated varying conditions into input to the growth rate of variables. Then, I simulated the response of the variables and compared predictions with variations in their real biomass trends. One major problem is the difficulty to establish the timing of input occurrence and that of response of the variables. To overcome the latter problem I considered time intervals of 5 and 10 years in which the response of the variables could be detected, in agreement with the literature (Daskalov 2002; Daskalov et al. 2007; Oguz and Gilbert 2007). As for the timing of changing conditions, the literature provided indications but this information is quite

heterogeneous. The exact period in which an input occurred could be defined only with a certain approximation (Gucu 2002; Oguz and Gilbert 2007; Llope et al. 2011). (2) I considered that changing conditions were targeted to specific components. However, it is clear that increasing fishing pressure acts on planktivores or piscivores only, while climate variations can concurrently affect multiple species in the community. It is acknowledged that higher winter temperatures boosted the growth of *M. leidyi*, but it is not certain whether and how climate affected the growth of other variables such as phytoplankton or zooplankton. Addressing this issue would require to consider additional inputs whose nature, however, is not presently known. (3) Identifying signs of regime shifts was not among my aims. Regime shift is considered when abundances change significantly in relation to a trend. Understanding such a type of pattern is partially precluded in presence of qualitative model predictions, although qualitative analysis was already applied to investigate regime shift phenomena (Marzloff et al. 2009). Here I used qualitative models to understand how the structure of the interactions can explain variations in the biomass of the variables and to test which drivers and mechanisms could be responsible for the observed changes. Loop analysis can be used to explore which backbone of trophic interactions reproduces cause-effect mechanisms compatible with observed trends of empirical data. This is because community-level responses can be assigned to changing parameters of target variables (e.g. overfishing that reduces the growth rate of fish) rather than being explained only as a function of variable fluctuations (e.g. environmental stochasticity). Therefore, it is important that changing conditions can be assigned to specific input on the variables. This chapter shows that the locus of control in the ecological community of the Black Sea is diffuse and that the behavior of the system depends on the structure of its interaction network.

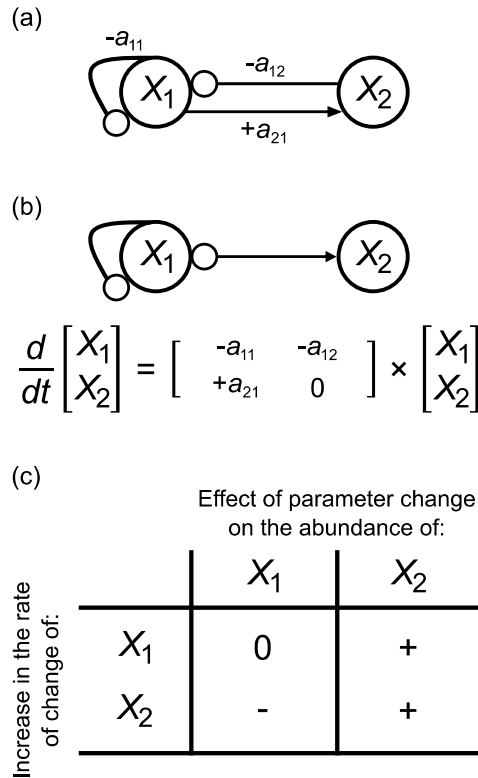
### 3.6 Supplemental Information

#### Appendix A - Loop analysis and simulation

##### *A1. Loop analysis*

Loop analysis is a qualitative modeling technique that uses signed digraphs to represent networks of interacting variables. The variables (single species or groups of species) are depicted as nodes, and each connection between two nodes represents a non-zero coefficient of the community matrix (Levins 1968). If the connection from variable  $X_1$  to variable  $X_2$  is an arrow (circle head), the effect of  $X_1$  on  $X_2$  is said to be positive (negative); this translates in pictorial terms a positive (negative) coefficient of the community matrix. The diagonal terms of the community matrix are self-effects on system variables. In signed digraphs, a self-limiting growth rate takes the form of a negative link connecting a variable with itself. In Figure 3.5, the correspondence between a community matrix and the related signed digraph is given for a simple predator-prey system. Loop analysis allows predicting the consequences that inputs on specific variables have on the level of all the variables in

the system. Such predictions are arranged in the table of predictions (Figure 3.5c). The table of predictions summarizes the variations expected in the level of all the column variables in response to positive parameter inputs that target the row variables.

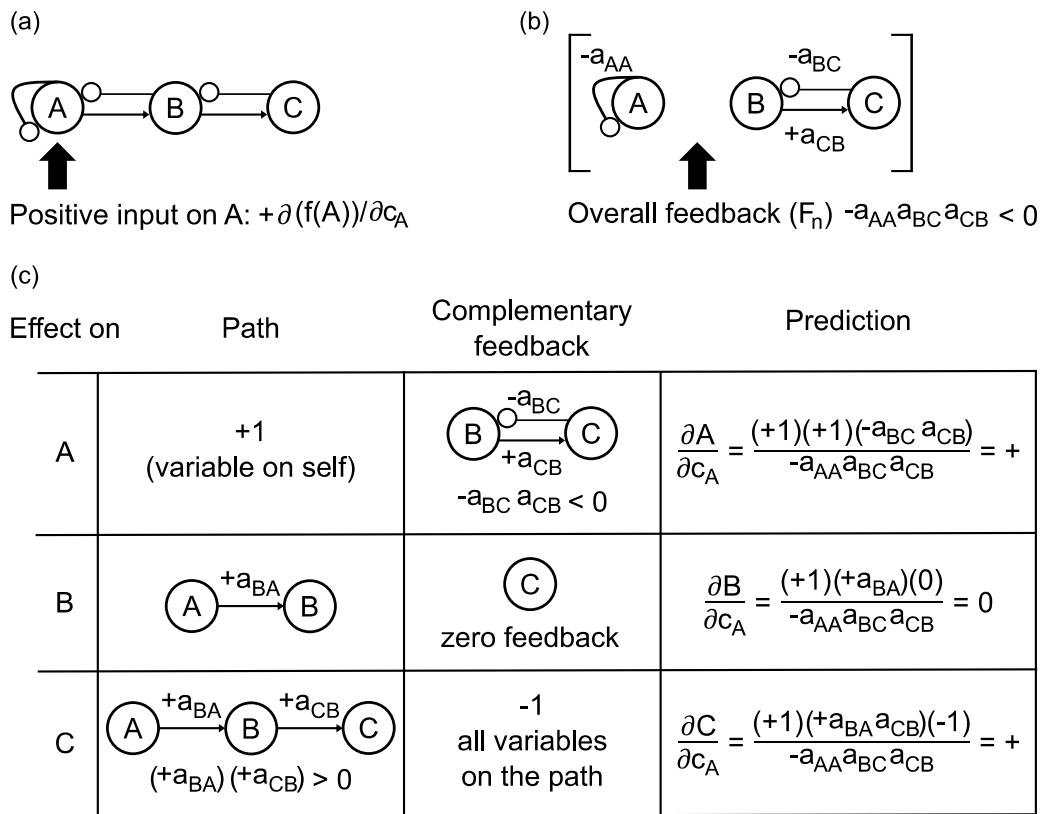


**Figure 3.5** - Mathematical and graphical elements of loop analysis: (a) signed digraph; (b) synthetic notation for signed digraph and community matrix; (c) table of predictions. This example refers to a resource-consumer interaction ( $X_1$  = resource,  $X_2$  = consumer). Directed connections depict positive (arrowhead) or negative (circle head) effects.

Press perturbations, also called inputs, may act on ecosystems by changing one or more parameters in the growth rate of the variables (Bender et al. 1984). In signed digraphs, any variable can be the target of impacts. That is there are as many entry points of impacts as the number of variables. Effects of these parameter changes may propagate beyond the direct target of the input because of the sequences of interactions that functionally link the components. Loop analysis identifies such pathways of interactions and feedbacks (that amplify or buffer the effects) and predicts whether the equilibrium value of system variables is expected to increase, decrease or remain the same following the perturbation. For any variable, changes can be calculated by the loop formula

$$\frac{\delta x_j}{\delta c} = \frac{\sum_{i,k} \left[ \frac{\delta f_i}{\delta c} \right] \times \left[ p_{ji}^{(k)} \right] \times \left[ F_{n-k}^{(comp)} \right]}{F_n} \quad (3.1)$$

Besides the sign of the input, indicated by the term  $[\partial f_i / \partial c]$ , the loop formula makes use of the concepts of circuit, overall feedback, path and complementary feedback. These refer to structural elements that can be identified in any graph. Their meaning can be fully understood by referring to the correspondence between matrix algebra and the formalism of loop analysis (see Puccia and Levins 1985). In the equation (3.1), which summarizes the elements of the algorithm,  $c$  is the changing parameter (e.g. mortality, fecundity, predation rate);  $[\partial f_i / \partial c]$  designates whether the growth rate of the  $i$ -th variable is increasing, decreasing or not;  $[p_{ij}^{(k)}]$  is the pathway connecting the variable that undergoes parameter change,  $x_i$ , with that whose equilibrium value is being calculated,  $x_j$ . The last factor of the numerator is the complementary feedback  $[F_{n-k}^{(comp)}]$ , which buffers or reverses the effect of the pathway.  $[F_n]$  indicates the overall feedback of the system, which is a measure of the inertia of the whole system to changes. Criteria to identify such elements in a graph are provided in the scheme depicted in Figure 3.6.



**Figure 3.6** - Signed digraph of a three-trophic level linear chain. Paths, complementary subsystems and feedbacks used to calculate expected changes in the equilibrium level of the variables in response to a positive input on A are explained. The first term of the numerator in the equations under the Prediction header is the sign of the input (+1).

**Circuits and feedbacks.** In loop analysis a pathway that starts at one node and, by following the direction of links, returns to it without crossing intermediate nodes more than once is called loop, or circuit. Any circuit produces a feedback that can be either positive or negative, depending on the product of the signs of the links that form the loop. As there may be circuits of different length (i.e.

with 1, 2, 3, ...,  $k$  variables involved), in a system there are as many levels of feedback as variables. Each level of feedback considers all the circuits (feedbacks) involving that particular number of variables. In the system of Figure 3.6a there are three levels of feedback. The first level of feedback comprises the one variable circuit that is present in the system: the self-damping on variable A. Two resource-consumer interactions [ $A \rightarrow B$ ] and [ $B \rightarrow C$ ] produce two feedbacks of the second level, and the three-variable feedback shown in Figure 3.6b (overall feedback) forms the third level of feedback, which is created by two independent loops: the self-damping on variable A and the resource-consumer interaction involving B and C.

**Overall feedback ( $F_n$ ).** It is computed only once and corresponds to the highest possible level of feedback in a system. It can be calculated either as associated to single circuits linking all the variables in the system or as a combination of shorter circuits involving smaller subsets of variables, in the understanding that such combinations must include all the variables in the system and do not share variables between themselves. In the hypothetical chain of three trophic levels depicted in Figure 3.6a, the overall feedback corresponds to a third level of feedback (i.e. a feedback effect involving all the three variables). Because the three variables cannot be connected simultaneously in unique circuits, the overall feedback comprises all the products of disjunct loops that have a combined number of variables equal to three. That is  $F_n$  is composed by the self-damping on A (a self-effect link is a loop of length 1) plus the two-node loop [ $B \rightarrow C$ ]. Its sign is obtained by multiplying the signs of the links involved, and this sign is further multiplied by  $(-1^{m+1})$ , where  $m$  is the number of disjunct loops entering the feedback. As the links involved are two negative and one positive, and there are two disjunct loops, the overall feedback is negative.

**Path [ $p_{ij}^{(k)}$ ].** A path is a series of links starting at one node and ending on another, without crossing any variable twice. Suppose a positive input occurs on A (its rate of change increases,  $\left[\frac{\partial f_i}{\partial c}\right] > 0$ ). To predict the new equilibrium of C, the path along which the effect travels is the positive link from A to B and the arrow from B to C. It involves three variables ( $k = 3$ ); its sign, given by the product of the signs of the links that form the path, is positive.

**Complementary feedback ( $F_{n-k}$ ).** If the  $k$  variables in the path were ideally excluded from the graph, what remains is called complementary subsystem. The complementary feedback is the feedback that groups all the variables in the complementary subsystem. In Figure 3.6c (second row of the table), for positive input on A and effect on B the complementary subsystem is formed by C only (A and B are on the path). So, the maximum feedback can be a one variable feedback. But because C has no self-effect link there will be a null (0) complementary feedback. For completeness, it has to be noted that a path from a variable to itself is equal to +1, no matter if it



has a self-effect or not, while if all the variables are in the path (i.e. input to A and effect on C) there is no complementary subsystem and the complementary feedback is set as equal to -1. These are two algebraic conveniences that are formally explained in Levins (1975) and Puccia and Levins (1985). Summation in the loop formula (1) considers the fact that two variables can be connected by more than one path.

#### **A2. Simulation**

In the case of multiple pathways with opposite effect a signed digraph yields ambiguous predictions and signs in the table of predictions are substituted by question marks. To solve these ambiguities, I applied a numerical simulation based on a routine that randomly assigns numerical values to coefficients of the community matrix (i.e. the coefficients of the links in the signed digraph). This procedure is executed  $n \times 1,000$  times, where  $n$  is the number of variables in the model. At each run, the community matrix that is formed is accepted if and only if it satisfies the asymptotic Lyapunov criteria. The  $z$  stable community matrices among the  $n \times 1,000$  that I constructed were accepted and inverted (Logofet 1993). The coefficient ( $c^{-1}_{ji}$ ) of each inverse community matrix shows the net effect of species  $i$  on species  $j$  due to the direct linkage with species  $i$  (e.g. predation) and all possible indirect pathways through which species  $i$  and  $j$  are connected via linkages with intermediate species (Bender et al. 1984; Wootton 2002; Montoya et al. 2009). Hence, the net effect (i.e. the sum of the direct effect plus all the individual indirect effects) on species  $j$  resulting from a perturbation on species  $i$  is given by the element of the inverse community matrix:

$$\frac{\partial \vec{x}^*}{\partial c_h} = (A_h)^{-1} \left( -\frac{\partial \vec{F}}{\partial c_h} \right) \quad (2)$$

$$\text{if } \left( \frac{\partial \vec{F}}{\partial c_h} = +1 \right) \text{ then } : \frac{\partial \vec{x}^*}{\partial c_h} = -(A_h)^{-1} \quad (3)$$

This means that  $A_h$  must have a non-zero determinant and must admit an inverse matrix  $(A_h)^{-1}$  whose eigenvalues must satisfy the Lyapunov condition of stability. The vector  $\left( -\frac{\partial \vec{F}}{\partial c_h} \right)$  is for simplicity taken equal to one because no information about the power (quantification) of inputs is available. For each simulated matrix a table of prediction is produced in which the response of the variables is given with no ambiguity (the signs are certain). Thus, each model in the simulation yields  $z$  table of predictions (considering the  $z$  stable matrices over the  $n \times 1,000$  community matrices that were constructed). An overall table of predictions is then constructed combining the  $z$  tables obtained from the simulation 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. However, there are cases in which for the same prediction a certain quota of the matrices yields a sign (e.g. +) and another part renders the opposite sign (-). The final decision about this prediction, whether it has to be a + or a -, is taken on the base of the percentage of matrices that render a sign in respect to those that yield the opposite sign. To this end, some rules of selections have been established for what concerns the percentages of cases in which +, - and 0 appear in any given entry of the table. These rules are summarized in Table 3.3.

% of +	Corresponding sign in the table
[0,25]	-
]25,40[	?- (tendency to -)
[40,60]	0*
]60,75[	?+ (tendency to +)
[75,100]	+
0 = 100%	0

**Table 3.3** - Rules to convert percentages of the signs obtained through simulations (% of +) to predictions (i.e. corresponding sign in the table). The open parenthesis stands for extreme excluded; 0\* is not a real zero, meaning no changes in the variable biomass, but a neutral result due to an equal amount of negative and positive effects.

### A3. R code for loop analysis

The procedure for simulations and the code are illustrated in what follows.

Inputs needed:

- (1) "names2.txt" = this is a row vector that contains labels for the variables (comma separated). The labels have to be the same as the ones used in the community matrix, namely the column heads, and in the same order as they appear along the rows and the columns of the community matrix.
- (2) "tab.txt" = the community matrix with values -1, 0, +1 has to be created in .txt format (with comma separated columns) and called "tab.txt".

Once in the R space, the following script should be used:

```
## load the library MASS, which is required for running the loop analysis script
library("MASS")

## input the information about the system that needs to be analyzed with loop
analysis
##
## examples for the files "names2.txt" and "tab.txt"
## these files refer to the model visualized in the Figure 3.1 of the manuscript
(i.e.
## the 5th model of the pre-invasion period in the Appendix B)
##
## "names2.txt"
## N,IP,EP,NC,EZ,J,PZ,LPZ,TP
##
## "tab.txt"
## -1,1,1,0,0,0,0,0,0
## -1,-1,0,0,0,0,0,0,0
## -1,0,-1,1,1,0,0,1,0
## 0,0,-1,-1,-1,0,0,0,0
## 0,0,-1,1,-1,1,1,1,1
## 0,0,0,0,-1,-1,0,-1,0
## 0,0,0,0,-1,0,-1,1,1
## 0,0,-1,0,-1,1,1,-1,0
## 0,0,0,0,-1,0,-1,0,-1

names <- scan("names2.txt", what = character(), sep = ",")
marcus <- read.table("tab.txt", col.names = names, row.names = names, sep = ",")

## script for loop analysis; it includes the community matrix in Levins' notation
Loop <- function(MM,NN){

  ## initializing count
  print("WARNING!!! MASS PACKAGE NEEDED")
  print("Community matrix")
  print(MM)

  k <- 1
  m <- 0
  h <- 0

  #####
  ## ##
  ## Community matrix as sign matrix: lev ##
  ## ##
  #####

  ## the matrix is: a11, a21, a31, etc.
  ## where aij = dfi/dxj change in the growth function of i due to j
```

```

lev <- t(MM)
Det_m <- det(lev)
print("Determinant")
print(Det_m)

dl <- sqrt(length(lev))
dl2 <- dl^2
## print("dl")
## print(dl)

nacc <- as.vector(k, mode = "integer")
nacc[1] = 0

n_p <- as.vector(m, mode = "integer")
n_m <- as.vector(m, mode = "integer")
n_oo <- as.vector(m, mode = "integer")

for(m in 1:dl2){
  (n_p[m] = 0) & (n_m[m] = 0) & (n_oo[m] = 0)
}

n_plus <- as.vector(n_p, mode = "integer")
n_min <- as.vector(n_m, mode = "integer")
n_o <- as.vector(n_oo, mode = "integer")

## number of runs (default is 1000)
## ntent <- (length(lev[1,]) * 100)
## ntent <- (length(lev[1,]) * 500)
ntent <- (length(lev[1,]) * 1000)
## ntent <- (length(lev[1,]) * 5000)
## ntent <- (length(lev[1,]) * 10000)

## print(ntent)

##
##
#####

for(k in 1:ntent){

#####
##          ##
## Random matrix: casuale ##
##          ##
#####

casuale <- matrix(rep(0,dl2), nrow = dl)

## random matrix generation (the name is: casuale) in [1e-6, 1]
for(i in 1:dl)
  for(j in 1:dl)casuale[i,j] <- runif(n = 1, min = 1e-6, max = 1)

#####
##          ##
## Weighted matrix (on degree tot for each variable) ##
##          ##
#####

num = 0
ww <- matrix(rep(NA, dl2), nrow = dl)

for(i in 1:dl)
  for(j in 1:dl){
    ww[i,j] <- (lev[i,j] * casuale[i,j])
  }

det_ww <- round(det(ww), digits = 6)

eig_vre <- round(Re(eigen(ww)$values), digits = 6)
eig_vim <- round(Im(eigen(ww)$values), digits = 6)

```

```

for(y in 1:dl){
  if(eig_vre[y] < 0) (num = num + 1)
}

## a minus sign is inserted during matrix inversion to take into account
the sign
## of coeff b = -dfi/dc

if((num-dl) == 0)
{
  (nacc[k] = nacc[k] + 1) & (inv_ww <- (-round(ginv(ww), digits = 6)))
  & (vector <- as.vector(inv_ww))
  for(m in 1:dl2)
  {
    if(vector[m] > 0) (n_plus[m] = n_plus[m] + 1)
    else if(vector[m] < 0) (n_min[m] = n_min[m] + 1)
    else if(vector[m] == 0) (n_o[m] = n_o[m] + 1)
  }
}

round(ginv(ww), digits = 6)

per_p <- round(matrix(c((n_plus * 100)/nacc[k]), nrow = dl, byrow = T), digits =
5)
per_m <- round(matrix(c((n_min * 100)/nacc[k]), nrow = dl, byrow = T), digits =
5)
per_o <- round(matrix(c((n_o * 100)/nacc[k]), nrow = dl, byrow = T), digits = 5)

v_p <- as.vector(per_p)
v_m <- as.vector(per_m)
v_o <- as.vector(per_o)

nacc[k+1] = nacc[k]

}

##
##
#####

ntot = nacc[k]
OUT <- as.list(rep(NA, 5))

OUT[[1]] <- ntot
OUT[[2]] <- k
OUT[[3]] <- per_p
OUT[[4]] <- per_m
OUT[[5]] <- per_o

print("Stable matrices")
print(OUT[[1]])
print("Simulated matrices")
print(OUT[[2]])
print(" (%) + ")

colnames(OUT[[3]]) <- NN
rownames(OUT[[3]]) <- NN
print(OUT[[3]])
print(" (%) - ")

colnames(OUT[[4]]) <- NN
rownames(OUT[[4]]) <- NN
print(OUT[[4]])
print(" (%) 0 ")

colnames(OUT[[5]]) <- NN
rownames(OUT[[5]]) <- NN
print(OUT[[5]])

tab <- as.vector(h, mode="any")

```

```

for(h in 1:dl2){
  if(v_o[h] == 100) (tab[h] <- 0)
  else if(v_p[h] >= 75) (tab[h] <- "+")
  else if(v_p[h] <= 25 & v_p[h] >= 0) (tab[h] <- "-")
  else if(abs(v_p[h] - v_m[h]) <= 20) (tab[h] <- "0*")
  else if(25 < v_p[h] & v_p[h] < 40) (tab[h] <- "?-")
  else if(60 < v_p[h] & v_p[h] < 75) (tab[h]
    <- "?+")
}

tab_m <- matrix(c(tab), nrow = dl, byrow = T)
table_of_predictions <- t(tab_m)

colnames(table_of_predictions) <- NN
rownames(table_of_predictions) <- NN

print("Table of predictions")
print.noquote(table_of_predictions)
}

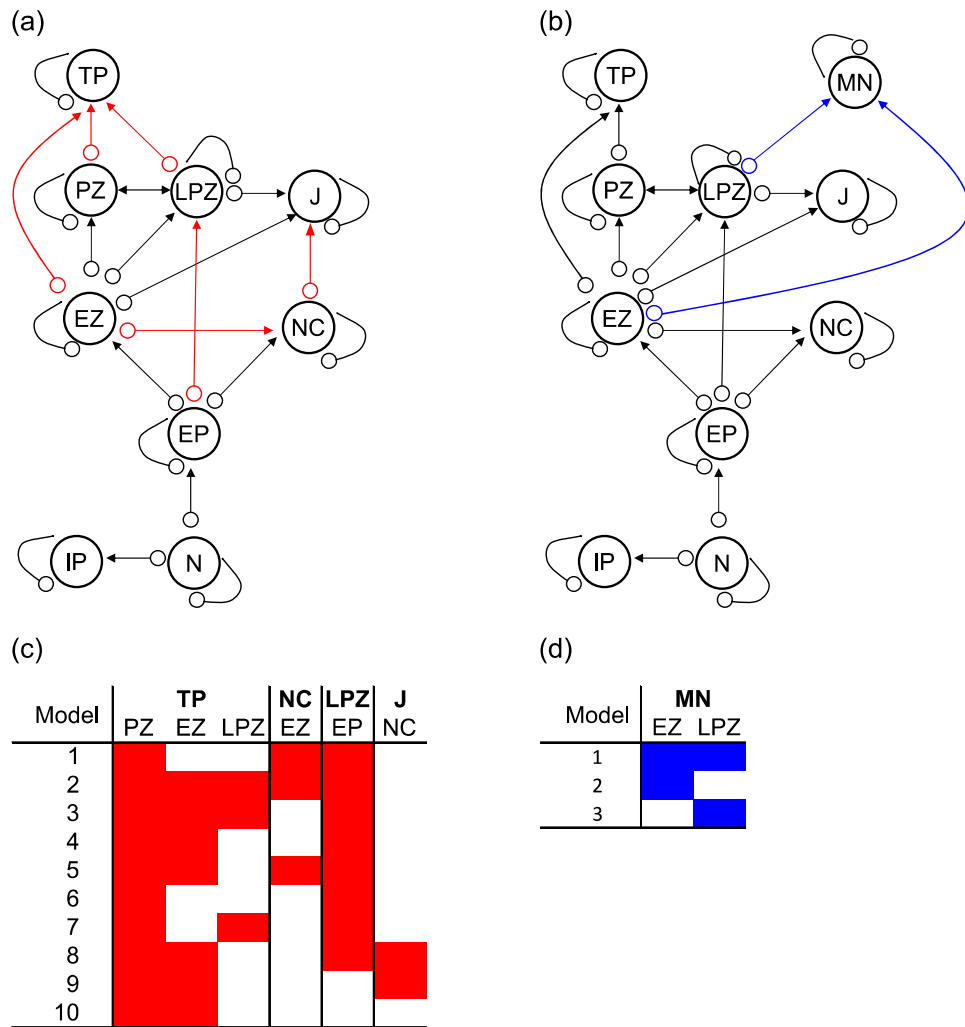
## launch: Loop(marcus, names)
## The output includes:
## (1) community matrix;
## (2) determinant;
## (3) number of stable matrices;
## (4) number of simulated matrices;
## (5) three matrices with the percentages of simulated stable matrices that give
a
## positive sign (+), a negative sign (-), and a zero (0);
## (6) table of predictions.

Loop(marcus, names)

```

## **Appendix B - Models and simulation**

The main criterion used for setting up the models was the ecological information about species feeding habits. Models were divided in two main periods, using the introduction of *Mnemiopsis leidyi* as a reference. *M. leidyi* is a gelatinous predator introduced accidentally through ballast water, and from the beginning of 1988 was observed in massive presence in the Black Sea (Vinogradov et al. 1989). I could not identify a unique representation of the system: ten alternative models for the pre-invasion period were constructed and analyzed. A condensed description of the pre-invasion graphs is provided in Figure 3.7a,c, and three alternative models represented the set of graphs for the post-invasion period (Figure 3.7b,d). All of them are equally plausible, on the basis of the ecological knowledge acquired. In the models, some variables represent single species (e.g. *Noctiluca scintillans*); however, most of the variables group many taxa (e.g. edible phytoplankton or planktivorous fish). This uneven resolution is supported by practical reasons. For species that could have a particular role in respect to some ecological processes (e.g. alien species *M. leidyi*), it was straightforward to represent them as individual species. In other cases (e.g. jellyfish), data were aggregated since discriminating the role of single populations could not be informative. Also for fish, although there are many different species that are important in various ways (ecological, economic), I considered that resolving the graph at the single species level would have led to obtain too complex models to be analyzed. Therefore, the architecture of the various models came out as a reasonable compromise that involved the need to describe the system in its complexity (i.e. to take into account the relevance of particular species), the availability of data, and the practical implementation of the predictive algorithms.

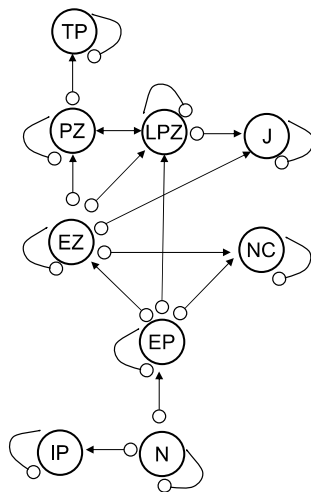


**Figure 3.7** - Alternative models for the pre-invasion and post-invasion periods. Pre-invasion and post-invasion are distinguished based on the introduction of *M. leidy* (MN) as additional component. For each period, the set of interactions that represents the backbone is in black. Red interactions (a) illustrate the configurations studied for the pre-invasion period (ten models); blue interactions (b) characterize the alternative models of the post-invasion period (three models). Two tables summarize the specific set of interactions considered in the alternative models for pre-invasion (c, in red) and post-invasion (d, in blue). The header of the tables is divided in two parts: the upper part (bold) indicates the predator, while the lower part (regular font) summarizes the prey. Each row stands for a different configuration, and the columns illustrate the trophic interactions that are considered. The fifth model of the pre-invasion period is the one explained and discussed in the manuscript (see Figure 3.1). Such model includes four red interactions (i.e. TP feeding on PZ and EZ, NC consuming EZ and LPZ preying upon EP) and consists of the backbone used for studying the post-invasion period. The three models of the post-invasion period match the ones depicted in Figure 3.4 of the manuscript; further details on the simulation are provided in this Appendix.



**B1. Models for the pre-invasion period**

(1) Model I



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0
NC	0	0	-1	-1	-1	0	0	0	0
EZ	0	0	-1	1	-1	1	1	1	0
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	0
TP	0	0	0	0	0	0	-1	0	-1

Determinant: -59  
 Stable matrices: 7538  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	97.45874	97.45874	99.06528	84.18285	16.09464	61.07784	59.83642	89.33840	59.83642
IP	2.54126	99.86856	0.93472	15.81715	83.90536	38.90755	40.16358	10.66160	40.16358
EP	0.93472	0.93472	99.06528	84.18285	16.09464	61.07784	59.83642	89.33840	59.83642
NC	77.66905	77.66905	22.33095	97.88228	24.93063	5.09712	10.98291	26.12823	10.98291
EZ	93.73448	93.73448	6.26552	64.20330	95.47247	90.91573	82.31342	41.41960	82.31342
J	25.28115	25.28115	74.71885	85.26362	57.55805	95.32642	9.59544	3.89952	9.59544
PZ	17.77421	17.77421	82.22579	18.21236	0.55499	41.21513	98.42267	95.07814	98.42267
LPZ	36.33708	36.33708	63.66292	10.80765	2.40981	71.16986	61.23850	99.82474	61.23850
TP	82.21119	82.21119	17.77421	81.78764	99.44501	58.78487	1.57733	4.92186	91.73361

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	2.54126	2.54126	0.93472	15.81715	83.90536	38.92216	40.16358	10.66160	40.16358
IP	97.45874	0.13144	99.06528	84.18285	16.09464	61.06324	59.82182	89.33840	59.83642
EP	99.06528	99.06528	0.93472	15.81715	83.90536	38.92216	40.16358	10.66160	40.16358
NC	22.33095	22.33095	77.66905	2.11772	75.06937	94.90288	89.01709	73.87177	89.01709
EZ	6.26552	6.26552	93.73448	35.79670	4.52753	9.08427	17.68658	58.58040	17.68658
J	74.71885	74.71885	25.28115	14.73638	42.44195	4.67358	90.40456	96.10048	90.40456
PZ	82.19658	82.22579	17.77421	81.78764	99.44501	58.78487	1.57733	4.92186	1.57733
LPZ	63.66292	63.66292	36.33708	89.19235	97.59019	28.83014	38.76150	0.17526	38.76150
TP	17.77421	17.77421	82.22579	18.21236	0.55499	41.21513	98.42267	95.07814	8.26639

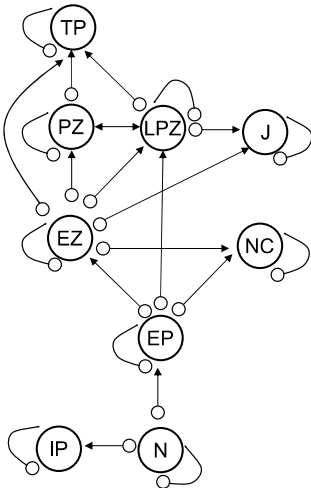
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.00000	0.0000	0	0	0	0.00000	0.0000	0	0
IP	0.00000	0.0000	0	0	0	0.02921	0.0146	0	0
EP	0.00000	0.0000	0	0	0	0.00000	0.0000	0	0
NC	0.00000	0.0000	0	0	0	0.00000	0.0000	0	0
EZ	0.00000	0.0000	0	0	0	0.00000	0.0000	0	0
J	0.00000	0.0000	0	0	0	0.00000	0.0000	0	0
PZ	0.02921	0.0000	0	0	0	0.00000	0.0000	0	0
LPZ	0.00000	0.0000	0	0	0	0.00000	0.0000	0	0
TP	0.01460	0.0146	0	0	0	0.00000	0.0000	0	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	-	?+	0*	+	0*
IP	-	+	-	-	+	?-	0*	-	0*
EP	-	-	+	+	-	?+	0*	+	0*
NC	+	+	-	+	-	-	-	?-	-
EZ	+	+	-	?+	+	+	+	0*	+
J	?-	?-	?+	+	0*	+	-	-	-
PZ	-	-	+	-	-	0*	+	+	+
LPZ	?-	?-	?+	-	-	?+	?+	+	?+
TP	+	+	-	+	+	0*	-	-	+

(2) Model II



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0
NC	0	0	-1	-1	-1	0	0	0	0
EZ	0	0	-1	1	-1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	1
TP	0	0	0	0	-1	0	-1	-1	-1

Determinant: -82  
 Stable matrices: 7271  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	Lpz	TP
N	97.24799	97.24799	99.23977	87.54751	22.38102	63.20511	45.61350	88.97674	62.52091
IP	2.75201	99.86316	0.76023	12.45249	77.61898	36.79489	54.38650	11.02326	37.47909
EP	0.76023	0.76023	99.23977	87.54751	22.38102	63.20511	45.61350	88.97674	62.52091
NC	78.72890	78.72890	21.27110	94.52638	13.63844	10.68876	47.65090	53.70230	10.58233
EZ	92.24570	92.24570	7.75430	76.06812	99.23977	80.02129	55.55724	13.66885	80.90315
J	19.76585	19.76585	80.23415	68.58750	40.01825	96.92869	50.47894	20.38924	7.55664
PZ	11.06888	11.06888	88.93112	29.45112	5.53444	22.24418	97.15676	75.26228	83.91364
Lpz	37.02296	37.00775	62.97704	10.74958	4.47012	69.66702	44.95971	99.63509	69.42375
TP	58.14201	58.14201	41.85799	87.33465	88.20131	30.84993	3.87715	2.79763	88.33815

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	2.75201	2.75201	0.76023	12.45249	77.61898	36.79489	54.38650	11.02326	37.47909
IP	97.24799	0.13684	99.23977	87.54751	22.38102	63.20511	45.61350	88.97674	62.52091
EP	99.23977	99.23977	0.76023	12.45249	77.61898	36.79489	54.38650	11.02326	37.47909
NC	21.27110	21.27110	78.72890	5.47362	86.36156	89.31124	52.34910	46.29770	89.41767
EZ	7.75430	7.75430	92.24570	23.93188	0.76023	19.97871	44.44276	86.33115	19.09685
J	80.23415	80.23415	19.76585	31.41250	59.98175	3.07131	49.52106	79.61076	92.44336
PZ	88.93112	88.93112	11.06888	70.54888	94.46556	77.75582	2.84324	24.73772	16.08636
LPZ	62.97704	62.97704	37.02296	89.25042	95.52988	30.33298	55.04029	0.36491	30.57625
TP	41.85799	41.85799	58.14201	12.66535	11.79869	69.15007	96.12285	97.20237	11.66185

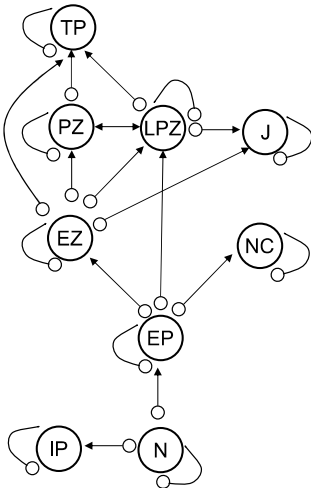
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0	0.0000	0	0	0	0	0	0	0
IP	0	0.0000	0	0	0	0	0	0	0
EP	0	0.0000	0	0	0	0	0	0	0
NC	0	0.0000	0	0	0	0	0	0	0
EZ	0	0.0000	0	0	0	0	0	0	0
J	0	0.0000	0	0	0	0	0	0	0
PZ	0	0.0000	0	0	0	0	0	0	0
LPZ	0	0.0152	0	0	0	0	0	0	0
TP	0	0.0000	0	0	0	0	0	0	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	-	?+	0*	+	?+
IP	-	+	-	-	+	?-	0*	-	?-
EP	-	-	+	+	-	?+	0*	+	?+
NC	+	+	-	+	-	-	0*	0*	-
EZ	+	+	-	+	+	+	0*	-	+
J	-	-	+	?+	0*	+	0*	-	-
PZ	-	-	+	?-	-	-	+	+	+
LPZ	?-	?-	?+	-	-	?+	0*	+	?+
TP	0*	0*	0*	+	+	?-	-	-	+

(3) Model III



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0
NC	0	0	-1	-1	0	0	0	0	0
EZ	0	0	-1	0	-1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	1
TP	0	0	0	0	-1	0	-1	-1	-1

Determinant: -68  
 Stable matrices: 7192  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	99.13286	99.13286	98.46702	98.46702	50.94456	83.95788	48.99350	78.46082	84.43791
IP	0.86714	99.70579	1.53298	1.53298	49.05544	16.04212	51.00650	21.53918	15.56209
EP	1.53298	1.53298	98.46702	98.46702	50.94456	83.95788	48.99350	78.46082	84.43791
NC	98.46702	98.46702	1.53298	98.00248	49.05544	16.04212	51.00650	21.53918	15.56209
EZ	80.67513	80.67513	19.32487	19.32487	99.10189	86.62124	57.06101	19.23196	87.81356
J	16.46020	16.46020	83.53980	83.53980	45.91205	97.67730	50.96005	16.50666	11.28832
PZ	19.95974	19.95974	80.04026	80.04026	6.39517	15.05110	97.21276	72.43729	77.09817
LPZ	52.09043	52.09043	47.90957	47.90957	1.44007	56.13193	43.20223	99.72128	54.72282
TP	45.13781	45.15330	54.84670	54.84670	92.24218	44.42552	5.18736	2.12140	91.88603

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.86714	0.86714	1.53298	1.53298	49.05544	16.04212	51.00650	21.53918	15.56209
IP	99.13286	0.29421	98.46702	98.46702	50.94456	83.95788	48.99350	78.44534	84.43791
EP	98.46702	98.46702	1.53298	1.53298	49.05544	16.04212	51.00650	21.53918	15.56209
NC	1.53298	1.53298	98.46702	1.99752	50.94456	83.95788	48.99350	78.46082	84.43791
EZ	19.32487	19.32487	80.67513	80.67513	0.89811	13.37876	42.93899	80.76804	12.18644
J	83.53980	83.53980	16.46020	16.46020	54.08795	2.32270	49.03995	83.49334	88.71168
PZ	80.04026	80.04026	19.95974	19.95974	93.60483	84.94890	2.78724	27.56271	22.90183
LPZ	47.90957	47.90957	52.09043	52.09043	98.55993	43.86807	56.79777	0.27872	45.27718
TP	54.84670	54.84670	45.15330	45.15330	7.75782	55.57448	94.81264	97.87860	8.11397

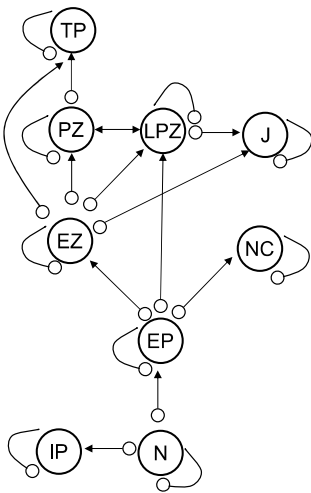
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.00000	0	0	0	0	0	0	0.00000	0
IP	0.00000	0	0	0	0	0	0	0.01548	0
EP	0.00000	0	0	0	0	0	0	0.00000	0
NC	0.00000	0	0	0	0	0	0	0.00000	0
EZ	0.00000	0	0	0	0	0	0	0.00000	0
J	0.00000	0	0	0	0	0	0	0.00000	0
PZ	0.00000	0	0	0	0	0	0	0.00000	0
LPZ	0.00000	0	0	0	0	0	0	0.00000	0
TP	0.01548	0	0	0	0	0	0	0.00000	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	0*	+	0*	+	+
IP	-	+	-	-	0*	-	0*	-	-
EP	-	-	+	+	0*	+	0*	+	+
NC	+	+	-	+	0*	-	0*	-	-
EZ	+	+	-	-	+	+	0*	-	+
J	-	-	+	+	0*	+	0*	-	-
PZ	-	-	+	+	-	-	+	?+	+
LPZ	0*	0*	0*	0*	-	0*	0*	+	0*
TP	0*	0*	0*	0*	+	0*	-	-	+

(4) Model IV



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	0	1
NC	0	0	-1	-1	0	0	0	0	0
EZ	0	0	-1	0	-1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	0
TP	0	0	0	0	-1	0	-1	0	-1

Determinant: -51  
 Stable matrices: 6798  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	99.04018	99.04018	98.21051	98.21051	31.95054	80.88498	79.99024	91.24776	57.96323
IP	0.95982	99.69091	1.78949	1.78949	68.03319	19.11502	20.00976	8.75224	42.03677
EP	1.78949	1.78949	98.21051	98.21051	31.95054	80.88498	79.99024	91.24776	57.96323
NC	98.21051	98.21051	1.78949	97.59232	68.04946	19.11502	20.00976	8.75224	42.03677
EZ	86.20465	86.20465	13.79535	13.79535	95.05450	93.06979	52.56223	45.46933	95.41240
J	20.22125	20.22125	79.77875	79.77875	71.18920	97.23442	13.87669	2.73304	40.86546
PZ	26.38686	26.38686	73.61314	73.61314	0.00000	20.92077	99.54449	87.76639	58.51635
LPZ	54.14023	54.14023	45.85977	45.85977	0.00000	57.65414	78.67252	99.88612	15.40589
TP	40.78412	40.78412	59.18334	59.18334	73.85717	39.64536	1.18757	11.74557	96.95787

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.95982	0.95982	1.78949	1.78949	68.04946	19.11502	19.99349	8.75224	42.03677
IP	99.04018	0.30909	98.21051	98.21051	31.93428	80.88498	79.99024	91.24776	57.96323
EP	98.21051	98.21051	1.78949	1.78949	68.04946	19.11502	20.00976	8.75224	42.03677
NC	1.78949	1.78949	98.21051	2.40768	31.95054	80.88498	79.99024	91.24776	57.96323
EZ	13.79535	13.79535	86.20465	86.20465	4.94550	6.93021	47.43777	54.53067	4.58760
J	79.77875	79.77875	20.22125	20.22125	28.81080	2.76558	86.12331	97.26696	59.13454
PZ	73.59688	73.61314	26.38686	26.38686	100.00000	79.07923	0.45551	12.23361	41.48365
LPZ	45.85977	45.85977	54.14023	54.14023	100.00000	42.34586	21.32748	0.11388	84.59411
TP	59.18334	59.18334	40.81666	40.81666	26.14283	60.35464	98.81243	88.25443	3.04213

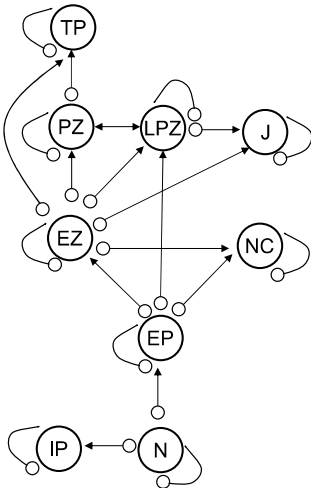
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.00000	0.00000	0	0	0.00000	0	0.01627	0	0
IP	0.00000	0.00000	0	0	0.03254	0	0.00000	0	0
EP	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0
NC	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0
EZ	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0
J	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0
PZ	0.01627	0.00000	0	0	0.00000	0	0.00000	0	0
LPZ	0.00000	0.00000	0	0	0.00000	0	0.00000	0	0
TP	0.03254	0.03254	0	0	0.00000	0	0.00000	0	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	?-	+	+	+	0*
IP	-	+	-	-	?+	-	-	-	0*
EP	-	-	+	+	?-	+	+	+	0*
NC	+	+	-	+	?+	-	-	-	0*
EZ	+	+	-	-	+	+	0*	0*	+
J	-	-	+	+	?+	+	-	-	0*
PZ	?-	?-	?+	?+	-	-	+	+	0*
LPZ	0*	0*	0*	0*	-	0*	+	+	-
TP	0*	0*	0*	0*	?+	?-	-	-	+

(5) Model V



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0
NC	0	0	-1	-1	-1	0	0	0	0
EZ	0	0	-1	1	-1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	0
TP	0	0	0	0	-1	0	-1	0	-1

Determinant: -52  
 Stable matrices: 6762  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	96.55115	96.55115	98.43386	81.00633	14.37854	64.17861	76.52449	91.20293	36.37121
IP	3.44885	99.73342	1.56614	18.99367	85.62146	35.82139	23.47551	8.79707	63.62879
EP	1.56614	1.56614	98.43386	81.00633	14.37854	64.17861	76.52449	91.20293	36.37121
NC	80.80640	80.80640	19.19360	95.81806	26.27458	8.06398	34.87171	30.13995	12.87904
EZ	92.65245	92.65245	7.34755	68.71043	96.80107	85.10497	45.46818	32.07264	93.13562
J	29.09030	29.09030	70.90970	84.90503	62.72909	94.48517	15.97801	5.44818	28.60713
PZ	14.86171	14.86171	85.13829	19.06031	0.18327	36.85438	99.46684	92.98567	66.24459
LPZ	37.00433	37.00433	62.99567	10.46318	1.94935	73.12562	84.45518	99.80007	28.79040
TP	49.86671	49.86671	50.13329	76.44119	72.14262	29.95668	1.39953	12.76241	94.98500

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	3.44885	3.44885	1.56614	18.99367	85.62146	35.82139	23.47551	8.79707	63.62879
IP	96.55115	0.26658	98.43386	81.00633	14.37854	64.17861	76.52449	91.20293	36.37121
EP	98.43386	98.43386	1.56614	18.99367	85.62146	35.82139	23.47551	8.79707	63.62879
NC	19.19360	19.19360	80.80640	4.18194	73.72542	91.93602	65.12829	69.86005	87.12096
EZ	7.34755	7.34755	92.65245	31.28957	3.19893	14.89503	54.53182	67.92736	6.86438
J	70.90970	70.90970	29.09030	15.09497	37.27091	5.51483	84.02199	94.55182	71.39287
PZ	85.13829	85.13829	14.86171	80.93969	99.81673	63.14562	0.53316	7.01433	33.75541
LPZ	62.99567	62.97901	37.00433	89.53682	98.05065	26.87438	15.54482	0.19993	71.20960
TP	50.13329	50.13329	49.86671	23.55881	27.85738	70.04332	98.60047	87.23759	5.01500

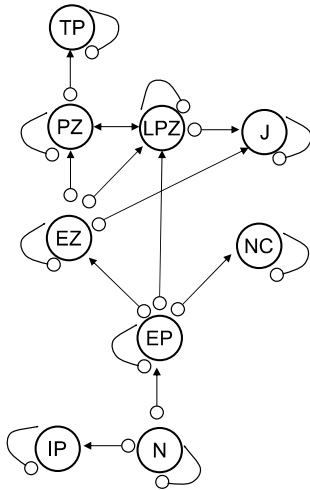
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0	0.00000	0	0	0	0	0	0	0
IP	0	0.00000	0	0	0	0	0	0	0
EP	0	0.00000	0	0	0	0	0	0	0
NC	0	0.00000	0	0	0	0	0	0	0
EZ	0	0.00000	0	0	0	0	0	0	0
J	0	0.00000	0	0	0	0	0	0	0
PZ	0	0.00000	0	0	0	0	0	0	0
LPZ	0	0.01666	0	0	0	0	0	0	0
TP	0	0.00000	0	0	0	0	0	0	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	-	?+	+	+	?-
IP	-	+	-	-	+	?-	-	-	?+
EP	-	-	+	+	-	?+	+	+	?-
NC	+	+	-	+	?-	-	?-	?-	-
EZ	+	+	-	?+	+	+	0*	?-	+
J	?-	?-	?+	+	?+	+	-	-	?-
PZ	-	-	+	-	-	?-	+	+	?+
LPZ	?-	?-	?+	-	-	?+	+	+	?-
TP	0*	0*	0*	+	?+	?-	-	-	+

(6) Model VI



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	0	1
NC	0	0	-1	-1	0	0	0	0	0
EZ	0	0	-1	0	-1	1	1	1	0
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	0
TP	0	0	0	0	0	0	-1	0	-1

Determinant: -58  
 Stable matrices: 7795  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	99.04272	99.04272	98.64266	98.64266	35.61937	82.62609	81.18303	92.37034	81.18303
IP	0.95728	99.74282	1.35734	1.34305	64.38063	17.35962	18.80269	7.62966	18.80269
EP	1.35734	1.35734	98.64266	98.64266	35.61937	82.64038	81.19731	92.37034	81.19731
NC	98.64266	98.64266	1.35734	98.19974	64.38063	17.35962	18.80269	7.62966	18.80269
EZ	89.45564	89.45564	10.54436	10.54436	94.72782	96.27090	88.18403	53.63623	88.18403
J	18.01686	18.01686	81.98314	81.98314	68.19546	99.07130	14.97357	1.57165	14.97357
PZ	27.87541	27.87541	72.11030	72.11030	0.00000	20.54579	98.67124	90.85584	98.67124
LPZ	52.03601	52.03601	47.96399	47.96399	0.00000	53.55051	46.50664	100.00000	46.50664
TP	72.11030	72.08173	27.88970	27.88970	100.00000	79.45421	1.32876	9.14416	93.85627

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.95728	0.95728	1.35734	1.35734	64.38063	17.35962	18.80269	7.62966	18.80269
IP	99.04272	0.25718	98.64266	98.64266	35.61937	82.64038	81.18303	92.37034	81.16874
EP	98.64266	98.64266	1.35734	1.35734	64.38063	17.35962	18.80269	7.62966	18.80269
NC	1.35734	1.35734	98.64266	1.80026	35.61937	82.64038	81.19731	92.37034	81.19731
EZ	10.54436	10.54436	89.45564	89.45564	5.27218	3.72910	11.81597	46.36377	11.81597
J	81.98314	81.98314	18.01686	18.01686	31.80454	0.92870	85.02643	98.42835	85.02643
PZ	72.09601	72.11030	27.88970	27.88970	100.00000	79.45421	1.32876	9.14416	1.32876
LPZ	47.96399	47.96399	52.03601	52.03601	100.00000	46.44949	53.49336	0.00000	53.49336
TP	27.88970	27.88970	72.11030	72.11030	0.00000	20.54579	98.67124	90.85584	6.14373

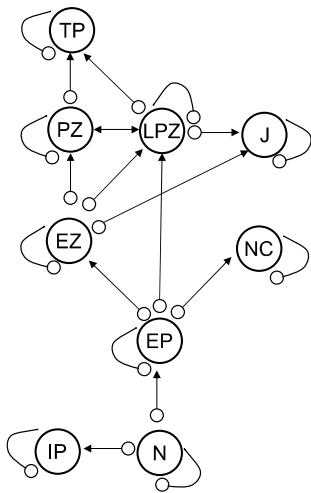
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.00000	0.00000	0	0.00000	0	0.01429	0.01429	0	0.01429
IP	0.00000	0.00000	0	0.01429	0	0.00000	0.01429	0	0.02858
EP	0.00000	0.00000	0	0.00000	0	0.00000	0.00000	0	0.00000
NC	0.00000	0.00000	0	0.00000	0	0.00000	0.00000	0	0.00000
EZ	0.00000	0.00000	0	0.00000	0	0.00000	0.00000	0	0.00000
J	0.00000	0.00000	0	0.00000	0	0.00000	0.00000	0	0.00000
PZ	0.02858	0.01429	0	0.00000	0	0.00000	0.00000	0	0.00000
LPZ	0.00000	0.00000	0	0.00000	0	0.00000	0.00000	0	0.00000
TP	0.00000	0.02858	0	0.00000	0	0.00000	0.00000	0	0.00000

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	?-	+	+	+	+
IP	-	+	-	-	?+	-	-	-	-
EP	-	-	+	+	?-	+	+	+	+
NC	+	+	-	+	?+	-	-	-	-
EZ	+	+	-	-	+	+	+	0*	+
J	-	-	+	+	?+	+	-	-	-
PZ	?-	?-	?+	?+	-	-	+	+	+
LPZ	0*	0*	0*	0*	-	0*	0*	+	0*
TP	?+	?+	?-	?-	+	+	-	-	+

(7) Model VII



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	0	1
NC	0	0	-1	-1	0	0	0	0	0
EZ	0	0	-1	0	-1	1	1	1	0
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	1
TP	0	0	0	0	0	0	-1	-1	-1

Determinant: -89  
 Stable matrices: 8246  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	99.64607	99.64607	99.63245	99.63245	62.33324	91.68255	61.16254	85.33896	91.88674
IP	0.35393	99.89110	0.36755	0.36755	37.66676	8.31745	38.83746	14.66104	8.09965
EP	0.36755	0.36755	99.63245	99.63245	62.33324	91.68255	61.16254	85.33896	91.90035
NC	99.63245	99.63245	0.36755	99.19684	37.66676	8.31745	38.83746	14.66104	8.09965
EZ	87.85734	87.85734	12.14266	12.14266	98.91097	95.90253	92.75796	36.61857	75.52409
J	8.45358	8.45358	91.54642	91.54642	34.00490	99.59161	37.73482	7.05146	2.80425
PZ	20.07895	20.07895	79.92105	79.92105	20.24231	13.05472	99.00626	53.28070	98.85652
LPZ	60.46828	60.49551	39.50449	39.50449	3.90689	63.24530	19.60250	100.00000	83.90961
TP	60.33215	60.34577	39.64062	39.64062	100.00000	64.93330	14.93330	1.37490	88.26572

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.35393	0.35393	0.36755	0.36755	37.65314	8.31745	38.83746	14.66104	8.09965
IP	99.64607	0.10890	99.63245	99.63245	62.33324	91.66894	61.14892	85.33896	91.90035
EP	99.63245	99.63245	0.36755	0.36755	37.66676	8.31745	38.83746	14.66104	8.09965
NC	0.36755	0.36755	99.63245	0.80316	62.33324	91.68255	61.16254	85.33896	91.90035
EZ	12.14266	12.12905	87.85734	87.85734	1.08903	4.09747	7.24204	63.38143	24.47591
J	91.54642	91.54642	8.45358	8.45358	65.99510	0.40839	62.26518	92.94854	97.19575
PZ	79.89382	79.92105	20.07895	20.07895	79.75769	86.94528	0.99374	46.71930	1.14348
LPZ	39.50449	39.50449	60.49551	60.49551	96.09311	36.75470	80.39750	0.00000	16.09039
TP	39.64062	39.64062	60.35938	60.35938	0.00000	35.06670	85.06670	98.62510	11.73428

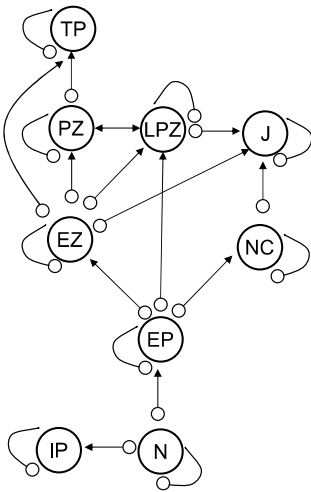
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.00000	0.00000	0	0	0.01361	0.00000	0.00000	0	0.01361
IP	0.00000	0.00000	0	0	0.00000	0.01361	0.01361	0	0.00000
EP	0.00000	0.00000	0	0	0.00000	0.00000	0.00000	0	0.00000
NC	0.00000	0.00000	0	0	0.00000	0.00000	0.00000	0	0.00000
EZ	0.00000	0.01361	0	0	0.00000	0.00000	0.00000	0	0.00000
J	0.00000	0.00000	0	0	0.00000	0.00000	0.00000	0	0.00000
PZ	0.02723	0.00000	0	0	0.00000	0.00000	0.00000	0	0.00000
LPZ	0.02723	0.00000	0	0	0.00000	0.00000	0.00000	0	0.00000
TP	0.02723	0.01361	0	0	0.00000	0.00000	0.00000	0	0.00000

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	?+	+	?+	+	+
IP	-	+	-	-	?-	-	?-	-	-
EP	-	-	+	+	?+	+	?+	+	+
NC	+	+	-	+	?-	-	?-	-	-
EZ	+	+	-	-	+	+	+	?-	+
J	-	-	+	+	?-	+	?-	-	-
PZ	-	-	+	+	-	-	+	0*	+
LPZ	?+	?+	?-	?-	-	?+	-	+	+
TP	?+	?+	?-	?-	+	?+	-	-	+

(8) Model VIII



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0
NC	0	0	-1	-1	0	1	0	0	0
EZ	0	0	-1	0	-1	1	1	1	1
J	0	0	0	-1	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	-1	0	-1	1	1	-1	0
TP	0	0	0	0	-1	0	-1	0	-1

Determinant: -63  
 Stable matrices: 6933  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	97.16966	97.16966	98.29862	77.78661	39.99046	92.01781	67.83272	73.36619	54.92129
IP	2.83034	99.69789	1.70138	22.21339	60.00954	7.98219	32.15138	26.63381	45.07871
EP	1.70138	1.70138	98.29862	77.78661	39.99046	92.01781	67.83272	73.36619	54.92129
NC	74.60646	74.60646	25.39354	93.38528	75.83082	80.21943	11.71887	1.81269	40.89680
EZ	70.94928	70.94928	29.05072	4.78613	89.64859	76.91207	62.31515	69.47050	95.94530
J	8.98394	8.98394	91.01606	17.14104	62.42646	98.18731	28.90762	21.95898	45.33312
PZ	35.80855	35.82446	64.17554	85.03737	0.69963	32.32628	98.91875	70.53586	57.79933
LPZ	51.34362	51.34362	48.65638	44.66529	0.55653	52.74288	80.66465	98.82334	16.36190
TP	45.36492	45.36492	54.63508	57.27461	77.03927	45.14231	0.58833	10.90793	97.61488

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	2.83034	2.83034	1.70138	22.21339	60.00954	7.98219	32.16728	26.63381	45.07871
IP	97.16966	0.30211	98.29862	77.78661	39.99046	92.01781	67.83272	73.36619	54.92129
EP	98.29862	98.29862	1.70138	22.21339	60.00954	7.98219	32.16728	26.63381	45.07871
NC	25.39354	25.39354	74.60646	6.61472	24.16918	19.78057	88.28113	98.18731	59.10320
EZ	29.05072	29.05072	70.94928	95.21387	10.35141	23.08793	37.68485	30.52950	4.05470
J	91.01606	91.01606	8.98394	82.85896	37.57354	1.81269	71.09238	78.04102	54.66688
PZ	64.17554	64.17554	35.82446	14.96263	99.30037	67.67372	1.08125	29.46414	42.20067
LPZ	48.65638	48.65638	51.34362	55.33471	99.44347	47.25712	19.33535	1.17666	83.63810
TP	54.63508	54.63508	45.36492	42.72539	22.96073	54.85769	99.41167	89.09207	2.38512

" (%) 0 "

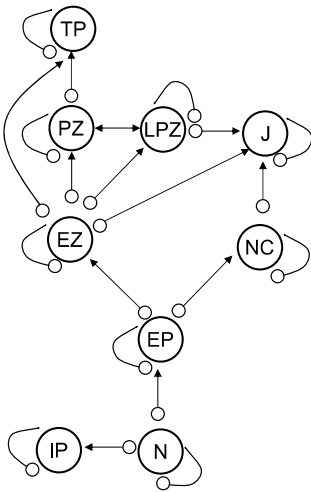
	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.0000	0	0	0	0	0	0.0000	0	0
IP	0.0000	0	0	0	0	0	0.0159	0	0
EP	0.0000	0	0	0	0	0	0.0000	0	0
NC	0.0000	0	0	0	0	0	0.0000	0	0
EZ	0.0000	0	0	0	0	0	0.0000	0	0
J	0.0000	0	0	0	0	0	0.0000	0	0
PZ	0.0159	0	0	0	0	0	0.0000	0	0
LPZ	0.0000	0	0	0	0	0	0.0000	0	0
TP	0.0000	0	0	0	0	0	0.0000	0	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	?-	+	?+	?+	0*
IP	-	+	-	-	?+	-	?-	?-	0*
EP	-	-	+	+	?-	+	?+	?+	0*
NC	?+	?+	?-	+	+	+	-	-	0*
EZ	?+	?+	?-	-	+	+	?+	?+	+
J	-	-	+	-	?+	+	?-	-	0*
PZ	?-	?-	?+	+	-	?-	+	?+	0*
LPZ	0*	0*	0*	0*	-	0*	+	+	-
TP	0*	0*	0*	0*	+	0*	-	-	+



(9) Model IX



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	0	0
NC	0	0	-1	-1	0	1	0	0	0
EZ	0	0	-1	0	-1	1	1	1	1
J	0	0	0	-1	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	0	0	-1	1	1	-1	0
TP	0	0	0	0	-1	0	-1	0	-1

Determinant: -71  
 Stable matrices: 7281  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	99.49810	99.49810	96.80608	76.82129	92.74525	97.12548	38.17490	28.76046	84.33460
IP	0.50190	99.33080	3.19392	23.17871	7.25475	2.87452	61.80989	71.23954	15.65019
EP	3.19392	3.19392	96.80608	76.82129	92.74525	97.12548	38.17490	28.76046	84.34981
NC	96.83650	96.83650	3.16350	95.57414	50.02281	79.43726	17.21673	5.04943	20.41065
EZ	55.23954	55.23954	44.76046	5.17110	89.56654	88.47148	65.96198	77.20152	96.86692
J	29.91635	29.91635	70.08365	3.20913	83.23954	96.94297	14.96578	4.73004	51.48289
PZ	21.46008	21.47529	78.52471	93.52091	0.24335	34.09886	99.71103	64.98859	61.94677
LPZ	7.07224	7.08745	92.91255	65.41445	1.58175	74.28137	82.93536	98.55513	21.04943
TP	81.03422	81.04943	18.95057	44.25856	75.75665	30.46388	0.38023	12.16730	97.24715

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.50190	0.50190	3.19392	23.17871	7.25475	2.87452	61.79468	71.23954	15.65019
IP	99.49810	0.66920	96.80608	76.82129	92.74525	97.12548	38.17490	28.76046	84.34981
EP	96.80608	96.80608	3.19392	23.17871	7.25475	2.87452	61.82510	71.23954	15.65019
NC	3.16350	3.16350	96.83650	4.42586	49.97719	20.56274	82.78327	94.95057	79.58935
EZ	44.74525	44.76046	55.23954	94.82890	10.43346	11.52852	34.03802	22.79848	3.13308
J	70.06844	70.08365	29.91635	96.79087	16.76046	3.05703	85.03422	95.26996	48.51711
PZ	78.50951	78.52471	21.47529	6.47909	99.74144	65.90114	0.28897	35.01141	38.05323
LPZ	92.91255	92.91255	7.08745	34.58555	98.41825	25.71863	17.06464	1.44487	78.95057
TP	18.93536	18.95057	81.04943	55.74144	24.24335	69.53612	99.61977	87.83270	2.75285

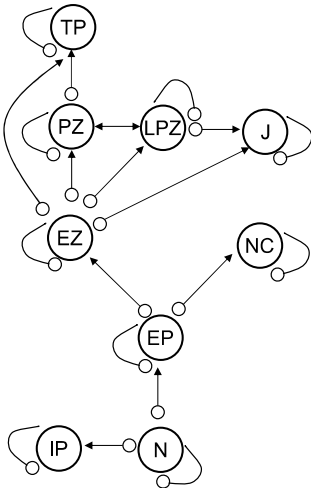
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.00000	0	0	0	0.00000	0	0.03042	0	0.01521
IP	0.00000	0	0	0	0.00000	0	0.01521	0	0.00000
EP	0.00000	0	0	0	0.00000	0	0.00000	0	0.00000
NC	0.00000	0	0	0	0.00000	0	0.00000	0	0.00000
EZ	0.01521	0	0	0	0.00000	0	0.00000	0	0.00000
J	0.01521	0	0	0	0.00000	0	0.00000	0	0.00000
PZ	0.03042	0	0	0	0.01521	0	0.00000	0	0.00000
LPZ	0.01521	0	0	0	0.00000	0	0.00000	0	0.00000
TP	0.03042	0	0	0	0.00000	0	0.00000	0	0.00000

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	+	+	?-	?-	+
IP	-	+	-	-	-	-	?+	?+	-
EP	-	-	+	+	+	+	?-	?-	+
NC	+	+	-	+	0*	+	-	-	-
EZ	0*	0*	0*	-	+	+	?+	+	+
J	?-	?-	?+	-	+	+	-	-	0*
PZ	-	-	+	+	-	-	?-	+	?+
LPZ	-	-	+	?+	-	?+	+	+	-
TP	+	+	-	0*	+	?-	-	-	+

(10) Model X



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	-1	1	1	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	0	0
NC	0	0	-1	-1	0	0	0	0	0
EZ	0	0	-1	0	-1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0
PZ	0	0	0	0	-1	0	-1	1	1
LPZ	0	0	0	0	-1	1	1	-1	0
TP	0	0	0	0	-1	0	-1	0	-1

Determinant: -51  
 Stable matrices: 7054  
 Simulated matrices: 9000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	99.76270	99.76270	97.27891	97.27891	92.73849	95.61778	54.94384	55.46591	95.34884
IP	0.23730	99.44629	2.72109	2.72109	7.22987	4.35058	44.96124	44.47081	4.60370
EP	2.72109	2.72109	97.27891	97.27891	92.77013	95.64942	54.97548	55.51337	95.38048
NC	97.27891	97.27891	2.72109	99.69941	7.22987	4.35058	45.02452	44.48663	4.61952
EZ	92.77013	92.75431	7.22987	7.22987	92.77013	95.64942	54.97548	55.51337	95.38048
J	75.73169	75.73169	24.26831	24.26831	75.73169	96.66192	10.67869	0.66445	37.38333
PZ	0.00000	0.00000	100.00000	100.00000	0.00000	18.96852	99.77852	82.86664	63.64499
LPZ	0.00000	0.00000	100.00000	100.00000	0.00000	64.67331	82.53441	99.79434	19.55387
TP	75.33618	75.33618	24.66382	24.66382	75.33618	36.97200	0.88594	10.69451	97.23145

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0.23730	0.23730	2.72109	2.72109	7.22987	4.35058	44.99288	44.48663	4.60370
IP	99.76270	0.55371	97.27891	97.27891	92.72267	95.61778	54.91220	55.46591	95.33302
EP	97.27891	97.27891	2.72109	2.72109	7.22987	4.35058	45.02452	44.48663	4.61952
NC	2.72109	2.72109	97.27891	0.30059	92.77013	95.64942	54.97548	55.51337	95.38048
EZ	7.22987	7.22987	92.77013	92.77013	7.22987	4.35058	45.02452	44.48663	4.61952
J	24.26831	24.26831	75.73169	75.73169	24.26831	3.33808	89.32131	99.33555	62.61667
PZ	100.00000	100.00000	0.00000	0.00000	100.00000	81.03148	0.22148	17.13336	36.35501
LPZ	100.00000	100.00000	0.00000	0.00000	100.00000	35.32669	17.46559	0.20566	80.44613
TP	24.66382	24.66382	75.33618	75.33618	24.66382	63.02800	99.11406	89.30549	2.76855

" (%) 0 "

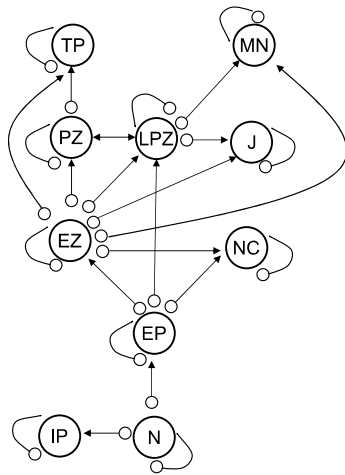
	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	0	0.00000	0	0	0.03164	0.03164	0.06328	0.04746	0.04746
IP	0	0.00000	0	0	0.04746	0.03164	0.12656	0.06328	0.06328
EP	0	0.00000	0	0	0.00000	0.00000	0.00000	0.00000	0.00000
NC	0	0.00000	0	0	0.00000	0.00000	0.00000	0.00000	0.00000
EZ	0	0.01582	0	0	0.00000	0.00000	0.00000	0.00000	0.00000
J	0	0.00000	0	0	0.00000	0.00000	0.00000	0.00000	0.00000
PZ	0	0.00000	0	0	0.00000	0.00000	0.00000	0.00000	0.00000
LPZ	0	0.00000	0	0	0.00000	0.00000	0.00000	0.00000	0.00000
TP	0	0.00000	0	0	0.00000	0.00000	0.00000	0.00000	0.00000

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP
N	+	+	+	+	+	+	0*	0*	+
IP	-	+	-	-	-	-	0*	0*	-
EP	-	-	+	+	+	+	0*	0*	+
NC	+	+	-	+	-	-	0*	0*	-
EZ	+	+	-	-	+	+	0*	0*	+
J	+	+	-	-	+	+	-	-	?-
PZ	-	-	+	+	-	-	+	+	?+
LPZ	-	-	+	+	-	-	?+	+	+
TP	+	+	-	-	+	-	-	-	+

## B2. Models for the post-invasion period

### (1) Model I



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	-1	1	1	0	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0	0
NC	0	0	-1	-1	-1	0	0	0	0	0
EZ	0	0	-1	1	-1	1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0	0
PZ	0	0	0	0	-1	0	-1	1	1	0
LPZ	0	0	-1	0	-1	1	1	-1	0	1
TP	0	0	0	0	-1	0	-1	0	-1	0
MN	0	0	0	0	-1	0	0	-1	0	-1

Determinant: 73  
 Stable matrices: 7310  
 Simulated matrices: 10000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	97.26402	97.26402	98.34473	82.48974	15.67715	63.47469	74.93844	91.20383	36.00547	64.40492
IP	2.73598	99.67168	1.65527	17.51026	84.32285	36.52531	25.04788	8.79617	63.96717	35.59508
EP	1.65527	1.65527	98.34473	82.48974	15.67715	63.47469	74.95212	91.20383	36.00547	64.40492
NC	84.71956	84.71956	15.28044	94.73324	22.39398	14.39124	41.65527	45.89603	14.04925	14.48700
EZ	89.13817	89.13817	10.86183	77.77018	98.59097	74.69220	39.23393	14.52804	91.58687	74.18605
J	31.03967	31.03967	68.96033	77.03146	59.78112	95.86867	21.08071	13.96717	31.96990	14.40492
PZ	17.59234	17.59234	82.40766	15.14364	0.19152	42.16142	99.43912	98.08482	67.87962	43.17373
LPZ	34.25445	34.25445	65.74555	9.76744	1.08071	66.73051	81.76471	99.91792	24.73324	66.77155
TP	50.17784	50.17784	49.82216	72.88646	69.31601	32.27086	2.31190	16.64843	95.47196	31.08071
MN	30.47880	30.47880	69.52120	77.15458	58.91929	14.11765	22.01094	13.54309	31.17647	95.89603

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	2.73598	2.73598	1.65527	17.51026	84.32285	36.52531	25.04788	8.79617	63.98085	35.59508
IP	97.26402	0.32832	98.34473	82.48974	15.67715	63.47469	74.93844	91.20383	36.00547	64.40492
EP	98.34473	98.34473	1.65527	17.51026	84.32285	36.52531	25.04788	8.79617	63.99453	35.59508
NC	15.28044	15.28044	84.71956	5.26676	77.60602	85.60876	58.34473	54.10397	85.95075	85.51300
EZ	10.86183	10.86183	89.13817	22.22982	1.40903	25.30780	60.76607	85.47196	8.41313	25.81395
J	68.96033	68.96033	31.03967	22.96854	40.21888	4.13133	78.91929	86.03283	68.03010	85.59508
PZ	82.40766	82.40766	17.59234	84.85636	99.80848	57.83858	0.56088	1.91518	32.12038	56.82627
LPZ	65.74555	65.74555	34.25445	90.23256	98.91929	33.26949	18.23529	0.08208	75.26676	33.22845
TP	49.82216	49.82216	50.17784	27.11354	30.68399	67.72914	97.68810	83.35157	4.52804	68.91929
MN	69.52120	69.52120	30.47880	22.84542	41.08071	85.88235	77.98906	86.45691	68.82353	4.10397

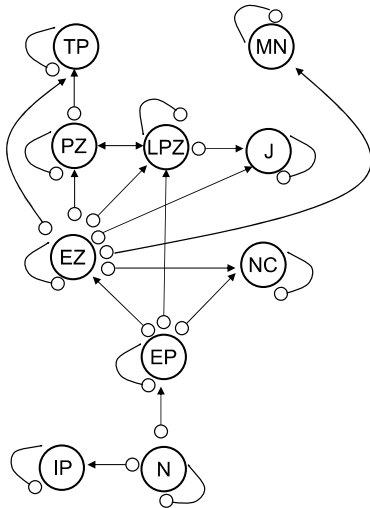
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	0	0	0	0	0	0	0.01368	0	0.01368	0
IP	0	0	0	0	0	0	0.01368	0	0.02736	0
EP	0	0	0	0	0	0	0.00000	0	0.00000	0
NC	0	0	0	0	0	0	0.00000	0	0.00000	0
EZ	0	0	0	0	0	0	0.00000	0	0.00000	0
J	0	0	0	0	0	0	0.00000	0	0.00000	0
PZ	0	0	0	0	0	0	0.00000	0	0.00000	0
LPZ	0	0	0	0	0	0	0.00000	0	0.00000	0
TP	0	0	0	0	0	0	0.00000	0	0.00000	0
MN	0	0	0	0	0	0	0.00000	0	0.00000	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	+	+	+	+	-	?+	?+	+	?-	?+
IP	-	+	-	-	+	?-	?-	-	?+	?-
EP	-	-	+	+	-	?+	?+	+	?-	?+
NC	+	+	-	+	-	-	0*	0*	-	-
EZ	+	+	-	+	+	?+	?-	-	+	?+
J	?-	?-	?+	+	0*	+	-	-	?-	-
PZ	-	-	+	-	-	0*	+	+	?+	0*
LPZ	?-	?-	?+	-	-	?+	+	+	-	?+
TP	0*	0*	0*	?+	?+	?-	-	-	+	?-
MN	?-	?-	?+	+	0*	-	-	-	?-	+

(2) Model II



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	-1	1	1	0	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0	0
NC	0	0	-1	-1	-1	0	0	0	0	0
EZ	0	0	-1	1	-1	1	1	1	1	1
J	0	0	0	0	-1	-1	0	-1	0	0
PZ	0	0	0	0	-1	0	-1	1	1	0
LPZ	0	0	-1	0	-1	1	1	-1	0	0
TP	0	0	0	0	-1	0	-1	0	-1	0
MN	0	0	0	0	-1	0	0	0	0	-1

Determinant: 71  
 Stable matrices: 7837  
 Simulated matrices: 10000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	97.84356	97.84356	98.04772	83.32270	13.99770	70.97103	80.13270	92.71405	45.70627	13.99770
IP	2.15644	99.71928	1.95228	16.67730	86.00230	29.02897	19.86730	7.28595	54.28097	86.00230
EP	1.95228	1.95228	98.04772	83.32270	13.99770	70.97103	80.13270	92.71405	45.71903	13.99770
NC	85.28774	85.28774	14.71226	97.26936	27.37017	6.32895	31.87444	26.03037	11.20327	27.37017
EZ	92.03777	92.03777	7.96223	69.83540	97.00140	83.46306	43.62639	30.54740	91.29769	97.00140
J	23.92497	23.92497	76.07503	87.61005	64.29756	93.91349	12.45375	4.26183	21.50057	64.29756
PZ	21.94717	21.95993	78.04007	15.27370	0.39556	47.67130	99.82136	95.24053	78.15491	0.39556
LPZ	47.83718	47.83718	52.16282	7.69427	2.43716	80.70690	88.96261	99.91068	41.67411	2.43716
TP	43.70295	43.70295	56.29705	79.23950	71.41763	23.31249	1.25048	10.41215	92.99477	71.41763
MN	7.96223	7.96223	92.03777	30.16460	2.99860	16.53694	56.37361	69.45260	8.70231	94.55149

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	2.15644	2.15644	1.95228	16.67730	86.00230	29.01621	19.86730	7.28595	54.28097	86.00230
IP	97.84356	0.28072	98.04772	83.32270	13.99770	70.97103	80.13270	92.71405	45.71903	13.99770
EP	98.04772	98.04772	1.95228	16.67730	86.00230	29.02897	19.86730	7.28595	54.28097	86.00230
NC	14.71226	14.71226	85.28774	2.73064	72.62983	93.67105	68.12556	73.96963	88.79673	72.62983
EZ	7.96223	7.96223	92.03777	30.16460	2.99860	16.53694	56.37361	69.45260	8.70231	2.99860
J	76.07503	76.07503	23.92497	12.38995	35.70244	6.08651	87.54625	95.73817	78.49943	35.70244
PZ	78.04007	78.04007	21.95993	84.72630	99.60444	52.32870	0.17864	4.75947	21.84509	99.60444
LPZ	52.16282	52.16282	47.83718	92.30573	97.56284	19.29310	11.03739	0.08932	58.32589	97.56284
TP	56.29705	56.29705	43.70295	20.76050	28.58237	76.68751	98.74952	89.58785	7.00523	28.58237
MN	92.03777	92.03777	7.96223	69.83540	97.00140	83.46306	43.62639	30.54740	91.29769	5.44851

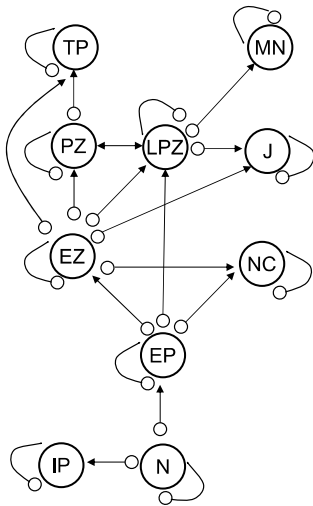
" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	0.00000	0	0	0	0	0.01276	0	0	0.01276	0
IP	0.00000	0	0	0	0	0.00000	0	0	0.00000	0
EP	0.00000	0	0	0	0	0.00000	0	0	0.00000	0
NC	0.00000	0	0	0	0	0.00000	0	0	0.00000	0
EZ	0.00000	0	0	0	0	0.00000	0	0	0.00000	0
J	0.00000	0	0	0	0	0.00000	0	0	0.00000	0
PZ	0.01276	0	0	0	0	0.00000	0	0	0.00000	0
LPZ	0.00000	0	0	0	0	0.00000	0	0	0.00000	0
TP	0.00000	0	0	0	0	0.00000	0	0	0.00000	0
MN	0.00000	0	0	0	0	0.00000	0	0	0.00000	0

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	+	+	+	+	-	?+	+	+	0*	-
IP	-	+	-	-	+	?-	-	-	0*	+
EP	-	-	+	+	-	?+	+	+	0*	-
NC	+	+	-	+	?-	-	?-	?-	-	?-
EZ	+	+	-	?+	+	+	0*	?-	+	+
J	-	-	+	+	?+	+	-	-	-	?+
PZ	-	-	+	-	-	0*	+	+	+	-
LPZ	0*	0*	0*	-	-	+	+	+	0*	-
TP	0*	0*	0*	+	?+	-	-	-	+	?+
MN	-	-	+	?-	-	-	0*	?+	-	+

(3) Model III



Community matrix

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	-1	1	1	0	0	0	0	0	0	0
IP	-1	-1	0	0	0	0	0	0	0	0
EP	-1	0	-1	1	1	0	0	1	0	0
NC	0	0	-1	-1	-1	0	0	0	0	0
EZ	0	0	-1	1	-1	1	1	1	1	0
J	0	0	0	0	-1	-1	0	-1	0	0
PZ	0	0	0	0	-1	0	-1	1	1	0
LPZ	0	0	-1	0	-1	1	1	-1	0	1
TP	0	0	0	0	-1	0	-1	0	-1	0
MN	0	0	0	0	0	0	0	-1	0	-1

Determinant: 10  
 Stable matrices: 8274  
 Simulated matrices: 10000

" (%) + "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	98.11458	98.11458	99.20232	89.17090	22.02079	60.90162	74.24462	91.24970	41.89026	91.26178
IP	1.88542	99.89123	0.79768	10.82910	77.97921	39.08629	25.75538	8.72613	58.10974	8.72613
EP	0.79768	0.79768	99.20232	89.17090	22.02079	60.91371	74.24462	91.26178	41.89026	91.26178
NC	81.19410	81.19410	18.80590	97.22021	16.48538	4.93111	39.02586	32.22142	8.81073	32.22142
EZ	94.53710	94.53710	5.46290	70.02659	98.19918	89.83563	45.15349	29.94924	94.46459	29.94924
J	20.63089	20.63089	79.36911	75.36862	44.42833	97.17186	20.72758	6.84071	17.11385	6.84071
PZ	11.02248	11.02248	88.97752	20.41334	0.21755	27.29031	99.63742	93.72734	71.75489	93.72734
LPZ	35.69011	35.69011	64.30989	9.92265	2.12715	68.67295	85.65386	99.84288	30.23930	99.84288
TP	49.11772	49.12980	50.87020	72.93933	66.01402	32.43897	1.19652	12.90790	96.44670	12.90790
MN	64.29780	64.30989	35.69011	90.07735	97.87285	31.32705	14.34614	0.15712	69.76070	89.79937

" (%) - "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	1.88542	1.88542	0.79768	10.82910	77.96713	39.08629	25.75538	8.73822	58.10974	8.73822
IP	98.11458	0.10877	99.20232	89.17090	22.02079	60.91371	74.24462	91.24970	41.89026	91.26178
EP	99.20232	99.20232	0.79768	10.82910	77.97921	39.08629	25.75538	8.73822	58.10974	8.73822
NC	18.80590	18.80590	81.19410	2.77979	83.51462	95.06889	60.97414	67.77858	91.18927	67.77858
EZ	5.46290	5.46290	94.53710	29.97341	1.80082	10.16437	54.83442	70.05076	5.53541	70.05076
J	79.36911	79.36911	20.63089	24.63138	55.57167	2.82814	79.27242	93.15929	82.88615	93.15929
PZ	88.96543	88.97752	11.02248	79.58666	99.78245	72.70969	0.36258	6.27266	28.24511	6.27266
LPZ	64.30989	64.30989	35.69011	90.07735	97.87285	31.32705	14.34614	0.15712	69.76070	0.15712
TP	50.87020	50.87020	49.12980	27.06067	33.98598	67.56103	98.80348	87.09210	3.55330	87.09210
MN	35.69011	35.69011	64.30989	9.92265	2.12715	68.67295	85.65386	99.84288	30.23930	10.20063

" (%) 0 "

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	0.00000	0	0	0	0.01209	0.01209	0.00000	0.01209	0	0.00000
IP	0.00000	0	0	0	0.00000	0.00000	0.00000	0.02417	0	0.01209
EP	0.00000	0	0	0	0.00000	0.00000	0.00000	0.00000	0	0.00000
NC	0.00000	0	0	0	0.00000	0.00000	0.00000	0.00000	0	0.00000
EZ	0.00000	0	0	0	0.00000	0.00000	0.01209	0.00000	0	0.00000
J	0.00000	0	0	0	0.00000	0.00000	0.00000	0.00000	0	0.00000
PZ	0.01209	0	0	0	0.00000	0.00000	0.00000	0.00000	0	0.00000
LPZ	0.00000	0	0	0	0.00000	0.00000	0.00000	0.00000	0	0.00000
TP	0.01209	0	0	0	0.00000	0.00000	0.00000	0.00000	0	0.00000
MN	0.01209	0	0	0	0.00000	0.00000	0.00000	0.00000	0	0.00000

Table of predictions

	N	IP	EP	NC	EZ	J	PZ	LPZ	TP	MN
N	+	+	+	+	-	?+	?+	+	0*	+
IP	-	+	-	-	+	?-	?-	-	0*	-
EP	-	-	+	+	-	?+	?+	+	0*	+
NC	+	+	-	+	-	?-	?-	-	-	?-
EZ	+	+	-	?+	+	+	0*	?-	+	?-
J	-	-	+	+	0*	+	-	-	-	-
PZ	-	-	+	-	-	?-	+	+	?+	+
LPZ	?-	?-	?+	-	-	?+	+	+	?-	+
TP	0*	0*	0*	?+	?+	?-	-	-	+	-
MN	?+	?+	?-	+	+	?-	-	-	?+	+

## Appendix C - Data

### C1. Data sources

	Common name	Scientific name	References	Node name	Source of data
Phytoplankton	Edible - Inedible Phytoplankton		Simonov et al. 1992; Prodanov et al. 1997; Kideys et al. 2000; Parr et al. 2005; Oguz et al. 2006, 2008; BS-TDA 2007; Yunev et al. 2007, 2009; BSC 2008; Nicolaev et al. 2010; Dorofeyev et al. 2012	EP	Prodanov et al. 1997
	Small - Large Phytoplankton			IP	
Zooplankton	Edible zooplankton		Simonov et al. 1992; Prodanov et al. 1997; Zaitsev and Mamaev 1997; Kovalev et al. 1998; Shiganova et al. 1998, 2000, 2001, 2003; Mutlu 1999; Kideys et al. 2000; Purcell et al. 2001; Kamburska et al. 2006; Volovik 2006; Grishin et al. 2007; BS-TDA 2007; BSC 2008; Oguz et al. 2008; Nicolaev et al. 2010; Dorofeyev et al. 2012; Finenko et al. 2013	EZ	Prodanov et al. 1997
	Small and large zooplankton				
	Copepods				
	Cladocerans	<i>Parasagitta setosa</i>			
<i>Noctiluca scintillans</i>		<i>Noctiluca scintillans</i>	Simonov et al. 1992; Prodanov et al. 1997; Kideys et al. 2000; Parr et al. 2005; Oguz et al. 2006, 2008; BS-TDA 2007; Yunev et al. 2007, 2009; BSC 2008; Nicolaev et al. 2010; Dorofeyev et al. 2012	NC	Simonov et al. 1992
Jellyfish	Ctenophores			J	Simonov et al. 1992
	Moon jelly	<i>Aurelia aurita</i>	Kideys et al. 2000; Shiganova et al. 2000, 2001; Oguz et al. 2001; Gucu 2002; Grishin et al. 2007; BSC 2008; Dorofeyev et al. 2012		
	Sea gooseberry	<i>Pleurobrachia pileus</i>	Kideys et al. 2000; Shiganova et al. 2001; Gucu 2002; BSC 2008		
		<i>Beroe ovata</i>	Shiganova et al. 2003; Kamburska et al. 2006; BSC 2008; Finenko et al. 2013		
<i>Mnemiopsis leidyi</i>	Sea walnut	<i>Mnemiopsis leidyi</i>	Kideys et al. 2000; Shiganova et al. 2000, 2001; Oguz et al. 2001; Gucu 2002; Grishin et al. 2007; BSC 2008; Dorofeyev et al. 2012	MN	

**Table 3.4** - Data sources for plankton groups: phytoplankton, zooplankton, *N. scintillans*, jellyfish, and *M. leidyi*. I reported information on both common and scientific names, as well as correspondence between the groups and the nodes in the digraphs for loop analysis. References used to obtain the empirical data for statistical analysis are in the last column (all data illustrated in the Figure 3.2 of the manuscript are expressed as biomasses, mg m<sup>-3</sup>).

	Common name	Scientific name	References	Node name	Effective source of data	Stocks/Catches
Planktivorous fish	Black Sea anchovy	<i>Engraulis encrasicolus</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; Shiganova et al. 2003; BS-TDA 2007; BSC 2008, 2010; Nicolaev et al. 2010; Sea Around Us Project 2011 <sup>7</sup> ; Daskalov et al. 2012	PZ	Prodanov et al. 1997; Sea Around us Project 2011 <sup>7</sup>	Stocks, Catches
	Black Sea horse mackerel	<i>Trachurus mediterraneus</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; BSC 2008, 2010; Nicolaev et al. 2010; Sea Around Us Project 2011 <sup>7</sup> ; Daskalov et al. 2012	PZ	Prodanov et al. 1997; Sea Around us Project 2011 <sup>7</sup>	Stocks, Catches
	Atlantic horse mackerel	<i>Trachurus trachurus</i>	BS-TDA 2007; Sea Around Us Project 2011 <sup>7</sup>	PZ	Sea Around us Project 2011 <sup>7</sup>	Catches
	Black Sea mackerel	<i>Scomber scombrus</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997			
	Chub mackerel	<i>Scomber japonicus</i>	Prodanov et al. 1997			
	European sprat	<i>Sprattus sprattus</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; Shiganova et al. 2003; BS-TDA 2007; BSC 2008, 2010; Daskalov et al. 2009, 2012; Nicolaev et al. 2010; Sea Around Us Project 2011 <sup>7</sup>	PZ	Prodanov et al. 1997; Sea Around us Project 2011 <sup>7</sup>	Stocks, Catches
	Caspian Sea sprat	<i>Clupeonella cultriventris</i>	Sea Around Us Project 2011 <sup>7</sup>	PZ	Sea Around us Project 2011 <sup>7</sup>	Catches
	Golden grey mullet	<i>Liza aurata</i>	Prodanov et al. 1997; BSC 2008			
	Red mullet	<i>Mullus barbatus barbatus</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; BSC 2008; Maximov et al. 2008; Nicolaev et al. 2010; Daskalov et al. 2012			
	Mulletts (other species)	<i>Liza aurata, Liza saliens, Mugil cephalus</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; BS-TDA 2007; BSC 2008; Nicolaev et al. 2010			
	Gobies		Zaitsev and Mamaev 1997; Maximov et al. 2008; Nicolaev et al. 2010; Sea Around Us Project 2011 <sup>7</sup>	PZ	Sea Around us Project 2011 <sup>7</sup>	Catches
	European pilchard	<i>Sardina pilchardus</i>	Sea Around Us Project 2011 <sup>7</sup>	PZ	Sea Around us Project 2011 <sup>7</sup>	Catches
Piscivorous fish	Turbot	<i>Scophthalmus maximus</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; BSC 2008, 2010; Maximov et al. 2008; Daskalov et al. 2009, 2012; Nicolaev et al. 2010	TP	Prodanov et al. 1997	Stocks, Catches
	Whiting	<i>Merlangius merlangus</i>	Prodanov et al. 1997, 2003; BS-TDA 2007; BSC 2008, 2010; Maximov et al. 2008; Nicolaev et al. 2010; Sea Around Us Project 2011 <sup>7</sup> ; Daskalov et al. 2012	TP	Prodanov et al. 1997	Stocks
	Bluefish	<i>Pomatus saltatrix</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; BS-TDA 2007; Sea Around Us Project 2011 <sup>7</sup>	TP	Prodanov et al. 1997	Catches
	Atlantic bonito	<i>Sarda sarda</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; BS-TDA 2007; Sea Around Us Project 2011 <sup>7</sup>	TP	Prodanov et al. 1997	Catches
	Picked dogfish	<i>Squalus acanthias</i>	Prodanov et al. 1997; Zaitsev and Mamaev 1997; BS-TDA 2007; BSC 2008; Maximov et al. 2008; Nicolaev et al. 2010; Daskalov et al. 2012	TP	Prodanov et al. 1997	Stocks

**Table 3.5** - Data sources for piscivorous fish and planktivorous fish. FishBase (Froese and Pauly 2016) was used as a reference for common and scientific names. I indicated the correspondence between the digraph nodes and the various taxa. References consulted to obtain the data for statistical analysis are provided. The last column indicates whether biomasses refer to stocks or catches.

<sup>7</sup> <http://www.seaaroundus.org/data/#/lme/62?chart=catch-chart&dimension=taxon&measure=tonnage&limit=10>  
[last accessed on November 7, 2016]

## C2. Data set

Year	A	B	C	D	E	F	G	H
1950						134229		6206
1951						187225		1898
1952						163013		3795
1953						154430		9555
1954						132326		17305
1955						87077		52012
1956						77940		62894
1957						90825		49949
1958						43612		32693
1959						53062		20982
1960	36.0		239.0	79.0		39635		15734
1961	525.0		213.3	31.3		40059		43866
1962	362.5		376.7	48.7		47502		4690
1963	45.0		261.0	53.7		74807		20674
1964	411.0	119.15	184.3	31.3		108497		11916
1965	391.5	81.70	169.7	67.3		124575		18339
1966	315.5	82.25	288.3	18.7		137806		16420
1967	323.0	204.35	241.3	9.7	1419	138400		17136
1968	201.0	98.70	58.7	39.7	1454	104713		16362
1969	280.0	125.70	125.7	6.7	1710	56204		26274
1970	442.0	89.00	531.0	74.7	2092	319675		22708
1971	228.5	125.90	262.0	219.7	2172	280901	239	24293
1972	327.5	72.60	197.3	119.0	1832	303677	257	12964
1973	867.5	122.90	99.0	216.0	1595	319128	316	3620
1974	671.5	107.60	66.7	58.3	1555	367762	316	4677
1975	339.0	71.65	245.0	124.7	1882	334369	361	3397
1976	896.0	47.40	119.3	95.7	1977	365274	414	8070
1977	1331.5	43.95	167.7	285.3	2211	285344	521	5338
1978	571.0	44.10	148.7	123.3	2569	370704	548	3308
1979	1163.0	67.30	316.7	70.7	3098	463267	514	17095
1980	1337.5	169.15	285.7	31.0	2741	603670	553	14076
1981	778.5	92.70	378.3	81.0	2421	584795	565	5665
1982	1051.0	51.05	148.0	51.0	2391	665406	526	17555
1983	594.5	56.70	348.0	89.0	2960	671706	488	15319
1984	668.0	63.90	254.7	156.0	3347	745543	429	6473
1985	190.5	75.85	643.0	150.0	3742	633782	361	12464
1986	258.5	73.05	710.3	62.7	3133	705078	326	4684
1987	451.5	56.90	504.7	107.3	2585	590137	282	6719
1988	560.5	65.70	324.3	80.7	1899	704727	232	8360
1989	988.0	81.80			1482	391999		4427
1990		73.80			837	225205		4754
1991		52.75			852	151574		8617
1992		61.90			1019	220875		3702
1993					1222	262022		
1994						334428		
1995						428221		
1996						313848		
1997						257497		
1998						243533		
1999						361228		
2000						336765		
2001						396827		
2002						442042		
2003						365618		
2004						389079		
2005						223502		
2006						137965		

**Table 3.6** - Time series used for statistical analysis. If not explicitly mentioned, data refer to the whole Black Sea basin. (A) Phytoplankton biomass ( $\text{mg m}^{-3}$ ) in the Black Sea from Prodanov et al. (1997); I considered the mean of data relative to northwestern and eastern part of the Black Sea. (B) Zooplankton biomass ( $\text{mg m}^{-3}$ ) in the depth 0 - 100 m from Prodanov et al. (1997); I considered the mean of data relative to western and eastern part of the Black Sea. (C) *N. scintillans* biomass ( $\text{mg m}^{-3}$ ) in the Black Sea from Simonov et al. (1992); I considered the mean of data relative to northwestern and eastern part of the Black Sea and Crimea coast. (D) Ctenophores biomass ( $\text{mg m}^{-3}$ ) in the Black Sea from Simonov et al. (1992); I considered the mean of data relative to northwestern and eastern part of the Black Sea and Crimea coast. Data on ctenophores were used as a reference for the variable jellyfish (J) in the models. (E) Planktivorous fish stock (1,000 tonnes) accounts for available data of three species (Prodanov et al. 1997): Black Sea anchovy (*E. encrasicolus*), for which I considered the exploited biomass; Black Sea horse mackerel (*T. mediterraneus*); European sprat (*S. sprattus*). (F) Planktivorous fish catch (tonnes) accounts for online available data of several species (source: Sea Around us Project - [www.seaaroundus.org](http://www.seaaroundus.org)): Black Sea anchovy (*E. encrasicolus*); Caspian Sea sprat (*C. cultriventris*); European sprat (*S. sprattus*); Black Sea horse mackerel (*T. mediterraneus*); gobies; Atlantic horse mackerel (*T. trachurus*); European pilchard (*S. pilchardus*). (G) Piscivorous fish stock (1,000 tonnes) accounts for available data of three species (Prodanov et al. 1997): whiting (*M. merlangus*) - I considered the mean of data relative to western and eastern part of the Black Sea; turbot (*S. maximus*); picked dogfish (*S. acanthias*). (H) Piscivorous fish catch (tonnes) accounts for available data of three species (Prodanov et al. 1997): turbot (*S. maximus*); Atlantic bonito (*S. sarda*); bluefish (*P. saltatrix*) - data refer to total landings in different countries (i.e. Bulgaria, Romania, former USSR and Turkey).



## **The controlling factor in ecosystems: bottom-up/top-down models and patterns of response**

### **4.1 Direct perturbations and community-wide consequences**

Direct perturbations (e.g. eutrophication and overfishing) targeting top and bottom species (apical predators and primary producers, respectively) can propagate and have community-wide consequences, even reaching the opposite extremes of the food web (Fuller et al. 1995, Crooks and Soulé 1999, Donald et al. 2001, Daskalov et al. 2007, Oguz et al. 2007, Sandin et al. 2008).

Three general hypotheses (arising from the regulation study of trophic level biomass in freshwater pelagic ecosystems) have been proposed to test the propagation of direct and indirect effects: biomanipulation concept (Shapiro et al. 1975, 1982, Shapiro 1980), cascading trophic interaction theory (Carpenter et al. 1985) and bottom-up/top-down model (McQueen et al. 1986). The first two focus on the impact of predators (e.g. changes in piscivore abundance will cascade down through the food web and will cause chlorophyll to deviate from nutrient-predicted concentrations). The biomanipulation concept was conceived as alternative methods to eliminate excess algae that result from eutrophication meanwhile avoiding high costs and inapplicability of conventional techniques (Edmondson 1977, Ahlgren 1978). It consists of manipulating the abundance of piscivorous or planktivorous fish to reduce the abundance of the producers but essentially is based on the idea of trophic cascade (Shapiro et al. 1975, Shapiro 1980ab, Shapiro et al. 1982). The trophic cascade hypothesis is a general theory that could be defined as “top-down” control of community structure by predators (Carpenter et al. 1985, Carpenter and Kitchell 1987, Kennen et al. 2007), resulting in inverse patterns in abundance or biomass across trophic levels (Pace et al. 1999, Polis et al. 2000). The trophic cascade concept arose from the observations and experiments of field ecologists in the marine intertidal zone (Paine 1980) and in lakes (Hrbáček et al. 1961, Shapiro et al. 1975), and became a central concept in ecology (e.g. theoretical analyses, field studies and management

application; Pace et al. 1999, Polis et al 2000). The trophic cascade mechanism is ubiquitous (i.e. no restricted to ecosystem type, diversity, habitat complexity, types of top predators or the trophic mode of consumers; Pace et al. 1999). It often originates from top predators, but is not necessarily restricted to these taxa (i.e. it does not necessarily originate at the top of the food web). The third theory, bottom-up:top-down model (McQueen et al. 1986), is derived from Lewis' work (1979) and explicitly combines the predicted influences of both resource availability (bottom-up, BU) and predators (top-down, TD). In freshwater pelagic ecosystems this model predicts that “*maximum attainable biomass is determined by (bottom-up) nutrient availability, but that realized biomass is determined by the combined effects of top-down and bottom-up forces*” (McQueen et al. 1989). The BU:TD theory predicts that top-down forces should be strong at the top of the food web and weaken towards the bottom, whereas bottom-up forces should be strong at the bottom and weaken towards the top. This leads to the prediction that in eutrophic lakes, the impacts of changes in piscivore biomass will damp out as they cascade down through the food web so that there will be little or no influence on algae. This would explain the high number of failures registered in biomanipulation experiments (Carpenter and Kitchell 1987). “Bottom-up” (i.e. regulation of food-web components by either primary producers or the input of limiting nutrients to an ecosystem - nutrient driven) and “top-down” (i.e. regulation of lower food-web components by an upper-level predator - predator dominated) forces often act simultaneously (Hunter and Price 1992, DeAngelis 2012, Wollrab et al. 2012) and disentangling their effect in the net outcomes observed in the field is a difficult task. From a theoretical perspective, the balance between these two mechanisms provides a foundation for understanding ecosystem structure, function, evolution (Reid et al. 2000) and it is a challenge for predicting eco-evolutionary dynamics and ecosystem management. The diffusion of the indirect effects from basal species and top predators is particularly complex due to the diversity of roles played by intermediate species (Power 1992, Stouffer et al. 2012).

In this chapter I am interested in disentangling the contribution and balancing of bottom-up and top-down forces to the spreading of indirect effects from one extreme to the other of the food web. I test whether differences exist for what concerns the forces that influence the response of top and basal species to perturbations affecting basal and top species, respectively. In particular, I aim at finding whether a general pattern of response exists and whether this pattern depends on the structure (i.e. arrangement of trophic interactions) or on the patterning of interaction strengths in the food webs.

A variety of approaches, from field ecology to modeling, illustrates how the spread and the consequences of “bottom-up” vs. “top-down” effects in ecosystems can be explored (Pace et al. 1999, Ebenman et al. 2004, Duffy et al. 2015). In this work I exploit the features of loop analysis, a qualitative modeling technique that studies signed digraphs (Levins 1974). This technique is introduced and described in the chapter 3 of the thesis. Loop analysis allows identifying the consequences of impacts that spread along pathways of any length within the structure of the community. Accordingly, top-down cascades and bottom-up effects can be assessed by considering

the diffusion of perturbations that target bottom and top species. Main objective of this chapter is describing how the perturbations that enter the system at the level of bottom and top species travel to top and bottom species, respectively.

To obtain general patterns of top-down and bottom-up responses I selected a high number of real systems (representative of marine, freshwater and terrestrial habitats) and applied loop analysis. My goal was predicting community-wide changes triggered by perturbations at either the top or the bottom of the food web. I was searching for trends in top/basal responses (i.e. over or underrepresentation) in the tables of predictions following an input on basal/top species, respectively. For example, considering a positive input on basal species I compared the answers of top species to the total answers of all other nodes due to the same perturbation (i.e. disturbance of basal species). I hypothesized that the entire system behaves uniquely and looked for possible difference in top species responses. My analysis shows an over-representation of positive signs on top species when an input affects basal species, but this not occurs when I investigated the response of basal species following a perturbation on top species. For better understanding the reasons of such discrepancies I studied the patterning of interaction strengths and the topological properties of the signed digraphs. First, I analyzed whether the results depend on the way the coefficients of the community matrix are assigned. To answer this question I compared the responses in presence of uniform interaction strength distribution (Bodini et al. 1994, 1998, 2000) with alternative scenarios. Alternative scenarios investigate loop analysis outputs in presence of coefficients randomly obtained from either normal or power-law distributions. Then, I compared all the results I obtained for real systems to null models (i.e. random food webs). Finally, on the basis of loop analysis' algorithm (see equation 3.1 in chapter 3), I investigated how the result of predictions are dependet from topological properties such as for example the mean length of positive paths.

## 4.2 Methods

### 4.2.1 Database construction

I created a database from the Food Web Bank<sup>8</sup>, a collection of 113 real food webs extracted from the literature (see Table S2.1 in Appendix for a detailed description of the literature sources). I used the community matrices obtained after converting the original presence (1) or the absence (0) of a direct feeding interactions in a dynamical interaction with coefficients  $a_{ij} = -1$  and  $a_{ji} = 1$  if species  $j$  feeds on species  $i$ . For each species I included a negative self-loop to take into account the individual dynamics of internal relationships (e.g. competition and predation, self-limitation processes and density dependence, and self-regulation mechanisms; see Bodini 1998). The original dataset comprises food webs from marine (36), freshwater (17) and terrestrial (26) habitats but I restricted the investigation to 26, 15 and 21 food webs, respectively. This is because I excluded

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<sup>8</sup> <http://ipmnet.org/loop/foodweb.aspx>

systems without primary producers at the bottom of the food web, systems that included human nodes (i.e. nodes called “man”, some example as food web number 1, 6 and 7 can be retrieved from the following link: <http://ipmnet.org/loop/foodweb.aspx?id=1> [Last accessed: January 30, 2017]) and those with a few species connected through long trophic chains (i.e. those resembling more a linear chain than a real web). I deleted isolated nodes in one freshwater (i.e. CM 73, see Table 4.2 in Appendix 4.5.1.1) and two terrestrial (i.e. CM25 and CM58, see Table 4.2 in Appendix 4.5.1.1) systems. A detailed description of the characteristics of each food web is reported in Table 4.2 in Appendix 4.5.1.1.

## 4.2.2 Simulation

### 4.2.2.1 Probability distributions of coefficients in the community matrix

The coefficients of the community matrix were assigned according to three different probability distributions: (I) uniform (i.e. standard procedure), (II) normal (with mean = 0.5 and standard deviation = 0.2), and (III) power-law (with the parameters that reproduce the Pareto principle or 80/20 rule). For each distribution the values were randomly sampled from the interval  $[1e^{-6}, 1]$  and the procedure of assigning values to the coefficients of the community matrix was executed  $s \times 1000$  times, where  $s$  is the model size (i.e. the number of variables in the model). As an outcome I obtained three tables of predictions (i.e. one for each distribution used to generate the coefficients of the community matrices) for each food webs.

### 4.2.2.2 Null models

I built up a database of null models as benchmark to test the outcomes obtained from the analysis of the real food web. Null models were constructed on the basis of two criteria: (I) network density (i.e. number of nodes and links) should be preserved (i.e. referring to real systems analyzed), and (II) each random food web should include, at least, one basal and one top species. Considering the number of nodes in the real food webs analyzed ( $S_{real}$ ), I identified three categories: small ( $5 < S_{real} < 10$ ), medium ( $11 < S_{real} < 19$ ), and large ( $21 < S_{real} < 33$ ) networks. I defined the network density for the null models by taking the mean of the number of nodes ( $S_{null}$ ) and links ( $L_{null}$ ) through these categories: small ( $S_{null} = 9$ ,  $L_{null} = 16$ ), medium ( $S_{null} = 15$ ,  $L_{null} = 32$ ), and large ( $S_{null} = 25$ ,  $L_{null} = 61$ ). For each category I simulated 1000 null networks according to the Erdős-Rényi model (“`erdos.renyi.game`” function in `igraph` R library; such function generates a random graphs with a given number of nodes,  $S_{null}$  and links,  $L_{null}$ ). For each random network generated I tested the outcomes of loop analysis by adopting different probability distributions for the assignment of the coefficients in the community matrix.

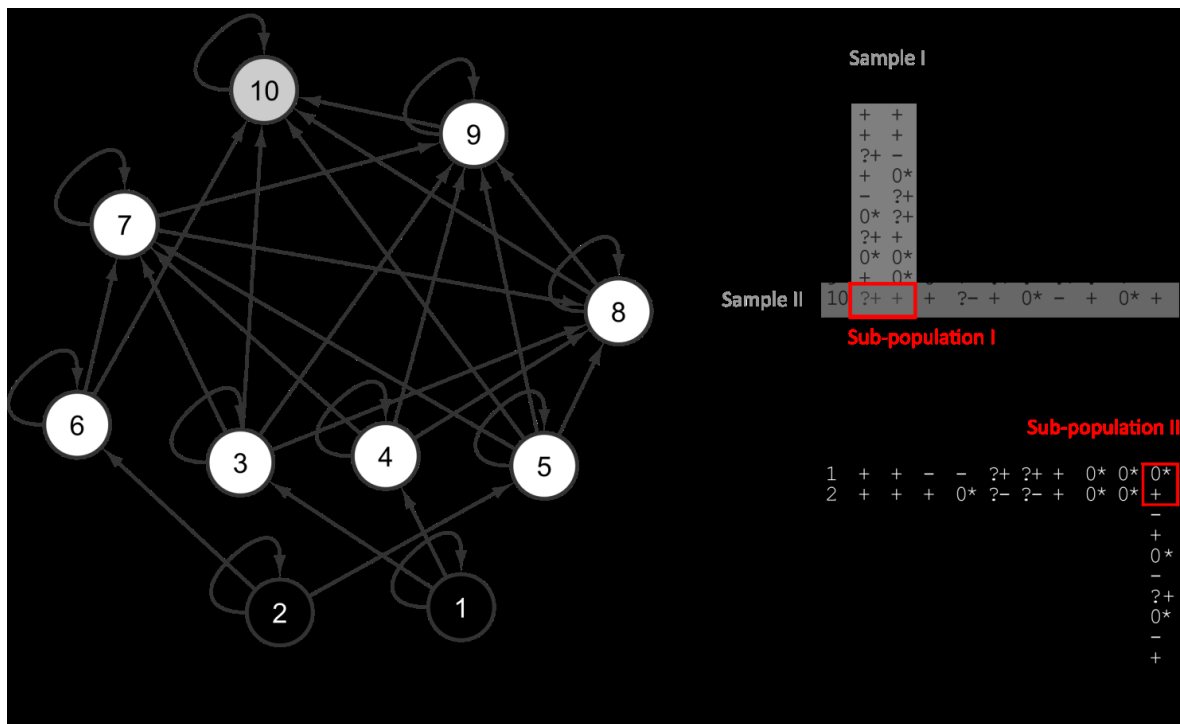
### 4.2.3 Statistical analysis

#### 4.2.3.1 Fisher's exact test

The Fisher's exact test is often used to identify if a sub-population is under- or over-represented (compared to random patterning) in a sample with the analysis of contingency tables. Sub-populations and samples in this case are subsets of specific predictions (i.e. +, ?+, -, ?-, 0\*, 0) extracted from the tables of predictions. Sub-populations are either the responses of top species when basal species are perturbed or the responses of basal species when top species are perturbed. Samples are both the responses of all species to perturbations affecting either basal or top species and the responses of basal and top species to input targeting all other species. With reference to Figure 4.1, which shows the model and its predictions for the rocky intertidal community in New England, Gulf of Maine (Edwards et al. 1982), table B1 highlights (in grey) the two samples (sample I and sample II) and the sub-population (red box) of predictions pertaining the response of the top species (node #10 in Figure 4.1A). Sample I is the subset of predictions about the response of all species for input to basal species (column in grey), and Sample II (rows in grey) is the subset of predictions expected for top species for input affecting all the species. I used these two samples in two different Fisher's exact tests. For each sign (i.e. +, ?+, -, ?-, 0\*, 0; see Tables 4.4 – 4.6 in Appendix 4.5.2) I investigated top species behavior. Considering "Sample I" vs "Sub-population I", for example, I applied the Fisher's exact test to investigate if positive predictions (i.e. +) in the sub-population I are under- or over-represented considering positive signs in the sample I. The contingency table that I analyzed contains four items: (1) the number of positive sign in sub-population, (2) the number of positive signs in sample I, (3) the difference between the number of items in sub-population I and the number of positive signs in sub-population I, and (4) the difference between the number of items in sample I and the number of positive signs in sample I. I looked for possible under- or over-representation for all other sign (Tables 4.4 – 4.6 in Appendix 4.5.2) considering appropriate contingency tables. In this way I assessed whether the responses of the top species (sub-population I) for each sign (i.e. +, ?+, -, ?-, 0\*, 0) were over or under-represented with respect to the respective responses in the samples (sample I and sample II). Table B2 in Figure 4.1 shows the samples and the subpopulation of responses concerning basal species. Here one sample is the subset of predictions about the response of all species for input to top species (sample III, column in black) and the other sample (Sample IV, rows in black) is the subset of predictions expected for basal species for input affecting all the species. Predictions in the red box are the responses of basal species and constitute the sub-population II. Using the appropriate contingency tables I performed the Fisher's exact tests to assess whether basal species show any over (or under) representation for what concerns the number of positive, negative or null (i.e. 0) responses if compared to the responses displayed in sample III and IV.

The Fisher's exact test was used to compare model predictions (i.e. possible differences between relative importance of particular responses in sub-populations and samples) obtained by simulating

the coefficients of community matrices from three different distributions. All calculations were performed in R (R Core Team 2014) using the routine developed by Bondavalli et al. (2009).



**Figure 4.1 – Graph and table of predictions: an example.** **A.** Graph representing the structure of the rocky intertidal community in New England, Gulf of Maine (Edwards et al. 1982). It comprises 10 nodes: plankton, detritus (1); algae (2); *Mytilus* sp. (3); *Balanus* (4); *Littorina* sp. (5); *Acmaea* (6); *Thais* (7); *Carcinus* (8); *Tautogolabrus* (9); fish, birds, mammals (10). Node colors indicate basal (black), intermediate (white) and top (grey) species. **B.** Table of prediction, obtained by assigning the coefficients of the community matrix according to uniform probability distribution. **B.1.** It is highlighted how input targeting basal species can influence top species (“Sub-population I”, red box). I compared the responses in the sub-population with the ones of two samples, either by considering the overall positive effect of basal on all food web species (columns highlighted in grey, “Sample I”), or by taking into account the positive responses generated by all food web species on top species (rows highlighted in grey, “Sample II”). **B.2** It is highlighted how input targeting top species can influence basal species (“Sub-population II”, red box): I compared the responses in the sub-population with the ones of two samples, either by considering the overall positive effect of top predators on all food web species (column highlighted in black, “Sample III”), or by taking into account the positive responses generated by all food web species on basal species (rows highlighted in black, “Sample IV”).

#### 4.2.3.2 Generalized Linear Model (GLM)

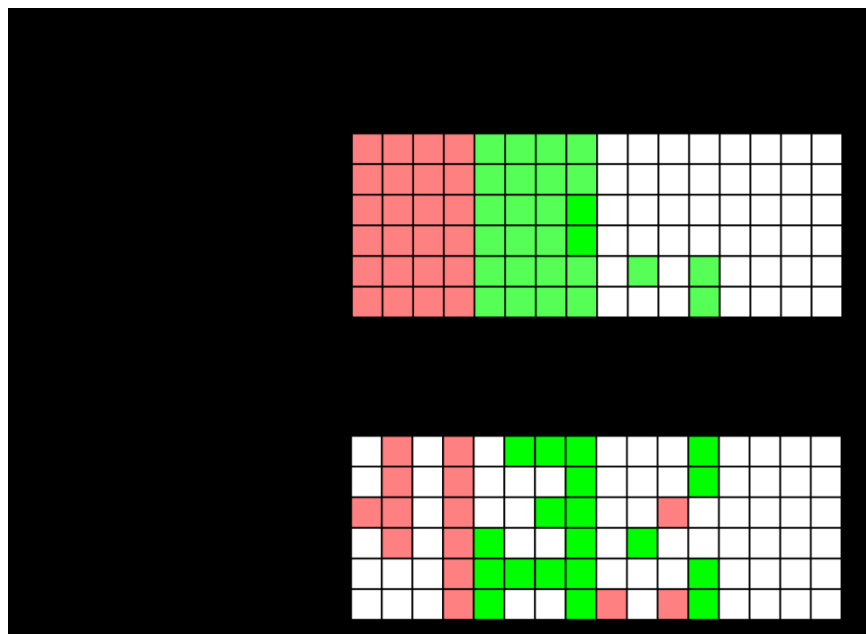
Using a Generalized Linear Model (GLM) I carried out regression analysis and ANOVA. Since my objective was to assess what determines a positive response (sing + in the table of prediction), I tested the response of a binomial variable (i.e. 1 for positive signs (+, ?+) and 0 for -, ?-, 0\*). The loop formula (see equation 3.1 in chapter 3) contains the elements that determine the sign of predictions. To facilitate the analysis I considered that within each community matrix the sign of the input  $[\partial f_i / \partial c]$  and that of the overall feedback ( $F_n$ ) are constant: the first is positive (as this is the convention adopted for loop analysis), while the second must be negative in order to meet the stability condition (Puccia and Levins 1986, Logofet 1992). Therefore, path  $(p_{ij}^{(k)})$  and

complementary feedback ( $F_{n-k}^{(comp)}$ ) are the two factors which determine the sign for the predictions. According to this I tested a model in which the dependent variable is the sign (binomial variable) and the predictors (the independent variables) are some features of the paths (e.g. mean length of positive and negative paths) and the sign of the complementary feedback. Finally, I investigate with a post-hoc Student's t-test the observed differences in the patterns from basal to top and from top to basal. All statistical analyses were carried out using the software R (2005), the data (Table 4.3) and form of the model I used is presented according to R syntax as an Appendix (i.e. 4.5.1.2 Generalized Linear Model) at the end of the chapter.

## 4.3 Results

### 4.3.1 Real systems: loop analysis and Fisher's exact test

I computed 186 tables of predictions (i.e. three for each of the 62 real food webs considered in this study) and reported detailed sign counts in Tables 4.4 - 4.6 in Appendix 4.5.2. Results of the Fisher's exact test are summarized in Table 4.1 (exact p-values are reported in Tables 4.4 - 4.6 in Appendix 4.5.2).



**Table 4.1 – Summary of Fisher’s exact test results for the comparison of sign counting between “population” and “sample” of real food web and random networks.** It is shown how a positive input targeting basal and top species can influence top (Table 4.1A, see also Figure 4.1B.1) and basal species (Table 4.1B, see also Figure 4.1B.2), respectively. Results obtained by using different distributions for the random sampling of community matrix coefficients (“C.A.”) are compared (i.e. uniform, normal - with mean = 0.5, sd = 0.2 and truncated distribution in the interval [1e-6, 1] – and power-law with Pareto distribution) for real (i.e. M, marine; F, freshwater; and T, terrestrial) and random (R) systems. The column “Norm” indicates if the comparison between “population” and “sample” refers to column or row (see Figure 4.1). The presence of significant differences is indicated by different colors: red underlies over-representation in the sample, while green stands for under-representation in the sample.

Considering the variation of top species in real systems (Table 4.1A) in response to an input on basal species (see “M”, “F” and “T” columns in Table 4.1A), I identified a clear overrepresentation of positive signs (and therefore an underrepresentation of the negative responses). This result seems to hold irrespective of the approach used to assign the coefficients to the community matrix (i.e. based on uniform, normal and power-law distributions) and the quantities used to perform the Fisher’s exact test (i.e. by assuming the sample along either the columns - where the response of all species to a positive input on basal species was examined, or the rows - where the reaction of top species to a positive input on all other species was measured; see Figure 4.1B.2). Such consequences were consistent with the direction of perturbation imposed on primary producers. Thus, positive (negative) perturbations targeting primary producers generated positive (negative) responses on top species in a significantly higher number than in other food web positions. Such overrepresentation does not characterize the response of basal species to inputs on top species. Only uniform assignment in freshwater systems and normal assignment in marine and freshwater food webs showed an overrepresentation of positive signs. Therefore, positive inputs on basal species determined a relative number of positive responses on top species that is significantly higher (see Tables 4.4 - 4.6 in the Appendix 4.5.2 for each p-values) than the one obtained for all other species (i.e. the net positive, bottom-up effect of basal species on top species is stronger if compared to the net positive effect generated on all other food web species). Also, top species show a significantly higher number of positive responses to positive inputs on basal species if compared to the number of positive responses triggered by positive inputs on any other species in the food web. These outcomes are not due to the patterning of the interaction strength. Rather, the reason of such differences should be investigated as a function of differences in network structure.

#### **4.3.2 Null models: loop analysis and Fisher’s exact test**

To investigate the significance of the results obtained with real food webs I studied null models. Goal of this analysis is identifying significant variation of top and basal species after inputs targeting either basal or top species, respectively. Results extracted with null models (i.e. random systems) are shown in Table 4.1 (“R” columns). With null models I identified for both the kinds of impacts (i.e. from basal species to top species and from top species to basal species) an overrepresentation of positive signs (and therefore an underrepresentation of negative signs). These outcomes hold irrespective of the method used to assign the coefficients to the community matrix (i.e. based on uniform, normal and power-law distributions) and the samples considered in the Fisher’s exact test (i.e. with samples taken along either the columns or the rows).

#### **4.3.3 Generalized Linear Model (GLM)**

I used a GLM model to understand which structural components were responsible for different pattern results of loop analysis going from basal to top or from top to basal. The factors that



determine positive responses on one extreme of the food web following positive inputs to the other extreme are the mean length of positive ( $p < 0.007$ ) and negative ( $p \ll 0.001$ ) paths, and the sign of complementary feedback ( $p < 0.009$ ). Short-positive and long-negative paths tend to confirm the sign of the input (i.e. positive) in the table of prediction, while long-positive and short-negative paths lean towards an inversion of input sign (i.e. to -, ?-, 0\* predictions, to 0 considering the binomial variable, see Figure 4.2 in the Appendix 4.5.2).

Through the post-hoc Student's t-test I investigated whether these structural differences can be found by comparing the topology from basal to top and from top to basal. A significant difference ( $p < 0.007$ ) emerged when comparing the numbers of negative odd paths from basal to top species and from top to basal species (Figure 4.3 in Appendix 4.5.2). The mean length of negative and odd paths from basal to top species is significantly higher. Therefore, the lower mean length of negative and odd paths is expected to be the factor responsible for the unpredictable response of basal species following perturbation on top species (i.e. short-negative paths tend to reverse the sign of the prediction if compared to the sign of the input, see Figure 4.2 in the Appendix 4.5.2).

#### **4.4 Discussion**

Bottom-up and top-down forces act simultaneously on ecosystems (Hunter and Price 1992, DeAngelis 2012). A variety of approaches, from field ecology to modeling, has been dedicated to the comparison of the effects generated by these two forces (Pace et al. 1999, Ebenman et al. 2004, Duffy et al. 2015). In this work I studied whether any characteristic pattern emerges from bottom-up and top-down control mechanisms. I investigated how variables that occupy the extremes of the trophic chain (i.e. basal and top species) respond to perturbations generated on the opposite part of the food web. To this end I focused on the response of top species to perturbations acting on basal species and the response of basal species for input to top species. I found that positive inputs on basal species triggered net positive feedback (i.e. expected abundances increase) on top species (both in real and random systems). This trend was significant when comparing the number of positive feedbacks on top species with: (I) the overall positive feedbacks generated by basal species on all other species in the food web, and (II) the total positive effects of all species in the food web on top species. Hence, positive perturbations on primary producers percolates until generating a consistent positive feedback on top species, independently on the way the frequency of such impact is normalized (i.e. either by considering the overall positive effect of primary producers on all food web species, or by taking into account the positive responses generated by all food web species on top predators). This pattern (i.e. higher probability of positive signs, see Table 2A) does not hold for the response of basal species following inputs that target top species in real systems (Table 2B). Studying how perturbations targeting primary producers spread throughout the whole food web is relevant to better understand the consequences of different human activities on ecosystems. In this work I analyzed 26 marine, 15 freshwater, and 21 terrestrial systems and the positive input on basal

species could approximate biomass increase in response to excess of nutrients as caused by water pollution, climate change or agricultural intensification (Asner et al. 1997, Behrenfeld et al. 2006, Haberl et al. 2007). Nixon and Buckley (2002) emphasized that nutrient supply is deeply connected to abundance and production of animals in marine ecosystems. These results show that positive inputs on primary producers (e.g. nutrient enrichment) propagate with positive consequences to the top of the trophic chain, where in general species that are commercially important can be found (Parsons 1992). Moreover, the management of biodiversity at the upper levels of the trophic chain deserves particular attention as top predators often include rare species that, due to their small population size, are more exposed to the risk of extinction (Simberloff 1988). In all real systems analyzed loop analysis identified non-random (predictable) feedbacks (i.e. positive responses in table of predictions) by the top species in response to perturbations targeting the primary producers. This has important consequences for biological conservation as the protection of rare species should also consider system-level solutions, rather than simply focus on the direct protection of species at the edge of extinction (Scotti and Jordán 2016).

Previous studies used loop analysis to make robust predictions about the effects of nutrient enrichment on top species in aquatic food webs (Bodini 1998, Hulot et al. 2000, Carey et al. 2013). Controversial patterns emerged and positive inputs on primary producers generated positive, negative or even ambiguous effects on top predators. For example, in the pelagic community of a mesoeutrophic lake the positive perturbation of phytoplankton did not result in any feedback on piscivorous fish at the top of the food chain (Bodini, 1998). In a mesocosm study reproducing the interactions of a lake ecosystem the results of the experiment were compared with the predictions of loop analysis (Hulot et al. 2000). The outcomes of loop analysis were in agreement with the findings of the mesocosm experiments: nutrient enrichment produced a reduction in the abundance of invertebrate carnivores, but such trend was changed by the presence of fish (i.e. as additional node) as top predator; this highlighted the importance of taking into account ecosystem complexity and indirect interactions. Reducing eutrophication in coastal food webs resulted in significant decrease of various top predators (e.g. piscivorous birds and piscivorous fish in the Chesapeake Bay; see Carey et al. 2013). Thus, the qualitative change predicted for input on primary producers is coherent with the direction of the perturbation exerted, a result that matches the findings of the present chapter.

Often, in topological studies (i.e. based on the static architecture of food webs) that consider the direction of energy flow in ecosystem it has been shown that bottom-up effects overcome top-down effects (Scotti and Jordán 2016). A common criticism to those outcomes is that the type of information used leads to such a prevalence in the importance of bottom-up effects (i.e. the findings are biased by data types and algorithms applied). However, here I show that also a study based on dynamics can identify a characteristic pattern for bottom-up effects but not for top-down responses.

To my knowledge, this work is the first attempt of searching for a general pattern of response under the constraints of top-down and bottom-up cascades. I observed that bottom-up perturbations on basal species reach the top of the trophic chain by producing univocal, significantly over-represented change if compared to the feedbacks on all other food web species. This does not hold for perturbations targeting top predators. The spread of indirect effects from top predators to basal species does not follow any clear pattern and cannot be significantly distinguished from the consequences involving intermediate species in the food web.

Coefficients of the community matrix are intended as interaction strength values along the trophic chain. The distributions used for extracting the coefficients of the community matrix (uniform, normal or power-law) support the robustness of the patterns identified for real food webs (i.e. all three approaches result in similar trends). The results of the GLM highlight that the structure of the interactions (i.e. their topology) is more important than the interaction strength. Generalized Linear Model revealed that positive responses on one extreme of the food web following positive inputs to the other extreme are influenced by the mean length of positive and negative paths, and by the sign of the complementary feedback. Short-positive and long-negative paths tend to confirm the input sign (i.e. positive) in the table of prediction, while long-positive and short-negative paths lean towards the inversion of the input sign. The relative disposition of weak vs. strong interactions is always random in my simulations and does not follow any regularity along the trophic chain. However, there are studies that emphasize how non-random patterning of interaction strengths can have deep consequences food web stability (de Ruiter et al. 1995, Neutel et al. 2002, 2007, but see Bondavalli and Bodini 2014).

In this study the primary goal was comparing the fate of indirect effects propagating from one extreme to the other of the food web. Future investigation could be extended to intermediate species. An interesting question to explore would be whether adding microbial pathways to the food webs might change the patterns observed in this study. For example, this investigation might clarify some aspects of the carbon shunt driven by jellyfish in coastal marine environments (Condon et al. 2011). Condon et al. (2011) investigated the voracious jellyfish predation and its consequences in the food web context. They have shown that jellyfish blooms contribute to convert large quantities of carbon into gelatinous biomass and lead to the release of colloidal and dissolved organic matter (jelly-DOM); these processes alter microbial nutrient and DOM pathways with fundamental transformations in the biogeochemical functioning and biological structure of food webs. The consumed jelly-DOM is shunted toward bacterial respiration rather than production, significantly reducing bacterial growth efficiencies and sequestering carbon from the planktonic food web (i.e., it potentially alters the transfers to higher trophic levels and shunts the carbon away from fish production). These shifts could have potentially significant environmental, societal, and economic implications (e.g., jelly carbon shunt can reduce fish production and decrease average size of individual fish thus having impacts on nutrient cycling, fisheries and adaptation to climate change; Brander 2007).

My study presents limitations. For example, (i) only one perturbation per simulation is considered (i.e. the concurrent effect of two or more perturbations can be obtained by combining single input scenarios only); (ii) changes in average or equilibrium values are not fully representative of the complex behavior displayed by ecological systems, even the simplest ones (Gilpin 1979, Shaffer 1985); (iii) the significant over-representation of the signs (e.g. in case of perturbations targeting primary producers and spreading effects at the top of the trophic chain) does not tell anything about the magnitude of such feedbacks. Loop analysis provides qualitative indications concerning the direction of change.

## 4.5 Appendix

### 4.5.1 Methods

#### 4.5.1.1 Database construction of real food web

	<b>H</b>	<b>S</b>	<b>L</b>	<b>LD</b>	<b>C</b>	<b>Ref</b>
<b>CM9</b>	M	10	16	1.60	0.16	Kitching et al. 1967
<b>CM10</b>	M	5	6	1.20	0.24	Menge et al. 1976
<b>CM11</b>	M	8	10	1.25	0.16	Menge et al. 1976
<b>CM12</b>	M	13	27	2.08	0.16	Menge et al. 1976
<b>CM13</b>	M	12	19	1.58	0.13	Menge et al. 1976
<b>CM16</b>	M	14	21	1.50	0.11	Copeland et al. 1974
<b>CM17</b>	M	14	24	1.71	0.12	Hiatt et al. 1960
<b>CM20</b>	M	19	33	1.74	0.09	Holdgate 1970
<b>CM21</b>	M	10	18	1.80	0.18	Halfon 1979
<b>CM23</b>	T	15	29	1.93	0.13	Bird 1930
<b>CM24</b>	T	12	19	1.58	0.13	Bird 1930
<b>CM25</b>	T	24	44	1.83	0.08	Bird 1930
<b>CM27</b>	T	22	42	1.91	0.09	Watson 1970
<b>CM29</b>	M	22	40	1.82	0.08	Dunbar 1954
<b>CM31</b>	M	14	52	3.71	0.27	Steele 1970
<b>CM34</b>	F	12	28	2.33	0.19	Jones 1949
<b>CM35</b>	F	13	38	2.92	0.22	Mninsall 1967
<b>CM40</b>	T	11	17	1.55	0.14	Harrison 1962
<b>CM41</b>	M	19	53	2.79	0.15	Dunbar 1954
<b>CM42</b>	M	16	43	2.69	0.17	Vinogradov 1978
<b>CM43</b>	M	21	43	2.05	0.10	Rosenthal 1974
<b>CM44</b>	M	12	29	2.42	0.20	Breymeyer & Van Dyne 1980
<b>CM46</b>	F	19	68	3.58	0.19	Patten 1975
<b>CM47</b>	T	27	52	1.93	0.07	Breymeyer & Van Dyne 1980
<b>CM50</b>	M	14	24	1.71	0.12	Dexter 1947
<b>CM51</b>	M	25	48	1.92	0.08	Dexter 1947
<b>CM54</b>	M	15	23	1.53	0.10	NA
<b>CM57</b>	M	9	19	2.11	0.23	Jones 1950

<b>CM58</b>	T	17	23	1.35	0.08	Smirnov 1961
<b>CM59</b>	T	30	71	2.37	0.08	Twomey 1945
<b>CM60</b>	T	33	75	2.27	0.07	Rasmussen 1941
<b>CM61</b>	T	9	13	1.44	0.16	Summerhayes & Elton 1928
<b>CM62</b>	T	12	14	1.17	0.10	Summerhayes & Elton 1928
<b>CM63</b>	F	18	75	4.17	0.23	Jones 1950
<b>CM64</b>	F	19	32	1.68	0.09	Cummins et al. 1966
<b>CM65</b>	F	16	46	2.88	0.18	Kajak & Hillbricht 1972
<b>CM66</b>	F	10	18	1.80	0.18	Kajak & Hillbricht 1972
<b>CM67</b>	F	21	63	3.00	0.14	Carlson 1968
<b>CM70</b>	F	14	30	2.14	0.15	Hall & Day 1977
<b>CM73</b>	F	9	16	1.78	0.20	Rasmussen 1941
<b>CM76</b>	F	14	20	1.43	0.10	Loeffler 1979
<b>CM83</b>	F	25	69	2.76	0.11	Carlson 1968
<b>CM85</b>	F	27	51	1.89	0.07	Furtado & Mori 1982
<b>CM87</b>	M	12	23	1.92	0.16	Bradstreet 1982
<b>CM88</b>	F	16	40	2.50	0.16	Furtado & Mori 1982
<b>CM89</b>	F	18	34	1.89	0.10	Hartley 1948
<b>CM90</b>	T	22	43	1.95	0.09	Shure 1973
<b>CM91</b>	T	10	14	1.40	0.14	Kitazawa 1977
<b>CM92</b>	T	18	22	1.22	0.07	Swan 1961
<b>CM93</b>	T	26	74	2.85	0.11	Pattie & Verbeek 1966
<b>CM94</b>	T	12	21	1.75	0.15	Bradstreet 1982
<b>CM95</b>	T	10	14	1.40	0.14	Kitazawa 1977
<b>CM96</b>	T	9	18	2.00	0.22	Osmolovskaya 1948
<b>CM97</b>	T	11	19	1.73	0.16	Dexter 1947
<b>CM98</b>	T	17	41	2.41	0.14	Holm & Scholtz 1980
<b>CM100</b>	T	22	61	2.77	0.13	Dunbar 1979b
<b>CM102</b>	M	9	25	2.78	0.31	Dunbar 1979a
<b>CM103</b>	M	23	135	5.87	0.26	Dunbar 1979b
<b>CM104</b>	M	27	63	2.33	0.09	Menge et al. 1986
<b>CM105</b>	M	10	22	2.20	0.22	Edwards et al. 1982
<b>CM109</b>	M	21	57	2.71	0.13	Castilla 1981
<b>CM110</b>	M	13	24	1.85	0.14	Dexter 1947

**Table 4.2** – Food web database. H: habitat (M, marine; F, freshwater; T, terrestrial); S: number of nodes; L: number of links; LD: link density, the average number of feeding links per species; C: connectance, computed as the ratio between existing and all possible trophic interactions (i.e.  $C = L/S^2$ , Martinez 1992); Ref: reference as reported in Food Web Bank<sup>9</sup>.

<sup>9</sup> <http://ipmnet.org/loop/foodweb.aspx>

#### 4.5.1.2 Generalized Linear Model (GLM)

**Table 4.3** – Data used for the GLM can be retrieved from the following link: <https://drive.google.com/open?id=0B6EOXgzXaPXLRF81X1p3SDVaVTA> [Last accessed: January 30, 2017]

The form of the model that I used, according to R syntax, is:

```
glm.fit <- glm(Signs ~ positive_paths_ML + negative_paths_ML + CFsign, data = DF, family = binomial)
```

where “Signs” is dependent binomial variable (i.e. 1 for positive signs (+, ?+) and 0 for -, ?-, 0\*), “positive\_paths\_ML”, “negative\_paths\_ML” and “CFsign” are the predictors and correspond to the mean length of positive and negative paths and the sign of the complementary feedback, respectively.

#### 4.5.2 Results

		Uniform distribution								
	Size	0	0*	+	?+	?+ & +	-	?-	?- & -	
$\Delta T$	Sample II	878	/	241	226	156	382	125	130	255
	Sample I	691	/	186	176	145	321	87	97	184
	Sub-population I	86	/	18	37	22	59	3	6	9
	Sample II vs. Sub-population I	p-value		0.205	<<0.001	0.055	<<0.001	0.002	0.027	<<0.001
					S > P	S > P	S > P	S < P	S < P	S < P
	Sample I vs. Sub-population I	p-value		0.298	<<0.001	0.331	<<0.001	0.005	0.042	<<0.001
				S > P		S > P	S < P	S < P	S < P	
$\Delta B$	Sample III	878	/	275	157	122	279	160	164	324
	Sample IV	691	/	206	125	115	240	113	132	245
	Sub-population II	86	/	32	18	11	29	6	19	25
	Sample III vs Sub-population II	p-value		0.276	0.466	0.871	0.717	0.004	0.471	0.160
								S < P		
	Sample IV vs Sub-population II	p-value		0.173	0.555	0.439	0.905	0.012	0.563	0.280
							S < P			
		Power-law distribution								
	Size	0	0*	+	?+	?+ & +	-	?-	?- & -	
$\Delta T$	Sample II	878	/	279	174	190	364	88	147	235
	Sample I	691	/	222	141	163	304	54	111	165
	Sub-population I	86	/	25	28	26	54	2	5	7
	Sample II vs. Sub-population I			0.715	0.006	0.049	<<0.001	0.008	0.003	<<0.001
					S > P	S > P	S > P	S < P	S < P	S < P
	Sample I vs. Sub-population I			0.624	0.009	0.184	<<0.001	0.039	0.005	<<0.001
				S > P		S > P	S < P	S < P	S < P	
$\Delta B$	Sample III	878	/	315	111	145	256	108	199	307
	Sample IV	691	/	222	106	130	236	84	149	233
	Sub-population II	86	/	36	15	14	29	5	16	21
	Sample III vs Sub-population II			0.291	0.239	1	0.387	0.046	0.419	0.056
								S < P		S < P
	Sample IV vs Sub-population II			0.047	0.636	0.660	1	0.051	0.579	0.051
			S > P				S < P		S < P	

		Normal distribution								
		Size	0	0*	+	?+	?+ & +	-	?-	?- & -
<b>ΔT</b>	Sample II	878	/	146	325	103	428	215	89	304
	Sample I	691	/	108	262	89	351	151	81	232
	Sub-population I	86	/	9	49	16	65	6	6	12
	Sample II vs. Sub-population I			0.166	<<0.001	0.052	<<0.001	<<0.001	0.449	<<0.001
					S > P	S > P	S > P	S < P		S < P
	Sample I vs. Sub-population I			0.263	<<0.001	0.179	<<0.001	<<0.001	0.125	<<0.001
				S > P		S > P	S < P		S < P	
<b>ΔB</b>	Sample III	878	/	179	247	87	334	270	95	365
	Sample IV	691	/	106	212	73	285	199	101	300
	Sub-population II	86	/	16	29	12	41	17	12	29
	Sample III vs Sub-population II			0.779	0.317	0.262	0.052	0.020	0.369	0.169
							S > P	S < P		
	Sample IV vs Sub-population II			0.433	0.621	0.359	0.297	0.048	1	0.053
							S < P		S < P	

**Table 4.4 - Marine systems: sign counts and Fisher’s exact test results.** It is shown how a positive input targeting basal and top species can influence top (“ΔT” section) and basal (“ΔB” section) species, respectively. Results of sign counts for “Sample” - columns and rows - and “Sub-population” for variation in top (Figure 4.1B.2) and basal (Figure 4.1B.1) species, and results of Fisher's exact test are reported. Results obtained by using different distributions for the random of interaction strengths in the community matrix are compared (i.e. uniform, power-law and normal). The presence of significant differences is indicated by S > P or S < P.



<b>Uniform distribution</b>										
	Size	0	0*	+	?+	?+ & +	-	?-	?- & -	
<b>ΔT</b>	Sample II	983	20	281	223	164	387	143	152	295
	Sample I	973	17	292	207	184	391	118	155	273
	Sub-population I	191	5	50	60	42	102	12	22	34
	Sample II vs. Sub-population I	p-value	0.585	0.539	0.007	0.051	<<0.001	<<0.001	0.182	<<0.001
					S > P	S > P	S > P	S < P		S < P
	Sample I vs. Sub-population I	p-value	0.388	0.299	0.002	0.319	<<0.001	0.010	0.072	0.002
				S > P		S > P	S < P	S < P	S < P	
<b>ΔB</b>	Sample III	983	20	264	173	148	321	185	193	378
	Sample IV	973	17	295	161	159	320	147	194	341
	Sub-population II	191	5	49	29	46	75	28	34	62
	Sample III vs Sub-population II	p-value	0.585	0.789	0.464	0.002	0.047	0.183	0.617	0.068
						S > P	S > P			S < P
	Sample IV vs Sub-population II	p-value	0.388	0.225	0.748	0.008	0.054	1	0.550	0.507
					S > P	S > P				
<b>Power-law distribution</b>										
	Size	0	0*	+	?+	?+ & +	-	?-	?- & -	
<b>ΔT</b>	Sample II	983	20	360	149	198	347	83	173	256
	Sample I	973	17	408	135	194	329	48	171	219
	Sub-population I	191	5	64	33	61	94	6	22	28
	Sample II vs. Sub-population I	p-value	0.585	0.459	0.261	<<0.001	<<0.001	0.005	0.022	<<0.001
						S > P	S > P	S < P	S < P	S < P
	Sample I vs. Sub-population I	p-value	0.388	0.018	0.217	<<0.001	<<0.001	0.189	0.023	0.008
			S < P		S > P	S > P		S < P	S < P	
<b>ΔB</b>	Sample III	983	20	363	118	149	267	115	218	333
	Sample IV	973	17	412	93	179	272	86	186	272
	Sub-population II	191	5	81	15	43	58	18	29	47
	Sample III vs Sub-population II	p-value	0.585	0.166	0.059	0.010	0.377	0.454	0.017	0.007
					S < P	S > P			S < P	S < P
	Sample IV vs Sub-population II	p-value	0.388	0.524	0.585	0.191	0.539	0.662	0.222	0.375

		Normal distribution								
		Size	0	0*	+	?+	?+ & +	-	?-	?- & -
<b>ΔT</b>	Sample II	983	20	165	334	105	439	253	106	359
	Sample I	973	17	157	329	121	450	229	120	349
	Sub-population I	191	5	26	92	20	112	30	18	48
	Sample II vs. Sub-population I	p-value	0.585	0.335	<<0.001	1	<<0.001	0.001	0.344	0.001
					S > P		S > P	S < P		S < P
	Sample I vs. Sub-population I	p-value	0.388	0.447	<<0.001	0.544	0.001	0.010	0.327	0.002
				S > P		S > P	S < P		S < P	
<b>ΔB</b>	Sample III	983	20	154	272	100	372	323	114	437
	Sample IV	973	17	158	282	101	383	285	130	415
	Sub-population II	191	5	21	59	30	89	55	21	76
	Sample III vs Sub-population II	p-value	0.585	0.965	0.380	0.021	0.015	0.155	0.902	0.133
						S > P	S > P			
	Sample IV vs Sub-population II	p-value	0.388	0.039	0.603	0.026	0.038	0.931	0.411	0.472
			S < P		S > P	S > P				

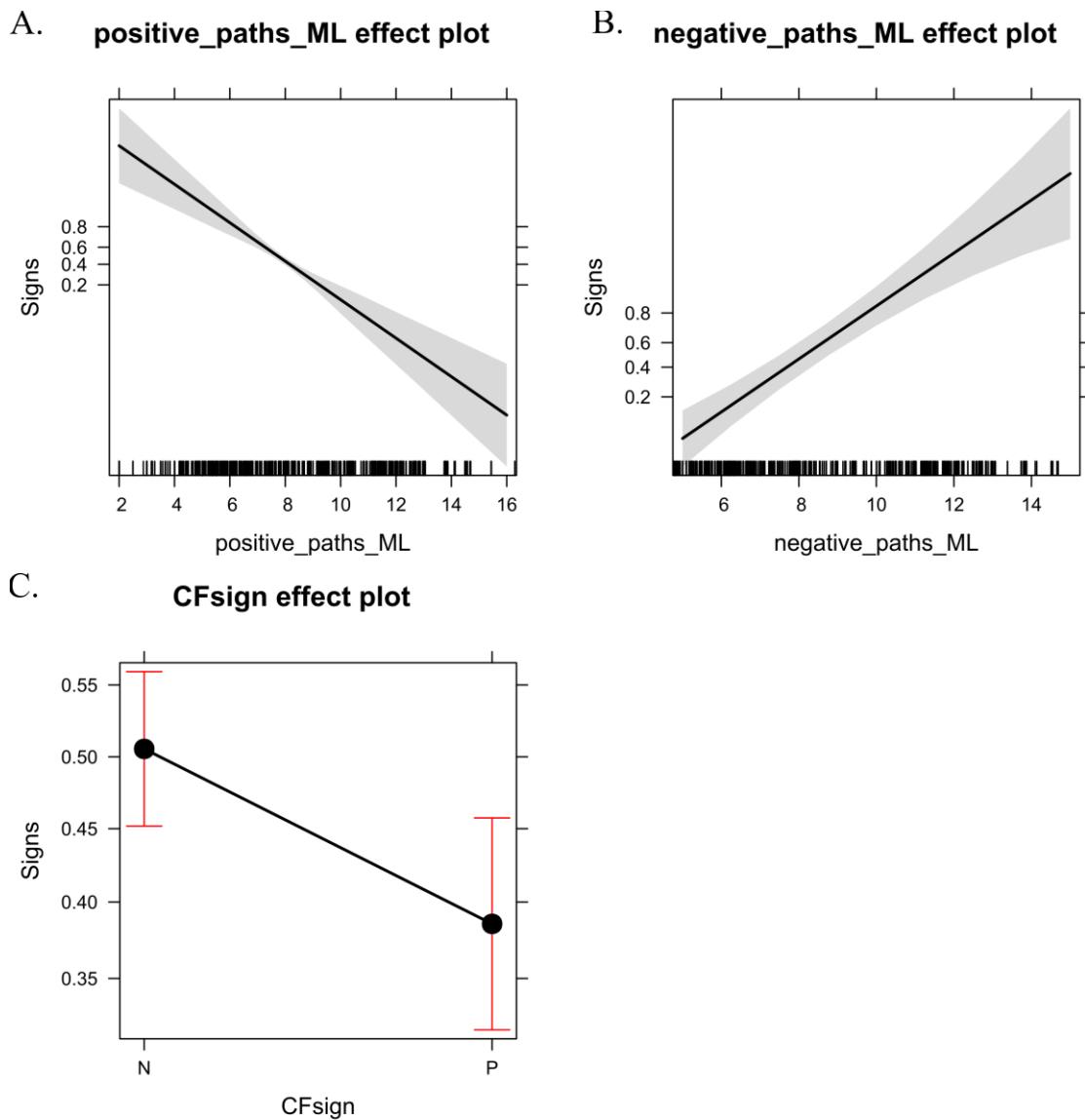
**Table 4.5 - Freshwater systems: signs counting and fisher test results.** It is shown how a positive input targeting basal and top species can influence top (“ΔT” section) and basal (“ΔB” section) species, respectively. Results of signs counting between “Sample” - columns and rows - and “Sub-population” for variation in top (Figure 4.1B.2) and basal (Figure 4.1B.1) species, and results of Fisher's exact test are reported. Results obtained by using different distributions for the random sampling of community matrix coefficients are compared (i.e. uniform, power-law and normal). The presence of significant differences is indicated by S>P or S<P.

<b>Uniform distribution</b>											
	Size	0	0*	+	?+	?+ & +	-	?-	?- & -		
<b>ΔT</b>	Sample II	2143	34	616	453	370	823	291	379	670	
	Sample I	1217	30	324	314	220	534	170	159	329	
	Sub-population I	342	8	100	102	64	166	27	41	68	
	Sample II vs. Sub-population I	p-value	0.362	0.847	<<0.001	0.539	<<0.001	0.001	0.005	<<0.001	
					S > P		S > P	S < P	S < P	S < P	
	Sample I vs. Sub-population I	p-value	1	0.336	0.079	0.812	0.071	0.001	0.648	0.004	
				S > P		S > P	S < P		S < P		
<b>ΔB</b>	Sample III	2143	34	632	367	375	742	372	363	735	
	Sample IV	1217	30	355	248	202	450	217	165	382	
	Sub-population II	342	8	110	62	66	128	49	47	96	
	Sample III vs Sub-population II	p-value	0.362	0.340	0.644	0.446	0.329	0.093	0.079	0.013	
									S < P	S < P	
	Sample IV vs Sub-population II	p-value	1	0.285	0.399	0.256	0.899	0.073	0.929	0.259	
							S < P				
<b>Power-law distribution</b>											
	Size	0	0*	+	?+	?+ & +	-	?-	?- & -		
<b>ΔT</b>	Sample II	2143	34	879	330	370	700	162	368	530	
	Sample I	1217	30	442	239	234	473	84	188	272	
	Sub-population I	342	8	129	76	80	156	13	36	49	
	Sample II vs. Sub-population I	p-value	0.362	0.260	0.001	0.005	<<0.001	0.005	<<0.001	<<0.001	
					S > P	S > P	S > P	S < P	S < P	S < P	
	Sample I vs. Sub-population I	p-value	1	0.657	0.287	0.054	0.015	0.020	0.012	<<0.001	
					S > P	S > P	S < P	S < P	S < P		
<b>ΔB</b>	Sample III	2143	34	908	236	366	602	245	354	599	
	Sample IV	1217	30	485	153	226	379	148	175	323	
	Sub-population II	342	8	157	37	60	97	33	47	80	
	Sample III vs Sub-population II	p-value	0.362	0.239	1	0.817	0.948	0.357	0.206	0.044	
										S < P	
	Sample IV vs Sub-population II	p-value	1	0.026	0.402	0.693	0.352	0.117	0.794	0.263	
				S > P							

		Normal distribution								
		Size	0*	+	?+	?+ & +	-	?-	?- & -	
<b>ΔT</b>	Sample II	2143	34	352	724	219	943	581	233	814
	Sample I	1217	30	215	490	95	585	294	93	387
	Sub-population I	342	8	66	158	28	186	60	22	82
	Sample II vs. Sub-population I	p-value	0.362	0.186	<<0.001	0.284	<<0.001	<<0.001	0.006	<<0.001
					S > P		S > P	S < P	S < P	S < P
	Sample I vs. Sub-population I	p-value	1	0.475	0.029	0.821	0.026	0.005	0.485	0.003
				S > P		S > P	S < P		S < P	
<b>ΔB</b>	Sample III	2143	34	346	656	223	879	627	257	884
	Sample IV	1217	30	234	405	101	506	342	105	447
	Sub-population II	342	8	71	107	37	144	84	35	119
	Sample III vs Sub-population II	p-value	0.362	0.022	0.801	0.849	0.723	0.041	0.415	0.013
					S > P			S < P		S < P
	Sample IV vs Sub-population II	p-value	1	0.537	0.515	0.161	0.901	0.216	0.392	0.525

**Table 4.6 - Terrestrial systems: signs counting and fisher test results.** It is shown how a positive input targeting basal and top species can influence top (“ΔT” section) and basal (“ΔB” section) species, respectively. Results of signs counting between “Sample” - columns and rows - and “Sub-population” for variation in top (Figure 4.1B.2) and basal (Figure 4.1B.1) species, and results of Fisher’s exact test are reported. Results obtained by using different distributions for the random sampling of community matrix coefficients are compared (i.e. uniform, power-law and normal). The presence of significant differences is indicated by S>P or S<P.

I used a GLM model to understand which structural components were responsible for different pattern emerged from loop analysis results going from basal to top or from top to basal.



**Figure 4.2 – Results of the GLM.** The model includes (A) mean length of positive path, (B) mean length of negative paths, and (C) complementary feedback sign. The vertical axis (“Signs”) is labelled on the probability scale of an occurring event (i.e. 1 for positive signs and 0 for all other), and a 95% confidence interval is drawn in grey around the estimated effects.



**Figure 4.3** – Box plots showing the mean length of all negative and odd paths both from basal to top species and from top to basal species ( $p < 0.007$ , calculated using the Student's t-test).

## Concluding remarks

Understanding how communities and ecosystems respond to environmental disturbance is a primary focus of the ecological research. Different avenues of inquiry have been unfolded in the last twenty years to answer the multiple and complex questions that pertain this issue. I developed the thesis along a line of research that privileges the use of mathematical models applied to complex systems. This choice is motivated by the fact that mathematical models are good instruments to disentangle the inherent complexity of ecosystems. In particular, the work of this thesis is dedicated to the analysis of the structural properties that emerge from the arrangement of the interactions in communities and ecosystems. Nevertheless, the use of mathematical tools and the associated findings need to be combined and integrated with field data and/or experimental indications. Thus, I compared model predictions with field data in chapter 3. In the absence of empirical information I performed simulations based on null models, and statistical analysis helped validating the results of the mathematical descriptions (see chapter 4).

One major problem of ecosystem management is to assess causes and effects of perturbations. The analysis that I present in this work can add some elements to the debate around such issue. The results discussed in the chapters 2, 3 and 4 in fact show that: 1) the structure of the interactions can be the appropriate locus for the explanation of system-scale and local-level patterns observed or simulated; 2) the structure of the interactions can help disentangling causative mechanisms that link the effect of the sources of change (disturbance) with the trends of change of the variables. For a better understanding of ecosystem behavior, it is thus essential the ability of depicting interaction diagrams that summarize the most important relationships at play in the system. This might contribute to elucidate how the system responds to perturbations that target specific variables. Often, in ecological studies the focus of the controlling factor is based on the correlation between abundance levels between populations. That is the search for shifts in population levels of one species that is accompanied by the population changes in another. Here I provide evidence that attention should be also given to parameters and structural components (e.g. the arrangement of feeding interactions in food webs) that regulate growth rate or the rate of change of the variables. So, the controlling factors in ecosystems are the changing parameters as mediated by the structure of the interactions.

The approach I have used for modelling is essentially qualitative. The qualitative analysis has certainly many limitations, among which the impossibility to make any quantitative statements is the most relevant. By recognizing these limitations, the reader should be aware that these methods are not alternative to quantitative models. Rather, I envision the potential for integration wherever parameter estimation is impossible or difficult to obtain, which is the rule rather than the exception in ecosystem management.

Ecosystem management will become more complex in the near future under the effects of global change. Impacts that can be hypothesized are many and will be due, among others, to altered CO<sub>2</sub> balance, increase of temperature, invasion of alien species and the growing human population. Making predictions will become more difficult because of the uncertainty associated with new, unknown events, changing dynamics and lack of quantitative data. An adaptive management approach that allows for continually assessing new evidence and changing approaches as the understanding increases has been called for. There is no recipe for modelling development, but great effort should be devoted to assimilation of facts, observation and generation of hypotheses. Therefore, qualitative models can be helpful in the new scenario that is approaching. They have the necessary adaptability to be used in changing contexts. When in doubt about critical linkages and dynamic features, alternative models can be easily developed to find out which difference matters the most, and such an iterative process might help to reach robust conclusions. Qualitative models are inherently flexible. They allow including and discarding variables easily, and above all they permit working with variables and links that are not readily measurable but are candidates for generating crucial effects.



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