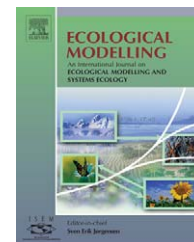


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# Topological keystone species in ecological interaction networks: Considering link quality and non-trophic effects

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## ABSTRACT

There is increasing evidence that non-trophic interspecific interactions play an at least as important role in community dynamics as trophic relationships. More and more studies on pollination, mutualism and facilitation are published but these effects are interpreted more like alternative explanations than being synthesized with results of trophic analyses. Here, we construct and analyze the interaction web of the well-studied Chesapeake Bay mesohaline ecosystem. By interaction web we mean a food web completed by a carefully selected set of non-trophic links. We quantify the interaction structure of the web and the positional importance of nodes by different network indices. We perform the suitable analyses for different variants of the network: combinations of direction, sign and weights, as well as considering also non-trophic links result in a set of webs of different information content. We also create a semi-quantitative variant of the web, in which only the order of magnitude of the mass flows are considered. The appropriate network indices for each web variant are calculated and compared. Finally, however our paper is primarily of methodological nature, we present some findings about the fish community of the Bay. We suggest that the multiple techniques presented here, adapted even from social network analysis, can help field conservation efforts by suggesting optimal preferences for data collection.

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## 1. Introduction

The construction and analysis of food webs is a traditional approach to understanding the structure and functioning of ecological systems. Food webs depict the collection of pairwise prey–predator interactions between species or their suitably defined groups (Pimm, 1982, 1991; Pimm et al., 1991). Although the information food web analysis provides is probably essential, notorious methodological problems weaken the predictions appearing during all of the three basic phases of the work (sampling during field data collection, right aggregation process during network construction, choosing sensible graph properties during network analysis).

Apart of the methodological problems of how to construct a network showing who eats whom, a number of additional issues are frequently claimed for: (1) trophic interactions are very important but other pairwise (direct) non-trophic interspecific interaction types are also of high importance (e.g. pollination: Memmott, 1999; mutualism: Bronstein, 2001; facilitation: Turner, 1983; Callaway, 1995; see also Kareiva and Bertness, 1997 and subsequent papers), (2) interactions could be characterized not only binarily (yes or no) but also by their strength, sign and direction. The direction and sign structure of a direct trophic interaction (a negative feeding effect in top–down direction and a positive food supply in bottom–up direction) is evident but still can be complemented by informa-

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tion on the magnitude of energy flows (strength). Non-trophic interactions are variable also in sign (e.g. the effects in both directions are positive in a mutualism) and direction (e.g. facilitation is a one-way positive effect with no response). Thus, a complex interaction network, defined as a general extension of a food web (but see Paine, 1980 for a different meaning), contains trophic and non-trophic, directed, signed and weighted effects between pairs of species. The combinations of co-occurring pairwise effects give rise to indirect interaction modules (e.g. trophic cascade or apparent competition; see Menge, 1995, for a classification) embedded in community-wide interaction networks. Indirect chain effects do spread in both bottom-up and top-down directions through trophic links and, as a result, may act also horizontally (Wootton, 1994; Menge, 1995; Abrams et al., 1996). If non-trophic interactions are also considered, the network may also have direct horizontal links.

The role non-trophic interactions have in organizing a community has traditionally been considered more local, and their analysis mostly focused on species pairs. The current need for taking also non-trophic effects into account while thinking within the network perspective is parallel with the recognition of their less local nature (e.g. diffuse mutualism; Jordano, 1987; Bronstein, 2001). We already have plant-pollinator (Jordano, 1987) and competitive networks, even with weighted interactions (Paine, 1984). However, to our knowledge, there is no community-wide interaction network showing a variety of both trophic and non-trophic links between species. An evident problem with weighting such a network is that there is no common currency, i.e. it is not easy to define the common denominator of material transfers and a facilitation effect (it is no problem in case of binary webs). Another problem is that mass-balance can comfortably be assumed in case of trophic flow networks but there are lots of problems with assuming “interaction balance”. This might be one reason for studying more intensively the trophic-dynamic aspect (Lindeman, 1942) in the past. We also have to note the problem of aggregation. It is frequently the case that trophic effects are less specific, so the aggregation process seriously affects how the two kinds of interactions will complement each other within a single graph (also, different interactions might suggest different aggregation procedures). Nevertheless, the dual nature of interaction networks could be helpful in better understanding, for example, the community-wide answers to stress and disturbance (Bertness and Shumway, 1993). An ultimate question to be addressed is whether to take into account non-trophic effects or to measure interaction strengths in a trophic network, if we want to optimize our efforts in improving a traditional, binary food web.

Both ecological research and conservation practice claim for quantitative, a priori approaches to characterizing the importance of different species in ecosystems. Keystone species have been defined variously and a number of studies report on their roles but their objective description is still immature. One of the very few quantitative approaches is their characterization based on the position they occupy within food webs: topological keystone species have been defined as being in key positions in trophic interaction networks (Jordán et al., 1999; Solé and Montoya, 2001; Montoya

and Solé, 2002; Jordán and Scheuring, 2002). New graph theoretical techniques have also been suggested for their finer characterization (Allesina and Bodini, 2004; Jordán et al., 2006). Here, we wish to extend these techniques to directed, signed and weighted interaction networks including also non-trophic links. We have to note that the “keystone” term is strictly used only for in “importance/biomass” context (Power et al., 1996), thus we should not use the term in the strictest sense. The topological importance indices could be easily combined with biomass data but, in this paper, our primary task is to compare different variants of the same web (and outline the methodological background of this problem), and our intention is to keep everything else as simple as possible.

Our primary concern is to develop the methodology of ecological network analysis, in other words, we are more interested in how to analyze such an “ideal” network than in how to construct it. The aims of our present paper are: (1) to construct an interaction network as a combination of a published food web and a collection of published data on non-trophic effects, (2) to construct the variants of this web according to different but only sensible combinations of link direction, strength and sign, as well as whether including non-trophic links, (3) to apply several graph theoretical indices for (3) mapping the direct and indirect interaction structure of these variants, and (4) determining the topological keystone species in the networks, and finally (5) to compare the network variants from the perspective of the fish community. We present results concerning the organization of the studied community but emphasize that this is more like illustration, since our paper is primarily of methodological nature.

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## 2. Data base

Energy flows between the trophic components of the Chesapeake Bay mesohaline community are well known (Baird and Ulanowicz, 1989; see Table 1 for carbon flow data and Table 2 for trophic groups) and have been analyzed extensively (see Baird et al., 1995 for nitrogen and Ulanowicz and Baird, 1999 for limiting nutrients). Since the Bay is well studied, there is a lot of information, even if more sporadic, about the functionally important and typical non-trophic effects between species inhabiting the Bay. We have collected a large number of non-trophic interspecific effects and selected the seemingly most characteristic and unambiguous links in order to complement our food web such that an interaction network can be constructed (Fig. 1). Table 3 shows the origin of non-trophic links considered in our study. Of course, our selection is subjective, but not intentionally biased, and we emphasize that the analysis of this interaction web is basically an illustration of our methodological investigation.

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## 3. Methods

### 3.1. Network construction

Our task is to complete a food web by considering also the seemingly most important non-trophic relationships between

**Table 1 – Carbon flow data<sup>a</sup> in mg C/m<sup>2</sup>/year in the food web of the Chesapeake Bay ecosystem (after Baird and Ulanowicz, 1989)**

| From | To | Annual flow | From | To | Annual flow | From | To | Annual flow |
|------|----|-------------|------|----|-------------|------|----|-------------|
| 5    | 6  | 88721       | 3    | 17 | 36169       | 14   | 27 | 316         |
| 1    | 7  | 31715       | 4    | 17 | 18086       | 15   | 27 | 97          |
| 2    | 7  | 22774       | 3    | 18 | 14156       | 16   | 27 | 55          |
| 6    | 7  | 31638       | 11   | 19 | 538         | 18   | 27 | 2           |
| 1    | 8  | 37139       | 12   | 19 | 215         | 22   | 27 | 14.5        |
| 2    | 8  | 44072       | 15   | 19 | 352         | 14   | 28 | 71          |
| 7    | 8  | 7555        | 16   | 19 | 4538        | 15   | 28 | 64          |
| 2    | 9  | 3457        | 18   | 19 | 967         | 22   | 28 | 14.6        |
| 7    | 9  | 3437        | 8    | 20 | 4.9         | 14   | 29 | 152.8       |
| 8    | 9  | 6842        | 8    | 21 | 25.7        | 15   | 29 | 22.6        |
| 8    | 10 | 1159        | 1    | 22 | 277         | 18   | 29 | 43.1        |
| 9    | 10 | 552         | 2    | 22 | 321         | 22   | 30 | 2.7         |
| 1    | 11 | 4199        | 8    | 22 | 1534        | 23   | 30 | 2.6         |
| 2    | 11 | 2751        | 1    | 23 | 20.8        | 27   | 30 | 10.2        |
| 7    | 11 | 290         | 2    | 23 | 111         | 22   | 31 | 91.4        |
| 1    | 12 | 2275        | 8    | 23 | 248.2       | 18   | 32 | 0.9         |
| 2    | 12 | 1489        | 8    | 24 | 5.2         | 22   | 32 | 12.3        |
| 7    | 12 | 156         | 14   | 25 | 7.2         | 23   | 32 | 8           |
| 1    | 13 | 4415        | 15   | 25 | 2.1         | 31   | 32 | 4.3         |
| 2    | 13 | 2892        | 18   | 25 | 0.3         | 19   | 33 | 2.4         |
| 7    | 13 | 304         | 12   | 26 | 9           | 21   | 33 | 0.2         |
| 3    | 14 | 161758      | 14   | 26 | 59          | 22   | 33 | 17.2        |
| 3    | 15 | 25207       | 15   | 26 | 14          | 23   | 33 | 10.6        |
| 3    | 16 | 57665       | 18   | 26 | 14          |      |    |             |

<sup>a</sup> We used data balanced by DATBAL, see Ulanowicz and Puccia (1990).

species, which we supposed to be comparable in strength of their effect with the trophic ones. Also, since our interest is primarily of methodological nature, we intend to incorporate as many interaction types as possible. Tables 1 and 2 show the original food web data, while Table 3 shows the non-trophic effects and Fig. 1 shows our complete interaction network. Note that the food web is a subgraph of the interaction network.

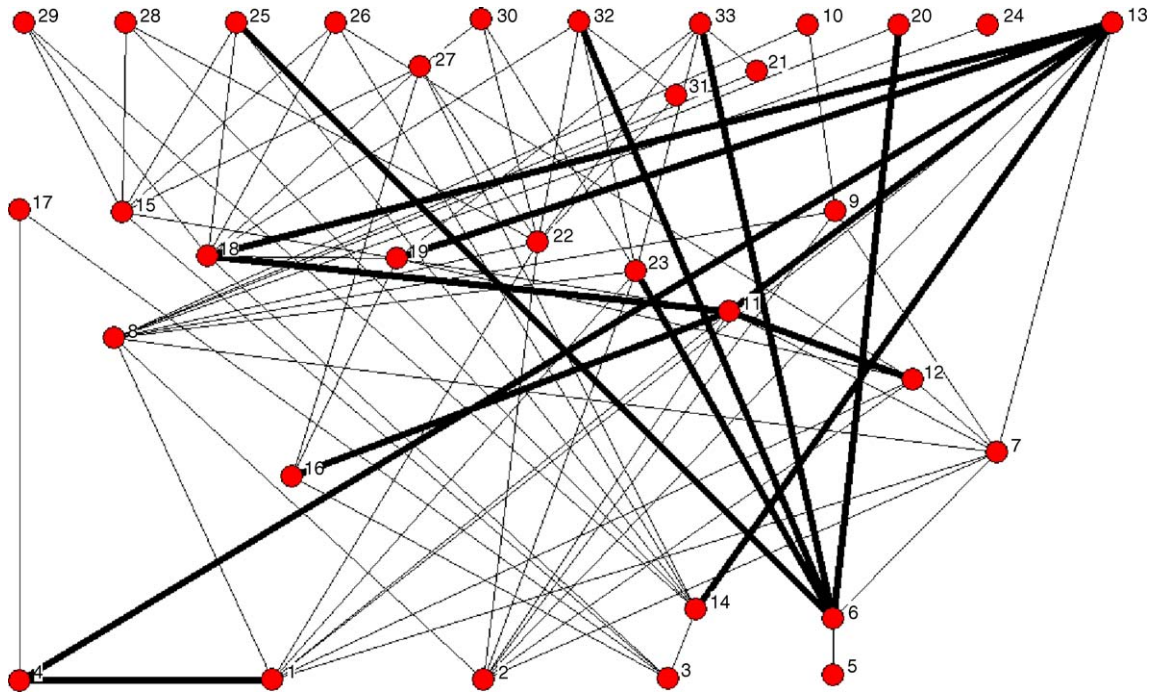
We mention that before the non-trophic links were incorporated, we slightly modified the original data base. Only interactions between living components were considered, since we are interested in the more biological aspect of community organization and not in mass-balance and the thermodynamics of the system. This is a deviation from the classical

traditions of “ecosystems ecology” but sounds more logical from a “community ecology” point of view. As far as we see, it is imperative to bridge the gap between these schools and our work is aimed to contribute to this. The major problem with non-living compartments, from a community-level interaction network viewpoint is that the interaction between “detritus” or “DOC” and a particular species as highly asymmetrical in many senses, i.e. very different from a classical “prey and predator” situation. If centrality is to be quantified, the directed nature of a couple of links produces serious artifacts. Also, each species and living group are linked to the detritus, so considering these “living–non-living” links would cause a serious artifact in mapping the topology of the interaction network in the case of the undirected variants (detritus

**Table 2 – Components of the carbon flow network (after Baird and Ulanowicz, 1989)**

|    |                                |    |                            |    |                            |
|----|--------------------------------|----|----------------------------|----|----------------------------|
| 1  | Phytoplankton                  | 13 | Oysters                    | 25 | Croaker                    |
| 2  | Suspended bacteria             | 14 | Other polychaetes          | 26 | Hog choker                 |
| 3  | Sediment bacteria              | 15 | Nereis                     | 27 | Spot                       |
| 4  | Benthic diatoms                | 16 | Macoma spp.                | 28 | White perch                |
| 5  | Free bacteria                  | 17 | Meiofauna                  | 29 | Catfish                    |
| 6  | Heterotrophic microflagellatae | 18 | Crustacean deposit feeders | 30 | Blue fish                  |
| 7  | Microzooplankton               | 19 | Blue crab                  | 31 | Weak fish                  |
| 8  | Zooplankton                    | 20 | Fish larvae                | 32 | Summer flounder            |
| 9  | Ctenophore                     | 21 | Alewife and blue herring   | 33 | Striped bass               |
| 10 | Sea nettle                     | 22 | Bay anchovy                | 34 | DOC <sup>a</sup>           |
| 11 | Other suspension feeders       | 23 | Menhaden                   | 35 | Suspended POC <sup>a</sup> |
| 12 | Mya                            | 24 | Shad                       | 36 | Sediment POC <sup>a</sup>  |

<sup>a</sup> Nodes #34–36 are only considered for the TUUU’ variant and are not shown in Fig. 1 (DOC and POC mean dissolved and particle organic carbon, respectively).



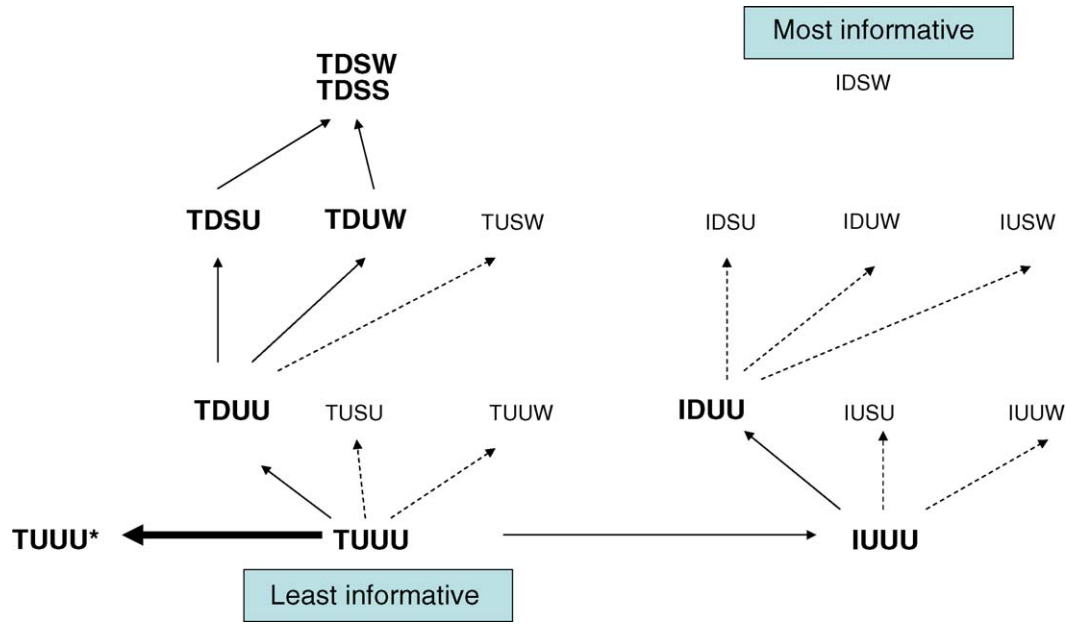
**Fig. 1 – The interaction network of the Chesapeake Bay ecosystem. Graph nodes represent species or suitably defined functional groups (for decoding, see Table 2). The thin links compose the food web graph (slightly modified after Baird and Ulanowicz, 1989, see explanation in text and also Table 1) complemented by selected non-trophic links marked bold (see explanation in text and Table 3). The network was drawn by the NetDRAW subroutine of UCINET (Borgatti et al., 2002).**

will inevitably be the “keystone species”, later we will illustrate the effect of this). So, dissolved and particle organic carbon pools (DOC and POC, respectively) are out of our interest, since these groups do not interact living groups in the same way as living entities do (detritus does not hunt for its “prey”). The links between groups #1 and #2 and between #2 and

#3 were deleted for the above reasons and the link between groups #3 and #19 was deleted following the secondary data base in Ulanowicz and Puccia (1990). However, we have not taken into account non-living components of the system, the methods make it very easy to incorporate them. For example, environment-mediated indirect interactions (Wootton, 2002;

**Table 3 – Non-trophic effects considered: their interaction type, sign and source are given**

| Effect                       | Sign | From | To | Reference                                   |
|------------------------------|------|------|----|---|
| Parasite                     | –    | 6    | 23 | Burkholder et al. (1992), Burkholder (1999) |
| Host                         | +    | 23   | 6  | Burkholder et al. (1992), Burkholder (1999) |
| Parasite                     | –    | 6    | 20 | Burkholder (1999)                           |
| Host                         | +    | 20   | 6  | Burkholder (1999)                           |
| Parasite                     | –    | 6    | 25 | Burkholder (1999)                           |
| Host                         | +    | 25   | 6  | Burkholder (1999)                           |
| Parasite                     | –    | 6    | 32 | Burkholder et al. (1992), Burkholder (1999) |
| Host                         | +    | 32   | 6  | Burkholder et al. (1992), Burkholder (1999) |
| Parasite                     | –    | 6    | 33 | Burkholder et al. (1992), Burkholder (1999) |
| Host                         | +    | 33   | 6  | Burkholder et al. (1992), Burkholder (1999) |
| Facilitation (surface, hide) | +    | 13   | 11 | Bahr and Lanier (1981)                      |
| Facilitation (surface, hide) | +    | 13   | 14 | Bahr and Lanier (1981)                      |
| Facilitation (surface)       | +    | 13   | 4  | Bahr and Lanier (1981)                      |
| Facilitation (hide)          | +    | 13   | 18 | Eggleston et al. (1998)                     |
| Facilitation (hide)          | +    | 13   | 19 | Eggleston et al. (1998)                     |
| Facilitation (surface)       | +    | 18   | 11 | Key et al. (1997)                           |
| Inhibition (shading)         | –    | 1    | 4  | McGlathery et al. (2001)                    |
| Facilitation (hide)          | +    | 11   | 16 | Skilleter (1994)                            |
| Facilitation (surface)       | +    | 16   | 11 | Skilleter (1994)                            |
| Facilitation (hide)          | +    | 11   | 12 | Skilleter (1994)                            |
| Facilitation (surface)       | +    | 12   | 11 | Skilleter (1994)                            |



**Fig. 2 – Relationships between the combinations of link qualities providing network variants. The theoretically possible but not reasonable or illogical combinations of directedness, signedness and weightedness are marked by small, normal letters and discussed in text. The flowchart of our interest shows the studied variants in large, bold letters. Solid arrows show steps of increasing complexity, while dashed arrows show impossible routes for increasing the information content of the interaction network. The variant marked by an asterisk is the only web containing non-biotic groups (like DOC).**

Bruno et al., 2003) can simply be considered as direct links. Before analyzing our interaction network, we assume that our construction is “perfect”: the nodes of the graph are the functionally sensible units of the community, the links of the graph are the functionally sensible interactions between them, and everything had been measured perfectly in the field.

Based on the information on the direction, sign and strength of interactions, and based on whether we take into account also non-trophic links, 16 variants of the same interaction network can be logically constructed (additionally, we provide both quantitative and semi-quantitative weighting in a special case, explained later). The least information is presented by the pure topological food web (coded as TUUU, i.e. Trophic, Undirected, Unsigned, Unweighted), while more information-rich webs are coded like TDSW (i.e. Trophic, Directed, Signed, Weighted) or IUUU (Interaction, Undirected, Unsigned, Unweighted). The theoretically most information-rich web (i.e. IDSW) is not presented, since at the moment it is impossible to express the weights on trophic and non-trophic links in the same units (e.g. a common currency for food provision by carbon transfer, substrate formation as a facilitative interaction and helping recruitment in a mutualism). Eight webs of the 17 variants have been analyzed; the others were excluded for various reasons (see next paragraph). Fig. 2 shows the relationships between the studied eight webs and also between the non-studied combinations. We note that ecological networks in one of the above combinations of link quality have been analyzed by Ulanowicz and Puccia (1990, TDSW), Ulanowicz (1995, IDSW), Montoya et al. (2003, IDSW), Levine (1980, IDSU) and Jordán et al. (2003a, TUUU and TUUW) but, as far as we see, this comparative methodological approach was

still needed for seeing more clearly how data quality modifies our predictions.

According to Fig. 2, there are many network variants constructed by different combinations of direction, sign and weight of links as well as the presence and absence of non-trophic links, and only some of these are analyzed. We briefly mention the reasons for these decisions. It is not logical to consider the signs of undirected links (in TUSU, TUSW and IUSU). It could be possible only if all of the links have symmetrical signs, i.e. +/+ and -/- links are exclusive. Thus, the combination of “U” on the second place (undirected) and “S” is forbidden. If links are not directed, it is illogical to weight them related to the carbon flows (in TUUW). (But see Jordán et al., 2003a, for weighting related to the interaction frequency.) A prey–predator link may have a weight, of course, in both directions, but not the same. So, “W” without “D” is excluded from the space of reasonable network variants. However, there are studies on weighting non-trophic links (like expressing the relative strengths of competition or mutualism); it is not possible to weight all the trophic and non-trophic links in the same unit. For a successful example for a special case, see Ulanowicz (1995). Thus, the combinations of “I” and “W” must be excluded. Considering the sign of interactions is possible by the IMPACTS software but it is based on mass-balance models (until non-trophic links are built in).

### 3.2. Network analysis

The network perspective on ecology is to say that in order to understand the behavior of the components of ecological systems (e.g. species), the graph properties of ecosystem networks must be analyzed. In other words, interaction networks

are built up and influenced by their species but also constrain the behavior of the constituent species. The topology of these networks shows the possibilities for indirect interactions (e.g. trophic cascade), the species occupying critically important positions within the graph (i.e. topological keystone species) and the constraints the web itself puts on population dynamics. Various graph indices characterize local, mesoscale and global system properties. We note that because of similar interest between ecological and social network analysis, the methodology of network analysis in these fields have common roots in the past (Harary, 1961) and similar future interest (Jordán et al., 1999; McMahon et al., 2001; Luczkovich et al., 2003).

We use the following indices for the analysis of the Chesapeake Bay interaction networks, the suitable ones for each network variant. These indices characterize and quantify the interaction structure of the networks, and particularly, the positional importance of graph nodes (representing the importance of the components within the community). The indices complement each other in showing different types of centrality, rather than giving competitive results, and their usefulness in network analysis depend on the question asked.

The indices range from very simple ones, dependent only on characteristics very local to the focal node, to those that include information on the widest web features. Throughout the paper, we define  $N$  as the number of nodes in a network.

The index that is most local and most widely used but probably least informative about network topology is the *degree* of a node ( $D$ ). This is the number of adjacent nodes (in a food web, the sum of prey and predator species; Wassermann and Faust, 1994). Several analyses on topological key species have been focusing on the number of neighbors in food webs, i.e. the degree of nodes and their distribution in trophic networks (Solé and Montoya, 2001; Dunne et al., 2002; Montoya and Solé, 2002; Williams et al., 2002). Degree considers only the links directly connected to a node. We also consider network indices reflecting short indirect effects, i.e. the neighbors of neighbors. We call these indices *mesoscale indices*, in contrast to the *local* nature of degree, and to the *global* nature of some indices characterizing the whole network (see later).

A mesoscale index quantifying how frequently a node  $i$  is on the shortest paths between every pair of nodes  $j$  and  $k$  is called *betweenness centrality* (BC) and used routinely in social network analysis (Wassermann and Faust, 1994). We calculated it using the UCINET VI programme (Borgatti et al., 2002). The standardized index for a node  $i$  ( $BC_i$ ) is:

$$BC_i = \frac{\sum_{j < k} g_{jk}(i)/g_{jk}}{(1/2)(N-1)(N-2)}$$

where  $i \neq j$  and  $k$ .  $g_{jk}$  is the number of equally shortest paths between nodes  $j$  and  $k$ , and  $g_{jk}(i)$  is the number of these shortest paths to which node  $i$  is incident (of course,  $g_{jk}$  may equal one). The denominator is the number of pairs of nodes without node  $i$ . This index thus measures how central a node is, in the sense of being incident to many shortest paths in the network. If  $BC_i$  is large for node  $i$ , it means that this group has an important role in mediating many rapidly spreading effects in the web.

The *ego-betweenness* of a node is the *betweenness* value within its own ego-network, i.e. the subgraph composed of

a particular node, its neighbors, and the connections between all of them. We use the normalized version of it, thus we can compare the values that the nodes have. If a node has a high ego-betweenness value, this means that the closest subcommunity around it strongly depends on its presence, i.e. it is a key mediator of various effects at a mesoscale.

We also calculate the *information centrality* index (IC), which considers all paths (including the shortest), weighted by path length (for detailed explanation, see Wassermann and Faust, 1994, calculated by UCINET VI, Borgatti et al., 2002), because the effects spreading through the shortest path may not be the most important ones.

*Closeness centrality* (CC) quantifies how short are the minimal paths from a given node to all others (Wassermann and Faust, 1994) and is again calculated using UCINET VI (Borgatti et al., 2002). The standardized index for a node  $i$  ( $CC_i$ ) is:

$$CC_i = \frac{N-1}{\sum_{j=1}^N d_{ij}}$$

where  $i \neq j$ , and  $d_{ij}$  is the length of the shortest path between nodes  $i$  and  $j$  in the network. This index thus measures how close a node is to others. The larger is  $CC_i$  for node  $i$ , the more rapidly will its effects spread to other groups.

In contrast to the mesoscale indices, the global ones provide information of the whole network. The *network centralization indices* for *degree*, *closeness*, *betweenness* and *information centrality* are calculated according to Wassermann and Faust (1994, p. 175 and for details, see also pp. 180, 186, 191 and 197). For the other indices, we define network centralization as the coefficient of the variation of the species' importance values.

Another measure we use, the *keystone index* ( $K$ ; Jordán et al., 1999) derives predominantly from the application and modification of the "net status" index in sociometry (Harary, 1959) used also in ecology (Harary, 1961). The keystone index of species  $i$  ( $K_i$ ) is defined as:

$$K_i = K_{bu,i} + K_{td,i} = K_{dir,i} + K_{indir,i} \\ = \sum_{c=1}^n \frac{1}{d_c} (1 + K_{bc}) + \sum_{e=1}^m \frac{1}{f_e} (1 + K_{te}),$$

where  $n$  is the number of predators eating species  $i$ ,  $d_c$  the number of prey of its  $c$ th predator and  $K_{bc}$  is the bottom-up keystone index of the  $c$ th predator. And symmetrically,  $m$  is the number of prey eaten by species  $i$ ,  $f_e$  the number of predators of its  $e$ th prey and  $K_{te}$  is the top-down keystone index of the  $e$ th prey. For node  $i$ , the first sum in the equation (i.e.  $\sum 1/d_c (1 + K_{bc})$ ) quantifies the bottom-up effect ( $K_{bu,i}$ ) while the second sum (i.e.  $\sum 1/f_e (1 + K_{te})$ ) quantifies the top-down effect ( $K_{td,i}$ ). After rearranging the equation, terms including  $K_{bc}$  and  $K_{te}$  (i.e.  $\sum K_{bc}/d_c + \sum K_{te}/f_e$ ) refer to indirect effects for node  $i$  ( $K_{indir,i}$ ), while terms not containing  $K_{bc}$  and  $K_{te}$  (i.e.  $\sum 1/d_c + \sum 1/f_e$ ) refer to direct ones ( $K_{dir,i}$ ). Both  $K_{bu,i} + K_{td,i}$  and  $K_{indir,i} + K_{dir,i}$  equals  $K_i$ . The keystone index emphasizes vertical over horizontal interactions (e.g. trophic cascades as opposed to apparent competition). Its conceptual counterpart is the trophic field of a species (Jordán, 2001) and has been applied several times in network analysis (e.g. Jordán, 2001). Its important feature is the sensitivity to both dis-

tance and degree: it quantifies positionality at an intermediate scale rather than giving very local or very global information (Jordán and Scheuring, 2002). We calculated the keystone indices of trophic groups by the FLKS 1.1 programme (available on request).

We must note that the keystone index is useful only for a single web type (TDUU), i.e. there is no possibility for comparisons. The other four indices presented above (*degree*, *betweenness*, *information centrality* and *closeness*) are insensitive to the direction, sign and strength of links, so we use them to analyze and compare TUUU and IUUU. Unlike them, one can calculate the importance of a node by summing the effects it has on each other nodes. The following two indices using this method assume that the indirect chain effects are multiplicative and additive.

An index useful for undirected, unsigned and unweighted networks is called *topological importance index* (TI). We use it for characterizing long indirect effects (cf. Yodzis, 2001) while it is not biased for vertical interactions, i.e. takes into account also exploitative and apparent competition. The index itself is the extension of an earlier one proposed for the analysis of two-steps long, horizontal, apparent competition interactions in weighted host–parasitoid networks (Müller et al., 1999). In an unweighted network, we define  $a_{n,ij}$  as the effect of  $i$  on  $j$  when  $j$  can be reached from  $i$  in  $n$  steps. The simplest mode of calculating  $a_{n,ij}$  is if  $n = 1$  (i.e. the effect of  $i$  on  $j$  in 1 step):  $a_{1,ij} = 1/D_j$ , where  $D_j$  is the degree of node  $j$ . When the effect of step  $n$  is considered, the effect received by species  $i$  from all species in the same network is equal to 1 (i.e. each species is affected by the same unit effect.). Furthermore, we define the  $n$ -step effect originated from a species  $i$  as:

$$\sigma_{n,i} = \sum_{i=1}^N a_{n,ij}$$

that may vary among different species (i.e. effects originated from different species maybe different). Here, we define the topological importance of species  $i$  when effects “up to”  $n$  step are considered as:

$$TI_i^n = \frac{\sum_{m=1}^n \sigma_{m,i}}{n} = \frac{\sum_{m=1}^n \sum_{j=1}^N a_{m,ij}}{n}$$

which is simply the sum of effects originated from species  $i$  up to  $n$  steps (one plus two plus three ... up to  $n$ ) averaged over by the maximum number of steps considered (i.e.  $n$ ).

In our study, we extend the TI index to directed networks. In this case, we define the direct effect  $i$  upon  $j$  as

$$a_{1,ij} = \frac{\alpha_{ij}}{\sum_{i=1}^D \alpha_{ij}}$$

where  $\alpha_{ij} = 1/D_{j,out}$  if  $i$  is a predator and  $\alpha_{ij} = 1/D_{j,in}$  if  $i$  is a prey of  $j$ . In the equations  $D_{i,in}$  is the number of  $i$ 's preys,  $D_{i,out}$  is the number of  $i$ 's predators and  $D$  is the sum of them (*degree*), while the other calculations remains the same. The method assumes that the effect each species receives from its predators and preys are equal. Further, each prey and predator has equal effects, respectively, which is normalized (the sum of them is defined as 1).

For a weighted network, all effects are defined in the same way as above with the exception of calculating  $\alpha_{ij}$ , which is

defined as:

$$\alpha_{ij} = \frac{\varepsilon_{ij}}{\mu_j},$$

where  $\mu_j$  is the sum of strength of links pointing to  $j$ , if  $i$  is a prey of  $j$  or the sum of strength of links originated from  $j$ , if  $i$  is a predator of  $j$ .  $\varepsilon_{ij}$  is the strength of the link connecting  $i$  and  $j$ . In this study, we define  $\varepsilon_{ij}$  as the absolute value of the strength calculated by the IMPACTS program (see next paragraph). The weighted approach of calculating two-step effects (i.e.  $a_{2,ij}$ ) was originally developed by Godfray and coworkers for assessing apparent competition in a host–parasitoid community (Müller et al., 1999; Rott and Godfray, 2000).

We also use the IMPACTS program developed by Ulanowicz and Puccia (1990) for measuring direct and indirect trophic impacts from trophic flow data. The dietary coefficient ( $g_{ij}$ ), quantifies the effect of prey  $i$  upon predator  $j$  (defined as the proportion of  $i$  within the menu of  $j$ ). The effect of predator  $j$  on its prey  $i$  ( $f_{ji}$ ) is measured by the fraction of net output (respiratory output is excluded) consumed by predator  $j$ . The net impact of  $i$  upon  $j$  equals  $g_{ij} - f_{ji}$  and defined as the one-step (direct) effect of  $i$  on  $j$ . Its values range from  $-1$  to  $+1$ . Taking every pair of  $N$  nodes, we calculate the above-defined direct net impacts and constitute the  $N \times N$  net impact matrix,  $[Q]$ . The total (direct and indirect) effects are calculated by summing the all integer powers of  $[Q]$ :

$$[M] = \sum_{h=1}^{\infty} [Q]^h.$$

Using the following equation known from the input–output theory (Hannon, 1973):

$$[M] = ([I] - [Q])^{-1} - [I],$$

where  $[I]$  is the identity matrix. Summing the rows of  $[M]$  equals the IMPACTS based importance. We use the summed absolute values of effects (later called IMA) in order to measure the interactive power of a group: keystones can be of high importance because of both positive and negative effects on others (otherwise mixed strong negative and strong positive effects might result in an effect around zero). Using the absolute of the resulting values does not lead to the loss of the information on sign structure. We use this method also for the TDSU variant. In this case, we calculate the direct, pairwise impacts as if each prey and predator would have had equal effects.

The reader can see that the method of IMPACTS is analogous to the calculation of the topological importance index. The latter is calculated for undirected and unsigned networks, by taking the average of the matrices while IMPACTS handles directed and signed graphs by summing them up. As expounded above, we extend these methods for all types of food webs analyzed in this study and used them to compare the different trophic variants of the network. Because of these methods suppose the additivity of the effects, which is not the case for interaction webs, they are not used. Note that while the calculation of the direct impacts with the IMPACTS method contains the flow to the non-living compartments as well, the TI method does not.

## 4. Results and discussion

Our results quantify the interaction structure of the networks and the positional importance of different nodes. First, we present the results of these quantifications, and then the comparative results. We are interested in: (i) comparing the results based on the food web to those based on the interaction web and (ii) comparing the values of the same network index in several network variants. Finally, (iii) we will present more detailed results on the structure of the fish community: since the level of aggregation is much more similar in the case of fish species, the value of comparative approaches is larger here.

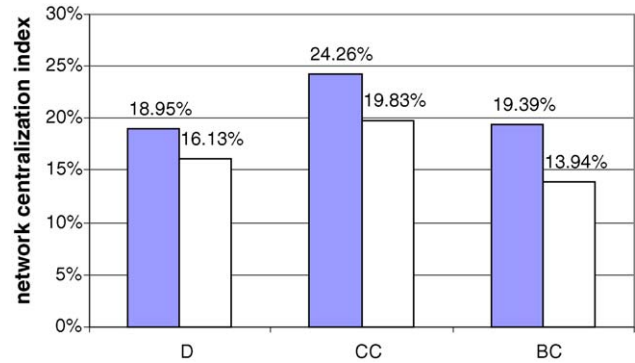
### 4.1. Species importance in network variants

The importance ranks of graph nodes in different network variants, according to the different sensible network indices presented above are shown in [Appendix A](#). (Note that the variant TUUU', the web with non-living components as well have the detritus as most important group.) Group #8 (zooplankton) is the leader in both the simplest (*D* in TUUU) and the most complex (TDSW and IDUU) calculations. Then, depending on the type of the web, groups #3 (bacteria in sediment), #1 (phytoplankton) and some six more groups appear among the key groups. The importance of the groups #8 and #3 are explained that they are the obligate prey of many species. The light assimilated by the phytoplankton is the energy source for the planktonic part of the food web and similarly, the most important benthic producers are the bacteria in sediment. Comparing the direct and indirect effects measured by TI and IMA, the observation is that the group #8 has rather direct, while the group #1 has rather indirect role in regulating the community. Bay anchovy (#22) is located in the centre of the food web, so it has an important role in transmitting impacts (*betweenness* and *information centrality*). It has the smallest average distance to the other nodes (*closeness centrality*). According to the top-down component of the *keystone index*, striped bass (#33) has an important role in the top-down control of the web.

### 4.2. Comparison of the food web (TUUU) and the interaction web (IUUU)

Different indices are not similarly sensitive to adding non-trophic links to the food web. In general, one can say that the adding of non-trophic links has a notable effect on the importance ranks of the species, suggesting that they may have an important role in organizing whole communities and do not have only local significance as thought before. For investigating the network's more local features, we calculate the *ego-betweenness* of the nodes. It increases only for group #13, the oysters (and very slightly to #1, phytoplankton) when considering the interaction web (see [Appendix A](#)). Thus, we can say that non-trophic effects are patterned in a way emphasizing more the importance of this group in its local subcommunity, outlining the subcommunity-organizing role of the oysters.

Analyzing the network from a global viewpoint, we find that if non-trophic links are taken into account, this increased complexity reduces the differences between the species' importance. First of all, the *network centralization index* is cal-



**Fig. 3 – The network centralization index for degree, closeness and betweenness, calculated for TUUU (grey) and IUUU (white), showing that considering the non-trophic interactions as well makes the web more homogenous.**

culated for the three basic topological measures (*D*, *CC* and *BC*) and always found lower in the interaction than in the food web ([Fig. 3](#)). Secondly, the observation that the most important nodes according to the different indices are approximately the same in the trophic web (#2, #7, #8 and #22) but different in the interaction web outlines the more diverse roles of species in the latter. Finally, the fact that the *ego-betweenness* values do not change or decrease for all but two groups means that the inbuilt non-trophic links make the network more redundant, with more alternative pathways.

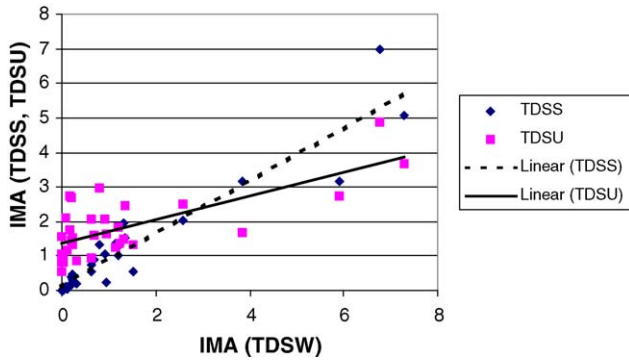
All these are suggesting that the community is more balanced than thought before, judging only by the food web (increasing stability, *sensu* MacArthur, 1955). The non-trophic links often represent interactions between the more or less independent parts of the trophic web, i.e. the plankton, the benthos and the nekton and besides, the seemingly most important non-trophic links belong to the trophically less important groups (cf. the rank positions of group #6 in [Appendix A](#)).

### 4.3. Comparisons of the different variants of the food webs

If only the order of magnitudes of the flows are known (TDSS), the results calculated by IMPACTS are very similar to those of TDSW (with exact flow data; [Fig. 4](#)). If only direct interactions are considered, there are only few changes in the importance ranks of the species, for example that the effect of #1 is underestimated. In the case of the overall (direct and indirect) effects, the differences between TDSW and TDSS are bigger, for example the importance of #3 is overestimated, but still very similar. TDSU considering no interaction strength show much more different results. The ranks of TDSS and TDSW are also much more similar to each other than to TDSU: groups #2, #19 and #33 decrease and groups #9 and #14 increase in significance as the quantitative weights are considered. TDSS already indicates these changes.

If we are examining only the direct interaction structure of the food web, the importance ranks of TDSW and the TDUU are nearly the same. This is showing that the two methods for calculating the effect of the direct interactions, i.e. topo-





**Fig. 4 – The IMA values of groups calculated for the TDSU and TDSS web variants plotted against the IMA indices calculated for TDSW web. Semi-quantitative weighting (TDSS) gives a much better approximation to the quantitative weighting (TDSW) than the unweighted index (TDSU).**

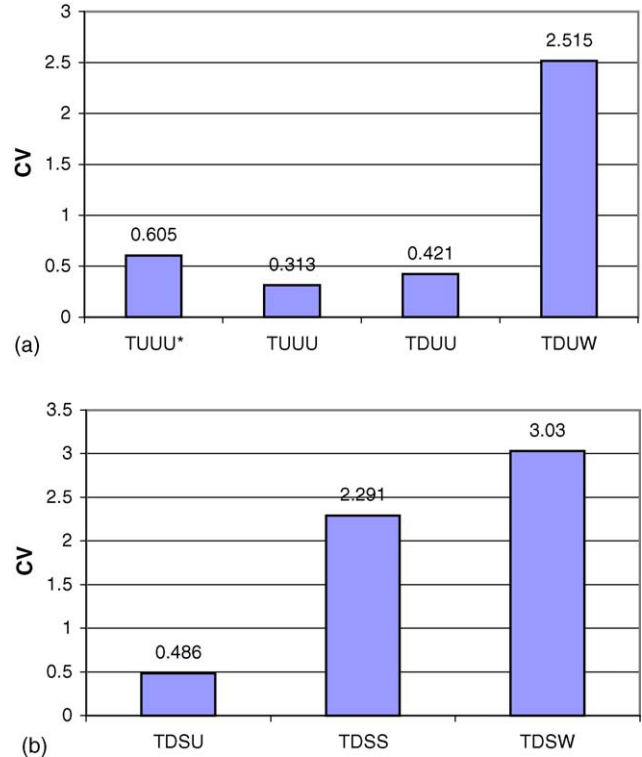
logical importance for unsigned and IMA for signed networks, are actually consistent. Examining the indirect effects as well, neglecting the signs of the interactions cause smaller differences in the most important (#8, #3 and #1 remains the three most important species, although in different order) and bigger differences in the least important species.

Summarizing the above-demonstrated results, our conclusions are the following. Despite the differences between the most and the least information-rich web's importance ranks, the most robust results, as it is the zooplankton's (#8) keystone rule, can be shown only by analyzing the simplest topological web. For a more detailed picture of the keystone structure, the web must be weighted and if indirect effects are taken into account it has to be signed. We must note that the longer indirect effects are considered, the more accurate data (both in weight and sign) is needed. The one of the most notable result for practice is that weighting links is important but a semi-quantitative approximation is accurate enough.

We characterize the centralization of the food web variants by the coefficient of variation of the importance values of graph nodes (Fig. 5). It is evident why the TUUU\* web is more heterogeneous than the TUUU web: it is an artifact caused by the non-living nodes' high importance. The centralization of the web is decreasing as we are losing information from TDSW through TDSS to TDSU and from TDUW through TDUU to TUUU. This is the case whether considering only direct or direct and indirect effects as well. The decrease of the coefficient of variation is caused by the decrease in the variation of the data analyzed. This indicates that comparing the centralization of different networks is only appropriate if the data bases contain the same quality of information.

#### 4.4. Fish community structure

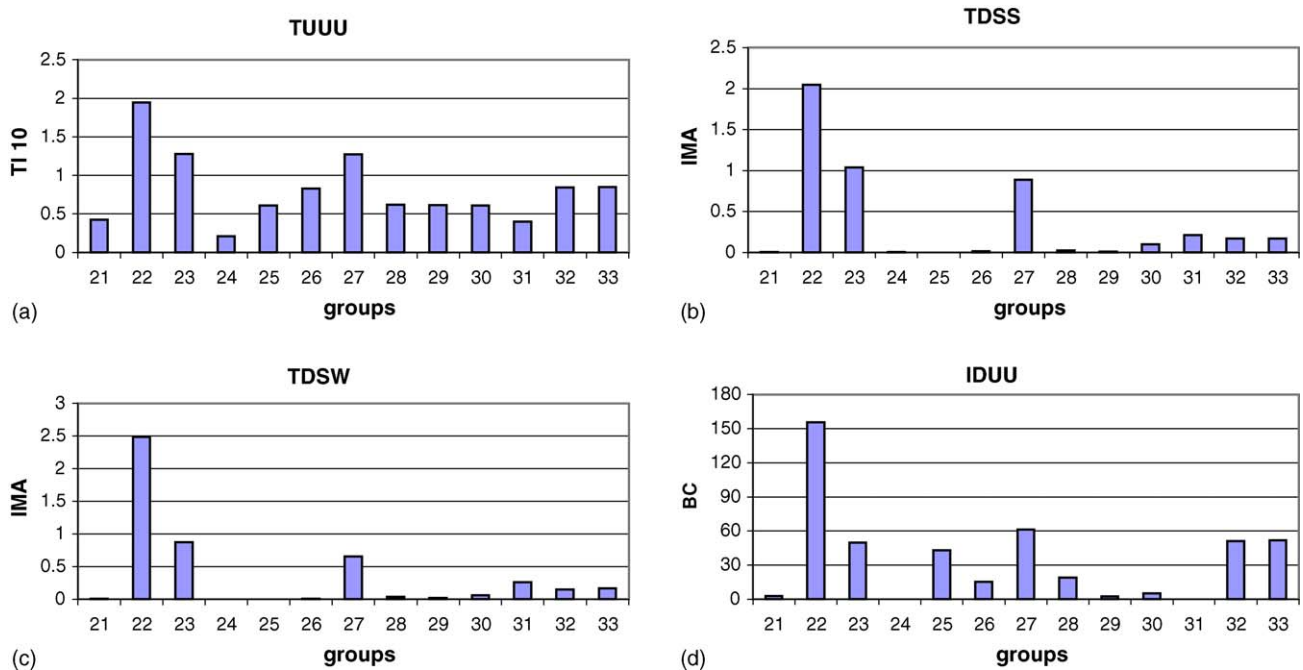
We analyzed the fish community (nodes #21–33) for two practical reasons. First, this part of the web is uniformly aggregated, i.e. the nodes represent one or two species. Second, there is heavy fisheries in the Bay, so there is a strong need to understand the roles fish play in the community.



**Fig. 5 – The coefficients of variation for: (a) TI 10 calculated for TUUU\*, TUUU, TDUU and TDUW and (b) IMA in TDSU, TDSS and TDSW. In both cases, the complexity of the networks leads to larger differences between the relative positional importance of groups. The keystone pattern is more characteristic and keystone species are easier to be identified if we have more data on the network.**

The most important fish, one of the keystone species of the community is Bay anchovy (#22). It's always among the first two species in the ranks for TUUU and IUUU. However, if the trophic web is directed, signed or weighted, it is ranked lower. As mentioned before, anchovy, consuming the plankton and consumed by most of the other fishes, has essential role in transmitting effects across trophic levels. That is why it is a key species in the food web considering *betweenness* and *information centrality* indices. Because of its central position, it has the smallest average distance to the other nodes (*closeness centrality*). The *topological importance* index is showing this effect as well, while assigning it the second highest importance value, even whether direct or all impacts are taken into account. Although anchovy is really common in the Chesapeake Bay today, its keystone role in the community suggests that it should not be neglected when setting the conservation priorities.

According to the top-down component of the *keystone index*, striped bass, one of the top predators (#33) is the most important top-down controller of the web and bluefish (#30) is the third most important. If we investigate the strength of pairwise interactions between it and the other species by considering the suitable component of the IMA index, the surprising result comes that it is mostly influenced indirectly, by group #8 and not by any of their direct neighbors. This is interesting



**Fig. 6 – The relative positional importance of fish species in different network variants. From the simplest (a) to more complex (c and d) cases the keystone pattern is more characteristic. This result comes already if weighting is semi-quantitative (TDSS). Species #22 is always the most important player in the community but the importance of others also becomes visible as soon as non-trophic links are also considered (e.g. #25).**

to be considered in analyses, where the number of neighbors ( $D$ ) is the only parameter characterizing a graph node. Also, in the first case, where top-species are mostly influenced by a bottom species, consequences might be drawn considering the possible relationships between fishing down and harmful algal blooms, especially because both are global, trendlike events.

Fig. 6a informs us about the relative positional importance of fish species in the TUUU web variant, according to the TI index for 10 steps long effects. If we consider more information (e.g. TDSW) and calculate the IMA values, we have a much less homogeneous distribution resulting in the more characteristic keystone pattern (Fig. 6c; IDUU in Fig. 6d is somewhat similar). This is still the case when only the order of magnitude of the mass flows are known (TDSS) (Fig. 6b). The relatively most important fish is always #22 but the relative importance of some others changes sensitively according to the different kinds of information the web variants represent.

## 5. Conclusions

We have quantified the importance of the different trophic groups composing the interaction network of the Chesapeake Bay mesohaline ecosystem. Different indices were used and different variants of the same web were studied, according to the combinations of whether to consider link direction, link sign, link strength and non-trophic links. Only the sensible combinations were studied and for each network variant only the sensible network indices were calculated. Our basic interest was whether and how do the positional importance rank

of trophic groups differ. Each rank was different. In contrast with previous ecological network analyses, we emphasized (1) the importance of mesoscale indices describing neither local nor global interactions and (2) analyzed a web containing both trophic and non-trophic interactions simultaneously. The first is important because of the dampening spread of indirect effects in food webs, while the second is timely because of recognizing the typically diffuse nature of mutualisms.

We emphasize that here we investigated an ‘effect’ network which is parallel in many ways with the ‘energy’ or ‘matter’ networks analyzed from the flow-storage perspective, also common in the literature (e.g. Borrett et al., 2006; Gattie et al., 2006; Schramski et al., 2006). The flow-storage analysis handles ecosystems as ‘structural, functional units that import, process and export energy, material and information’ (Gattie et al., 2006), hence gives insights into the origin and the fate of these three mediums. In this sense, Patten has shown that indirect effects tend to dominate direct ones (Patten, 1995; Borrett et al., 2006) and Fath and coworkers (Fath, 2004; Schramski et al., 2006) concluded that the control, defined as the extent to which elements contribute to the system’s overall flow-storage pattern, is widely, but not equally distributed among the components. However, these studies deal with only positive flows of medium, thus, the negative effects of predation fall out of their scope (Ulanowicz, 2004). In contrast, we were interested in how interacting species affect each other and how these effects spread through the network, using carbon flows as only the basis of effects. Hence, the ‘indirect effects’ and ‘control’ terms from the perspective of flow-storage analysis are related to the bottom-up effects in our terminology. Although there are many methodically sim-

ilar points in the analysis of interaction and flow-storage networks, several questions addressed are clearly different and a synthesis is needed if ecosystems are to be understood.

Our analysis is basically a methodological work and an illustrative case study, thus, our results and conclusions are statistically not sensible and one of the most important future tasks is to extend this analysis to further networks (for some examples, excellent trophic network data bases and additional non-trophic data exist for the Benguela upwelling system, the North Atlantic, or the Ythan River). This study is more like an illustration of some technical developments. Also, for testing the robustness of the results, i.e. their sensitivity to methodological noise, perturbation studies should also be welcome (cf. Jordán et al., 2003b). As a further theoretical development, the sign structure of interaction networks could also be taken into account, providing possibly helpful information about loop balance and structural stability.

We emphasize that more connections between ecologists and sociologists could be very helpful in both fields, either only for methodological developments or for better understanding comparative community dynamics within the network context. The common roots vary richly from conceptual to methodological crossroads (see Harary, 1959; Harary, 1961; Jordán et al., 1999; McMahon et al., 2001; Williams et al., 2002; Luczkovich et al., 2003; Krause et al., 2003).

Particular problems need different approaches suggesting basically the same but sometimes also different roles assigned to functional groups of species. Thus, the further developments in this field are proposed to help functional and

problem-centric ecology and conservation biology. We believe that this study may contribute to the theoretical development of how to set conservation priorities and how to optimize data collection. We suggest that it is imperative to make difference between the usefulness of different data types. Whether to make more effort on mapping non-trophic interaction pathways or measuring link weights is a practical question. Theoretically, both give important information but conservation biology is typically in decision situation. As for the more academic part of our work, it is a fundamental question how to quantify the relative importance of species and whether the proposed methods might consider only the trophic structure of communities or emphasis must be set also on non-trophic effects.

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**Appendix A**

The positional importance rank of trophic groups (in bold) according to the values (in normal) of different indices (in italics) characterising different network variants (in bold). See explanation in text.

|    | TUUU |    |       |    |          |      |       |    |        | TUUU' |      |    |      |    |    |    |      |  |
|----|------|----|-------|----|----------|------|-------|----|--------|-------|------|----|------|----|----|----|------|--|
|    | D    | CC | BC    | IC | n-ego-BC | TI 1 | TI 10 | D  | IC     |       |      |    |      |    |    |    |      |  |
| 8  | 10   | 22 | 47.76 | 22 | 123.13   | 22   | 1.48  | 14 | 100.00 | 8     | 3.92 | 8  | 2.46 | 36 | 29 | 36 | 3.45 |  |
| 22 | 9    | 2  | 43.24 | 8  | 113.32   | 8    | 1.42  | 15 | 100.00 | 22    | 2.20 | 22 | 2.03 | 35 | 14 | 35 | 2.92 |  |
| 2  | 8    | 8  | 43.24 | 7  | 76.71    | 2    | 1.42  | 16 | 100.00 | 7     | 1.90 | 7  | 1.91 | 8  | 11 | 22 | 2.82 |  |
| 7  | 8    | 23 | 43.24 | 19 | 68.62    | 1    | 1.38  | 17 | 100.00 | 15    | 1.78 | 2  | 1.79 | 22 | 11 | 8  | 2.75 |  |
| 1  | 7    | 1  | 42.67 | 18 | 65.97    | 7    | 1.38  | 18 | 100.00 | 18    | 1.70 | 15 | 1.59 | 2  | 10 | 2  | 2.72 |  |
| 15 | 7    | 27 | 42.67 | 3  | 64.15    | 19   | 1.36  | 19 | 100.00 | 14    | 1.62 | 18 | 1.58 | 1  | 9  | 1  | 2.59 |  |
| 18 | 7    | 19 | 42.11 | 27 | 53.18    | 18   | 1.35  | 21 | 100.00 | 2     | 1.54 | 1  | 1.55 | 7  | 9  | 23 | 2.56 |  |
| 14 | 6    | 12 | 41.56 | 12 | 51.73    | 23   | 1.35  | 25 | 100.00 | 19    | 1.32 | 14 | 1.37 | 15 | 8  | 7  | 2.56 |  |
| 19 | 6    | 7  | 40.51 | 15 | 46.18    | 15   | 1.33  | 26 | 100.00 | 1     | 1.29 | 27 | 1.34 | 18 | 8  | 18 | 2.48 |  |
| 23 | 6    | 18 | 40.51 | 2  | 41.99    | 27   | 1.33  | 28 | 100.00 | 3     | 1.29 | 19 | 1.34 | 23 | 8  | 15 | 2.46 |  |
| 27 | 6    | 32 | 40.00 | 6  | 31.00    | 12   | 1.30  | 29 | 100.00 | 27    | 1.23 | 23 | 1.34 | 12 | 7  | 12 | 2.46 |  |
| 3  | 5    | 11 | 39.51 | 17 | 31.00    | 14   | 1.26  | 3  | 100.00 | 17    | 1.20 | 3  | 1.28 | 14 | 7  | 19 | 2.43 |  |
| 12 | 5    | 15 | 39.51 | 1  | 30.14    | 11   | 1.20  | 33 | 100.00 | 23    | 1.20 | 12 | 1.09 | 19 | 7  | 27 | 2.40 |  |
| 9  | 4    | 28 | 39.51 | 32 | 28.27    | 33   | 1.19  | 6  | 100.00 | 6     | 1.13 | 9  | 0.93 | 27 | 7  | 14 | 2.33 |  |
| 11 | 4    | 33 | 39.51 | 14 | 26.18    | 26   | 1.18  | 27 | 93.33  | 33    | 0.94 | 33 | 0.90 | 3  | 6  | 11 | 2.31 |  |
| 26 | 4    | 26 | 38.10 | 23 | 26.04    | 3    | 1.17  | 22 | 87.50  | 32    | 0.92 | 32 | 0.90 | 9  | 6  | 9  | 2.27 |  |
| 32 | 4    | 30 | 37.65 | 26 | 24.64    | 32   | 1.17  | 23 | 83.33  | 9     | 0.85 | 26 | 0.88 | 11 | 6  | 3  | 2.21 |  |
| 33 | 4    | 14 | 36.78 | 11 | 19.90    | 9    | 1.13  | 32 | 83.33  | 12    | 0.81 | 11 | 0.87 | 13 | 5  | 13 | 2.12 |  |
| 13 | 3    | 16 | 35.96 | 33 | 19.46    | 30   | 1.09  | 12 | 75.00  | 26    | 0.65 | 17 | 0.69 | 26 | 5  | 33 | 2.11 |  |
| 16 | 3    | 31 | 35.96 | 28 | 19.17    | 28   | 1.08  | 8  | 68.33  | 11    | 0.56 | 16 | 0.68 | 32 | 5  | 26 | 2.11 |  |
| 25 | 3    | 21 | 34.41 | 16 | 13.17    | 13   | 1.06  | 30 | 66.67  | 16    | 0.53 | 29 | 0.66 | 33 | 5  | 32 | 2.10 |  |
| 28 | 3    | 9  | 33.68 | 9  | 3.91     | 16   | 1.06  | 11 | 58.33  | 4     | 0.50 | 25 | 0.66 | 10 | 4  | 30 | 1.93 |  |
| 29 | 3    | 3  | 32.65 | 30 | 3.33     | 25   | 1.03  | 1  | 50.00  | 5     | 0.50 | 28 | 0.66 | 16 | 4  | 10 | 1.92 |  |
| 30 | 3    | 13 | 32.00 | 21 | 2.28     | 29   | 1.03  | 2  | 46.43  | 29    | 0.45 | 6  | 0.65 | 25 | 4  | 28 | 1.91 |  |
| 6  | 2    | 10 | 30.77 | 25 | 1.19     | 21   | 0.88  | 7  | 40.00  | 25    | 0.45 | 13 | 0.65 | 28 | 4  | 16 | 1.89 |  |
| 10 | 2    | 25 | 30.77 | 29 | 1.19     | 31   | 0.87  | 13 | 16.67  | 30    | 0.44 | 30 | 0.65 | 29 | 4  | 25 | 1.88 |  |

Appendix A (Continued)

| TUUU |   |    |       |    |      |    |      |          |       | TUUU* |      |       |      |    |   |    |      |
|------|---|----|-------|----|------|----|------|----------|-------|-------|------|-------|------|----|---|----|------|
| D    |   | CC |       | BC |      | IC |      | n-ego-BC |       | TI 1  |      | TI 10 |      | D  |   | IC |      |
| 17   | 2 | 29 | 30.77 | 13 | 0.14 | 10 | 0.85 | 9        | 16.67 | 28    | 0.42 | 10    | 0.47 | 30 | 4 | 29 | 1.88 |
| 21   | 2 | 20 | 30.48 | 4  | 0    | 6  | 0.62 | 10       | 0     | 13    | 0.39 | 21    | 0.46 | 5  | 3 | 21 | 1.64 |
| 31   | 2 | 24 | 30.48 | 5  | 0    | 20 | 0.61 | 31       | 0     | 31    | 0.36 | 31    | 0.44 | 6  | 3 | 31 | 1.63 |
| 4    | 1 | 6  | 29.63 | 10 | 0    | 24 | 0.61 | 4        | -     | 10    | 0.35 | 4     | 0.37 | 17 | 3 | 6  | 1.50 |
| 5    | 1 | 17 | 25.20 | 20 | 0    | 17 | 0.58 | 5        | -     | 21    | 0.35 | 5     | 0.35 | 21 | 3 | 17 | 1.50 |
| 20   | 1 | 5  | 23.02 | 24 | 0    | 5  | 0.39 | 20       | -     | 20    | 0.10 | 20    | 0.23 | 31 | 3 | 5  | 1.38 |
| 24   | 1 | 4  | 20.25 | 31 | 0    | 4  | 0.38 | 24       | -     | 24    | 0.10 | 24    | 0.23 | 4  | 2 | 20 | 1.32 |
|      |   |    |       |    |      |    |      |          |       |       |      |       |      | 20 | 2 | 24 | 1.32 |
|      |   |    |       |    |      |    |      |          |       |       |      |       |      | 24 | 2 | 4  | 1.19 |
|      |   |    |       |    |      |    |      |          |       |       |      |       |      | 34 | 2 | 34 | 1.13 |

| IUUU |    |    |       |    | IDUU  |    |      |          |        | TUUU |        |                 |      |    |      |      |      |       |      |
|------|----|----|-------|----|-------|----|------|----------|--------|------|--------|-----------------|------|----|------|------|------|-------|------|
| D    |    | CC |       | BC |       | IC |      | n-ego-BC |        | BC   |        | K <sub>td</sub> |      | K  |      | TI 1 |      | TI 10 |      |
| 8    | 10 | 1  | 52.46 | 8  | 89.05 | 22 | 2.14 | 14       | 100.00 | 8    | 174.44 | 33              | 6.93 | 3  | 9.98 | 8    | 3.87 | 3     | 2.94 |
| 18   | 9  | 22 | 52.46 | 22 | 71.13 | 18 | 2.12 | 15       | 100.00 | 22   | 155.61 | 19              | 3.88 | 2  | 7.66 | 3    | 2.50 | 8     | 2.33 |
| 22   | 9  | 2  | 51.61 | 6  | 59.10 | 8  | 2.09 | 17       | 100.00 | 6    | 124.75 | 30              | 3.27 | 1  | 7.16 | 22   | 2.11 | 7     | 1.89 |
| 1    | 8  | 13 | 50.79 | 18 | 55.05 | 1  | 2.09 | 20       | 100.00 | 18   | 119.57 | 10              | 2.33 | 8  | 7.01 | 7    | 1.77 | 2     | 1.84 |
| 2    | 8  | 7  | 50.00 | 1  | 44.88 | 13 | 2.08 | 21       | 100.00 | 3    | 86.64  | 7               | 2.27 | 33 | 6.93 | 15   | 1.67 | 22    | 1.78 |
| 7    | 8  | 11 | 49.23 | 13 | 38.34 | 2  | 2.08 | 25       | 100.00 | 7    | 79.29  | 32              | 2.23 | 7  | 6.38 | 18   | 1.59 | 1     | 1.69 |
| 11   | 8  | 18 | 49.23 | 7  | 37.85 | 7  | 2.07 | 26       | 100.00 | 1    | 75.08  | 26              | 1.60 | 19 | 4.13 | 14   | 1.55 | 18    | 1.41 |
| 13   | 8  | 23 | 49.23 | 2  | 29.58 | 11 | 2.07 | 28       | 100.00 | 11   | 67.11  | 27              | 1.50 | 30 | 3.27 | 2    | 1.50 | 15    | 1.38 |
| 6    | 7  | 8  | 47.76 | 19 | 29.09 | 19 | 2.00 | 29       | 100.00 | 2    | 65.73  | 17              | 1.20 | 22 | 3.23 | 19   | 1.42 | 19    | 1.35 |
| 14   | 7  | 6  | 47.06 | 27 | 26.09 | 23 | 2.00 | 3        | 100.00 | 27   | 61.23  | 9               | 1.05 | 5  | 2.70 | 1    | 1.33 | 23    | 1.34 |
| 15   | 7  | 19 | 47.06 | 14 | 25.83 | 14 | 1.92 | 27       | 93.33  | 19   | 60.00  | 6               | 1.00 | 6  | 2.70 | 17   | 1.20 | 14    | 1.22 |
| 19   | 7  | 32 | 46.38 | 33 | 24.86 | 15 | 1.91 | 18       | 91.67  | 15   | 55.66  | 8               | 0.92 | 10 | 2.33 | 23   | 1.17 | 17    | 1.15 |
| 23   | 7  | 33 | 46.38 | 23 | 24.42 | 6  | 1.90 | 33       | 90.00  | 33   | 51.78  | 11              | 0.92 | 32 | 2.23 | 6    | 1.17 | 33    | 1.09 |
| 12   | 6  | 27 | 45.71 | 11 | 23.70 | 12 | 1.89 | 6        | 88.10  | 32   | 51.11  | 12              | 0.92 | 15 | 1.97 | 33   | 1.13 | 27    | 0.98 |
| 27   | 6  | 14 | 45.07 | 15 | 22.85 | 27 | 1.87 | 22       | 87.50  | 23   | 49.71  | 13              | 0.92 | 18 | 1.88 | 27   | 0.93 | 12    | 0.95 |
| 3    | 5  | 12 | 44.44 | 32 | 22.42 | 33 | 1.75 | 16       | 83.33  | 14   | 46.21  | 28              | 0.70 | 27 | 1.83 | 32   | 0.83 | 9     | 0.88 |
| 32   | 5  | 15 | 43.24 | 25 | 18.60 | 32 | 1.74 | 32       | 81.00  | 25   | 42.82  | 25              | 0.64 | 14 | 1.72 | 9    | 0.80 | 30    | 0.85 |
| 33   | 5  | 25 | 42.11 | 3  | 18.23 | 3  | 1.68 | 23       | 76.19  | 17   | 36.58  | 29              | 0.64 | 26 | 1.60 | 30   | 0.75 | 16    | 0.80 |
| 9    | 4  | 28 | 41.56 | 4  | 16.27 | 25 | 1.62 | 8        | 68.33  | 12   | 36.36  | 22              | 0.54 | 9  | 1.55 | 12   | 0.74 | 11    | 0.79 |
| 16   | 4  | 30 | 40.51 | 12 | 14.79 | 26 | 1.60 | 30       | 66.67  | 13   | 31.77  | 23              | 0.54 | 12 | 1.42 | 10   | 0.57 | 6     | 0.77 |
| 25   | 4  | 4  | 40.00 | 28 | 7.11  | 16 | 1.60 | 4        | 66.67  | 16   | 28.31  | 20              | 0.27 | 23 | 1.38 | 26   | 0.52 | 32    | 0.67 |
| 26   | 4  | 16 | 40.00 | 16 | 6.56  | 9  | 1.51 | 19       | 64.29  | 28   | 19.02  | 21              | 0.27 | 17 | 1.20 | 4    | 0.50 | 13    | 0.63 |
| 4    | 3  | 26 | 39.51 | 26 | 5.51  | 30 | 1.41 | 1        | 51.19  | 4    | 15.99  | 24              | 0.27 | 11 | 1.17 | 5    | 0.50 | 10    | 0.61 |
| 28   | 3  | 9  | 39.02 | 9  | 5.16  | 28 | 1.41 | 13       | 51.19  | 26   | 15.37  | 31              | 0.26 | 13 | 0.92 | 11   | 0.49 | 26    | 0.58 |
| 29   | 3  | 31 | 38.55 | 20 | 2.75  | 29 | 1.38 | 12       | 45.56  | 9    | 10.11  | 14              | 0.20 | 16 | 0.72 | 16   | 0.43 | 4     | 0.57 |
| 30   | 3  | 20 | 38.10 | 30 | 2.45  | 4  | 1.32 | 2        | 42.26  | 20   | 5.50   | 15              | 0.20 | 28 | 0.70 | 13   | 0.37 | 21    | 0.43 |
| 10   | 2  | 3  | 37.65 | 17 | 2.08  | 20 | 1.13 | 7        | 37.32  | 30   | 5.16   | 16              | 0.20 | 25 | 0.64 | 31   | 0.33 | 5     | 0.40 |
| 17   | 2  | 21 | 37.21 | 21 | 1.39  | 21 | 1.11 | 11       | 28.39  | 21   | 2.86   | 18              | 0.20 | 29 | 0.64 | 21   | 0.32 | 28    | 0.38 |
| 20   | 2  | 29 | 35.56 | 29 | 0.87  | 31 | 1.09 | 9        | 16.67  | 29   | 2.26   | 1               | 0    | 21 | 0.52 | 28   | 0.27 | 29    | 0.35 |
| 21   | 2  | 10 | 32.99 | 5  | 0     | 10 | 1.05 | 10       | 0      | 5    | 0      | 2               | 0    | 31 | 0.51 | 29   | 0.27 | 25    | 0.35 |
| 31   | 2  | 17 | 32.99 | 10 | 0     | 17 | 1.01 | 31       | 0      | 10   | 0      | 3               | 0    | 4  | 0.50 | 25   | 0.27 | 31    | 0.32 |
| 5    | 1  | 24 | 32.65 | 24 | 0     | 24 | 0.71 | 5        | -      | 24   | 0      | 4               | 0    | 20 | 0.27 | 24   | 0.07 | 24    | 0.16 |
| 24   | 1  | 5  | 32.32 | 31 | 0     | 5  | 0.68 | 24       | -      | 31   | 0      | 5               | 0    | 24 | 0.27 | 20   | 0.07 | 20    | 0.16 |

| TDUW |      | TDSU  |      |       |      | TDSS |      | TDSW  |      |     |      |       |      |     |      |
|------|------|-------|------|-------|------|------|------|-------|------|-----|------|-------|------|-----|------|
| TI 1 |      | TI 10 |      | IMA 1 |      | IMA  |      | IMA 1 |      | IMA |      | IMA 1 |      | IMA |      |
| 8    | 6.76 | 3     | 6.03 | 8     | 4.97 | 3    | 4.88 | 8     | 4.86 | 3   | 6.98 | 8     | 5.91 | 8   | 7.28 |
| 3    | 4.29 | 1     | 4.57 | 3     | 4.50 | 8    | 3.65 | 3     | 3.61 | 8   | 5.07 | 3     | 4.63 | 3   | 6.76 |
| 14   | 3.72 | 8     | 4.36 | 7     | 2.93 | 19   | 2.98 | 14    | 2.89 | 1   | 3.17 | 14    | 3.58 | 1   | 5.90 |
| 1    | 3.62 | 7     | 3.58 | 22    | 2.78 | 33   | 2.72 | 22    | 1.99 | 14  | 3.16 | 1     | 2.75 | 14  | 3.85 |

Appendix A (Continued)

|    | TDUW |    | TI 10 |    | TDSU  |    | IMA  |    | TDSS  |    | IMA   |    | TDSW  |    | IMA   |  |
|----|------|----|-------|----|-------|----|------|----|-------|----|-------|----|-------|----|-------|--|
|    | TI 1 |    | TI 10 |    | IMA 1 |    | IMA  |    | IMA 1 |    | IMA   |    | IMA 1 |    | IMA   |  |
| 22 | 2.40 | 14 | 3.36  | 2  | 2.66  | 1  | 2.71 | 1  | 1.63  | 22 | 2.05  | 22 | 2.45  | 22 | 2.57  |  |
| 7  | 1.87 | 6  | 2.40  | 19 | 2.58  | 2  | 2.68 | 6  | 1.23  | 9  | 1.94  | 7  | 1.37  | 16 | 1.52  |  |
| 6  | 1.37 | 16 | 1.37  | 1  | 2.34  | 22 | 2.49 | 19 | 1.19  | 7  | 1.52  | 6  | 1.29  | 7  | 1.35  |  |
| 15 | 1.18 | 5  | 1.27  | 33 | 2.00  | 7  | 2.47 | 23 | 1.02  | 5  | 1.35  | 15 | 1.15  | 9  | 1.31  |  |
| 17 | 1.12 | 17 | 1.14  | 15 | 1.82  | 30 | 2.12 | 5  | 1.00  | 6  | 1.32  | 5  | 1.00  | 6  | 1.23  |  |
| 16 | 0.97 | 9  | 1.12  | 18 | 1.73  | 23 | 2.09 | 9  | 0.87  | 19 | 1.31  | 23 | 0.87  | 15 | 1.22  |  |
| 23 | 0.87 | 15 | 0.62  | 32 | 1.67  | 18 | 2.06 | 27 | 0.85  | 23 | 1.04  | 16 | 0.77  | 5  | 1.15  |  |
| 19 | 0.69 | 22 | 0.52  | 14 | 1.65  | 15 | 1.85 | 15 | 0.75  | 15 | 1.02  | 19 | 0.67  | 17 | 0.95  |  |
| 27 | 0.63 | 4  | 0.42  | 27 | 1.54  | 32 | 1.77 | 18 | 0.60  | 27 | 0.89  | 27 | 0.63  | 23 | 0.92  |  |
| 9  | 0.62 | 19 | 0.37  | 30 | 1.50  | 14 | 1.69 | 7  | 0.58  | 18 | 0.76  | 18 | 0.55  | 19 | 0.79  |  |
| 18 | 0.59 | 18 | 0.37  | 6  | 1.33  | 17 | 1.63 | 4  | 0.50  | 4  | 0.56  | 9  | 0.54  | 27 | 0.68  |  |
| 5  | 0.58 | 11 | 0.30  | 23 | 1.24  | 27 | 1.58 | 12 | 0.29  | 16 | 0.55  | 17 | 0.45  | 18 | 0.64  |  |
| 4  | 0.38 | 13 | 0.27  | 17 | 1.20  | 26 | 1.56 | 16 | 0.28  | 11 | 0.46  | 4  | 0.38  | 4  | 0.62  |  |
| 31 | 0.24 | 10 | 0.23  | 10 | 1.14  | 12 | 1.51 | 11 | 0.25  | 2  | 0.39  | 31 | 0.24  | 31 | 0.33  |  |
| 12 | 0.21 | 12 | 0.17  | 26 | 1.03  | 9  | 1.50 | 2  | 0.21  | 12 | 0.31  | 12 | 0.16  | 11 | 0.23  |  |
| 11 | 0.21 | 2  | 0.17  | 5  | 1.00  | 10 | 1.45 | 31 | 0.13  | 17 | 0.24  | 32 | 0.13  | 12 | 0.22  |  |
| 2  | 0.14 | 23 | 0.14  | 9  | 0.97  | 6  | 1.36 | 17 | 0.12  | 31 | 0.21  | 2  | 0.11  | 2  | 0.21  |  |
| 32 | 0.13 | 27 | 0.09  | 12 | 0.88  | 16 | 1.32 | 10 | 0.11  | 33 | 0.17  | 11 | 0.11  | 10 | 0.20  |  |
| 10 | 0.12 | 31 | 0.06  | 11 | 0.64  | 11 | 1.31 | 32 | 0.09  | 32 | 0.17  | 10 | 0.10  | 32 | 0.18  |  |
| 33 | 0.10 | 32 | 0.03  | 16 | 0.57  | 5  | 1.25 | 33 | 0.09  | 10 | 0.15  | 33 | 0.09  | 33 | 0.17  |  |
| 13 | 0.10 | 33 | 0.03  | 28 | 0.53  | 13 | 1.17 | 30 | 0.06  | 30 | 0.10  | 30 | 0.05  | 13 | 0.13  |  |
| 30 | 0.05 | 28 | 0.01  | 29 | 0.53  | 21 | 1.04 | 13 | 0.01  | 28 | 0.03  | 13 | 0.03  | 30 | 0.08  |  |
| 28 | 0.01 | 30 | 0.01  | 25 | 0.53  | 28 | 1.02 | 26 | 0.01  | 13 | 0.03  | 28 | 0.01  | 28 | 0.04  |  |
| 26 | 0.01 | 29 | 0.01  | 4  | 0.50  | 4  | 0.95 | 28 | 0.01  | 26 | 0.02  | 29 | 0.01  | 29 | 0.02  |  |
| 29 | 0.01 | 21 | 0.01  | 13 | 0.47  | 31 | 0.86 | 29 | 0.01  | 29 | 0.01  | 26 | 0.01  | 21 | 0.01  |  |
| 21 | 0.01 | 26 | 0.003 | 31 | 0.42  | 29 | 0.84 | 21 | 0.01  | 21 | 0.01  | 21 | 0.01  | 26 | 0.01  |  |
| 20 | 0    | 20 | 0     | 21 | 0.39  | 25 | 0.84 | 20 | 0     | 20 | 0.002 | 20 | 0     | 20 | 0.001 |  |
| 24 | 0    | 24 | 0     | 24 | 0.14  | 24 | 0.56 | 24 | 0     | 24 | 0.002 | 24 | 0     | 24 | 0.001 |  |
| 25 | 0    | 25 | 0     | 20 | 0.14  | 20 | 0.55 | 25 | 0     | 25 | 0.001 | 25 | 0     | 25 | 0     |  |

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