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Architectural classes of aquatic food webs based on link distribution

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Abstract. Link distribution is an important architectural feature of ecological networks, since it is thought to influence community dynamics. Several attempts have been made in order to characterize the typical link distribution of food webs, but the number of webs studied thus far is low and their quality is unbalanced. Comparability is a rarely asked methodological question, and as far as we see only two data bases are available which allow reliable comparison of food webs: one for terrestrial, high resolution, host-parasitoid webs and another for highly aggregated, marine trophic networks. We present an analysis of a set of food webs belonging to the latter type, since the host-parasitoid networks are only subgraphs and therefore uninformative on the structure of the entire community. We address the following three questions: (1) how to characterize the link distribution of these small networks which cannot always be fitted statistically to well-known distributions (such as the exponential or the Poisson, etc.), (2) are these distributions of more or less similar shape or they belong to different „architectural classes", and (3) if there are different classes, then what are their distinctive topological and biological properties. We suggest that link distribution of such small networks can be compared to each other by principal coordinates ordination and clustering. We conclude that (1) the webs can be categorized into two different classes, and (2) one of the classes contains significantly larger and topologically more heterogeneous webs for which net output of material is also of higher variance. We emphasize that link distribution is an interesting and important property not only in case of complex, speciose food webs, but also in highly aggregated, low-resolution webs.

Abbreviations: DOC – Dissolved Organic Carbon, NO CV – Coefficient of Variation of Net Output Values, PCA – Principal Components Analysis, PCoA – Principal Coordinates Analysis, POC – Particulate Organic Carbon.

Introduction

Comparative analyses of food webs synthesize results for population, community and ecosystem levels and are therefore applicable to seek unifying ecological principles. This question has long attracted interest in ecological research (Briand 1983, Cohen 1978, Cohen et al. 1990) and current studies are no exception (e.g., Dunne et al. 2002, Solé and Montoya 2001, Williams et al. 2002). A fundamental problem of comparative analyses is to find a common logical basis of comparison regarding field methods of data collection and subsequent network construction by aggregation. Without methodological standardization, the results may be strongly biased so that the conclusions drawn are frequently misleading and irrelevant. For instance, it is unreasonable to compare a network of highly aggregated functional groups with a web that includes only species or genera. Furthermore, it seems illogical to look for generalities in a set of food webs containing both *community* and *sink* webs (*sensu* Cohen 1978). Methodological standardization is difficult to achieve, however, and only a few noted examples represent the appropriate comparative approach. Baird and Ulanowicz (1989) and Ulanowicz (1996) compared seasonally and spatially different food webs, respectively, that were described in the same way. In most other cases, the methodology of food web studies is still highly subjective and is restricted to the qualitative aspects only.

To our best knowledge, two data bases representing comparable food webs are available, both in state of continuous expansion. The first one summarizes a set of host-parasitoid communities described from temperate and tropical territories (Müller et al. 1999). In these, the vertices of the food web graph are almost always species. The second set comprises food web data from aquatic environments (both marine habitats and estuaries, lakes, rivers are included) compiled following the standards of the EcoPath and EcoSim procedures (Christensen and Pauly 1992, Pauly et al. 2000). These are highly aggregated networks containing components such as „phytoplankton" or „benthic invertebrates". We note that some, much smaller data sets presenting comparable food webs also exist (de Ruiter et al. 1995, Kitching 2000) and it is also possible to compare differently aggregated versions of the same food web (Jordán 2003, Jávor et al. 2005).

A seminal paper by Cohen et al. (1993) gave the impression for many ecologists that old-fashioned and imprecise food webs are being replaced by updated and more perfect ones. Extensive field work allowed increasing the accuracy of food webs (Goldwasser and Roughgarden 1993, Martinez 1991, Polis 1991) and it is frequently stated that these are „high quality" webs. The „modern webs" are certainly improved in several aspects (e.g., in identifying indirect interactions) but basically it is not the size of a food web that matters. The adequate level of resolution can only be determined after clearly defining the actual problem to be solved. Since ecology is the science of functions and interactions, usually functional groups are in focus rather than species (e.g., Steneck and Dethier 1994). Thus, a simple web describing the relationships between functional groups defined cautiously can be much more helpful, depending on the actual problem, than a complex network of species (Jordán and Scheuring 2002). Arguments against species-level resolution of food webs include difficulities with the species concept in many taxonomic groups (e.g., bacteria or species complexes of higher organisms), the high functional relevance of groups both below (tadpoles and adult frogs feed differently) and above (large desert spiders regardless of species identity eat smaller ones) the species level, and other functional aspects (for modelling energetics, low-resolution webs are satisfactory). Larger (higher resolution) food webs are therefore not necessarily better than the small (more aggregated) ones. Consequently, there are no "good" food webs in the general sense: the only choice is to study comparable webs even if they are highly aggregated. If food web theory needs to be improved, then the comparative approach has to be strengthened by a methodologically robust definition of comparability.

Comparative studies may reveal fundamental architectural properties of food webs. Recently, nodal degree and its distribution (link distribution) have been the most intensively studied local and global topological properties of networks that are not necessarily ecological (e.g., Newman 2003). However, the results coming from such analyses are highly sensitive to field methodology, aggregation procedure and possible data transformation (cf. the re-analysis of networks already studied, compare the variants of the Chesapeake Bay network in Baird and Ulanowicz 1989, Baird et al. 1991, and Dunne et al. 2002, all authors providing different link distribution patterns). Of the food webs whose link distributions have been studied recently (and found to be exponential, scale-free and uniform by Dunne et al. 2002, and scale-free by Montoya and Solé 2002), the Chesapeake Bay food web is the only „large and complex" network with comparable counterparts in the literature. Our objective is to provide a meta-analysis of many, recently described, comparable food webs. Note that the other available sets of comparable webs, i.e., host-parasitoid networks, are not suitable for studying link distributions due to the „subcommunity" property: these networks are bipartite graphs representing interactions between two sets of animals (i.e., hosts and parasitoids) and their analyses cannot be informative on other types of webs.

Data

We screened recent issues of relevant journals that usually publish web data (e.g., Ecological Modelling) and a conference proceedings volume (Christensen and Pauly 1993). A total of 50 aggregated trophic networks described by similar methods were chosen for the present study. This number is many more than ever used in previous comparative analyses.

Trophic mass balance models consider information on biomass, carbon transfers, respiration and production of compartments represented by trophic flow networks (typically of carbon, but also of nitrogen, Baird et al. 1995, and phosphorus, Ulanowicz and Baird 1999). The methodology of preparing these data for network analysis is highly standard and robust (including the typical names of trophic compartments).

Table 1 shows the name and various structural properties of the 50 networks, while the Appendix presents the references and the link distributions. The latter gives how many (n_i) compartments have links to exactly i other com-

Table 1. Basic information on the food webs studied. Note that in case of 4 webs, net output (and *NO CV)* data were not available. Link distributions are presented in Appendix.

Web no.	Web name	*n*	*NO CV*	D_{max}	*Range*	*Cat*	*Peak*	*Med*	*KNS*
1	Baltic Sea	12	1.57	5	5	5	4	3	0.50
2	Benguela upwelling	22	2.80	15	15	13	3	8	2.33
3	Benguela upwelling, aggr.	14	2.29	10	10	9	3	5	1.67
4	Bolinao Reef	25	2.89	17	16	13	3	7	3.33
5	Brunei Darussalam	12	2.20	10	6	6	3	7	1.00
6	Campeche Bank	18	2.32	18	15	11	3	9	3.00
7	Caribbean Reef	20	1.68	19	14	11	3	12	2.33
8	Celestun lagoon	18	2.47	14	12	10	3	8	2.00
9	Chesapeake Bay	34	2.89	10	10	10	7	4	0.86
10	Chesapeake Bay, aggr.	12	1.56	5	5	5	3	2	1.00
11	Crystal River, control	16	3.95	10	8	7	5	5	1.00
12	Crystal River, stressed	16	3.94	9	9	8	5	3	1.20
13	Ems estuary	12	1.55	6	6	5	4	3	0.75
14	Etang de Thau Lagoon	10	1.47	9	5	4	5	8	0.20
15	French Frigate Schoals	12	2.39	9	9	7	3	4	1.67
16	Garonne River	9	2.59	7	3	3	4	6	0.38
17	Goose Creek Bay	47							
18	Gulf of Mexico	23	2.20	18	16	11	6	11	1.25
19	Gulf of Mexico / aggr.	14	3.05	8	7	7	4	5	0.75
20	Kromme estuary	13	2.33	6	6	5	4	3	0.75
21	Laguna de Bay, no fishpen	14	3.41	10	9	5	4	6	1.00
22	Laguna de Bay, with fishpen	15	3.68	12	12	8	5	5	1.40
23	Lake Aydat, France	10	2.32	10	8	6	3	5	1.67
24	Lake Chad	14	1.85	10	5	5	4	8	0.50
25	Lake George	13	2.95	12	8	5	5	8	0.80
26	Lake Kariba, Africa	9	2.40	5	5	4	3	3	0.67
27	Lake Kinneret, Israel	13	2.34	10	9	8	3	5	1.67
28	Lake Malawi	8	2.35	7	5	5	3	4	1.00
29	Lake Tanganyika	6	2.06	6	3	3	3	5	0.33
30	Lake Turkana	7	2.20	6	6	6	2	3	1.50
31	Lake Victoria	15	2.71	17	11	9	3	10	2.33
32	Malawi pond	9	1.93	4	4	4	3	2	0.67
33	Mandinga Lagoon	19	3.21	13	12	10	5	6	1.40
34	Maputo Bay	9	1.20	7	5	5	3	5	0.83
35	Monterey Bay, CA	15							
36	Ontario Lake	13	2.41	8	6	5	5	4	0.80
37	Peruvian upwelling	13	2.49	7	7	7	3	4	1.00
38	River Thames	10	1.68	8	7	5	5	3	1.00
39	Schlei Fjord	9	2.02	5	5	5	4	4	0.38
40	South China Sea	8	2.80	6	6	5	3	3	1.00
41	Swartkops estuary	12	2.08	5	5	4	7	3	0.29
42	Tamiahua Lagoon	12	3.10	10	8	6	4	7	0.75
43	Tampamachoco lagoon	22	2.90	14	14	12	4	8	1.50
44	Tongoy Bay	23							
45	Veli Lake, India	13	2.54	9	7	6	4	6	0.88
46	Venezuela Shelf	15	2.5	12	10	8	3	8	1.33
47	Venice lagoon	15							
48	wetland ricefield	11	2.81	13	13	7	3	5	2.83
49	Ythan River	11	2.66	4	4	3	7	3	0.14
50	Yucatan Shelf	20	2.91	19	17	9	5	10	1.80

partments in the web, where Σn_i provides n. The largest degree was $i_{max} = 19$ for three compartments. Some compartments had no link to others ($i_{min} = 0$), these were out of our interest, although they do appear in the Appendix (there are 7 nodes with $D = 0$, while we have 735 nodes with $D > 0$). These all are trophic groups consuming inorganic or dead material and not consumed by others. Here, it is important to note that the original networks were slightly but consistently modified: we were interested only in biotic trophic interactions. Thus, „exogeneous input", „energy and nutrients", detritus, POC, DOC and similar non-living compartments were not included in our webs. The explanation of this choice is straightforward. First, if detritus is taken into account, each single compartment will have a link to it (if not disappearing by only respiration and predation) and the resulting highly linked node provides no useful information on network structure. Second, consumption of an organism by another is an interaction remarkably different from the situation in which a dead organism sinks into the detritus pool. In fact, the second one is not an *inter*action. Link distribution studies typically intend to draw conclusions concerning community dynamics and organisation, and from this viewpoint it would be irrelevant and misleading to confuse these kinds of effects (of course, these effects cannot be excluded energetically). All in all, link distributions start at $D = 1$. Self loops were out of interest and were also excluded from this analysis (since we are basically interested in the architecture of interactions betwen components). If an ecosystem was found in two or more alternatives in the literature (and these did not differ seriously in the level of aggregation), we always used the most recent version (e.g., in case of Lake Tanganyika, Christensen and Pauly 1993, pp. 141-142).

Methods

Distributions of the number of vertices per degree differ considerably from one another. Therefore, comparing distributions on the basis of their shapes rather than on their size properties requires standardization and an appropriate dissimilarity function. Each frequency distribution was standardized by the total number of vertices in the corresponding web, to obtain relative frequencies. The dissimilarity of relativized distributions j and k was defined as the Manhattan distance obtained by finding the best fit of the categories in j to those in distribution k. In order to find the optimum match and to output the distances, a simple algorithm was written in FORTRAN. The Manhattan distance matrix of distributions was subjected to ordination by principal coordinates analysis (PCoA) and to numerical classification by complete linkage analysis using the SYN-TAX 2000 software package (see Podani 2001, for details). The results give us some insight regarding the existence of groups or trends among the food webs examined. Ordination scores on the first 2 axes were correlated with six web properties using principal components analysis (PCA) to examine potential explanatory factors affecting the configuration of webs in the PCoA ordination. In this analysis, only 46 webs are represented, because data were incomplete for 4 webs. The two clusters of webs (the so-called architectural classes) were also compared based on biological and geographical variables and a combined index discussed below, using the Mann-Whitney test with ranks.

The architecture of the interaction structure of components was quantified by several topological measures and their combination. These values are given in Table 1. The degree (*D,* number of neighbours) is the simplest and most local property of nodes. In small networks, its distribution can be characterised by a combination of several topological statistics, like its maximum and minimum (D_{max} and D_{min}), its *Range* ($D_{max} - D_{min} + 1$), the number of $D > 1$ categories within the range (*Cat*), the median of the distribution (*Med*), the number of nodes possessing the most frequent degree value (*Peak*) and by the number of nodes, n. In order to identify a particular kind of food web architecture that can be characterised by the presence of structural keystone species, we constructed a combined index, called "keystonedness", defined as $KNS = (D_{max} - Med) / Peak$. *KNS* is high if there is a highly connected node (with a large D_{max}), while most of the others have lower degrees (small *Med*), and the distribution is "flat" (small *Peak* reflecting a relatively even link distribution except for the keystone node). *KNS* can be used either for separating different sets of webs or for looking for correlations between various network properties.

A non-topological measure of functional relevance is the coefficient of variation of net output values (*NO CV*), quantifying the variability of the energy outflow from the components (providing food for others). Other variables examined are the average distance from the Equator (*Lat* for latitude) and salinity (*Salt*, expressed by 1 for marine, 2 for mesohaline and 3 for freshwater systems). These are variables of possible interest at both macroecological and local scales.

Results

Cluster analysis suggests the existence of two „architectural classes" (Figure 1). This separation is at least partly confirmed by the ordination results (Figure 2): networks from group B of the classification are on the left side of the ordination. That separation is not clear-cut on the ordination plane is due to the different explanatory

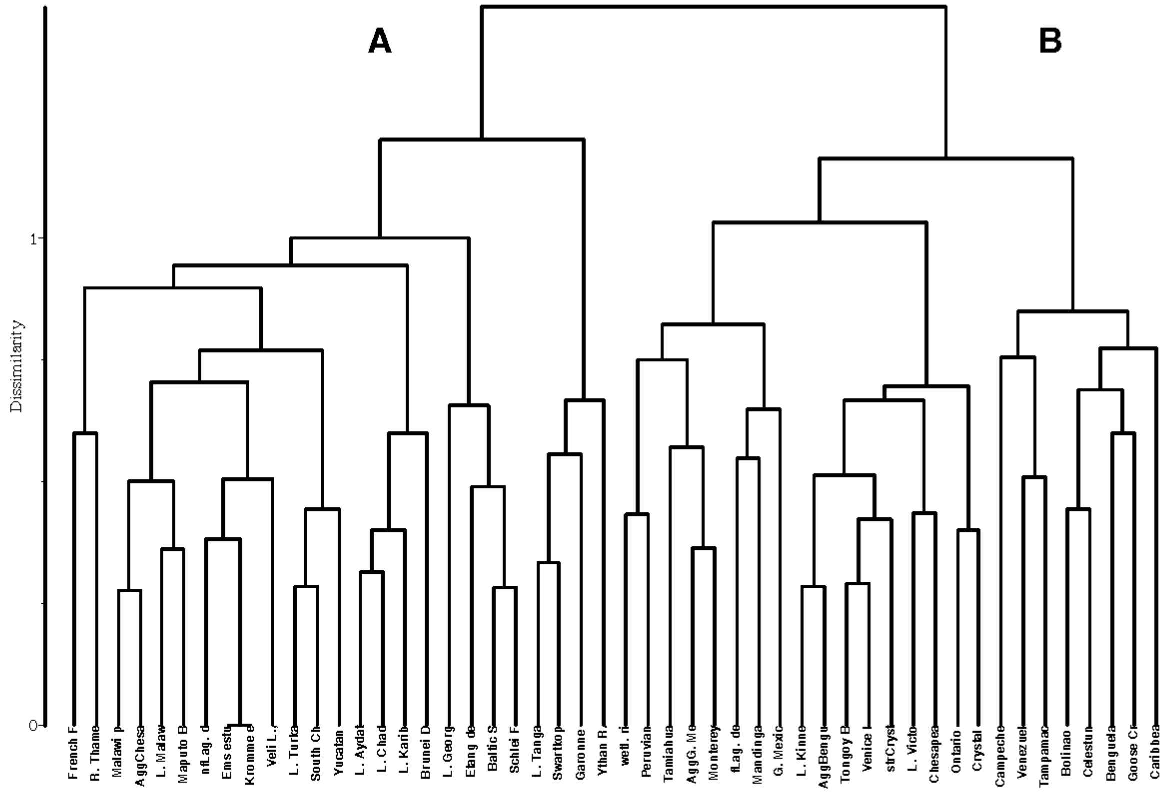

Figure 1. Classification of 50 food webs based on standardized data and Manhattan distances calculated by finding the optimum match for every pair of webs. See text, for the discussion of groups A and B.

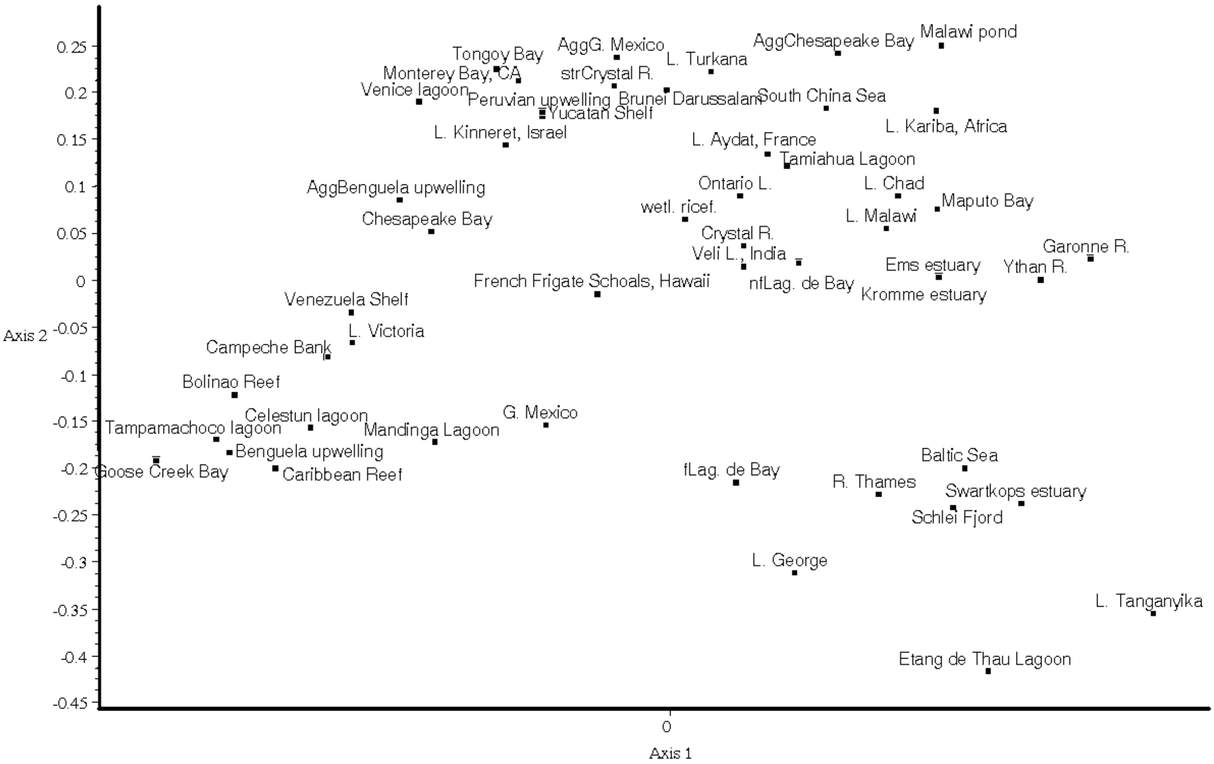

Figure 2. PCoA ordination of 50 food webs based on the same distances used in the classification of Fig. 1.

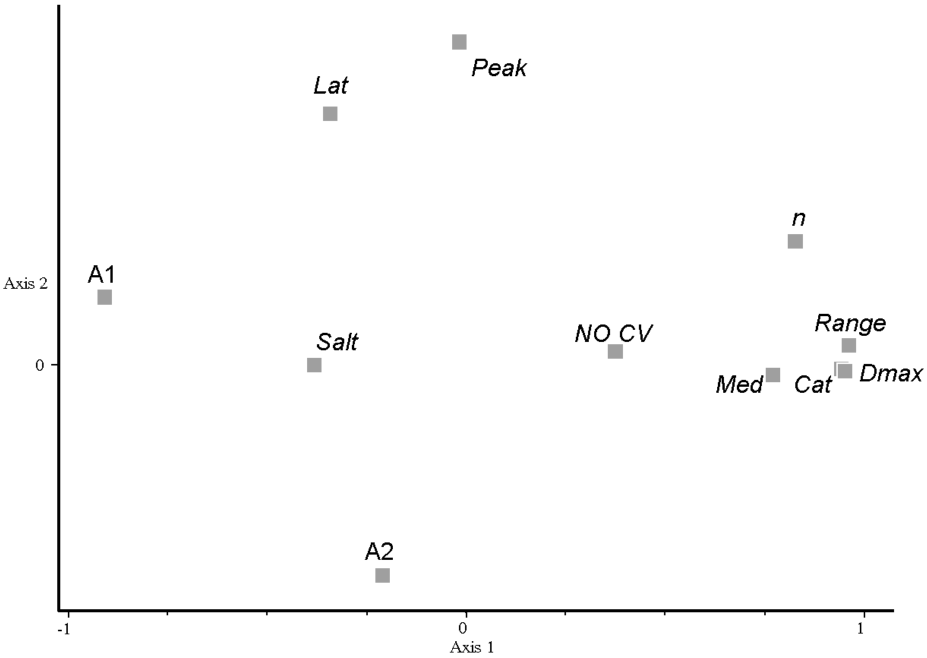

Figure 3. PCA ordination of two PCoA axes (A1: Axis 1 and A2: Axis 2), topological (*Peak, n, D_{max}, Range, Med,* and *Cat*) and non-topological (*Lat, Salt* and *NO CV*) network properties.

power of the two results. Whereas clustering attempts to compress all information in the distances into a single dendrogram, the principal coordinates ordination explains only 18% of the total variation by the first axis (A1), and 9% by the second (A2), thus leaving considerable stochastic variation for the remaining, even less important dimensions.

The two major PCoA ordination dimensions exhibit a clear correlation structure with the six simple topological properties of the networks, as shown by PCA (Fig. 3). D_{max}, *Range*, *Cat* and *n* are highly correlated with one another and are responsible for variation along PCoA axis 1 (D_{max}: -0.7875, *Range*: -0.8538, *Cat*: -0.9424 and *n*: -0.7363, *Med*: -0.5702), whereas *Peak* is correlated with the second PCoA dimension (-0.2862). (The sign does not matter for the positions of PCoA axes, because direction is arbitrary in PCA. Note, also, that *KNS* was not included because it is a combination of three other topological measures.) Thus, these two PCoA axes reflect respectively the horizontal and vertical components determining the shape of the distributions. As for the non-topological properties of the webs, Axis 1 of the PCoA has the following correlations: *Salt* (0.3471), *Lat* (0.3180) and *NO CV* (-0.3203) whereas Axis 2 has the following values: *Salt* (0.3913), *Lat* (-0.1444) and *NO CV* (0.1331).

Although the separation of the two clusters was not sharp, comparison of the two clusters in terms of external and derived variables may give insight into the fundamental properties that affect trends in the distributions. Thus, a crucial question is how are the topological measures related to the non-topological ones. The strongest correlations are: *NO CV* with *Range* (0.3672, the second highest is with *n*: 0.3563), *Salt* with *Cat* (-0.3926, the second highest is with *Range*: -0.3489) and *Lat* with *Peak* (0.3917, the second highest is with *Med*: -0.3666). The two groups of webs differ significantly in the coefficient of variation for net outputs (*NO CV*, Mann-Whitney test, p = 0.001285). This is higher in group B of Figure 1. If network heterogeneity is measured by the newly introduced keystonedness index (*KNS*), we again find significant difference (Mann-Whitney test, p = 0.000186), suggesting that group B (Figure 1) contains more keystone-like webs. *KNS* is typically larger for higher *NO CV* webs, independently of the classification (Figure 4). The average distance from the Equator and salinity did not differ significantly between the two groups. This is in good agreement with the PCA, because they have low scores on PCA axis 1.

Discussion

We were interested in how the general architectural properties of classes of fifty comparable food webs are related to certain characteristics of the ecological systems they represent. Classes of food webs can be defined based on the typical „shape” of degree distribution, although separation of these classes is not sharp. Because of the small size of the networks, it was not possible to fit these distributions statistically to standard reference distributions (such as exponential, normal or Poisson). Neverthe-

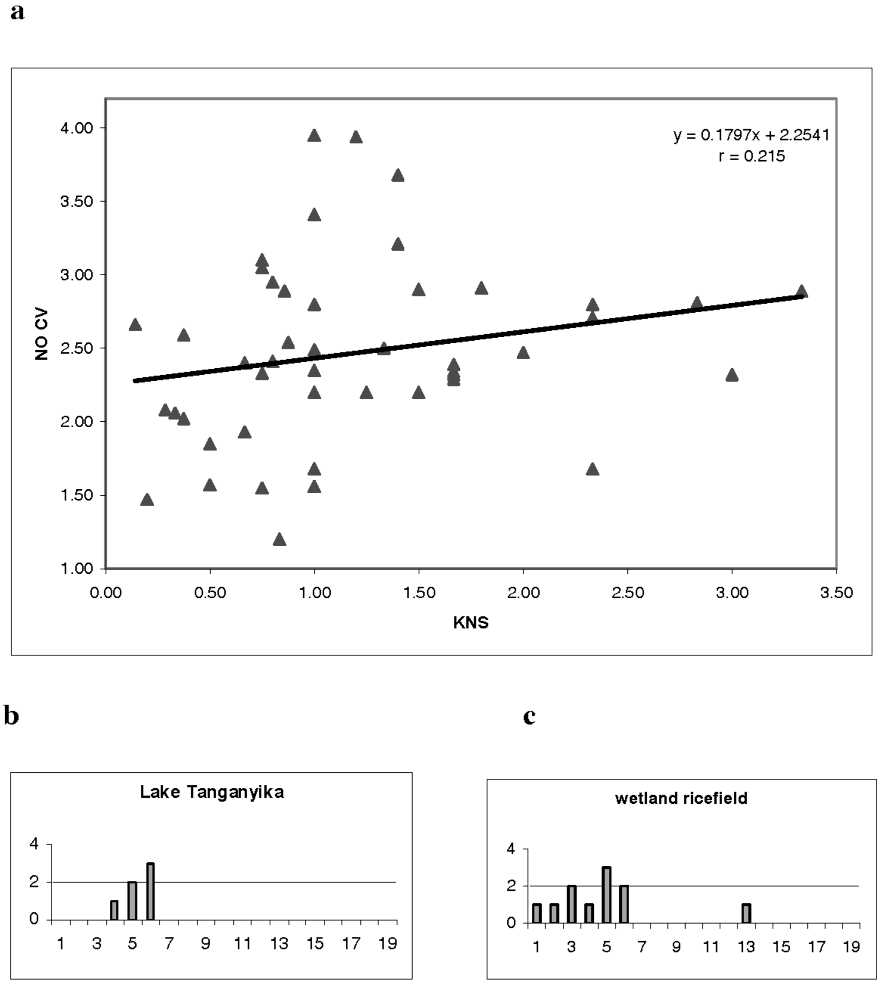

Figure 4. a. Relationship between network „keystonedness” (*KNS*) measuring structure and the coefficient of variation for net output values (*NO CV*) characterising function. **b**. A link distribution without nodes of extremely high degree (*KNS* = 0.33). **c.** An example for a link distribution in which one node has outstanding degree and the others have more or less uniform, smaller *D* values (*KNS* = 2.83). The node with *D* = 13 is a candidate topological keystone species (or trophic component).

less, they provided sufficient information to characterize link distribution patterns in terms of similar shape. We have to emphasize that our results are sensitive to aggregation level and are valid probably for webs made at similar levels of aggregation (but cf. Dunne et al. 2002). Important ecological problems have to be approached by selecting the adequate level of aggregation in food webs: here we do not attempt to reveal findings about species interactions represented in high resolution food webs aggregated only slightly but provide a statistically robust description of the architecture of low-resolution, highly aggregated food webs.

The classification and ordination of food webs were based on optimized distances, and the two main PCoA dimensions were correlated with the topological properties. Since the distributions were standardized before PCoA, this result is not a trivial consequence of absolute differences among the networks but it does reflect underlying properties. It is also interesting to note that the separation of the two groups can be explained by two independent properties as well, such as *KNS* and *NO CV*, i.e., structural and functional heterogeneity, respectively. In the group where the webs are typically characterised by structural hubs (the presence of outstandingly connected nodes), the variability of the net output of material flows is also higher. At the global level (entire food web), this is a parallel between structure and function, independently of the possibility of local level (species or trophic component) correlations. This might suggest that a topological analysis gives probably more realistic results than thought before (see also Jordán et al. 2002, 2003). We emphasise that robust results provided by meta-analyses are valuable only if the data sets are comparable, i.e., methodologically homogeneous.

Distance from the equator (*Lat*) and salinity (*Salt*) are not reflected in network shape. We note that there are no clear macroecological theories explaining how salinity or latitude is correlated with food web structure. However, case studies of more local nature are abundant for both salinity (effect on phytoplankton: Lionard et al. 2005, on microorganisms: Pedros-Alio et al. 2000; on invertebrates: Herbst 2001) and latitude (effect on protozoa and bacteria: Buckley et al. 2003, on herbivore fish: Pauly, manuscript).

Finally, although many types of networks, including food webs, have recently been found to have scale-free properties (e.g., Strogatz 2001), our results suggest that aquatic food webs at the present level of aggregation do not follow the power law. Examination of the distributions themselves indicate that they are mostly of unimodal shape and are far from the very asymmetric shapes, suggesting either the absence of the scale free property or its sensitivity to aggregation (cf. Dunne et al. 2002).

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References

Baird, D. and Ulanowicz, R. E. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* 59:329-364.

Baird, D., McGlade, J. M. and Ulanowicz, R. E. 1991. The comparative ecology of six marine ecosystems. *Philosophical Transactions of the Royal Society, London, series B* 333:15-29.

Baird, D. and Ulanowicz, R. E. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Marine Ecology Progress Series* 99:221-237.

Baird, D., Ulanowicz, R. E. and Boynton, W. R. 1995. Seasonal nitrogen dynamics in Chesapeake Bay: a network approach. *Estuarine, Coastal and Shelf Science* 41:137-162.

Briand, F. 1983. Environmental control of food web structure. *Ecology* 64: 253-263.

Buckley, H. L., Miller, T. E., Ellison, A. M. and Gotelli, N. J. 2003. Reverese latitudinal trends in species richness of pitcher-plant food webs. *Ecology Letters* 6: 825-829.

Carrer, S. and Opitz, S. 1999. Trophic network model of a shallow water area in the northern part of the Lagoon of Venice. *Ecological Modelling* 124:193-219.

Christensen, V. 1995. Ecosystem maturity – towards quantification. *Ecological Modelling* 77:3-32.

Christensen, V. and Pauly, D. 1992. ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61:169-185.

Christensen, V. and Pauly, D. (eds.) 1993. *Trophic Models of Aquatic Ecosystems.* ICLARM Conf. Proc. 26, 390 p.

Christian, R. R. and Luczkovich J. J. 1999. Organising and understanding a winter's seagrass foodweb network through effective trophic levels. *Ecological Modelling* 117:99-124.

Cohen, J. E. 1978. *Food Webs and Niche Space.* Princeton Univ. Press, Princeton.

Cohen, J. E., Briand, F. and Newman, C. M. 1990. *Community Food Webs: Data and Theory*. Springer Verlag, Berlin.

Cohen, J. E., Beaver, R. A., Cousins, S. H., De Angelis, D. L., Goldwasser, L., Heong, K. L., Holt, R. D., Kohn, A. J., Lawton, J. H., Martinez, N. D., O'Malley, R., Page, L. M., Patten, B. C., Pimm, S. L., Polis, G. A., Rejmánek, M., Schoener, T. W., Schoenly, K., Sprules, W. G., Teal, J. M., Ulanowicz, R. E., Warren, P. H., Wilbur, H. M. and Yodzis, P. 1993. Improving food webs. *Ecology* 74:252-258.

De Ruiter, P. C. et al. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269: 1257-1260.

Dunne, J. A., Williams, R. J. and Martinez, N. D. 2002 Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5:558-567.

Goldwasser, L. and Roughgarden, J. 1993. Construction and analysis of a large Caribbean food web. *Ecology* 74:1216-1233.

Herbst, D. B. 2001. Salinity-dependent changes in the organization of aquatic food webs in salt evaporation ponds in the Mojave Desert. ESA Annual Meeting, Abstract Volume, #0709.

Heymans, J. J. and Baird, D. 2000. A carbon flow model and network analysis of the northern Benguela upwelling system, Namibia. *Ecological Modelling* 126:9-32.

Jávor, B., Jordán, F. and Török, J. 2005. A comparative sink web analysis of two birds in two habitats: trophic structure, functionality, aggregation and system-level indication. *Community Ecology* 6:13-22.

Jordán, F. 2003. On the functional trophic height of whiting. *Ecological Indicators* 3:223-225.

Jordán, F., Scheuring, I. and Vida, G. 2002. Species positions and extinction dynamics in simple food webs. *Journal of Theoretical Biology* 215:441-448.

Jordán, F. and Scheuring, I. 2002. Searching for keystones in ecological networks. *Oikos* 99:607-612.

Jordán, F., Scheuring, I. and Molnár, I. 2003. Persistence and flow reliability in simple food webs. *Ecological Modelling* 161:117-124.

Kitching, R. L. 2000. *Food Webs and Container Habitats.* Cambridge University Press, Cambridge.

Lionard, M., Muylaert, K., Van Gansbeke, D. and Vyverman, W. 2005. Influence of changes in salinity and light intensity on growth of phytoplankton communities from the Schelde river and estuary (Belgium/The Netherlands). *Hydrobiologia* 540: 105-115.

Martinez, N. D. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs* 61: 367-392.

Montoya, J. M. and Solé, R. V. 2002. Small world patterns in food webs. *Journal of Theoretical Biology* 214:405-412.

Müller, C. B., Adriaanse, I. C. T., Belshaw, R. and Godfray, H. C. J. 1999. The structure of an aphid-parasitoid community. *J. Anim. Ecol.* 68: 346-370.

Newman, M. E. J. 2003. Ego-centered networks and the ripple effect. *Social Networks* 25: 83-95.

Ortiz, M. and Wolff, M. 2002. Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios. *Ecological Modelling* 148:277-291.

Pauly, D., Christensen, V. and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci.* 57:697-706.

Pedros-Alio, C., Calderon-Paz, J. I., MacLean, M. H., Medina, G., Marrase, C., Gasol, J. M. and Guixa-Boixereu, N. 2000. The microbial food web along salinity gradients. *FEMS Microbiol. Ecology* 32: 143-155.

Podani, J. 2001. *SYN-TAX 2000. User's Manual.* Scientia, Budapest.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* 138: 123-155.

Rosado-Solórzano, R. and Guzmán del Próo, S. A. 1998. Preliminary trophic structure model for Tampamachoco lagoon, Veracruz, Mexico. Ecological Modelling 109:141-154.

Solé, R. V. and Montoya, J. M. 2001. Complexity and fragility in ecological networks. *Proc. Roy. Soc. L. B* 268: 2039-2045.

Steneck, R. S. and Dethier, M. N. 1994. A functional group approach to the structure of algal- dominated communities. *Oikos* 69: 476-498.

Strogatz, S. H. 2001. Exploring complex networks. *Nature* 410: 268-276.

Ulanowicz, R. E. 1996. Trophic flow networks as indicators of ecosystem stress. In: Polis, G. A. and Winemiller, K. O. (eds.) *Food Webs: Integration of Patterns and Dynamics.* Chapman and Hall, London. pp. 358-368.

Ulanowicz, R. E. and Baird, D. 1999. Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community. *Journal of Marine Systems* 19:159-172.

Vega-Cendejas, M. E. and Arreguín-Sánchez, F. 2001. Energy fluxes in a mangrove ecosystem from a coastal lagoon in Yucatan Peninsula, Mexico. *Ecological Modelling* 137:119-133.

Walters, C. J., Christensen, V. and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass balance assessments. *Reviews in Fish Biology and Fisheries* 7:139-172.

Williams, R. J., Berlow, E. L., Dunne, J. A., Barabási, A.-L. and Martinez, N. D. 2002. Two degrees of separation in complex food webs. *Proc. Natl. Acad. Sci. USA* 99: 12913-12916.

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Appendix

Degree distribution data and references

The original references for the food webs studied and the degree-vectors for each web. A degree vector shows the number of nodes with the degree value given at the top. Names of webs are given in Table 1. The seven nodes with $D = 0$ remaining after deleting the non-living trophic components were excluded form the analyses, but are shown here for completeness.

		Degree																			
Web No.	References	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Baird et al. (1991)	1	1	1	4	4	1														
2	Heymans and Baird (2000)	1	1	2	1	0	2	1	2	2	3	0	2	2	1	1	1				
3	Baird et al. (1991)	0	1	0	2	2	3	1	1	2	1	1									
4	Christensen and Pauly (1993), p.256	1	0	3	1	1	2	3	3	2	3	2	1	1	1	0	0	0	1		
5	Christensen and Pauly (1993), p.304	0	0	0	0	0	1	3	2	2	1	3									
6	Christensen and Pauly (1993), p.210	0	0	0	0	1	1	3	2	1	3	1	0	1	0	2	2	0	0	1	
7	Christensen and Pauly (1993), p.265	0	0	0	0	0	0	3	1	0	1	3	1	1	2	3	2	0	1	0	2
8	Christensen and Pauly (1993), p.190	0	0	0	3	1	1	1	2	3	2	2	0	0	2	1					
9	Baird and Ulanowicz, R.E. (1989)	0	3	7	6	5	1	3	4	1	2	2									
10	Baird et al. (1991)	0	3	3	2	3	1														
11	Ulanowicz (1996)	1	0	0	2	1	5	3	2	0	1	1									
12	Ulanowicz (1996)	1	1	5	2	3	1	1	1	0	1										
13	Baird et al. (1991)	0	2	2	4	3	0	1													
14	Christensen and Pauly (1993), p.228	0	0	0	0	0	1	1	0	3	5										
15	Christensen and Pauly (1993), p.7	0	1	0	2	3	2	1	1	0	2										
16	Christensen and Pauly (1993), p.178	0	0	0	0	0	4	1	4												
17	Christian and Luczkovich (1999)	0	0	3	3	5	3	3	3	5	5	3	2	1	2	2	1	3	0	3	
18	Christensen and Pauly (1993), p.202	0	0	0	1	0	1	2	0	1	1	5	6	1	2	2	0	0	0	1	
19	Christensen and Pauly (1993), p.281	0	0	1	3	1	4	1	1	3											
20	Baird and Ulanowicz, R.E. (1993)	1	2	2	4	3	0	1													
21	Christensen and Pauly (1993), p.82	0	0	1	0	2	3	4	3	0	0	1									
22	Christensen and Pauly (1993), p.82	0	1	1	1	1	5	4	1	0	0	0	0	1							
23	Christensen and Pauly (1993), p.100	0	0	0	1	1	3	1	3	0	0	1									
24	Christensen and Pauly (1993), p.157	0	0	0	0	0	0	2	1	4	3	4									
25	Christensen and Pauly (1993), p.128	0	0	0	0	0	1	0	3	5	0	1	0	3							
26	Christensen and Pauly (1993), p.134	0	2	0	3	1	3														
27	Christensen and Pauly (1993), p.104	0	0	1	2	2	3	1	1	2	0	1									

28	Christensen and Pauly (1993), p.113	0	0	0	1	3	2	1	1												
29	Christensen and Pauly (1993), p.141	0	0	0	0	1	2	3													
30	Christensen and Pauly (1993), p.120	0	1	1	2	1	1	1													
31	Christensen and Pauly (1993), p.146	0	0	0	0	0	0	0	1	2	3	2	0	1	2	2	1	0	1		
32	Christensen and Pauly (1993), p.67	0	3	2	2	2															
33	Christensen and Pauly (1993), p.195	0	0	2	2	1	2	5	2	1	1	2	0	0	1						
34	Christensen and Pauly (1993), p.221	0	0	0	2	2	3	1	1												
35	Christensen and Pauly (1993), p.319	0	1	3	0	3	2	1	4	1											
36	Christensen and Pauly (1993), p.33	0	0	0	5	3	2	0	1	2											
37	Christensen and Pauly (1993), p.308	0	1	1	3	2	1	3	2												
38	Christensen and Pauly (1993), p.168	0	0	2	5	1	1	0	0	1											
39	Christensen and Pauly (1992)	0	1	1	2	4	1														
40	Walters et al. (1997)	1	1	0	3	1	1	1													
41	Baird et al. (1991)	0	2	2	7	0	1														
42	Christensen and Pauly (1993), p.184	0	0	0	1	0	0	2	3	1	4	1									
43	Rosado-Solórzano and Guzmán del Proó (1998)	0	2	0	1	2	1	0	4	1	2	1	2	3	2	1					
44	Ortiz and Wolff (2002)	0	0	2	2	6	2	4	3	2	2										
45	Christensen and Pauly (1993), p.88	0	0	0	1	2	3	4	0	1	2										
46	Christensen and Pauly (1993), p.294	0	0	0	1	2	0	3	0	2	1	2	2	2							
47	Carrer and Opitz (1999)	0	1	1	4	1	3	1	1	2	1										
48	Christensen and Pauly (1993), p.61	0	1	1	2	1	3	2	0	0	0	0	0	0	1						
49	Baird and Ulanowicz (1993)	0	3	0	7	1															
50	Vega-Candejas & Arreguin-Sanchez (2001)	0	0	0	1	0	0	0	1	3	0	5	3	2	3	1	0	0	0	0	1