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The effects of taxonomic aggregation on network analysis

Luis G. Abarca-Arenas [a,*], Robert E. Ulanowicz [b]

[a] *Centro de Ecología y Pesquerías, Apartado Postal 663, C.P. 91000, Xalapa, Veracruz, Mexico*
[b] *Chesapeake Biological Laboratory, University of Maryland System, Solomons, MD 20688-0038, USA*

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Abstract

In their search for ever better trophic models, ecologists have often tried aggregating the number of species in order to better focus upon the variables that most interest them. Previous attempts at aggregating food webs have yielded varied results. We studied a series of different taxonomic aggregations on the same trophic network model of the Chesapeake Bay. The original 50-compartment model, which served as the control configuration, exhibited the highest value for the ascendency index. As expected, in those systems with fewer compartments the ascendency declined in monotonic fashion. The ascendency dropped precipitously for systems with fewer than 40 compartments and achieved its lowest value for systems with less than 29. Systems with the same number of compartments but different aggregations of species yielded different values of the ascendency. The aggregation of bacteria and ciliates resulted in a precipitous drop in the information of the network, revealing perhaps the significance of the microbial loop. Direct and indirect trophic impacts were also affected by the nature of the aggregation, and the impacts seemed to be exaggerated whenever species were lumped into single compartments.

Keywords: Ascendency; Network analysis; Chesapeake Bay; Trophic impact

1. Introduction

The practice of grouping species is an exercise common to all forms of ecological modeling, and the reasons why particular species might be grouped are many. One reason why species are combined is that they are difficult to segregate, either physically or taxonomically. Another reason might be that the modeling of a food web or network is the collateral result of a much broader task. Under such circumstances, the creation of a trophic web may not have been contemplated among the original objectives, so that there remains a lack of information with which to segregate certain species.

Taxonomic aggregation carries with it a series of problems. The effects of lumping upon food web analysis have received some attention (e.g. Pimm, 1982; Yodzis, 1984; Lawton and Warren, 1988; Martinez, 1993, 1994; Martinez and Lawton, 1995; Polis and Hurd, 1995; Winemiller, 1996), but less effort has been expended to illu-

* Corresponding author. Tel./fax: +52-2-813-6059.
E-mail address: labarca@bugs.invest.uv.mx (L.G. Abarca-Arenas).

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Table 1
Compartments, ecological parameters and the source of the data used to compile the trophic network for the Chesapeake Bay model

Compartment	Parameter	Reference
Phytoplankton	Biomass	McManus and Ederington-Cantrell (1992)
	$P/R = 0.24$/d	Sellner (1987)
DOC	Biomass	Wiebe and Smith (1977)
		Larsson and Hagstrom (1979)
		Fenchel (1982)
		Woltes (1982)
		Ulanowicz and Baird (1986)
Bacteria		
Acartia tonsa	Biomass	Tuttle (1997, pers. comm.)
Other Zooplankton	Biomass	White and Roman (1992)
	$P/B = 0.8$/d	Ulanowicz and Baird (1986)
	$P/R = 0.71$/d	Vezina and Pace (1994)
	Assim. Eff. = 0.75	Sanders and Wickham (1993)
Cladocera	Biomass	Purcell and Nemazie (1992)
	$P/B = 0.79$/d	Jorgensen et al. (1991)
	$P/R = 1.13$/d	Jorgensen et al. (1991)
	Assim. Eff. 0.65	Vezina and Pace (1994)
Chrysaora quinquecirrha	Density	Purcell (1992)
	Biomass in carbon = 0.000215 × $Diam^{2.903}$	Purcell (1992)
	$P/B = 0.12$/d	Ulanowicz and Baird (1986)
	$P/R = 0.17$/d	Ulanowicz and Baird (1986)
Mnemiopsis leidyi		
Nemopsis bachei	Density-Biomass	Purcell et al. (1994), Purcell and Nemazie (1992)
	$P/B = 0.12$/d	Ulanowicz and Baird (1986)
	$P/R = 0.17$/d	Ulanowicz and Baird (1986)
Ciliates		
Microphagous	10×12 to 60×25 μm^2	Dolan (1991a)
Macrophagous	20×10 to 100×45 μm^2	Dolan (1991a)
Predaceous	30×25 to 150×50 μm^2	Dolan (1991a)
	Volume to carbon constant	0.088 pgC/μm^3
	$P/B = 0.64$/d	Dolan (1991b)
	$P/R = 0.75$/d	Ulanowicz and Baird (1986)
	Ass. Eff. = 0.75	Ulanowicz and Baird (1986)
Amphipoda	Density	Duguay and Shoemaker (1995)
	Biomass: indiv. dry weight = 0.037 mg	Jorgensen et al. (1991)
	37% of DW as carbon	Jorgensen et al. (1991)
	$P/B = 0.0088$/d	Ulanowicz and Baird (1986)
	$P/R = 0.0011$/d	Ulanowicz and Baird (1986)
Polychaetes	Density	Duguay and Shoemaker (1995)
	Biomass: 0.34 mg C/ind.	Vega-Cendejas et al. (1993)
	$P/B = 0.03$/d	Ulanowicz and Baird (1986)
	$P/R = 0.005$/d	Ulanowicz and Baird (1986)
	Ass. Eff. = 20%	Vega-Cendejas et al. (1993)
Macoma balthica	Density	Gerritsen et al. (1994)
	Biomass = AFDW:Carbon 0.4	Jorgensen et al. (1991)
	$P/B = 1.49$	Ulanowicz and Baird (1986)
	$P/R = 0.33$	Ulanowicz and Baird (1986)
Macoma mitchelli	Density	Gerritsen et al. (1994)
	Biomass = AFDW:Carbon 0.4	Jorgensen et al. (1991)

Table 1 (*Continued*)

Compartment	Parameter	Reference
	$P/B = 1$	Ulanowicz and Baird (1986)
	$P/R = 0.35$	Ulanowicz and Baird (1986)
Rangia cuneata	Biomass	Ulanowicz and Baird (1986)
	$P/B = 1$	Ulanowicz and Baird (1986)
	$P/R = 0.37$	Ulanowicz and Baird (1986)
Mulinea lateralis	Density	Gerritsen et al. (1994)
	$P/B = 1$	Ulanowicz and Baird (1986)
	$P/R = 0.5$	Ulanowicz and Baird (1986)
Mya arenaria	Density	Gerritsen et al. (1994)
	$P/B = 2$	Ulanowicz and Baird (1986)
	$P/R = 0.37$	Ulanowicz and Baird (1986)
Crasostrea virginica	Biomass	Ulanowicz and Baird (1986)
	$P/B = 1.3$	Ulanowicz and Baird (1986)
	$P/R = 1.3$	Ulanowicz and Baird (1986)
Callinectes sapidus	Biomass	Ulanowicz and Baird (1986)
	$P/B = 2$/d	Ulanowicz and Baird (1986)
	$P/R = 0.35$/d	Ulanowicz and Baird (1986)
Anchoa mitchilli	Biomass	Ulanowicz and Baird (1986)
	$P/B = 1$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.26$/d	Ulanowicz and Baird (1986)
Micropogon undulatus	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.49$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.45$/d	Ulanowicz and Baird (1986)
Trinectes maculatus	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.48$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.35$/d	Ulanowicz and Baird (1986)
Leiostomus xanthusrus	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.56$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.49$/d	Ulanowicz and Baird (1986)
Cynoscion regalis	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.48$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.4$/d	Ulanowicz and Baird (1986)
Alosa sapidissima	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.6$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.5$/d	Ulanowicz and Baird (1986)
Alosa pseudoharengus	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.96$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.5$/d	Ulanowicz and Baird (1986)
Alosa chrysocloris	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.96$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.5$/d	Ulanowicz and Baird (1986)
Brevortia tyranus	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.4$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.13$/d	Ulanowicz and Baird (1986)
Morone americana	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.4$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.42$/d	Ulanowicz and Baird (1986)
Morone saxatilis	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.4$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.42$/d	Ulanowicz and Baird (1986)

Table 1 (*Continued*)

Compartment	Parameter	Reference
Pomatomus saltatrix	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.41$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.42$/d	Ulanowicz and Baird (1986)
Paralichthyes dentatus	Biomass	Ulanowicz and Baird (1986)
	$P/B = 0.35$/summer	Ulanowicz and Baird (1986)
	$P/R = 0.42$/d	Ulanowicz and Baird (1986)
Arius felis	Biomass	Ulanowicz and Baird (1986)
	$P/B = 2.21$/summer	Ulanowicz and Baird (1986)
	$P/R = 3.08$/d	Ulanowicz and Baird (1986)

mine the effects of grouping upon trophic networks (food webs wherein the transfers of matter between compartments have been quantified to some degree, e.g. Hirata and Ulanowicz, 1985 or Christensen and Pauly, 1993). The probable reason for the emphasis on food webs is that the amount of information needed for their construction is far less than that required for weighted networks, and food web analysis thereby has a longer history.

The classical way to group species, regardless of whether one is working with a food web or a network, is to aggregate according to similarities in diet. That is, species are grouped in conformance with trophic guilds, or collections of species all having a similar trophic niche (Pielou, 1977, 1984). Although grouping species according to trophic guilds might seem appropriate, it is also known that species within a guild exhibit many dissimilarities like competition between members of the guild or different food preferences due to size (Pielou, 1977).

Baird and Ulanowicz (1993) pointed out that the number of system compartments should be, if not equal, at least very similar among different ecosystems before they can be compared. Whence, their identification of taxa was made only after considering trophic similarities. The species aggregation they chose ensured that the major community components—plankton, benthos, and nekton—would remain intact.

In her doctoral dissertation, Optiz (1993) compressed a coral reef network of more than 60 species into one with only 30 compartments. In order to test whether there were changes in the information content of the network after it had been reduced in size, Opitz performed two further aggregations. As little further changes in the network ascendency (a scaled measure of the information inherent in a network configuration) were noticed, she concluded by extrapolation that the reduction from 60 to 30 compartments did not appreciably affect the results. Arias-Gonzalez (1993), studying two Polynesian reefs, applied the ECOPATH program (Christensen and Pauly, 1992) to a matrix of 41 compartments that had been condensed from an original network of more than one hundred species. Unlike Optiz, Arias did not compare the information inherent in successive stages of aggregation.

Hirata and Ulanowicz (1985) proposed a method for aggregating networks whereby the network's compartments were combined in iterative pair-wise fashion in such a way as to produce the minimum decrease in the value of the ascendency at each iteration. The rationale of this methodology is quite different from the structural approach mentioned earlier in that species are aggregated according to the optimal behavior of a *functional* index.

The goal of this exercise was to study the effect that grouping species has on system-level information by regarding how the calculated information index (ascendency) changes as a series of networks are generated via the systematic aggregation of a 50-compartment Chesapeake Bay trophic network.

2. Methods

The Chesapeake Bay trophic network is one of the first to be studied in terms of both its structure and functionality (e.g. Baird and Ulanowicz,

1989; Ulanowicz and Baird, 1998). Recently, Abarca-Arenas (1999) expanded the original 36 compartment network (Baird and Ulanowicz, 1989) to a one with 50 components by resolving (segregating) several of the taxonomic groupings made in formulating the original model. The model represents an average trophic interactions during the summer in the mesohaline reach of the Chesapeake Bay. The names of the compartments, the basic model inputs and the accompanying references are all presented in Table 1.

The expanded 50-compartment model was considered to be the control, from which a series of aggregated variations would be produced. Although a numerical classification method of the 50 compartments could have been used, the objective of this work was to assume the role of a researcher, who normally would lump species, or groups of species in an intuitive way (as if no quantitative data were available, and species groupings were effected solely on the basis of qualitative food preferences.) The aggregations used here were based on predator–prey relationships and food preferences—e.g. various ciliates (predators) were aggregated into a single compartment, while three sizes of bacteria (prey) were kept separated. In another aggregation, both bacteria and ciliates were condensed into single compartments. Proceeding in this manner, 19 different matrices were created, all variations of the original network. Each matrix consisted of a distinct combination of aggregated species.

Summing all inputs and outputs of the individual compartments provided a check on mass conservation within each data matrix. In this way the total amount of matter flowing in each system (total system throughput) was maintained constant and equal to that of the original matrix. Keeping the throughflow constant is important in order to keep system size from affecting the results. Once each new flow matrix has been checked, the informational indices were calculated (Ulanowicz, 1986; Ulanowicz and Norden, 1990; Ulanowicz and Abarca-Arenas, 1997).

The magnitudes of trophic impacts between compartments were also analyzed along with the information indices. Although the effects of all combinations of component upon the trophic impacts were computed, only some of those combinations are presented here in order to emphasize the effect of that particular scenario. Also, only the control system and the most aggregated network (25 components) are presented as full examples. Because indirect effects between species (compartments) could provide important information pertaining to the management of a species, it is important to clarify the consequences of compartment lumping on trophic impacts. The method used to compute trophic impacts was that proposed by Ulanowicz and Puccia (1990).

3. Results and analysis

The various combinations of compartments effected upon the original 50-compartment system are presented in Table 2. The key to the combinations given in the table will be the one to be used throughout this work, and the cluster heading denotes the kind of species or group of species joined to form a new compartment in that particular matrix. The names of the compartments in the original model are given in Table 1. The most aggregated system contained a total of 22 living compartments, while the control counted 45. Some of the aggregated systems contained an equal number of living compartments (e.g. GI, GIII, GV and GVIII); but, as can be seen in Table 2, the types and combinations of clusters are distinct.

As an example of how the compartments were aggregated, Fig. 1 depicts the zooplankton community as it appears in the original model (control) and in aggregation GIX. Bacteria (all three size classes), ciliates (all three classes), medusa and ctenophores, and *Acartia tonsa*, cladocera and other zooplankton, are combined into four different compartments as shown in Table 2. The rest of the compartments in this particular combination remained as in the original trophic model.

The calculated values of the internal ascendency, overhead and capacity (the informational variables calculated using internal exchanges only) for all 20 systems are presented in Table 3. The systems are arranged in order of decreasing number of living compartments and are accompanied

Table 2
Key to the systems used for analysis after aggregation

Key to system	No. of total compartments	No. of living compartments	Clusters
Original	50	47	Original system
GI	48	45	*Free living bacteria
GII	47	44	*Free living bacteria *POC attached bacteria
GIII	48	45	*Ciliates
GIV	46	43	*Ciliates *Free living bacteria
GV	48	45	*Medusa & Ctenophores
GVI	46	43	*Ciliates *Medusa & Ctenophores
GVII	44	41	*Free living bacteria *Ciliates *Medusa & Ctenophores
GVIII	48	45	**A. tonsa* & Cladocera & O. Zoopl.
GIX	42	39	*Free living Bacteria *Ciliates *Medusa & Ctenophores **A. tonsa* & Cladocera & O. Zoopl.
GX	45	42	*Polychaetes *Meiofauna
GXI	37	34	*Free living bacteria *Ciliates *Medusa & Ctenophores **A. tonsa* & Cladocera & O. Zoopl. *Polychaetes *Meiofauna
GXII	45	42	*Mollusks
GXIII	43	40	*Free living bacteria *Mollusks
GXIV	32	29	*Free living bacteria *Ciliates *Medusa & Ctenophores **A. tonsa* & Cladocera & O. Zoopl. *Polychaetes *Meiofauna *Mollusks
GXV	29	26	*Free living bacteria *Ciliates *Medusa & Ctenophores **A. tonsa* & Cladocera & O. Zoopl & *A. mitchilli* laravae and eggs *Polychaetes *Meiofauna *Mollusks
GXVI	27	24	*Free living bacteria *Ciliates *Medusa & Ctenophores **A. tonsa* & Cladocera & O. Zoopl & *A. mitchilli* laravae and eggs *Polychaetes

Table 2 (*Continued*)

Key to system	No. of total compartments	No. of living compartments	Clusters
			*Meiofauna *Mollusks *Alosid Fish
GXVII	46	43	*Fish Cluster
GXVIII	44	41	*Fish Cluster **A. tonsa* & Cladocera & O. Zoopl. & *A. mitchilli* laravae and eggs
GXIX	25	22	*Free living bacteria *Ciliates *Medusa & Ctenophores **A. tonsa* & Cladocera & O.Zoop & *A. mitchilli* laravae and eggs *Polychaetes *Meiofauna *Mollusks *Fish Cluster

The column cluster identifies those compartments that were aggregated maintaining the other compartments as in the original system.

by their respective informational values. The original system posted the highest values for all three internal indices. System GXVII, wherein only the fishes were aggregated, yielded the next highest values of these variables, followed by the systems with combinations of medusa with ctenophore, and polychaetes with meiofauna—GV and GX, respectively.

In order better to analyze the pattern by which the index values obtained from the aggregated systems deviate from those yielded by the original, the differences between the original and each aggregation were computed and plotted in Fig. 2. The trend in these differences shows how the total number of compartments is not the sole factor determining the difference, but that the quality or type of clustering is also an important factor affecting the magnitude of the ascendency.

The first thing to notice in Fig. 2 is that the departure from the original system is greatest for those systems with the fewest number of compartments. The highest difference corresponds to system GXIX, which contains all of the clusters and only 22 living compartments. As the number of compartments approaches that of the original system, a monotonic tendency towards an increasing value of the informational indices can be discerned. There appears to be a monotonic decrease in the difference as the number of compartments approaches that of the original. This trend is broken, however, by a few of the systems that maintain a relatively large distance from the original, despite the total number of their compartments being close to that of the original.

The second point to note is that systems with the same number of compartments yielded different values for the informational indices. The four systems with 45 compartments varied markedly, from a difference of almost zero to around 25 thousand bits mg C/m^2 summer. The system in this quartet with the lowest difference was the one containing the cluster of medusa and ctenophores (GV), while the system with the ciliate cluster (GIII) provided the highest difference. The system that aggregates all three-size classes of bacteria yielded a difference of almost 20 thousand bits.

Systems with 43 compartments varied in their informational values as well. The system wherein only the fish were clustered (GXVII) yielded informational indices closest to those of the control. The other two systems were relatively distant from the original model.

A common characteristic for these two series of systems is that clusters of small species of zoo-

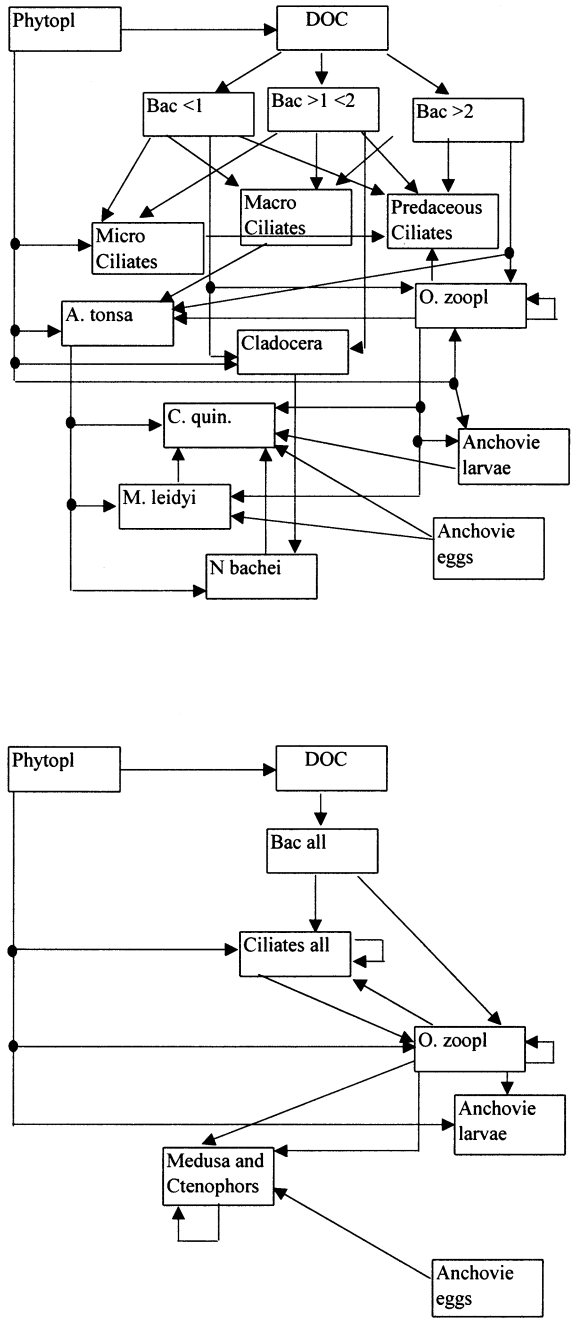

Fig. 1. Example on how the original system was aggregated: (a) original system showing the planktonic sub-system as was in the original trophic network, (b) aggregated network of the planktonic sub-system as used for the system labeled as GIX (see Table 2), the rest of trophic network remains as in the original model.

plankton characterized those systems that deviated more from the control. Similarly, a significant drop in information due to the aggregations of bacteria and ciliates could reveal the importance of the microbial loop within the bay's ecosystem. This view is supported by the results from the system with a single cluster in the fish, where the informational values were the closer to he original than those of any other combinations. Also, for those systems where bacteria were maintained as segregated units, the informational indices changed little from those of the original.

Analyzing Fig. 2 further, a monotonic decrease of the internal ascendency (increasing deviation from the control system) is evident for systems with 41 or fewer compartments. In each of these systems, the zooplanktonic and the bacterial communities were clustered (Table 2). Those systems with higher deviation of the ascendancy from the control system all contained aggregated zooplankton and bacteria communities. When predators of these communities were clustered but their prey were left segregated, the informational values remained closer to that of the control. This circumstance may suggest bottom-up control of the trophic network of the Chesapeake Bay community.

Concerning the trophic impact analysis, comparison of the control system with the more aggregated ones reveals some small differences. When the three size classes of bacteria were left unclustered, the category of those less than one micrometer had a positive effect on the phytoplankton. When the three size classes are joined as a single compartment, a higher positive influence was observed (although the effect of the cell between one and two micrometers on those greater than two micrometers was negative.) The impact of bacteria on ciliates depended on the size of the bacteria. Larger bacteria had a negative effect on microphagous ciliates, while the other size classes affected all ciliates positively. When the bacteria were all joined into a single component, the bacterial compartment exerted a negative impact on the ciliate cluster. Overall, clustering bacteria and other members of the zooplankton community had mixed effects on trophic impacts.

The clustering of other network compartments yielded similar effects on the trophic impacts.

Table 3
Results for the Internal ascendency, overhead and capacity for each one of the distinct systems obtained after the aggregation of compartments

System key	Total compartments	Living compartments	Internal ascendancy (bits mgC/m^2 summer)	Internal overhead (bits mgC/m^2 summer)	Internal capacity (bits mgC/m^2 summer)
GXIX	25	22	2976385.55	2764479.75	5740865.30
GXVI	27	24	2976414.32	2764465.65	5740879.97
GXV	29	26	2977092.52	2765315.31	5742407.83
GXIV	32	29	2977826.91	2766644.39	5744471.30
GXI	37	34	3006302.92	2778437.57	5784740.49
GIX	42	39	3008739.50	2818880.53	5827620.03
GXIII	43	40	3014604.30	2855128.73	5869733.03
GVII	44	41	3017411.22	2843709.35	5861120.57
GXVIII	44	41	3048080.52	3042098.51	6090179.04
GX	45	42	3058053.11	3019314.53	6077367.65
GXII	45	42	3035988.93	3043999.93	6079988.85
GIV	46	43	3018820.87	2847151.97	5865972.84
GVI	46	43	3032028.51	3042118.46	6074146.96
GXVII	46	43	3060342.60	3059743.90	6120086.50
GII	47	44	3021091.16	2878904.57	5899995.72
GI	48	45	3043080.18	2866921.91	5910002.09
GIII	48	45	3033428.37	3045600.20	6079028.57
GV	48	45	3059080.48	3056323.07	6115403.55
GVIII	48	45	3048228.07	3042120.12	6090348.19
Original	50	47	3060490.18	3059765.66	6120255.84

For system's characteristics refer to Table 2 and the corresponding key.

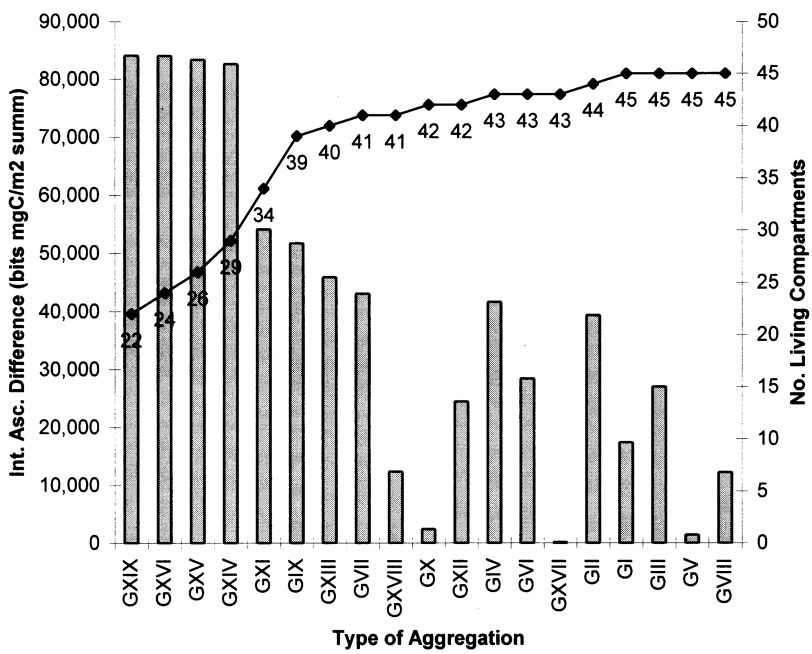

Fig. 2. Difference between the internal ascedency of the original system and each reduced system, and the number of living compartments for each system. Key to systems and their characteristics are as in Table 2.

Although the differences in impacts between the control and the reduced system were relatively small in most cases, in some instances there was a change of sign in the impact. That is, segregated compartments yielded trophic impacts in a given direction, whereas after clustering, the impacts were in the opposite directions. The intent in this paper has been to use the Chesapeake Bay for illustrative purposes, but if the objective were actually to manage the ecosystem, the indirect effects of clustered compartments could have masked species relationships that are important to the ecosystem's structure and functioning.

As mentioned earlier, the relationship of bacteria with the phytoplankton, ciliates, and mesozooplankton indicates the importance of the microbial loop within the system. When the bacteria clustered, some of the trophic impacts are depressed, thereby masking the intricate structure of this community. Results presented by Ulanowicz and Baird (1998) suggests a complex interaction between the bacteria and ciliates regarding the use of phosphorous, carbon and nitrogen. The results of this exercise show that the relationship is perhaps even more complex by implying that phytoplankton and some members of the mesozooplankton community are also involved.

4. Summary and conclusions

In the ongoing search to elaborate ecosystem structure and functioning, ecologist have tended to simplify system components in order to make their models more manageable. On the other hand, several investigators have proposed indices that portray ecosystem characteristics in a more synthetic way, e.g. goal functions (Mueller and Leupelt, 1998.) In this context, increasing ascendency has been widely used to quantify the growth and development of ecosystems. In order to assess the consequences that aggregating ecosystem compartments has on the ascendancy index, a series of compartment clusterings were performed on the Chesapeake Bay trophic network.

Although the matter of species lumping as it pertains to food web analysis has been addressed, almost no work has focused on how component clustering affects weighed trophic networks. Christensen and Pauly (1993) and Christensen (1995) have considered the optimization of goal variables (e.g. ascendency) after a reduction in the number of compartments. Their goal differs from the objective of this work, which was to investigate the effect of the aggregation process itself upon the value of the ascendancy.

As had been expected, the original (control) system maintained the highest values of the ascendancy and related indices. (This was in accordance with the theoretical expectations of Hirata and Ulanowicz (1985), who used information theory to show that the ascendency value for a system could not rise after a reduction in the number of compartments.) Along the same lines, the effect of clustering was clear for those systems that were reduced to the fewest number of compartments. They revealed the lowest values of the informational indices.

An interesting observation flowing from the current work was that, even when the number of compartments remains the same, the type of aggregation can significantly affect the value of the ascendancy. That is, the reduction of system components not only decreases the information inherent in the system, but may also affect the structural and functional representation of the system. The change in network structure also can impinge upon a specie's direct and indirect interactions. Hence, whenever one is analyzing a system in terms of an aggregated model (which is almost always the case), strict attention should be paid to the degree of species clustering.

It was clearly shown how the effects of species clustering affect not only the final values of goal functions like the ascendancy index, but also can change the global structure of the trophic network itself. Before analyzing a trophic network, care should always be taken as to how and when species are to be clustered.

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