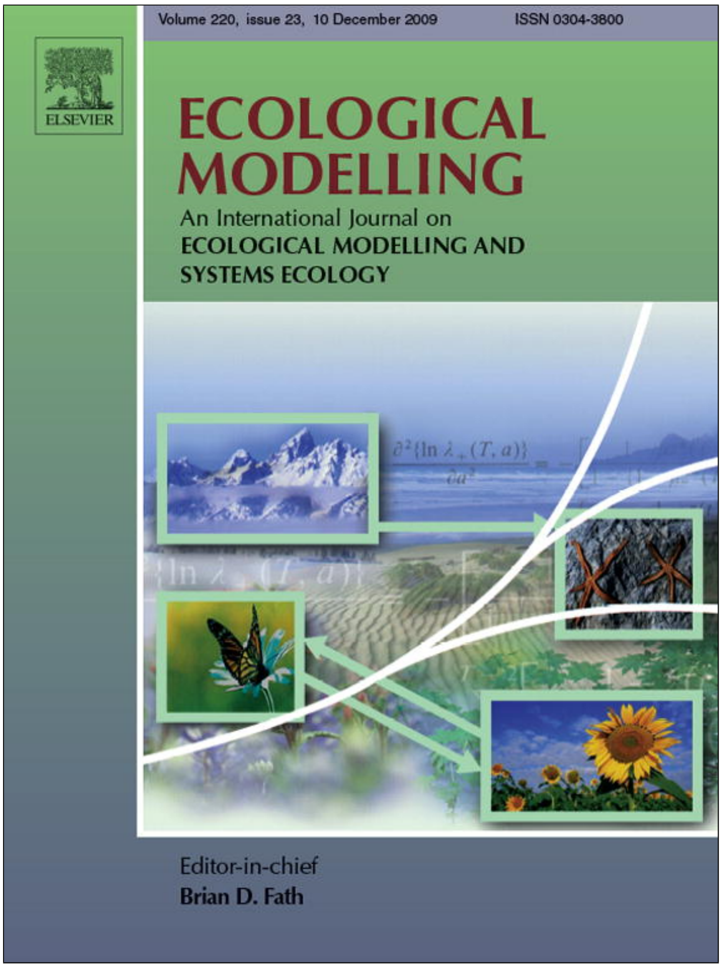
Volume 220, issue 23, 10 December 2009
ISSN 0304-3800
ELSEVIER
ECOLOGICAL MODELLING
An International Journal on
ECOLOGICAL MODELLING AND SYSTEMS ECOLOGY
Editor-in-chief
Brian D. Fath

Ecological Modelling 220 (2009) 3465–3471

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

On the consequences of aggregation and balancing of networks on system properties derived from ecological network analysis

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ARTICLE INFO

Article history:
Received 25 June 2009
Received in revised form 2 September 2009
Accepted 4 September 2009
Available online 8 October 2009

Keywords:
Ecological network analysis
Steady state models
Non-steady state models
Balancing
Aggregation
Trophic dynamics
System indices
Sylt–Rømø Bight

ABSTRACT

In the ecological network analysis (ENA) of complex flow food webs the assumption is often made that the models characterizing the flows and stocks of ecosystems occur in a steady state where inflows equals outflows. An assessment of the system indices derived from ENA of six balanced and unbalanced system models, respectively, indicate to differences between indices. The aggregation of highly articulated flow models into models with fewer compartments also has drastic effects on the system metrics, particularly on the information indices.

1. Introduction

The construction of quantitative networks depicting the mass of living and non-living components and flows of energy and material between them is today practiced on a global basis. The objectives for doing so are often to describe the trophic dynamics of an ecosystem, for comparative purposes between systems, for the assessment of the same system over temporal scales, and to obtain some understanding of how ecosystems function. Ecological network analysis (ENA) is a methodology developed to holistically assess the complex interactions within an ecosystem (see Fath et al., 2007 and references therein). A large number of system properties results from ENA which are used to satisfy the objectives mentioned above, and are often also used for management purposes (Patricio et al., 2006; Christian et al., 2009). Once a network is constructed it can be analyzed by network analysis (a set of algorithms derived from input–output analysis, information theory, trophic and cycle analysis), to compute structural (e.g. cycling and throughput) and functional (e.g. dissipation, development, redundancy and relational) properties of the network. The theoretical foundations and the basic concepts of ENA have been adequately described by, for example, Wulff et al. (1989), Ulanowicz (1986, 2004), Fath and Patten (1999), Fath et al. (2004) and Jørgensen and Fath (2004), while the software to do these analyses are readily available (Ulanowicz and Kay, 1991; Allesina and Bondavalli, 2004; Christensen and Pauly, 1992; Fath and Borret, 2006, http://www.glerl.noaa.gov/EcoNetwrk/).

Two of the fundamental “problems” confronting the construction of a network are (a) that the model network must represent a steady-state condition; i.e. that the inputs into the system equal all outputs, and (b) that species, or even communities, often have to be aggregated into functional guilds (not necessarily taxonomic ones) resulting in highly aggregated networks (e.g. 15 compartments or less; Wilson et al., 2007; Baird and Ulanowicz, 1993; Monaco and Ulanowicz, 1997), or by highly articulated ones (e.g. 50 compartments or more; Baird et al., 2004, 2007; Heymans et al., 2002). Here we address both the issues: firstly the effects of the balancing of non-steady models into balanced ones on the output results (i.e. system metrics) derived from ecological network analysis (ENA) of six intertidal subsystems, based on carbon flow models of six highly articulated intertidal systems (networks comprising of 59 compartments each) which differ in habitat structure and biodi-

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doi:10.1016/j.ecolmodel.2009.09.008

Table 1
Imbalances and percent difference in system attributes between balanced and unbalanced networks of six intertidal systems of the Sylt–Rømø Bight ecosystem, German Wadden Sea. A positive percent value indicates a smaller attribute value in the unbalanced network (+Difference = increase in balanced models). A negative percent value indicates a larger attribute in the unbalanced network (−Difference = decrease in balanced models).

Imbalances	Subsystem					
	Mussel banks	Arenicola Flats	Sparse *Z. noltii*	Dense *Z. noltii*	Mud Flats	Muddy-sand Flats
Sed POC imbalance (mgCm^{-2} day^{-1})	1103.2	885.6	775.5	759.4	330.3	269.3
Unbalanced prey production (mgCm^{-2} day^{-1})	1101	72.7	214.7	0	58.4	0
Sum of unbalances (mgCm^{-2} day^{-1})	2204.2	958.3	990.2	759.4	388.7	269.3
TSTP in Unblanced models (mgCm^{-2} day^{-1})	33,584	4,928	5,639	7,566	5,248	5,852
TSTP in Balanced models (mgCm^{-2} day^{-1})	35,056	5,886	6,629	8,326	5,666	6,121
System Attribute	Percent difference between steady state (balanced) and non-steady state (unbalanced) subsystem models					
Trophic efficiency	0	0	0	0	0	0
No. of cycles	0	0	0	0	0	0
Finn cycling index	−3.56	−15.76	−12.47	−9.13	−7.72	−4.40
Total system throughput (TSTP)	4.42	19.44	17.56	10.04	7.96	4.60
Development capacity (DC)	7.98	19.47	18.29	10.32	10.19	5.59
Flow diversity (DC/TSTP)	3.40	0.03	0.63	0.25	2.06	0.95
Ascendency (A)	0.85	26.09	19.30	14.16	7.01	6.42
Relative ascendency (A/DC)	−6.63	5.50	1.27	3.27	−2.87	0.84
Average mutual information (A/TSTP)	−3.42	5.57	4.89	3.74	−0.88	1.74
Internal development capacity (DCi)	1.37	5.22	4.68	2.64	2.06	1.21
Internal acendency (Ai)	−2.15	−2.34	−2.89	−3.63	−3.68	−1.97
Relative internal acendency (Ai/DCi)	−3.39	−7.11	−7.16	−6.09	−5.57	−3.20
Average internal mutual information (Ai/TSTP)	−6.29	−18.23	−17.39	−12.43	−10.78	−6.28
Overhead on imports	24.87	31.85	52.46	0	68.92	0
Overhead on exports	164.3	25,081.8	5,925.6	8,069.4	3,926.7	39,633.3
Overhead on dissipation	0.03	0	0	0	0	0
Redundancy (R)	5.85	9.85	9.84	6.17	4.79	2.88
Relative redundancy (R/DC)	−1.69	−8.16	−7.18	−3.85	−4.90	−2.56
Relative internal redundancy (Ri/Dci)	7.73	4.35	4.87	3.44	2.66	1.68
Φ (sum of overheads/TSTP)	10.18	−6.77	−4.19	110.02	3.64	0.05
Average path length (APL = TSTP – Z)/Z)	6.70	25.97	18.75	14.10	10.51	5.99
Average residence time (ART)	−8.43	−15.87	−53.05	−34.97	−24.29	−19.73
Overall connetance	3.49	−0.29	1.82	4.20	7.16	4.86
Intercompartmental connectance	0.06	0.00	0.00	0.00	0.00	0.00
Foodweb connectance	0.00	0.00	0.00	0.00	0.00	0.00

versity (see Baird et al., 2007). Secondly, we address the effect of the aggregation of a 59 compartment model (see Baird et al., 2004) to ones comprising of 36 and 18 compartments, respectively, on ENA output results.

2. Study site, materials and methods

The study area in both instances is the Sylt–Rømø Bight (54°52′ to 55°10′N and 8°20′ to 8°40′E), a large semi-enclosed basin situated between islands of Sylt, Germany, and Rømø, Denmark. The Bight covers an area of 404 km^2 with an intertidal area of about 138 km^2. The intertidal regions of the Bight ecosystem have been subdivided into eight subsystems characterized by differences in sediment characteristics and biodiversity (Gätje and Reise, 1998; Asmus and Asmus, 2005). Habitats show variation in species composition and extension over time. The status presented here represent the years 1990–1998. The various habitat types, or intertidal subsystems, are contiguous, but nevertheless separated by the nature of the substrate of each, and by its characteristic species composition. The "naming" of the different contiguous subsystems was done according to either the dominant species (e.g. mussel beds [0.36 km^2], where the mussel *Mytilus edulis* predominates, the lugworm *Arenicola* on the *Arenicola* Flats [91 km^2], the dwarf seagrass *Zostera noltii* as the dominant macrophytic species on the *Z. noltii* beds [4.76 km^2 where the seagrass is sparse, and 10.8 km^2 where it is dense], or to typical substrate types (e.g. mud flats [3.9 km^2], a mixture of mud and sand [13.3 km^2], sandy shoals [3.7 km^2], and sandy beaches [7.3 km^2]). Each subsystem differs substantially in species composition, standing stocks and productivity of the constituent species, and in habitat structure so that their recognition and treatment as different subsystems of the intertidal Bight is justified. Detailed network models have been developed based on empirical data collected by staff of the Alfred Wegener Institute for Polar and Marine Research in List, Sylt, and from numerous published and unpublished information residing in the Institute. The network models were analyzed by ENA for the Bight ecosystem as a whole (Baird et al., 2004), as well as for each of the constituent subsystems (Baird et al., 2007). The data used in the network analysis of the intertidal systems can be downloaded on-line at http://www.int-res.com/articles/meps2007/351/m351p025.pdf filed under Appendix 2. The data used for the three aggregations of the 59, 36 and 18 compartment models can be down loaded from the electronic store of this journal as Appendix 1. Both sets of data are cast in the readily useable recommended SCOR format. Results from these studies form the basis of this communication. We refer specifically to ENA outputs that reflect on the functioning of an ecosystem such as the magnitude of cycling (the Finn cycling index, FCI [Finn, 1976]), trophic efficiency (calculated from the logarithmic mean of the efficiency of energy transfers between discreet trophic levels of an ecosystem derived from the Lindeman Spine), system activity (or total systems throughput, TSTP), development capacity (DC), ascendency (A), redundancy (R), average mutual information (AMI = A/TSTP), flow diversity (DC/TSTP), average path length (APL = (TST − Z)/Z where Z = sum of exogenous inputs [Kay et al., 1989]), and Φ (sum of overheads/TSTP). These and various other attributes and ratios are also included in Table 1, which gives the percent differences between the system indices for balanced and unbalanced models.

The 59 compartments in the original network were aggregated into models comprising 36 and 18 compartments, respectively. This was done by grouping compartments together having the same mode of feeding and which obtain their food from common prey resources. The AGGREGATION subroutine was then used to cast the aggregated models into the SCOR format to be analyzed by the software package NETWRK 4.2a. Both of the software routines that perform the abovementioned analyses and its supporting documentation can be downloaded from http://www.cbl.umces.edu/~ulan/ntwk/network.hmtl.

3. Results and discussion

3.1. Steady and non-steady state comparison

The "original" network model is seldom constructed in a perfect steady or balanced state; errors in estimation of population/community energy budgets (for parameters such as consumption, production, respiration, excretion, and mortality), incomplete empirical data on biomass, diet, and rates of flow from prey to predator, various assumptions on the feeding topology (predator–prey connections), invariably contribute to an unbalanced network. Ulanowicz and Scharler (2008) have proposed least-inference methods to construct ecosystem budgets (input data) under minimal inference. They proposed a "joint apportionment" (MATBLD) and a "reverse mold-filling" (MATLOD) methodologies to balance the flows associated with each component (or node) in a network so that inflows equals outflows. Allesina and Bondavalli (2003) discussed and formulated input and output based methods to balance system networks, including DATBAL, also a balancing routine developed by Ulanowicz (1989). Balancing can also be achieved by an ECOPATH routine (Christensen and Pauly, 1992) at http://www.ecopath.org.

In the study conducted by Baird et al. (2007) the living components were assumed to be in balance; for plants GPP = NPP + respiration and for heterotrophs according to the general energy budget of C = P + R + E where C = consumption, P = secondary production, R = respiration, and E = egestion. These assumptions would imply that each of the subsystems is also in balance. However, six of the eight subsystems were found not to be in balance. Imbalances occurred firstly in subsystems where predator demand exceeded prey production, and secondly by sediment POC. Excess sediment POC, which normally consists of benthic egestion and mortality of pelagic and benthic fauna, and non-utilized dead plant material, is usually artificially exported in networks to balance the *in situ* production and utilization of this material. Here no attempt was made to balance sediment POC and was subsequently retained in the subsystem models, with the exception of the sandy shoal and sandy beach subsystems where tidal water movements are known to remove excess material (Baird et al., 2007; Asmus and Asmus, 1998). Sediment POC accumulation in the intertidal zone appears to be a common phenomenon in the Bight, and it is removed and exported to the near-shore ocean only during episodic storm events. The magnitudes of the imbalances are given in Table 1 (first five rows). It shows that the retention of sediment POC, and to a lesser extent prey production (particularly in the Mussel Banks), were the flows involved in the analyses of the unbalanced and balanced models. These differences are also reflected in the TST of balanced and balanced models (see Table 1).

To follow convention, the models were also balanced using DATBAL (linear donor controlled routine) and mainly by the manual manipulation of unbalanced components by importing shortfalls in prey production, exporting excess production and sediment POC, and adjusting consumption and production rates. No algorithm was used in these balancing procedures. Table 1 shows the magnitude of the imbalances in the percent difference between system properties of balanced and unbalanced models. Results in the table indicate that several indices (trophic efficiency, number of cycles, dissipation, intercompartmental and food web connectance) show minimal or no changes between the balanced and unbalanced networks. The differences in exports are, however, very high because sediment POC were not exported in order to balance the networks; an ecological phenomenon with substantial impact on the system indices. Also, because the shortfall prey production in the mussel banks, Arenicola Flats, the Sparse *Z. noltii* sea grass beds, and the mudflats was not adjusted to balance those affected nodes the difference of the overheads on imports in those four subsystems are rather large between the balanced and unbalanced networks. Several indices showed persistent negative or positive responses between balanced and unbalanced models. For example, the FCI, internal ascendency (Ai), relative internal ascendency (Ai/DCi), internal AMI (Ai/TSTP), relative redundancy (R/DC), and the ART declined in all the balanced networks, most probably because in these cases (with the exception of relative redundancy) only internal connections were considered. Other indices, such as TSTP, DC, ascendency, DCi, flow diversity, redundancy, relative redundancy, and the APLs increased in all the balanced networks. A few other indices show inconsistent responses to results from ENA between balanced and unbalanced networks. E.g. both the relative ascendency (A/DC) and the AMI (A/TSTP) declined in the mussel beds and mud flats, but increased in the other subsystems of the balanced models. Wilson et al. (2007) reported on the comparison of system metrics of balanced vs. unbalanced networks (using DATBAL) of 8 and 12 compartment models each for Dublin Bay and Baie de Somme. Their results show an increase from the unbalanced to the balanced 12 compartment model in TSTP, DC, A, R, and DCi, and a decline in the Ai/Ci ratio, similar to the trends observed for the subsystems in the Sylt–Rømø Bight. The Ai shows an increase in the balanced models for Dublin Bay and Baie de Somme, but a persistent decline in the Bight. The percentage differences between the balanced and unbalanced models of Dublin Bay and Baie de Somme vary however considerably. For example, the TSTP increased by 56 and 59% in Dublin Bay and the Somme, respectively, the DC by 60 and 70%, and the FCI by 53 and 60% from the unbalanced to the balanced models (see Wilson et al., 2007 for further details). These differences are high when compared to the differences between system indices in the Bight (see Table 1).

We calculated the coefficients of variation (CVs) of the percent difference between balanced and unbalanced models of selected system level attributes which have either a positive or negative sign for all the intertidal systems (see Table 1). The CVs of the differences vary between 26% (relative internal ascendency) and high CVs of 77% (ascendency) and 105% (flow diversity) as illustrated in Fig. 1. Flow diversity and ascendency appear to be most affected by the balancing procedure and since these are key system attributes it would impact on the interpretation of ecosystem growth, health, and flow dynamics.

The emerging idea, when indices from (artificially) balanced models are compared with those derived from models which are unbalanced because of ecological reasons, is that there appears to be a consistent pattern, at least amongst the subsystems of the Bight discussed here, of an increase or decrease in important system indices such as the FCI, TSTP, DC, A, DCi/Ai, Ai/DCi, Internal AMI, relative redundancies, APLs and ARTs. Allesina and Bondavalli (2003) focused the effects of balancing specifically on TST and ascendency, and compared the resultant indices derived from a donor (or input)- and predator (or output)-based-approaches, as well as from four newly developed balancing algorithms. They concluded that balancing procedures may well affect system level indices as pointed out in their assessment of a comparison between balancing methods. Ulanowicz and Scharler (2008) also noted that balancing routines changes the magnitude of flows in order to achieve a balanced network. They concluded that MATBLD and MATLOD nevertheless produce several flows that match the original flows in the Cone Spring network closely, although some do not.

Table 2
Aggregation of 59 network model to a 36 and 18 compartment models of the Sylt–Rømø Bight ecosystem, German Wadden Sea.

Original 59 compartment network		Aggregated 36 compartment network			Aggregated 18 Compartment model		
Compartment #	Species/compartment	New compartment #	Original compartment #	Compartment name	New compartment #	Original compartment #	Compartment name
1	Phytoplankton	1	1	Phytoplankton	1	1	Phytoplankton
2	Microphytobenthos	2	2	Microphytobenthos	2	2	Microphytobenthos
3	Macrophytes	3	3	Macrophytes	3	3	Macrophytes
4	Freeliving bacteria	4	4	Freeliving bacteria	4	4	Freeliving bacteria
5	Zooplankton	5	5	Zooplankton	5	5	Zooplankton
6	Hydrobia ulvae	6	6, 7	Benthic grazers	6	6, 7	Benthic grazers
7	Littorea littorea	7	7	Arenicola	7	8, 9, 10, 11, 12, 16, 17	Invertebrate benthic detritus feeders
8	Arenicola marina	8	8	Scoloplos	8	13, 15, 19, 20, 21, 23, 24	Invertebrate benthic suspension feeders
9	Scoloplos armiger	9	10, 11, 12	Benthic detritivores	9	14, 18, 26, 22, 25, 27, 28, 29	Benthic omnivorous invertebrates
10	Capitella capitata	10	16, 17	Corophium spp.	10	34	Planktivorous fishes
11	Oligochaeta	11	13, 15	Benthic suspension feeders	11	30, 31, 32, 33, 35, 36, 37	Benthic feeding fishes
12	Heteromastus	12	19	Mytilus	12	38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51	Benthic feeding birds
16	Corophium arenarium	13	20	Cerastoderma		52, 53, 54	Herbivorous birds
17	Corophium volutator	14	21, 23	MyaTharyx	13	55	Sediment bacteria
13	Lanice conchilega	15	24	Macoma	14	56	Meiobenthos
15	Pygospio elegans	16	14	Nereis	15	57	Suspended POC
19	Mytilus edulis	17	18	Gammarus	16	58	Sediment POC
20	Cerastoderma edule	18	22, 25, 26	Benthic invertebrate omnivores	17	59	DOC
21	Mya arenaria	19	27, 28	Crabs	18		
23	Tharyx killariensis	20	29	Nepthys			
24	Macoma balthica	21	30, 31	Gobies			
14	Nereis diversicolor	22	32, 33	Flat fishes			
18	Gammarus	23	34	Herring			
22	Small polychaetes	24	35, 36, 37	Demersal fish			
26	Small Crustacea	25	38, 39	ShellduckEider			
25	Phyllodocidae	26	41, 42	Plovers			
27	Carcinus maenas	27	43, 44	Small waders			
28	Crangon crangon	28	45, 46	Large waders			
29	Nephthys hombergi	29	47, 48, 49	Gulls			
34	Herring	30	50, 51	Mallard other birds			
30	Pomatoschistus minutus	31	52, 53	Herbivorous birds			
31	Pomatoschistus microps	32	55	Sediment bacteria			
32	Pleuronectes platessa	33	56	Meiobenthos			
33	Pleuronectes flesus	34	57	Suspended POC			
35	Whiting	35	58	Sediment POC			
36	Cod (kabeljauw)	36	59	DOC			
37	Bull rout						
38	Shelduck						
39	Eider						
40	Oystercatcher						
41	Avocet						
42	Golden plover						
43	Knot						
44	Dunlin						
45	Bar-tailed godwit						
46	Curlew						
47	Black-headed gull						
48	Common gull						
49	Herring gull						
51	Mallard						
50	Other birds						
52	Pintail						
53	Widgeon						
54	Brent goose						
55	Sediment bacteria						
56	Meiobenthos						
57	Suspended POC						
58	Sediment POC						
59	DOC						

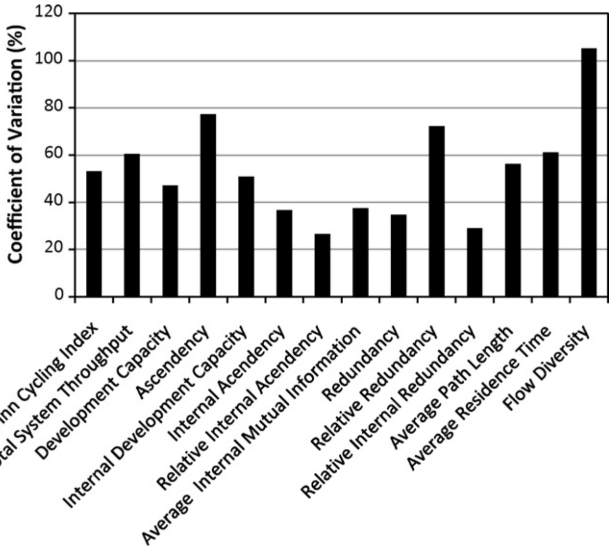

Fig. 1. Coefficients of variation of the percent differences between selected system indices of balanced and unbalanced flow models of six intertidal subsystems of the Sylt–Rømø Bight ecosystem, German Wadden Sea.

3.2. Consequences of aggregation

The grouping of species into single compartments of ecosystem network is universally practiced. There may be many reasons why this is done, but one of the major reasons is the lack of information on all the species comprising the system. For example, phytoplankton, microbenthic algae, bacteria, and meiofauna, to mention but a few, are lumped because of the difficulty to segregate the composite species taxonomically in these communities, or to assess their energetics individually. More is usually known of species at higher trophic levels, such as fish, birds, and other top predators. Usually species are grouped according to trophic similarities such as feeding mode or diet.

It is important to note that most of what falls under the rubric of "Food Web Theory" (e.g. Pimm, 1982; Paine, 1988) treats only binary connections and ignores the relative weights of the connections. For the most part, the same lacunae characterize much of the work in social networks (although Luczkovich et al. (2003) do make allowances for weightings). Cohen et al. (1993) remarked that "When quantitative information about the strength of feeding links is collected, . . . lumping organisms into trophic species may obliterate differences in the strengths of connections between different kinds of organisms that have identical sets of predators and prey." To avoid that and similar ambiguities, other investigators have developed "Ecological Network Analysis" to emphasize and treat the quantitative differences among the manifold connections. As regards the problems that Cohen cites with aggregation, Hirata and Ulanowicz (1995) have proposed a method of aggregation according to the optimal behavior of a functional index such as ascendency (A), while Abarca-Arenas and Ulanowicz (2002) pointed out that species aggregation may affect both the final values of system indices (such as ascendency), as well as changing the global structure of the trophic network. Allesina et al. (2005) addressed the serious consequences of the aggregation of detritus pools (commonly DOC, suspended POC, and sediment POC) into one compartment on the results of network analysis, while the important role of detritus in the cycling of energy in ecosystems is discussed by Fath and Halnes (2007). Johnson et al. (2009) assessed the effects of aggregation on system indices using direct and inverse methods. They concluded that these metrics are sensitive to aggregation, particularly when aggregations are made low in the food web, confirming the findings of Fath and Halnes (2007).

The original 59 compartment balanced network model of the Sylt–Rømø Bight has been described and analyzed in detail by Baird et al. (2004) using network analysis. This 59 compartment model was reduced to 36 and 18 compartment models for comparison with other system models. The aggregations of species into trophic guilds were based on the knowledge of the biologists working for many years on the ecology of the Bight. Table 2 illustrates the aggregations and Table 3 the differences in system properties, derived from network analysis, between the three models.

For this second investigation, we have also calculated the impact that aggradation has on additional network properties used in network environ analysis (Patten, 1981, 1982; Fath and Patten, 1999; Fath, 2007). In this environ analysis, the main aim is to ascertain the role that indirect, or higher level, pathways (as expressed in the powers of the pertinent flow matrices) has on the overall organization of the system. Specifically, we look at total system throughflow (TSTF), flow partitioning (boundary, first passage, and cycled), and the network properties: indirect effects, synergism, mutualism, homogenization, and amplification. Since these have all been described elsewhere only brief overview is given here. First, note there is a difference between the total system throughput (TSTP), described above, and total system throughflow (TSTF). These differences are described clearly in Latham (2006), in that TSTP is the sum of all link magnitudes whereas, TSTF is the sum of compartmental throughflow, Thus, TSTP > TSTF since it counts both inputs and outputs simultaneously. The flow partitioning is a more refined way to allocate the flow to each node according to whether it originated directly from external import, or internal without or with cycling. Latham (2006) also contains a nice discussion of the different internal cycling measures.

Strength of indirect effects is measured as the ratio of all flow carried on higher order pathways versus the direct flow. The synergism ratio is the degree to which a network exhibits quantitative positive utility (value), mutualism the degree of qualitative positive utility (ratio of mutualists to competitors), homogenization, the amount of mixing due to indirect flow connections, and amplification, the ratio of the number of compartments which receive more than one unit of integral (direct plus indirect flow). All these measures provide different perspectives of viewing the impact of structural connectivity and flow cycling within the system. Except for the last one, amplification, these properties are usually observed to be greater than one in ecological networks.

Table 3 shows negligible differences in the indices between the original 59 model and the aggregated 36 compartment model. Only the calculation of the trophic efficiency, number of cycles, the FCI, and the overhead on imports differ significantly more than 5% between these two aggregations. It seems that these attributes could be the most sensitive to compartmental aggregation. The network environ properties were also generally invariant (<6.5%) under the aggradation from 59 to 36 compartments with only amplification showing large difference. The amplification ratio is particular sensitive because of the small numbers involved. Essentially, the difference was 9 out of 3422 possibilities for $n = 59$ and 7 out of 1260 for $n = 36$. In both cases, the presence of amplification was rare. The differences between the 59 and 18 aggregated compartment models and between the aggregated 36 and 18 compartment models are much higher than those between the 59 and 36 models. This could be because the initial aggregations (59–36) condensed the less important compartments while further aggregation forces one to amalgamate more important compartments. The trophic efficiency, which increased towards the smaller aggregations, and number of cycles, which decreased towards the smaller 18 compartment model, appear to be the most affected by the aggregation process as mentioned above. Other large differences

Table 3

Global measures of the Sylt–Rømø Bight ecosystem. The original 59 compartment model was aggregated into models consisting of 36 and 18 compartments, respectively.

Attribute Model compartments	Value 59	Value 36	% Difference 59–36 compartments	Value 18	% Difference 59–18 compartments	% Difference 36–18 compartments
NNP efficiency (%)	57.5	57.5	0.00	57.5	0.00	0.00
APL (trophic steps)	2.789	2.788	−0.02	2.868	2.85	2.87
ART (resident time, days)	19.17	19.54	1.91	19.29	0.63	4,8791.27
Trophic efficiency of system (geometric mean, %)	2.56	3.61	41.02	4.86	89.84	34.63
Detrivory:herbivory ratio	1.44:1	1.44:1	0.00	1.44:1	0.00	0.00
Number of cycles	1,197	1,077	−10.03	107	−91.06	−90.06
Finn cycling index (%)	17.21	16.00	−7.03	16.14	−6.22	0.88
Total system throughput (TSTP, mgCm^{-2} day^{-1}, bits)	6,752	6,659	−1.38	6,693	−0.87	0.51
Development capacity (DC, mgCm^{-2} day^{-1}, bits)	32,945	32,813	−0.40	30,565	−7.22	−6.85
Ascendancy (A, mgCm^{-2} day^{-1}, bits)	12,793	12,758	−0.27	12,588	−1.60	−1.33
Relative ascendancy (A/DC, %)	38.83	39.9	2.50	41.18	6.05	3.47
Average mutual information AMI (Normalized Ascendancy, A/TST)	1.895	1.916	1.12	1.881	−0.74	−1.83
Overheads on imports (Oi, mgCm^{-2} day^{-1}, bits)	3,424	3,192	−6.78	3,226	−5.78	0.00
Overheads on exports (Oe, mgCm^{-2} day^{-1}, bits)	1,040	1,058	1.73	1,050	0.96	−0.76
Dissipative overheads (Od, mgCm^{-2} day^{-1}, bits)	4,576	4,522	−1.18	4,344	−5.07	−3.94
Redundancy (R, mgCm^{-2} day^{-1}, bits)	11,112	10,624	−4.39	9,357	−15.79	−11.93
Relative redundancy (R/DC, %)	33.7	33.7	0.00	30.6	−9.20	−9.20
Normalized redundancy (R/TST)	1.646	1.595	−3.06	1.398	−15.05	−12.37
Internal development capacity (DCi, mgCm^{-2} day^{-1}, bits)	17,577	17,152	−2.42	15,716	−10.59	−8.37
Internal ascendancy (Ai, mgCm^{-2} day^{-1}, bits)	6,465	6,528	0.97	6,359	−1.64	−2.59
Relative internal ascendancy (Ai/DCi, %)	36.78	38.10	3.59	40.46	10.01	6.20
Internal redundancy (Ri, mgCm^{-2} day^{-1}, bits)	11,112	10,624	−4.39	9,357	−15.79	−11.93
Realtive internal redundancy (Ri/DCi, %)	63.2	61.9	−2.02	59.5	−5.82	−3.88
Overall connectance	2.280	2.273	−0.31	2.099	−7.94	−7.66
Intercompartmental connectance	2.845	2.816	−1.02	2.335	−17.93	−17.08
Foodweb connectance	2.200	2.186	−0.64	1.733	−21.23	−20.72
Flow diversity (DC/TST, %)	4.879	4.928	0.99	4.567	−6.41	−7.32
Total system throughflow (TSTF, mgCm^{-2} day^{-1}, bits)	4,879	4,786.6	−1.89	4,843.9	−0.71	1.20
Boundary flow (%)	38.38	38.14	−0.63	38.17	−0.55	0.08
First passage flow (%)	52.2	52.6	0.77	52.4	0.44	−0.32
Cycled flow (%)	9.42	9.26	−1.70	9.4	−0.21	1.51
Average change over all system properties			0.17		−4.55	−5.60
Dimensionless network environ properties						
Indirect effect ratio	1.1397	1.2129	6.42	1.3276	16.49	9.46
Synergism ratio	3.2045	3.1925	−0.37	3.3062	3.17	3.56
Mutualism ratio	0.7888	0.8357	5.95	1.0124	28.35	21.14
Homogenization ratio	1.7343	1.7722	2.19	1.8728	7.99	5.68
Amplification ratio	0.0026	0.0056	115.38	0.0131	403.85	133.93
Average change overnetwork environ properties			25.91		91.97	34.75

between the 59 and 18, and 36 and 18 aggregations are noted in the redundancy values and its associated ratios, and in the inter-compartmental and food web connectance indices. It is noteworthy that no large differences were observed in important system indices such as the TST, DC, A, relative ascendency, AMI, and flow diversity. Network environ properties also showed larger difference in the aggradation to 18 compartments, particularly in the indirect effects, mutualism, and amplification. The smaller model had across the board higher values in each network environ property. The indirect effects jumped almost 10% from the 36 compartment version, and the mutualism value crossed the unitary threshold indicating that this model, unlike the others, now has more mutualistic relations than competitive ones. This is consistent with earlier results that show smaller networks are more mutualistic (Fath, 2004). Regarding amplification, while there were only 4 out of 306 possible occurrences this still represented a large increase its ratio.

4. Concluding remarks

In a study to determine the impact of size on network properties, Fath (2004) constructed models ranging from 60 to 600 compartments using a community assembly rule algorithm. Results showed that indirect effects and homogenization increase with model size, whereas synergism decreases with size. In that study, the networks did not represent aggradations of specific models. The ENA results discussed here were derived from highly articulated networks of the Sylt–Rømø Bight ecosystem based on reliable quantitative empirical data. Confining analysis to quantitative networks fulfills a major desideratum put forth by Cohen et al. (1993). Having access to quantified networks allows one to evaluate the differences between indices of balanced and unbalanced models, which comparison remains impossible using “Food Web” methodology. Results indicate persistent increases in the indices of balanced models with the exception of the FCI, and the internal ascendency and its associated ratios. Balancing of original models clearly affects the ENA outcomes; it is the magnitude of the differences that need scrutiny before the outcomes of balanced models can be accepted. The same principle applies when the aggregation of species in trophic or other guilds are considered.

Acknowledgements

We thank the Alfred Wegener Institute for Polar and Marine Research (AWI) for providing the facilities for this project. DB would like to thank the AWI and the University of Stellenbosch for support during the course of this study.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2009.09.008.

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