

Quantification of species as functional units within an ecological network

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ABSTRACT

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A new index referred to as “scope for change in ascendancy” has been suggested recently by Genoni and Pahl-Wostl to measure overall ecosystem performance. In this paper we derive an amended version of their original formulation that we suggest be called the “scope for growth and development.” The amended measure can be decomposed into terms that correspond to the contribution of each system component toward total system performance. Those system compartments that are acknowledged often to exert top-down trophic control on their supporting resources make strong positive contributions to the community scope, whereas those thought to limit the availability of resources from below impart negative terms to the new scope index. On a per unit flow basis, system performance seems to be most sensitive to exports of usable materials from the system and least affected by losses due to dissipation. The qualitative description of the system performance in terms of contributions by its components appears to be robust with respect to the level of aggregation of system elements.

INTRODUCTION

Historically, ecology has been divided along the lines of autecology, or the study of individual organisms, and synecology, the study of groups of organisms associated together as a unit (Odum and Odum, 1959). The problem with such categorization is that it is sometimes an impediment to putting theory into practice. For example, the burgeoning field of ecotoxi-

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cology is still mostly concerned with the effects of toxics on particular target organisms, when it should be devoted more to describing how such impacts are manifested as changes in the organizational pattern of the entire community.

It is a cliché that in ecosystems, each component can affect every other. But as anyone who has studied whole systems is aware, any impact upon a particular component is propagated forcefully to a few others, moderately to many more and almost not at all to the remaining majority. Thus, there have been many efforts to quantify the sensitivity of a given population to an impact occurring somewhere else in the system. Perhaps the most oft-employed technique for this purpose is first to simulate the impacted system as if it were a mechanical clockwork, i.e., to perform ecosystems simulation modeling. Within the framework of simulation modeling one then may compute the sensitivities of any given population to changes in others. For example, O'Brien and Wroblewski (1973) catalogued the sensitivities of the various components of the marine pelagic community off the West Coast of Florida and concluded that, on the average, most components exhibited greatest sensitivity to changes in the population level of mesozooplankton.

Of course, ecosystems are not mechanical clockworks, and overlapping circuits of non-linear feedbacks can cause ecosystems dynamics to resemble organisms more than they do machines. As a result, simulation models possess only very limited prediction ability, and to complement their investigations of whole systems, ecologists have turned to the analysis of trophic structures, i.e., networks of material and energy transfers. Matrix methods developed to trace indirect effects in economic systems (Leontief, 1951) have been adapted for ecology to quantify the amounts of a particular conservative medium that flow along concatenated trophic pathways of arbitrary lengths (Hannon, 1973; Patten et al., 1976; Szyrmer and Ulanowicz, 1987). Although such input-output (I-O) methods treat only material causalities, it is commonly assumed that the results are correlated as well to the pathways of efficient causalities, i.e., dynamical interactions. Within the matrix framework of I-O analysis, it becomes possible to quantify the sensitivities of ecosystem components one to another (e.g. Bossermann, 1981; Szyrmer and Ulanowicz, 1987).

The problem with all the sensitivity analyses mentioned thus far is that they deal with indirect influence on a bilateral basis, that is, how population x responds to changes in component y . One infers from the aggregate of such pairwise interactions how sensitive the overall system structure might be to changes in each component. It would be preferable if one could identify an index of overall community structure and investigate how that measure is affected by impacts to each part of the system.

To date, relatively few community properties have been investigated. Community production and respiration (Odum, 1969), system throughput or power (Odum and Pinkerton, 1955), and aggregate available work or exergy (Jørgensen and Mejer, 1981; Schneider and Kay, in press) are several extensive properties of ecosystems that have been suggested as possible measures to characterize system status. None of these, however, appears to address the trophic structure of the system, or how it is linked together (an intensive attribute). It was Rutledge et al. (1976) who first employed information theory and conditional probabilities to quantify the degree of organization inherent in a flow structure.

Ulanowicz (1980, 1986) has suggested that autocatalytic feedbacks are agents which configure ecosystems and engender changes in *both* their extensive and intensive attributes. Accordingly, he proffered an analog to the thermodynamic Gibbs or Helmholtz work functions, which he called the system "ascendency". Ascendency is the product of an extensive factor, the activity level (as measured by the total system throughput), times the average mutual information of the flow structure. Following Rutledge et al. (1976), the various fractions which observed macroscopic flows comprise of the compartmental and system throughputs can be taken as estimators of the transition probabilities that appear in the formula for the mutual information of a given weighted network. That is, if: T_{ji} is the measured flow from compartment j to compartment i ; $T_{.i}$ is the sum of all the inputs into i ; $T_{j.}$ is the sum of all outputs from j ; and T is the total system throughput; then the system ascendency, A , of an n -compartment system becomes

$$A = \sum_{j=0}^n \sum_{i=1}^{n+2} T_{ji} \log \left(\frac{T_{ji} T}{T_{j.} T_{.i}} \right) \quad (1)$$

where exogenous inputs to the system emanate from virtual compartment 0 (zero), exports of useful materials or energy exit the system into the figurative compartment $n + 1$, and dissipations are imagined to be collected into compartment $n + 2$.

SYSTEM SENSITIVITIES

We choose A as the most comprehensive index available that incorporates both system size and structure. We now wish to demonstrate how one may compute the sensitivities of this overall property to changes in its various constituent elements. One begins by calculating the sensitivities of A to minute changes in each component flow, i.e.,

$$\frac{\delta A}{\delta T_{ji}} = \log \left(\frac{T_{ji} T}{T_{j.} T_{.i}} \right) \quad (2)$$

Relationship (2) was derived recently by Gannon (1992). Earlier, Ulanowicz (1986) had identified the right hand side of (2) as a generalized ecological "force" in analogy to the force-flux couples of irreversible thermodynamics (Onsager, 1931). Unfortunately, he did not follow through with a systematic investigation of the utility of these "forces".

In what follows we shall call the partial derivative in (2) the weight, W_{ji} , of a flow as distinct from its straightforward physical magnitude, T_{ji} . Accordingly, W_{ji} attains high values if

$$(a) \frac{T_{ji}}{T_j} \text{ or } \frac{T_{ji}}{T_i} = 1$$

and/or

$$(b) \frac{T}{T_j} \text{ or } \frac{T}{T_i} = \gg 1$$

Each of these conditions describes a type of flow specificity: (a) when only a single exchange leaves or enters a particular compartment, and (b) when the flow in question leaves or enters a compartment that makes but a minor contribution to the total system throughput. The two cases pertain to different hierarchical levels. Condition (a) refers to the specificity which a single flow exhibits relative to the level of the individual compartment. Condition (b) quantifies the specificity of an individual compartment relative to the level of the whole system. This latter condition implies that respirations and other flows that enter high throughflow compartments along with many other contributors will have small weights.

As an example of the rather low weights assigned to respirations, we consider the network of carbon flows among the 36 major compartments of the mesohaline Chesapeake ecosystem (see Fig. 1 and Baird and Ulanowicz, 1989). The first two columns in Table 1 contain the aggregated weights for inputs and outputs, respectively. One sees that the mean weight of one unit of carbon being respired is 1.1, whereas that for a unit entering the top predator bluefish is 11.5. Because they usually comprise small fractions of the total system activity, exchanges occurring at higher trophic levels tend to be highly specific and therefore are usually weighted more. Despite their high weightings, the contributions of the upper trophic level flows to the system ascendancy usually are not large, because the flows themselves are disproportionately small. One sees this from the definition of ascendancy (eqn. 1) rewritten as

$$A = \sum_{j=0}^n \sum_{i=1}^{n+2} T_{ji} W_{ji} \quad (3)$$

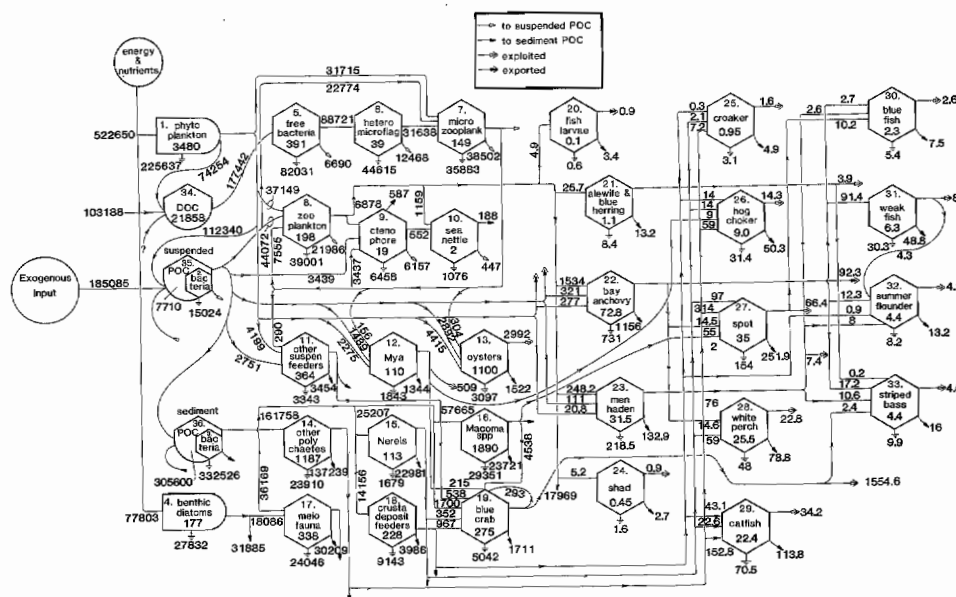


Fig. 1. Exchanges of carbon (in $\text{mg m}^{-2} \text{ y}^{-1}$) among 36 compartments comprising the ecosystem of the mesohaline reach of Chesapeake Bay. Values inside the boxes refer to standing stocks of carbon in mg m^{-2} .

SYSTEM PERFORMANCE AND FLOW STRUCTURE

One may regard each compartment as embedded in a structural environment comprised of the flows linking it to other compartments (Fig. 2). The total amount which compartment i contributes to the system ascendancy is

$$A_i = \sum_{j=0}^n T_{ji} W_{ji} + \sum_{k=1}^{n+2} T_{ik} W_{ik} \quad (4)$$

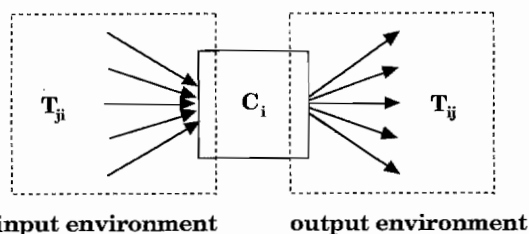


Fig. 2. An arbitrary ecosystem compartment, i , showing its input and output environments.

The various terms in (4) are partitioned into two groupings – the first generated by all flows entering i (its input environment) and the second by flows leaving i (cf. the environ concept by Patten et al., 1976).

As regards the long-term energy balance for a population or a system, there is a basic asymmetry between the inputs and the outputs. Whenever inputs exceed outputs, the population in question grows, and vice-versa. This amount by which inputs to a compartment exceed its outputs is a measure of its performance and has been termed by Winberg (1960) as its “scope for growth”. Genoni and Pahl-Wostl (1991a) have suggested that anthropogenic impacts on entire ecosystems could be monitored by tracing changes in its overall energy balance. At first they considered using just the difference between aggregate inputs to and exports from the system as a straightforward extension of the “scope for growth” concept to the level of the whole system. It soon became apparent, however, that such an index would be insensitive to the *structure* of the trophic interactions, so an alternative formulation was suggested (Genoni and Pahl-Wostl, 1991b).

We wish to show in the following that one way of introducing the potential for change in trophic structure into the scope for growth is to weight each transfer according to its impact on the whole system. Accordingly, we define

$$fin_i = \sum_{j=0}^n \frac{T_{ji} W_{ji}}{A_i} \quad (5)$$

$$fout_i = \sum_{k=1}^{n+2} \frac{T_{ik} W_{ik}}{A_i} \quad (6)$$

$$\Delta f_i = fin_i - fout_i \quad (7)$$

That is, Δf_i is the difference between the contributions of i 's input and output environments to the total ascendancy, as normalized by its total contribution. It should constitute a sensitive measure for characterizing the performance of compartment i within the context of the overall ecosystem network.

In particular, at steady-state the inputs to and outputs from each compartment balance, and the *structural* differences between the input and output environments alone determine the sign and magnitude of Δf_i . These structural differences may be quantified as the numerical difference between the weighted inputs and outputs

$$\langle W_{*i} \rangle = \frac{\sum_{j=0}^n T_{ji} W_{ji}}{\sum_{j=0}^n T_{ji}} = \frac{\sum_{j=0}^n T_{ji} W_{ji}}{T_i} \quad (8)$$

$$\langle W_{i*} \rangle = \frac{\sum_{j=1}^{n+2} T_{ij} W_{ij}}{\sum_{j=1}^{n+2} T_{ij}} = \frac{\sum_{j=1}^{n+2} T_{ij} W_{ij}}{T_i} \quad (9)$$

$$\Delta W_i = \langle W_{*i} \rangle - \langle W_{i*} \rangle \quad (10)$$

At steady-state $T_i = T_{i*}$, so that under such circumstances (and only then)

$$\Delta f_i = \frac{\langle W_{*i} \rangle - \langle W_{i*} \rangle}{\langle W_{*i} \rangle + \langle W_{i*} \rangle} \quad (11)$$

The W_{ij} , Δf_i and ΔW_i are component weightings that variously can be recombined into an amended version of what Genoni and Pahl-Wostl called the “scope for change in ascendancy”, S , which they suggested as an index of overall system performance. In general

$$\begin{aligned} S &= \sum_{i=1}^n \left(\sum_{j=0}^n T_{ji} W_{ji} - \sum_{k=1}^{n+2} T_{ik} W_{ik} \right) \\ &= \sum_{i=1}^n (T_{0i} W_{0i}) - \sum_{k=n+1}^{n+2} T_{ik} W_{ik} \end{aligned} \quad (12)$$

On the level of the whole system the scope measure includes the external exchanges only as in an energy balance scheme corresponding to the original scope for growth measure. However, each exchange with the environment is given a weighting according to its relevance for the self-organization potential of the whole ecosystem.

A more appropriate name for S might be the “scope for growth and development”, as this phrase indicates more clearly the nature of Genoni and Pahl-Wostl’s extension of the scope of growth concept, while at the same time incorporating the intention of Ulanowicz (1986) that an increase in ascendancy become a quantitative surrogate for the common notions of growth and development. We suggest that the latter term be adopted in all further discourse on the topic.

APPLICATION OF STRUCTURAL INDICES

The utilities of the measures defined in (5) through (10) are best demonstrated by way of some examples. One of the simplest input–output configurations is the linear food chain, like the one illustrated in Fig. 3. Here each compartment receives but a single input from the one preceding it and transfers a fraction k of this input to the next level. If the initial

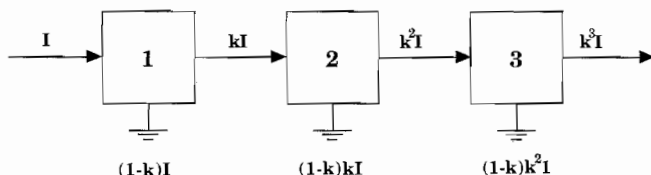


Fig. 3. A linear food chain representing a simple structural element of a trophic network. A flow of magnitude, I enters compartment 1. Each compartment transfers a fraction k to the next higher level and loses a fraction $(1-k)$ as respiration.

input to the chain is I , then the difference between the weighted inputs and outputs for compartment 2 become

$$\begin{aligned}\Delta W_2 &= \frac{kI}{kI} \log\left(\frac{kIT}{IkI}\right) - \frac{k^2I}{kI} \log\left(\frac{k^2IT}{kIk^2I}\right) - \frac{(1-k)kI}{kI} \log\left(\frac{(1-k)kIT}{kIT_d}\right) \\ &= \log\left(\frac{T}{I}\right) - k \log\left(\frac{T}{kI}\right) - (1-k) \log\left(\frac{(1-k)T}{T_d}\right)\end{aligned}$$

where T_d represents the sum of all dissipative flows out of the system. ΔW_2 is zero only when $k = 1$ – a thermodynamic impossibility. Thus, we see that dissipation serves to depreciate the mean weight of *all* outputs, making $\Delta W > 0$ and $\Delta f > 0$ in most of the cases when these differences are calculated across living (i.e. respiring) components.

One sees in Table 1 that ΔW and Δf are indeed positive for 31 of the 33 living compartments. The two exceptions, however, demonstrate that, although thermodynamics imparts a positive bias to ΔW and Δf , it does not entirely determine the sign of these quantities. As intended, the structural configuration strongly influences their actual values.

To illustrate this last point, we have chosen the two extreme cases portrayed in Fig. 4. In case 1 (Fig. 4a) a single input is distributed over many outputs, while in case 2 (Fig. 4b) many inputs are focused into a single (non-respiratory) output. (Thermodynamically speaking, case 2 is impossible and can be only approximated by real components.) For notational convenience we define d as the fraction which any input comprises of the total output from the compartment in which it originates. (Without loss of generality, this may be assumed equal for all input flows in case 2.) The parameter r is the fraction that an output from the compartment in question comprises of the total input into its recipient. (Again, no generality is lost by assuming r to be equal for all outputs in case 1.) By definition, $1 \geq d \geq 0$ and $1 \geq r \geq 0$.

Substituting into the definition for ΔW_i , we see, after simplification, that in case 1, $\Delta W_x = \log(nd/r)$. Similarly, for case 2, $\Delta W_x = \log(d/nr)$. Be-

TABLE 1

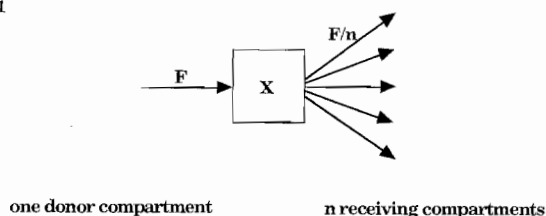
Results for the Chesapeake Bay network shown in Fig. 1

i	NAME ^a	$\langle W_{*i} \rangle$	$\langle W_{i*} \rangle$	ΔW_i	f_{in_i}	f_{out_i}	Δf_i
0	External input		1.9				
1	Phytoplankton	2.2	1.3	0.9	0.62	0.38	0.24
2	Bacteria in susp. POC	3.4	1.0	2.4	0.77	0.23	0.54
3	Bacteria in sedi. POC	2.7	1.5	1.2	0.64	0.36	0.28
4	Benthic diatoms	2.2	1.9	0.3	0.54	0.46	0.08
5	Free bacteria	4.5	2.7	1.8	0.62	0.38	0.24
6	Heterotr. microflag.	4.5	2.1	2.4	0.68	0.32	0.36
7	Microzooplankton	2.4	1.7	0.7	0.58	0.42	0.16
8	Zooplankton	2.0	2.4	-0.3	0.46	0.54	-0.08
9	Ctenophores	3.4	1.7	1.7	0.67	0.33	0.34
10	Seanettle	5.4	1.3	4.1	0.81	0.20	0.61
11	Other susp. feeders	2.0	1.7	0.3	0.55	0.45	0.10
12	<i>Mya arenaria</i>	2.0	1.8	0.2	0.53	0.47	0.06
13	Oysters	2.0	2.9	-0.8	0.41	0.58	-0.17
14	Other Polychaetes	2.7	2.0	0.7	0.57	0.43	0.14
15	Nereis	2.7	2.3	0.4	0.54	0.46	0.08
16	Macoma SPP	2.7	1.7	1.0	0.62	0.38	0.24
17	Meiofauna	2.9	1.5	1.4	0.66	0.34	0.32
18	Crust. deposit feeders	2.7	1.7	1.0	0.62	0.38	0.24
19	Blue crab	4.3	2.0	2.3	0.68	0.32	0.36
20	Fish larvae	5.5	2.3	3.1	0.70	0.30	0.40
21	Alewife + blue herring	5.5	1.9	3.6	0.74	0.26	0.48
22	Bay anchovy	3.7	2.1	1.6	0.64	0.36	0.28
23	Menhaden	3.5	1.9	1.6	0.65	0.35	0.30
24	Shad	5.5	1.9	3.5	0.74	0.26	0.48
25	Croaker	4.7	1.9	2.8	0.71	0.29	0.42
26	Hogchoker	4.8	1.8	2.9	0.72	0.28	0.44
27	Spot	4.4	2.0	2.4	0.69	0.31	0.38
28	White perch	5.3	1.9	3.4	0.74	0.26	0.48
29	Catfish	4.7	1.9	2.9	0.72	0.28	0.44
30	Blue fish	11.5	1.9	9.6	0.86	0.14	0.72
31	Weak fish	10.9	2.1	8.7	0.84	0.16	0.68
32	Summer flounder	10.7	1.9	8.8	0.85	0.15	0.70
33	Striped bass	10.4	1.8	8.5	0.85	0.15	0.70
34	DOC	1.6	4.5	-2.9	0.26	0.74	-0.48
35	Suspended POC	1.2	2.3	-1.1	0.35	0.65	-0.30
36	Sediment POC	1.8	2.7	-0.9	0.40	0.60	-0.20
37	Exports	5.2					
38	Respiration	1.1					

^a The corresponding scientific names are given in the appendix.

cause $n > 1$, and in most cases $d \cong r$, we see that ΔW_x tends to be positive in case 1 and negative in case 2. The reasons for exceptions to this scheme also become apparent. In case 1, ΔW_x would be negative only in the (very

CASE 1



CASE 2

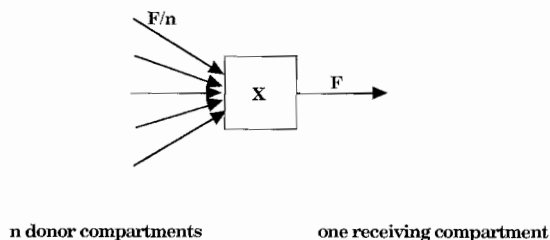


Fig. 4. Two hypothetical extremes of compartmental flow structure, (a) facultative, dispersing a single input among several outputs, and (b) inhibiting, channeling many inputs into but a single outflow.

rare) circumstances that all the recipients were highly specialized *and* compartment x were a very minor predator of its prey. Conversely, ΔW_x in case 2 could become positive only in the unlikely event that it were the dominant predator of all its various prey species and a minor element in the diet of its predator.

Returning to the elements of Table 1, we note that the two compartments with negative ΔW_i (and Δf_i) are the mesozooplankton and the oysters, respectively. Both components are filter feeders, having relatively broad diets that include items shared by many other filter feeders (i.e. d is small) and contributing to comparatively few predators, which in turn have relatively narrower diets. Hence, the resemblance of these filter feeders to case 2 is strong enough to overcome the positive bias imparted by their respiratory activities. The remaining negative values belong to abiotic compartments (dissolved and particulate carbon) that exhibit almost no respiration, receive input from many sources and are consumed largely by populations that specialize as detritivores. Hence, they strongly resemble case 2, and all have negative values of ΔW_i .

DISCUSSION AND CONCLUSIONS

The implications of scope for growth and development to the ecosystem dynamics of the Chesapeake ecosystem become evident once one studies

the extremes in ΔW_i . Those populations contributing the most per capita to S include the populations at the top of the food chain, e.g., bluefish, summer flounder, weakfish, striped bass and (interestingly) the seaneettle. Their inputs are weighted strongly because they tend to be specialists and to be the dominant predators on most of their prey. At the same time, their significant respirations per unit biomass do not weight their outputs proportionately, because aggregate respiration from these species is but a small fraction of total community respiration. We note that it is these compartments that are most likely to exert top-down control on the pyramids of resources that support them.

At the other extreme in ΔW_i are those components that serve to focus and concentrate material and energy before it can flow elsewhere in the system. Such components include the suspended POC, sediment POC, DOC, oysters and mesozooplankton – all with negative ΔW_i . A failure of these system elements to carry out their transfer functions would negatively affect those populations higher up the trophic chain. As Fig. 4b suggests, case 2 species are capable of acting as a “bottleneck” in the pattern of material and energy flows, so that the system components with negative ΔW_i are those most likely to exert bottom-up control.

These examples should make it clear that the sign of the measure of a component’s structural environment does not convey its importance to the functioning of the overall system, but rather indicates *how* it may contribute. The Δf_i and the ΔW_i themselves represent analytical tools for the investigation of structural characteristics of a given network configuration indicating:

- the functional role of a compartment (and its seasonal variation);
- the diversity of functional elements within a system.

Focusing on the presumably anthropogenically induced changes in a network’s flow structure over time, our hypothesis is that a drop in Δf_i (or ΔW_i) should signify a negative impact of that species on overall system performance. Whenever a large, positive Δf_i decreases, the compartment in question probably is exerting less top-down influence on the trophic web than it previously had been. In corresponding fashion, whenever a component with a large, negative Δf_i becomes even more negative, it is somehow impeding the circulation of material and energy through the remainder of the system.

It is interesting to generalize about how weightings usually correlate with the four types of system flows. The exports of usable medium from the system tend to have the heaviest W_{ij} ’s, followed closely by the exogenous inputs and the internal transfers rank third. The respirations frequently receive the smallest weightings. These rankings accord with the intuition that losses of high quality medium from a particular compartment to

outside the system are more costly than losses from the same compartment to another within the system, where it may still support other community activities. Medium being dissipated from the system appears to be the most affordable loss in that it minimally impacts overall community function.

Accordingly, the scope of the whole system defined in (12) attains high values if the energy enters the system via a multitude of specialized compartments and if it is lost from the system mainly via dissipation. Such behaviour characterizes a diverse and highly autonomous system. Let us

TABLE 2

Results for the aggregated Chesapeake Bay network

<i>i</i>	NAME	$\langle W^*_i \rangle$	$\langle W_i^* \rangle$	ΔW_i	f_{in_i}	f_{out_i}	Δf_i
0	External Input		1.9				
1	Phytoplankton	2.2	1.3	0.9	0.62	0.38	0.24
2	Bacteria in susp. POC	3.4	1.0	2.4	0.77	0.23	0.55
3	Bacteria in sedi. POC	2.7	1.5	1.2	0.64	0.36	0.28
4	Benthic diatoms	2.2	1.9	0.3	0.54	0.46	0.09
5	Free bacteria	3.4	2.7	0.6	0.62	0.38	0.25
6	Heterotr. microflag.	4.5	2.1	2.4	0.68	0.32	0.35
7	Ciliates	2.4	1.7	0.7	0.58	0.42	0.16
8	Mesozooplankton	2.0	2.4	-0.3	0.46	0.54	-0.08
9	Ctenophores	3.4	1.7	1.7	0.67	0.33	0.33
10	Seanettle	5.4	1.3	4.1	0.81	0.20	0.61
11	Other susp. feeders	2.0	1.6	0.4	0.55	0.45	0.10
12	Oysters	2.0	2.9	-0.8	0.41	0.58	-0.17
13	Other deposit feeders	2.7	1.8	0.9	0.60	0.40	0.21
14	Meiofauna	2.9	1.5	1.4	0.66	0.34	0.31
15	Blue crab	3.2	2.0	1.2	0.62	0.38	0.24
16	Filter feeding fish	3.7	2.0	1.7	0.65	0.35	0.29
17	Benthic feeding fish	4.2	1.9	2.3	0.69	0.31	0.38
18	Pelagic carnivores	10.1	1.9	8.2	0.84	0.16	0.68
19	DOC	1.6	4.5	-2.9	0.26	0.74	-0.49
20	Suspended POC	1.2	2.3	-1.1	0.35	0.65	-0.30
21	Sediment POC	1.8	2.7	-0.9	0.4	0.6	-0.20
22	Exports	5.2					
23	Respiration	1.0					

Compartments of the network as listed in Table 1 were aggregated into groups of trophically equivalent species:

Resolved (Table 1)	aggregated (Table 2)
11 + 12	11
14 + 15 + 16 + 18	13
20 + 21 + 22 + 23 + 24	16
25 + 26 + 27 + 28 + 29	17
30 + 31 + 32 + 33	18

recall that the weighting of a flow corresponds to the sensitivity of the whole system's ascendancy to an incremental change in that flow. Short-term changes in flows will affect the organization of the whole system in the long run. One expects effects to be most pronounced for a reduction in the diversity of the receiving input compartments, for a decrease in the magnitude of the inputs, or for energy losses from the system via external exports. The various changes at the system's boundaries then may be traced to the changes they engender in the input and output environments of the individual compartments. Thereby one may achieve a better understanding of the dualistic interplay between the level of the constituent elements, and the level of the system as a whole. An additional goal might be to identify the most sensitive compartments and(or) flows of an ecosystem so as to provide focus for work on conservation of individual species and monitoring of system performance.

A concern which many express about whole systems analyses is to question how robust the conclusions remain in the face of changes in the level of system aggregation. To test how the components of S change after aggregation, we coalesced the 36 compartments designated by Baird and Ulanowicz (1989) into 21 compartments by lumping 20 of the original boxes into 5 new components in such a way that functionally nearly equivalent species were grouped together (see Hirata and Ulanowicz, 1985). The weightings used in the calculation of the scope of the aggregated system (see eqn.'s (12) and (13)) are shown in Table 2. One sees that all of the qualitative conclusions drawn thus far could have been supported as well by the components of the reduced system.

We conclude by recommending the "scope for growth and development" as a robust gauge of overall system performance. When this index is decomposed into terms that correspond to system components or to transfers among those elements, the values of these terms provide clues as to how each entity is functioning within the context of overall material and energy processing. Such analysis provides a much-needed quantitative bridge between studies of population level phenomena and the observations on the behavior of entire ecosystems. We feel that after further testing and application the scope measure should develop into a fundamental tool useful in synecology.

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APPENDIX

Scientific names of species whose common names are used in the text

Common name	Scientific name
Alewife	<i>Alosa pseudoharengus</i>
Atlantic croaker	<i>Micropogonius undulatus</i>
Bay anchovy	<i>Anchoa mitchilli</i>
Blue crabs	<i>Callinectes sapidus</i>
Bluefish	<i>Pomatomus saltatrix</i>
Sea catfish	<i>Arius felis</i>
Clam, soft shell	<i>Mya arenaria</i>
Herrings	<i>Clupeidae</i> (family)
Hogchoker	<i>Trinectes maculatus</i>
Atlantic menhaden	<i>Brevoortia tyrannus</i>
Oyster, American	<i>Crassostrea virginica</i>
Perch	<i>Percidae</i> (family)
Seanettle	<i>Chrysaora quinquecirrha</i>
Shad, American	<i>Alosa sapidissima</i>
Striped bass	<i>Morone saxatilis</i>
Summer flounder	<i>Paralichthys dentatus</i>
Spot	<i>Leiostomus xanthurus</i>
Weakfish	<i>Cynoscion regalis</i>
White perch	<i>Morone americana</i>

100

100