Ulanowicz, R.E. and F. Wulff. Comparing ecosystem structures: The Chesapeake Bay and the Baltic sea. pp. 140-166

Reprinted from

Jonathan Cole Gary Lovett Stuart Findlay
Editors

Comparative Analyses of Ecosystems

Patterns, Mechanisms, and Theories

Printed in United States of America.

Springer-Verlag
New York Berlin Heidelberg London
Paris Tokyo Hong Kong Barcelona

8

Comparing Ecosystem Structures: The Chesapeake Bay and the Baltic Sea

ROBERT E. ULANOWICZ AND FREDRIK WULFF

Abstract

Much can be learned about the differences in how two distinct ecosystems are functioning by studying their respective quantitative networks of trophic exchanges. The feeding processes occurring in the ecosystems of the Baltic Sea and the Chesapeake Bay have been parsed into similar 17-node networks of carbon flows, and the use of network analysis to compare the structures reveals that the Baltic ecosystem functions less as a hypertrophic system than does the community in the Chesapeake: The diversity of trophic connections is higher in the Baltic community and the specificity of feeding (trophic articulation) is greater there as well. More pathways for recycle are evident in the Baltic system, and they involve a larger proportion of higher species. Trophic efficiencies are generally greater in the Baltic than they are in the Chesapeake. On a relative basis, about four times as much carbon fixed in primary productivity reaches the fishes of the Baltic than is transferred up the trophic web of the Chesapeake. This disparity is explained in part by a large indirect subsidy that Chesapeake fishes receive from inputs of allochthonous carbon that is processed for them by the benthic community of deposit feeders.

Introduction

The reasons for comparing ecosystems are both academic and practical. On the academic side, by juxtaposing different ecosystems, or configurations of the same ecosystem at different times, one hopes to discover why and how natural communities come to be structured as they are (e.g., Odum 1969). Motivating this activity is the widespread (but not universal) belief that ecosystems develop in a way that can be generalized and possibly quantified.

While academicians may be concerned with the process of ecosystems “becoming,” the popular lay belief seems to be that ecosystems already

Analysis and synthesis of grassland ecosystem dynamics. In: *Patterns of Primary Production in the Biosphere*, H. Leith, ed. Dowden Hutchison & Ross, Stroudsburg, pp. 199–204.

Whicker, A.D. and J.K. Detling. (1988). Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.

White, T.C.R. (1976). Weather, food and plagues of locusts. *Oecologia* 22:119–134.

Wiegert, R.G. and F.C. Evans. (1967). Investigations of secondary productivity in grasslands. In: *Secondary Productivity of Terrestrial Ecosystems*, K. Petrusewicz, ed. Krakow, Poland, pp. 499–518.

Wielgolaski, F.E. (1975). Functioning of Fennoscandian tundra ecosystems. In: *Fennoscandian Tundra Ecosystems*, F.E. Wielgolaski, ed. Springer-Verlag, Heidelberg, pp. 300–326.

exist in some ideal natural state that too often is degraded by the activities of humankind. Regardless of one's opinions about "ecogenesis," managers are continually being asked to judge how much a particular ecosystem as a whole has been damaged. To be able to render such judgments requires a background of copious ecosystem comparisons that, it is hoped, indicates some fundamental ecological principles.

How to compare ecosystems is no trivial question, as evidenced by the contents of this volume. At the core of the issue stands the matter of scale—which temporal and spatial scales are best for comparing systems?

At the smaller scales, investigating mechanisms behind the fluctuations of individual populations is almost sure to provide useful information about what ails a disturbed ecosystem. Some contend that the mechanistic approach is the only legitimate route to ecological knowledge (e.g., Lehman 1986). But others question the sufficiency of mechanistic descriptions. They contend that cybernetic and homeostatic processes inextricably involve entire groups of populations and function in a way that makes the prediction of overall behavior from a knowledge of the component mechanisms a highly problematic activity at best (e.g., Platt et al. 1981; Ulanowicz 1986).

As an alternative to reductionistic ecology, the investigator might identify one, or at most a few, measurable properties thought to characterize the status of a system. For example, Vollenweider (1969) employed the magnitude of nutrient loading and water residence time to classify the trophic status of lakes. Peters (1986) identified more than 30 other correlations, such as phosphorous burden versus chlorophyll level or fish yield versus nutrient concentration, that have been used to classify aquatic systems in an activity that he calls "empirical limnology." While such phenomenological endeavors afford useful comparisons at the whole-system level, they usually do not divulge exactly where in the system difficulties are arising. Furthermore, marine ecologists would find it hard to pursue an analogous "empirical marine ecology." It is far more difficult to perform experiments in the ocean than in lakes, and at this time one cannot easily identify a number of independent marine ecosystems that would compare with Peters' 48 Canadian Shield lakes.

Ideally, one seeks a comparison of at least two ecosystems that quantifies the differences in the overall structure and allows one to trace the origins of those differences.

Networks—A Bridge between Holism and Reductionism

We wish to argue that a compromise exists between the need for overwhelming amounts of data to pursue reductionism and the often unsatisfactory loss of information inherent in phenomenological holism, such as that advocated by Peters. Ecologists long have been fond of constructing whole-system budgets of material and energy transactions in ecosystems.

Their results are usually represented as a network of exchanges among the elements of the communities under study. Because these frameworks are cast in the material or energetic units common to any system, the task of system intercomparison is greatly facilitated. One could say metaphorically that such quantified networks resemble a skeletal structure of ecosystem processes.

There are investigators who will regard any representation of ecosystems in such simplistic terms as a brutish attempt to sidestep or ignore the wonderful intricacies at play in ecosystems (e.g., Engleberg and Boyarsky 1979). Virtually all naturalists (including these authors) will regret that elements such as mating rituals, territorial displays, or rates of flagellation by algae do not appear explicitly in the network of ecosystem exchanges. Our assumption is not that such processes are unimportant. Quite the opposite: Because they are important, their effects are broadly impressed upon the ecosystem, and, in particular, these nonmaterial agents play a significant (but not exclusive) role in organizing the framework of palpable exchanges. To continue the earlier analogy, the discovery of a skeleton of a prehistorical individual does not allow the anthropologist to perceive directly the physiology or environment of that distant ancestor. However, modern osteologists are able to infer a surprising amount about the life and times of the deceased through a meristic study of its remains.

It should be noted that one may relate the flow network to the "corpus" of an ecosystem without subscribing to the Clementsian notion of the ecosystem as a "superorganism." To claim that an ecosystem possesses structure and undergoes development is not to elevate its ontological status above that of an individual organism. However, the analogy with anatomy does cast the current status of ecosystems science in an enlightening perspective. Leonardo da Vinci sketched the structure of the human body long before the functions of many of the body parts were fully appreciated and certainly before most physiological mechanisms were discovered. Anatomical description was a prerequisite to the advances in physiology that were to follow. Ecology today needs a clearer picture of ecological structure if ever a full understanding of ecosystem functioning is to be achieved some distant tomorrow.

No sooner does one decide to use ecosystem flow networks to effect a "comparative anatomy" than one is immediately beset by two significant practical difficulties: (1) Considerable effort and resources are required to describe quantitatively the networks of two or more ecosystems. (2) The networks that result can be disturbingly complicated, sometimes so complex as to cause one to wonder whether any meaningful comparison is possible.

As regards the first obstacle, progressively more ecosystem networks are being described with moderate resolution (say 15 or more compartments). After enough quantified networks appeared, it was only a matter of time before the probability became high that two or more of them could serve as the basis of a "comparative anatomy." In this instance, Wulff had collected copious data on exchanges in the Baltic Sea ecosystem, while Baird and Ulanowicz (1989) had delimited a counterpart for the Chesapeake Bay. In late 1986, the authors became aware of each other's work and of the potential benefits that might derive from comparing their respective systems.

As for complexity, it lately has been the subject of much interest in physics and biology. Recent work in applied mathematics (described later) allows one to analyze complex networks in a systematic fashion, hereinafter referred to as "network analysis." In what follows, we wish to show how network analysis can be applied to the ecosystem networks of the Baltic Sea and the Chesapeake Bay to identify significant differences and similarities between the two communities.

The Ecosystems and Their Accompanying Networks

Reasonably detailed descriptions of the ecosystems of the Baltic Sea and the mesohaline region of the Chesapeake Bay can be found in Wulff and Ulanowicz (1989). Only a few pertinent observations are repeated here.

The Baltic Sea consists of three major basins, the Baltic proper, the Bothnian Sea, and the Bothnian Bay, which together span an area of 373,000 km^2. The Baltic proper connects over a shallow sill and through the Kattegat Strait to the North Sea (Fig. 8.1A). The average salinity at the surface of the Baltic is barely in the mesohaline range (about 7 ppt). The Baltic proper has a permanent halocline at 65 m, below which salinities range from 10 to 15 ppt. A seasonal thermocline forms during the summer at about 20 m. Salt-water replenishment enters sporadically via the Kattegat and is driven by meteorological events.

The Baltic proper has undergone considerable eutrophication during the last 50 years because of increased anthropogenic nutrient input (Larsson et al. 1985). Anoxic conditions in the deep waters are now common, and the deep sediments have turned anoxic, resulting in the extirpation of some associated benthic species. On the other hand, benthic biomass (Cederwall and Elmgren 1980) and fish catches (Ojaveer 1981) both have increased during the same period.

The Chesapeake Bay is a drowned river valley situated along the middle of the eastern North American coastline that covers a much smaller surface area of 12,500 km^2. The full range of salinities extends along its 290-km length, but attention here will be confined to the mesohaline zone (6–18 ppt) as shown in Fig. 8.1B. The bay has a relatively shallow average depth of only 9 m and exceeds 60 m at only a few isolated spots along its channel. During the summer months, a moderately strong combined halothermocline forms at about 8–10 meters depth.

The Chesapeake has always been slightly eutrophic, but during the past half century (since about 1940) nutrient loads have increased appreciably from domestic sewage and agricultural runoff. During the warmer months,

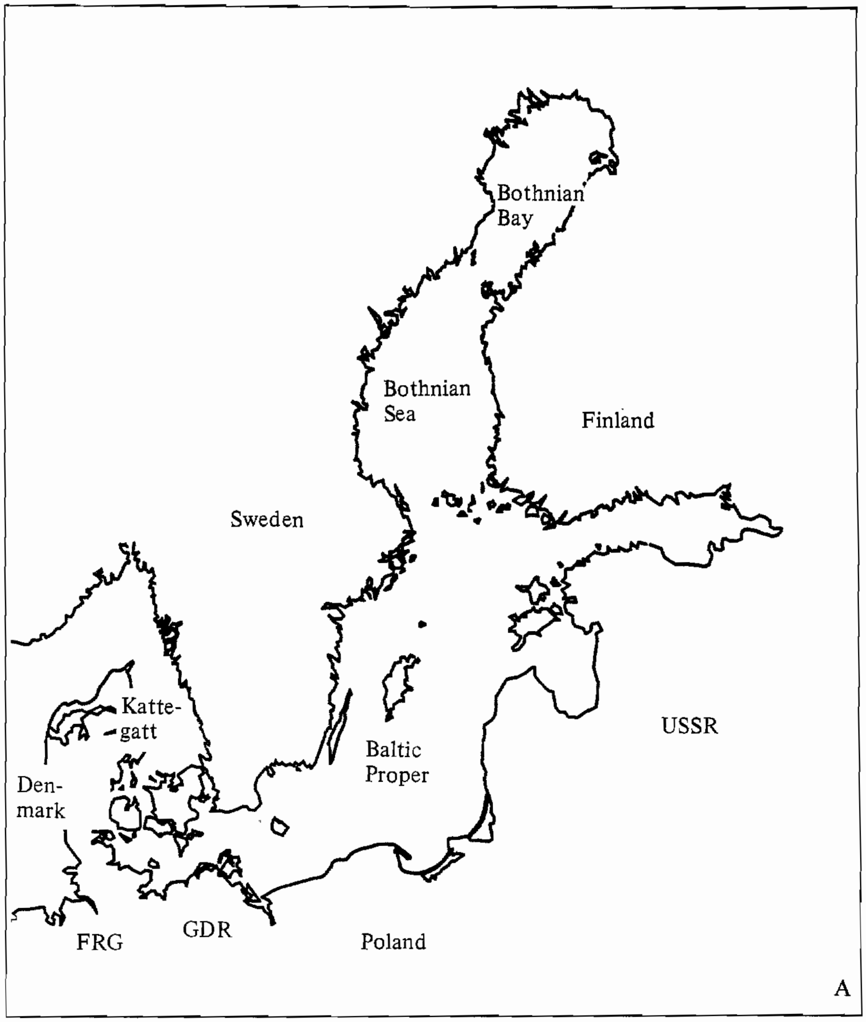

FIGURE 8.1. (A) Baltic Sea. (B) Chesapeake Bay.

anoxia is quite common below the thermocline. During the past 20 years, dinoflagellate blooms (mostly *Gymnodynium splendens*) have been occurring with increasing frequency and duration, and submerged aquatic grasses have fallen to a tiny fraction of their former stocks. Harvests of almost all commercial fish have declined.

One can safely conclude that both systems have been stressed during recent decades; however, it is not obvious which of the two communities is more heavily impacted. The rise in the Baltic fish catch and the corresponding decline in Chesapeake harvests indicate that the Chesapeake might be more hypertrophic. However, there is strong evidence that fish stocks in Chesapeake Bay have been overharvested (MDDNR 1985), and the remain-

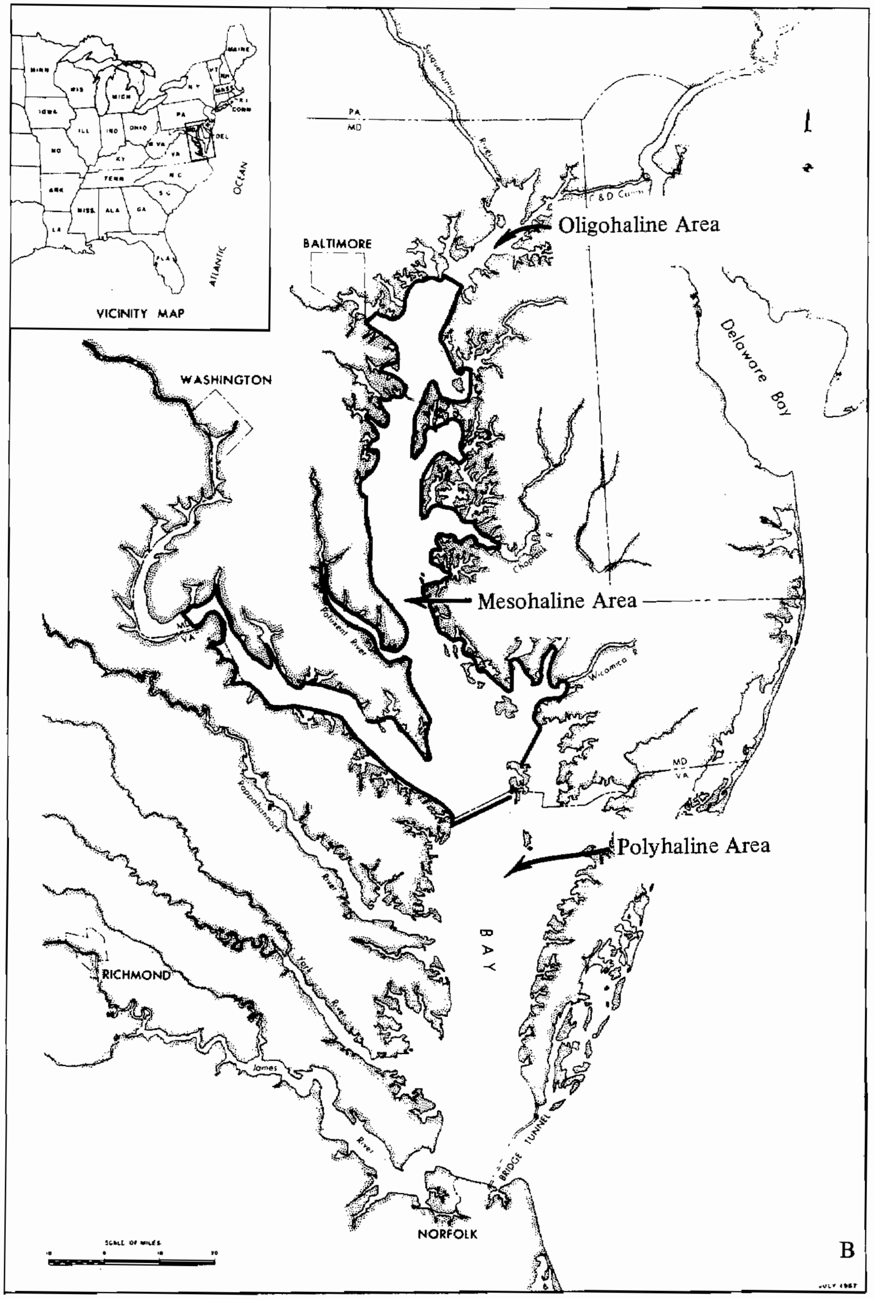

FIGURE 8.1. *Continued*

der of the ecosystem might not be as stressed as its Baltic counterpart. Conventional wisdom holds that the more oligohaline Baltic should be less resilient to nutrient stress. A systematic comparison of the two ecosystem networks should resolve which of the systems has sustained more overall damage, and network analysis should spotlight just where the functioning of each system has been impaired.

The compartments of the ecosystems, their annually averaged standing stocks of carbon (mg C m^{-2}) and the exchanges among them (mg C m^{-2} d^{-1}) are given in Figs. 8.2A and 8.2B. Those wishing to trace the derivation of any particular value in the schematics are referred to Wulff and Ulanowicz (1989) for Baltic values or Baird and Ulanowicz (1989) for Chesapeake magnitudes. The one-to-one correspondence between the compartments of the two networks is intentional. Several of the calculated network properties depend strongly on the choice of compartments, and it was thought that numerical comparisons would remain equivocal unless the systems were partitioned in exactly the same way. Originally, a 17-compartment flow model of the Baltic ecosystem had been created by Wulff, whereas 36 taxa were used by Baird and Ulanowicz (1989) to represent the biotic community in Chesapeake. It was difficult to settle on a common set of compartments into which both the original networks could be aggregated.

Although both networks represent spatial averages over the whole systems, the temporal frequencies of available data differed in the two cases. Networks characterizing the Chesapeake ecosystem during spring, summer, fall, and winter had been described (Baird and Ulanowicz 1989). Most of the Baltic flows were known only as annual averages, although the planktonic community could have been parsed on a finer scale. As data on all flows in both systems were available on an annual basis, this became the interval to be used for the comparison.

This search for common dimensions exemplifies the necessary tendency toward choosing "least common denominators" as the basis for comparison. Just as two fractions cannot be compared until their denominators have been changed to a common (and generally larger) reference value, the comparison of two ecosystems necessitates choosing the least resolved (i.e., largest) spatial, temporal, and taxonomic intervals for which data are available from both systems.

It should be noted in Figs. 8.2A and 8.2B that despite the common compartments, the biomasses, fluxes, and topologies of the networks differ in places. With regard to the differences in topology, during the past 20 years a considerable literature has evolved under the rubric of "food web theory," wherein regularities among trophic topologies of diverse ecosystems have been catalogued (see Cohen 1989 for overview). If one considers only those connections among the living elements in both systems (those numbered 1–12 in Figs. 8.2A and 8.2B), one may readily see how these two networks fit into the overall patterns that Cohen cites and how they stand in relation to each other.

Among the 12 living compartments in each system, there are 20 connections in the Baltic and 18 in the Chesapeake. Cohen cited how most food webs contain roughly twice as many links as the number of nodes. By such a yardstick both networks seem slightly underconnected, but not egregiously so. The convention among food web investigators is to classify taxa as top predators (those that are predators but never prey), intermediate taxa (those that act as both predator and prey), and basal compartments (those that are consumed but never consume other living materials). Cohen states that "on average, top species make up about one fourth of the total, intermediate species about one half, and basal species the remaining fourth." In the Chesapeake the percentages are 33%, 50%, and 17%, respectively, while in the Baltic the proportions are 33%, 58%, and 8%. Although the Baltic is somewhat sparse in top predators, the two food webs reasonably fit the general pattern.

Food web investigators also have observed that the proportions of trophic links between members of the three categories of compartments likewise exhibit reasonable regularity among all systems that have been catalogued. Thus, about 35% of the total linkages connect top predators to intermediate taxa; 30% link intermediates to other intermediates; 32%, intermediates to basals; and 8%, tops to basals. In the Chesapeake these ratios are 6 : 50 : 33 : 11, whereas in the Baltic they are 25 : 45 : 30 : 0. Both systems are more highly connected among the intermediates than is generally observed, and scarce in links from the intermediate to top consumers. The proportions of linkages from basal to intermediate species is virtually identical to Cohen's ensemble averages, but the Baltic appears to lack any basal-top connections. This latter irregularity results from the way meiofauna were treated in the two networks. In the Baltic, meiofauna are an intermediate species, serving as host to deposit feeders and benthic invertebrate carnivores. In the Chesapeake, most meiofauna are considered to be recycled to the sediment particulate organic matter (POC) and do not appreciably contribute to benthic predators, that is, it stands as a "top" species in that network.

These minor topological differences notwithstanding, the food web portions of both networks appear to be typical of the collection of webs that have been catalogued by food web theorists. The analysis of trophic topology does uncover a few discrepancies in the way the system was parsed, but any system-level differences that may exist are not made apparent. To compare the workings of the system as a whole, it becomes necessary to take explicit account of differences in flow magnitudes and the routes of transfers through the detrital pools.

Whole-System Comparisons

Table 8.1 lists the values of some properties of the Chesapeake and Baltic ecosystem networks. The total system throughput is the sum of all the flows occurring in each network. It measures the total activity of each system.

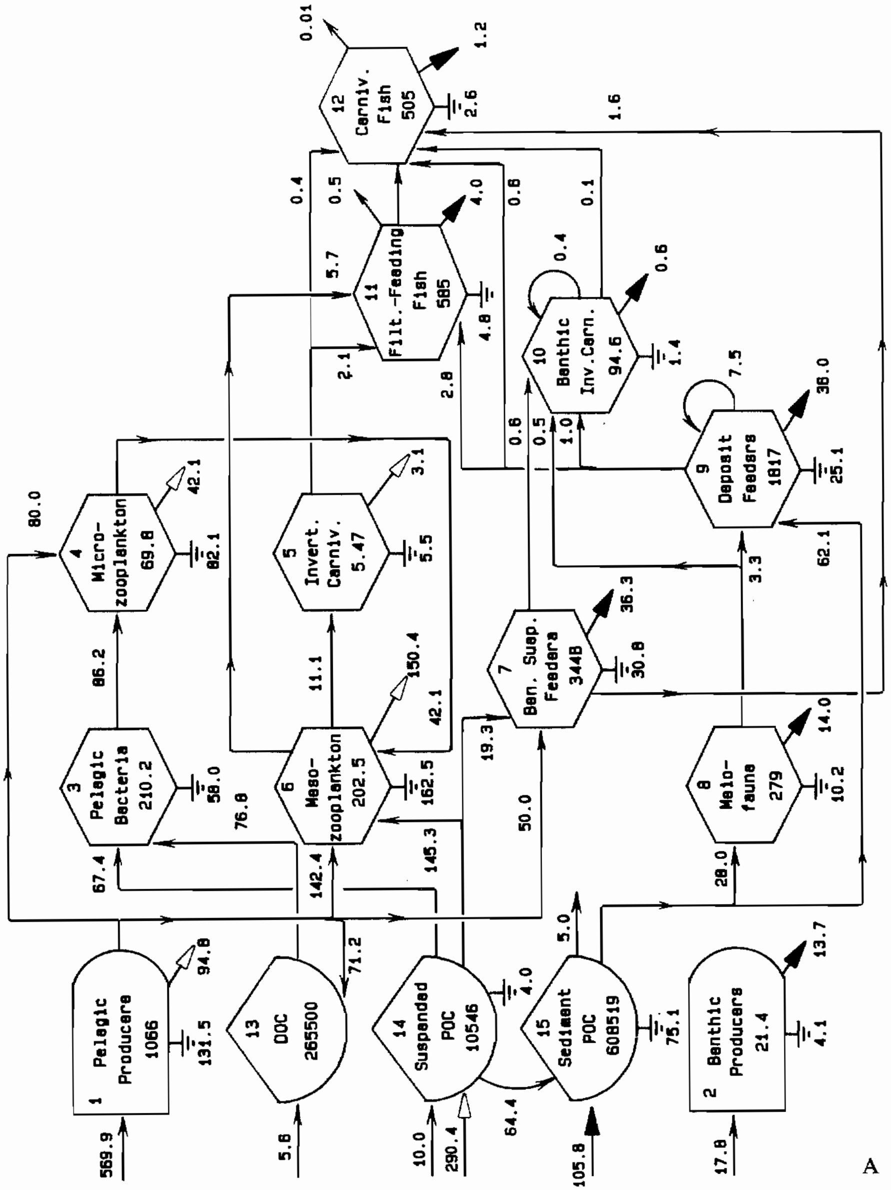

FIGURE 8.2. Diagrams of annually averaged carbon flows: (A) ecosystem of Baltic Proper; (B) Chesapeake Bay. Units of biomass (inside boxes), mg C m^{-2}; units of flows, mg C m^{-2} d^{-1}. For simplicity, particulate organic carbon (POC) flows between compartments are not connected: open arrows into space indicate flows to suspended POC; filled arrows into space, flows to sediment POC. Ground symbols indicate dissipative respirations.

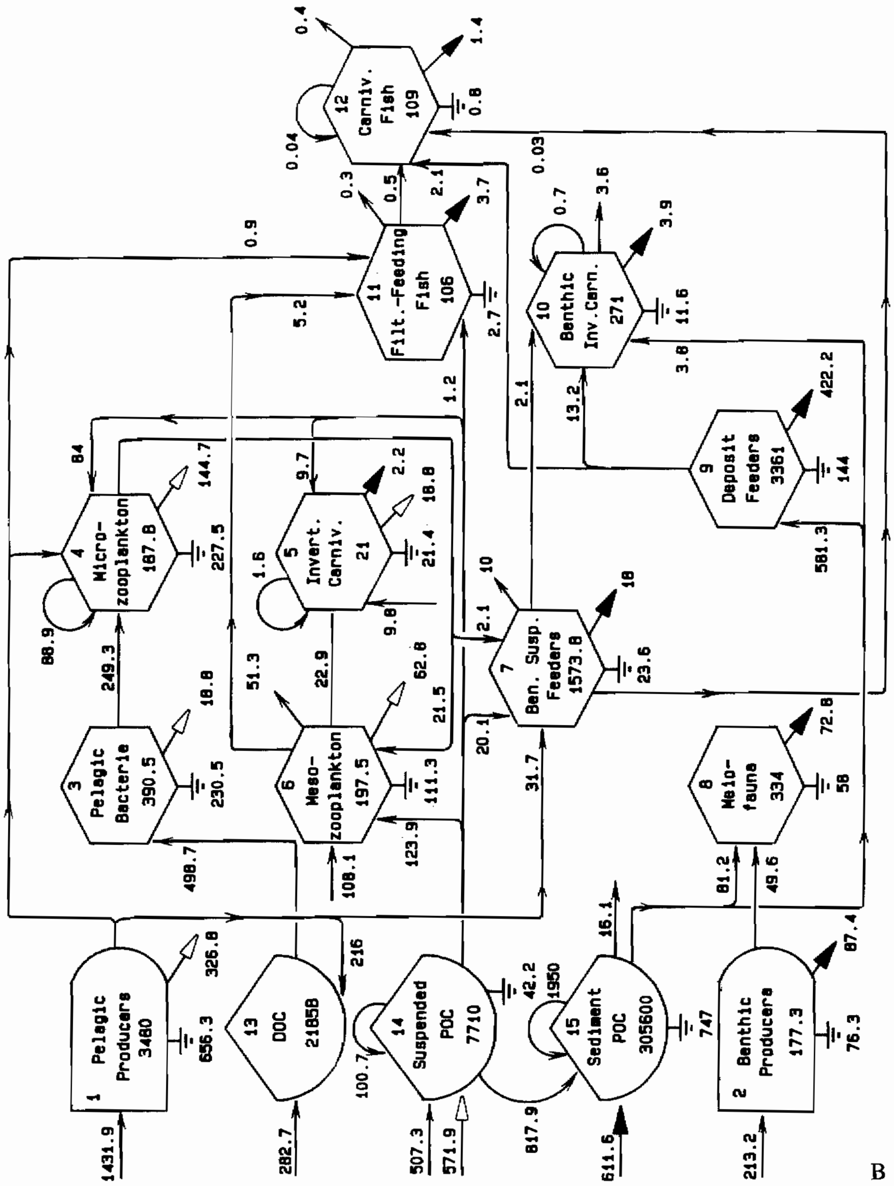

FIGURE 8.2. *Continued*

TABLE 8.1. Indices of total system behavior.

Index (units)[a]	Chesapeake	Baltic
Total system throughput (mgC m^{-2} d^{-1})	11,224	2,577
Flow diversity (bits)	2.94	3.10
Development capacity (mgC m^{-2} d^{-1} bits)	33,000	8,007
Relative ascendency (%of 3)	49.5	55.6
Overhead on inputs (% of 3)	2.6	0.9
Overhead on exports (% of 3)	0.4	0.0
Overhead on respirations (% of 3)	19.4	21.4
Redundancy (% of 3)	28.1	22.0
Finn cycling index (% of 1)	29.7	22.8

[a] See glossary for definitions.

This activity in the Chesapeake is about four times greater than that in the Baltic, because primary production in the former system exceeds that in the latter by almost the same ratio. Some of the elevated activity in the Chesapeake can be attributed to the higher annual temperatures at that latitude.

A second measure by which to compare whole systems is flow diversity. This was first suggested by MacArthur (1955) as a measure of the capacity of a system for homeostasis. Rutledge et al. (1976) later improved on MacArthur's index, and Ulanowicz (1986) scaled the improved flow diversity by the total system throughput to create a measure of the capacity of the system for development. The flow diversity is calculated using the Shannon–Weaver measure of complexity, which is logarithmic in nature. Hence, small differences in the value of this index can reflect much larger qualitative disparities. The Baltic network has a higher flow diversity (see Table 8.1), and this leads one to expect that this system has more remaining ability to cope with disturbance. This difference was unanticipated and constitutes the first clue that the Baltic might not be as strongly impacted as the Chesapeake.

Ulanowicz (1986) separated the development capacity into five components, each of which relates to some qualitative property of the overall structure. The component most relevant here is the relative ascendency, or the articulation of the network. In a system that is more highly articulated (or better organized), the effects of an event at any one compartment are propagated to only a small subset of other compartments. Ulanowicz (1980, 1986) suggested that ecosystems naturally develop in the direction of greater articulation. Articulation is presented in Table 8.1 as the percentage of development capacity that is expressed as organized flow. One sees that about 6% more of the capacity of the Baltic network appears as organized structure.

Odum (1969) proposed that mature ecosystems recycle a greater percentage of material and energy than do pioneer or disturbed communities. The last entry in Table 8.1 is the Finn cycling index, the fraction of the total system activity comprised by recycling. The Chesapeake community appears to recycle considerably more carbon than does the Baltic, which seems to contradict the emerging picture of the Baltic as the less disturbed system. However, Ulanowicz (1984) has remarked that perturbed systems often exhibit greater degrees of recycling. Presumably, augmented cycling in a disturbed system is its homeostatic response to retain in circulation resources that, before the perturbation, had been stored in the biomass of higher organisms. To determine if the Chesapeake is functioning in this fashion requires more details about the patterns of individual cycles in both ecosystems.

Structure of Cycling

A knowledge of the aggregate amount of cycling in a system is often insufficient information on which to judge how well an ecosystem is functioning. Ulanowicz (1983) constructed an algorithm that enumerates all the simple cycles present in a network and then removes those cycles from the underlying framework of dissipative flows. This program uncovered 22 routes for recycle in the Baltic network and 20 in that of the Chesapeake. More importantly, however, most of the recycling in the Chesapeake occurs over two short benthic cycles, where 424 mg C m^{-2} d^{-1} circulates between the deposit feeders and the sediment POC and 72.8 units circulates between the benthic meiofauna and the sediment detrital pool (Fig. 8.3). It is clear from Fig. 8.3 that a greater proportion of the recycled flow in the Baltic courses over longer cycles. For example, 42.1 units of flow traverse the circuit from suspended POC → pelagic bacteria → microzooplankton → mesozooplankton and back again.

That longer cycles are relatively more important to the Baltic system is shown in Fig. 8.4, where the proportions of recycle activity that occur over loops of various trophic lengths are plotted for the two systems. One concludes that the higher Finn cycling index for the Chesapeake networks was indeed misleading. Once the pattern and nature of the recycling was considered, it became apparent that the Baltic possesses a more developed apparatus for recycling.

One notices in Figs. 8.3A and 8.3B that two of the six Chesapeake compartments that engage in no cycling whatsoever are seen to facilitate the reuse of Baltic carbon (pelagic bacteria and planktivorous fish). The "microbial loop" appears to be more important to the dynamics of the plankton community in the Baltic than is the case in the Chesapeake.

Trophic Structure

From the analysis thus far, it appears that the Baltic remains less hypertrophic than the Chesapeake ecosystem. To test such a conclusion, we wish to elaborate the actual trophic structure of the two communities.

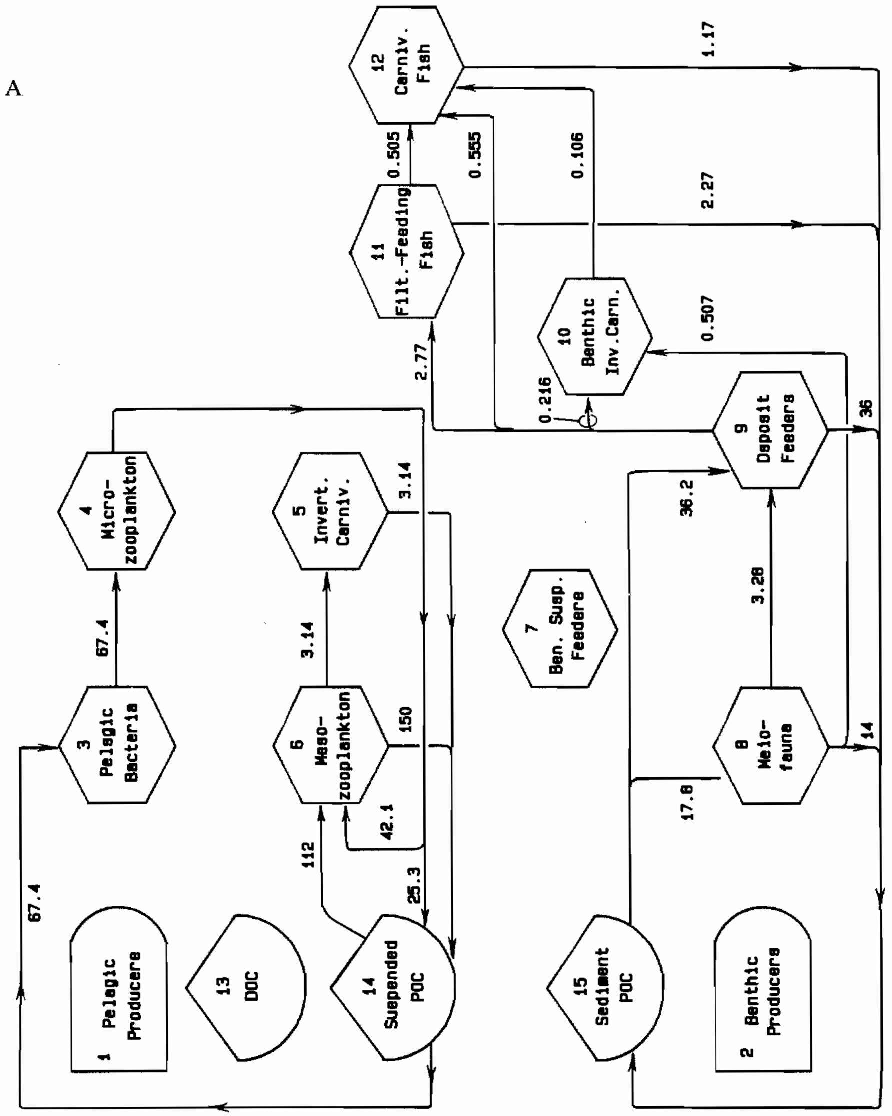

FIGURE 8.3. Networks for Baltic (A) and Chesapeake (B) show only cycled flows, that is, the amount of any compartmental throughput that returns to that compartment after traversing indicated loop.

B

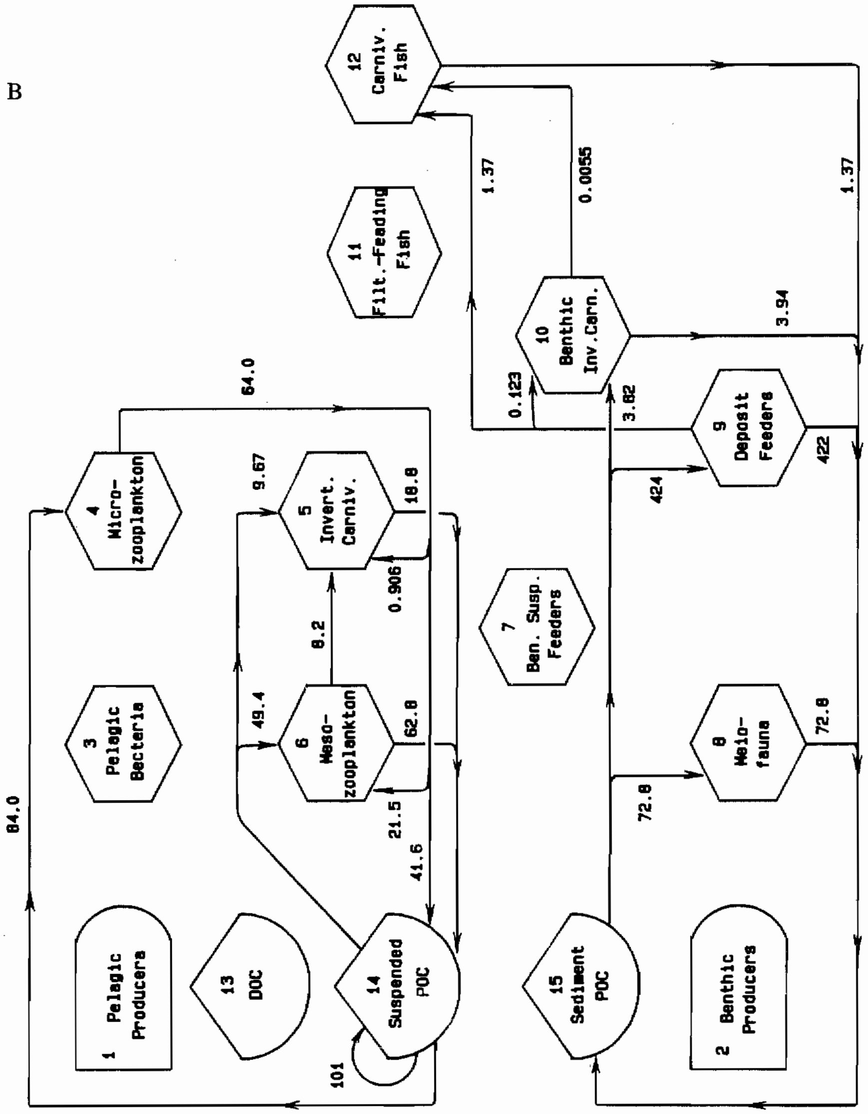

FIGURE 8.3. *Continued*

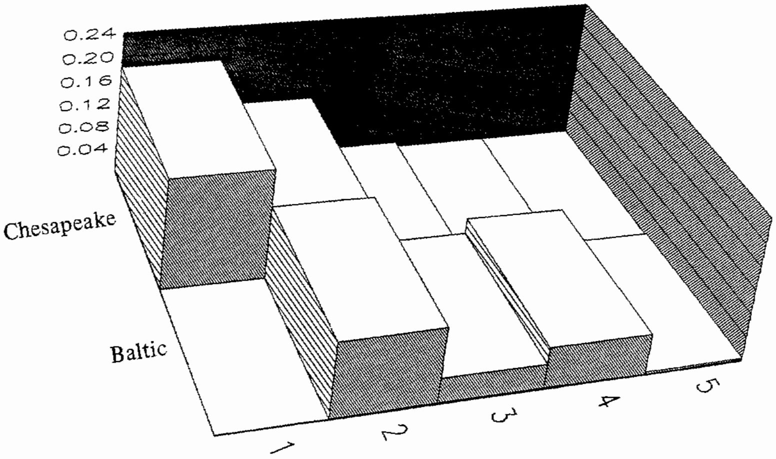

FIGURE 8.4. Proportions of total activity devoted to recycle (vertical axis) over cyclic pathways of various lengths (horizontal axis) in Chesapeake and Baltic ecosystems.

Depicting the trophic structure of a network, like other tools in network analysis, builds upon representing the exchanges in matrix form. That is, the magnitude of each exchange occurring in an *n*-compartment community can be entered into an n × n matrix in such a way that the row index designates the donor of the medium and the column location shows the recipient. It becomes useful to normalize each column of this exchange matrix by the total amount of all medium flowing into that recipient. The entries of each column then represent the fractions that each donor (prey) constitutes in the overall diet of that recipient (predator). The reason for normalizing in this fashion becomes apparent as soon as one multiplies this matrix of dietary coefficients by itself. Each element in the resulting product matrix represents the fraction of the predator's (column index) diet that is derived from each donor (row index) along all pathways exactly two trophic exchanges in length. Subsequent multiplication of the product matrix by the original matrix reveals the dietary contributions along all pathways of trophic length 3, etc.

The powers of the dietary matrix are useful in numerous ways, two of which are relevant to elaborating the trophic structure of the system. Levine (1980) showed how the amounts arriving at various trophic distances from primary sources can be used as weighting factors to estimate the average trophic level at which each heterotroph is feeding. In effect, each compartment is assigned a point along a trophic continuum. Levine's "trophic positions" for the 15 compartments (Fig. 8.5) show little disparity (< 0.3 trophic units) between the trophic positions of most compartments in the two communities, except for those of the planktivorous and carnivorous fishes. The planktivorous fish in the Baltic appear on the average to feed a full trophic position higher than their Chesapeake counterparts. This difference suggests examining the feeding behaviors of the filter-feeding fishes in both systems for more insight. In the Chesapeake, the dominant filter feeding fish species is the menhaden (*Brevoortia tyrannus*), which acts mostly as a herbivore on phytoplankton. In contrast, the Baltic counterparts consume mostly zooplankton (one trophic level higher) during the warmer months and switch to consuming benthic invertebrates during colder periods.

As an alternative to the trophic continuum, one may envision all transfers as occurring between a set of integral trophic levels. In reality, heterotrophic species often feed at several trophic levels. However, the power sequence of the dietary matrix discussed earlier indicates just how much each species feeds at each trophic level. Hence, this information can be used to apportion the activity of a given compartment among the imagined integral levels (Ulanowicz and Kemp 1979; Fig. 8.6). Only the living members of the ecosystem are apportioned in this manner. The attendant recycle through the nonliving detritus (which confounds the trophic apportionment scheme) is treated separately (Ulanowicz, in press). Virtually all ecosystem networks can be mapped into concatenations like the ones shown in Fig. 8.6. Therefore, one may speak of these chains as canonical trophic forms that should be particularly useful for comparing ecosystems widely disparate in structure.

The canonical trophic forms of the two systems reveal several obvious differences. The Baltic trophic chain possesses one more link than its Ches-

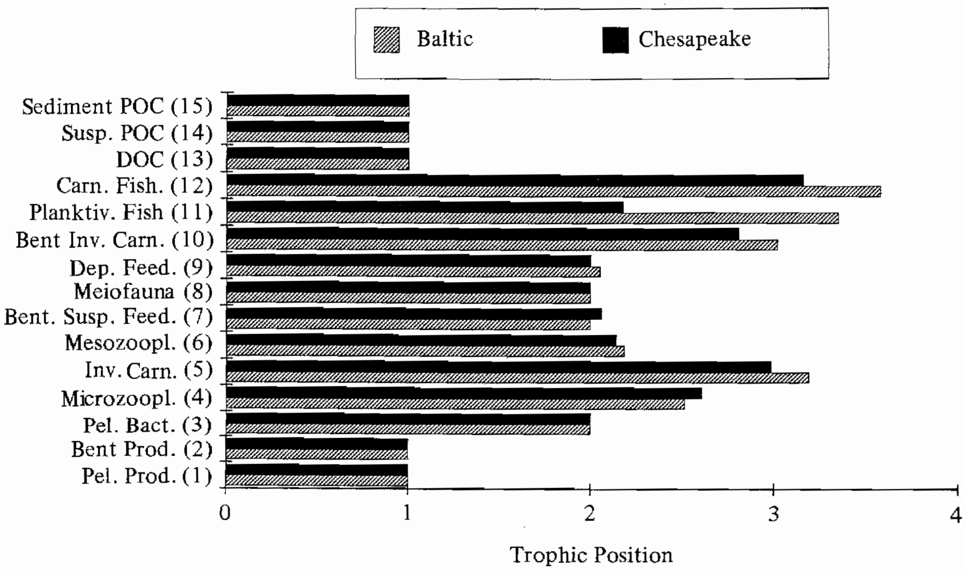

FIGURE 8.5. Average trophic position for each compartment in Chesapeake and Baltic networks.

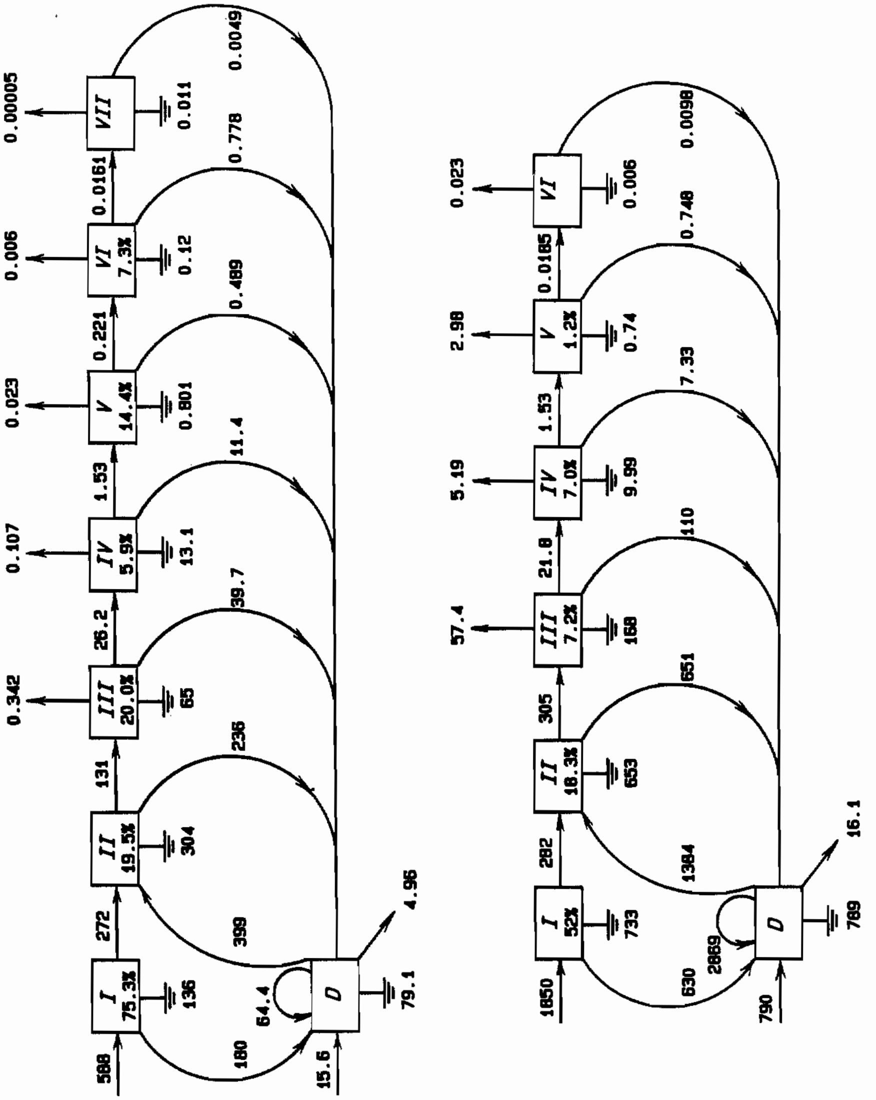

FIGURE 8.6. Canonical trophic aggregations of Baltic (A) and Chesapeake (B) ecosystem networks (see Figs. 8.2A and 8.2B). Boxes represent virtual trophic levels that are linear combinations of actual taxa. Percentages inside boxes refer to aggregate efficiencies of each virtual level.

apeake counterpart, probably because trophic efficiencies are higher in the Baltic. (The efficiency of a trophic level is calculated by dividing its output to the next level by its total input.) Furthermore, one sees that detritivory (the flows from D to II) are much larger in the Chesapeake system. Detritivory in the bay strongly predominates over herbivory (the flow from I to II) by a ratio of 4.9 to 1, whereas the corresponding quotient in the Baltic is 1.5 to 1.

Bilateral Indirect Relationships

Evidence that the trophic structure of the Baltic ecosystem appears less impacted than that of the Chesapeake concludes the macroscopic comparison of the two systems. However, an ecologist or ecosystem manager could still gain much from further comparison of the networks at finer resolution. For example, one might be charged with managing a particular species and wish to know the effects that all other compartments have on the given taxon over all trophic pathways, direct and indirect. The tool for quantifying indirect bilateral relationships is the power series of the dietary matrix discussed early. To be more specific, Leontief (1951) discovered that the infinite series generated by the powers of matrices normalized like the dietary matrix would always converge. Further, he showed that the limit of this series could be calculated through a few simple matrix operations on the dietary array. The end result is a "structure matrix" whose elements estimate the indirect trophic effects of any one compartment on any other element over all pathways of all lengths. Hannon (1973) introduced this econometric tool into ecology, and Szyrmer and Ulanowicz (1987) later modified the analysis to yield results with clearer ecological meanings.

Here we are interested in using "input-output" analysis to estimate how much of the various exogenous inputs eventually reach the "commercially useful products" that issue from the system. Once again, it is clear that the Baltic is more effective at producing valuable resources (Table 8.2). For example, one unit of Baltic phytoplankton production results in about four

TABLE 8.2. Percentage of input from three major sources that reaches the four commercially important compartments.

Source	Source	Benthic filter feeders	Planktivorous fish
Phytoplankton production	Baltic	11.9	1.7
	Chesapeake	2.9	0.4
Benthic production	Baltic	0	1.8
	Chesapeake	0	0
Allochthonous input	Baltic	8.9	0.8
	Chesapeake	2.0	0.2

times as much planktivorous fish as does its counterpart in the Chesapeake (and this despite the earlier observation that planktivorous fish in the Baltic feed at higher levels of the food chain).

Turning matters around, one might ask how much of the medium ingested by a particular heterotroph was once incorporated by various other components during its transit through the trophic web. In other words, one can calculate the "indirect diet" of each heterotroph. Elsewhere, Baird and Ulanowicz (1989) observed how two carnivorous fish populations in Chesapeake Bay exhibited apparently minor differences in their behaviors and direct diets; however, considerable niche separation arose once the ultimate sources of their diets were calculated. Pelagic primary production is obviously much more important to the carnivorous fish of the Baltic (95%) than it is to the same populations in Chesapeake Bay (42%) (Table 8.3). The Baltic fishes depend more heavily on the pelagic producers, mesozooplankton, and benthic suspension feeders, whereas benthic deposit feeders and detrital material are the primary resources for carnivorous fishes in the bay. There is a sharp disparity in the Chesapeake between the carnivorous fish, which depend on detrital food sources, and the plankton-feeding finfish, which rely mostly on the grazing food chain. In the Baltic this difference is much less pronounced. The contrast in system behavior of the two systems can be traced to the fact that primary and secondary production are both sufficiently high during the Maryland winter to support plankton feeding by fish in the bay. However, pelagic production becomes so

TABLE 8.3. Indirect diets (in % of total intake) of carnivorous and filter-feeding fishes in both systems.[a]

	Carnivorous fish		Planktivorous fish	
Compartment	Baltic	Chesapeake	Baltic	Chesapeake
Pelagic producers (1)	94.8	41.5	94.1	68.3
Benthic producers (2)	2.9	9.6	3.0	0
Pelagic bacteria (3)	8.0	13.2	11.7	9.6
Microzooplankton (4)	15.5	13.2	22.6	13.8
Invertebrate carnivores (5)	16.4	1.6	20.7	1.0
Mesozooplankton (6)	48.2	19.0	83.2	72.5
Benthic suspension feeders (7)	49.8	2.6	8.2	0
Meiofauna (8)	4.6	5.8	4.3	0
Deposit feeders (9)	24.5	79.8	26.3	0
Benthic invertebrate carnivores (10)	2.9	0.5	0.1	0
Planktivorous fish (11)	32.7	19.5	1.0	0
Carnivorous fish (12)	0.2	1.5	0.3	0
Dissolved Organic matter, DOC (13)	4.6	9.8	6.7	9.6
Suspended POC (14)	43.4	79.5	51.7	52.6
Sediment POC (15)	25.0	79.8	26.3	0

[a] Percents add to more than 100, because the same material visits several compartments along its way to the designated consumer. POC, particulate organic matter.

sparse in the wintertime Baltic that most zooplankton are forced to overwinter in diapause, thereby compelling the planktivorous fish to go to the bottom and utilize the benthic deposit feeders (Aneer 1980).

It appears that the Chesapeake ecosystem relies more on its benthic processes than does its Baltic counterpart. This is understandable, given the large difference in mean depths between the two systems. The predominant role of benthic metabolism in the Chesapeake becomes quite visible when one uses input-output analysis to calculate how much of the net primary production leaves the systems from each compartment (Fig. 8.7). It is immediately evident that the major egress of carbon from the Chesapeake ecosystem is via the respiration of benthic detritus, whereas the Baltic mesozooplankton (predominantly mysids) respire most of the carbon from that system.

Finally, it is often informative to take explicit account of the antagonistic nature of predator–prey trophic interactions. That is, the immediate effect of feeding is positive to the predator population, but negative to the prey stocks. Ulanowicz and Puccia (1990) have outlined a variation on input-output techniques that permits simultaneous bookkeeping of both positive and negative trophic influences. The technique allows one to quantify indirect interactions such as competition for prey, indirect mutualism (e.g., the predator of a predator is beneficial to the original prey population), self-damping of heterotrophic populations, autocatalytic loops, etc.

As can be seen from Figs. 8.2A and 8.2B, the trophic topologies of the two networks are reasonably similar and only a few indirect influences bear mention. It was just remarked how the mesozooplankton play a strong role in the Baltic ecosystem, so it comes as no surprise that the indirect effects originating in this compartment are more obvious than those of its counterpart in Chesapeake Bay. In both systems, the mesozooplankton act as predators on the microzooplankton, which in turn consume pelagic bacteria. The method of Ulanowicz and Puccia (1990) reveals that the indirect mutualism inherent in this trophic concatenation is about eight times stronger in the Baltic than in the Chesapeake network, where the beneficial effect of mesozooplankton on bacteria is confounded by a subsidy of suspended POC to the microzooplankton. The same subsidy ameliorates the negative direct impact that mesozooplankton in the Chesapeake have upon the microzooplankton. Input-output analysis shows that the negative effect that mesozooplankton exert on benthic suspension feeders in the Baltic is about twice as strong as the same competitive relationship (mesozooplankton and benthic suspension feeders both consume suspended POC) in the Chesapeake.

It was remarked earlier that sediment POC played a much more significant role in the community metabolism of the Chesapeake. Further, the cycle analysis spotlighted how large amounts of sediment carbon are being recycled by the meiofauna and deposit feeders. So reflexive are these loops that sediment POC comes to exert a large autocatalytic effect on itself.

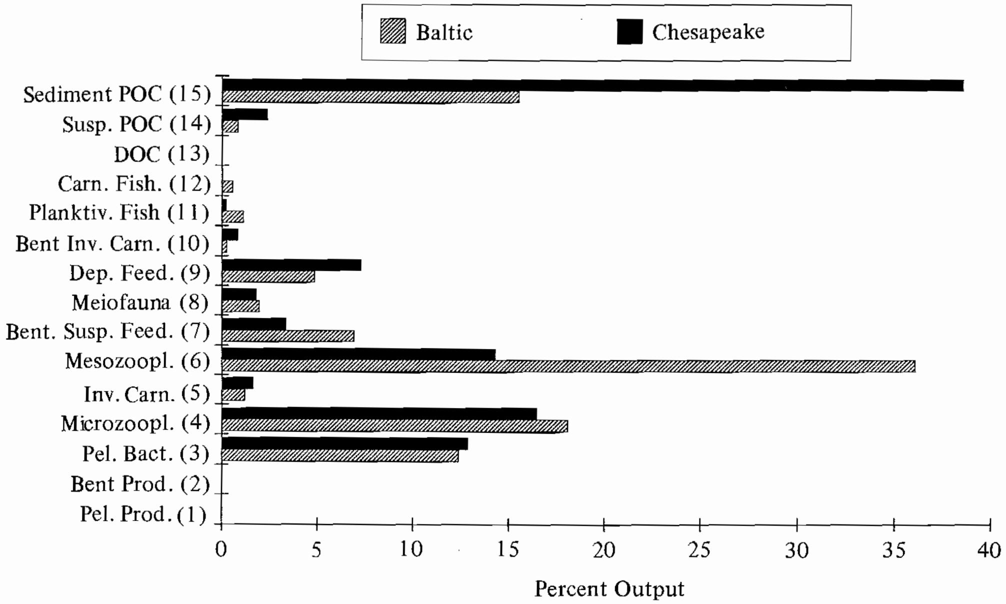

FIGURE 8.7. Fraction of net primary productivity that exits from the systems at each compartment.

Summary and Conclusions

In summary, the Baltic ecosystem appears to be less prone to hypertrophy than is the community in the Chesapeake. Evidence for this conclusion appears at all levels of comparison. The diversity of trophic processes is higher in the Baltic, and its species are trophically linked together in more narrow, or articulated, fashion. The amount of activity devoted to cycling is higher in the Chesapeake, but this fact is an indicator more of stress than of maturity. Routes of recycle are more numerous in the Baltic ecosystem, and individual cycles there are longer and contain a greater proportion of higher trophic level species. Overall trophic efficiencies are greater in the Baltic; one unit of primary production in that system creates four times as much fish as does a unit of productivity in the Chesapeake. The Baltic may be characterized as more pelagic than the Chesapeake. Carnivorous fish in the Sea ultimately depend on phytoplankton, mesozooplankton, and benthic suspension feeders for most of their sustenance, whereas Chesapeake fish rely indirectly on deposit feeders and particulate detritus for the better part of theirs.

Ideally, we would like to quantify the confidence level of each of the aforementioned conclusions. Unfortunately, explicitly stating the significance of most of the results of network analysis is not an easy task. For example, the statistical behavior of the Shannon–Weaver uncertainty or of the average mutual information used to compute the system articulation is recondite (Kullback 1978), and the tests are difficult to implement. Somewhat more accessible progress has been made toward evaluating the credibility of results issuing from input-output analysis by running sensitivity analyses on the constituent matrix manipulations (Bosserman 1981). Implementing these analyses involves a total effort comparable to that already expended up to this point. While such evaluations are in all ways desirable, a lack of time and resources has precluded their application to this study. Suffice it here to mention that in searching the various outputs for notable differences, we took care to confine our attention only to clear-cut disparities and never yielded to the temptation to employ marginal differences to paint any preconceived picture of how the systems compared one to another.

Perhaps the outcome of this comparison would have been better anticipated by everyone had the authors begun by contrasting the nutrient-loading characteristics of both systems. One notes, for example, that the ratio of catchment area to water surface area in the Chesapeake is sevenfold greater than it is in the Baltic. Furthermore, when one prepares a simple Vollenweider (1982) diagram of phosphorous loading versus the ratio of mean depth to water residence time (Fig. 8.8), the Chesapeake system plots in the region of excessively enriched systems, whereas the Baltic falls in the borderline region between undesirable and permissible zones. Presumably, several decades ago the Baltic was well inside the oligotrophic half of the

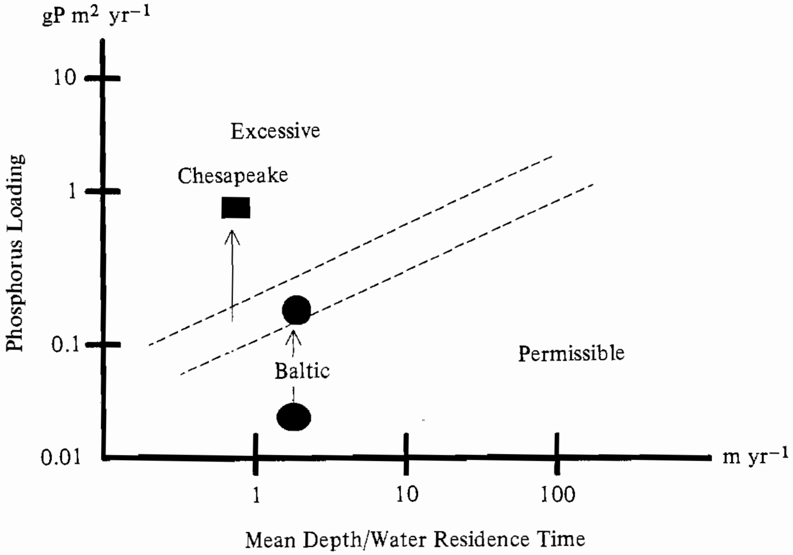

FIGURE 8.8. Diagram (Vollenweider 1982) of phosphorous loading plotted against ratio of mean depth to water residence time. Lower Baltic point represents estimated conditions in Baltic Sea earlier in the twentieth century.

plot and has since moved toward the zone characterizing degraded systems. Such preliminary shifts often are accompanied by increases in fish harvests (as was the case in the Baltic), whereas yields are likely to decrease with further degradation. We do not mean to imply that plotting a system on Vollenweider diagrams gives sufficient information to judge its trophic status. Useful as the Vollenweider technique may be, it nevertheless would be highly speculative to categorize a system on the basis of that analysis alone. The point of this essay has been to show that the quantified networks of two systems permit one to carry out an entire suite of comparisons. The breadth of the results issuing from the exercise allows not only the manager to draw some very defensible conclusions about the relative trophic status of the communities, but also affords the ecologist a bridge with which to connect analyses at the whole-system level to those concerning individual populations. Ecologists have long preached that reductionism and holism go hand in glove. The wherewithal to act on that notion is now available.

Acknowledgments. R.E. Ulanowicz was supported in part by LMER Grant #BSR-8814272 from the Division of Biotic Systems and Resources, the National Science Foundation. F. Wulff's work was underwritten by the Swedish National Science Foundation (NFR) and the Environmental Protection Board (SNV).

REFERENCES

Aneer, G. (1980). Estimates of feeding pressure on pelagic and benthic organisms by Baltic herring (*Clupea harentus* v: *membras L.*). *Ophelia* (Suppl.) 1:265–275.

Baird, D. and R.E. Ulanowicz. (1989). The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59:329–364.

Bosserman, R.W. (1981). Sensitivity techniques for examination of input-output flow analyses. In: *Energy and Ecological Modelling*, W.J. Mitsch, R.W. Bosserman, and J.M. Klopatek, eds. Elsevier, New York, pp. 653–660.

Cederwall, H. and R. Elmgren. (1980). Biomass increase of benthic marcrofauna demonstrates eutrophication of the Baltic Sea. *Ophelia* (Suppl.) 1:287–304.

Cohen, J.E. (1989). Big fish, little fish: the search for patterns in predator-prey relationships. *The Sciences* 29:37–42.

Engelberg, J. and L.L. Boyarsky. (1979). The noncybernetic nature of ecosystems. *Am. Nat.* 114:317–324.

Finn, J.T. (1976). Measures of ecosystem structure and function derived from analysis of flows. *J. theor. Biol.* 56:363–380.

Hannon, B. (1973). The structure of ecosystems. *J. theor. Biol.* 41:535–546.

Kullback, S. 1978. *Information Theory and Statistics*. Peter Smith, Gloucester.

Larsson, U., R. Elmgren, and F. Wulff. (1985). Eutrophication and the Baltic Sea: causes and consequences. *Ambio* 14:9–14.

Lehman, J.T. (1986). The goal of understanding in ecology. *Limnol. Oceanogr.* 31: 1160–1166.

Leontief, W. (1951). *The Structure of the American Economy, 1919–1939*, 2d Ed. Oxford University Press, New York.

Levine, S. (1980). Several measures of trophic structure applicable to complex food webs. *J. theor. Biol.* 83:195–207.

MacArthur, R.H. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–536.

MDDNR. (1985). First Annual Status Report on Striped Bass. Tidewater Administration, Maryland Department of Natural Resources, Annapolis, Maryland.

Odum, E.P. (1969). The strategy of ecosystem development. *Science* 164:262–270.

Ojaveer, E. (1981). Marine pelagic fishes. In: *The Baltic Sea*, A. Voipio, ed. Elsevier, Amsterdam, pp. 276–292.

Peters, R.H. (1986). The role of prediction in limnology. *Limnol. Oceanogr.* 31: 1143–1159.

Platt, T., K.H. Mann, and R.E. Ulanowicz. (1981). *Mathematical Models in Biological Oceanography*. UNESCO Monographs on Oceanography Methodology 7, UNESCO Press, Paris.

Rutledge, R.W., B.L. Basorre, and R.J. Mulholland. (1976). Ecological stability: an information theory viewpoint. *J. theor. Biol.* 57:355–371.

Szyrmer, J. and R.E. Ulanowicz. (1987). Total flows in ecosystems. *Ecol. Model.* 53:123–136.

Ulanowicz, R.E. (1980). An hypothesis on the development of natural communities. *J. theor. Biol.* 85:223–245.

Ulanowicz, R.E. (1983). Identifying the structure of cycling in ecosystems. *Math. Biosci.* 65:219–237.

Ulanowicz, R.E. (1984). Community measures of marine food networks and their possible applications. In: *Flows of Energy and Materials in Marine Ecosystems*, M.J.R. Fasham, ed. Plenum Press, New York, pp. 23–47.

Ulanowicz, R.E. (1986). *Growth and Development: Ecosystems Phenomenology*. Springer-Verlag, New York.

Ulanowicz, R.E. Ecosystem trophic foundations: Lindeman exonerata. In: *Complex Ecology: The Part-Whole Relation in Ecosystems*, B.C. Patten and S.E. Jorgensen, eds. Prentice-Hall, New York (in press).

Ulanowicz, R.E. and W.M. Kemp. (1979). Toward canonical trophic aggregations. *Am. Nat.* 114:871–883.

Ulanowicz, R.E. and C.J. Puccia. (1990). Mixed trophic interactions in ecosystems. *Coenoses* 5:7–16.

Vollenweider, R.A. (1969). Moeglichkeiten und Grenzen Elementarer Modelle der Stoffbilanz von Seen. *Arch. Hydrobiol.* 66:1–36.

Vollenweider, R.A., ed. (1982). *Eutrophication of Waters: Monitoring, Assessment and Control*. OECD, Paris. 154 pp.

Wulff, F. and R.E. Ulanowicz. (1989). A comparative anatomy of the Baltic Sea and Chesapeake Bay ecosystems. In: *Flow Analysis of Marine Ecosystems*, F. Wulff, K.H. Mann and J.G. Field, eds. Springer-Verlag, Berlin, pp. 232–256.

Glossary

To assist the reader in following the text, we attempt to clarify the words and terms listed below that either are newly coined, used by analogy or otherwise unusual:

Anatomy: The structural characteristics of a living or a once- living system. Used here in reference to ecosystems to mean the configuration of trophic relationships among the compartments of an ecosystem.

Articulation: Degree of specificity or definition in the effect of a given event. In a highly articulated trophic network, each prey has only one, or very few, predators, and vice versa.

Ascendency: A property of a network of flows describing both the aggregate intensity of process activities and the level of definition (see *articulation*) or specificity with which these processes occur. Mathematically, it is the product of the total system throughput (see following) and the average mutual information inherent in the network (Rutledge et al. 1976; Ulanowicz 1986).

Autocatalysis: A circumstance wherein the activity of a network element augments itself, usually via one or more intermediaries. If the activity of element A catalyzes the activity of B, B catalyzes C, and C in turn catalyzes A, then the cycle or loop A-B-C-A is said to be autocatalytic in all its members. Autocatalysis inherent in networks of ecosystem interactions (not limited to feeding relations) is assumed to be the principal agent driving the system toward configurations with ever-higher network ascendencies.

Canonical form: The most elementary or simplest of a group of equivalent mathematical expressions, used here in reference to flow networks. If a network can be mathematically transformed into another aggregated representation, then the results of repeated application of the transform will converge to the simplest possible representation, or canonical form.

Complexity: The degree to which a system or network is difficult to analyze or separate, used here mostly in reference to the multiplicity and overlap of the various pathways through the system. Assumed to be equivalent to the flow diversity (see following).

Cycle: A pathway in which the beginning and terminal compartments are the same. The object of the analysis described here is to decompose all cycles into simple ones, that is, those in which no compartment appears more than once.

Development: Any change in network topology that contributes toward an increase in *ascendency* (see earlier). The *development capacity* is a measure of system activity and complexity and is equal to the product of the *total system throughput* times the *flow diversity*. The development capacity is always greater than or equal to the network ascendency and thereby appears as an upper bound on the growth and development of the system.

Finn Cycling Index: That fraction of the total system activity (*total system throughput*) devoted to the recycling of medium (see Finn 1976).

Flow Diversity: A measure of the complexity of flow pathways inherent in a network. This property is taken to be the result of applying the Shannon–Weaver index to the fractions of the total activity represented by the individual intercompartmental transfers and exogenous connections (i.e., inputs, exports, and respirations).

Gain: The factor by which an input to a compartment is amplified in the output. The gain of a *cycle* is the amplification a signal undergoes in one circuit around the cycle and usually is a small number, less than 1.

Hypertrophy: Ecosystems that are well nourished are called eutrophic. Those that for either natural or anthropogenic reasons are adversely overenriched are termed hypertrophic.

Information: That which causes one to change a probability assignment. It is equivalent to the decrease in uncertainty such reassignment engenders. The information inherent in the network structure is manifested by the constraints the connection topology places upon the calculated flow diversity. (See "average mutual information" in Rutledge et al. 1976.)

Input-Output Analysis: The quantitative study of the origins or fates of a medium after more than a single transfer. The study of indirect material causality (see Hannon 1973).

Organization: A flow network is said to be more highly organized the more articulated it becomes.

Overhead: That fraction of the *development capacity* encumbered from appearing as coherent activity (*system ascendency*). Generally, in any flow network there are four categories of overhead: (1) that caused by uncertainties in the inputs, (2) multiplicities of exports and (3) respirations, and (4) parallelism among internal pathways (see *redundancy*).

Reductionism: The search for explanation at smaller scales. In its strictest applications it becomes the belief that all causes behind any observed event lie at smaller temporal and spatial scales.

Redundancy: The degree to which pathways in a network are duplicated so that the connection between any two arbitrary compartments cannot be severed by elimination of a single intervening link. One of four components of the network *overhead* (see earlier).

Reflexivity: The degree to which an event is turned back on itself as its own cause.

Relative Ascendency: The fraction of the *development capacity* that appears as structured activity. The quotient of the *ascendency* by the *development capacity*. A relative measure of a system's organization.

Taxon: One of a group of elements that collectively define a formal system. A node in a flow network, not necessarily related to a Linnean taxonomic unit.

Throughput: The amount of flow of medium through an entity. That flowing through a system node or compartment is called *compartmental throughput*. The aggregate of all compartmental throughput in a system is called the *total system throughput*, which gauges the total activity of the system.

Trophic Level: (1) The average number of times an arbitrary particle is ingested by system *taxa* on its way to being incorporated by a given component (see Levine 1980). (2) An abstract element in a virtual chain of trophic transfers representing the totality of feeding relations in a system (see Ulanowicz, in press).