

## CONTRIBUTORY VALUES OF ECOSYSTEM RESOURCES

**Robert E. Ulanowicz**  
*University of Maryland*  
*Chesapeake Biological Laboratory*  
*Solomons, MD 20688-0038 USA*

### ABSTRACT

Ecologists and economists use different methods for keeping track of transactions occurring in their respective systems. Until now, those investigators who have sought to analyze indirect influences in multimedia (multiple commodity) ecosystems have employed a supply-side analysis and have advocated that ecologists adopt the style of accounting framework commonly used in economics. Existing ecological bookkeeping practices, however, are more compatible with a complementary demand-side, or input treatment that describes the contributory value of each flow or process towards specified final outputs. The values of these products are determined by an extant market.

The contributory values assigned to each trophic transaction also serve to convert all flows of various media into common dimensions. When combined with an appropriate discounting, or costing scheme, this conversion permits comparison of all the inputs into a compartment, allowing one to identify which nutrient is limiting the production of each node in the network.

### INTRODUCTION

In his most recent book, Eugene Odum (1989) repeatedly stresses how urgent a task is the incorporation of ecological support functions into economic theory. Of course, one may attempt to bridge the separation of ecology and economics from either direction. That is, one could try to adopt the "ecological" standpoint and recast economic values in physical or biological terms; or alternatively, one could approach the problem as an economist and endeavor to impart monetary significance to ecological externalities.

To date, most efforts at combining ecology and economics have proceeded from the first viewpoint, i.e., interpreting market goods and services in terms of primary ecological inputs—giving rise to what has become known as the "energy theory of value." That the "ecological" perspective was the first to develop merely reflects the necessity that one first had to perceive the human economy as a threat to the natural order before economists could be informed of the long-term dangers of economic overexpansion. Thus it was that Hannon's (1973) application of Leontief's (1951) Input-Output Theory to the analysis of ecological systems soon was followed by efforts to reinterpret the units of economic transactions in physical terms (Costanza and Neill 1984; Odum 1988; Hannon et al. 1991).

There are also dimensional reasons why more progress has been made to date toward quantifying the ecological viewpoint. In economic communities, the inputs of goods and services are usually reckoned in variegated units, e.g., tons of coal, numbers of televisions, or manhours of sales effort. By assuming that outputs of a single commodity from any process are valued equally by all users of that product, it becomes possible to assign weights (or prices) to each commodity which then permit their intercomparison. These weights allow one to interpret the relative worth of each transaction with respect to some primary input to the system. The most obvious and prevailing input to the combined ecological-economic system is that of solar energy, so that most ecological values for artificial goods have been estimated as "solar equivalents."

Because the converse assumption that a consumer values its different inputs equally is considered economic nonsense, input-side evaluations of transfers are practically never made. (See Augustinovic 1970 for very special exceptions.) Hence, projects to hindcast the monetary contributions of natural subsidies to the functioning of the human economy have languished. The goal of this exercise is to make some modest progress toward rehabilitating the "economic" perspective, so as to lend credibility to the notion that heretofore unassessed natural subsidies (externalities) have made at least nominal cash contributions to the marketplace.

Before proceeding with the technical analysis, it is useful to note several interesting differences between the habits and concerns of economists and those of ecologists. For example, in economics most interest focuses upon exchanges between a given community and the next larger hierarchical unit, i.e., how changes in transfers affect final supplies and demands (whence the name "Input-Output Analysis.") In ecology, more stress is placed upon reckoning how the intermediate transfers affect each other (Szyrmer and Ulanowicz 1987). Concerning preferences for quantitative units, it has already been remarked how economists often deal with idiosyncratic units reflecting the particular nature of the commodity being measured. American ecologists, believing that systems reflect their underlying chemistries, seem less concerned with individual units (organisms) than with the amounts of energy or chemical constituents that accompany feeding transfers. There remains, however, a strong Eltonian tradition in British ecology for quantifying organism sizes and numbers (Ulanowicz 1989).

Differences are marked as well in how economists and ecologists perceive the concept of "value." "Value" in economics has manifest cognitive associations, and for that reason

is eschewed by most biologists as inapplicable to nonhuman systems. If they think about value at all, most ecologists gravitate towards physicochemical notions, such as entropy and its derivative property, free energy. However, a few (notably H. T. Odum 1988), feel that expressing magnitudes of trophic exchanges in terms of measured energy or material, without scaling their observations by the "qualities" these media possess in context, will lead to erroneous conclusions. As a measure of quality or value they suggest that I-O supply-side techniques be invoked to calculate how much of the primary inputs are "embodied" downstream in the intermediate flows and final outputs. Embodied flows magnify the otherwise small, higher trophic interactions to portray more accurately their significance in the overall scheme of the ecosystem.

With these distinctions as background, it is most interesting to note that virtually all of the work that led to an energy theory of value (the *ecological* viewpoint) was cast entirely in the lexicon of *economic* discourse. Such orthodoxy has not precluded a host of other ecologists from adapting input-output mathematics for a variety of other purposes (e.g., Patten et al. 1976; Finn 1976; Ulanowicz and Kemp 1979; Levine 1980; Bosserman 1981; Szyrmer and Ulanowicz 1987; Ulanowicz and Puccia 1990), but the larger body of ecologists remains distinctly cool towards the introduction of "foreign" terms and unfamiliar methods of bookkeeping. For their part, economists have shown even less enthusiasm for employing input-output theory to reconcile economics with ecology, feeling instead that I-O methods are academically passe. It would indeed prove ironic should the extension of *economics* into ecology proceed via arguments that are basically *ecological* in form; however, it is precisely this interwoven and mutually dependent nature of the ecological-economic dialogue that I wish to demonstrate.

## QUANTITATIVE FORMULATION

Ecologists are wont to create "mass and energy balances" for the ecosystems they study. For example, one might choose the medium carbon, and make an account of the magnitudes of each influx into and efflux out of every element in the system. The bookkeeping on a single element does not constitute a unique description of the flow system, inasmuch as parallel balances of energy, nitrogen, phosphorous or any number of other media are possible. Each account gives rise to a different network description of the system (see also Herendeen 1990). Because the various media are transported together, embodied in the biomass of the component species, the connection topologies of the parallel networks are often very similar. The weightings of the connecting arcs, however, can be quite dissimilar.

To be more precise, it is assumed that the system consists of  $n$  distinct compartments and that  $m$  different media are considered relevant to the description of the system. The transfer of the  $k$ th medium leaving the  $i$ th compartment and entering the  $j$ th will be denoted by  $T_{ijk}$ . In addition to the  $n$  specified components, it will be convenient to define three virtual compartments with which to represent the exogenous transfers. All primary inputs to the system will be considered to emanate from compartment zero (0). Similarly, all exports of useful products from any compartment will be regarded as

flowing to node  $n + 1$ , and all egress of degraded, or useless, medium will be denoted as entering  $n + 2$  (Hirata and Ulanowicz 1984). Often, the system is considered to be at steady-state, that is, the amount of each medium that enters each compartment balances the amount of the same medium that exits, or

$$\sum_{p=0}^n T_{pik} = \sum_{q=1}^{n+2} T_{iqk} \quad (1)$$

for all  $i$  and  $k$ . Assumption (1) is not required in what follows.

One now wishes to calculate the relative contribution that one unit of medium  $k$  entering compartment  $i$  makes towards creating final products (to be denoted by  $\lambda_{ik}$ . They are analogous to the "shadow prices" of equilibrium I-O Theory.) A key assumption will be that the per-unit value of  $k$  entering  $i$  is independent of the source of  $k$ . This is the mirror conjugate to the assumption made by Costanza, Hannon, et al. They assume that the per-unit value of a product from a given node is the same to all compartments that utilize that product. In economics, the latter assumption makes good sense. For example, a telefax machine usually is sold at the same price, regardless of whether the customer is a law firm, a grocery, a baseball club or whatever. Any attempt at differential pricing would be eroded by market forces. It usually does not make economic sense to break products into their material components and equate the value of, say, the copper in a telefax machine with that of the copper in a personal computer purchased from another vendor. The customer uses the telefax and the personal computer in the forms they were received and (usually) doesn't render them into component parts for reconstitution into some radically different configuration. But such is precisely the nature of trophic transformations! A predator captures a prey organism and catabolizes it (digests it) into elementary chemical forms (not elements, but simple compounds dominated by specific elements) and thereafter anabolizes (assimilates) those simple forms according to a new *bauplan*. The anabolic process incorporates simple elements in nearly fixed ratios, and the residuals are discarded. Glutamine, for example, is required at the same rate by the anabolic system of a fox, regardless of whether it comes from a rabbit or from a mouse. Hence, equivalence of elements as seen from the demand side seems an eminently reasonable assumption to make as a prelude to assigning values to ecological components.

It is useful to compare the values of the inputs with those of the outputs from the same compartment. If the contribution (value) of all the inputs to a node is the same as the contribution its outputs make to their consumers, then

$$\lambda_{ik} \sum_{l=0}^n T_{lik} = \sum_{p=1}^{n+2} \lambda_{pk} T_{ipk} \quad (2)$$

for all components  $i = 1, 2, \dots, n$  and all media  $k = 1, 2, \dots, m$ . In general, however, the contributory values of inputs and outputs are not equal. The outputs from a compartment often contribute more to the final product than the inputs that sustain them. The

difference may be regarded either as the "value-added" by processes that occur within the compartment, or conversely the amount by which subsequent users discount<sup>1</sup> the value of inputs to the given compartment. The fraction by which the users of output from  $i$  discount the value of medium  $k$  flowing into  $i$  will be denoted by  $D_{ik}$ . It follows that (2) should read

$$\lambda_{ik} \sum_{l=0}^n T_{lik} = (1 - D_{ik}) \sum_{p=1}^{n+2} \lambda_{pk} T_{ipk} \quad (3)$$

Not all of the  $\lambda_{ik}$  are unknown. In particular, one assumes that the degraded products are of no value whatsoever to the sink that receives them, i.e.,  $\lambda_{n+2} = 0$ . By way of contrast, the exports of  $i$  to the economic community have values set by the market. Call the market value of exports from compartment  $i$ ,  $V_i$ . It is now assumed that products passing into the market are used in the same forms that they are harvested or otherwise delivered. That is, each of the  $m$  elements is necessary to the final product in its natural proportions. Then,

$$V_i = \lambda_{n+1,k} T_{i,n+1,k} \quad (4)$$

for all  $i$  and  $k$ . (This assumption is *not* crucial to what follows. In the event the various elements in a product are valued differently by the market, one can replace  $V_i$  in eqn 4 by  $V_{ik}$ , the value of element  $k$  in the export from  $i$ , and proceed accordingly.)

Substituting (4) into (3) yields

$$\lambda_{ik} \sum_{l=0}^n T_{lik} - (1 - D_{ik}) \sum_{p=1}^n \lambda_{pk} T_{ipk} = V_i \quad (5)$$

or

$$\sum_{p=1}^n K_{pik} \lambda_{pk} = V_i \quad (6)$$

where

$$K_{pik} = \delta_{pi} \sum_{l=0}^n T_{lpk} - (1 - D_{ik}) T_{ipk} \quad (7)$$

<sup>1</sup> This is not discounting in the traditional sense of the word, which always implies an evaluation over time. Rather, it refers to what might be called "trophic discounting," or that done across trophic levels. Hannon has suggested that "costing" might be the more orthodox terminology, but "discounting" will be retained here in the spirit of transdisciplinary discourse.

and

$$\delta_{pi} = 1 \quad \forall p = i$$

$$\delta_{pi} = 0 \quad \forall p \neq i$$

There are  $m \times n$  unknown  $\lambda_{pk}$  in the  $m \times n$  equations represented by (6). Once the discount rates have been specified, (6) can be solved for the contributions per unit flow,  $\lambda_{pk}$ .

In formulating the discount rates,  $D_{ik}$ , it might seem that one should regard the  $T_{i,n+2,k}$  as wasted and discount the input flows by the fraction of the input that is dissipated by  $i$ . That is,

$$D_{ik} = T_{i,n+2,k} / \sum_{l=0}^n T_{lik} \quad (8)$$

However, discounting everything that is dissipated is too radical an assumption. Although the values of the dissipated flows to the sink that receives them is null, it is likely that some of the dissipated energy or material served the purpose of organizing and/or maintaining the internal structure of  $i$ . Therefore, some portions of the dissipated media contributed to the values of the outputs from  $i$ , and their effects are embodied therein (cf., "basal metabolism" in Costanza and Hannon 1989).

A rational estimate of the discount rates may be achieved by searching for the "limiting element" flowing into each  $i$ . If the amount of medium  $k$  stored in  $i$  is  $B_{ik}$ , then the characteristic rate at which element  $k$  appears to pass through stock  $B_{ik}$  is

$$r_{ik} = \left( \sum_{l=0}^n T_{lik} \right) / B_{ik} \quad (9)$$

However, population  $i$  incorporates media only in fixed proportions<sup>2</sup> (cf., stoichiometry), so the actual rate at which all media pass through biomass  $i$  becomes identical to the slowest, or limiting (Liebig 1840) rate of passage—call it  $r_{iq} = \min(r_{ik})$  over all  $k = 1, 2, \dots, m$ . Media being received by  $i$  faster than this limiting rate are assumed to be wasted in proportion to the relative amounts by which their throughput rates exceed the limiting pace and should be discounted accordingly (cf., Gigantes 1970.) Hence, the discount rate for medium  $k$  through component  $i$  becomes

$$D_{ik} = (r_{ik} - r_{iq}) / r_{ik} \quad (10)$$

<sup>2</sup> Margalef (personal communication), however, warns that molar ratios are prone to shift with succeeding generations.

Nonliving compartments (e.g., detrital pools) are assumed to add no value to the resources passing through them and hence exhibit no discounting. (Of course, microbiota acting on detritus do change the values of the media they process and thus should appear *explicitly* in the network.) In the event that biomass proportions are unknown, the discount rate can be approximated by setting

$$r_{ik} = \left( \sum_{l=0}^n T_{lik} \right) / \left( \sum_{p=1}^{n+1} T_{ipk} \right) \quad (9')$$

and proceeding in similar manner to calculate  $D_{ik}$  with (10).

### A SIMPLE EXAMPLE

Flows in ecological communities usually are reckoned in terms of a single reference medium. Although budgets of various media appear in the literature, the instances of bookkeeping on more than a single medium for a given system are few. In one such case, Fasham (1985) estimated both carbon and nitrogen flows occurring in the ecosystems of the marine euphotic zone in neritic areas such as the North Sea. Fasham's networks were reported as the flows that would result from a unit of primary input of each element. The carbon network is readily converted into actual mass flows by scaling up the primary production to  $90 \text{ g carbon m}^{-2}\text{y}^{-1}$ , as is typical of the North Sea (Steele 1974). The results are shown in figure 17.1.

Nitrogen enters Fasham's system into the dissolved pool and could not be scaled directly. Fortunately, the molar ratio of C:N in the phytoplankton is known rather precisely to be 6.625, so that the nitrogen output from the phytoplankton is obtained accordingly. Back-calculating through the dissolved pool of nitrogen reveals that an input of  $3.47 \text{ g nitrogen m}^{-2}\text{y}^{-1}$  into the system at that point replicates the desired output of nitrogen from the phytoplankton. The network of nitrogen flows appears as figure 17.2.

Fasham gives no values for the standing stocks of carbon and nitrogen in each compartment. Actually, the absolute magnitudes of the stocks are not necessary, as they cancel out in eqn (10). Knowing only the C:N ratios is sufficient to calculate the discount coefficients. The C:N ratios of 5 of Fasham's 7 compartments appear as the ratios of carbon to nitrogen in predatory losses from these nodes. Only the C:N ratios for the fish and the dissolved nutrient pool are not evident from his diagrams, and the latter is moot, because discounting by nonliving compartments is assumed to be zero. As to the carnivores (fish), Jorgensen (1979) reports that the dry weight of fish nominally consists of 16.3% nitrogen and 50% carbon. Thus, the C:N ratios (by weight) are taken to be:

1. Phytoplankton	5.68	5. Protozoa	5.06
2. Planktobacteria	4.54	6. Detritus and Bacteria	2.92
3. Carnivores	3.07	7. Dissolved nutrients	****
4. Omnivorous Zooplankton	5.23		

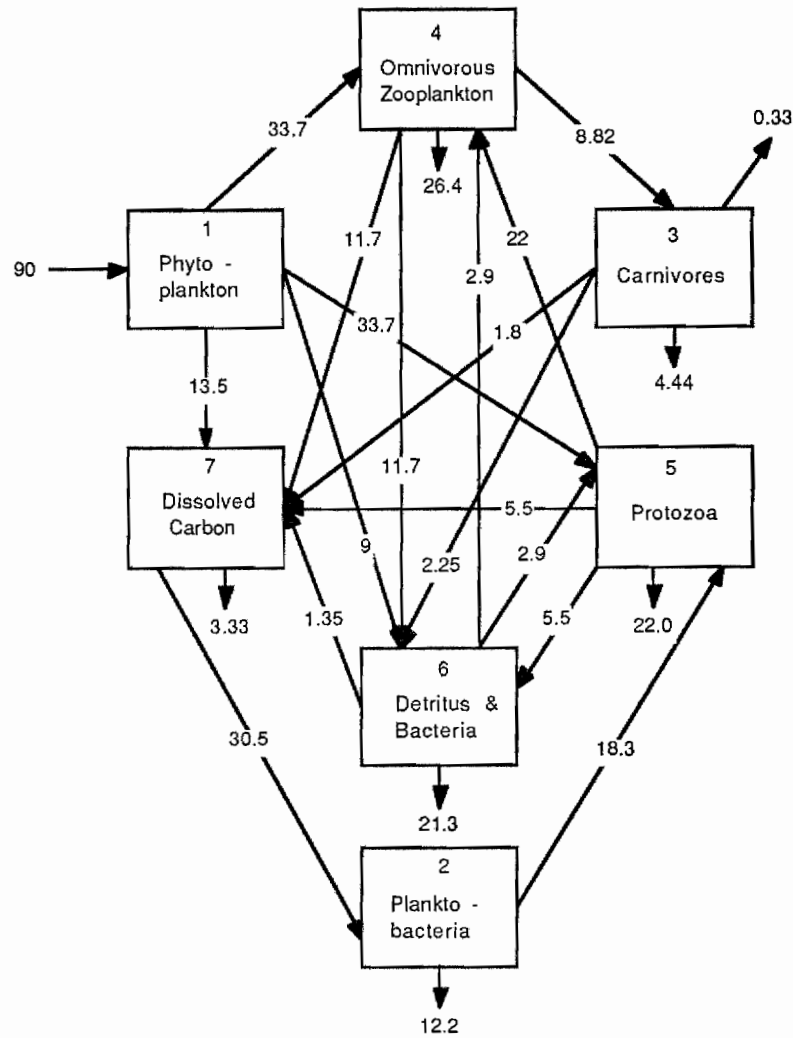


FIGURE 17.1 Flows of carbon in  $\text{mg m}^{-2}\text{y}^{-1}$  among the components of the euphotic zone of the North Sea ecosystem (after Fasham 1985).

The final market product is the carnivores, or fish. Here, it is assumed that all the nitrogen exported from that compartment ( $0.11 \text{ g Nitrogen m}^{-2}\text{y}^{-1}$ ) appeared in the harvest and was accompanied by a proportionate amount of carbon. The value of the harvest was set arbitrarily to 100 units.

The contributory values per unit flow (the  $\lambda_{pk}$  in eqn. 6) were calculated and multiplied by their corresponding flows (the  $T_{ipk}$ ) to assign a contributory value to each flow



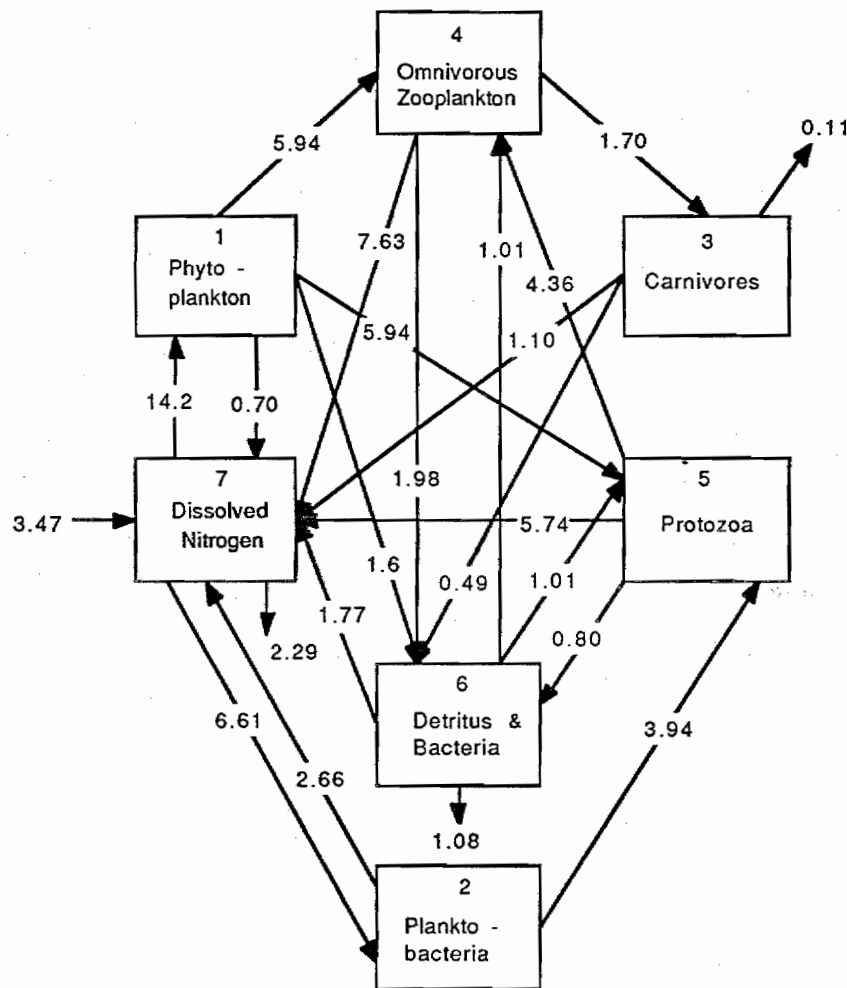


FIGURE 17.2 Exchanges of nitrogen in  $\text{mg m}^{-2}\text{y}^{-1}$  among seven compartments comprising the ecosystem of the North Sea euphotic zone.

in the system. The values corresponding to the flows of carbon are shown in figure 17.3, and those for nitrogen appear in figure 17.4.

One notices immediately that the contributory values of the nitrogen flows are generally higher than their carbon counterparts. The final output from the carnivores (fish) is set equal to 100 for both media, but farther back in the network, the carbon flows diminish rapidly in value. The primary production of carbon contributes only 56 units to the final output, as contrasted with the 95 units contributed by the nitrogen upwelling into the dissolved nutrient compartment. Perusal of the discount coefficients reveals that the

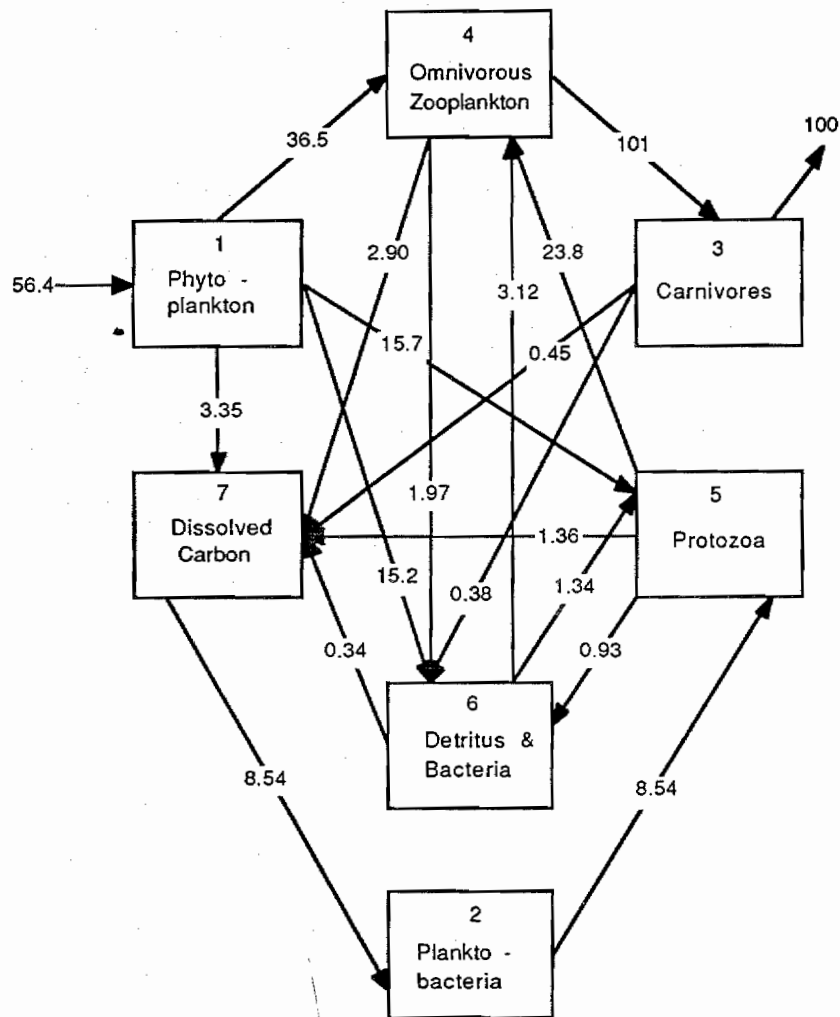


FIGURE 17.3 Relative contributions that each flow of carbon in figure 17.1 makes towards 100 arbitrary units exported from the fish compartment (carnivores).

inputs of carbon and nitrogen are virtually balanced (i.e., near their stoichiometric proportions) coming into the zooplankton and protozoan compartments and limited only slightly by nitrogen going into the phytoplankton (10.5% discounting of carbon) and planktobacteria (2%) compartments. Major nitrogen limitation occurs at the inputs to the detritus-bacteria compartment (50% discounting of carbon) and during carnivore feeding (41%). These two nodes account for most of the excess consumption (i.e., discounting) of carbon by the system.

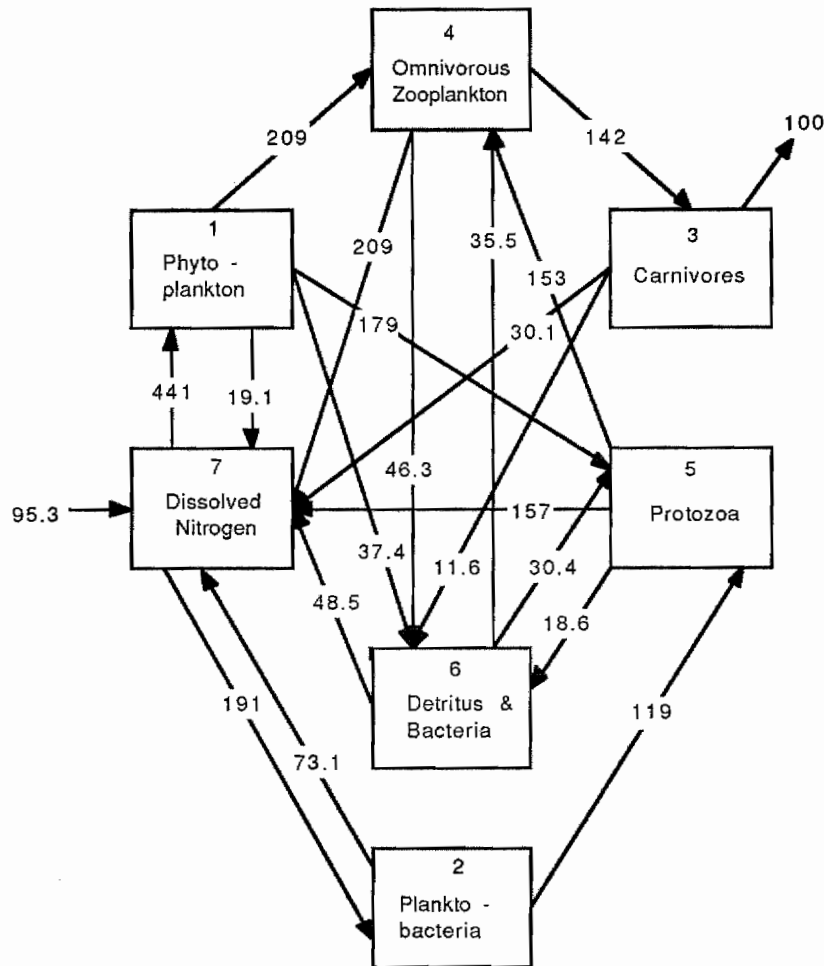


FIGURE 17.4 Relative contributions of nitrogen flows to the 100 units produced by the fish compartment.

The values of many nitrogen flows are high, sometimes even exceeding the value of the exported nitrogen. These high values are due to the large fraction of nitrogen recycling activity within the system (Finn cycling index  $>87\%$ ). In particular, the uptake of nitrogen by phytoplankton contributes 441 units to the final output. This contribution exceeds the 100 unit value of the final output; however, it should be remembered that this nitrogen will spend considerable time recycling within the system. Before it finally leaves the system, it will have contributed not only to the 100 units of fish now being produced, but to several-fold that output during later circuits through the system. It is interesting to note that the major pathways for recycle of valuable nitrogen do not include

the detrital stage. (Detritus is prone to settling out of the euphotic zone.) Rather, the planktobacteria, zooplankton and protozoa are the principal agents that keep the scarce nitrogen circulating within the system.

An algorithm exists that is able to separate the cycled components in figure 17.4 from their once-through counterparts (Ulanowicz 1983). Figure 17.5 shows such "circulation" of nitrogen value. As Fasham himself pointed out, the system is strongly nitrogen limited, and one can see in figure 17.5 the emergence of nitrogen as a "proto-currency," which remains in the system for a long time.

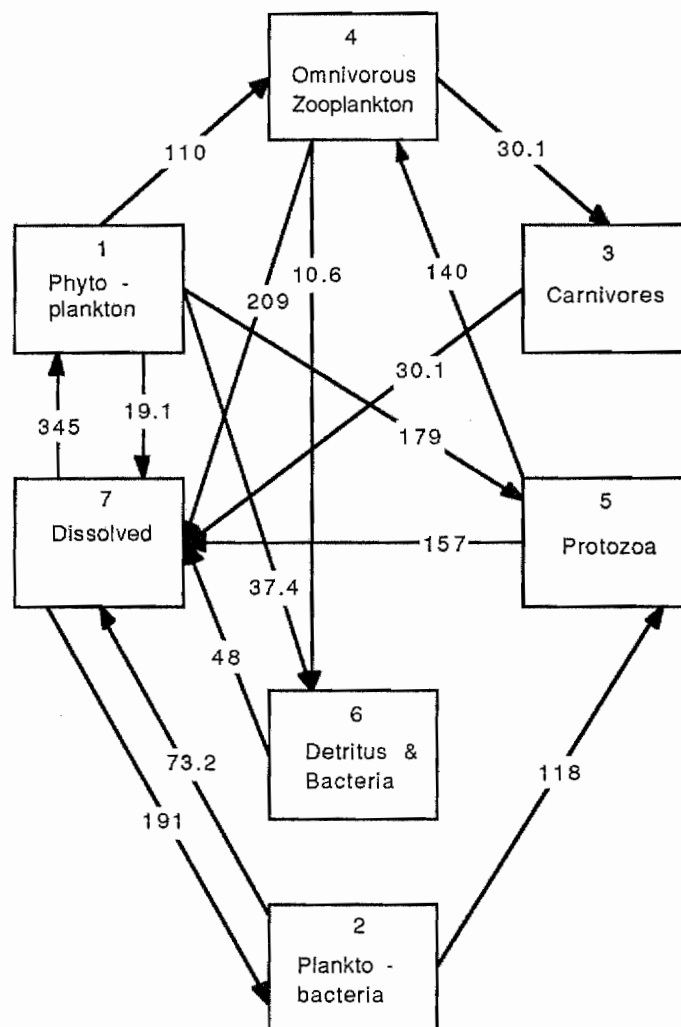


FIGURE 17.5 The circulation of nitrogen value in the North Sea ecosystem.

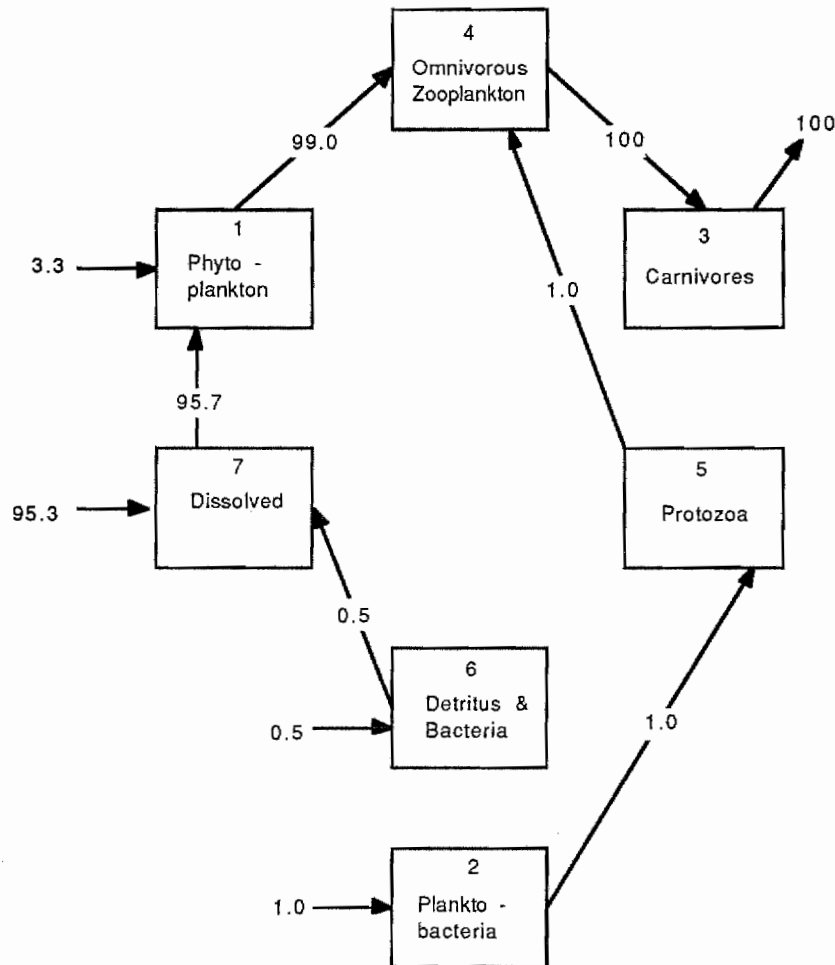


FIGURE 17.6 Residual sources and transfers of nitrogen values.

The actual sources for the nitrogen values appear in figure 17.6, where the residual nitrogen values are depicted. One sees that the "new" nitrogen contained in the upwelling is the primary contributor of *net* nitrogen value to the system. The remaining value-added sources are small by comparison.

## DISCUSSION

Like all measures of value, contributory value is a relative concept. It refers specifically to the potential for a particular medium in a given form to contribute towards a

designated end product. The magnitude of any contribution is always scaled by the value of the final product, which in turn is set outside the system. For example, the  $33.7 \text{ g carbon m}^{-2}\text{y}^{-1}$  of phytoplankton consumed by the zooplankton potentially contributes 36.5 units to the output of fish valued at 100 arbitrary units. This contributory value does not measure the value of the phytoplankton to the zooplankton, much less any intrinsic worth phytoplankton may have in some other context. This last point deserves emphasis, lest any reader be tempted to use the method described here to assess the absolute worth of an ecological resource per se. Trees in a forest will contribute via the food web to the creation of, say, pelts taken from resident furbearing mammals. If one knows the quantified web of trophic interactions that culminate in the growth of furbearers and the economic value of the harvested pelts, it becomes possible to use the method described above to calculate the contribution of the trees to the harvested pelts via the web of trophic transfers. The same result, however, does not assess the value of the trees in creating habitat for the mammals, nor does it begin to encompass the host of other roles (utilitarian and otherwise, e.g., aesthetic) that trees play in the ecosystem.

These limitations notwithstanding, the calculation of contributory values can prove very useful. Justifiable or not, the perceived value of familiar ecosystems to some segments of the public will be in terms of one or a few items that the natural system provides to these individuals. For example, the primary association that legislators (or many natural resources managers, for that matter) make with the Chesapeake Bay is to a sports-fish, the striped bass (*Morone saxatilis*). Understandably, these individuals wish (for both personal and political reasons) to maintain the value of striped bass provided by the Bay ecosystem at a high level. The same group probably would never give a thought to the condition of ciliate populations (microscopic heterotrophs) in the same water column, until it is pointed out to them that the ciliates contribute 35 units to every 100 units of striped bass taken from the Bay (Baird and Ulanowicz 1989; and eqn. 6 above). At the very least, the contributory values of the supporting members of an ecosystem provide a *conservative* estimate of the values of the ecological foundations underlying a given resource.

In the end, the most important application of contributory values may not be explicitly economic in nature. The index could prove most useful in expanding the utility of the notion of limiting nutrients. Marine and aquatic ecosystems often are characterized as nitrogen-limited or phosphorous-limited, respectively. Some question remains as to what limits the productivity of estuarine systems—it probably would be simplistic to think of estuarine systems as being limited by either one element or the other. It is likely that phosphorous is limiting to some populations at certain times and nitrogen (or even carbon) to the remaining species at other times. Exactly which compartments are controlled by what elements, at which times and places could be addressed by computing the contributory values of each element using quantified networks of carbon, nitrogen and phosphorous flows for the estuarine ecosystem.

Like its supply-side counterpart, the calculation of contributory values converts flows having different sundry physical dimensions into a common currency. Networks with common units are of great advantage to those seeking to characterize ecosystem status in

terms of whole-system indices (Kay et al. 1989). Heretofore, such indices have been reckoned in terms of a single medium. However, the magnitudes of flows of other media bear different proportions to each other than do those of the chosen medium, and useful information is lost by neglecting the exchanges of other media (Herendeen 1990). By expressing all flow networks of relevant media in terms of a common currency, one obtains a three-dimensional array ( $n \times n \times m$ ) of flows to which one may then attach appropriate three dimensional information measures (see Ulanowicz 1986, p. 146; and Pahl-Wostl 1990). These expanded indices encompass all aspects of multimedia kinetics that comprise the system's organization.

It might further be asked how the demand-side calculations presented here could be related to the results from the supply-side treatment (e.g., Costanza and Hannon 1989). The system topologies used in the two methods are different, and comparing the values of intermediate products could be problematical. The primary inputs and the final products are easier to compare, however, and it would be interesting to calculate the contributory values of sunlight to a number of ecosystem products in order to observe the range in values that would result. Determining a *lower bound* on the economic utility of sunlight and primary production could be a significant step toward attributing value to many ecosystem components whose contributions to human welfare have heretofore languished in the realm of "common property natural resources."

Finally, it bears repeating that this exercise yields a valuable glimpse into the nature of ecological economics. It was mentioned before how progress by others in quantifying an *ecological* description of the natural world and its embedded marketplace was predicated on the methods and conventions of *economic* theory. The work just described points out the complement: How articulation of the *economic* perspective on the same interactions depends crucially on invoking bookkeeping methods peculiar to *ecology*. It may appear trite or self-evident to read that a transdisciplinary endeavor relies on a sufficient knowledge of both separate fields of study, but perhaps nowhere else is the mutually obligatory nature of such a relationship made more starkly evident than in the case of ecological economics!

### Acknowledgments

The author would like to thank Dr. Robert Costanza for pointing out to him the existing notion of "contributory value." Drs. John Cumberland, Bruce Hannon, Robert Herendeen, and Ramon Margalef read the draft manuscript and offered many useful suggestions for revision. This work was supported as an element of the National Science Foundation's "Land Margin Ecosystems Research" Program, Grant no. BRS8814272.

### REFERENCES

- Augustinovic, M. 1970. Methods of International and Intertemporal Comparison of Structure. In A. P. Carter and A. Brody, eds., *Contributions to Input-Output Analysis*, vol. I, pp. 249-269. Amsterdam: North Holland.

- Baird, D. and R. E. Ulanowicz. 1989. The Seasonal Dynamics of the Chesapeake Bay Ecosystem. *Ecological Monographs*. 59:329-364.
- Bosserman, R. W. 1981. Sensitivity Techniques for Examination of Input-Output Flow Analyses. In W. J. Mitsch and J. M. Klopatek, eds., *Energy and Ecological Modelling*, pp. 653-660. Amsterdam: Elsevier.
- Costanza, R. and B. Hannon. 1989. Dealing With the "Mixed Units" Problem in Ecosystem Network Analyses. In F. Wulff, J. G. Field and K. H. Mann, eds., *Network Analysis in Marine Ecology: Methods and Applications*, pp. 90-115. Berlin: Springer-Verlag.
- Costanza, R. and C. Neill. 1984. The Energy Embodied in the Products of Ecological Systems: A Linear Programming Approach. *Journal of Theoretical Biology* 106:41-57.
- Fasham, M. J. R. 1985. Flow Analysis of Materials in the Marine Euphotic Zone. In R.E. Ulanowicz and T. Platt, eds., *Ecosystem Theory for Biological Oceanography*, pp. 139-175. Canadian Bulletin of Fisheries and Aquatic Sciences, 213.
- Finn, J. T. 1976. Measures of Ecosystem Structure and Function Derived from Analysis of Flows. *Journal of Theoretical Biology* 56:363-380.
- Gigantes, T. 1970. The Representation of Technology in Input-Output Systems. In A. P. Carter and A. Brody, eds., *Contributions to Input-Output Analysis*, vol. 1, pp. 270-290. Amsterdam: North Holland.
- Hannon, B. 1973. The Structure of Ecosystems. *J. theor. Biol.* 41:535-546.
- Hannon, B., R. Costanza and R. E. Ulanowicz. 1991. In press. A General Accounting Framework for Ecological Systems: A Functional Taxonomy for Connectionist Ecology. *Theoretical Population Biology*.
- Herendeen, R. 1990. System-Level Indicators in Dynamic Ecosystems: Comparison Based on Energy and Nutrient Flows. *Journal of Theoretical Biology* 143:523-553.
- Hirata, H. and R. E. Ulanowicz. 1984. Information Theoretical Analysis of Ecological Networks. *International Journal of Systems Science*. 15:261-270.
- Jorgensen, S. E., ed. 1979. Handbook of Environmental Data and Ecological Parameters. Copenhagen: International Society for Ecological Modelling.
- Kay, J. J., L. A. Graham and R. E. Ulanowicz. 1989. A Detailed Guide to Network Analysis. In F. Wulff, J. G. Field and K. H. Mann, eds., *Network Analysis in Marine Ecology: Methods and Applications*. Berlin: Springer-Verlag, pp. 15-61.
- Leontief, W. 1951. *The Structure of the American Economy, 1919-1939*. 2d ed. New York: Oxford University Press.
- Levine, S. 1980. Several Measures of Trophic Structure Applicable to Complex Food Webs. *Journal of Theoretical Biology* 83:195-207.
- Liebig, J. 1840. *Chemistry in Its Application to Agriculture and Physiology*. London: Taylor and Walton.
- Odum, H. T. 1989. Self-Organization, Transformity, and Information. *Science* 242:1132-1139.
- Pahl-Wostl, C. 1990. Temporal Organization: A New Perspective on the Ecological Network. *Oikos* 58:293-305.
- Patten, B. C., R. W. Bosserman, J. T. Finn and W. G. Cale 1976. Propagation of Cause in Ecosystems. In B. C. Patten, ed., *Systems Analysis and Simulation in Ecology* 4:457-479. New York: Academic Press.
- Steele, J. H. 1974. *The Structure of Marine Ecosystems*. Oxford: Blackwell.
- Szyrmer, J. and R. E. Ulanowicz. 1987. Total Flows in Ecosystems. *Ecological Modelling* 35:123-136.
- Ulanowicz, R. E. 1983. Identifying the Structure of Cycling in Ecosystems. *Mathematical Biosciences* 65:219-237.
- Ulanowicz, R. E. 1986. *Growth and Development: Ecosystems Phenomenology*. New York: Springer-Verlag.
- Ulanowicz, R. E. 1989. Energy Flows and Productivity in the Oceans. In P. J. Grubb and J. B. Whittaker, eds., *Toward a More Exact Ecology*, pp. 327-351. Oxford: Blackwell.
- Ulanowicz, R. E. and W. M. Kemp 1979. Toward Canonical Trophic Aggregations. *American Naturalist* 114:871-883.
- Ulanowicz, R. E. and C. J. Puccia 1990. Mixed Trophic Impacts in Ecosystems. *Coenoses*, 5:7-16.