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MIXED TROPHIC IMPACTS IN ECOSYSTEMS

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Abstract. When conventional economic input-output (I-O) analysis is applied to ecological networks, it traces only the positive benefits that material and energetic exchanges impart to their recipients, *i.e.*, the vertical structure of ecosystem trophodynamics. However, unlike their economic counterparts, most predator-prey exchanges in ecology are not accompanied by a compensating counterflow, so that the immediate effect of depredation upon the prey population is negative in character. It is possible to amend the I-O calculus to assess simultaneously the indirect consequences of both positive and negative impacts of trophic interactions, thereby expanding I-O methods to explore also the horizontal dimension of indirect competitions and mutualisms. For example, the new method shows that in the network of carbon exchanges occurring in the Chesapeake Bay estuarine ecosystem, the ctenophores and coelenerates engage in indirect mutualism with the phytoplankton and in extended competition with most other heterotrophs. These invertebrates are seen to play a heretofore unappreciated role in the eutrophic dynamics of the Chesapeake system.

Introduction

It is often remarked in the popular literature that in ecosystems "everything is connected with everything else". Ecologists are usually quick to caution against interpreting this aphorism too literally, citing that each component of an ecosystem interacts directly with only a small subset of other species (May 1973, Yodzis 1980, Pimm 1982). But exactly how far throughout the system does the *indirect* influence of a particular element extend?

Indirect influences have intrigued biologists throughout the history of modern science. The biologist-philosopher Quesnay set forth an algorithm for tracing indirect effects in diagrammatic/arithmetic form as early as 1758 (Rosenblatt 1960). But it fell to economists to make the first concrete strides toward quantifying the magnitudes and extents of indirect influences. Leontief (1951) demonstrated how a knowledge of all the direct exchanges occurring in an economic community could be used to infer the level of activity within any economic sector necessary to meet the final demand by any other sector. Some twenty years passed before Hannon (1973) imported this highly useful methodology into ecology, where it has been refined and adapted to assess indirect influences in ecosystems (*e.g.*, Patten *et al.* 1976, Finn 1976, Ulanowicz and Kemp 1979, Bosserman 1981, Ulanowicz 1986, Szyrmer and Ulanowicz 1987). It is now possible to estimate the probable sources and sinks for material flowing anywhere in a system. With regard to the connectedness of indirect effects, these input-output techniques revealed that a particular component usually receives material indirectly from only a subset of all system elements, and in turn contributes to only another subset of species. That is, even the network of indirect material exchanges is not fully connected. But this depiction of the vertical structure of material flows is not the full story of trophic impacts.

To be more specific, ecosystems differ from their economic counterparts in that conjugate compensatory flows are virtually absent from the former. That is, in economic systems each exchange of materials, goods, or services is always accompanied by an approximately compensating counterflow of currency, labor or barter. While such direct mutualism does occur in ecosystems, uncompensated predator-prey interactions are far more common. Trophic feeding has an *immediate* effect that is positive to the predator and negative to the prey. Ecological input-output analysis, as it now stands, treats the propagation of the positive benefits to predators, but ignores the ultimate impacts of the losses to the prey.

Levins (1974) did include the negative effects of predation in his qualitative analysis of foodwebs, commonly referred to as loop-analysis. In his scheme, ecosystem compartments are treated as boxes, and the interactions, (material or otherwise) between the boxes are depicted as arrows connecting the boxes. Two kinds of arrows are used, one for enhancement and another for depredation. Thus, a single trophic transfer is represented by one arrow of each kind pointed in opposite directions. No other information beyond the qualitative nature of the effects (+ or −) is used in his analysis. Among the definitive statements one can make about

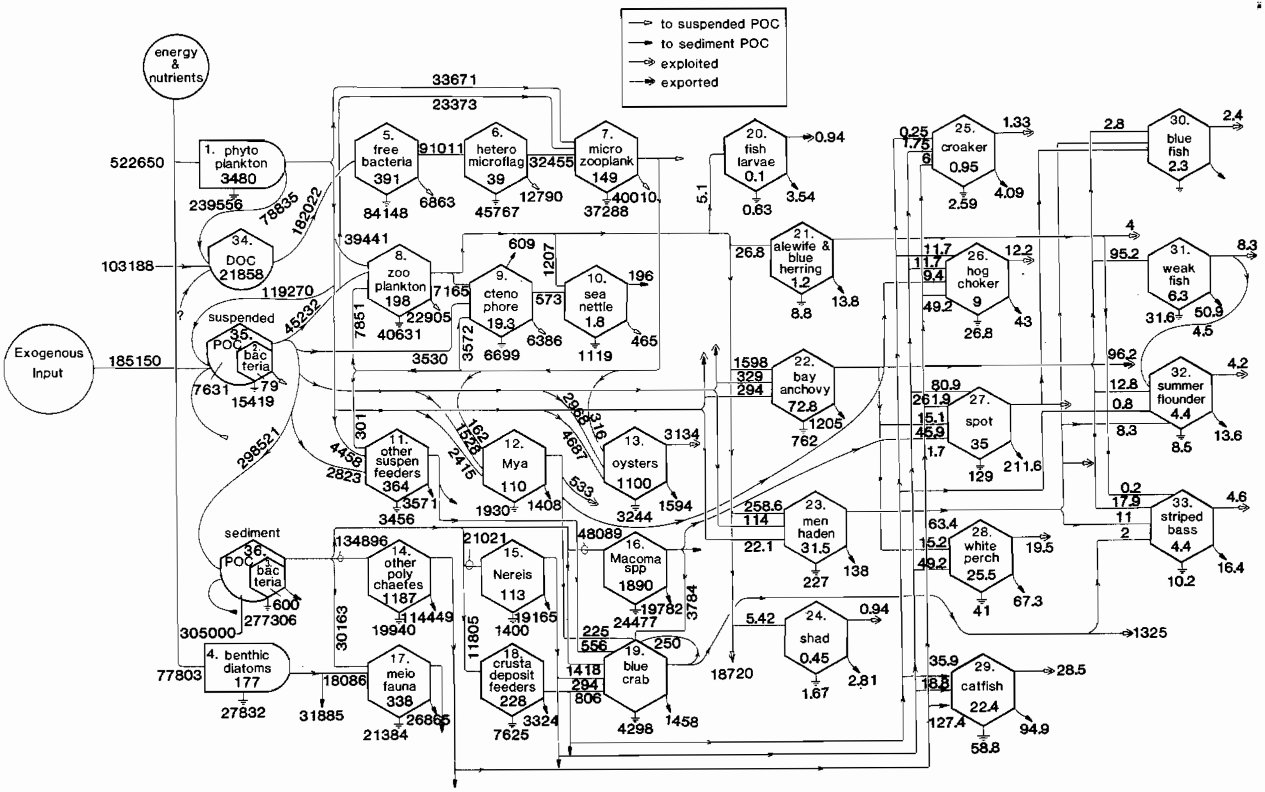

Fig. 1. Estimated exchanges of carbon (mg m^{-2} y^{-1}) among the 36 principal components of the Chesapeake mesohaline ecosystem (Baird and Ulanowicz, 1989).

such qualitative networks is that any directed cycle consisting exclusively of positive arrows is by definition autocatalytic and potentially important in defining the structure of the community. Of course, a particular species also may be a part of a multitude of other feedback loops, and estimating the outcomes of various interacting routes of self-enhancement is treated in Puccia and Levins (1985).

Perhaps the major source of ambiguity in loop analysis is the multiplicity of pathways that may connect any two nodes of the system, or what Ulanowicz (1980) calls the pathway redundancy. When only one pathway connects two species, its overall effect is always positive or negative, according to whether the number of negative arrows in the pathway is even or odd, respectively. However, when two or more paths connect two species, and the overall effects of the various pathways differ in sign, there is no way using qualitative data alone to resolve whether the cumulative effect is positive or negative (Legovic and Patten 1981). Of course, pathway redundancy is more often the rule rather than the exception. In a graph of trophic transfers that is simply connected (*i.e.*, one in which one can identify at least one tree containing all the elements) many pathways connecting any two nodes usually can be found. The situation is further complicated as soon as one accounts for the presence of negative trophic impacts. One or more pathways will then connect any two elements in the graph, so that every node is literally connected with every other in the system! Intuition suggests that not all connections are equivalent, and it remains somehow to ordinate the indirect impacts, *i.e.*, a quantitative form of loop-analysis is called for.

Quantifying trophic impacts

Confining further discussion to trophic interactions only, the positive effect that a prey has upon a predator was quantified by Leontief when he originated input-output analysis: If T_{ij} represents the amount of prey i consumed by predator j, then $g_{ij} = T_{ij}/\sum_k T_{kj}$ represents the fraction of j's diet comprised by prey item i[1]. The summation on k is taken over all elements of j's diet, so that $0 \le g_{ij} \le 1$. The dietary coefficients (called technical coefficients in economic parlance) assign weights to the various items in each predator's diet.

Weighting the negative impact that a predator has upon its prey is but marginally more complicated. Augustinovics (1970) defined technical coefficients based on outputs from a compartment as $f_{ij} = T_{ij}/\sum_m T_{im}$. That

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[1] All the T_{ij} are assumed to have the same physical units. However, even when units are consistent, some investigators argue that the flows still need to be weighted according to their qualities (*e.g.*, Hannon and Costanza, 1985).

is, f_{ij} represents the fraction of i's total production that is consumed by predator j. For ecological purposes it is necessary to amend this definition slightly to exclude respiratory output from the denominator, *i.e.*, f_{ij} is defined as the fraction of *net* output by i that is consumed by j. Net output should be a better gauge of the impacted population than is the gross output, because dissipation is largely decoupled from the rate of predation (Kay 1984). When the receiving compartment j is not an active feeder, but simply a collection of passive material, one should equate f_{ij} to zero, because such detrital flows usually do not directly impact their donors to the same negative degree as do active predators.

A typical ecosystem network is presented in Fig. 1. The nodes represent 36 major compartments of the ecosystem inhabiting the mesohaline reach of the Chesapeake Bay estuary along the East Coast of North America. The lines and arrows between the nodes depict the cumulative annual flows of carbon $mgCm^{-2}y^{-1}$) as estimated by Baird and Ulanowicz (1989).

For examples of how one calculates the g's and f's the reader's attention is drawn to compartment 7 representing the microzooplankton (mostly ciliates) that are dispersed throughout the water column. The inputs into 7 from compartments 1, 2, 6 and 35 sum to 89,499 $mgCm^{-2}y^{-1}$. Of that total, 32,455 units are coming from 6, so that $g_{67} = 0.363$. The dissipation (respiration) by the ciliates is 37,288 $mgCm^{-2}y^{-1}$, making the net output equal 52,211 $mgCm^{-2}y^{-1}$. Of this net production, 3,572 units are cropped by compartment 9, the ctenophores, so that the host coefficient $f_{79} = 0.068$.

The net impact of i upon j will equal the amount that i serves as a prey item for j minus any detrimental impact that i might have as a predator upon j. Calling q_{ij} the net impact of i upon j, we see that

$$q_{ij} = g_{ij} - f_{ji} \tag{1}$$

It happens that either g_{ij} or f_{ji} is zero for most pairs of interacting i and j. Because the g_{ij} and f_{ji} are normalized, *i.e.*,

$$0 \leq g_{ij} \leq 1 \qquad \text{and} \qquad 0 \leq f_{ji} \leq 1 \tag{2}$$

the values of q_{ij} range from -1 to $+1$, inclusive. Due to the fact that g_{ij} and f_{ji} are the components of n x n matrices, their differences constitute the components of an n-dimensional *net impact matrix.*

Indirect impacts

The object of applying input-output theory to ecology is to evaluate how impacts are exerted via indirect routes. If A influences B, and B interacts with C, then an indirect pathway exists for A to impact C. Indirect influences can be propagated along pathways containing negative influences as well. If A adversely affects B, and B catalyzes the activity of C, then A will exert a negative influence upon C along this particular causal route. However, if the impact of B upon C were negative, then A would have a salutary effect upon C by virtue of its inhibition of B's suppression of C. It should be clear, as has been pointed out in loop analysis, that the qualitative nature of any indirect effect is determined by the sign of the product of the sequential actions along the pathway by which such influence is exerted. That is, any pathway containing an odd number of negative direct effects will inhibit the end member, whereas any route containing an even number of depredatory impacts will stimulate its last node.

It remains to quantify the magnitudes of sequential actions. Here it should be noted that in writing equation (1) it was implicitly assumed that the g's and f's are comparable quantities. That is, one cannot subtract apples from oranges (again, see Hannon and Costanza, 1985). In keeping with established practice in I-O analysis, we will assume that the overall trophic impact of any concatenation of direct effects is measured by the product of all the q's along that pathway. We will assume furthermore that if more than one pathway of action impinges upon a given node, the cumulative effect upon that node will be reflected in the algebraic sum of the weights assigned to the various pathways impinging upon the given compartment. In quantitative terms, if i, j, k, ..., y, z, are the nodes along a particular pathway of action, then

$$p_{iz} = q_{ij}\, q_{jk} \cdots q_{yz} \tag{3}$$

will characterize the strength of that particular interaction from i to z. Secondly, if p_{iz} and p_{hz} are two distinct pathways ending at z, then their combined impact is assumed to be $p_{iz} + p_{hz}$. (We stress these assumptions because they are not necessarily unique, and other investigators might wish to explore the results of a different set of algebraic postulates.)

This particular method of weighting and comparing indirect effects was chosen because it allows one to invoke the same matrix methods as are employed in standard input-output analysis. In particular, the coefficients, q_{ij}, of the mth algebraic power of the net impact matrix, [Q], will then quantify the cumulative effects of i upon j along all pathways of exactly length m. Consequently, the total impact of i upon j will appear as the i-jth entry in a matrix, say [M], that is the sum of all integer powers of [Q], *i.e.*,

$$[M] = \sum_{h=1}^{\infty} [Q]^{h} \tag{4}$$

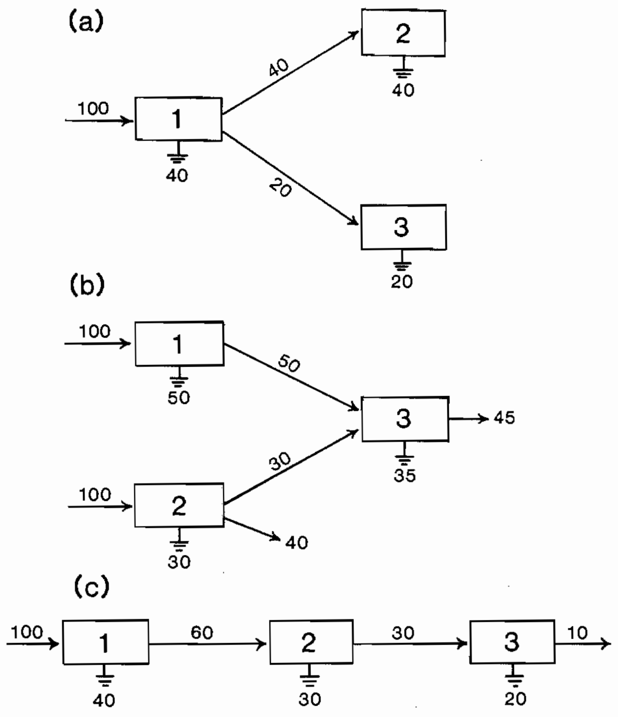

Fig. 2. Three simple hypothetical configurations of trophic exchanges (arbitrary units). (a.) Two predators on a single prey. (b.) Two prey sustaining a single predator. (c.) A linear trophic chain of three compartments.

Because of the normalization schemes used, the row and column sums of [Q] will all fall between −1 and +1 in magnitude. This condition guarantees that the infinite series in (4) will converge to a finite limit -- one well-known from input-output theory to be

$$\sum_{h=0}^{\infty} [Q]^h = \{[I]-[Q]\}^{-1} \tag{5}$$

where [I] is the identity matrix (ones along the diagonal and zeroes elsewhere), and the exponent −1 signifies matrix inversion. Substituting (5) into (4) and recognizing that $[Q]^0 = [I]$, yields

$$[M] = \{[I]-[Q]\}^{-1} - [I] \tag{6}$$

Equations (1) and (6) allow one to calculate all the mixed trophic impacts that occur in the system.

Elementary examples

The three very elementary networks shown in Fig. 2 illustrate several points about the nature of indirect mixed impacts. In Fig. 2a a single prey is host to two predators. The [Q] matrix for this configuration is

$$[Q] = \begin{bmatrix} 0.0 & 1.0 & 1.0 \\ -0.667 & 0.0 & 0.0 \\ -0.333 & 0.0 & 0.0 \end{bmatrix}$$

The first thing to notice is that mixed impacts are not strictly antisymmetric. For example, the prey 1 is all-beneficial to both predators 2 and 3. However, compartment 2 engenders only 2/3 of the total depredation to 1, and the remainder is lost to predator 3. Although the absolute amount lost by 1 to 3 is identical to that received by 3 from 1, it is clear that the relative benefit of this transfer to 3 exceeds its detriment to 1.

The indirect impacts over pathways of length 2 are given by

$$[Q]^2 = \begin{bmatrix} -1.0 & 0.0 & 0.0 \\ 0.0 & -0.667 & -0.667 \\ 0.0 & -0.333 & -0.333 \end{bmatrix}$$

Here the competition between the two predators is manifested in the negative values for q_{23} and q_{32}, and it further appears that predator 2 is more of a detriment to 3 than vice-versa. Interestingly enough, all the diagonal terms in $[Q]^2$ are negative. What this fact seems to reflect is the irreversible nature of uncompensated flows, such as trophic transfers. In donating medium to a predator the prey strengthens the consumer for still further depredation. Meanwhile, from the receptor's vantage each act of consumption diminishes the predator's wellspring of potential sustenance. Negative values along the diagonal abet the stability of the system (May 1973) and appear to be a consequence of mass conservation.

Higher powers of [Q] seem only to mitigate the absolute values of the components of the first two powers, and the matrix of overall impacts converges to

$$[M] = \begin{bmatrix} -0.500 & 0.500 & 0.500 \\ -0.333 & -0.333 & -0.333 \\ -0.167 & -0.167 & -0.167 \end{bmatrix}$$

In Figure 2b two prey compartments sustain a single predator. The associated matrix of total impacts is

$$[M] = \begin{bmatrix} -0.350 & -0.150 & 0.350 \\ -0.210 & -0.090 & 0.210 \\ -0.560 & -0.240 & -0.440 \end{bmatrix}$$

Once again, all the diagonal terms turn out to be negative. But more interestingly, the two prey items stand in competition with one another (M_{12} and M_{21} are both negative). This competitive relationship counters the intuition that an increase in either prey, by satisfying more of the consumer's demands, should relieve some of the predation pressure on the other host. But such logic ignores the fact that the alternative prey is strengthening the consumer to redouble its predation upon the given host. Appeasement by a few rarely benefits the total community at risk!

These two simple examples bespeak of competition as an agent that mitigates against multiple connections into and out of each compartment. That is, one should include simple trophic competition in addition to autocatalytic feedback (Ulanowicz 1980), as a cause behind the tendency towards more articulated, or streamlined trophic networks. Ulanowicz (1986) has suggested the measure network ascendency as a gauge of this ecological succession towards more articulated trophic configurations.

Lastly, a straight trophic chain is illustrated in Fig. 2c. This simple structure yields

$$[M] = \begin{bmatrix} -0.333 & 0.333 & 0.333 \\ -0.333 & -0.667 & 0.333 \\ 0.333 & -0.333 & -0.333 \end{bmatrix}$$

The interesting feature of this network is the autocatalytic-like relationship between primary host (1) and top predator (3). Such indirect mutualism is easy to rationalize. The top-predator feeds indirectly on the production of the primary host, whereas the first host benefits as the top consumer constrains the activities of the intermediate predator (2). This alternating sequence of enhancements and repressions along a linear trophic chain has been suggested by Kitchell (1989) to explain the abundances and types of phytoplankton and fishes in the Great Lakes.

Numerous other interaction configurations are considered in Puccia and Levins (1985).

Trophic impacts in Chesapeake Bay

To learn more about the nature of mixed trophic impacts as they occur in real ecosystems we return to the network of trophic transfers depicted in Fig. 1. Those interested in the scientific names of the members of each compartment and in the details of how the flow values and biomasses were estimated are referred to Baird and Ulanowicz (1989). Here we wish to apply the matrix methods just described to highlight indirect trophic interactions that might not be apparent from visual inspection of Fig. 1.

The matrix of total trophic impacts is given in Table 1. This matrix is fully connected; but, for clarity, interaction coefficients with absolute magnitudes below 1/10000 will appear as zeroes in the table. The reader will probably be quick to notice that sifting through the myriad of components in the [M] matrix is about as formidable a task as analyzing the interaction patterns in Fig. 1. The investigator would be helped in evaluating [M] by resorting to computer search methods[2]. One of the easiest searches is for - beneficial predators. A beneficial predator directly impacts the host in a negative manner, but this detrimental effect is overshadowed by positive indirect influences[3]. Patten (1984) has noted the potential for indirect influences to overwhelm direct interactions, and this eclipse is most obvious when the indirect impacts are strong enough to reverse the qualitative nature of an immediate exchange.

There are six instances of beneficial predation in Fig. 1: Spot (27) feeding on crustacean deposit feeders (18), ctenophores (9) upon bacteria attached to suspended particulate organic carbon (POC) (2), bay anchovy (22) and menhaden (23) each upon phytoplankton (1) and attached bacteria (2). All six cases fit the same pattern. Each prey is a secondary item in the diet of its predator, which in turn feeds mostly on other predators or strong competitors of the given host. For example, the crustacean deposit feeders comprise only 0.4% of the diet of the spot. But nearly 86% of the spot's diet consists of assorted polychaetes (14)-(15) and *Macoma* (16), all strong competitors of the crustaceans for space and sediment POC.

The components of [M] also may be searched for cycles of mutual benefaction. As an example, phytoplankton (1) are ultimately beneficial to suspended POC (35). This pool of organic carbon has a positive effect upon the ctenophores (9), which in turn augment the phytoplankton. An estimate of the autostimulatory gain in such a cycle can be obtained by serially multiplying the components of the [M] matrix that form the loop, i.e., the gain would be estimated by the product $m_{1,35}\ m_{35,9}\ m_{9,1} = .00175$, or about 0.2% gain. While this amplification is not overwhelmingly large, it should be recalled that small percentages compounded over long intervals yield large returns, which can grow to allow the participants in autocatalysis to dominate other compartments.

The algorithm for finding cycles of mutual benefaction is based on the method of backtracking with pruning (Ulanowicz, 1983). Because the density of positive components in [M] is relatively high, the potential number of autocatalytic loops is enormous. To keep the search within manageable bounds it is necessary to introduce stringent pruning criteria into the backtracking routine. Because one wishes to concentrate only on cycles having appreciable gain, one method of abbreviating the search is to establish a lower threshold of impact below which a positive connection in the [M] matrix is ignored. By raising the threshold in iterative fashion, it is possible to narrow upon only those cycles with the highest autocatalytic gains.

As might have been expected, those cycles in the

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[2] The authors can supply the reader with a copy of an algorithm that calculates [M] and performs several helpful search and ordering tasks. Anyone desiring the program is asked to enclose a blank 5 1/4 inch floppy diskette and appropriate SASE with his/her request.

[3] Here beneficial predation is considered only in the trophic sense of the word, and we neglect other positive influences predators may have on their prey populations, such as genetic pruning, etc.

Chesapeake network having the highest gain factors were mostly short, two member feedbacks. Furthermore, the most intense autocatalysis was engendered by the recycle of carbon among the benthic deposit feeders. Compartments 14 through 18 each separately exchange benefaction with the sediment POC (36) at gain factors that range from 10.5% (14-36) to a low of 0.4% (18-36). All deposit feeders utilize sediment POC via the mediation of the bacteria attached to the detritus. As discussed above, the presence of an intermediary fosters a degree of mutual benefit between the members thus separated. Nevertheless, the major contribution to autocatalysis appears to derive from the large amounts of carbon that are recycled through the sediment POC.

Autocatalysis of lesser intensity is exhibited by the members of the microbial loop (compartments 5-7). The heterotrophic microflagellates (6) and the dissolved organic carbon (34) are separated by the free bacteria (5) and abet one another with an impressive 7.7% gain. The microflagellates in turn are bracketed by the free bacteria (5) and the microscopic zooplankton (7, mostly ciliates), allowing the latter two to augment each other's activities with a gain of 1.7%. It is interesting to note that linear, highly articulated chains, such as comprise the pelagic microbial community in Chesapeake Bay, contain autocatalytic pairings that leapfrog each other up the trophic chain. The mutual aggrandizements inherent in linear trophic configurations constitute another factor that, in the absence of perturbation, fosters the tendency away from highly connected food webs towards more articulated, chain-like concatenations.

Next on the list of autocatalytic loops is the above-mentioned example of mutual reinforcement among the ctenophores, phytoplankton and suspended POC. The ctenophores also interact bilaterally with the phytoplankton and POC with gains of 0.6% and 0.7%, respectively.

The taxa in all the loops described thus far appear to be associated with the increasing eutrophication of Chesapeake Bay: the phytoplankton productivity has risen dramatically in recent decades; the microbial components have surfaced only recently as major elements contributing to community metabolism; and the deposit feeders now strongly dominate the benthos as the filter-feeding stocks continue to decline. Very few of the populations of commercial or recreational importance engage in autocatalytic loops having any appreciable gain. Many of the nekton participate in no mutually beneficial trophic interactions whatsoever. The mesozooplankton, a critical bridge between primary production and higher trophic populations, exchange reciprocal benefits with the weakfish (31) and the flounders (32), but the gains are a weak 0.08% and 0.01%, respectively. All the remaining autocatalytic loops involving the zooplankton or nekton pale by comparison.

The investigator can examine particular rows and columns of the [M] matrix to elucidate those species that most significantly affect a population of especial interest. To analyze these series of matrix elements it helps to employ a computer to rank the components of a given row or column according to their magnitudes. For example, judging from what has been discussed, the ctenophores (9) seem to be a key taxon in the community dynamics of the Chesapeake ecosystem. In ranking the values appearing in row 9, one notices that only one other species receives significant benefit from the comb jellies-their chief predator, the medusae (10). The next group to be aided by the ctenophore activity consists of (in order) the attached bacteria (2), the phytoplankton (1), the heterotrophic microflagellates (6), and the suspended POC (35), but the succor they receive from the comb jellies is less than a tenth of the boost that the ctenophores give to the medusae. At the other end of the list, the comb jellies compete with a host of fishes, mostly filter-feeders, but also carnivorous nekton.

Those compartments that contribute to the welfare of the comb jellies are (in order) the suspended POC (35), the phytoplankton (1), the mesozooplankton (8), the microzooplankton (7), the heterotrophic microflagellates (6), the free bacteria (5) and the DOC pool (34) --all save one of which (8) are actors in the eutrophication scenario.

The striped bass (33) is a troubled species that long has been emblematic of the Chesapeake Bay. The three greatest benefactors to the trophic welfare of striped bass are the bay anchovy (22), the mesozooplankton (8) and the phytoplankton (1), respectively. These are the three elements of the grazing chain from which this top carnivore draws most of its sustenance. The most inimical competitor to striped bass turns out to be none other than the ctenophore populations. Because of its relatively small stock size and share of the community activity, the effects that striped bass exert upon other organisms are quite small, save for the detriment it visits upon those in its immediate diet (23, 22 and 21), upon itself and on three competing top carnivores (32, 30 and 31). The striped bass engages in no autocatalytic interactions.

Conclusions

The negative effects that a predator directly exerts upon its prey may be quantified in much the same way as that used in I-O analysis to assay the benefits that a prey yields to its predator. Furthermore, the indirect effects should propagate along the trophic network in much the same way as do the dietary benefits. The estimates of mixed trophic impacts can be calculated using the formal methods of input-output analysis that have been applied to ecosystem networks now for well over a decade.

The newfound capability to trace indirect competi-

Table 1. Matrix of Total Mixed Trophic Impacts [M] Chesapeake Bay Mesohaline Ecosystem (see Fig. 1).

	1	2	3	4	5	6	7	8	9	10	11	12
1	-.1215	.1672	.0543	-.0108	.1956	-.0116	.2889	.4440	.3224	.4048	.6006	.6038
2	.0021	-.0642	-.0069	.0014	.0010	-.0011	.0029	-.0158	-.0135	-.0150	-.0012	-.0050
3	.0005	.0007	-.5518	-.0893	.0002	-.0001	.0004	.0006	.0005	.0006	-.0281	-.0232
4	.0000	.0001	.0137	-.1222	.0000	-.0000	.0000	.0000	.0000	.0000	-.0022	-.0017
5	-.0129	.0065	.0033	-.0007	-.6376	.2899	.1012	.0059	.0310	.0140	.0017	.0018
6	-.0246	-.0017	.0033	-.0007	-.2754	-.4192	.2006	.0058	.0553	.0217	-.0013	-.0012
7	-.0947	-.0642	.0004	-.0001	.1689	-.4074	-.1966	.0008	.1972	.0639	-.0233	-.0233
8	-.0929	-.1086	-.0144	.0029	-.0531	.0709	-.1728	-.1650	.3088	.6657	-.0845	-.0849
9	.0190	.0197	.0040	-.0008	-.0036	.0167	-.0283	-.1160	-.0777	.2180	.0156	.0157
10	.0006	.0020	.0004	-.0001	.0015	-.0030	.0063	-.0103	-.0765	-.0316	.0011	.0011
11	-.0127	-.0165	.0011	-.0002	-.0041	.0029	-.0098	-.0090	-.0086	-.0089	-.0201	-.0180
12	-.0069	-.0082	.0001	-.0000	-.0022	.0016	-.0053	-.0049	-.0047	-.0049	-.0096	-.0093
13	-.0135	-.0146	-.0011	.0002	-.0044	.0031	-.0104	-.0097	-.0093	-.0096	-.0119	-.0119
14	-.0000	-.0000	-.0916	.0182	-.0000	.0000	-.0001	.0003	.0001	.0002	.0019	-.0008
15	.0001	.0001	-.0129	.0026	.0000	-.0000	.0000	.0002	.0001	.0002	-.0044	-.0039
16	.0010	.0013	-.0434	.0086	.0003	-.0002	.0008	.0008	.0007	.0008	-.0566	-.0430
17	-.0000	-.0000	-.0247	-.3138	-.0000	.0000	-.0000	-.0000	-.0000	-.0000	.0011	.0009
18	.0002	.0003	-.0118	.0024	.0001	-.0001	.0002	.0002	.0002	.0002	-.0118	-.0096
19	.0021	.0027	.0089	-.0018	.0007	-.0005	.0016	.0015	.0014	.0015	-.1141	-.0871
20	.0000	.0000	.0000	-.0000	.0000	-.0000	.0000	-.0001	-.0000	-.0001	.0000	.0000
21	.0000	.0001	.0000	-.0000	.0000	-.0000	.0001	-.0004	-.0002	-.0003	.0000	.0000
22	.0018	.0016	.0011	-.0002	.0013	-.0019	.0045	-.0243	-.0093	-.0195	.0016	.0016
23	.0004	.0000	.0001	-.0000	.0002	-.0003	.0008	-.0040	-.0015	-.0032	.0003	.0003
24	.0000	.0000	.0000	-.0000	.0000	-.0000	.0000	-.0001	-.0000	-.0001	.0000	.0000
25	-.0000	-.0000	.0000	-.0000	-.0000	.0000	-.0000	-.0000	-.0000	-.0000	.0000	.0000
26	.0000	.0000	.0001	-.0000	.0000	-.0000	.0000	.0000	.0000	.0000	.0001	-.0043
27	-.0000	-.0000	.0005	-.0001	-.0000	.0000	-.0001	.0003	.0001	.0002	.0001	.0001
28	-.0000	-.0000	.0001	-.0000	-.0000	.0000	-.0000	.0003	.0001	.0002	-.0000	-.0000
29	-.0000	-.0000	.0003	-.0001	-.0000	.0000	-.0000	-.0000	-.0000	-.0000	.0001	.0001
30	-.0000	-.0000	-.0000	.0000	-.0000	.0000	-.0000	.0001	.0000	.0001	-.0000	-.0000
31	-.0001	-.0001	-.0000	.0000	-.0001	.0001	-.0003	.0016	.0006	.0013	-.0001	-.0001
32	-.0000	-.0000	-.0000	.0000	-.0000	.0000	-.0001	.0003	.0001	.0002	-.0000	-.0000
33	-.0000	-.0000	-.0000	.0000	-.0000	.0000	-.0001	.0006	.0002	.0005	.0000	.0000
34	-.0129	.0065	.0033	-.0007	.3624	.2899	.1012	.0059	.0310	.0140	.0017	.0018
35	-.0718	.8599	.1953	-.0389	.0128	-.0609	.1027	.3422	.3927	.3585	.2704	.2755
36	.0009	.0012	.4499	-.0896	.0003	-.0002	.0007	.0009	.0007	.0009	-.0502	-.0400

Table 1 Cont'd

	13	14	15	16	17	18	19	20	21	22	23	24
1	.6148	.0540	.0521	.0379	.0299	.0339	.1012	.4440	.4395	.4335	.3593	.4440
2	-.0091	-.0069	-.0068	-.0059	-.0038	-.0057	-.0061	-.0158	-.0156	-.0135	-.0143	-.0158
3	.0005	.4464	.4417	.4134	.2467	.4023	.2122	.0006	.0005	-.0079	-.0043	.0006
4	.0000	.0137	.0134	.0111	.3376	.0104	.0163	.0000	.0000	-.0002	-.0001	.0000
5	.0021	.0033	.0033	.0029	.0018	.0027	.0030	.0059	.0058	.0043	.0069	.0059
6	-.0008	.0033	.0033	.0029	.0018	.0028	.0027	.0058	.0058	.0029	.0063	.0058
7	-.0231	.0004	.0004	.0007	.0002	.0008	-.0018	.0008	.0009	-.0109	-.0035	.0008
8	-.0870	-.0144	-.0142	-.0111	-.0079	-.0104	-.0203	.8350	.8295	.5345	.4635	.8350
9	.0162	.0040	.0040	.0032	.0022	.0031	.0049	-.1160	-.1152	-.0726	-.0622	-.1160
10	.0011	.0004	.0004	.0003	.0002	.0003	.0004	-.0103	-.0102	-.0066	-.0056	-.0103
11	-.0113	.0011	.0002	-.0092	.0006	-.0113	.0647	-.0090	-.0090	-.0089	-.0086	-.0090
12	-.0062	.0001	-.0003	-.0040	.0001	-.0051	.0257	-.0049	-.0049	-.0048	-.0046	-.0049
13	-.0121	-.0011	-.0011	-.0008	-.0006	-.0007	-.0020	-.0097	-.0096	-.0095	-.0090	-.0097
14	-.0000	-.0940	-.0956	-.0903	-.0504	-.0957	-.0146	.0003	.0004	-.0096	-.0041	.0003
15	.0001	-.0137	-.0152	-.0185	-.0071	-.0204	.0329	.0002	.0002	-.0054	-.0013	.0002
16	.0009	-.0434	-.0498	-.1119	-.0239	-.1250	.4267	.0008	.0004	.0002	-.0014	.0008
17	-.0000	-.0246	-.0244	-.0233	-.1330	-.0228	-.0081	-.0000	-.0000	.0004	.0002	-.0000
18	.0002	-.0121	-.0134	-.0261	-.0065	-.0310	.0893	.0002	.0001	.0002	-.0014	.0002
19	.0019	.0089	-.0039	-.1291	.0049	-.1569	-.1390	.0015	.0009	.0010	-.0018	.0015
20	.0000	.0000	.0000	.0000	.0000	.0000	.0000	-.0001	-.0001	-.0001	-.0000	-.0001
21	.0000	.0000	.0000	.0000	.0000	.0000	.0000	-.0004	-.0005	-.0003	-.0007	-.0004
22	.0017	.0010	.0007	.0009	.0006	.0008	.0007	-.0243	-.0300	-.0869	-.0792	-.0243
23	.0003	.0001	.0001	.0001	.0001	.0001	-.0001	-.0040	-.0078	-.0079	-.0419	-.0040
24	.0000	.0000	.0000	.0000	.0000	.0000	.0000	-.0001	-.0001	-.0001	-.0000	-.0001
25	-.0000	-.0000	-.0001	.0000	.0000	-.0000	-.0000	-.0000	-.0000	.0000	.0000	-.0000
26	.0000	-.0003	-.0005	.0002	.0001	-.0026	-.0003	.0000	.0000	.0000	.0000	.0000
27	-.0000	-.0017	-.0035	-.0013	.0003	.0003	-.0008	.0003	.0004	-.0102	-.0083	.0003
28	-.0000	-.0004	-.0024	.0001	.0001	.0001	-.0000	.0003	.0003	-.0095	.0008	.0003
29	-.0000	-.0008	-.0007	.0004	.0002	-.0081	-.0007	-.0000	-.0000	.0000	.0000	-.0000
30	-.0000	.0001	.0001	.0000	-.0000	-.0000	.0000	.0001	.0002	-.0013	-.0150	.0001
31	-.0001	-.0000	-.0000	-.0000	-.0000	-.0001	-.0000	.0016	.0020	-.0601	-.0028	.0016
32	-.0000	-.0000	-.0000	.0000	-.0000	-.0002	-.0000	.0003	.0005	-.0034	-.0466	.0003
33	-.0000	-.0000	-.0000	.0001	-.0000	.0001	-.0006	.0006	-.0107	-.0107	-.0619	.0006
34	.0021	.0033	.0033	.0029	.0018	.0027	.0030	.0059	.0058	.0043	.0069	.0059
35	.2964	.1945	.1908	.1643	.1075	.1561	.1910	.3422	.3380	.3373	.4338	.3422
36	.0008	.4481	.4409	.3884	.2477	.3719	.3787	.0009	.0007	-.0077	-.0046	.0009

Table 1 Cont'd

	25	26	27	28	29	30	31	32	33	34	35	36
1	.0529	.1141	.0599	.0984	.0498	.1919	.4058	.3940	.3856	.1849	.2356	.0875
2	-.0068	-.0065	-.0067	-.0076	-.0066	-.0095	-.0125	-.0134	-.0133	-.0001	-.0652	-.0113
3	.4440	.3854	.4168	.3905	.4372	.2512	-.0082	.0049	.0079	.0001	.0004	-.2585
4	.0135	.0114	.0125	.0119	.0130	.0076	-.0002	.0001	.0009	.0000	.0000	.0511
5	.0033	.0031	.0032	.0034	.0032	.0041	.0040	.0050	.0052	-.3680	.0157	.0055
6	.0033	.0027	.0031	.0032	.0032	.0037	.0026	.0039	.0041	.2647	.0159	.0055
7	.0004	-.0023	.0001	-.0009	.0005	-.0028	-.0103	-.0081	-.0076	-.2099	.0044	.0008
8	-.0142	-.0219	.0004	.0510	-.0136	.1959	.5000	.4907	.4750	.0128	-.0670	-.0234
9	.0040	.0052	.0019	-.0051	.0038	-.0253	-.0679	-.0663	-.0641	.0119	.0166	.0066
10	.0004	.0005	.0002	-.0004	.0004	-.0023	-.0061	-.0060	-.0058	-.0012	.0014	.0007
11	.0005	-.0030	-.0005	-.0004	-.0014	-.0037	-.0083	-.0087	-.0039	-.0014	-.0090	-.0000
12	-.0001	.1132	-.0006	-.0006	-.0010	-.0022	-.0045	-.0047	-.0028	-.0008	-.0050	-.0006
13	-.0011	-.0023	-.0012	-.0021	-.0010	-.0044	-.0088	-.0090	-.0088	-.0015	-.0100	-.0018
14	.6556	.5165	.5450	.4114	.6048	.3289	-.0089	-.0102	-.0079	.0000	-.0000	.2354
15	.2045	.1287	.1819	.3717	.0883	.1094	-.0051	-.0045	-.0014	.0000	.0001	.0377
16	-.0474	-.0559	.0609	-.0407	-.0602	.0368	.0005	-.0038	.0276	.0001	.0007	.0537
17	-.0245	-.0214	-.0230	-.0215	-.0242	-.0139	.0005	-.0003	-.0002	-.0000	-.0000	.0358
18	.0183	.1278	-.0092	-.0111	.1813	-.0059	-.0017	.0270	.0055	.0000	.0002	.0115
19	.0009	-.0276	-.0100	.0030	-.0251	-.0063	.0013	-.0044	.0564	.0002	.0015	-.0108
20	.0000	.0000	.0000	-.0000	.0000	-.0000	-.0000	-.0000	-.0000	-.0000	.0000	.0000
21	.0000	.0000	.0000	-.0000	.0000	-.0002	-.0003	-.0004	.0062	-.0000	.0000	.0000
22	.0009	.0010	.0292	.1094	.0009	.1850	.8732	.5676	.4967	-.0005	.0011	.0017
23	.0001	.0001	-.0057	-.0008	.0001	.1786	-.0285	.2933	.3336	-.0001	.0001	.0002
24	.0000	.0000	.0000	-.0000	.0000	-.0000	-.0001	-.0001	-.0000	-.0000	.0000	.0000
25	-.0001	-.0000	-.0000	-.0001	-.0000	-.0000	.0000	-.0000	.0000	-.0000	-.0000	-.0000
26	-.0004	-.0011	-.0003	-.0003	-.0008	-.0002	.0000	-.0000	.0000	.0000	.0000	-.0001
27	-.0021	-.0015	-.0207	-.0034	-.0015	.5923	-.0096	-.0092	-.0088	.0000	-.0000	-.0006
28	-.0008	-.0006	-.0010	-.0023	-.0005	-.0024	-.0091	-.0059	-.0052	.0000	-.0000	-.0002
29	-.0010	-.0017	-.0006	-.0007	-.0022	-.0004	.0000	-.0002	-.0000	-.0000	-.0000	-.0003
30	.0001	.0000	-.0304	-.0001	.0000	-.0216	-.0009	-.0055	-.0061	.0000	-.0000	.0000
31	-.0000	-.0000	-.0018	-.0072	-.0000	-.0137	-.0692	.1281	-.0355	.0000	-.0001	-.0001
32	-.0000	-.0000	.0002	-.0004	-.0000	-.0095	-.0718	-.0285	-.0184	.0000	-.0000	-.0000
33	-.0000	.0000	.0000	-.0013	.0000	-.0140	-.0088	-.0262	-.0281	.0000	-.0000	-.0000
34	.0033	.0031	.0032	.0034	.0032	.0041	.0040	.0050	.0052	-.3680	.0157	.0055
35	.1925	.1978	.1873	.2101	.1865	.2645	.3121	.3582	.3617	-.0439	-.1001	.3201
36	.4441	.3801	.4148	.3910	.4323	.2500	-.0080	.0040	.0188	.0001	.0007	-.2605

tive interactions through the foodweb reveals significant couplings that did not appear in earlier applications of input-output methods to ecosystems. For example, in the Chesapeake Bay ecosystem there exist strong competitive and inhibitory relationships between the ctenophore population and many of the commercially and recreationally important species that inhabit the system. The siphoning away of large amounts of mesozooplankton secondary production by ctenophores not only deprives other desirable species of sustenance, but it also fuels autocatalytic reactions within the planktonic community that further contribute to the profile of the Chesapeake Bay as a eutrophic system.

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