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 tropohdynamics. 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.

1. 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 is 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 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.

2. 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 Tij represents the amount of prey i

consumed by predator j, then gij = Tij/ Tkj represents the fraction of j's diet comprised by prey item i1. The summation on k is taken over all elements of j's diet, so that O < gij < 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 fij = Tij/ Tim. That is, fij 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., fij 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. When the receiving compartment j is not an active feeder, but simply a collection of

passive material, one should equate fij 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 Figure 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-2y-1) as estimated by Baird and Ulanowicz (in press).

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)

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1 All the Tij 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).------------------

that are dispersed throughout the water column. The inputs into 7 from

compartments 1, 3, 6 and 35 sum to 86,127 mgCm-2y-1. Of that total, 31,638 units are coming from 6, so that g67 = 0.367. The dissipation (respiration) by the ciliates is 35,883 mgCm-2y-1, making the net output equal 50,244 mgCm-2y-1. Of this net production, 3,437 units are cropped by compartment 9, the ctenophores, so that the host coefficient f79 = 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 qij the net impact of i upon j, we see that

qij = gij - fji. (1)

It happens that either gij or fij is zero for most pairs of interacting i and

j. Because the gij and fji are normalized, i.e.,

0 < gij < 1 and (2)

0 < fji < 1,

the values of qij range from -1 to +1, inclusive. Due to the fact that gij and fji are the components of n x n matrices, their differences constitute the components of an n-dimensional net impact matrix.

3. 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

piz = qijqjk...qyz (3)

will characterize the strength of that particular interaction from i to z.

Secondly, if piz and phz are two distinct pathways ending at z, then their combined impact is assumed to be piz + phz. (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, qij, 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] = [Q]h . (4)

h=1

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

[Q]h = {[I] -[Q]}-1, (5) h=0

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]. (6)

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

4. Elementary Examples

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

0.0 1.0 1.0

[Q] = -0.667 0.0 0.0 .

-0.333 0.0 0.0

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

- 1.0 0.0 0.0

[Q]2 = 0.0 -0.667 -0.667 .

0.0 -0.333 -0.333

Here the competition between the two predators is manifested in the negative values for q23 and q32, 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

-0.500 0.500 0.500

[M] = -0.333 -0.333 -0.333 .

-0.167 -0.167 -0.167

In Figure 2b two prey compartments sustain a single predator. The

associated matrix of total impacts is

-0.350 -0.150 0.350

[M] = -0.210 -0.090 0.210 .

-0.560 -0.240 -0.440

Once again, all the diagonal terms turn out to be negative. But more

interestingly, the two prey items stand in competition with one another (M12 and M21 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 Figure 2c. This

simple structure yields

-0.333 0.333 0.333

[M] = -0.333 -0.667 0.333 .

0.333 -0.333 -0.333

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).

5. 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

Figure 1. Those interested in the details of how the flow values and

biomasses were estimated are referred to Baird and Ulanowicz (in press). Here

we wish to apply the matrix methods just described to highlight indirect

trophic interactions that might not be apparent from visual inspection of

Figure 1.

The matrix of total trophic impacts is given in Table 1. 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 Figure 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

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2The 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.

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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 Figure 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 crustacea 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 m1,35 m35,9 m9,1=.00175, or about 0.2%

gain. While this amplification is not overwhelmingly large, it should be

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3Here 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.

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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 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.

6. 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 competitive 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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Figure Legends

Figure 1. Estimated exchanges of carbon (mg m-2y-1) among the 36

principal components of the Chesapeake mesohaline ecosystem (Baird and

Ulanowicz, Ecol. Mongr. in press.

Figure 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.