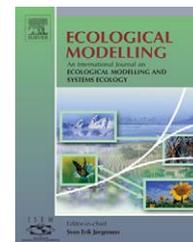


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Effective trophic positions in ecological acyclic networks

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ABSTRACT

In the tropho-dynamic analysis of ecosystems the heuristic, discrete concept of trophic level has been replaced by the more realistic, continuous definition of trophic position. In ecological network analysis (ENA) the suite of matrix manipulations called canonical trophic aggregation (CTA) apportions each species' feeding activity to a series of discrete trophic levels sensu Lindeman. The effective trophic position is computed as the sum of the fractions of trophic activity that each species performs at different trophic levels. In this paper we present an extension of the CTA that combines matrix manipulation and sensitivity analysis. Applying this "extended" CTA to an hypothetical network and to real ecosystems we show how trophic position can be computed taking into account the contribution of external inflows, making it scale-insensitive. Moreover "extended" CTA solves ambiguities related to trophic position in the presence of multiple non-living nodes, considering them as imports.

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1. Introduction

The trophic level ideal of a simple linear chain of energy passages had great appeal as an easy and intuitive description of complex energy-based ecosystem processes. Further, this approach has inspired several applications in ecology and management such as the cascade trophic interaction theory (Carpenter et al., 1986; Carpenter and Kitchell, 1993) and the associated biomanipulation idea (Gophen, 1990; Shapiro, 1990). On the other hand, the structural intricacy (e.g. richness and topology of connections between species) of food webs gives rise to a vast array of functional behaviors that do not easily accommodate into the framework of the "green world"

theories (Polis and Strong, 1996). Donor-controlled diffuse omnivory, for example, shunts the flow of matter and energy away from adjacent trophic components thus challenging the idea that populations aggregate into discrete homogeneous trophic levels each of which receives energy solely from its adjacent level nearer the ultimate source of energy (the outside or abiotic environment) and passes it to the next (Vadas, 1990; Winemiller, 1990; Polis, 1991, 1994). The "...hawk that feeds at five trophic levels ..." (Cousins, 1985, 1987) embarrasses less the ecologists now that the trophic-dynamic description of the ecosystem needs not exclude the reticulate connections between the diversity of consumers and resources. Mapping energy movements according to feeding relation in

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complex ecological communities yields to ecological flow networks (Ulanowicz, 1986), from which one can appreciate the continuum of trophic positions of the species in the ecosystem. Matrix manipulation on flow coefficients allows one to calculate trophic positions: while some species do behave as obligate autotrophs or herbivores, many heterotrophs assume fractional trophic position, as the result of their feeding at multiple levels (Christian and Luczkovich, 1999). This scenario remains problematic to many, essentially because the recognition of trophic levels implies the acceptance of the trophodynamic viewpoint of ecosystem organization (Cousins, 1987; Oksanen, 1991). The more realistic notion of trophic position or trophic role has gained ground among ecologists because of its potential both for conceptual developments and practical applications (Burns, 1989; Pauly et al., 1998; Luczkovic et al., 2003). In particular, investigating trophic position allows insights into trophic transfer efficiencies (Christensen and Pauly, 1993), the overall energy budget in ecosystems (Wulff and Ulanowicz, 1989; Burns et al., 1991; Gaedke and Stralle, 1997) and ecosystems response to stress (Ulanowicz, 1996; Bondavalli et al., 2006). The emphasis in all of these studies has been at the ecosystem level but effective trophic position can be used also to infer controlling factors in ecological communities (Christian and Luczkovich, 1999), showing the potential of the concept for community-level investigations. At present, the bulk of ecological trophic analysis conducted in the framework of ecosystem network analysis (Ulanowicz and Kay, 1991; Christensen and Pauly, 1993; Christian and Luczkovich, 1999) makes use of the canonical trophic aggregation (CTA, Ulanowicz and Kemp, 1979; Ulanowicz, 1995) a matrix-based algorithm that defines trophic positions as the weighted average distance of the compartment from the ultimate source of energy (imports—outside environment). When analyzed in detail, however, we found that this method can give rise to some inconsistencies. In particular, we noted that: (1) there are ambiguities for the role of migratory imports (inflows to the system coming from another ecosystem); (2) there is scale dependency (i.e. a species trophic position varies when one considers just a subset of the original network); (3) the computation can lead to ecologically unrealistic values for trophic position when performed on networks that use currencies others than carbon (i.e. phosphorous and nitrogen), or from multiple non-living nodes (nutrient pools, detritus, etc.). In this work we present a natural extension of the original formulation of the CTA algorithm (Ulanowicz and Kemp, 1979; Ulanowicz, 1995) for computing trophic positions, showing how all the inconsistencies vanish after its implementation. In what follows we briefly describe the method proposed by Ulanowicz and Kemp (1979) (detailed information can be found in Appendix in Supplementary data) and the possible drawbacks. Finally we explain in detail how this procedure can be generalized, and contrast the two approaches.

2. Canonical trophic aggregation

Ecological network analysis (Ulanowicz, 1986; Baird and Ulanowicz, 1989; Fath and Patten, 1999; Christensen and Pauly, 1992) is a technique that depicts ecosystems as composed of compartments (that represent species or aggregates of

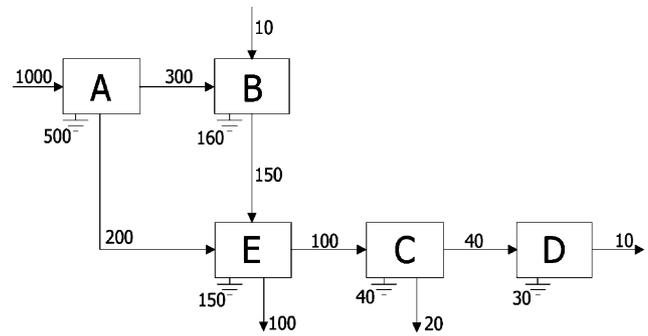


Fig. 1 – Hypothetical five species network.

species, nutrient pools, etc.) exchanging flows (that can stand for energy or matter nutrients) with each other. One can discriminate between several types of fluxes: intercompartmental fluxes denote internal exchanges (t_{ij} that stands for a flux from compartment i to compartment j), while exchanges with the external world can be divided into imports from the outside (z_j indicates an external input flow to compartment j), exports to the outside (e_j indicates an outflow from compartment j), and respirations (symbolized, for the compartment j , as r_j). Such scheme is given in matrix form with three column vectors, namely (Z): Import, (E): Export and (R): Respiration and the matrix [T] of internal exchanges. All vectors will have S coefficients, where S is the number of compartments, and the matrix [T] will have dimension $S \times S$. As an example, consider the network depicted in Fig. 1.

The five compartment network of Fig. 1 can be represented in matrix form as:

$$T = \begin{bmatrix} 0 & 300 & 0 & 0 & 200 \\ 0 & 0 & 0 & 0 & 150 \\ 0 & 0 & 0 & 40 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 100 & 0 & 0 \end{bmatrix} \quad Z = \begin{bmatrix} 1000 \\ 10 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad E = \begin{bmatrix} 0 \\ 20 \\ 10 \\ 100 \end{bmatrix} \quad R = \begin{bmatrix} 500 \\ 160 \\ 40 \\ 30 \\ 150 \end{bmatrix}$$

Effective trophic position is defined as the weighted average length of all the pathways that originate from outside the system and reach a given compartment. Autotrophs will have distance (and therefore trophic position (TP)) equal to 1, herbivores 2 and so on. Usually TPs are fractionary: for a species that bases half of its diet on primary producers and the other half on herbivores, the TP will be $2 \times 0.5 + 3 \times 0.5 = 2.5$ (one pathway of length 2: outside → primary producers and one of length 3: outside → primary producers → herbivores). Organisms feeding on this latter species would have TP=3.5 and so forth. If one considers the network in Fig. 1, it is clear that species A receives flows just from the outside, having therefore TP=1. Computing the other TPs is more difficult, as there are multiple pathways connecting the external environment to each compartment. After some computation, we see that species B is almost herbivore (TP=1.968), as the energy (or matter) it receives from the outside (10) is much smaller than the amount it gets from species A (300). So it acts as a primary producer by a 3.22% ($10/(10+300)$) and for the remaining 96.78% as a primary consumer. Computation yields

to $0.0322 \times 1 + 0.9678 \times 2 = 1.968$. Similarly, one can compute the trophic positions of all species in the network. When the network under examination comprises non-living compartments, such as detritus and nutrient pools, the classical analysis considers only the subsystem formed by the ensemble of living compartments. Non-living nodes are then assigned to trophic level 1, equipping their outflows as imports to the living subsystem. Even though this is the most common procedure (Cousins, 1985; Baird and Ulanowicz, 1989), other studies calculate trophic positions of non-living compartments as the number of transfers required to reach the given compartment starting from the outside (imports) (Burns et al., 1991; Higashi et al., 1989, 1991, 1992; Whipple and Patten, 1993; Whipple, 1998). Cycles embedded in the network would therefore imply an infinity of pathways connecting any two nodes in the same strongly connected component (Allesina et al., 2005), making the actual trophic level computation more complicated. The vast majority of cycles, however, involves non-living compartments as an intermediate step (Pimm, 1982; May, 1983; Ulanowicz, 1983, 1995): removing the non-living nodes would therefore leave just a few residual cycles. Nevertheless, recent studies highlight the presence of cycles involving only living compartments (Dunne et al., 2002, 2004; Williams and Martinez, 2000). According to these evidences, while we leave to a more detailed study the problem of assigning trophic positions in the presence of cycles, in what follows we discuss the question in the framework of CTA by analyzing simple networks, both hypothetical and extracted from real ecosystems, in which living compartments do not form cycles.

2.1. Drawbacks of CTA

Having sketched the basic idea behind CTA, we can discuss some general drawbacks.

2.1.1. Migratory Imports

In CTA, as it was initially conceived, all imports, corresponding to inputs from outside the system, are assigned to virtual trophic position 0, thus considering them as nutrients received by primary producers. But this is not always true. When individuals of a prey species migrate from another area (e.g. think about stream-forest ecosystems) there is an import with effective trophic position different from 0. Therefore, setting these inflows to trophic level 0 will affect the final outcome of trophic aggregation and the trophic positions of the various compartments are likely to be underestimated. The principal software packages for network analysis are NETWRK (Ulanowicz and Kay, 1991), WAND (Allesina and Bondavalli, 2004) and ECOPATH (Pauly et al., 2000; Christensen et al., 2005). The first version of NETWRK set all imports to trophic level 0, while a more recent one (Ulanowicz, 2002) assigns migratory inputs to heterotrophs to the same trophic position of the receiving node, whereas imports to primary producers are set to $TP = 0$. WAND and ECOPATH use an approach similar to the older NETWRK version.

2.1.2. Scale dependency

Assigning external input to trophic level 0, trophic positions of network compartments are sensible to scale. If a compart-

ment is computed to have a trophic position equal to, say, x , considering a sub-network, “external environment” boundary changes and some intercompartmental flows in the original network appear now as import flows, that will be assigned to trophic level 0. Recomputing the trophic position of the compartment yields to a value $y \leq x$. The lack of a clear procedure for handling migratory imports makes the computation of trophic positions scale-dependent.

2.1.3. Non-living compartment trophic level

In carbon based networks primary producers receive their requisite medium from outside the system in form of atmospheric carbon dioxide and their TP is 1. Considering different currencies, such as nitrogen or phosphorous, or also multiple non-living nodes (i.e. nutrient pool and detritus) in a carbon based network, the calculation is not that straightforward. To include the contribution of non-living components to the budget of the other nodes in the network one could either decide to assimilate inflows coming from these nodes to imports (that is to say assigning a virtual trophic position 0 to non-living compartments), or treat those inflows, as suggested by Ulanowicz (1995), as primary production (assigning virtually detritus and nutrient pools to level 1). The latter approach is axiomatically utilized in NETWRK (Ulanowicz and Kay, 1991) and ECOPATH (Pauly et al., 2000) softwares, because: “... it’s sometime difficult to separate living from dead plant tissue ...” (Kay et al., 1989). It is clear that assimilating inflows from non-living nodes as of level 1 does not always hold. In the case of nitrogen, in fact, this would lead to an unfeasible $TP = 2$ for primary producers. The same problem may arise in carbon based network with multiple non-living nodes (e.g. nutrient pool, suspended POC, sediment POC; see Table 4). This problem has been analyzed in detail by Gaedke and Straile (1997). They compared four different definitions for the trophic position of dead autochthonous organic material, from a logical and descriptive point of view, suggesting to allocate all the dead organic material to the “zeroth” trophic level. In what follows, we will describe a procedure able to cope with migratory imports. The outflows of non-living compartments will be considered to be imports with: (1) $TP = 0$ when non-living nodes apportion flows to, at least, a primary producer; (2) $TP = 1$ when non-living nodes act as autotrophic compartments and exclusively show outflows to heterotrophs.

3. Extending CTA

To deal with all the above inconsistencies we extended canonical trophic aggregation introducing multiple imports of different trophic position. The new algorithm naturally extends the one presented by Ulanowicz (1995). We define an import vector $(Z)^0$ (energy or nutrients to plants) of trophic level 0, and an import vector $(Z)^\alpha$ for any trophic position α different from 0. Also we define a $[T]_{\text{living}}$ sub-matrix that accounts only for exchanges between living compartments (species or group of species), while non-living nodes become imports aggregated in a non-living import vector $(K)^\alpha$. In the next paragraphs we present the building blocks of the algorithm and in the last paragraph of this section we assemble them into a general framework.

3.1. Partial feeding matrix [G]

If we divide every non-zero coefficient in the [T]_{living} matrix by the column sum plus all the imports to that column compartment we obtain a matrix [G]_{living} that specifies the fractionary diet of each compartment. The columns of [G]_{living} will sum to 1 in case the compartment does not receive imports, and to less than 1 elsewhere:

$$g_{ij} = \frac{t_{ij}}{\sum_{k=1}^{\text{living}} t_{kj} + z_j + k_j} \tag{1}$$

where (Z) is an undifferentiated vector with z_j coefficient that sums all the external imports (z_j^α), and (K) is a vector with k_j coefficient that sums all the flows from non-living nodes (k_j^α).

For the network in Fig. 1, [G]_{living} becomes:

$$G_{\text{living}} = \begin{bmatrix} 0 & 0.968 & 0 & 0 & 0.571 \\ 0 & 0 & 0 & 0 & 0.429 \\ 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \end{bmatrix}$$

The powers of [G]_{living} are defined as repeated product of [G] by itself: [G]_{living}⁰ stands for the identity matrix [I], [G]_{living}¹ = [G]_{living}, [G]_{living}² = [G]_{living} × [G]_{living}, and so forth. These powers account for the fraction of matter flowing from the row compartment to the column compartment in exactly x steps, being x the exponent of the [G]_{living} matrix.

3.2. Normalized import vectors (N)^α

These vectors quantify what amount of the flows to a given compartment comes from external subsidies. They are expressed similarly to [G]_{living} coefficients. If a compartment j bases its diet only on external inflows of trophic position α, then n_j^α will be 1. Conversely, a value of 0 means that the compartment is not directly connected to the surrounding system; if 0 < n_j^α < 1 the node j receives matter, or energy, both from outside and from internal exchanges. Then we may calculate normalized import vectors (N)^α, using

$$n_j^\alpha = \frac{z_j^\alpha}{\sum_{k=1}^{\text{living}} t_{kj} + z_j + k_j} \tag{2}$$

In the example network there is an import to plants (node A) which can be classified as of trophic level 0 (α = 0). Plus, an additional import to node B (omnivores) exists. For the sake of the methodological explanation this matter/energy is assumed to be at trophic position 2.825 (α = 2.825). We get now

$$N^0 = \begin{bmatrix} 1.000 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad N^{2.825} = \begin{bmatrix} 0 \\ 0.032 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

3.3. Normalized non-living import vectors (W)^α

These vectors are obtained with the same procedure used for normalized import vectors. The coefficients of normalized non-living import vectors (W)^α are computed as:

$$w_j^\alpha = \frac{k_j^\alpha}{\sum_{k=1}^{\text{living}} t_{kj} + z_j + k_j} \tag{3}$$

where the trophic position α is set to 0 when non-living compartments appertain to primary producers, and 1 elsewhere. Fig. 1 network does not have non-living imports, but the calculation is straightforward once one know how to compute normalized vector of living matter.

3.4. Trophic positions

Two types of trophic transformation matrices (Ulanowicz, 1995) can be computed: [A]^α, that considers imports of living matter with various trophic positions, and [D]^α that refers to non-living compartments. Computation can be conducted one row at a time, using the formulas:

$$a_i^\alpha = (N^\alpha)^T \times G_{\text{living}}^{i-1} \tag{4}$$

$$d_i^\alpha = (W^\alpha)^T \times G_{\text{living}}^{i-1} \tag{5}$$

where i stands for the row number and the superscript T stands for transpose form. Putting the rows together we define the final form of matrices [A]⁰ and [A]^{2.825} for the example network of Fig. 1:

$$A^0 = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 0 & 0.968 & 0 & 0 & 0.571 \\ 0 & 0 & 0.571 & 0 & 0.415 \\ 0 & 0 & 0.415 & 0.571 & 0 \\ 0 & 0 & 0 & 0.415 & 0 \end{bmatrix}$$

$$A^{2.825} = \begin{bmatrix} 0 & 0.032 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.014 \\ 0 & 0 & 0.014 & 0 & 0 \\ 0 & 0 & 0 & 0.014 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Therefore, there are two vectors of trophic positions (TP)_j⁰ and (TP)_j^{2.825} whose coefficients (i.e. trophic positions) are computed as:

$$TP_j^0 = \sum_{i=1}^N A_{ij}^0 \cdot i \tag{6}$$

$$TP_j^{2.825} = \sum_{i=1}^N A_{ij}^{2.825} \cdot (i + 2.825) \tag{7}$$

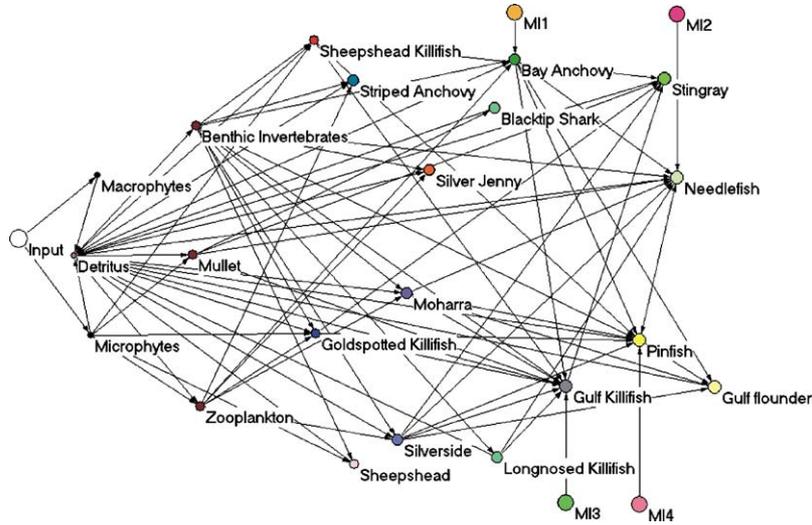


Fig. 2 – Crystal River Creek network.

yielding to:

$$TP^0 = \begin{bmatrix} 1 \\ 1.935 \\ 3.373 \\ 4.359 \\ 2.387 \end{bmatrix} \quad TP^{2.825} = \begin{bmatrix} 0 \\ 0.123 \\ 0.081 \\ 0.095 \\ 0.067 \end{bmatrix}$$

The final vector of trophic positions results from the sum of $(TP)^0$ and $(TP)^{2.825}$:

$$TP^{Final} = \begin{bmatrix} 1 \\ 2.058 \\ 3.454 \\ 4.454 \\ 2.454 \end{bmatrix}$$

This procedure can be generalized into

$$TP^{Final} = \left(\sum_{i=1}^b (\alpha_i \cdot \bar{1} + [12345]) \times [M]^{\alpha_i} \right)^T \quad (8)$$

This relation allows computing the trophic position in the system with different types of import flows. In particular, α_i represents the scalar TP of the i th import and b the total number of imports (including non-living compartments). $[M]^{\alpha_i}$ is the trophic transformation matrix associated to the input with TP α_i . In our example $b = 2$, in fact we have $\alpha_1 = 0$, and $\alpha_2 = 2.825$. The number of nodes in the system is five, and the trophic transformation matrices are: $[M]^{\alpha_1} = [A]^0$, and $[M]^{\alpha_2} = [A]^{2.825}$. So, for the five-species system of Fig. 1 the compact representation becomes explicit as follows:

$$TP^{Final} = ((0 \cdot \bar{1} + [12345]) \times [A]^0)^T + ((2.825 \cdot \bar{1} + [12345]) \times [A]^{2.825})^T$$

4. Results

4.1. Crystal River network with multiple migratory imports

We now apply the “extended” CTA to the Crystal River Creek ecosystem (Homer and Kemp, unpublished data; see also Ulanowicz, 1983, 1986), to highlight differences in trophic positions of each compartment respect to the outcomes obtained with “classical” CTA. In this example (Fig. 2) flows are measured in mg C/(m² day), and there are 21 compartments: 20 living nodes (mainly vertebrate fish) and 1 non-living compartment (detritus). The network consists of 6 imports (to compartment microphytes, macrophytes, bay anchovy, needlefish, gulf killifish and pinfish), 20 exports (one for each compartment, excluding microphytes), 21 respiratory flows and 82 internal exchanges. Although much currency cycles through detritus and various living compartments, there is no need for decyclization because our trophic analysis treats non-living nodes (detritus) like exogenous inputs. Therefore, we carry out “extended” CTA on 20 living compartments. The new subsystem (Fig. 2) is comprised of 2 imports of light or energy (to microphytes and macrophytes), 4 migratory imports (to bay anchovy, needlefish, gulf killifish and pinfish), 20 exports, 21 respiratory flows, 52 internal exchanges, 10 non-living imports from detritus to living compartments (zooplankton, benthic invertebrates, striped anchovy, bay anchovy, sheepshead killifish, goldspotted killifish, silverside, moharra, silver jenny and mullet) and 20 exports from living nodes to detritus. We consider imports to primary producers (microphytes and macrophytes) as light or energy with trophic level equal to 0, while other imports are migratory income with trophic position far from 0 because they are directed to fish. There is no logic to think of these imports to fish as light or energy. To fish receiving migratory imports in Crystal River Creek network, we assign the following trophic positions, according to the Florida Bay network dataset (Ulanowicz et al., 1998):

- TP import to bay anchovy = 2.55.
- TP import to needlefish = 2.9.
- TP import to gulf killifish = 2.24.
- TP import to pinfish = 2.07.

The trophic position of migrating prey is estimated by subtracting 1 from the average trophic position of the receiving compartment. This method is what we recommend to apply. The average trophic position of a compartment should be obtained from existing datasets and literature (i.e. FishBase database available on the web site <http://www.fishbase.org>, Florida Bay network dataset), or should be set to the trophic position of the receiving node without the contribution of the imported prey.

The trophic level of imports from detritus, in Crystal River Creek ecosystem, is fixed to 1 because this compartment does not show flows directed to primary producers.

4.2. Comparison with “classical” CTA

We stress now the differences between the trophic positions of species in Crystal River Creek determined using our “extended” CTA with respect to those computed with the “classical” CTA (see Table 1).

It is evident that microphytes and macrophytes conserve the same trophic level of 1 both in “classical” and in “extended” CTA because their inflows are exclusively external inputs that maintain trophic level 0 in both the methods. Also zooplankton, benthic invertebrates and mullet maintain their trophic level (2) since they are strictly herbivores depending on microphytes (primary producers) and detritus (placed to trophic level 1 as default in both CTA versions in this case). Longnosed killifish and blacktip shark maintained their trophic level (3), being placed in an hypothetical linear chain without other inflows (detritus → benthic invertebrates → longnosed killifish,

and microphytes → mullet → blacktip shark), playing the role of primary carnivores. Migratory imports that change their trophic values from 0 to a scalar number α , in the “extended” CTA, affect directly bay anchovy, needlefish, gulf killifish and pinfish, and indirectly gulf flounder (that feeds on bay anchovy and on pinfish), and stingray (that feeds on gulf killifish). It is interesting to notice that with the exception of the bay anchovy the others compartments show both direct and indirect dependence on migratory imports: needlefish that feeds on bay anchovy and pinfish; gulf killifish and pinfish that feed on bay anchovy. The last column of Table 1 presents the percentage of variation produced by considering the trophic position of imports with a scalar number α far from 0 respect to what happens in “classical” CTA. The percentage of variation is calculated as the difference between the trophic position obtained considering migratory import trophic positions different from 0 and the trophic position calculated setting all the imports to 0, divided by the latter and multiplied by 100.

4.3. Sensitivity analysis of migratory imports

Prey migration counts for about 49% ($1.57/(1.57 + 0.64 + 1)$) of bay anchovy diet, while other species rely less on external inputs: needlefish = 1.3%; gulf killifish = 2.4%; pinfish = 3.4%. Bay anchovy distributes its outflows in some intra-compartmental exchanges (to needlefish, gulf killifish, pinfish and gulf flounder), and it is more connected than needlefish, gulf killifish and pinfish. Therefore, we decided to perform a sensitivity analysis on migratory imports to bay anchovy. We carry out 10,000 random samplings of migratory import amounts to bay anchovy, into a range that is $\pm 50\%$ its original value, obtaining the following interval: $0.755 \text{ mg C}/(\text{m}^2 \text{ day}) \leq 1.57 \text{ mg C}/(\text{m}^2 \text{ day}) \leq 2.355 \text{ mg C}/(\text{m}^2 \text{ day})$. The relative importance of prey migration flow with respect to total inflows into bay anchovy, in this simulation, varies between 32% ($0.785/(0.785 + 1 + 0.64)$) and 59% ($2.355/(2.355 + 0.64 + 1)$). For each value sampled, considered as a possible amount of prey migration, we apply the “extended” CTA to calculate trophic positions of different compartments and their confidence interval at 95 and 99% (see Table 2).

Only compartments that are directly (bay anchovy) or indirectly (stingray, striped anchovy, needlefish, gulf killifish, silverside, silver jenny, pinfish and gulf flounder) affected by the prey migration to bay anchovy show a confidence interval around their mean values. Confidence interval are bigger for bay anchovy, needlefish, gulf killifish, pinfish and gulf flounder, because these nodes are closer to prey migration than others.

4.4. Scale independence

Trophic positions of compartments depicted in Fig. 2 are summarized in the column labeled “extended” CTA of Table 1. If we selected a subsystem (Fig. 3) composed by gulf killifish and longnosed killifish, CTA would treat inflows to these nodes from benthic invertebrates, bay anchovy, sheepshead killifish, goldspotted killifish, silverside, moharra and mullet as energy fluxes with trophic level equal to 0, while our “extended” CTA allows to maintain the same trophic positions they had in the whole network.

Table 1 – Trophic positions for living compartments in Crystal River Creek, calculated according to “classical” CTA (CTA) and its extended version (“extended” CTA)

Species	CTA	“Extended” CTA	Variation (%)
Microphytes	1.000	1.000	0.000
Macrophytes	1.000	1.000	0.000
Zooplankton	2.000	2.000	0.000
Benthic invertebrates	2.000	2.000	0.000
Blacktip shark	3.000	3.000	0.000
Stingray	3.833	3.847	0.364
Striped anchovy	2.667	2.667	0.000
Bay anchovy	2.020	3.138	55.373
Needlefish	3.438	3.949	14.864
Sheepshead killifish	2.109	2.109	0.000
Goldspotted killifish	2.446	2.446	0.000
Gulf killifish	3.392	3.531	4.105
Longnosed killifish	3.000	3.000	0.000
Silverside	2.937	2.937	0.000
Moharra	2.859	2.859	0.000
Silver jenny	2.846	2.846	0.000
Sheepshead	2.500	2.500	0.000
Pinfish	3.225	3.706	14.930
Mullet	2.000	2.000	0.000
Gulf flounder	3.820	4.155	8.759

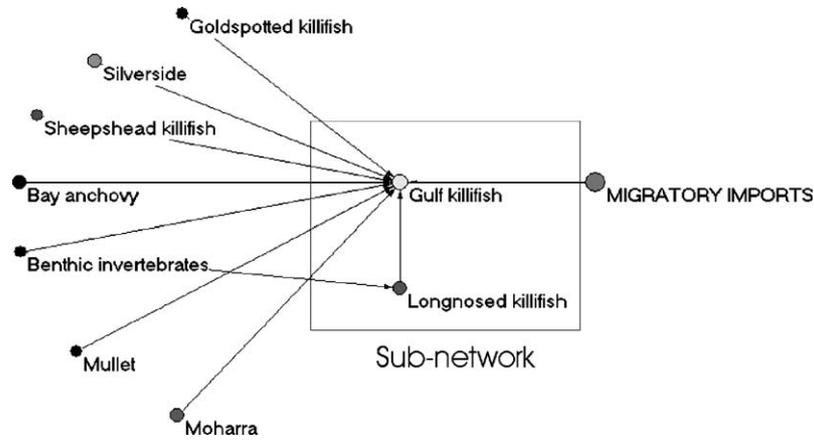


Fig. 3 – Crystal River Creek: a sub-network.

Table 2 – Trophic position sensitivity analysis for migratory imports to bay anchovy (Crystal River Creek ecosystem): confidence interval at 95 and 99%

Species	95%	99%
Microphytes	1.000 ± 0.000e+00	1.000 ± 0.000e+00
Macrophytes	1.000 ± 0.000e+00	1.000 ± 0.000e+00
Zooplankton	2.000 ± 0.000e+00	2.000 ± 0.000e+00
Benthic invertebrates	2.000 ± 0.000e+00	2.000 ± 0.000e+00
Blacktip shark	3.000 ± 0.000e+00	3.000 ± 0.000e+00
Stingray	3.844 ± 3.028e-05	3.844 ± 4.542e-05
Striped anchovy	2.667 ± 8.882e-18	2.667 ± 1.332e-17
Bay anchovy	2.708 ± 3.990e-03	2.708 ± 5.986e-03
Needlefish	3.767 ± 1.681e-03	3.767 ± 2.522e-03
Sheepshead killifish	2.109 ± 0.000e+00	2.109 ± 0.000e+00
Goldspotted killifish	2.446 ± 0.000e+00	2.446 ± 0.000e+00
Gulf killifish	3.498 ± 3.028e-04	3.498 ± 4.542e-04
Longnosed killifish	3.000 ± 0.000e+00	3.000 ± 0.000e+00
Silverside	2.937 ± 8.882e-18	2.937 ± 1.332e-17
Moharra	2.859 ± 0.000e+00	2.859 ± 0.000e+00
Silver jenny	2.846 ± 8.882e-18	2.846 ± 1.332e-17
Sheepshead	2.500 ± 0.000e+00	2.500 ± 0.000e+00
Pinfish	3.548 ± 1.462e-03	3.548 ± 2.193e-03
Mullet	2.000 ± 0.000e+00	2.000 ± 0.000e+00
Gulf flounder	4.034 ± 1.124e-03	4.034 ± 1.686e-03

In Table 3 results of “extended” CTA are compared with those of “classical” CTA. The trophic position of gulf killifish and longnosed killifish remains the same in the whole network and in the selected subsystem when using “extended” CTA.

4.4.1. The role of inorganic nutrients

“Extended” CTA permits to consider flows from non-living nodes of a system as inputs from outside. We may set non-living nodes trophic position to 0 when primary producers (plants, phytoplankton, etc.) receive flows from them, or 1 elsewhere. Here follows an application to Ythan estuary ecosystem (Baird and Milne, 1981), whose scheme is depicted in Fig. 4.

Flows are measured in gC/(m² year). There are 13 compartments: 10 living (benthic macrophytes, phytoplankton, benthic microflora, herbivorous birds, zooplankton, invertebrate suspension feeders, meiofauna, invertebrate deposit feeders, carnivorous birds and carnivorous fish) and 3 non-living (nutrient pool, suspended POC and sediment POC). Non-living nodes apportion to living ones as follows:

- Nutrient pool → benthic macrophytes, phytoplankton and benthic microflora (three primary producers).

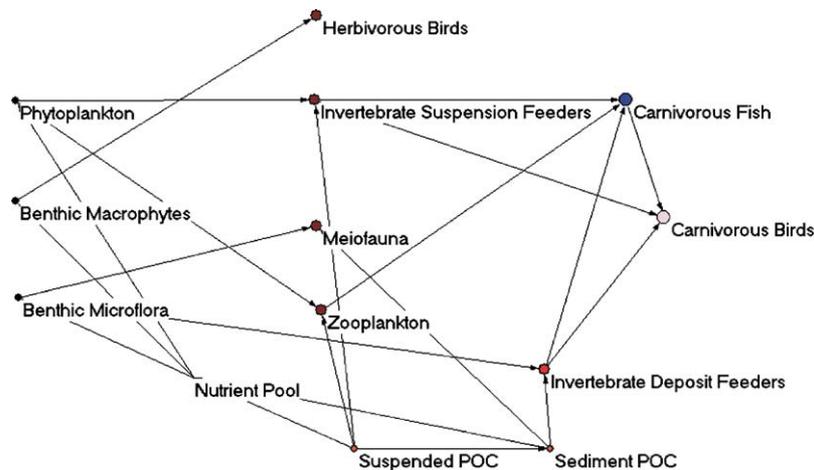


Fig. 4 – Ythan estuary ecosystem.

Table 3 – Gulf killifish and longnosed killifish trophic positions investigated with “classical” and “extended” CTA, at different scale levels (Crystal River Creek ecosystem)

	Gulf killifish	Longnosed killifish
Whole network “classical” CTA	3.392	3.000
Whole network “extended” CTA	3.531	3.000
Subsystem “classical” CTA	1.005	1.000
Subsystem “extended” CTA	3.531	3.000

- Suspended POC → zooplankton and invertebrate suspension feeders.
- Sediment POC → meiofauna and invertebrate deposit feeders.

The network consists of 2 imports into nutrient pool and suspended POC, 10 exports (from benthic macrophytes, phytoplankton, zooplankton, invertebrate suspension feeders, meiofauna, invertebrate deposit feeders, carnivorous birds, carnivorous fish, nutrient pool and suspended POC), 12 respiration flows (one for each node, excluding nutrient pool) and 40 intercompartmental exchanges. We isolated a sub-network that includes only living compartments, using flows from non-living nodes as imports. We set to 1 the trophic level of suspended POC and sediment POC, while to 0 the trophic level of the nutrient pool flowing to primary producers (benthic macrophytes, phytoplankton and benthic microflora). The “living subsystem” that we isolated from the whole network is comprised of 7 imports (formerly flows from non-living to living nodes), 8 exports, 10 respiratory flows, 12 internal exchanges and 17 “non-living exports” (formerly flows to non-living compartments). Results after applying CTA and “extended” CTA are summarized in Table 4.

“Classical” CTA yields to strange results: primary producers appear at trophic level 2 (benthic macrophytes, phytoplankton and benthic microflora), with a consequent shift in the trophic position of herbivorous birds, that now feed at trophic level 2. These incongruities arise because in the “classical” trophic analysis all the non-living nodes are positioned at trophic level

Table 4 – Trophic positions in the Ythan estuary living sub-network, calculated according to “classical” CTA (CTA) and its extended version (“extended” CTA)

Species	CTA	“Extended” CTA	Variation (%)
Benthic macrophytes	2.000	1.000	50.000
Phytoplankton	2.000	1.000	50.000
Benthic microflora	2.000	1.000	50.000
Herbivorous birds	3.000	2.000	33.333
Zooplankton	2.143	2.000	6.667
Invertebrate susp. feed.	2.151	2.000	7.006
Meiofauna	2.049	2.000	2.411
Invertebrate dep. feed.	2.053	2.004	2.411
Carnivorous birds	3.125	3.030	3.047
Carnivorous fish	3.062	3.003	1.918

1, including those that contribute to primary producers (nutrient pool). In “extended” CTA we distinguish the trophic level of non-living nodes (0 if the compartment outflows flux to primary producers, and 1 elsewhere). Trophic positions of the Ythan estuary sub-network are ecologically consistent when computed using “extended” CTA:

- Benthic macrophytes, phytoplankton and benthic microflora (primary producers) = TP 1.
- Herbivorous birds = TP 2.

Applying the “extended” CTA instead of the “classical” approach, these nodes largely change their trophic position. The other compartments (zooplankton, invertebrate suspension feeders, meiofauna, invertebrate deposit feeders, carnivorous birds and carnivorous fish) present a lower variation.

5. Discussion and conclusion

Canonical trophic aggregation is a matrix-based device that has been developed for ecosystem trophic analysis. One of its outcomes is the trophic position that species occupy in an ecosystem (Kercher and Shugart, 1975; Levine, 1983; Higashi et al., 1989; Christian and Luczkovich, 1999; Heymans et al., 2002). In the algorithm for calculus, inputs from outside the system are all allocated to the “zeroth” trophic level. The consequences of this assumption is that organisms first assimilating this energy are allocated to trophic level 1. In doing so, however, the procedure completely excludes from the analysis the question of ecosystem subsidies, that is, imports of energy and nutrients from other ecosystems (Polis and Hurd, 1996). There is a vast array of publications that highlight the importance of ecosystem subsidies (Polis et al., 1997, 2004 and citations in there) and other address the problem of the import of nutrients or non-living organic matter (Gaedke and Straile, 1997). Whereas non-living imports can easily be treated in the “classical” canonical trophic aggregation, the many other forms of living material exchanges between ecosystems, such as immigration, prey migration and so forth, still need to be accommodated in the CTA. Living imports and their effect on the trophic position of species has not been treated extensively in the literature. Gaedke and Straile (1997) consider this as a scale problem, stating that “... If physical ecosystem boundaries are chosen in such a way that species immigrating from other systems constitute major prey items, we suggest that they maintain the trophic position they had in their previous food web, and that this number is included into the calculations ...”. However, they do not treat the question in detail and restricted their analysis to dead material. In this paper, while we generalize the CTA procedure by including any kind of import (i.e. living and non-living), we also show how this approach can overcome the difficulties posed by ecosystem boundaries and related scale problems. The “extended” CTA allows, in fact, to maintain the same trophic position when sub-models of the original food web are analyzed. Often, incidentally, the trophic position of an immigrating prey is not known. In those cases it is not possible to calculate exactly the trophic position of the species that receive this incoming energy (detailed information on simulation approaches can be found in Appendix in Supplementary data). However, in this respect a reason-

able guess can be made considering the type of organism and its ecology, by taking into account that no organism can efficiently combine different ways of energy intake (Oksanen, 1991). Although the main object of investigation of this work are import flows, the “extended” CTA provides insight into the problem of trophic position as related to flows from inorganic nutrients and non-living organic matter present in the system. Assigning all non-living organic matter to the first trophic level like autotrophs (Pimm, 1988; Wulff et al., 1989) raises the problem of having plants feeding at trophic level 2 when the currency is inorganic nutrients. Gaedke and Straile (1997) criticized this approach and emphasized that the trophic position of the various species is largely independent from the currency (organic or inorganic) when all the non-living organic material is considered as system input. Accordingly, primary producers and bacteria would be allocated to trophic level 1; we think that this assumption underestimates the trophic role played by bacteria that can perform either as autotrophs and heterotrophs (Azam et al., 1983; Pomeroy, 1984; Bratbak, 1987; Sherr et al., 2003; Bennett et al., 1990). The “extended” CTA results show that bacteria can be allocated either at trophic level 1 or higher according to their function but this requires that non-living material be allocated: (1) to trophic level 1 if bacteria act as heterotrophs; (2) to trophic level 0 when bacteria are autotrophs. Through the “extended” CTA we have been able to solve some ambiguities related to trophic position in the presence of multiple non-living nodes connected to living compartments. Instead of considering non-living matter as part of the system, we propose to place it as import flows (see Fig. 4). Setting the nutrient pool trophic level to 0 avoids the strange trophic position 2 that happens to characterize benthic macrophytes, phytoplankton and benthic microflora, changing it to a more reasonable first level (Table 4). Conversely, if suspended POC and sediment POC trophic levels are equal to 1 we obtain ecologically robust outcomes for meiofauna, zooplankton and invertebrate feeders (herbivores with trophic level 2). What comes out from suspended POC and sediment POC (Fig. 4) substantially corresponds to what Gaedke and Straile (1997) call autochthonous dead organic matter. Although our choice of considering suspended POC and sediment POC as inflows into the system matches with their “biospheric point of view” that abolish the distinction between allochthonous and autochthonous material, still a difference remains in assigning these compartments to a trophic level. We set up these flows (to herbivores) at trophic level 1, whereas the above cited authors keep them at trophic level 0. Their approach seems beneficial for the clarity and meaningfulness of various trophic measures such as trophic position as indicative of number of assimilation events, transfer efficiency between trophic levels, homogeneity of trophic level composition. However, it seems that the same achievements could be obtained by setting up dead organic material (irrespective of its endogenous or exogenous origin) to trophic level 1 or to the respective trophic position of its sources, as likely, what matters in their context is the difficulty of treating dead organic material as part of the system. We reiterate, however, that dead organic material, as external source of energy (i.e. inorganic nutrients), should be allocated to trophic level 0 if inconsistencies involving the trophic positions of plants have been noticed, while it should be set up to 1 when

it just apportion its outflows to heterotrophic compartments. Lindeman (1942) allocated dead organic material at trophic level 1, and this choice was criticized as an arbitrary convention (Cousins, 1987). However, while we show that in doing so one avoids many inconsistencies in the trophic aggregation scheme and that the entire CTA acquires internal coherence, we also point out that a distinction should be made between detritus (i.e. suspended POC and sediment POC in our example) and dead organic material. In many cases detritus includes living organisms and in this case particular attention should be devoted in separating living from non-living things before calculating the trophic position of this entity (Gaedke and Straile, 1997). The same authors draw their conclusion discussing the trophic position of autochthonous dead organic material from a logical–empirical point of view. They make evident how the various approaches used in the literature to calculate trophic position in ecosystems generate inconsistencies when dead organic material is included in the computation and show how these inconsistencies can be resolved. Although they provide a logical – step by step – reconstruction of the potential consequences of the different assumptions concerning the trophic position of the dead organic matter, they do not generalize their point of view in a rigorous procedure for calculation. Because we developed our arguments within the canonical trophic aggregation framework, which is basically manipulation of ecosystem flow matrices, our outcomes are fairly general. Despite the fact that conclusions drawn in this paper differ from Gaedke and Straile’s, rather than seeing the two approaches in contrast with one another we perceive the potential for their integration. In recent times, the shift of emphasis from local stability dynamics, toward a more comprehensive analysis of ecosystem persistence and nonlinear dynamics, has allowed to reconsider the importance of cycles in networks. As a consequence, the fact that we used simple acyclic ecosystem models to derive our “extended” CTA may cast doubts on the realism of our approach. We stress, however, that our aim was to resolve the inconsistencies arising in CTA. Therefore, we started from the very same set of assumptions (Ulanowicz, 1995, 2004), and we treated flows from non-living compartments as imports to living. The choice of using an acyclic model is coherent within this framework. Since cycles play a major role in ecosystems, and recent studies show a greater evidence of cycles involving living nodes (Dunne et al., 2002, 2004; Williams and Martinez, 2000), next amendment to CTA should deal with them, replacing decyclization routine that over simplifies the networks. We have not tested the consequences of our approach on the trophic attributes of real ecosystems such as efficiency of transfer, trophic pyramids and interpretation of analysis of the overall energy flow. Applications to real ecosystems are required to perform these investigations, and they will certainly be carried out in the near future. Also a more functional CTA should explore the effect of cycling but this is a question that we inherited from the original formulation of the canonical trophic aggregation. Whether the concept of trophic position has resolved many ambiguities associated with that of trophic level, this latter idea remains as a reference point because the calculation of the trophic position is made in relation to a classification scheme that sets plants as the first level.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2006.06.005.

REFERENCES

- Allesina, S., Bodini, A., Bondavalli, C., 2005. Ecological subsystems via graph theory: the role of strongly connected components. *Oikos* 110, 164–176.
- Allesina, S., Bondavalli, C., 2004. WAND: an ecological network analysis user-friendly tool. *Environ. Model. Software* 19, 337–340.
- Azam, F., Fenichel, T., Field, J., Gray, J., Meyer-Reil, L., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.* 10, 257–263.
- Baird, D., Milne, H., 1981. Energy flow in the Ythan Estuary, Aberdeenshire, Scotland. *Estuarine, Coastal Shelf Sci.* 13, 455–472.
- Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59 (4), 329–364.
- Bennett, S., Sanders, R., Porter, K., 1990. Heterotrophic, autotrophic, and mixotrophic nanoflagellates: seasonal abundances and bacterivory in a eutrophic lake. *Limnol. Oceanogr.* 35, 1821–1832.
- Bondavalli, C., Bodini, A., Rossetti, G., Allesina, S., 2006. Detecting stress at a whole ecosystem level. The case of a mountain lake: Lake Santo (Italy). *Ecosystems* 9, 1–56.
- Bratbak, G., 1987. Carbon flow in an experimental microbial ecosystem. *Mar. Ecol. Prog. Ser.* 36, 267–276.
- Burns, T.P., 1989. Lindeman's contradiction and the trophic structure of ecosystems. *Ecology* 70, 1355–1362.
- Burns, T.P., Higashi, M., Wainright, S.C., Patten, B.C., 1991. Trophic unfolding of a continental-shelf energy-flow network. *Ecol. Model.* 55 (1–2), 1–26.
- Carpenter, S., Kitchell, J., 1993. *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge, UK.
- Carpenter, S., Kitchell, J., Hodgson, J., 1986. Cascading trophic interactions and lake productivity. *BioScience* 35, 634–639.
- Christensen, V., Pauly, D., 1992. Ecopath II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Model.* 61 (3–4), 169–185.
- Christensen, V., Pauly, D. (Eds.), 1993. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings, p. 26.
- Christensen, V., Walters, C.J., Pauly, D., 2005. *Ecopath with Ecosim: a User's Guide*. Fisheries Centre, University of British Columbia, Vancouver, Canada, <http://www.ecopath.org>.
- Christian, R.R., Luczkovich, J., 1999. Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. *Ecol. Model.* 117, 99–124.
- Cousins, S., 1985. Ecologists build pyramids again. *New Scientist* 107 (1463), 50–54.
- Cousins, S., 1987. The decline of the trophic level concept. *Trends Ecol. Evol.* 2, 312–316.
- Dunne, J., Williams, R., Martinez, N., 2002. Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. U.S.A.* 99, 12917–12922.
- Dunne, J., Williams, R., Martinez, N., 2004. Network structure and robustness of marine food webs. *Mar. Ecol. Prog. Ser.* 273, 291–302.
- Fath, B.D., Patten, B.C., 1999. Review of the foundations of network environ analysis. *Ecosystems* 2 (2), 167–179.
- Gaedke, U., Straile, D., 1997. The trophic position of dead autochthonous organic material and its treatment in trophic analysis. *Environ. Model. Assess.* 2 (2), 13–22.
- Gophen, M., 1990. Biomanipulation: retrospective and future development. *Hydrobiologia* 200/201, 1–11.
- Heymans, J.J., Ulanowicz, R.E., Bondavalli, C., 2002. Network analysis of the South Florida everglades graminoid marshes and comparison with nearby cypress ecosystems. *Ecol. Model.* 149, 5–23.
- Higashi, M., Burns, T.P., Patten, B.C., 1989. Food network unfolding: an extension of trophic dynamics for application to natural ecosystems. *J. Theor. Biol.* 140, 243–261.
- Higashi, M., Burns, T.P., Patten, B.C., 1992. Trophic niches of species and trophic structure of ecosystems—complementary perspectives through food network unfolding. *J. Theor. Biol.* 154, 57–76.
- Higashi, M., Patten, B.C., Burns, T.P., 1991. Network trophic dynamics: an emerging paradigm in ecosystems ecology. In: Higashi, M., Burns, T.P. (Eds.), *Theoretical Studies of Ecosystems—The Network Perspective*. Cambridge University Press.
- Kay, J.K., Graham, L.A., Ulanowicz, R.E., 1989. A detailed guide to network analysis. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), *Network Analysis in Marine Ecology*. Coastal and Estuarine Studies Series. Springer-Verlag, Berlin, pp. 15–61.
- Kercher, J.R., Shugart, H.H., 1975. Trophic structure, effective trophic position, and connectivity in food webs. *Am. Nat.* 109, 191–206.
- Levine, S., 1983. Several measures of trophic structure applicable to complex food webs. *J. Theor. Biol.* 83, 195–207.
- Lindeman, R., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 399–418.
- Luczkovic, J., Borgatti, D., Johnson, J., Everett, M., 2003. Defining and measuring trophic role similarity in food webs using regular equivalence. *J. Theor. Biol.* 220 (3), 303–321.
- May, R., 1983. The structure of foodwebs. *Nature* 301, 566–568.
- Oksanen, L., 1991. Trophic level and trophic dynamics: a consensus emerging? *Trends Ecol. Evol.* 6, 58–60.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.J., 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, ecosim, and ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci.* 57, 697–706.
- Pimm, S., 1982. *Food Webs*. Chapman & Hall, New York.
- Pimm, S., 1988. Energy flow and trophic structure. *Concepts of Ecosystem Ecology*. Springer-Verlag, New York.
- Polis, G., 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* 138, 123–155.
- Polis, G., Anderson, W., Holt, R., 1997. Toward and integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28, 289–316.
- Polis, G., Hurd, S., 1996. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: examples from the ocean-land interface. *Food Webs: Integration of Patterns and Dynamics*. Chapman-Hall, NY, pp. 275–285.
- Polis, G., Power, M., Huxel, G., 2004. *Food webs at the Landscape Level*. University of Chicago Press, Chicago.
- Polis, G., Strong, D., 1996. Food web complexity and community dynamics. *Am. Nat.* 147, 813–846.
- Polis, G.A., 1994. Food webs, trophic cascades and community structure. *Aust. J. Ecol.* 19, 121–136.
- Pomeroy, L., 1984. Significance of microorganisms in carbon and energy flow in marine ecosystems. *Current Perspectives in Microbial Ecology*. American Society for Microbiology, Washington, DC, pp. 405–411.
- Shapiro, J., 1990. Biomanipulation: the next phase making it stable. *Hydrobiologia* 200/201, 13–27.
- Sherr, E., Sherr, B., Fessenden, L., Gosselin, M., Thibault, D., Wheeler, P., 2003. Heterotrophic Bacteria and Protists in the Upper Water Column of the Central Arctic Ocean. National Snow and Ice Data Center, Boulder, CO.

- Ulanowicz, R., 1983. Identifying the structure of cycling in ecosystems. *Math. Biosci.* 65, 219–237.
- Ulanowicz, R., 1986. *Growth and Development—Ecosystems Phenomenology*. Springer-Verlag, New York.
- Ulanowicz, R., 1995. *Ecosystem trophic foundations: Lindeman exonerata. Complex Ecology: The Part-Whole Relation in Ecosystems*. Prentice-Hall, New Jersey.
- Ulanowicz, R., 1996. Trophic flow networks as indicators of ecosystem stress. *Food Webs: Integration of Patterns and Dynamics*. Chapman-Hall, NY, pp. 358–368.
- Ulanowicz, R., 2002. NETWRK 4.2b: A Package of Computer Algorithms to Analyze Ecological Flow Networks. University of Maryland, Center for Environmental & Estuarine Studies, Chesapeake Biological Laboratory, Solomons, MD, <http://www.cbl.umces.edu/~ulan/ntwk/network.html>.
- Ulanowicz, R., 2004. Quantitative methods for ecological network analysis. *Comput. Biol. Chem.* 28, 321–339.
- Ulanowicz, R., Bondavalli, C., Egnotovitch, M., 1998. *Network Analysis of Trophic Dynamics in South Florida Ecosystems (1445-ca09-95-0093 sa#2). fy 97: The Florida Bay ecosystem*. Tech. Rep. [UMCES] CBL 98–123, Annual Report to the United States Geological Service Biological Resources Division, University of Miami, Coral Gables, FL.
- Ulanowicz, R., Kay, J., 1991. A package for the analysis of ecosystem flow networks. *Environ. Software* 6, 131–142.
- Ulanowicz, R.E., Kemp, W.M., 1979. Toward canonical trophic aggregations. *Am. Nat.* 114 (6), 871–883.
- Vadas, R.J., 1990. The importance of omnivory and predator regulation of prey in freshwater fish assemblages of North America. *Environ. Biol. Fish.* 27, 285–302.
- Whipple, S., 1998. Path-based network unfolding: A solution for the problem of mixed trophic and non-trophic processes in trophic dynamic analysis. *J. Theor. Biol.* 190, 263–276.
- Whipple, S.J., Patten, B.C., 1993. The problem of nontrophic processes in trophic ecology—toward a network unfolding solution. *J. Theor. Biol.* 163, 393–411.
- Williams, R.J., Martinez, N.D., 2000. Simple rules yield complex food webs. *Nature* 404, 180–183.
- Winemiller, K., 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* 60, 331–367.
- Wulff, F., Field, J., Mann, K., 1989. *Network Analysis in Marine Ecology. Methods and Applications*. Springer-Verlag, Berlin.
- Wulff, F., Ulanowicz, R.E., 1989. A comparative anatomy of the Baltic Sea and Chesapeake Bay ecosystems. In: Wulff, F., Field, J.G., Mann, K.H. (Eds.), *Network Analysis in Marine Ecology. Coastal and Estuarine Studies Series*. Springer-Verlag, Berlin, pp. 232–256.