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A draft guide to the ECOPATH II program (ver. 1.0)

V. CHRISTENSEN
D. PAULY

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Abstract

This guide documents the use and background of a program written for MSDOS Computers, in QUICKBASIC 4.5, for straightforward construction and parametrization of steady-state trophic models of aquatic ecosystems.

The ECOPATH II program is structured around a system of linear equations as suggested by J.J. Polovina and coworkers, and also incorporates routines from the computation of various network flow indices derived from a theory presented by R.E. Ulanowicz.

Introduction

The ECOPATH II model program combines an approach proposed by J.J. Polovina (1984) for estimation of biomass and food consumption of the various elements (species or species groups) of an aquatic ecosystem with an approach proposed by R.E. Ulanowicz (1986) for the analysis of the flows between the elements of ecosystems.

The implications of this marriage of two approaches initially proposed in 1987 (Pauly et al. in press) have not all been followed up, and the present notes are not meant to remedy this situation. Rather, these notes shall attempt to clarify some of the terminology and operations involved with ECOPATH II.

This is achieved through two tables presenting definitions of terms relevant to the interpretation of outputs of ECOPATH II (Tables 1 and 2) and through describing a number of "algorithms", in which the equations used to estimate certain parameters, along with relevant comments and descriptions of special cases. Table 1 presents some concepts relevant to the construction of trophic ecosystem models, as proposed or used by theoretical ecologists (notably R.E. Ulanowicz) and as commonly used by fishery biologists such as ourselves. Table 2 presents definitions of the major ecosystem indices presented in Ulanowicz (1986). The aim of this table is not to replace the book from which the definitions were extracted, but hopefully, to facilitate its comprehension.

Indeed, even the title of this book ("Growth and Development: Ecosystem Phenomenology") needs explaining. This is so because the words "growth" and "development", as used by R.E. Ulanowicz, are not used to mean what most people would assume they do. Thus, "growth" refers to the <u>size</u> of an ecosystem, while "development" refers to the <u>information contents</u> embodied in ecosystem structure. This implies that the <u>time dimension</u>, an important aspect of standard definition of growth and development, is not an explicit part of the theory leading to Ulanowicz' various key concepts (in Table 2).

Also, the last word of the title needs to be defined. Phenomenology, a term first proposed and used by the German philosopher E.G.A. Husserl (1859-1938) is a branch of philosophy devoted to the careful, detailed description of "phenomena" (i.e., observed fact and occurrences) and which deemphasizes (or even denies) the need to <u>explain</u>, i.e., to identify the cause(s) of phenomena. The use of this term by R.E. Ulanowicz is to emphasize his contention that the flows (of energy or matter) between the components of ecosystems are sufficient for a "complete" description of those system - a contention with which many may disagree. However, there is no reason not to use his indices and the theory from which they were derived to improve our (partial) descriptions.

The ECOPATH II Model

As described in Pauly et al. (in press), the ECOPATH II model is derived from the ECOPATH program of Polovina and Ow (1983) and Polovina (1984a, 1984b, 1985, 1986).

Basically, the approach is to model an ecosystem using a system of simultaneous linear equations (one for each (group of) species i), i.e.,

Production by (i) - all predation on (i) - non predation losses of (i) - export of (i) = 0, for all i.

Or using the notations of Appendix 1,

$$P_i - M2_i - P_i\,(1\text{-}EE_i) - EX_i = 0 \qquad \text{...1)}$$

where P_i is the production of (i), $M2_i$ is the predation mortality of (i), EE_i is the Ecotrophic Efficiency of (i) and EX_i is the Export of (i).

The equation can be expressed

$$B_i\,PB_i - \sum_j B_j{*}QB_j{*}DC_{ji} - PB_i{*}B_i\,(1\text{-}EE_i) - EX_i = 0$$

or

$$B_i{*}PB_i{*}EE_i - \sum_j B_j{*}QB_j{*}DC_{ji} - EX_i = 0 \qquad \text{...2)}$$

where B_i is the biomass of i, PB_i is the production/biomass ratio, QB_i is the consumption/biomass ratio, and DC_{ji} is the fraction of prey (i) in the average diet of predator j (see also Table 3).

Based on (2), a number (n) of linear equations can be expressed as

$$B_1PB_1EE_1\text{-}B_1QB_1DC_{11}\text{-}B_2QB_2DC_{21}\text{-}...\text{-}B_nQB_nDC_{n1}\text{-}EX_1 = 0 \qquad \text{...3.1)}$$
$$B_2PB_2EE_2\text{-}B_1QB_1DC_{12}\text{-}B_2QB_2DC_{22}\text{-}...\text{-}B_nQB_nDC_{n2}\text{-}EX_2 = 0 \qquad \text{...3.2)}$$
$$\vdots$$
$$\vdots$$
$$B_nPB_nEE_n\text{-}B_1QB_1DC_{1n}\text{-}B_2QB_2DC_{2n}\text{-}...\text{-}B_nQB_nDC_{nn}\text{-}EX_n=0 \qquad \text{...3.n)}$$

This system of simultaneous linear equations can be reexpressed (using some substitutions that are described in Algorithm 5) as

$$a_{11}\,X_1 + a_{12}\,X_2 + ... + a_{1m}\,X_m = Q_1 \qquad \text{...4.1)}$$
$$a_{21}\,X_1 + a_{22}\,X_2 + ... + a_{2m}\,X_m = Q_2 \qquad \text{...4.2)}$$
$$\vdots$$
$$\vdots$$
$$a_{p1}\,X_1 + a_{p2}\,X_2 + ... + a_{pm}\,X_m = Q_p \qquad \text{...4.n)}$$

with P being equal to the number of equations, and m to the number of unknowns.

This can be written in matrix notation as

$$[A]_{p,m} * [X]_m = [Q]_m \qquad \text{...5)}$$

If we can find the inverse A^{-1} of the matrix A, we have

$$[X]_m = [A^{-1}]_{m,m} * [Q]_m \qquad \text{...6)}$$

If the determinant of a matrix is zero, or if the matrix is not square, it has no ordinary inverse. However, a generalized inverse can be found in most cases (Mackay 1981). In the ECOPATH II model, we have adopted the program of Mackay (1981) to estimate the generalized inverse.

If the set of equations is overdetermined (more equations than unknowns, and the equations are not consistent with each other, the generalized inverse method is used to obtain least squares estimates, which minimize the discrepancies.

If, on the other hand, the system is underdetermined (more unknowns than equations, an answer that is consistent with the data may still be obtained.

To optimize the ECOPATH II model, a number of algorithms have been included in order to calculate (some of the) missing parameters without using the generalized inverse method. These algorithms, which make the program faster, take advantage of the fact that many of the elements of the diet composition matrix are known to be zero, and use this knowledge of the trophic interactions to increase the number of parameters that can be estimated.

It should be noted, however, that there are certain requirements that must be met. Thus, according to the basic equation (1) of the ECOPATH II model, we have, for any (species) group i:

$$B_i * PB_i * EE_i = EX_i + \sum_j B_j * QB_j\, DC_{ji} \qquad \text{...2)}$$

Therefore, only one of the parameters B_i, PB_i or EE_i may be unknown. In addition, QB_i may in some cases be unknown as well (see Algorithm 3).

The energy balance of a box

A box may, in the ECOPATH II model, be a group of (ecologically) related species, a single species, or a size/age group (see Table 2).

In the model, the energy input and output of all boxes must be balanced, as we are only dealing with "steady-state" systems (see Table 2).

However, the basic ECOPATH equation (1) models only the production of a box, i.e., production equals predation mortality + export + contribution to the detritus. When balancing the energy flow of a box, other flows should be included. Thus,

$$\text{Import} + \text{Consumption} = \begin{array}{l}\text{Export} + \text{Predation Mortality}\\ + \text{Contribution to Detritus}\\ + \text{Respiration}\end{array} \qquad \text{...7)}$$

From this equation, the respiration can be estimated (see Algorithm 10).

Algorithm 1 **Estimation of PB**

From equation (2), we have

$$PB_i = \frac{EX_i + M2_i}{B_i * EE_i} = \frac{EX_i + \sum_j B_j\, QB_j\, DC_{ji}}{B_i * EE_i} \qquad ...8)$$

This expression can be solved if both the catch, biomass and Ecotrophic Efficiency of group (i), and the biomasses and consumption rates of all predators on group (i) are known (including group (i) if a zero order cycle, i.e., "cannibalism" exists). It should be noted that for a top predator where $M2_i$ is zero, the production biomass ratio can be estimated from knowledge of group (i) alone.

Problem: How to deal with top predators

For a top predator i with Ecotrophic efficiency $EE_i = 0$, in is necessary to obtain independent estimates of PB_i. This parameter cannot be estimated from equation (9) as EE_i, Ci and s $B_j\, QB_j\, DC_{ji}$ are, in this case, all equal to 0.

In most cases (at least for fisheries biologists), this will not pose serious problems as PB (i.e., total mortality see Table 1) for top predators can be readily estimated from the age/size structure of the population.

If no data of this type should exist, $PB_i = 0$ can also be entered; although biologically unrealistic, this value will not have any detrimental effect on other estimates*).

Finally, it should be noted that for top predators with EE = 0, it is impossible to estimate QB (see the problem description pertaining to Algorithm 5).

Algorithm 2 **Estimation of EE**

Once again, rearranging equation (2), we have

$$EE_i = \frac{EX_i + M2_i}{B_i * PB_i} = \frac{EX_i + \sum_j B_j{*}QB_j{*}DE_{ji}}{B_i * PB_i}$$

The data requirements are as mentioned for Algorithm 1.

The Equation also implies the definition of EE, i.e., the ecotrophic efficiency is the part of the production that goes to export and predation mortality. This may seem inconsistent if one expects the ecotrophic efficiency to be a measure of "predation" within the system. This is, however, a consequence of the definition of the ecotrophic efficiency given by Polovina (1984).

---

*)An attempt to estimate PB using the program will result in the trivial solution $PB_i = 0$.

Algorithm 3 Dealing with B_i and QB_i as unknowns

We define i as a (species) group for which estimates of B and QB are not available, and k as a prey group (i.e., $DC_{ik} > 0$) for which B, PB, QB and EE are known or can be estimated. For groups that do not prey on either i nor k, B or QB may be unknown; other groups must have known B and QB.

From equation (2), we have

$$B_i{*}PB_i{*}EE_i = EX_i + \sum_j B_j\, QB_j\, DC_{ji} \qquad \text{...8)}$$

If $EE_i > 0$, then

$$B_i{*}PB_i = (EX_i + \Sigma_j\, B_j\, QB_j\, DC_{ji}) \,/\, EE_i \qquad \text{...9)}$$

Predation mortality $M2_i$ is, per definition (see Table 3),

$$M2_i = \sum_j B_j{*}QB_j{*}DC_{ji} = \sum_{j(j<>i)} B_j{*}QB_j{*}DC_{ji} + B_i{*}QB_i{*}DC_{ii}$$

$$= PARTM2_i + B_i{*}QB_i{*}DC_{ii} \qquad \text{...10)}$$

Further, as

$$B_k{*}PB_k{*}EE_k = EX_k + \sum_j B_j{*}QB_j{*}DC_{jk}$$

$$= EX_k + \sum_{j(j<>i)} B_j{*}QB_j{*}DC_{jk} + B_i{*}QB_i{*}DC_{ik}$$

and we have as $DC_{ik} <> 0$,

$$B_i{*}QB_i = (B_k{*}PB_k{*}EE_k - EX_k - \sum_{j(j<>i)} B_j{*}QB_j{*}DC_{jk}) \,/\, DC_{ik} \qquad \text{...11)}$$

or

$$QB_i = (B_k{*}PB_k{*}EE_k - EX_k - \sum_{j(j<>i)} B_j{*}QB_j{*}DC_{jk}) \,/\, (DC_{ik} * B_i) \qquad \text{...12)}$$

Now, from equations (2) and (10), we have

$$B_i = \frac{EX_i + PARTM2_i + DC_{ii} * (B_k{*}PB_k{*}EE_k - EX_k - \sum_{j(j<>i)} B_j{*}QB_j{*}DC_{jk})/DC_{ik}}{EE_i\, PB_i} \qquad \text{...13)}$$

Finally QB_i can be found using equation (12).

Algorithm 4 Estimating biomasses (B_i) only

From equation (2) and (10), we have

$$B_i\, PB_i\, EE_i = EX_i + M2_i$$

$$= EX_i + PARTM2_i + B_i\, QB_i\, DC_{ii}$$

and thus

$$-B_i = \frac{EX_i + PARTM2_i}{(PB_i\, EE_i - QB_i\, DC_{ii})} \qquad \text{...14)}$$

if $PB_i\, EE_i = QB_i\, DC_{ii}$, i.e., if group i is the only predator on group i, the equation above cannot be solved. In such a case, group i should be split into (at least) two groups.

Please note that if

$$PB_i * EE_i < QB_i\, DC_{ii}$$

(that is, "cannibalism" exceeds predation mortality) equation (13) will produce a negative estimate of B_i. If so, an error message will give a warning and program execution will be aborted.

If the biomasses are unknown for all groups and if there is no export (including fishery) for any of the groups, it is necessary to enter an estimate of at least one of the biomasses (or of several of the exports).

Algorithm 5 **The Generalized Inverse**

Looking again at the equation system (3), we have

$$B_1PB_1EE_1\text{-}B_1QB_1DC_{11}\text{-}B_2QB_2DC_{21}\text{-}...\text{-}B_nQB_nDC_{n1}\text{-}EX_1 = 0 \qquad \text{...3.1)}$$
$$B_2PB_2EE_2\text{-}B_1QB_1DC_{12}\text{-}B_2QB_2DC_{22}\text{-}...\text{-}B_nQB_nDC_{n2}\text{-}EX_2 = 0 \qquad \text{...3.2)}$$
:
:
$$B_nPB_nEE_n\text{-}B_1QB_1DC_{1n}\text{-}B_2QB_2DC_{2n}\text{-}...\text{-}B_nQB_nDC_{nn}\text{-}EX_n=0 \qquad \text{...3.n)}$$

As mentioned earlier in the equation system (4), this can be reexpressed as

$$a_{11}\, X_1 + a_{12}\, X_2 + ... + a_{1m}\, X_m = Q_1 \qquad \text{...4.1)}$$
$$a_{21}\, X_1 + a_{22}\, X_2 + ... + a_{2m}\, X_m = Q_2 \qquad \text{...4.2)}$$
:
:
$$a_{p1}\, X_1 + a_{p2}\, X_2 + ... + a_{pm}\, X_m = Q_p \qquad \text{...4.n)}$$

The substitutions leading to system (4) depends on which of the parameters that are unknown in each of the equations (after algorithms 1-2 have been used repeteadly).

For each of the i (possible) equations, the following routines, i.e. substitutions, are performed:

a. **PB_j or EE_j unknown**

In addition to PB_j or EE_j, either B_j or QB_j will be unknown (otherwise algorithm 1 or 2 would have calculated the missing parameter).

Equation (j) is not included in the A, X and Q matrices. Instead, the missing value of the parameters B_j and QB_i is estimated from the other equations, and PB_j or EE_j is calculated from algorithm 1 or 2.

b. **B_j and QB_j both unknown**

If it has not been possible to estimate these parameters using algorithm 3, program execution will be aborted at this point in algorithm 5, and the following message will appear:

"Insufficient data make it impossible to calculate both the missing B and the missing QB for group j"

c. **Only B_j is unknown**

If $i <> j$, then $A_{ij} = -QB_j * DC_{ji}$.

If $i = j$, then $A_{ij} = PB_j * EE_j - QB_j * DC_{jj}$

d. **Only QB_j is unknown**

$A_{ij} = -B_j * DC_{ji}$

e. **The X matrix**

The i^{th} element of the x-matrix will be either B_i or QB_i depending on which of these is unknown.

f. **The Q matrix**

The Q matrix contains "the Right Hand Side" elements.

For each box (i), the Q_i's are derived from the sums over each of the (j) elements of each equation

$$Q_i = EX_i + \sum_j q_{ij}$$

where

$$q_{ij} = \left[\begin{array}{ll} 0 & \text{if } B_j \text{ is unknown} \\ +B_j*QB_j*EE_j & \text{if } QB_j \text{ is unknown} \\ B_j*QB_j*DC_{ji} & \text{if } B_j \text{ and } QB_j \text{ are known} \\ & \quad \text{and } B_i \text{ is unknown} \\ B_iQB_iDC_{ii} - B_iPB_iEE_i & \text{if } B_i \text{ and } QB_i \text{ are} \\ & \quad \text{known and } i = j. \end{array} \right.$$

where the index (j) again covers all the boxes included.

Problem: Estimation of QB for a top predator

The QB ratio can, in most cases, be estimated using Algorithm 5. However, for a top predator (m) for which $DC_{jm} = 0$ (i.e. no one eats m) for all possible predators) (j), it in not possible to estimate QB_m.

Algorithm 6 **Contribution to detritus as used when computing the trophic level of detritus**

All that is not eaten, caught or exported, must eventually end in the detritus box. Also, a part of what is eaten (i.e., the part that is excreted or egested) ends up as detritus. This can be expressed as:

$$DET_i = (1\text{-}EE_i) * P_i + (\text{Fraction excreted} + \text{Fraction egested}) * Q_i \qquad ...15)$$

where DET_i is the contribution to the detritus from species i. This can be used to derive an equation for estimating the contribution to the detritus. However, when calculating the trophic level of the detritus, this equation must be amended to take the fact into account that the products of egestion and excretion should not have the trophic level of the egesting and excreting organism, but that of its food item.

Therefore, equation (15) is reexpressed as

$$DET_i = B_i\, PB_i\, (1\text{-}EE_i) - \sum_j B_j * QB_j ** DC_{ji} * (XC + GS)/100$$

where XC and GS are excretion and egestion in percentage of consumption.

The "diet composition" of detritus, as it is used for computing its trophic level, is thus:

$$DC_D = DET_i \,/\, \sum_i DET_i$$

Algorithm 7 **Trophic levels**

Primary producers such as phytoplankton and benthic producers have, by definition, a trophic level equal to zero. For all other groups except detritus, the (mean weighted) trophic level (T) of group (i) is defined as one plus the sum of the trophic level of its preys multiplied by the prey's proportion in the diet of species (i).

$$T_i = 1 + \sum_j DC_{ij} * T_j \qquad ...16)$$

where DC_{ij}, referred to as the diet composition, is the proportion of prey (j) in the diet of species (i).

Detritus is that part of the ecosystem resources that is not bound to living organisms. Its trophic level (T_D) poses a small problem; we have chosen to define T_D as the sum of the trophic levels of species contributing to the detritus box multiplied by the fraction of the species' contribution over the total amount of contribution to the detritus. The computation of these proportions was discussed in Algorithm 6 and it is expressed in terms of the diet composition as in equation (16).

$$T_D = \sum_j DC_{Dj} * T_j \qquad ...17)$$

The trophic levels for all species may be expressed as a system of equations in the form:

$$
\begin{array}{lllllll}
1 & = & t_1(1-DC_{11}) & -t_2DC_{12} & -t_3DC_{13} & ...-t_nDC_{1n} & -t_DDC_{1D} \\
1 & = & -t_1DC_{21} & +t_2(1-DC_{22}) & -t_3DC_{23} & ...-t_nDC_{2n} & -t_DDC_{2D} \\
: & & : & : & : & : & : \\
: & & : & : & : & : & : \\
: & & : & : & : & : & : \\
1 & = & -t_1DC_{n1} & -t_2DC_{n2} & -t_3DC_{n3} & ...+t_n(1-DC_{nn}) & -t_DDC_{nD} \\
0 & = & -t_1DC_{D1} & -t_2DC_{D2} & -t_3DC_{D3} & ...-t_nDC_{nD} & +t_D(1-DC_{DD})
\end{array}
$$

Putting the above in matrix form:

$$
\begin{bmatrix} 1 \\ 1 \\ : \\ : \\ : \\ 1 \\ 0 \end{bmatrix}
\begin{array}{c} = \\ = \\ = \\ = \\ = \\ = \\ = \end{array}
\begin{bmatrix}
(1-DC_{11}) & -DC_{12} & ...-DC_{1n} & -DC_{1D} \\
-DC_{21} & (1-DC_{22} & ...-DC_{2n} & -DC_{2D} \\
: & : & : & : \\
: & : & : & : \\
: & : & : & : \\
-DC_{n1} & -DC_{n2} & ...\ (1-DC_{nn}) & -DC_{nD} \\
-DC_{D1} & -DC_{D2} & ...\ -DC_{Dn} & (1-DC_{DD}
\end{bmatrix}
\begin{bmatrix} t_1 \\ t_2 \\ : \\ : \\ : \\ t_n \\ t_D \end{bmatrix}
$$

or $Y = DT$

which has the solution $T = (D^{-1})Y$

The solution to matrix T is obtained by taking the inverse of D (i.e., D^{-1}), using the generalized inverse method (Mackay 1981).

Algorithm 8 **Omnivory index**

The feeding behavior of group (i) can be partly described by its "omnivory index", i.e., the variance of the trophic levels of its preys.

$$OI_i = \sum_j (T_j - T)^2 * DC_{ij} \qquad ...18)$$

A large omnivory index indicates that the trophic position of its preys and its prey preference are variable.

If a predator only has one type of prey, its omnivory index will equal zero.

Algorithm 9 **Contribution to detritus**

As discussed previously (Algorithm 6), the contribution to the detritus from group (i) can be expressed as`

$$DET_i = (1-EE_i) * P_i + (\text{Fraction Excreted} + \text{Fraction Egested}) * Q_i \qquad ...15)$$

This equation is used for calculating the contributions to the detritus, as they are displayed in the program output.

The total flow into the detritus box is calculated as

$$DT = \sum_{i} DET_i \qquad \text{...19)}$$

Note that when calculating the trophic level of the detritus box, a modified version of equation (15) is used (see Alg. 6).

Algorithm 10 **Respiration**

From equation (7), we have the respiration of group (i) defined as:

$$RESP_i = IM_i + Q_i - EX_i - M2_i - DET_i$$

This can also be expressed as

$$RESP_i = IM_i + B_i\,(QB_i - PB_i - QB_i\,(XC_i + GS_i) / 100) \qquad \text{...20)}$$

Further, the contribution to the detritus can, from equation (15), be expressed as

$$DET = B_i * [(1\text{-}EE_i) * PB_i + QB_i * (XC_i + GS_i)/100]$$

$$= B_i*[PB_i - EE_i*PB_i + QB_i * (XC_i + GS_i)/100]$$

$$= B_i*PB_i - B_i*EE_i\,PB_i*+ B_i*QB_i\,(XC_i + GS_i)/100$$

$$\text{or } DET_i + B_i + B_i*PB_i*EE_i = B_i*PB_i + B_i*QB_i\,(XC_i + GS_i)/100 \qquad \text{...21)}$$

That is, (20) + (21)

$$RESP_i = IM_i + B_i*QB_i - EE_i*B_i*PB_i - DET_i \qquad \text{...22)}$$

Equation (22) is used for the calculation of RESP in the program.

Algorithm 11. **Network information indices**

In the introduction to these notes, attention was drawn to the new ecosystem parameters (Table 2) derived by Ulanowicz (1986).

For calculation of the indices in the ECOPATH II model, the program given by Ulanowicz (1986, Appendix B) has been adopted. The procedure is described below.

The first step is to make a (n +3) by (n + 3) matrix P with the following elements:

$$P = \begin{bmatrix} Q_{11} & Q_{21} & \dots Q_{n1} & 0 & EX_1 & RESP_1 \\ Q_{12} & Q_{22} & \dots Q_{n2} & 0 & EX_2 & RESP_2 \\ \vdots & & \vdots & & & \\ \vdots & & \vdots & & & \\ Q_{1n} & Q_{2n} & \dots Q_{nn} & 0 & EX_n & RESP_n \\ IM_1 & IM_2 & \dots IM_n & 0 & 0 & 0 \\ 0 & 0 & \dots 0 & 0 & 0 & 0 \\ 0 & 0 & \dots 0 & 0 & 0 & 0 \end{bmatrix}$$

Now, let

$Q_i =$ The sum of the flow out of box (i), i.e., the sum of the elements of the i^{th} row (Consumption by all predators of group (i), plus export to (i), plus respiration of group (i).

$U_i =$ The sum of all flow into box (i), i.e., the sum of the elements of the i^{th} column (Food intake by group (i) plus the import to the group).

T = The total throughput, that is, the sum of all components of the P matrix, $(T = \sum_{ij} P_{ij})$.

Thus T is the sum of all flows within the system plus all exports, respirations and imports.

If further

$$G_{ij} = (P_{ij} * T) / (Q_i * U_j) \qquad \text{...23)}$$

then the Ascendency (A) is calculated (using all $G_{ij} > 0$) from

$$A = \sum_{ij} P_{ij} * \log G_i \qquad \text{...24)}$$

Full Development capacity (C), equivalent to the upper bound on ascendency, is calculated from

$$C = C' - \sum_i C' \qquad \text{...25)}$$

where

$$C' = \left[\begin{array}{ll} -\log (\sum_i IM_i / T) * (\Sigma IM_i) & \text{if } IM_i > 0 \\ 0 & \text{if } IM_i \leq 0 \end{array} \right.$$

and

$$C'' = \left[\begin{array}{ll} \log (Q_i/T) * (Q_i) & \text{if } Q_i > 0 \\ 0 & \text{if } Q_i \leq 0 \end{array} \right.$$

System overheads (Φ) is the difference between development capacity (C) and ascendency (A). The overheads consist of four components, i.e., $\Phi = \Phi_o + \Phi_e + \Phi_s + \Phi_V$ (see below and Table 2).

Overhead on inputs (Φ_o) is obtained from

$$\Phi_o = -\sum_i \Phi'_o \qquad \text{...26)}$$

where

$$\Phi'_o = \left[\begin{array}{ll} \log (IM_i/V_i) * IM_i & \text{if } IM_i > 0 \\ 0 & \text{if } IM_i \leq 0 \end{array} \right.$$

Similarly, overheads on exports (Φ_e) and on respirations (Φ_s) come from:

$$\Phi_e = -\Sigma \Phi'_e \qquad \text{...27)}$$

$$\Phi'_e = \left[\begin{array}{ll} \log (EX_i / Q_i) * (Q_i) & \text{if } EX_i > 0 \\ 0 & \text{if } EX_i \leq 0 \end{array} \right.$$

$$\Phi_s = -\Sigma \Phi'_s \qquad \text{...28)}$$

$$\Phi'_s = \left[\begin{array}{ll} \log (RESP_i / Q_i) * Q_i & \text{if } RESP_i > 0 \\ 0 & \text{if } RESP_i \leq 0 \end{array} \right.$$

The System Redundancy (Φ_r or R) is an overhead that can be calculated from

$$R = -\sum_{i=1}^{n} R' \qquad \text{...29)}$$

where

$$R' = \sum_{j=1}^{n} R^n$$

$$\text{and } R^n = \left[\begin{array}{ll} \log (Q_{ij} / \sum_{j=1}^{n} Q_{ij} * (Q_{ij}) & \text{if } Q_{ij} > 0 \\ 0 & \text{if } Q_{ij} \leq 0 \end{array} \right.$$

Internal capacity (C_i) and Internal ascendency (A_i) are calculated as full capacity and full ascendency excluding, however, all exports, respirations and imports from the calculations.

The tribute to other system (E) is the sum of the contributions of the exports from a system to the overheads (F_e) and to ascendency (A). The tribute is calculated as

$$E = -\sum_{i} E' \qquad \text{...30)}$$

where

$$E' = \left[\begin{array}{ll} \log (Q_i / T) * EX_i & \text{if } EX_i > 0 \\ 0 & \text{if } EX_i \leq 0 \end{array} \right.$$

Finally, Dissipation (S) is the sum of the contributions of respiration to the overhead of a system (Φ_S) and to its ascendency (A). It is calculated as

$$S = -\sum_i S' \qquad \text{...31)}$$

where

$$S' = \begin{cases} \log (Q_i/T) * RESP_i & \text{if } RESP_i > 0 \\ 0 & \text{if } RESP_i \leq 0 \end{cases}$$

Note that the results given in the program's written outputs are calculated using Base 2 logarithms. Therefore, the unit is "bits" where one "bit" is the probability that is associated with a single binary decision.

Table 1 **Definition of some terms relevant to the construction of steady-state trophic ecosystem model**

Equivalent concepts, by discipline Theoretical ecology[a]	Fishery biology	Definition and/or remarks
P/B ratio (PB)	Total mortality (Z)	These two concepts were shown by Allen (1971, J. Fish. Res. Board Can. 28: 1573-1581) to be identical under steady-state, when von Bertalanffy growth and exponential mortality are assumed)
Node [also elements or compartment]	Box	A population (or group of single-species population belonging to the same guild), explicitly included in a model, and whose members can be represented by the same diet compo-sition, food consumption and PB ratio.
Arc	Arrow	A trophic flow of matter (or energy) between two boxes, or a flow of material or energy from or into a box. Arrows may be either "weighted" (i.e., quantified) or unweighted (i.e., represent only the existence of a flow).
Edge	Link	An "arc" from which the direction of flow is lacking.
T_{ij} "Throughput"	DC_{ji} "Diet Composition"	Represents flow of energy/matter from box j to box i (note different sequence of subscripts).
Respiration (R_i)	Respiration	A flow (or flows) of mass or energy that is (are) not directed toward, nor could be used by any other box(es). When carbon is used as "currency", respiration appears as CO_2, (biologically) the most degenerate form of carbon (Ulanowicz 1986, p. 18).
Exports (E_i)	Sum of fishery catches plus emigration to adjacent ecosystem(s)	A flow (or flows) of usable mass or energy that is not directed toward any of the boxes explicitly included in an ecosystem model [Note difference to respiration, where the flows represent unusable mass or energy.]

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[a] Emphasis is given here to concepts and symbols (T_{ij}, R_i, E_i, D_i) used by Ulanowicz (1986).

Equivalent concepts, by discipline Theoretical ecology[a]	Fishery biology	Definition and/or remarks
"Steady-state" population	"Average" population	A steady-state population is a theoretical construct, never occurring in reality. It can be approximated by averaging time series data over longer periods without major changes of biomass or size/age composition.
Network, directed network, graph, weighted graph	Trophic model, box model	A (graphic) representation of the flows (and often of diagraph, the biomasses) in a given ecosystem. A "graph" is "weighted" when the flows linking the boxes are quantified (e.g., in gCm^{-2} $year^{-1}$).
Inputs (D_i)	Primary production (in most cases)	Models of ecosystems must always include an "input", because such system dissipate energy. In most practical cases, the input will consist of primary production, except for some cave and deep sea ecosystems, in which the inputs may consist of detritus.

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[a] Emphasis is given here to concepts and symbols (T_{ij}, R_i, E_i, D_i) used by Ulanowicz (1986).

Table 2 **Dimensions, units and definitions of some ecosystem indices presented in Ulanowicz (1986)**

Index (with symbol, ftsdimension and units)	Definition and remarks with page and equation no.
Total System Throughput (T); mass (or energy) * area^{-1} * time^{-1} (e.g., gCm^{-2}d^{-1}, or kcal m^{-2}y^{-1})	Sum of all flows into and from the boxes in an ecosystem, i.e., including imports, exports of usable materials or energy (e.g., fishery catches, or emigration), respiration and flows to and from the detritus box. When put on a per area basis, T expresses the relative size of an ecosystem better than the sum of the biomass would (p. 35, eq. 3.4).
Ascendency (A); The dimensions and units of A also apply to all indices further below (except A/C, which is dimensionless). The dimension mass (or energy) * bits * area^{-1} * time^{-1} (e.g., gC bits * m^{-2}y^{-1}). [A is also referred to as "full" ascendency, since there is also an "internal" ascendency (A_i), see below.]	The product of total system throughput (T) times an index of the "average mutual information", or information content of an ecosystem. Hence, the uncommon dimension of A, which may be rendered as "flowbits" (p. 102, eq. 6.9).
Development capacity (C) [or "full" development capacity, since there is also an "internal" capacity (C_I), see below	Upper bound on ascendency; the value A would take if the overheads (Φ, see below) were zero (which they cannot be, for thermodynamical reasons; see p. 105, eq. 6.16 and further below).
System overheads (Φ)	The difference between development capacity (C) and ascendency (A), or Φ = C-A; Φ is the sum of four components ($\Phi_o + \Phi_e + \Phi_s + \Phi_r$) defined (on p. 107, eq. 6.18 and) further below.

Index (with symbol, ftsdimension and units)	Definition and remarks with page and equation no.
Overhead on inputs (Φ_o)	The loss of flowbits due to the fact that knowledge of the input flows into an ecosystem does not provide information on the boxes from which the flows originated (because they are outside of the system). Φ_o is minimized (=0) when all inputs into a system occur via one single arrow (see p. 107-108).
Overhead on exports (Φ_e)	The loss of flowbits due to the fact that knowledge of the export flows out of an ecosystem does not provide information on the boxes to which the flow are going (because they are outside the system). Φ_e equals zero when there are no exports, or when all exports out of a system occur via one single arrow (see p. 107, eq. 6.18).
Overhead on respiration (Φ_s)	The loss of flowbits due to the fact that respiratory flows do not connect boxes, and hence, do not involve any mutual information between boxes. Hence, Φ_s increase with respiration and must always be >>0.
Overhead on redundancy (Φ_r), also called "system redundancy" (R)	The loss of flowbits due to the occurrence of multiple flows between boxes. Φ_r is minimized when only one arrow enters or leaves any one box, or when several arrows leaving one box have the same magnitude of flow. Thus, R (or Φ_r) is "a measure of the internal ambiguity of the internal connections within the system" (see pp. 107 and 114).
Internal development (C_I)	Same as development capacity, but capacity computed without considering external inputs.
Internal ascendency (A_I)	Same as full ascendency (A, see above) but computed without considering the contribution to A of the flows related to inputs (A_O), exports (A_e) and respiration (A_s). Note that $A_I = C_I -$ (E + S + R) with E and S defined below and R = Φ_r.

Index (with symbol, ftsdimension and units)	Definition and remarks with page and equation no.
Tribute to other (E)	The sum of $\Phi_e + A_e$, i.e., of the systems contributions of the exports from a system to the overheads (Φ_e) and to Ascendency (A_e) (p. 114-115).
Dissipation (S)	The sum of Φ_s and A_s, i.e., of the contributions of respiration to the overhead of a system (Φ_s) and to its ascendency (A_s).
Ascendency/development capacity (A/C)	A measure of ecosystem network efficiency (see p. 111).

Table 3 **Definitions and symbols**

Symbol	Equations	Definitions	Dimensions
B_i	-	Biomass of group (i).	UNIT
EX_i		Exports (including catches) out of the system.	UNIT/time
DC_{ij}	$\sum_j DC_{ij} = 1$,	The fraction that prey j constitutes in predator i's food intake; DC_{ij} is weighted over species, sizes and seasons included in a box.	Dimensionless
DC (N1%,I)	DET_i/DT	Diet composition of detritus box	Dimensionless
DET_i	See Alg. (9)	Flow from group i to detritus	UNIT/time
DT	$\sum_i DET_i$ (E_q19)	Sum of all flows to detritus	UNIT/time
DIFF	TOTPP-PPROD	The difference between input total primary production (TOTPP) and calculated PPROD. DIFF should be > = 0. DIFF is assumed to be "unaccounted contribution to detritus from primary producers" and is treated as input to the detritus, not as flow from the primary producers to the detritus.	UNIT/time
DTPP	$\sum_{i(QB_i=0)} DET_i$	Sum of all flows to detritus from producers	UNIT/time
Ecosystem		A system where input balances output, and where TRPUT > EXPORT + IMPORT	
EE_i	(Algorithm 2), $EE_i*P_i = EX_i+M2_i$	Ecotrophic Efficiency is that part of production that goes to predation and catches (including exports).	
GE_i	PB_i/QB_i	Gross efficiency (of food conversion).	
Group (box)	Equation (7)	See "The energy balance of a box"	
GS		Egestion. A required input; the default value used is 15% for all consumers (Winberg 1956). Egesta go to the detritus.	%, dimensionless

Symbol	Equations	Definitions	Dimensions
I_{ij}	$(DC_{ij} - \frac{B_j}{\sum_j B_j}) / (DC_{ij} + \frac{B_j}{\sum_j B_j})$	Ivlev's Electivity Index (Ivlev 1961)	dimensionless
$M2_i$	$\sum_j B_j QB_j DC_{ji}$	Predation mortality of (i)	UNIT/time
N		Number of boxes.	dimensionless
N1	N + 1	Number of boxes when detrivores are included.	dimensionless
NE	P/(Q-(XC+GS)/100)	Net efficiency	dimensionless
OI	(Equation 18)	Omnivvory index	dimensionless
PARTM2	$M2_i - B_i QB_i DC_{ii}$ (Equation 10)	Partial predation mortality of (i)	UNIT/time
PB_i	(Equation 8)	Production/biomass ratio of (i).	UNIT/time
P_i	$B_i * PB_i$	Production rate of (i).	UNIT/time
PPROD	$\sum_{(QB_j=0)} B_j PB_j$	Calculated total primary production.	UNIT/time
Producers	$QB_i = 0$	All groups for which consumption (QB) is zero.	
QB_i	(Equation 12)	Consumption/biomass ratio of (i). QB is >0 for producers.	1/time
Q_i	$B_i * QB_i$	Consumption rate of (i).	UNIT/time
TOTPP	TOTPP ≥ PPROD	Total net primary production of all producers. TOTPP is a required input.	
TRPUT	Algorithm 11	Total system throughput, i.e., the sum of all production, catches in- and exports, respiratory flows and flows to the detritus	UNIT/year
$TTLX_i$	Algorithms 6 and 7	Trophic level of (i)	

Symbol	Equations	Definitions	Dimensions
UNIT		Units used for masses/energy; the units are only for display.	
XC		Excretion. A required input. The default values used is 5% of consumption for all consumers (Winberg 1956). Excreta go to the detritus.	%

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