

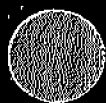
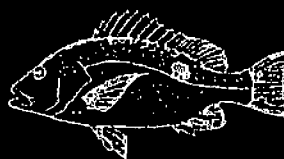
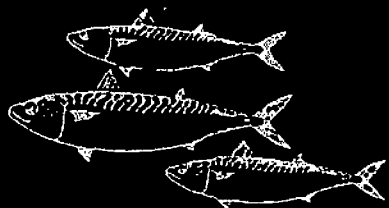
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A GUIDE TO THE ECOPATH II SOFTWARE SYSTEM (VERSION 2.1)

Villy Christensen

and

Daniel Pauly



IICLARM

MANILA, PHILIPPINES



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A GUIDE TO THE ECOPATH II SOFTWARE SYSTEM (VERSION 2.1)

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Villy Christensen

and

Daniel Pauly

SOFTWARE 6

INTERNATIONAL CENTER FOR LIVING AQUATIC RESOURCES MANAGEMENT
MANILA, PHILIPPINES

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**A guide to the ECOPATH II
software system (version 2.1)** MAY 19 1997

V. CHRISTENSEN
D. PAULY

Reprinted February 1993

Published by the International Center for Living
Aquatic Resources Management
MC P.O. Box 2631, Makati
Metro Manila 0718, Philippines

Christensen, V. and D. Pauly. 1992. A guide to the ECOPATH II
software system (version 2.1). ICLARM Software 6, 72 p.
International Center for Living Aquatic Resources Management
Manila, Philippines.

Cover : Selected organisms from the Bolinao reef ecosystem,
Northern Luzon, Philippines (Drawing by O. Espiritu).

ISSN 0116-6964

ICLARM Contribution No. 637

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No fish is an island...

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Christensen, V. and D. Pauly. 1992. A guide to the ECOPATH II software system (version 2.1). ICLARM Software 6, 72 p. International Center for Living Aquatic Resources Management, Manila, Philippines.

ABSTRACT

This guide documents the use and background of the ECOPATH II software system written for MS DOS computers for straightforward construction and parametrization of steady-state trophic models of aquatic ecosystems.

ECOPATH II is structured around a system of linear equations initially proposed by J.J. Polovina and coworkers, and also incorporates routines from the computation of several maturity and network flow indices proposed by various theoretical ecologists, notably E.P. Odum and R.E. Ulanowicz.

2. INTRODUCTION

The software described in the present guide is designed to help you construct a simple model of an aquatic ecosystem.

The word "model" has several meanings; for scientists, and more specifically for biologists working at the ecosystem level, "models" may be defined as *consistent* descriptions, emphasizing certain aspects of the system investigated, as required to *understand* their function.

Thus, models may consist of a text ("word models") or a graph showing the interrelationships of various components of a system. Models may also consist of equations, whose parameters describe "states" (the elements included in the models) and "rates" (of growth, mortality, food consumption, etc.), of the elements of the model.

The behavior of mathematical models is difficult (often impossible) to explore without computers. This is especially the case for "simulation models", i.e., those representations of ecosystems which follow, through time, the interactive behavior of the (major) components of an ecosystem.

Simulation models are difficult to build, and even more difficult to get to realistically simulate the behavior of a system over a long period of time, without "crashing". This is one reason why most aquatic biologists shy away from constructing such models, or even interacting with "modellers" (who, often being nonbiologists, may have scant knowledge of the intricate interactions between living organisms).

However, "modelling" does not necessarily imply "*simulation* modelling".

There are various ways of constructing quantitative models of ecosystems which avoid the intricacies of simulation modelling, yet still give most of the benefits of fully-fledged modelling, *viz*:

- (i) requiring the biologist/ecologist to review and standardize all available data on a given ecosystem, and identify information gaps;
- (ii) requiring the would-be modeller to identify estimates (of states, or rates) that are mutually incompatible, and which would prevent the system from running, (e.g., prey productions that are lower than assumed food requirements of predators);
- (iii) requiring the same would-be modeller to interact with specialities other than her/his own, e.g., a plankton specialist will have to either cooperate with fish biologists and other colleagues working on various consumer groups, or at least read the literature they produce.

To avail of these and other related advantages without having to get involved in simulation modelling, one's models can be limited to describing "average" (or "steady-state") states and rates.

This limitation, as we shall see is not as constraining as it may appear at first sight. It is consistent with the work of most aquatic biologists, whose state and rate estimates also represent "averages", applying to a certain period (although this generally is not stated).

The approach we propose is thus to use state and rate estimates for single species in a multispecies context, to describe aquatic ecosystems in rigorous, quantitative terms, during the (arbitrary) period to which their state and rate estimates apply.

In many cases, the period considered will be one year but the state and rate estimates used for model construction may pertain to different years. Models may represent a decade or more, during which little changes have occurred.

When ecosystems have undergone massive changes, two or more models may be needed, representing the ecosystem before, (during), and after the changes. This can be illustrated by an array of models of the Peruvian upwelling ecosystem representing periods before and after the collapse of the anchoveta fishing there (Jarre et al. 1991a). Several other examples of the same can be found in Christensen and Pauly (in press).

When seasonal changes are to be emphasized, different models may be constructed for each season, or for extreme situations ("summer" vs. "winter"). As an example Baird and Ulanowicz (1989) constructed four models describing the seasons in Chesapeake Bay, and one "average" model to represent the whole year. The same idea can be applied to aquaculture situations, where a pond and its producers and consumers can be described for instance at the beginning, midpoint, and end of a growing season. Examples of this can be found in Christensen and Pauly (in press).

Judicious identification of periods long enough for sufficient data to be available, but short enough for massive changes not to have occurred, will thus solve most problems associated with lack of a time dimension in "steady-state models".

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

The implications of this marriage of two approaches (initially proposed in 1987, see Pauly et al., in press) have not all been followed up, and the present guide is not meant to remedy this situation. Rather, we shall attempt to clarify some of the terminology and operations involved with ECOPATH II modelling. This is done throughout this guide, including in the appendices, several of which present definitions of terms relevant to the interpretation of outputs of ECOPATH II.

Appendix 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 fisheries biologists. Appendix 2 presents definitions of the major ecosystem indices presented in Ulanowicz (1986). The aim of these appendices is not to replace the book from which the definitions were extracted, but hopefully, to facilitate its comprehension.

Technical details describing a number of "algorithms", in which the equations used to estimate certain parameters are presented along with relevant comments and descriptions of special cases, are given in Appendices 3 and 4.

A brief description of the ECOPATH II software has been published elsewhere (Christensen and Pauly (1992, reprints available from the authors). In addition a description in French of the ECOPATH model can be requested from ICLARM; French and Portuguese versions of the manual are under preparation.

3. THE ECOPATH II MODEL

The core routine of ECOPATH II is derived from the ECOPATH program of Polovina and Ow (1983) and Polovina (1984b, 1985).

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

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

Using the notations of Appendix 3, this can also be put as

$$P_i - B_i M_{2i} - P_i (1 - EE_i) - EX_i = 0 \quad \dots 1)$$

where: P_i is the production of (i),
 B_i is the biomass of (i),
 M_{2i} is the predation mortality of (i),
 EE_i is the Ecotrophic Efficiency of (i), $(1 - EE_i)$ is the "other mortality", and
 EX_i is the Export of (i).

Equation (1) can be re-expressed as

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

or

$$B_i PB_i EE_i - \sum_j B_j QB_j DC_{ji} - EX_i = 0 \quad \dots 2)$$

where: PB_i is the production/biomass ratio,
 QB_j is the consumption/biomass ratio, and
 DC_{ji} is the fraction of prey (i) in the average diet of predator j.

Based on (2), for a system with n groups, n linear equations can be given, in explicit terms,

$$\begin{aligned} B_1 PB_1 EE_1 - B_1 QB_1 DC_{11} - B_2 QB_2 DC_{21} - \dots - B_n QB_n DC_{n1} - EX_1 &= 0 \\ B_2 PB_2 EE_2 - B_1 QB_1 DC_{12} - B_2 QB_2 DC_{22} - \dots - B_n QB_n DC_{n2} - EX_2 &= 0 \\ &: \\ &: \\ B_n PB_n EE_n - B_1 QB_1 DC_{1n} - B_2 QB_2 DC_{2n} - \dots - B_n QB_n DC_{nn} - EX_n &= 0 \end{aligned} \quad \dots 3)$$

This system of simultaneous linear equations can be reexpressed (using some substitutions that are described in Appendix 4, Algorithm 5, as

$$\begin{aligned} a_{11} X_1 + a_{12} X_2 + \dots + a_{1m} X_m &= Q_1 \\ a_{21} X_1 + a_{22} X_2 + \dots + a_{2m} X_m &= Q_2 \\ &: \\ &: \\ a_{n1} X_1 + a_{n2} X_2 + \dots + a_{nm} X_m &= Q_n \end{aligned} \quad \dots 4)$$

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

This can be written in matrix notation as

$$[A]_{n,m} * [X]_m = [Q]_m \quad \dots 5)$$

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

$$[X]_m = [A^{-1}]_{n,m} \cdot [Q]_m \quad \dots 6)$$

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 others, the generalized inverse method provides 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 will still be output.

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 run faster, take advantage of the fact that many of the elements of the diet composition matrix are known to be zero, and use this characteristic of the trophic interactions to increase the number of parameters that can be estimated. The algorithms are described in Appendix 4.

It should be noted that there are certain requirements that must be met. Thus, generally only one of the parameters B_i , PB_i , QB_i or EE_i may be unknown. In special cases, QB_i may be unknown in

addition to one of the other parameters (see Appendix 4, Algorithm 3). Exports and diet estimates are always required.

4. ON ECOPATH II VERSION 2.1

4.1 Changes from Version 1.0 to 2.0

A major change from Version 1.0 is that the data file structure has been modified; Version 1 '.EII' files need editing before they can be used with the present version. Thus, for example, if the previous consumption/biomass ratio was QB_o , the biomass B_o , and the import IM_o , the new consumption/biomass ratio is $QB_n = ((QB_o \cdot B_o + IM_o) / B_o)$. In addition you will have to change the diet compositions of the groups with import, so that the import is reflected in the diet. If your QB estimate is from an independent source you should probably not change it, but note that you may have had a bias in the previous version.

In addition to removal of known bugs, the following new features are included in Version 2.0 and later releases,

1. It is possible to include groups for which the consumption is smaller than the production (this feature is relevant to consumers that are also autotrophic such as corals or tridacnid clams).
2. It is not necessary to include primary producers (a feature important for those who want to model cave or abyssal ecosystems).
3. The detritus is strictly defined as dead matter, and hence does not have a respiration term.
4. A detritus box will by default, be, included in all model descriptions.

5. A number of new indices has been added to the parameter estimation and network programs.
6. A method proposed by R.E. Ulanowicz to allocate the throughput of the groups ("boxes") of an ecosystem into discrete trophic levels has been adopted. The routine enables calculation of trophic efficiencies by trophic level.
7. The calculation of fractional trophic level has been changed to comply with the approach adopted by the previous International Biological Program and others. Here the trophic level of producers and of detritus is defined to be 1.
8. A standardized forage ratio was included which is independent of prey abundance (in contrast to the Ivlev electivity index).
9. A method for calculating mixed trophic impacts was included. This uses the Leontief matrix, as suggested in recent publications by Hannon and Joiris (1989) and by Ulanowicz and Puccia (1990). This routine calculates direct and indirect impacts within a system, to some extent making it possible to answer "what if" questions.
10. A new routine was implemented for aggregating groups. Any specified pairs of groups can be aggregated, or the routine can be used to identify the pair of groups which, if aggregated, will lead to the smallest possible decrease in ascendancy. The aggregated dataset can subsequently be used for further aggregation and/or other analysis with other routines of ECOPATH II.
11. The program for finding cycles and pathways was improved.

4.2 New Features in Version 2.1

Here is a quick summary of the changes from Version 2.0:

Menu:	No substantial changes
<D> Data entry:	Not in Vers. 2.1, use <E> instead
<E> Edit data:	Now also used for creating new files
<H> Hard copy:	No substantial changes
<P> Parameter estimation	Substantial changes
<C> Cycles and pathways	No substantial changes
<N> Network flow indices	Substantial changes
<A> Aggregation	No substantial changes
<X> Export file	No substantial changes
<S> SCOR/ECOPATH bridge	No substantial changes

1. No changes in data file format have been made, so you can simply use Vers. 2.0 files.
2. The programs no longer manipulates the Num Lock, nor the Caps Lock keys.
3. To avoid incompatibility problems with printers, the programs no longer uses page feed.
4. Hard Disk Installation program: A new program is used for installation from one 5¼" diskette. Some bugs have been removed from the installation program for 3½" diskettes.
5. Parameter estimation program: A bug in Vers. 2.0 causing gross efficiency to be equal to net efficiency has been removed.
6. Parameter estimation program: A bug in the display of natural mortality coefficients on screen causing at most 18 groups of a system to be displayed has been removed. In addition natural mortalities may now be displayed for all files, not just for systems with catches.

7. Parameter estimation program: The calculation of trophic level has been changed to so that for strict consumers ($PP=0$), it is assumed that any import has the same trophic level as all the other preys. For producers, the import does not affect trophic levels.
8. Network flow indices program: A bug that aborted the ascendancy routine when the cycling index could not be calculated has been removed. Now, an error message is given instead.
9. Network flow indices program: The ascendancy routine has been modified to include the information content from the calculation of ascendancy.
10. Network flow indices program: Finn's mean pathlength ($\text{Throughput} / (\Sigma\text{Export} + \Sigma\text{Respiration})$), and straight-through pathlength ($\text{Throughput-Cycled} / (\Sigma\text{Export} + \Sigma\text{Respiration})$), have been included.
11. Network flow indices program: The calculation of the cycling index has been changed to include cycling through detritus, to make the calculations consistent with those described by Ulanowicz (1986, p. 63). In addition a cycling index which totally excludes detritus flows from the calculations has been included. The latter index has been termed the Predatory Cycling Index. For both indices the Finn's straight-through-pathlength is calculated.
12. Network flow indices program: The mixed trophic impact routine has been changed to include the fishery (if occurring) as a predator.
13. Network flow indices program: An inconsistency in the treatment of detritus in the mixed trophic impact routine was removed. The inconsistency affected mainly the lower trophic level.
14. Network flow indices program: For calculation of the trophic transfer efficiencies, it is now assumed that import to consumer groups has the same trophic level as other prey of the consumer. This assumption is in contrast to that made by Ulanowicz (1986) who assumed all imports to be primary production. For a mixed producer/consumer (e.g. corals, giant clams) it is assumed that all import is primary production. For a facultative producer ($PP=1$) the diet composition must sum to 0 if there is no import (i.e. $QB=0$), and to 1 if there is import ($QB>0$).
15. Network flow indices program: A bug in the trophic aggregation routine leading to inconsistencies in flow calculations for systems with imports has been removed. In addition imports have been included on the tables for this routine.
16. Network flow indices program: A bug in the trophic aggregation routine which suppressed flows on the highest trophic levels if this trophic level was not preyed upon nor exported has been removed.
17. Network flow indices program: A new routine displaying the relative distribution of flow on different trophic levels has been incorporated in the trophic aggregation routine.

18. Network flow indices program: The calculation of transfer efficiencies in the trophic aggregation routine has been changed to include catches/harvest. The transfer efficiencies are now calculated as: (predation + harvest)/ throughput.

4.3 Future upgrades

We anticipate that we will be able to maintain the ECOPATH II software for a number of years. At present the main upgrade that is planned is a new version programmed in Turbo C++. This new version (3.0) will include graphic routines and a new user interface presently under development at ICLARM as a standard for new ICLARM software. Until Version 3.0 is ready for release we intend to upgrade the present version at irregular intervals.

4.4 Copyright and liability

Neither the present software, nor any other software released by ICLARM, is copy protected or copyrighted. You may freely copy and distribute the program and the documentation as long as this is not done commercially. We would, however, appreciate to be informed when you copy the software to anyone, or if you received it from someone else; this will enable us to register you (free of charge) as a user, and thus to keep you informed of new developments, bugs, etc. At the same time, we invite you to send brief descriptions of your ecosystem models to us, possibly as submissions for publication in Naga, the ICLARM Quarterly. We look forward to a good interaction with you.

Note that we cannot guarantee the present version of ECOPATH II to be free of bugs, (nor can we take responsibility for any miscalculations that might occur). However, we have removed all known bugs. Please consult the READ.ME files for updates to this manual. Should you encounter problems or have questions, please do not hesitate to write or fax us.^{a)}

5. DEFINING THE SYSTEM

The ecosystems to model with ECOPATH II can be of nearly any kind. The modeller sets the limits. We suggest that you define a system such that the interactions within the system add up to a larger flow than the interactions between the system and the outside world. In practice, this means that the import to and export from a system should not exceed the sum of the transfer between the groups of the system. If necessary, one or more groups from outside the system should be included in order to achieve this.

The groups of a system may be (ecologically or taxonomically) related species, single species, or size/age groups. Using single species as the basic unit has clear advantages, especially as one then can use consumption and mortality rates without having to average these between species. On the other hand, averaging is straightforward and leads to unbiased estimates if one has information on all the components of the group. The input parameters of the combined groups should simply be the (weighted) means of the component parameters. Often one does not,

^{a)} ICLARM Software Project, International Center for Living Aquatic Resources Management, MC P.O. Box 2631, Makati, Manila, Philippines, Fax No: (63-2) 816-3183. E-mail: (CGNET) ICLARM.

however, have all the data needed for the weighting. If so, aim to group species that have similar sizes, growth, mortality and food compositions.

For tropical applications, grouping of species is nearly always needed: there are simply too many species for a single-species approach to be appropriate for more than a few important populations. It is difficult to give general guidelines for how to make the groupings as this is mainly a function of the modelling approach. Generally we do recommend, however, that one includes the *whole* ecosystem, i.e., detritus, phytoplankton, benthic producers, zooplankton, benthos, herbivorous fish, planktivorous fish, predatory fish, etc., and that at least 10 groups are included. But most important is the personal judgment of what is appropriate for *your* system.

Special consideration needs to be given to the detritus box. This group can be defined in several ways. One can opt to include in that box the bacteria associated with the detritus. However, unless special emphasis needs to be given to bacterial biomasses and production, it may be best to disregard the flows associated with these processes. Otherwise the bacterial flows will totally overshadow the other flows in the system. Note also that detritus is not assumed to respire in our ECOPATH II model. If bacterial processes are to be modelled explicitly, bacteria must be given their own "box".

6. THE ENERGY BALANCE OF A BOX

A box, in an ECOPATH II model, may be a group of (ecologically) related species, a single species, or a single size/age group of a given species.

In a model, the energy input and output of all living groups must be balanced, as we are only dealing with "steady-state" systems.

The basic ECOPATH equation (1) includes only the production of a box. Here production equals predation mortality + export + other mortality. When balancing the energy flow of a box, other flows should be included. Thus,

$$\text{Consumption} = \text{production} + \text{respiration} + \text{un-assimilated food} \quad \dots 7)$$

From this equation, the respiration can be estimated (see Appendix 4, algorithm 9). If the model currency is a nutrient there is no respiration, and the proportion of food that is not assimilated will be higher.

6.1 Consumption

6.1.1 Producer

Normally, ecologists separate living organisms into two large groups, the "primary producers" and the "consumers".

One can however choose to treat the "primary producers" as consumers and let these groups "consume" energy or nutrients. In ECOPATH II one can, in this case, enter a Q/B ratio for the "primary producers". When prompted in the diet

composition screen, one then enter as prey either "import" or "detritus". Or of course, if this is more appropriate, one can include the energy/nutrient sources as "primary producers", i.e., as groups with a Q/B ratio of zero. Generally, we recommend that one treats the autotrophs as producers, at least if the model currency is not a nutrient.

6.1.2 Import

Import to a system is consumption of prey that are not a part of the system. Import excludes immigration, which should be included in the production/biomass (PB) ratio.

Import is treated as a "prey" in the diet composition, and should be entered as a proportion of the total diet.

In ECOPATH II, the difference between input total primary production and calculated total primary production is treated as "import" to the detritus (see section 9.3.3).

6.2 Mortality Coefficients

In steady-state systems, each group can be represented by an average organism of an average weight. This makes it possible to use standard equations based on numbers for estimating mortality coefficients even in a regime based on weight. One such equation is

$$N_t = N_0 e^{-Zt}$$

where: N_0 is a number of organism at time = 0,

N_t is the number of survivors at time = t, and

Z is the instantaneous rate of mortality.

Under the assumption that Z_i , the mortality of group i is constant for the organisms included in i , we have for a large number of growth functions (including the von Bertalanffy Growth Function, VBGF)

$$Z_i = (\text{Production/Biomass})_i = PB_i$$

or instantaneous mortality equals total production over mean biomass (Allen 1971).

The mortality coefficient can be split into its components following a procedure well known among fisheries biologists, i.e.,

$$Z_i = PB_i = \text{other mortality} + \text{predation mortality} + \text{harvest} + \text{other exports}$$

$$\text{or } PB_i = M0_i + M2_i + F_i + E_i$$

where: PB_i is production/biomass (production includes immigration),

$M0_i$ = "other mortality". In some models, this component is split between $M1_i$, predation by other predators in the system, and $M0_i$, other mortality, caused by diseases, etc.* $M0_i$ is not entered directly but is computed from the ecotrophic efficiency, EE_i ,

$M2_i$ is the predation mortality coefficient,

F_i is the fishing mortality coefficient,

* In ECOPATH II $M1$ is not included as this kind of predation mortality should be treated as an export (included in E_i).

E_i is the coefficient for other exports, and represents the part of the mortality that is attributed to exports other than harvest, e.g., emigration out of the system, or food intake of predators that are not part of the system. Here, total export, $EX_i = F_i + E_i$.

The mortality coefficients are estimated from the following equations:

$$Z_i = PB_i$$

$$M0_i = (1 - EE_i) * PB_i$$

$$M2_i = (E_j B_j QB_j DC_{ji}) / B_i$$

$$F_i = C_i / B_i$$

$$E_i = (EX_i - C_i) / B_i$$

where: QB_j is the consumption/biomass ratio of predator j ;
 DC_{ji} is the proportion prey i constitutes to the diet of predator j ,
 B_i is the average biomass of i , and
 C_i is the catch of i

If any component of the system is harvested, a table summarizing the mortality coefficients can be obtained from ECOPATH II.

6.2.1 Immigration

The production of a system as defined here includes not only what is added due to recruitment and growth, but also the biomass added via immigration (from outside the system) to any of the groups considered.

6.2.2 Export

Export from a group consists of catches and emigration. These are entered separately, as estimates of catches and as estimates of total export.

6.2.2.1 Catches

In a model of an ecosystem exploited by a fishery, the "catches" are the total withdrawals over the time period, (e.g., a year) for each of the groups modelled. Similarly "catches" for an aquaculture system are the harvests from each group over the time period, (e.g., a growing season).

Fishery catches are normally based on landing statistics. This may cause a problem as official statistics are generally on a regional basis, not on an ecosystem basis. This can be of importance in defining the system to be modelled, either as a geographical/political region or as an ecosystem. It is necessary to consider the availability of appropriate data in such decisions.

6.2.2.2 Emigration

Emigration is rarely considered and even more rarely quantified by fisheries biologists; here, it is treated as a part of the exports. If emigration occurs, but is not included, the main effect will be that, a) if the production has been entered, a larger part of this will be directed towards the detritus, and b) if production is to be estimated, this estimate will be biased downwards.

6.2.3 Predation mortality

The predation mortality of a group (i) is the sum of the consumption of (i) by the other groups, divided by the biomass of group (i). The predation mortality is calculated in the program, i.e., it is not an input parameter. Predation mortality corresponds to what is termed "M2" in some other models.

6.2.4 Other mortality

Other mortality is the difference between total production and the sum of export and predation mortality. Other mortality is termed "M0" in some other models. Some of these other models also include a term for mortality, called "M1" which is the mortality caused by other predator groups that are not included in the system. This kind of mortality is, in ECOPATH II, a part of emigration (the prey "migrates" out of the system and may then be eaten.) This is however normally not a problem as ECOPATH II is intended to include *all* the groups that occur in the system, not just a part of them.

Other mortality consists of organisms dying due to diseases, starvation, etc., where the animals or plants concerned end up as part of the detritus. This mortality is entered in ECOPATH II as the ecotrophic efficiency (EE), i.e., as (1 - other mortality). The ecotrophic efficiency is, thus, the proportion of the production that is exported or consumed by the predators included in the system.

6.3 Respiration

Respiration includes all nonusable "model currency" that leaves an organism or a "group". If the model currency is

energy or carbon, the bulk of the food intake will end up as respiration. If, however, phosphorus or nitrogen is used as currency, all nutrients that leave an organism or a group is reutilized; in these cases respiration is nil.

Respiration is calculated in the program as the difference between the assimilated part of the consumption and the total production. For mixed producers/consumers, only the part of the production that is not attributed to primary production is subtracted. For reasons of consistency, in ECOPATH II, detritus is assumed not to respire, although it should if bacteria are included in the detritus group (which is the reason why it may be best to create a "box" for the bacteria).

The respiration of any living group (i) can be expressed as,

$$RESP_i = (1 - GS_i) \cdot Q_i - (1 - PP_i) \cdot P_i$$

where: $RESP_i$ is the respiration of group i,

GS_i is the proportion of i's consumption that is not assimilated,

Q_i is the consumption of i,

PP_i is the proportion of the production that can be attributed to primary production; if the unit is a nutrient PP_i is equal to zero in this equation, irrespective of if the group is an autotroph or not (as nutrients are not produced), and,

P_i is the total production of group i.

Respiration cannot be entered. Its value, computed internally for each box is used for checking that the estimated balance makes sense from a physiological and thermodynamical point of view.

7. PARAMETRIZATION

The data requirements for an ECOPATH II steady-state model are very limited in comparison to those for simulation models. At the same time ECOPATH II gives a summary of the available data and of the trophic flows in the system. Also, and quite importantly, ECOPATH II helps identify gaps in one's knowledge about an ecosystem. Together, this makes ECOPATH II a good starting point for ecosystem modelling. Realizing that gaps in available data may make it difficult to parametrize models, we invite users to contact us, as we may have information from the literature^{a)} or from other models that may be of use.

7.1 Consumption

Consumption is the intake of food by a group over the time period considered. It is entered as a consumption over biomass ratio, (QB). Absolute consumption computed by ECOPATH II is a flow expressed, e.g., in t km⁻² year⁻¹, while the corresponding QB is in year⁻¹.

There are various approaches for obtaining estimates of the consumption/biomass ratio (QB); we may split these into (i) analytical methods and (ii) holistic methods.

(i) The analytical methods involve estimation of ration, pertaining to one or several size/age classes, and their subsequent extrapolation to a wide range of

size/age classes, representing an age-structured population exposed to a constant or variable mortality.

The required estimates of ration are obtained from laboratory experiments, from studies of the dynamics of stomach contents in nature (Jarre et al. 1991b), or by combining laboratory and field data (Pauly 1986).

(ii) The existing holistic methods for estimation of QB are empirical regressions for prediction of QB from some easy to quantify characteristics of the animals for which the QB values are required.

One such model for finfishes is,

$$QB = 3.06 \cdot W_{\infty}^{-0.2018} \cdot T_c^{0.6121} \cdot A_r^{0.5156} \cdot 3.53 H_d$$

derived by Palomares and Pauly (1989) from 33 analytical estimates of QB, from data on marine fishes. Here,

QB is the annual food consumption/biomass ratio (in year⁻¹, not in % day⁻¹ as in Palomares and Pauly 1989)

T_c is the mean habitat temperature for the fishes in question (in °C),

W_∞ is the asymptotic (or maximum) weight of these same fishes (wet weight, in g),

A_r is the aspect ratio of their caudal fin, as defined in Exhibit 7.1, and

H_d is the food type (0 for carnivores and 1 for herbivores and detritivores).

^{a)} An excellent source of ecological parameters is the 'Handbook of Ecological Parameters and Ecotoxicology' edited by S.E. Jørgensen, S.N. Nielsen and L. Jørgensen. This handbook gives estimates for some 55,000 parameters, and is published by Elsevier, Amsterdam.

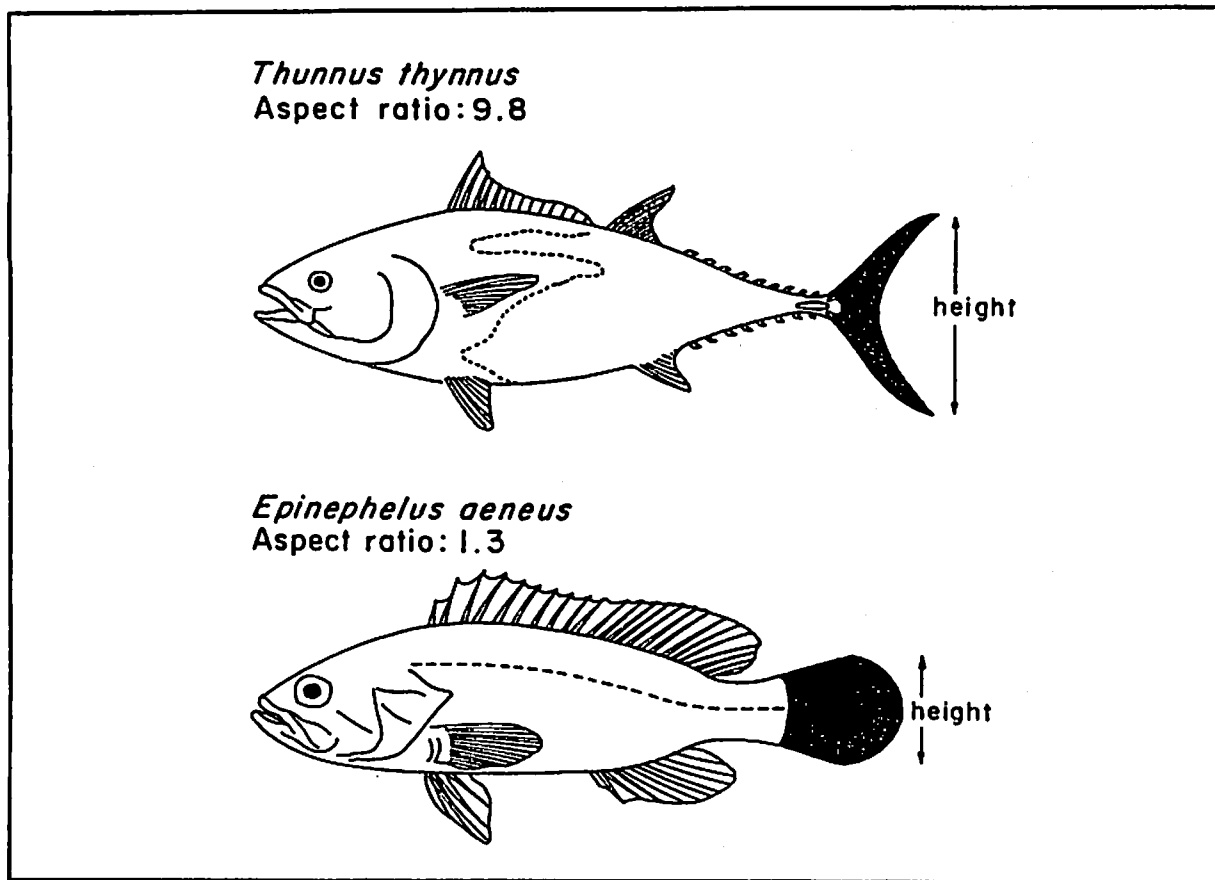


Exhibit 7.1. Schematic representation of method to estimate the aspect ratio ($= h^2/s$) of the caudal fin of fish, given height (h) and surface area (s , in black).

This relationship can be used only for fish groups which use the caudal fin as the (main) organ of propulsion. As a general approach, one can use the model

$$QB = 10^{6.37 + 0.0313T_k} \cdot W_\infty^{-0.168} \cdot 1.38P_f \cdot 1.89H_d$$

derived by Pauly et al. (1990)^{a)} from 73 estimates of QB used in various models. Here

QB, W_∞ and H_d are as defined above,

T_k is a convenient expression for mean annual habitat temperature, suggested by Regier et al. (1990), i.e. $TK = 1000/(T^\circ C + 273.1)$, and P_f is 1 for apex and/or pelagic predators and/or zooplankton feeders, and 0 for other feeding types.

^{a)} The version of the equation above published in that paper included an error, corrected here.

7.2 Production

Production refers to the elaboration of tissue (whether it survives or not) by a group over the period considered, expressed in whatever currency has been selected. Total mortality, when constant and defined as in (6.2) above, is equal to production over biomass. Therefore, it is safe to use estimates of total mortality (Z) as input values for the production over biomass ratio (PB) in ECOPATH II models.

Total mortalities can be estimated from linearized catch curves, i.e., from catch composition data. The estimation can be carried out using an appropriate system for analysis, such as LFSA (Sparre 1987) or the Compleat ELEFAN (Gayaniilo et al. 1989; Pauly 1990).

Production rate is the sum of natural mortality ($M = M_0 + M_2$) and fishing mortality (F), that is $Z = M + F$. In the absence of catch-at-age data from an unexploited population, natural mortality for finfish can be estimated from an empirical relationship (Pauly 1980) linking M and two parameters of the von Bertalanffy Growth Function (VBGF), i.e.,

$$M = K^{0.65} \cdot L_{\infty}^{-0.279} \cdot T_c^{0.463}$$

where: M is the natural mortality (year⁻¹),
 K is the curvature parameter of the VBGF (year⁻¹),
 L_{∞} is the asymptotic length (total length, cm), and
 T_c is the mean environmental temperature, in °C .

In a steady-state situation, fishing mortality can be estimated directly from the catches:

$$\text{Fishing mortality} = \text{catch} / \text{biomass}$$

where the catch is a rate, (e.g., t km⁻² year⁻¹), the biomass lacks a time dimension, (e.g., is expressed as t km⁻²), and thus the fishing mortality is an instantaneous rate, (e.g., year⁻¹).

7.3 Predation

No fish is an island. In a trophic model such as constructed by ECOPATH II, it is predation that links the groups in a system together. Thus, what is consumption for one group is mortality for another. Therefore, information on predation is important for understanding the dynamics of ecosystems. Unfortunately information on diet composition is sparse - fish population dynamics has traditionally treated fish populations as if they were isolated. Further, much of the available information on diet compositions is expressed on a "per cent occurrence" basis or as "dominance," both of which are of little use for quantification of diets. What are needed are measures based on weights or volumes, not on numbers.

For the ECOPATH II model, the diet compositions should be expressed as the proportion (weight or volume) each prey constitutes to the overall diet. The same holds true for other multispecies models where the diet is not estimated from size and suitability distributions.

A warning about zero order cycles ("cannibalism"): Make sure that the preys actually belong to the group that is modelled, e.g., if the preys are juveniles or larvae of the group in question it may be more appropriate to model these in a separate group, as their dynamics, (e.g., high PB) otherwise may not be captured.

7.4 Nonassimilated food

Information of proportion of the food that is not assimilated must be entered if the currency of your model is energy related. Following Winberg (1956) we suggest the use of a default value of 20% for carnivorous fish groups if other estimates are not available. Thus, 80% of the consumption is assumed to be physiologically useful while the non-assimilated food is directed to the detritus. For herbivores, the proportion not assimilated may be considerably higher.

If the currency is a nutrient, there is no respiration costs, and the proportion of the food that is not assimilated is calculated in the program as $(1 - \text{production}/\text{consumption})$. In this case it is not possible to input the proportion of the food that is not assimilated.

7.5 Other mortality

Organisms experiencing "other mortality" end up as part of the detritus. Thus, "other mortality" is the difference between total production and the sum of export and predation mortality. Other mortality is expressed in ECOPATH II in terms of the ecotrophic efficiency (EE) which is the same as $(1 - \text{other mortality})$. Thus, EE is the proportion of the production that is exported or consumed by predators (see also section 6.2.4).

It is difficult to estimate EE independently, and we are aware of only few direct estimates. Intuitively one would expect EE to be very close to 1 for nearly all groups, diseases and starvation probably not often being direct agents of mortality. For some groups EE, may however, be

lower. It is often seen that phytoplankton simply die off in systems where blooms occur ($EE \approx 0.5$ or less), that kelps and seagrasses are hardly consumed when alive ($EE \approx 0.1$ or so), and that apex predators have very low EEs when fishing intensity is low: incidences of tunas dying and sinking have been reported from open oceans.

Ecotrophic efficiencies of 0.95, based on Ricker (1968) have been used for many groups in Polovina's original model (Polovina 1984a) and in other later models.

8. INSTALLING AND RUNNING ECOPATH II

ECOPATH II is programmed in Microsoft Basic 7.0, Professional Developers Version, and is made available with the present documentation in an executable version requiring no commercial software. It can be run on any IBM-compatible personal computer, and on Apple Macintosh computers if you have the SoftPC IBM to MAC Conversion software.^{a)}

This manual refers to version 2.1 of ECOPATH II, which consists of the following files:

- | | | |
|----|--------------|---------------------------------|
| a. | ECOPATH2.EXE | (The information screen) |
| b. | ECOMENU.EXE | (The main menu) |
| c. | ECOEDIT.EXE | (Data entry and edit) |
| d. | ECOPRINT.EXE | (Print of input data) |
| e. | ECOPAR.EXE | (Estimation of parameters) |
| f. | ECOCYCLE.EXE | (Ecosystem cycles and pathways) |
| g. | ECONET.EXE | (Network flow indices) |
| h. | ECOAGG.EXE | (Aggregation of groups) |
| i. | ECOCOMMA.EXE | (Export to spreadsheets) |
| j. | ECOSCOR.EXE | (ECOPATH/SCOR bridge) |
| k. | BRT70ENR.EXE | (System file) |
| l. | READ.ME | (Information) |
| m. | *.EII files | (Application examples) |

^{a)} SoftPC is available for various Macintosh models from Insignia Solutions Inc., 254 San Geronimo Way, Sunnyvale, CA 94806, USA.

The file named BRT70ENR.EXE is a library file that must be in the same directory as the ECOPATH II EXE files. (We distribute the BRT70ENR.EXE with permission from Microsoft Inc.).

8.1 Installation

ECOPATH II can no longer be run from the supplied 360 KB 5¼" disk, as we have opted to compress the files (thus we only need one disk). Use the install routine to uncompress the files and transfer them to two 360 KB disks. It is then necessary to transfer some of the EXE files from the disk without the BRT70ENR.EXE (no. 2) to a third disk (no. 3), and then to copy the BRT70ENR.EXE file from disk no. 1 to disk no. 2 and disk no. 3.

You will also have to have access to your data files. If you have two disk drives leave your data diskette in one of them during sessions, and always save and load your data file with the proper drive specified.

If ECOPATH II was supplied as a 720 KB 3½" disk you can run ECOPATH II from this disk without installation. Just change Directory (CD) to A:\ECOPATH (or B:\ECOPATH, if you use drive B:) and enter: <ECOPATH2>.

If you have a hard disk it is preferable to install ECOPATH II onto it. Proceed as follows:

Insert diskette no. 1 in a floppy drive and type

```
INSTALL <enter>
```

Answer the questions, and all files on the diskette will then be copied to a directory named ECOPATH on a specified drive. If the ECOPATH directory does not exist already, it will be created. If you have the ECOPATH directory from a previous version, the new ECOPATH files will be copied on top of the existing ones.

8.2 Running ECOPATH II

When ready to run the ECOPATH II program you should type (assuming that your programs have been installed on drive C:, directory C:\ECOPATH)

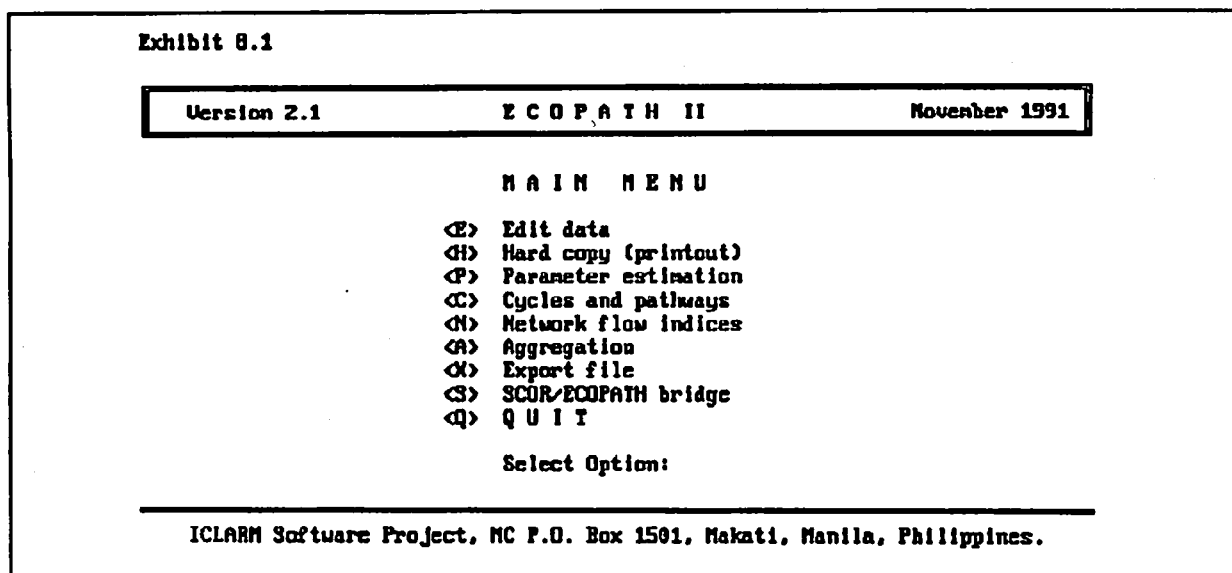
```
C: <enter>
```

```
CD C:\ECOPATH <enter>
```

then type

```
ECOPATH2 <enter>
```

You will then get an information screen, followed by the main menu of the system (Exhibit 8.1). Throughout this guide a number of Exhibits like this presents screens from ECOPATH II. Most of the exhibits will be employing data from a model of the open ocean part of the South China Sea (Pauly and Christensen, in press).



If you are running ECOPATH II from a floppy drive, you should place diskette no. 1 in the drive and, as above, type <ECOPATH2>.

If you have problems running ECOPATH II from a diskette drive you may wish to consult an experienced PC user locally, or write to us for advice. If you do the latter please describe your system, approach and problem carefully.

The main menu gives the option of selecting which of a number (p.t. 8) of separate programs to run next, see sections 9 - 17.

Note that in most cases, <F3> is used to abort the program, <F6> to list data files, <F7> to override defaults, <F9> and <return> to accept defaults and to continue to the next screen. Generally you cannot move backwards through the screens of a program. Thus, if it is necessary, abort the routine, save your data, return to the main menu, and run the program again.

On most screens where input is needed you will get help on what to enter in the lower left text box. Additionally some help

screens have been included. Where these exists it is mentioned in the lower right text box that help can be availed of by pressing the <F1> function key.

9. ENTERING THE DATA - ECOEDIT

If you want to choose the first possibility in the main menu, type

<E>

for "Edit Data". You will then get the data edits program, where you can enter data for up to 50 groups. It may be a good practice to enter only a few groups first, save, and edit the file using the edit data program again.

Notice that in addition to the group name you must enter at least two of the major input parameters (B, PB, QB and EE) before trying to save. Groups with less entries will be deleted before saving.

The first screen prompts for creation of a new file. Choose Yes or No as appropriate.

Exhibit 9.1

Edit Entry Routine for Currency

Currency unit used is : (t/km²)

Energy related units	Nutrient related units
<1> Joules : J/m ²	<7> Nitrogen : mg N/m ²
<2> Calorie : kcal/m ²	<8> Phosphorous : mg P/m ²
<3> Carbon : g/m ²	<9> Other units :
<4> Dry weight : g/m ²	
<5> Wet weight : t/km ²	
<6> Other units :	

Select currency :

Please enter model currency Note: 1 g/m ² = 1 t/km ² = 10 kg/ha	[F3]- quit [F9]- accept default & proceed
--	--

9.1 File comments

As a first entry, you can enter one line of comments about the file you are about to create. These comments will reappear, whenever you edit the file, and be printed together with the results from the other programs included in ECOPATH II.

9.2 Parameter units

The units of the parameters, i.e., the model "currency" should be entered. Units are available on two screens, one for choosing energy/nutrients, the other for selecting time units.

9.2.1 Energy-related units

A total of 6 choices are given (joules, calories, carbon, dry weight, wet weights, and "other," see Exhibit 9.1). The last of these gives the possibility of entering any unit of your choice. If one of the energy-related units is chosen, the program will calculate the respiration for all groups except the detritus.

9.2.2 Nutrient-related units

The choices for nutrient-related units are nitrogen, phosphorous and "other units". The last of these choices, provides,

again, possibility of entering any unit of your choice. For nutrient-related units, respiration will be set to zero for all groups; all nutrients are assumed to be recycled. This is not strictly correct due to interactions between nitrogen and the atmosphere. We will disregard these interactions as they are not of importance for the type of models discussed here.

9.2.3 Time units

A choice can be made between day, year, and others. The last of these offers the possibility of entering a unit of one's own choice. The screen is shown on Exhibit 9.2.

Exhibit 9.2

Time Unit Entry Routine for ECOPATH II

The time unit for this model is : year

Time units

<1> for day
 <2> for year
 <3> for others

Select time unit :

Please choose the time unit for the currency you have entered.	[F3]- quit [F9]- accept default & proceed
--	--

9.3 Detritus and total primary production

The big brown fox The next screen is for entry of detritus and total primary production (Exhibit 9.3). There will always be a detritus group included in an ECOPATH II model, whether the biomass of detritus is entered or not. If the biomass is entered, it will be possible to calculate selection indices, and these will be included in the printed output of the parameter estimation program (see section 12.8). If the biomass of detritus is not entered and detritivores are included in the system, the selection indices will be suppressed. This, however, will not influence the other analyses.

9.3.1 Detritus biomass

The approximate biomass of detritus in an aquatic ecosystem can be estimated using an empirical relationship derived by Pauly et al. (in press),

$$\log_{10}D = 0.954 \log_{10}PP + 0.863 \log_{10}E - 2.41$$

where: D is the detritus standing stock in $gC\ m^{-2}$,
PP is primary production in $gC\ m^{-2}\ year^{-1}$, and
E is the euphotic depth, in m.

For a crude approximation like this, a conversion factor of 10 g wet weight = 1 gC is suggested.

The relationship is based on a data set containing only 14 observations and explaining only 52% of their variance. However, estimates of detrital biomass obtained from this relationship may be useful for modelling ecosystems about which little is known, but for which the selection indices are of interest.

9.3.2 Detritus export and import

Enter export and import of detritus as rates, e.g., in $t\ km^{-2}\ year^{-1}$. If these are unknown, and you have no reason to assume that they are important, it may be appropriate, as a first approach, to assume zero export and import (default values).

Exhibit 9.3

Edit Screen for Detritus & Primary Production	
Enter the primary production (in $t\ km^{-2}\ year$)	
BIOMASS =	1.000
IMPORT =	0.000
(TOTPP) =	
<p>A detritus box is included in all cases. If detritivores are included the biomass should be entered or the selection indices will be suppressed. If detritivores are not included, the input on this screen can be skipped.</p>	
(If unknown enter a negative number or press ENTER)	

9.3.3 Total primary production

This entry is optional, but enter the total primary production (as t km⁻² year⁻¹) if you have an independent estimate based on e.g., C₁₄ experiments. This sort of information is readily available for many systems, such as the global maps of primary production, in FAO (1981).

In the program, the sum of the production of all groups that have been identified as primary producers will be estimated, and the difference between the entered primary production and that estimated within the model will (if positive) be treated as import to the detritus group. If the difference is negative the entered total primary production will be disregarded but a warning will be displayed. For mixed consumers/producers, only the part of the production that is attributed to primary production is included.

9.4 Entering values for basic input parameters

Data entry for a given ecosystem is distributed over several program screens. The required entries are described further below. Generally, leaving an input blank implies it is unknown. This can also be made explicit by entering a negative value. For some parameters that must be entered (e.g., exports), defaults (usually of zero) are supplied; skipping over these means accepting the default values.

It is necessary to use the <enter> key to indicate that an input has been made. One cannot exit an input box with the arrow keys as in spreadsheets.

9.4.1 Naming the groups/species

In this field (Exhibit 9.4) you can enter up to 15 alphanumeric characters. A name that is descriptive of the group should be chosen. Note that if this field is left blank, the program will delete all entries for the group before saving the input.

Exhibit 9.4

Edit Data Routine of ECOPATH II							page 1
Group name	PP	Export	Biomass	PB	QB	EE	GE.
1. Apex predators	0.00	0.050	0.050	1.200	15.000		
2. Epipelagic nect	0.00	0.000	0.500	2.000	9.300		
3. Mesopelagics	0.00	0.000	2.600	0.600	2.900		
4. Bathypelagics	0.00	0.000	0.020	0.100	0.400		
5. Benthic fish	0.00	0.000	1.500	0.075	0.300		
6. Benthos	0.00	0.000	5.000	0.100	0.400		
7. Zooplankt. large	0.00	0.000	10.000	0.500	2.500		
8. Phytoplankton	1.00	0.000	1.000	400.000	0.000		
9. MicroZooplankt.	0.00	0.000	2.500	20.000	96.000		
10.	0.00	0.000					

Please enter group name	[F3]-quit	[F7]-prev. page
	[F8]-next page	[F9]-done
	[F2]-↑ [F4]-↓	[F5]-← [F6]-→

Detritus should not, and indeed must *not* be entered as a named group. This group is included by default, and will always appear on subsequent screens and in subsequent programs as the last group of the system.

Further, a group name starting with "Detritu" should not be used as this would confuse things.

9.4.2 *Producer, consumer or both?*

A group can be a producer and a consumer at the same time; examples are corals and tridacnid clams, which host symbiotic algae. Therefore it is not (as in ECOPATH II Ver. 1.0) sufficient to check whether the consumption is zero to decide if a group is a consumer or not. We have consequently included a variable titled "PP?" (see Exhibit 9.4) where 0 should be entered if the group is a consumer only, 1 if it is a facultative primary producer, and a value between 0 and 1 if it is a mixed consumer/producer. The value represents the proportion of the production that is due to primary production.

9.4.3 *Exports include catch or harvest*

Export should be entered in this column using appropriate units (e.g., t km⁻² year⁻¹). Export estimates must always be entered; the default values are zero, and omitting entry means accepting these defaults. All catches and harvests should be included under exports. In addition, emigration can be included (see the discussion in section 6.2.2).

9.4.4 *Total biomass*

The biomass of a group is assumed to be constant for the period covered by the model, i.e. it is assumed that an average

biomass can be used as representative for the biomass of each group (this applies even if the biomasses do change during the time period modelled). Appropriate units should be used, (e.g., t km⁻²) for the biomasses. Entry of biomass is optional. However, if biomasses are unknown for *all* groups and there are no exports from any of the groups, it is necessary to enter at least one estimate of biomass, preferably of a top predator.

9.4.5 *PB - the production/biomass ratio*

Enter the PB ratio for each group using consistent units, (e.g., year⁻¹). Entry of PB ratios is optional. Production itself is described in more detail in section 7.2.

9.4.6 *QB - the consumption/biomass ratio*

Consumption/biomass ratios are entered using the same units as for PB. Entry of consumption/biomass ratios is optional. Consumption is described in sections 6.1 and 7.1

9.4.7 *EE - the ecotrophic efficiency*

The ecotrophic efficiency (EE) is a measure of what is not "other mortality"; it is the part of the production that is either passed up the trophic foodweb or exported. Ecotrophic efficiency is difficult to measure directly; it varies between 0 and 1, and can be expected to approach 1 for most groups (see section 7.5). EE has no unit, and the entry of EE is optional.

9.4.8 *GE - the food conversion efficiency*

The (gross) food conversion efficiency (GE) is the ratio between production and consumption and is thus a parameter

without units. The entry of a GE is optional and not even possible if both QB and PB have been entered. In cases when, e.g., PB and a GE are entered, the parameter estimation program will estimate QB. If a QB value is entered for the same model in a subsequent editing session, the program will check if the GE value is consistent with the PB and QB values, and display a warning if not.

In normal cases, the GE will be in the range 0.1 to 0.3, as the consumption of most groups is about 3-10 times higher than their production. This is tested in ECOPATH II and warnings are given if production exceeds consumption (as it may for corals and giant clams), or if the production exceeds half the consumption (which may be acceptable for bacteria, small nauplii and small larvae but usually not for other groups).

9.4.9 The harvest screen

The harvests or catches should be entered on the next screen (Exhibit 9.5). The harvests are in the same units as the

other flows in the system (e.g., t km⁻² year⁻¹). Harvest data must always be entered; the default values are zero, and omitting their entry means accepting the defaults.

If the harvest of a group exceeds the export given on the previous screen, or if exports are entered but the harvests are omitted, warning messages will be displayed.

The harvests on this screen are only used for calculating the "efficiency of the fishery", i.e., the ratio between total catch and the total primary production.

9.4.10 Nonassimilated food

A part of the food consumed by any consumer group is always excreted as urine and feces and is not used by the organism. This nonassimilated food has only been quantified for few aquatic organisms of interest to fisheries biologists and we recommend the use of the default value of 20% if no other estimate is available (see section 7.4).

Exhibit 9.5

Edit Entry Routine for Harvests

Please enter the harvests, e.g. fishery catches, by group:

Harvests	
1.	0.050
2.	0.000
3.	0.000
4.	0.000
5.	0.000
6.	0.000
7.	0.000
8.	0.000
9.	0.000
10.	0.000

Cursor position

Group name: apex predators

[F3]-quit	[F7]-prev. page
[F8]-next page	[F9]-done
[F2]-↑	[F4]-↓
[F5]-←	[F6]-→

The parameter for nonassimilated food does not have a unit, it is entered as a percentage, ranging from 0 to 100 (Exhibit 9.6). A routine checks whether the sum of gross efficiency plus percentage of food not assimilated exceeds 100% and displays a warning if so. Then, a new and consistent percentage for the nonassimilated food

should be entered. If one does not want to change the value for non-assimilated food, it is possible to leave the screen by pressing the <F5> key repetitively. The problem will then remain and the input file should be edited (check PB, QB and GE) before parameter estimation is attempted (see section 10).

Exhibit 9.6

Edit Entry Routine for Unassimilated Food

Please enter the percentage of food that is not assimilated.

1.	20
2.	20
3.	20
4.	20
5.	20
6.	20
7.	20
8.	0
9.	20

Cursor position

Group name: Apex predators

[F3]-quit	[F7]-prev. page
[F8]-next page	[F9]-done
[F2]-↑	[F4]-↓
[F5]→	[F6]←

9.4.11 The diet composition

As discussed in section 7.3, the diet should be expressed as the proportion (on a weight or volume basis) each prey contributes to the diet. Import to a group is considered to be consumption (while immigration is production) and should be entered as a "prey" in the diet composition.

All diet composition screens will have a prey group with the code "IM" and the name "Import". Here the proportion of the food that is imported can be entered (Exhibit 9.7). The "DE" (or "Detritus") is for entering the part of consumption that comes from detritus.

Exhibit 9.7

Edit Entry Routine for Diet Composition

Diet composition of (1) Apex predators

DIET

1.	0.0000
2.	0.7500
3.	0.1500
4.	0.0000
5.	0.0000
6.	0.0000
7.	0.1000
8.	0.0000
9.	0.0000
DE.	0.0000
IM.	0.0000

Cursor position

Sum =

[F3]-quit	[F7]-prev. page
[F8]-next page	[F9]-done
[F2]-↑	[F4]-↓
[F5]→	[F6]←

Group name: Apex predators

The diet composition needs to sum to 1 before this screen can be left. A counter displays the current sum of the food composition for guidance. Use <F9> when the diet compositions have all been entered, and proceed to the save routine.

9.5 On the need for input parameters

All parameters used to construct a model need not be entered. ECOPATH II "links" the production of each group with the consumption of all groups, and uses the linkages to estimate missing parameters, based on the notion in equation (1) that production from any of the groups has to end somewhere else in the system. This can be expressed as,

$$\text{Production} = \text{Export} + \text{Predation Mortality} + \text{Other Mortality},$$

where the predation mortality term is the parameter that links the groups together. ECOPATH balances the system using one production equation for each group in the system. For a system with three groups three production equations like the one above are used, i.e.,

$$P_1 = EX_1 + B_1 \cdot QB_1 \cdot DC_{11} + B_2 \cdot QB_2 \cdot DC_{21} + B_3 \cdot QB_3 \cdot DC_{31} + B_1 \cdot PB_1 \cdot (1 - EE_1)$$

$$P_2 = EX_2 + B_1 \cdot QB_1 \cdot DC_{12} + B_2 \cdot QB_2 \cdot DC_{22} + B_3 \cdot QB_3 \cdot DC_{32} + B_2 \cdot PB_2 \cdot (1 - EE_2)$$

$$P_3 = EX_3 + B_1 \cdot QB_1 \cdot DC_{13} + B_2 \cdot QB_2 \cdot DC_{23} + B_3 \cdot QB_3 \cdot DC_{33} + B_3 \cdot PB_3 \cdot (1 - EE_3)$$

where,

P_i is the total production of group i .

EX_i is the export of group i .

DC_{ij} is the proportion of the diet predator group i obtains from prey group j .

B_i is the biomass of group i .

QB_i is the consumption/biomass ratio of group i .

PB_i is the production/biomass ratio of group i .

EE_i is the ecotrophic efficiency, i.e. (1 - other mortality), of group i .

EX_i , and DC_{ij} must always be entered, while entry is optional for any of the other four parameters (B_i , QB_i , PB_i , EE_i). The set of linear equations can be solved even if, for any of the groups, one or more (see below) of these four parameters is/are unknown. It is not necessary that the same parameter is unknown for all groups, the program can handle any combination of unknowns. The algorithms involved in the estimation of missing parameters are described in detail in Appendix 4. A number of algorithms have been incorporated which take advantage of the fact that most entries in the diet composition matrix will be zero, to estimate more than one missing parameter for each group. In some cases it may thus be possible to estimate the value of QB in addition to B , PB , or EE of a group.

It is generally not possible to estimate the biomasses or PB of apex predators from which there is no exports.

If too many input parameters are missing when running the estimation program (section 12) a message to this effect will be displayed and the program will be aborted. In such cases, the data set will need to be complemented (see section 11).

9.6 Saving the data

Once the input data have been entered, the final operation in the data entry program is to create a file and save it (Exhibit 9.8). This is done by entering an optional drive letter, ":", and a filename following the usual DOS rules, (e.g., A:FileName). You should not include an extension name. Up to 8 characters can be used for the filename and these may include any characters except the following,

. " / \ [] | < > + = ; : ,

Moreover, DOS control codes (i.e., ASCII codes 0 through 31) are invalid.

Before entering the filename you have the option of pressing <F6>, which will give you a listing of the filenames already in the default directory on the specified drive. Notice that you can specify the drive (A: or B: or C: etc.) but not the directory of the drive, as the file will be saved in your default directory. If this is not where you want to save the file, you should change the default directory from outside ECOPATH II (e.g., C: <Enter>, cd C:\Ecopath <Enter>.)

Select a descriptive filename made up only of alphabetic and/or numeric characters. You may choose to let the last

letter of the filename be a numeric character indicating the version of the dataset you are using, e.g., ModelA1 is the first version of ModelA, and ModelA38 is the thirty-eightth version.

10. EDITING THE DATA

Upon return to the ECOPATH II main menu you select

<E> Edit Data

to load the data editing program again.

10.1 Selecting an input file

The filename of the file to be edited should be entered (without the ".EII" file extension) on the first screen to appear after you have chosen <E> Edit Data on the main menu and press <N> or <Return> to indicate that you do not want to enter a new datafile. Pressing <F6> and later the drive letter (A, or B, or C, etc.) will give you a list of all filenames in use in the default directory. Retype the filename if appropriate.

10.2 Changing parameter values

As you work your way through the screens, you may add, change or delete parameters, group names, etc.

Exhibit 9.8	
Save Routine of ECOPATH II - ECOEDIT	
Enter filename to save these data : OCEANSCS	
Please use letters (A-Z) and/or numbers only.	[F1]-redo routine [F3]-quit [F10]-change disk

10.3 Adding new groups

You can add new groups to the system by simply adding a new group name and the corresponding input parameter values. The diet composition screens etc. will automatically change to reflect the incorporation of the new group.

10.4 Deleting groups

Deleting groups is only slightly more complicated than adding new groups: a group is deleted by entering a negative value for all parameters of the group (Export, B, PB, QB, EE, and GE) that are displayed on the screen. Then, press <F9> repetitively, until you get to the 'save screen', where you save the file. Next, re-edit the file. The group will have disappeared; if not check that you actually deleted all parameters.

10.5 Saving the changes

The last screen in the edit program is the save screen. Once you reach this screen, you can save the data file by entering its file name. If, for some reason you do not want to save the changes you just entered, press <F3> to abort the edit program.

11. PRINTING THE INPUT DATA

The third option on the main menu is,

<H> Hard copy (printout).

As in the edit data program, you will have to select an input file (do not include the ".EII" file extension). A copy of the selected input file will then be directed to your default printer.

12. ESTIMATING THE MISSING PARAMETERS

Select from the main menu

<P> Parameter Estimation

to load the program which estimates missing parameters based on the assumption that the system is in a balanced or "steady" state.

12.1 Selecting an input file

The first screen in the parameter estimation program prompts for a filename. This should be entered following the guidelines given above (section 10.1).

12.2 The estimation procedure

The estimation is performed using a number of algorithms and a routine for matrix inversion described above in general terms. (Appendix 4 presents the computational aspects).

Once the parameters have been estimated by the program the system balances input and output of each group, using the respiration for adjustments. The relationship used is;

$$\text{Consumption} = \text{Production} + \text{Respiration} \\ + \text{Nonassimilated food}$$

where,

Consumption is the total consumption of a group, i.e., biomass * (consumption / biomass).

Production excludes primary production, i.e., is defined by biomass * (production / biomass) * (1 - PP), where PP is the proportion of total production that can be attributed to primary production (thus (1 - PP) = 0 in plants, 1 in heterotrophic consumers, and intermediate in corals or tridacnid clams).

Respiration is the part of the consumption that is not used for production or egestion (feces). Respiration is nonusable currency, i.e., it cannot be used by the other groups in the system. Facultative autotrophs with $QB = 0$ and detritus have zero respiration.

Nonassimilated food is an input parameter expressing the fraction of food that is not assimilated, (i.e., is excreted plus egested). For systems where the model currency is energy, the default is 20 % of consumption for all groups, though this may be most applicable for finfish groups (see section 7.4). The non-assimilated food is directed to the detritus.

If the model currency is a nutrient, then there is no respiration; instead the model is balanced so that egestion equals the difference between consumption and production.

12.3 Evaluation of an ECOPATH II run

The program estimates the missing parameters and a number of indices without further input. These results are displayed over a number of screens. You may choose to consider these one by one, or move on (pressing any key) to the print routine at the end of the program (section 12.4), and make a hard copy of parts or all of the run.

Your model will probably not look very convincing the first time you run it. Keep an eye open for warning messages while you make your way through the screens. In the more serious cases, the program will be aborted, and you will have to edit your data. To improve your chances of identifying problems, you will in some cases only get a warning and the program will continue. The following items are provided to help you evaluate the results of a run.

Exhibit 12.1

Parameter Estimation for ECOPATH II

GROUP NAME	PP	BIOMASS	P/B	Q/B	EE	GROSS EFF.
1. Apex predators	0.00	0.050	1.200	15.000	0.833	0.080
2. Epipelagic nekt	0.00	0.500	2.000	9.300	0.940	0.215
3. Mesopelagics	0.00	2.600	0.600	2.900	0.854	0.207
4. Bathypelagics	0.00	0.020	0.100	0.400	0.600	0.250
5. Benthic fish	0.00	1.500	0.075	0.300	0.600	0.250
6. Benthos	0.00	5.000	0.100	0.400	0.561	0.250
7. Zooplankt. large	0.00	10.000	0.500	2.500	0.764	0.200
8. Phytoplankton	1.00	1.000	400.000	0.000	0.626	-
9. MicroZooplankt.	0.00	2.500	20.000	96.000	0.428	0.208
10. Detritus	0.00	1.000	-	-	0.009	-

Press any key to continue ...

12.3.1 Are the EE's between 0 and 1?

When examining the output of a run, the first and perhaps most important items to consider are the ecotrophic efficiencies. The relevant values are given in the column headed "EE" (Exhibit 12.1). These values should be between 0 and 1. Here the lower bound indicates that the group is not caught nor eaten by any other group. Similarly, the upper bound indicates that the group is being heavily preyed upon and/or that the fishing pressure is high, i.e., not much dies of old age. The whole range of ecotrophic efficiencies can be found in nature. However, a few guidelines appear to have emerged from our modelling exercises. For most groups, the EE should be close to one. The exceptions are top predators and primary producers (see section 7.5 for a discussion of these).

If any of the EE values is larger than 1, something is wrong: it is not possible that more of something is eaten and/or caught than is produced. The problem can of course be due to the steady-state assumption not being met, e.g., for a new fishery on a previously unexploited stock. Unless this is known to be the case, we recommend that you have a closer look at the input parameters.

It may be worthwhile to check the food consumption of the predators, and the production estimates of the group. Compare the food intake of the predators (section 12.5.2) with the production of their prey. Most often, the diet compositions will have to be changed - often the diets are more "pointers" to, than reliable estimates of the real values.

Often "cannibalism" in the sense of within-group predation causes problems. If

a group contributes 10% or more to its own diet, this alone may result in consumption being higher than the production of the group. The solution to this is to split the group in two, with only one of the two subgroups acting as predator on the other. The smaller prey (sub)group will have a higher production rate, as production is inversely related to size.

We recommend that you make one change at a time when editing input parameters. Make that one change, rerun the parameter program for estimation of parameters, re-examine the run, and if necessary edit again the data file, etc. Continue with one change at a time until you get a run you consider acceptable. Be sure to note down *en route* what you do and why.

12.3.2 Ecotrophic efficiency of detritus

The ecotrophic efficiency, EE, of detritus is defined as the ratio between what flows out of the detritus group and what flows into the detritus group. Under steady state, this ratio should be equal to 1.

Estimates of EE of less than 1 indicate that more is entering the detritus group than is exiting. The difference is assumed to end up as accumulated detritus to be buried as sediment, i.e., as an export from the detritus group.

Estimates of EE of more than 1 for the detritus also require attention. They indicate that the primary production and/or the inputs to the lower parts of the food web are too small to support overall consumption in the system. It will be necessary to study the production and consumption of the lower parts of the food web closely.

12.3.3 Are the "efficiencies" possible?

Recall that the gross efficiency, GE, is defined as the ratio between production and consumption, (section 9.4.8.). In most cases, GE values will range from 0.1 to 0.3 but exceptions may occur (e.g. for coral reefs or small fast-growing organisms). If the GE values are unrealistic (Exhibit 12.1), check the input parameters, especially for groups whose productions have been estimated. In such cases, careful editing of the diet composition matrix of the predators of the problem groups will generally help.

12.4 Printing the results

After having examined the summary screens, you may choose to:

1. print the mortality coefficients, and/or
2. print the summary screens, and/or
3. print the diet compositions (with selection indices).

Finally, the file should be saved, as in the other programs. This is done on the final screen. The printouts are discussed further below.

12.5 Estimated parameters, indices and ratios

The parameter estimation program outputs a number of indices and ratios of parameters that can be of use for assessing the status of the overall ecosystem and of the constituent groups (Exhibits 12.3-12.5). We have only included indices which we think will become generally used. We invite users to send us suggestions on additional indices that should be considered for inclusion in future versions. Likewise, we welcome interpretations of and experiences with the present indices. If you send us a diskette with your datafile or a hard copy of the print from the parameter estimation program we will give you our comments on your model.

12.5.1 Flows to the detritus

For each group, the flow to the detritus consists of what is egested (the non-assimilated food) and those elements of the group which die of old age, diseases, etc. (the "other mortality" or 1-EE). The flow to the detritus should be positive for all groups (Exhibit 12.2). The flows are rates, expressed, e.g., in $t\ km^{-2}year^{-1}$.

Exhibit 12.2

Parameter Estimation for ECOPATH II				
GROUP NAME	EXPORT *)	CATCHES	Unassim. Food	FLOW TO DETRITUS
1. Apex predators	0.050	0.050	0.200	0.160
2. Epipelagic nekt	0.000	0.000	0.200	0.990
3. Mesopelagics	0.000	0.000	0.200	1.737
4. Bathypelagics	0.000	0.000	0.200	0.002
5. Benthic fish	0.000	0.000	0.200	0.135
6. Benthos	0.000	0.000	0.200	0.620
7. Zooplankt. large	0.000	0.000	0.200	6.170
8. Phytoplankton	0.000	0.000	0.000	149.535
9. MicroZooplankt.	0.000	0.000	0.200	76.616
10. Detritus	233.866	0.000	0.000	0.000

*) 'Exports' refer to 'losses' to other systems and include catches.

Press any key to continue ...

12.5.2 Food intake

The food intake of a group is the product of its biomass times its consumption/biomass ratio. The food intake is a rate expressed, e.g., as $t\ km^{-2}\ year^{-1}$ (Exhibit 12.3).

12.5.3 Amounts exported or eaten

The ecotrophic efficiency, EE_i , is the part of the production ($PB_i * B_i$) of group i that is exported from or consumed by predators included in the model. Thus, $PB_i * B_i * EE_i$ is the total amount of i that is exported from or is eaten within the system. This is given in the column marked "Prod * EE" on the printout (Exhibit 12.3). The amount exported and/or eaten is a rate expressed, e.g., in $t\ km^{-2}\ year^{-1}$.

12.5.4 Net efficiency

The net food conversion efficiency is calculated as the production divided by the assimilated part of the food, i.e.,

$$\text{Net efficiency} = PB / (QB * (1 - GS))$$

where:

PB is the production/biomass ratio,
QB is the consumption/biomass
ratio, and

GS is the proportion of the food that
is not assimilated.

The net efficiency is a proportion and thus without unit (Exhibit 12.3). It is positive and, in nearly all cases, less than 1, the exceptions are groups with symbiotic algae (discussed in section 9.4.8).

12.5.5 Trophic levels

Lindeman (1942) introduced the concept of trophic levels. In ECOPATH II the trophic levels are not integers (1, 2, 3...) as proposed by Lindeman, but fractional (e.g., 1.3, 2.7, etc.) as suggested by Odum and Heald (1975). A routine assigns trophic levels (TL) of 1 to producers and detritus and a trophic level of $1 +$ [the weighted average of the preys' trophic level] to consumers.

Exhibit 12.3

Parameter Estimation for ECOPATH II

GROUP NAME	FOOD INTAKE	PROD * EE	NET EFF.	TROPHIC LEV.	OMNIV IND.
1. Apex predators	0.750	0.050	0.100	4.218	0.0432
2. Epipelagic nekt	4.650	0.940	0.269	3.275	0.3503
3. Mesopelagics	7.540	1.332	0.259	3.349	0.2316
4. Bathypelagics	0.008	0.001	0.313	2.615	0.5005
5. Benthic fish	0.450	0.068	0.313	2.672	0.4111
6. Benthos	2.000	0.280	0.313	2.053	0.0526
7. Zooplankt. large	25.000	3.822	0.250	2.600	0.2400
8. Phytoplankton	0.000	250.465	-	1.000	0.0000
9. Microzooplankt.	240.000	21.384	0.260	2.000	0.0000
10. Detritus	-	-	-	1.000	0.3061

Press any key to continue ...

Following this approach, a consumer eating 40% plants (TL = 1) and 60% herbivores (TL = 2) will have a trophic level of $1 + [0.4 * 1 + 0.6 * 2] = 2.6$. The trophic level is an index without units (Exhibit 12.3).

12.5.6 The omnivory index

The "omnivory index" was introduced in 1987 (see Pauly et al., in press), in the initial version of the ECOPATH II model. This index (OI) is calculated as the variance of the trophic level of a consumer's prey groups. We have

$$OI_i = \sum_j (TL_j - (TL_i - 1))^2 * DC_{ij}$$

where: TL_j is the trophic level of prey j ,
 TL_i is the trophic level of the predator i , and,
 DC_{ij} is the proportion prey j constitutes to the diet of predator i .

When the value of the omnivory index is zero, the consumer in question is specialized, i.e., it feeds on a single trophic level. A large value indicates that the consumer feeds on many trophic levels. The omnivory index has no units.

12.5.7 Respiration

Respiration is, in ECOPATH II, a factor used for balancing the flows between groups. Thus, it is not possible to enter respiration data. But, of course known values of the respiration of a group can be compared with the output (Exhibit 12.4), and the input parameters can be adjusted to achieve the desired respiration.

Respiration is calculated as the difference between the assimilated part of the consumption and the part of the production that is not attributable to primary production (i.e., $1 - PP$), since the assimilated food ends up as either production or respiration.

Exhibit 12.4

Parameter Estimation for ECOPATH II

GROUP NAME	RESPIRATION	ASSIMILATION	RESP/ASSIM	PROD/RESP	RESP/BIO
1. Apex predators	0.540	0.600	0.900	0.111	10.800
2. Epipelagic nekt	2.720	3.720	0.731	0.360	5.440
3. Mesopelagics	4.472	6.032	0.741	0.349	1.720
4. Bathypelagics	0.004	0.006	0.688	0.455	0.220
5. Benthic fish	0.248	0.360	0.688	0.455	0.165
6. Benthos	1.100	1.600	0.688	0.455	0.220
7. Zooplankt. large	15.000	20.000	0.750	0.333	1.500
8. Phytoplankton	0.000	-	-	-	-
9. MicroZooplankt.	142.000	192.000	0.740	0.352	56.800
10. Detritus	0.000	-	-	-	-

Press any key to continue ...

Respiration is a non-negative flow expressed, e.g., in $t\ km^{-2}\ year^{-1}$. If the currency is a nutrient, (e.g., N or P) the respiration is zero, since nutrients are not respired, but egested and recycled within the system.

12.5.8 Assimilation

The part of the food intake that is assimilated is computed for each consumer group from

$$B_i \cdot QB_i \cdot (1 - GS_i)$$

where

B_i is the biomass of group i ,
 QB_i is the consumption / biomass ratio of group i , and
 GS_i is the part of the consumption that is not assimilated.

The three values needed for the estimation are all input parameters. Assimilation is a flow expressed, e.g., in $t\ km^{-2}\ year^{-1}$ (Exhibit 12.4).

12.5.9 Respiration/assimilation

This column gives the ratio of respiration to assimilation (Exhibit 12.4). Respiration cannot exceed assimilation, so this ratio should be less than 1 (no units). For top predators, whose production is relatively low, the respiration/assimilation ratio can be expected to be close to 1, while it should be lower for organisms at lower trophic levels.

12.5.10 Production/respiration

This ratio expresses the fate of the assimilated food. Computationally, the ratio can take any positive value, though

thermodynamic constraints limit the realized range of this ratio to values lower than 1 (no units). The ratio is presented on Exhibit 12.4.

12.5.11 Respiration/biomass

This ratio can take any positive value (no units, Exhibit 12.4). It can be useful when balancing the system, if previous experience is available.

12.6 Summary statistics

A number of statistics describing the whole system have been included into ECOPATH II (Exhibit 12.5). Several of these can be of use for assessing the status of an ecosystem, e.g., to express its state of maturity *sensu* Odum (1969), Exhibit 12.6.

Exhibit 12.5	
SUMMARY STATISTICS	
Sum of all consumption	= 280.4
Sum of all exports	= 233.9
Sum of all respiratory flows	= 166.1
Sum of all flows into detritus	= 236.0
<hr/>	
Total system throughput	= 916.4
Sum of all production	= 458.2
<hr/>	
The fishery has a 'mean trophic level'	= 5.22
Its gross efficiency (catch/prim. prod.) is	= 0.0001
<hr/>	
Calculated total net primary production	= 400.0
Total primary production/total respiration	= 2.4084
Net system production	= 233.916
Total primary production/total biomass	= 17.2637
Total biomass/total throughput	= 0.025
Total biomass (excl. detritus)	= 23.170
Total catches	= 0.050
<hr/>	
Connectance Index	= 0.284
System Omnivory Index	= 0.173
<hr/>	
Press any key to continue ...	

Exhibit 12.6. A tabular model of ecological succession: trends to be expected in the development of ecosystems (from Odum 1969). The "ECOPATH II" column gives reference to the section in this guide where the attribute is discussed.

Ecosystem attributes	Developmental stages	Mature stages	ECOPATH II Reference
<i>Community energetics</i>			
1 Gross production/community respiration (P/R ratio)	Greater or less than 1	Approaches 1	12.6.3
2 Gross production/standing crop/biomass (P/B ratio)	High	Low	12.6.4
3 Biomass supported/unit energy flow (B/E ratio)	Low	High	12.6.5
4 Net community production (yield)	High	Low	12.6.6
5 Food chains	Linear predominantly grazing	Weblike, predominantly detritus	12.6.10 and 12.6.11
<i>Community structure</i>			
6 Total organic matter	Small	Large	12.6.9
7 Inorganic nutrients	Extrabiotic	Intrabiotic	
8 Species diversity-variety component	Low	High	
9 Species diversity-equitability component	Low	High	
10 Biochemical diversity	Low	High	
11 Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well organized	
<i>Life history</i>			
12 Niche specialization	Broad	Narrow	12.5.6
13 Size of organism	Small	Large	12.6.9
14 Life cycles	Short, simple	Long, complex	
<i>Nutrient cycling</i>			
15 Mineral cycles	Open	Closed	15.2
16 Nutrient exchange rate, between organisms and environment	Rapid	Slow	
17 Role of detritus in nutrient regeneration	Unimportant	Important	15.3
<i>Selection pressure</i>			
18 Growth form	For rapid growth ("r-selection")	For feedback control ("K-selection")	12.6.9
19 Production	Quantity	Quality	
<i>Overall homeostasis</i>			
20 Internal symbiosis	Undeveloped	Developed	
21 Nutrient conservation	Poor	Good	15.2
22 Stability (resistance to external perturbations)	Poor	Good	15.1 (Overhead)
23 Entropy	High	Low	12.6.7
24 Information	Low	High	15.1 (Ascendency)

12.6.1 Total system throughput

The total system throughput (Exhibit 12.5) is the sum of all flows in a system, expressed, e.g., in $t\ km^{-2}\ year^{-1}$. It is estimated as the sum of four components of the flows, i.e.,

$$\begin{aligned} & \text{Total consumption} \\ & + \text{Total export} \\ & + \text{Total respiration} \\ & + \text{Total flows to detritus} \\ & = \text{Total system throughput.} \end{aligned}$$

The total system throughput is seen to represent the "size of the entire system in terms of flow" (Ulanowicz 1986). As such it is an important parameter for comparisons of flow networks (see section 15). The total production is presented independently.

12.6.2 Total primary production

Two values of total net primary production may be presented (Exhibit 12.5). The first is the primary production that may have been entered independently of ECOPATH II calculations (see section 9.3.3.). The second estimate is calculated as the sum of the part of the production of all groups that can be attributed to primary production. The difference between the two estimates of primary production will (if positive) be treated as import to the detritus group. A warning (which should be considered more as an information) will be displayed on the summary screen stating that there is an unaccounted contribution to detritus. If the difference is negative another warning will be displayed. In this case the input primary production will be

disregarded, but the estimates need reconsidering. The calculated primary production should not exceed the input total primary production. Primary productions are flows expressed, e.g., in $t\ km^{-2}\ year^{-1}$.

12.6.3 System primary production/respiration

This is the ratio between total primary production (P_p) and total respiration (R) in a system. It is considered by Odum (1971) to be an important ratio for description of the "maturity" of an ecosystem. In the early developmental stages of a system, production is expected to exceed respiration, leading to a ratio greater than 1. In systems suffering from organic pollution, this ratio is expected to be less than 1. Finally, in "mature" systems, the P_p/R ratio should approach 1; the energy that is fixed is approximately balanced by the cost of maintenance. The P_p/R ratio can take any positive value and is dimensionless (Exhibit 12.5).

12.6.4 System primary production/biomass

The ratio between a system's primary production (P_p) and its total biomass (B) is expected to be a function of its maturity. For immature systems, production will exceed respiration (section 12.6.3); as a consequence, one can expect biomass to accumulate over time. This in turn will influence the system P_p/B ratio, which can be expected to diminish. The system P_p/B ratio behaves like that of individual groups: unit is $time^{-1}$ and it can take any positive value (Exhibit 12.5).

12.6.5 System biomass/throughput

The total system biomass that is supported by the available energy flow in a system can be expected to increase to a maximum for the most mature stages of a system (Odum 1971). For the estimation of this ratio, we use the total system throughput (defined in section 12.6.1) as a measure consistent with ECOPATH II as a whole (E.P. Odum used the sum of the total primary production and total system respiration). The system biomass/throughput ratio can take any positive value, and has time as unit (Exhibit 12.5).

12.6.6 Net system production

Net system production (or yield) is the difference between total primary production and total respiration. As can be inferred from the discussion in section 12.6.3, system production will be large in immature systems and close to zero in mature ones. Systems with large imports may have a negative system production. Systems production has the same unit as the flows from which it is computed, e.g., $t\ km^{-2}\ year^{-1}$.

12.6.7 System respiration/biomass

In an ecosystem, the ratio of total respiration (R) to total biomass (B) can be seen as a thermodynamic order function (Odum 1971). Odum call it the "Schrödinger ratio", after the physicist E. Schrödinger who showed that biological systems must continuously be pumping out "disorder" if they are to maintain their internal "order" in the presence of thermal vibrations. Thus, the larger the biomass, the greater the maintenance cost. Whether biological systems (individual organisms,

or ecosystems) tend to maximize the R/B ratio over evolutionary time or not is a matter of debate. The ratio has the unit of $time^{-1}$, and can take any positive value.

12.6.8 The efficiency of the fishery

Correlations between primary production and (potential) fishery yields have been presented by various authors, (see e.g., Polovina and Marten 1982). To encourage future comparative work along this line, we have added to the outputs of ECOPATH II (Exhibit 12.5) an index of the efficiency of a fishery computed as $\Sigma C/P_p$, where ΣC represents the sum of all (fisheries) catches (C) and P_p represents the total primary production. This ratio will have a wide range between different systems, with high values for systems with a fishery harvesting fish low in the food chain (e.g., upwelling fishery), and low values in systems whose fish stocks are underexploited, or where the fishery is concentrated on apex predators, (e.g., oceanic tuna fisheries).

We encourage users to include this index in their model descriptions to enable future comparative work. The index is the ratio between two flows, and is thus without unit. It is generally much lower than 1.0 (the weighted global average is about 0.0002).

12.6.9 Total system biomass and catches

These variables are simply the sums of the group biomasses of the harvests. They have the same unit as the group biomasses and catches, e.g., $t\ km^{-2}$, and $t\ km^{-2}year^{-1}$ respectively (Exhibit 12.5).

The production of a group in a system is size-specific, and it has been demonstrated that the inverse of the group production/biomass ratio is a measure of size (see e.g., in Christensen and Pauly, in press). We suggest that the same is the case on a system level, and propose to use the ratio between total biomass and total production (both given on Exhibit 12.5) as an index of the size of organisms in a system (see Exhibit 12.6). The size of an average organism will be a function of the system growth form (Exhibit 12.6), and we see these two attributes as closely correlated.

12.6.10 Connectance index

The connectance index (CI) is for a given food web, the ratio of the number of actual links to the number of possible links (Exhibit 12.5). *Feeding* on detritus (by detritivores) is included in the count, but the opposite links (i.e., detritus "feeding" on other groups) are disregarded.

The number of possible links in an ECOPATH II model can be estimated as $(N - 1)^2$.

It has been observed that the actual number of links in a foodweb is roughly proportional to the number of groups in the system (Nee 1990). Thus

$$CI \propto N/(N - 1)^2 \approx 1/(N - 1),$$

which defines a hyperbolic relationship. Odum (1971) expected food chain structure to change from linear to weblike as systems mature. Hence, we assume the connectance index to be correlated with maturity.

12.6.11 System omnivory index

The system omnivory index is a new index defined as the average omnivory

index of all consumers weighted by the logarithm of each consumer's food intake (recall that the latter is estimated as biomass times the consumption/biomass ratio). We used the logarithms as weighting factors because we expect the intake rates to be approximately log normally distributed.

The system omnivory index is a measure of how the feeding interactions are distributed between trophic levels. (See the discussion of the omnivory index, section 12.5.6, for a further description of the component omnivory indices). The idea of system omnivory index was inspired by perceived drawbacks of the connectance index. The connectance index is strongly dependent on how the groups of the system are defined. As this is quite arbitrary in aquatic systems, where interactions of nearly all groups are possible at some development stage, connectance would be close to 1 in most systems described. Moreover, a prey has the same "score" in the connectance index whether it contributes 1, 10 or 100% of its predators' diet. Both of these drawbacks are overcome by the system omnivory index. We recommend the use of the latter index to characterize the extent to which a system has weblike features.

12.7 Breakdown of mortalities

A table can be printed giving the breakdown of total mortality ($Z = PB$) into fishing mortality (F), predation mortality (M2), other exports (E), and other mortality (M0) (Exhibit 12.7). Predation mortality is further broken down, so that one can see how much each consumer group contributes to the total predation mortality of each prey group.

Exhibit 12.7

MORTALITY COEFFICIENTS (per year)

Group	Z	F	E	M0	MZ
1. Apex predators	1.20	1.00	0.00	0.20	0.00
2. Epipelagic nek	2.00	0.00	0.00	0.12	1.88
3. Mesopelagics	0.60	0.00	0.00	0.09	0.51
4. Bathypelagics	0.10	0.00	0.00	0.04	0.06
5. Benthic fish	0.08	0.00	0.00	0.03	0.05
6. Benthos	0.10	0.00	0.00	0.04	0.06
7. Zooplankt. larg	0.50	0.00	0.00	0.12	0.38
8. Phytoplankton	100.00	0.00	0.00	149.53	250.46
9. MicroZooplankt.	-	-	-	-	-

MORTALITY COEFFICIENTS (per year)

GROUP	M2 due to consumer								
	1	2	3	4	5	6	7	8	9
1. Apex predators	-	-	-	-	-	-	-	-	-
2. Epipelagic nekt	1.13	-	0.75	-	-	-	-	-	-
3. Mesopelagics	0.04	0.18	0.29	-	-	-	-	-	-
4. Bathypelagics	-	-	-	0.06	-	-	-	-	-
5. Benthic fish	-	-	-	-	0.05	-	-	-	-
6. Benthos	-	-	-	0.00	0.04	0.02	-	-	-
7. Zooplankt. large	0.01	0.19	0.19	0.00	-	-	-	-	-
8. Phytoplankton	-	0.47	-	-	-	-	10.00	-	240.00
9. MicroZooplankt.	-	0.74	1.81	-	-	-	6.00	-	-

Press any key to continue ...

Z = PB = F + E + M0 + MZ = total mortality
 F = fishing mortality; E = other exports coefficients
 M0 = other mortality; MZ = predation mortality

12.8 Selection indices

One of the most widely used indices for selection is the Ivlev electivity index, E_i (Ivlev 1961) defined as:

$$E_i = (r_i - P_i) / (r_i + P_i)$$

where r_i is the relative abundance of a prey in a predator's diet and P_i is the prey's relative abundance in the ecosystem. Note that within ECOPATH II, r_i and P_i refer to biomass, not numbers. E_i is scaled so that $E_i = -1$ corresponds to total avoidance of, $E_i = 0$ represents non-selective feeding on, and $E_i = 1$ shows exclusive feeding on a given prey i .

We have included the Ivlev electivity index because it often shows up in the literature (Exhibit 12.8). This index has, however, a major shortcoming, seriously limiting its usefulness as a selection index: as shown by several authors, e.g., Jacobs (1974), the Ivlev index is not independent of prey density.

A better approach may be to use the standardized forage ratio (S_i) as suggested by Chesson (1983). This index, independent of prey availability, is given by:

$$S_i = (r_i/P_i) / (\sum_n r_n/P_n)$$

where r_i and P_i are defined as above, and n is the number of groups in the system. The standardized forage ratio as originally presented takes values between 0 and 1, with $S_i = 0$ representing avoidance and $S_i = 1$ exclusive feeding.

As implemented in ECOPATH II (Exhibit 12.8), the forage ratio has been transformed such as to vary between -1 and 1, so that -1, 0 and 1 can be interpreted as for the Ivlev index.

13. GRAPHICAL REPRESENTATION OF FLOWS

One of the characteristics of steady state ecosystem models is that all flows and biomasses can be shown in a single graph. Some see this as a major advantage, while others, in view of the absence of a time factor and because of their arrangement of boxes and paths, feel that such models resemble cemeteries. No matter how the interpretation may be, the output should be presented in a graph to be interpretable.

Exhibit 12.8				
	(1) Diet Compo- sition	(2) Food Intake	(3) Ivlev's Elec. Index	(4) Standardized Forage Ratio
Predator : (1) Apex predators				
2. Epipelagic nekt	0.750	0.56	0.944	0.990
3. Mesopelagics	0.150	0.11	0.144	-0.488
7. Zooplankt.large	0.100	0.08	-0.624	-0.891
	-----	-----		
	1.000	0.75		
Predator : (2) Epipelagic				
3. Mesopelagics	0.100	0.47	-0.058	0.071
7. Zooplankt.large	0.400	1.86	-0.038	0.093
8. Phytoplankton	0.100	0.47	0.397	0.581
9. MicroZooplankt.	0.400	1.86	0.575	0.779
	-----	-----		
	1.000	4.65		

12.9 Saving the results

The last screen in the parameter estimation program is the save screen. Here you may enter a filename, press <F6> and a drive letter to get a list of existing filenames, or accept the displayed default filename. The file to be saved (with all estimated basic parameters) will get the filename ".RUN". Your original input data file (the ".EII" file) will not be affected by the run, and remains available for reanalysis.

13.1 The do-it-yourself approach

The present version of ECOPATH II does not contain a graphic component to draw the boxes and the flows between them (but we expect that Version 3.0 will do so). However, several commercial computer software systems can be used for drawing the graphs. We have tested two systems for designing electronic hardware (Schema II and OrCad) and found both useful. In addition to the features of simple drawing programs, these sophisticated

systems can check for inconsistencies in the connections (arrows) between groups; they have routines for grouping connecting arrows and numerous other features. The systems are, however, designed for completely different purposes, and using them is to some extent like shooting at sparrows with missiles.

Another possibility is the use of a system designed for producing organograms for organizations and similar graphs. Interactive EasyFlow is an example. They are often easy to use but may include rigid rules (such as not allowing arrows to cross) that make them difficult to use in multiflow systems. Finally, standard graphics programs such as Harvard Graphics, SlideWrite, Dr. Halo or Paintbrush can be of use; we have also had success using Borlands Quattro Pro, a spreadsheet with remarkably good drawing facilities.

13.2 Rules and recommendations

The traditional method of representing steady-state ecosystem models, usually by scattering interconnected boxes across a page, both underutilizes the potential descriptive and explanatory power of graphical representations and makes it difficult to compare different system representations.

13.2.1 Using the Y-axis

Often, trophic models are drawn such that the boxes representing organisms low in the food web are placed in the lower part of the graph, along with the plants, while the boxes representing organisms high in the food web are put higher up.

We propose to make explicit use of this mode of graphing, i.e., to plot the boxes representing the organisms of an ecosystem such that the horizontal axis of symmetry of each box is aligned with the (functional)

trophic level of the box in question (Exhibit 13.1).

13.2.2 Using the X-axis

Using trophic level as the Y-axis is not sufficient to define the relative position of the elements of a model, and two approaches may be considered for ordering the boxes along the X-axis:

(i) arranging the boxes such that they do not overlap, and/or with emphasis on some symmetry, such that the resulting graph is esthetically pleasing, or,

ii) arranging the boxes such that the arrows linking the boxes cross each other as little as possible, hence maximizing clarity of the graph.

We have tried to incorporate (i) and (ii) in the construction of Exhibit 13.1. The sizes of the boxes plotted are proportional to the logarithm of the biomass in each box. We found this trick to be particularly useful in helping to visualize the relative role and impact of the organisms in each box - something which boxes of equal sizes do not attempt, and which boxes with dimensions directly proportional to biomass fail to do as well.

We have introduced another rule of construction in Exhibit 13.1. Flows entering a box do this on the lower half of the box, while flows exiting a box do it from the upper half. Flows that enter a box can be combined, while flows that leave a box cannot branch, but can be merged with flows exiting other boxes. This ensures compatibility with shortcut circuit checks in software for electronic hardware design, and more importantly, it simplifies the flow chart. "Cannibalism" or zero-order flows can be shown as arrows originating from the top half of a box, and moving in a (semi)circle before entering the lower half.

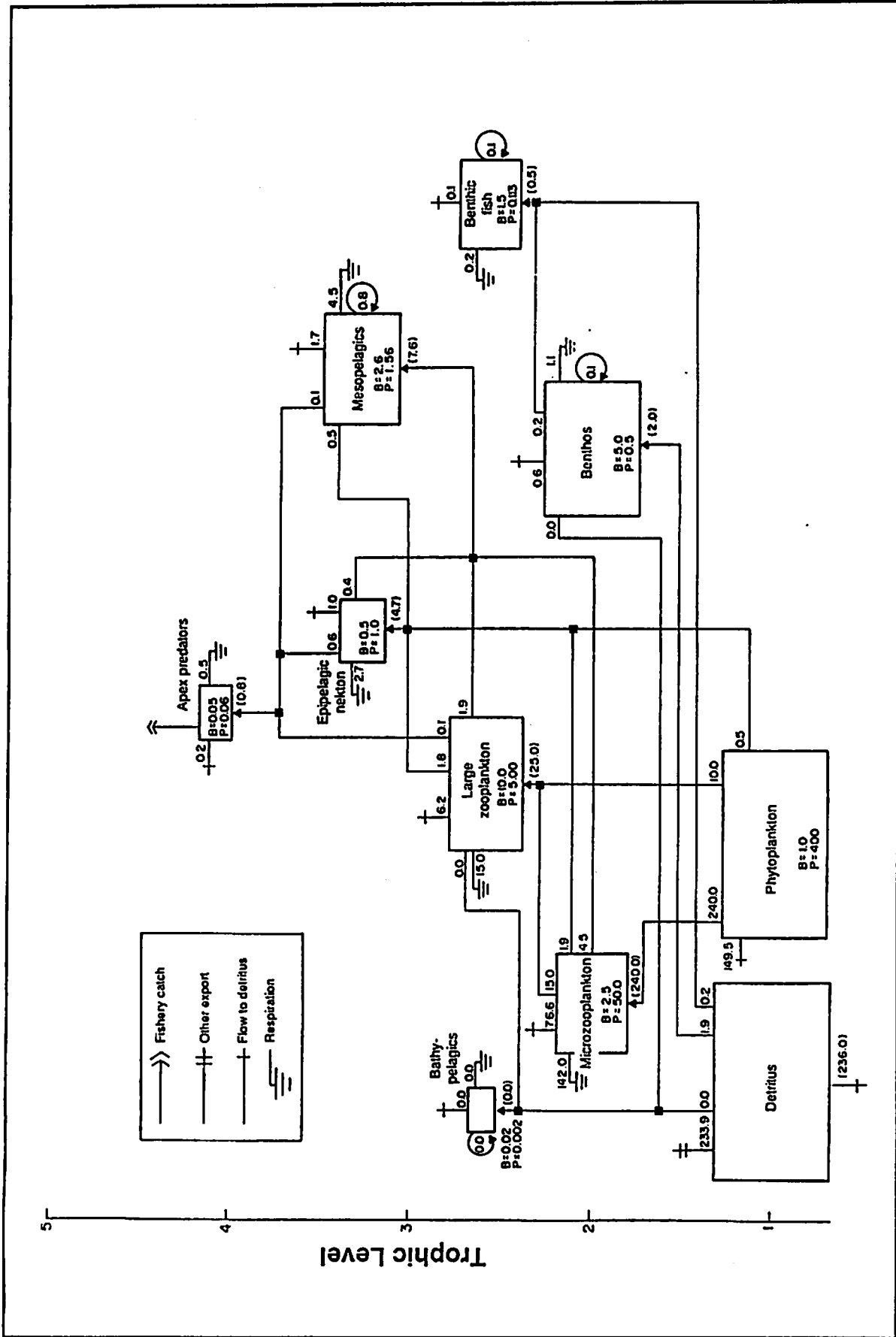


Exhibit 13.1 Flow diagram of a model of the open ocean part of the South China Sea (Pauly and Christensen, in press). Flows are expressed in tons km²year⁻¹. B indicates biomass and P production.

On the other hand, we abstain here from representing flows through arrows of different sizes (i.e. with thickness proportional to the flow) because we found that this cluttered up our models. Indeed, it is often necessary to omit, for clarity's sake, lesser flows from graphs representing highly interconnected systems.

14. CYCLES AND PATHWAYS

A routine based on an approach suggested by Ulanowicz (1986) has been implemented to describe the numerous cycles and pathways that are implied in an ecosystem.

14.1 Selecting an input file

As in other programs the first screen gives the possibility of entering a filename (or accepting the default that will be displayed if you are already in a session with a data file). You may press <F6> and a subsequent drive letter to get a list of

data files. The cycles and pathways program (ECOCYCLE.EXE) works with files describing systems whose parameters have all been estimated, i.e., with files with the extension ".RUN". You will not be able to run the cycles and pathways program before you have run the parameter estimation program (Section 12).

14.2 Printer or screen?

After the input filename has been selected, a new screen will require a choice of either screen only or paper and screen output. Make sure that your printer is on and ready if you select the latter option.

14.3 The cycles and pathways menu

The following screen (Exhibit 14.1) gives six options, five of which call different routines, while the last allows one to leave the program. The five first options are described below.

Exhibit 14.1

ECOPATH II - ECOCYCLES	
C Y C L E S - M E N U	
<1> Print all pathways from primary producer(s) to a specific consumer	
<2> Print pathways from primary producer(s) to a consumer via a selected prey	
<3> Print pathways from a selected prey to all top predators	
<4> Print all cycles in the system	
<5> Total number and mean length of all pathways from primary producers	
<6> Quit ECOCYCLE	
Select option	[F3]- quit

14.3.1 From primary producers to consumer

The first routine lists all pathways leading from all primary producers to any selected consumer. A list of all consumers in the system will be displayed (Exhibit 14.2), and one can choose from this. The program then searches through the diet

compositions, finds all the pathways from primary producers to the specified consumer, and then presents the pathways (Exhibit 14.3). A summary screen will next present the total number of pathways and the mean length of the pathways (Exhibit 14.4). The latter is calculated as the total number of trophic interactions divided by the number of pathways.

Exhibit 14.2

ECOPATH II - Cycles and Pathways

GROUP

1. Apex predators
2. Epipelagic nekt
3. Mesopelagics
4. Bathypelagics
5. Benthic fish
6. Benthos
7. Zooplankt. large
9. MicroZooplankt.

Enter consumer number :

Exhibit 14.3

Pathways leading to Apex predators (1) (cycles are excluded)

1. 1 ← 2 ← 3 ← 7 ← 8
2. 1 ← 2 ← 3 ← 7 ← 9 ← 8
3. 1 ← 2 ← 3 ← 9 ← 8
4. 1 ← 2 ← 7 ← 8
5. 1 ← 2 ← 7 ← 9 ← 8
6. 1 ← 2 ← 8
7. 1 ← 2 ← 9 ← 8
8. 1 ← 3 ← 2 ← 7 ← 8
9. 1 ← 3 ← 2 ← 7 ← 9 ← 8
10. 1 ← 3 ← 2 ← 8
11. 1 ← 3 ← 2 ← 9 ← 8
12. 1 ← 3 ← 7 ← 8
13. 1 ← 3 ← 7 ← 9 ← 8
14. 1 ← 3 ← 9 ← 8
15. 1 ← 7 ← 8
16. 1 ← 7 ← 9 ← 8

Press any key to continue ...

Exhibit 14.4

ECOPATH II - Cycles and Pathways

SUMMARY OF PATHWAYS:

Pathways leading to Apex predators (1)

Total no. of pathways = 16

Mean length of pathways = 3.50

**Mean length of pathways is calculated as total number of 'arrows'
(see previous screen) divided by number of pathways.**

Press any key continue ... **[F3]- quit**

14.3.2 From producers to consumer via a specified prey

This routine resembles the previous one, but differs from it in that one has to enter both a predator and a prey. The pathways included in the output will be those that pass to the specified predator via the prey selected. A summary screen similar to the one above will then be presented.

14.3.3 From a prey to all top predators

Here, one enters a prey group, and the program will find all pathways leading from this prey to all top predators. A summary screen then presents the total number of pathways and the mean length of the pathways.

14.3.4 All cycles

The routine will identify all cycles in the system and display these, in ascending order, starting with "zero order" cycles (cannibalism). In addition the total number and mean length of the cycles will be displayed.

14.3.5 From producers to all top predators

This routine counts the number of all pathways leading from primary producers to top predators. (These pathways will not be displayed automatically; for this purpose, use the first routine repetitively). The mean pathlength will be calculated and displayed. This mean path length is calculated as the total number of trophic links divided by the number of pathways.

14.3.6 Saving - no

The results obtained from this program cannot be saved. Rather, once a routine has been run, you will be brought back to the cycles and pathways menu. You may leave the program by entering <6> or <F3>.

15. NETWORK FLOW INDICES

The ECOPATH II software links concepts developed by theoretical ecologists, especially the theory of Ulanowicz (1986), with those used by biologists involved with fisheries and aquaculture. The following sections gives

only brief accounts of the concepts from theoretical ecology that we have included in ECOPATH II. We do not give full descriptions; for these, the user is referred to the literature cited as sources in the respective section.

15.1 Ascendency

Ascendency is a measure of the average mutual information in a system, scaled by system throughput. These quantities are derived from information theory, see Ulanowicz and Norden (1990). If one know the location of a unit of energy the uncertainty of where it will go next is reduced by an amount known as the "average mutual information",

$$I = \sum_{ij} f_{ij} Q_i \log(f_{ij} / \sum_k f_{kj} Q_k),$$

where, if T_{ij} is a measure of the energy flow from j to i , f_{ij} is the fraction of the total flow from j that is represented by T_{ij} , or,

$$f_{ij} = T_{ij} / \sum_k T_{kj}.$$

Q_i is the probability that a unit of energy passes through i , or

$$Q_i = \sum_k T_{ki} / \sum_{lm} T_{lm}.$$

Q_i is a probability and is scaled by multiplication with the total throughput of the system, T , where

$$T = \sum_{ij} T_{ij}.$$

Further

$$A = T \cdot I$$

where, it is A that is called "ascendency". The ascendency is symmetrical and will have the same value whether calculated from input or output.

There is an upper limit for the size of the ascendency. This upper limit is called the "development capacity" and is estimated from

$$C = H \cdot T,$$

where H is called the "statistical entropy", and is estimated from

$$H = - \sum_i Q_i \log Q_i.$$

The difference between the capacity and the ascendency is called "system overhead". The overheads provide limits on how much the ascendency can increase and reflect the system's "strength in reserve" from which it can draw to meet unexpected perturbations (Ulanowicz 1986). As an example, the part of the ascendency that is due to imports, A_o , can increase at the expense of the overheads due to imports, Q_o . This can be done by either diminishing the imports or by importing from a few major sources only. The first solution would imply that the system should starve, while the latter would render the system more dependent on a few sources of imports. The system thus does not benefit from reducing Q_o below a certain system-specific critical level (Ulanowicz and Norden 1990).

The ascendency, overheads and capacity can all be split into contributions from imports, internal flow, exports and dissipations (respiration). These contributions are additive and are presented on Exhibit 15.1.

Exhibit 15.1

ECOPATH II - Network Flow Indices						
Source	Ascendency		Overhead		Capacity	
	Flowbits	%	Flowbits	%	Flowbits	%
Import	0.0	0.0	0.0	0.0	0.0	0.0
Internal flow	442.3	17.6	1060.8	42.2	1503.2	59.8
Export	457.6	18.2	3.9	0.2	461.5	18.4
Respiration	283.8	11.3	263.9	10.5	547.6	21.8
Totals	1183.7	47.1	1328.6	52.9	2512.3	100.0
Total system thrupt	=		916	t/km ² /year		
Information content	=		1.292	bits		
Thruput cycled (excl detritus)	=		1.0	t/km ² /year		
Predatory cycling index	=		0.2	(% thrupt w/o detr.)		
Thruput cycled (incl detritus)	=		1.7	t/km ² /year		
Finn's cycling index	=		0.2	(% of total thrupt)		
Finn's mean path length	=		2.29	(dimensionless)		
Finn's straight-thru path length	=		2.29	(w/o detritus)		
Finn's straight-thru path length	=		2.29	(w/ detritus)		

The unit for these measures is "flowbits", or the product of flow (e.g., t km⁻² year⁻¹) and bits. Here the "bits" is an information unit corresponding to the amount of uncertainty associated with a single binary decision.

We see the overheads on imports and internal flows (redundancy) as measure of system stability *sensu* Odum (Exhibit 12.6) and the ascendency/system throughput ratio as a measure of information as included in Odum's attributes of ecosystems.

15.2 Cycling index

The "cycling index" is the fraction of an ecosystem's throughput that is recycled (Exhibit 15.1). This index, developed by Finn (1976), is expressed here as percentage of total throughput that is recycled. It was originally intended to quantify one of Odum's (1969) 24 properties of system maturity (Exhibit 12.6). However, its interpretation is apparently not as simple as E.P. Odum

conceived, with recycling increasing as a system matures. Wulff and Ulanowicz (1989) suggest that the opposite may indeed be the case. One added problem is that this index varies with the "currency" used: nutrients are recycled more than energy-related indices (such as weight).

In addition to Finn's cycling index we have included a slightly modified "predatory cycling index" which excludes cycling through the detritus.

15.3 Trophic aggregation

Apart from the a routine for calculating fractional trophic levels, we have included a routine that aggregates the entire system into discrete trophic levels *sensu* Lindeman. This routine which is based on an approach suggested by Ulanowicz (in press), reverses the routine for calculation of fractional trophic levels. Thus, for the example given previously, where a group obtains 40% of its food as a herbivore and 60% as a first-order carnivore, the relevant fractions of

the flow through the group are attributed to the herbivore level and the first consumer level (Exhibit 15.2).

The result of these analyses is presented in four tables (Exhibit 15.3), where the import (on trophic level I only), consumption by predators, export, flow to the detritus, respiration, and throughput are given by trophic levels. The throughput is the sum of the flows in the other columns. The first table presents flows originating from the primary producers, the second summarizes the flows originating from the detritus, while the third table presents the summed flow for the system as a whole.

The table with transfer efficiencies can be used for constructing a figure presenting the trophic flows in form of a pyramid (Exhibit 15.4). We have modified the traditional two-dimensional Lindeman pyramid, consisting of a number of rectangles placed on top of each other, by creating a three-dimensional pyramid.

The pyramid can be scaled so that the volume of each of the trophic level compartments is proportional to the total throughput of that level. In addition we

found it useful for various 'comparisons' to make the topangle inversely proportional to the geometric mean system transfer efficiency (see Exhibit 15.4 for examples).

Based on the three tables discussed above, the efficiency of transfer between the discrete trophic levels can be calculated as the ratio between sum of the exports and the flow that is transferred from one trophic level to the next, and the throughput on the trophic level. This is presented in a fourth table of transfer efficiencies (%) by trophic levels on Exhibit 15.3. Efficiency of detritus is not defined since detritus is non-living.

Further, we have included the ratio of total flow originating from the detritus to total flow originating from both primary producers and detritus. This ratio, which we propose as index of the importance of detritus in a system is the quantitative form of yet another of E.P. Odum's (1969) measures of ecosystem maturity (see Exhibit 12.6). The index is complementary to the proportion of the total flow that originates from the primary producers.

Exhibit 15.2

TROPHIC TRANSFORMATION MATRIX FOR FILE: e:ocean2

No.	Group	Relative flows by trophic level					
		I	II	III	IV	V	VI
1	Apex predators	-	-	0.122	0.641	0.235	0.003
2	Epipelagic nek	-	0.109	0.609	0.278	0.004	-
3	Mesopelagics	-	-	0.824	0.176	-	-
4	Bathypelagics	-	0.706	0.153	0.141	-	-
5	Benthic fish	-	0.529	0.471	-	-	-
6	Benthos	-	1.000	-	-	-	-
7	Zooplank. larg	-	0.400	0.600	-	-	-
8	Phytoplankton	1.000	-	-	-	-	-
9	Microzooplankt	-	1.000	-	-	-	-
10	Detritus	1.000	-	-	-	-	-

15.4 Mixed trophic impacts

Leontief (1951) developed a method to reveal the direct and indirect interactions in the economy of the USA, using what has since been called the Leontief matrix. This matrix was introduced to ecology by Hannon (1973) and Hannon and Joiris (1989). Using this method, it becomes possible to assess the effect that changes

the biomass of a group will have on the biomass of the other groups in a system. Ulanowicz and Puccia (1990) developed a similar approach, and a routine based on their method has been implemented in the ECOPATH II system. An example of the use of mixed trophic impacts is given in Exhibit 15.5 for the South China Sea open ocean ecosystem.

Exhibit 15.3

FLOWS ORIGINATING FROM THE PRIMARY PRODUCERS							
TROPHIC LEVEL	IMPORT	CONSUMED BY PREDAT.	EXPORT	FLOW TO DETRITUS	RESPIRATION	THROUGH-PUT	
I	0.000	250.465	0.000	149.595	0.000	400.000	
II		22.974	0.000	79.195	148.296	250.465	
III		2.801	0.006	5.760	14.407	22.974	
IV		0.192	0.032	0.685	1.892	2.801	
V		0.002	0.012	0.041	0.137	0.192	
VI		0.000	0.000	0.000	0.001	0.002	
VII		0.000	0.000	0.000	0.000	0.000	
FLOWS ORIGINATING FROM THE DETRITUS							
I	0.000	2.107	239.866	0.000	0.000	235.973	
II		0.180	0.000	0.693	1.234	2.107	
III		0.000	0.000	0.064	0.117	0.180	
IV		0.000	0.000	0.000	0.000	0.000	
V		0.000	0.000	0.000	0.000	0.000	
VI		0.000	0.000	0.000	0.000	0.000	
VII		0.000	0.000	0.000	0.000	0.000	
VIII		0.000	0.000	0.000	0.000	0.000	
FLOWS ALL COMBINED							
TROPHIC LEVEL	IMPORT	CONSUMED BY PREDAT.	EXPORT	FLOW TO DETRITUS	RESPIRATION	THROUGH-PUT	
I	0.000	252.572	239.866	149.595	0.000	635.973	
II		23.154	0.000	79.888	149.530	252.572	
III		2.801	0.006	5.824	14.523	23.154	
IV		0.192	0.032	0.685	1.892	2.801	
V		0.002	0.012	0.041	0.137	0.192	
VI		0.000	0.000	0.000	0.001	0.002	
VII		0.000	0.000	0.000	0.000	0.000	
Sum						914.695	
Amount extracted to break cycles						1.677	
Total throughput						916.371	
TRANSFER EFFICIENCIES (%) BY TROPHIC LEVEL							
SOURCE	I	II	III	IV	V	VI	VII
Producers	-	9.2	12.2	8.0	7.2	6.7	
Detritus	-	8.6					
All flows	-	9.2	12.1	8.0	7.2	6.7	

Proportion of total flow originating from detritus: 0.26

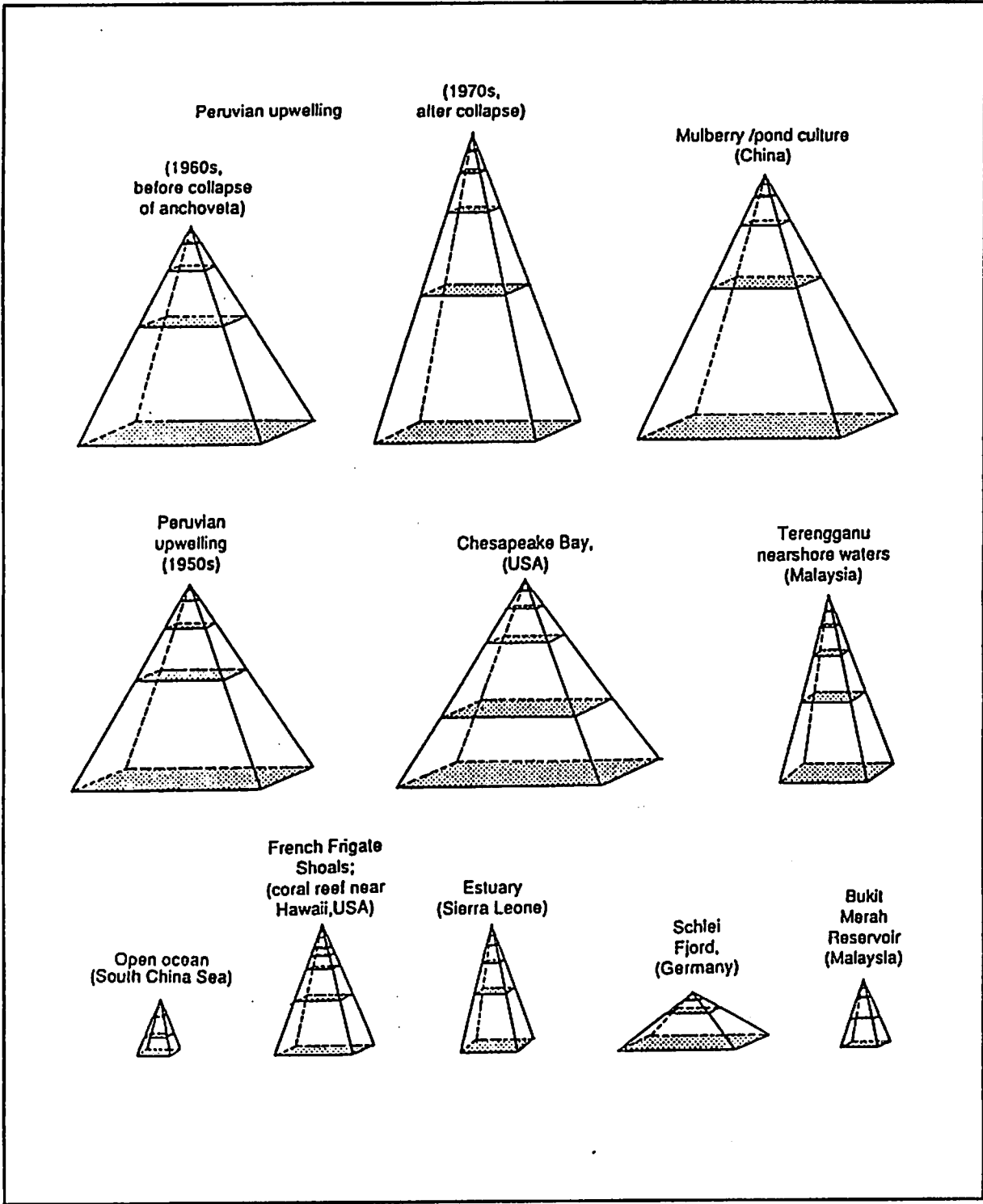


Exhibit 15.4. Trophic pyramid of flows in various ecosystems. The volume of each discrete trophic level is proportional to the throughput (total flow) at the level. The top angle is inversely proportional to the mean system transfer efficiency. The bottom compartment represent herbivory (trophic level II) in all cases.

Exhibit 15.5 shows the direct and indirect impact the group mentioned to the left of the histograms has on the other groups mentioned above the histograms. Positive impacts are indicated by the bars pointing upwards, while the bars pointing downwards shows negative impacts. The bars should not be interpreted in an absolute sense; the impacts are relative, but comparable between groups.

For the example in Exhibit 15.5 the apex predators will have a negative impact on the preferred prey, the epipelagic nekton, and an indirect, slight positive impact on the prey of the prey, the larger zooplankton. The impact on the zooplankton is positive even though the large zooplankton feeds on zooplankton directly. This is because the predation pressure from the epipelagics will be lessened (they suffer heavier predation), and this overrules the direct impact.

The phytoplankton is seen to have a positive impact on all other groups in the system; not surprisingly the impact is seen to be greatest on the microzooplankton and the zooplankton. In contrary the impact of the bathypelagics is negligible on all other groups in the system, as the bathypelagics are too scarce to be of quantitative importance in the system.

Most groups have a negative impact on themselves, reflecting increased within-group competition for resources. Exceptions exists: if a group cannibalizes itself (0-order cycle) the impact may be positive.

The mixed trophic impact routine can also be regarded as a form of an "ordinary" sensitivity analysis (Majkowski 1982). Thus, in this case, it can be concluded, e.g., that the impact of the bathypelagics on any other group is negligible. This can be seen to indicate that one need not allocate much effort in getting better parameters for this group, it may be better to concentrate on other groups.

It can also be concluded for the zooplankton that the production estimate is sensitive to variation in the production estimates of phytoplankton, microzooplankton, and to a lesser extent of apex predators. Further it is sensitive to changes in the consumption estimates (i.e. in consumption/biomass ratios and in biomass) of mesopelagics and epipelagic nekton.

One should therefore regard the impact routine as a tool for indicating the possible impact of direct and indirect interactions (including competition) in a steady-state system, not as an instrument for making predictions.

15.4.1 Graphical representation

A simple routine has been included for CGA/VGA graphic cards which presents the mixed trophic impact of changes of a single group in graphical form. This routine can be activated after the mixed trophic impact calculations have been performed. This routine does not produce hard copies of these graphs.

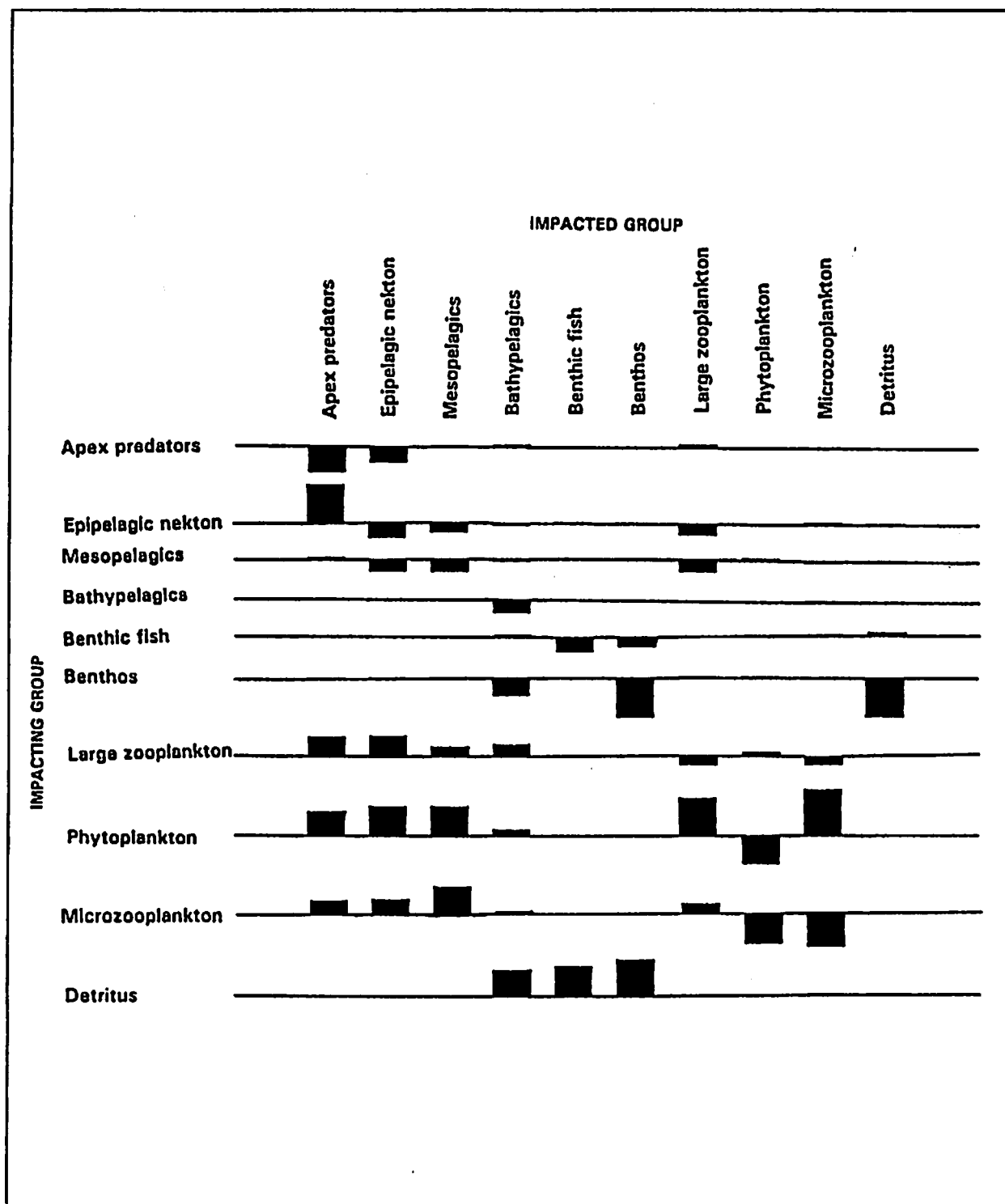


Exhibit 15.5 Mixed trophic impacts in the South China Sea open ocean ecosystem (Pauly and Christensen, in press). The figure shows the direct and indirect impacts on the living groups in the system that would result from an increase in the biomass of the groups given at the left. Positive impacts are shown above the base line, negative below. The impacts are relative, but comparable between groups.

15.4.2 Hard copy

The numerical results of the mixed trophic impact routine can be printed using the appropriate print routine. The impacts will be shown as positive and negative numbers, which can be compared between groups (Exhibit 15.6). The numbers cannot be interpreted in some absolute sense, but their graphical representation (Exhibit 15.5) still allows qualitative inferences as discussed above.

15.5 Saving

Some of the results from the network flow indices program can be saved using the last screen of the program (the others will be recalculated when needed in other programs). An extension name should not be included; the data file will be saved with the same extension as before, i.e. ".RUN".

16. AGGREGATION OF GROUPS

The ascendancy and several other features of an ecosystem are affected by the number of groups included in the description. Ulanowicz (1986) suggested an algorithm for aggregation of groups, based on stepwise combination of the pairs of groups that lead to the least reduction in system ascendancy. We have included in ECOPATH II a routine based on this suggestion. The aggregation routine can be run only after the network flow indices program.

16.1 Selecting an input file

The input files for the aggregation program are the ".RUN" files. The extension name should, however, not be included when entering the input file name. As in other programs, selection of <F6> and of a drive letter gives an overview of the available data files on the default directory. A filename can then be entered, or the default accepted by pressing <Enter>.

Exhibit 15.6

MATRIX OF MIXED TROPHIC IMPACTS

IMPACTING GROUPS	IMPACTED GROUPS									
	1	2	3	4	5	6	7	8	9	10
1. APEX PREDATORS	-.31	-.19	0.00	0.01	-.00	-.00	0.03	0.00	-.00	-.00
2. EPIPELAGIC NEXT	0.47	-.18	-.11	-.02	0.00	0.00	-.13	-.00	0.01	0.00
3. MESOPELAGICS	0.01	-.14	-.15	-.02	0.00	0.00	-.14	0.01	-.01	0.00
4. BATHYPELAGICS	-.00	-.00	-.00	-.16	-.00	-.00	-.00	-.00	0.00	-.00
5. BENTHIC FISH	-.00	-.00	-.00	0.01	-.18	-.12	-.00	-.00	0.00	0.03
6. BENTHOS	0.00	0.00	0.00	-.22	-.00	-.48	0.00	0.00	-.00	-.47
7. ZOOPLANKY.LARGE	0.23	0.24	0.11	0.15	-.00	-.00	-.11	0.04	-.10	-.00
8. PHYTOPLANKTON	0.29	0.35	0.35	0.08	-.00	-.00	0.46	-.35	0.56	-.00
9. MICROZOOPLANKY.	0.16	0.18	0.32	0.02	-.00	-.00	0.12	-.36	-.40	-.00
10. DETRITUS	-.00	-.00	-.00	0.31	0.36	0.44	-.00	-.00	0.00	0.00
11. FISHERY	-.17	0.05	-.00	-.00	0.00	0.00	-.01	-.00	0.00	0.00

Press any key to continue ...

16.2 Aggregation of specified groups

The second screen in the aggregation program asks if you want to aggregate pairs of groups that you identify yourself. Enter <Y> for "Yes" and <N> or <Enter> for "No". If you choose <Y> you will see a new screen, displaying all the group names in the system. You can then enter the numbers of the two groups to be aggregated. The aggregation involves calculation of new weighted biomasses, production, consumption, trophic level, diet composition, etc. The new group resulting from the aggregation will get a new group name. If you have 20 groups in your system when you start this routine, the aggregated group will be named "Agg. 19", as you now have only 19 groups in the system.

Next, you will be asked if you want to aggregate another pair. If <Y> you repeat the process, if <N> you proceed to the save routine, and *save the aggregated data file under a new name*. The new data file can then be run with the edit data program.

16.3 Minimizing the decline in ascendancy

If you answer <N> to the question in section 16.2, above, you will be led to a routine which automatically identifies any pairs of groups whose aggregation will result in the least decline in ascendancy.

The aggregation is performed so that only groups which are separated by less than a given (optional) difference in trophic levels can be combined. The default value for the difference in trophic level is six (6). Using this high default value ensures that any group in the system can be combined

with any other. Entry of a small value for the difference of trophic level forces the routine to consider only pairs of groups with similar trophic levels.

You will further be asked if you want to direct the output to a printer or to the screen, and to how many groups you want to aggregate the system. If you have directed the output to a printer, printing will start with a list of the groups and the trophic level and throughput of each group in the original system (this list is sorted after decreasing trophic levels, which is useful for drawing the flows in the system).

An example of how the aggregation then proceeds is given in Exhibit 16.1. The inset in this exhibit shows that the ascendancy diminishes strongly only when the system is aggregated to less than about six groups. Further, the pairing of groups is closely related to the trophic levels of the groups that are paired even when the above difference is set at the high value of six. The figure shows a remarkable resemblance with figures illustrating clustering techniques, but this is coincidental: trophic level was not used as an input parameter for this run.

Both features of the aggregation, i.e. that the ascendancy only drops off when a system is aggregated to very few groups, and that the groupings are closely linked with trophic levels, are generally valid, according to analysis of more than 30 ecosystems using ECOPATH II by various authors (Christensen and Pauly 1992b). Our findings support those of Ulanowicz (1986) who applied a similar routine to the Crystal River system in Florida, USA, and found that the aggregation gave the same result as "intuitive guesswork".

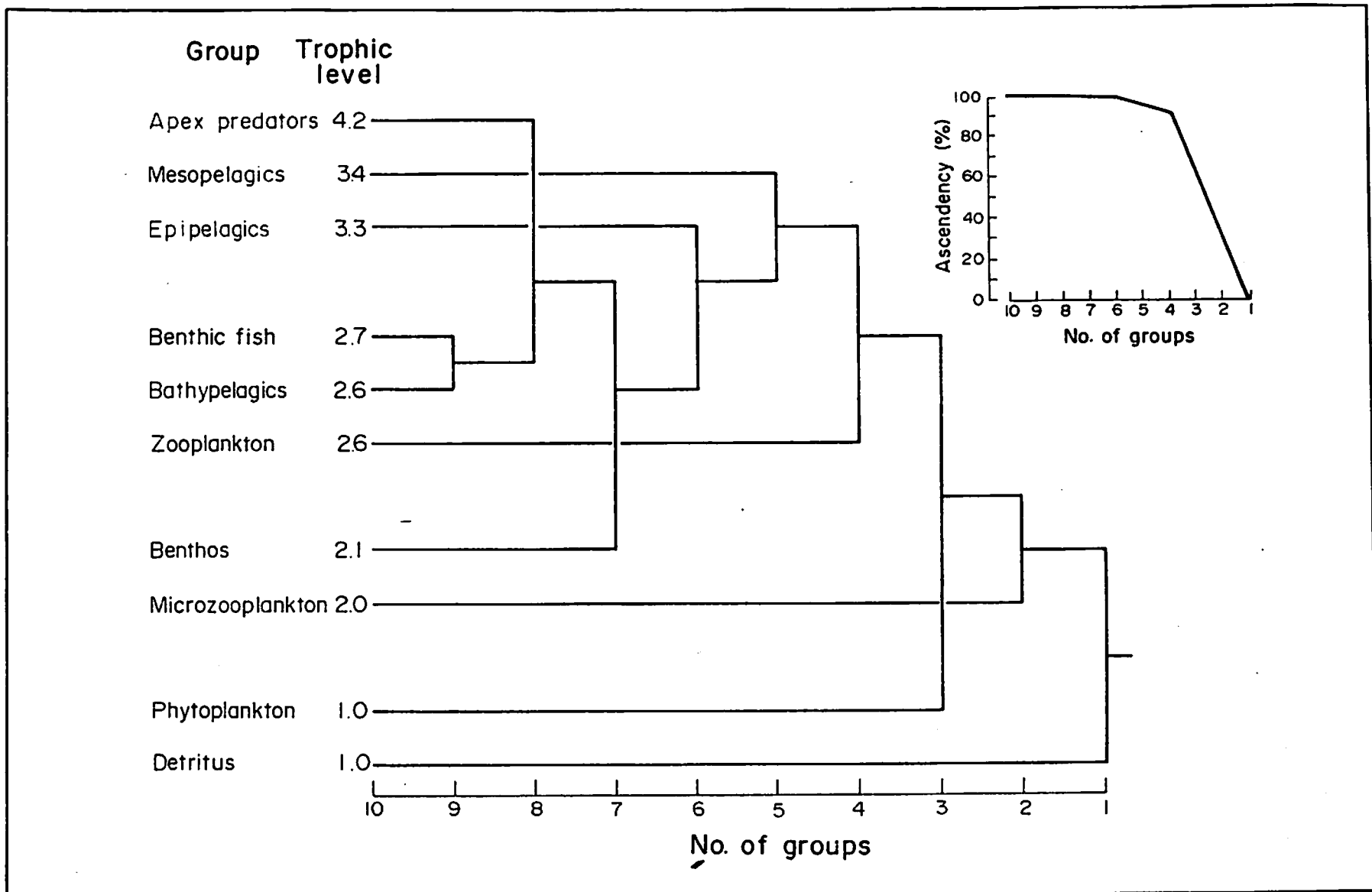


Exhibit 16.1

The main graph (South China Sea open ocean) shows the pairwise aggregation of groups that results in the least decrease in system ascendency. Note that groups with similar trophic levels are aggregated first. The small inset shows the decrease in ascendency resulting from the aggregation.

16.4 Saving and using the aggregated file

The aggregated file should be saved under a new filename. The file will automatically receive the extension name ".EII" and should subsequently be edited with the edit data program and run with the parameter estimation program. You should not include an extension name; this will cause an error.

17. EXPORT TO SPREADSHEETS

A routine has been included into ECOPATH II, which allows export of data files (".RUN"), in a format that can be read by most commercial spreadsheets. As in other programs, either enter a file name (use <F6> to get a list) or accept the default if such is supplied. The export will be performed without user interaction and the export file will be saved with the same filename and the extension ".prn".

To use the file in the spreadsheet, exit ECOPATH II and load your spreadsheet program. If you are using the LOTUS 123 spreadsheet, invoke the menu and select the <File>, <Import>, <Numbers> command. If you are using the Quattro Pro spreadsheet, select <Import> and <Comma & "" Delimited File>.

18. SCOR WG

A program has been developed to import files from and export files to the file format used by the theoretical ecologists associated with Working Group 59/73 of the SCOR (UNESCO/IOC Scientific Committee on Oceanographic Research) (Platt et al. 1981; Ulanowicz and Platt 1985).

The SCOR/ECOPATH bridge is chosen by entering <S> on the main menu. Next choose the direction in which you want to translate data, and enter a filename. As in other programs <F6> and drive letter will give you a list with available filenames (*.SCO in SCOR format and *.RUN in ECOPATH format).

The program runs without further user interaction and automatically saves the translated file with the appropriate extension. You can then run the translated file either in ECOPATH or with the SCOR system.

The SCOR/ECOPATH bridge program is called ECOSCOR.EXE.

In the SCOR files, all flows directed from a group to the detritus are pooled irrespective of whether the flow consists of undigested food or dying organisms. Therefore the ecotrophic efficiency is set to 1 (one) for all groups in files translated from SCOR format to ECOPATH format. In other words it is assumed that all flow from a group to the detritus is due to unconsumed food. The bridge is generally not reversible - you should not translate from one format to the other and back again.

19. ACKNOWLEDGMENTS

We take this opportunity to thank Ms. Mina Soriano who wrote an initial and not released version of the ECOPATH II program during her work with ICLARM's Software Project from 1985 to the end of 1989. Thanks to Ms. Carmela C. Janagap for programming effort from mid 1990 to mid 1991, to Mr. Felimon C. Gayanilo, Jr. for brushing up, and to Ms. Sandra A. Gayosa for checking the programs and models.

We also wish to thank Dr. J.J. Polovina for his permission to carry further the model and the name he initiated, and Prof. R.E. Ulanowicz for inspiration and support. Version 2.0 of ECOPATH was distributed to some 190 users. We thank all for their interest, especially those who supplied us with comments and experiences.

The finalization of ECOPATH II was made possible through a project grant for "Global Comparisons of Aquatic Ecosystems" from the Danish International Development Agency, DANIDA.

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APPENDICES

Appendix 1. Definition of some terms relevant to the construction of steady-state trophic ecosystem models.

Equivalent concepts, by discipline theoretical ecology ^{a)}	Fisheries biology	Definition and/or remarks
P/B ratio (PB)	Total mortality (Z)	These two concepts were shown by Allen (1971) to be identical, under steady-state, when von Bertalanffy growth and exponential mortality are assumed).
Node [also elements or compartment]	Box/group	A population (or group of single-species populations belonging to the same guild), explicitly included in a model, and whose members can be represented by the same diet composition, 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 <u>existence</u> 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 i to box j (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 <u>usable</u> mass or energy that is not directed toward any of the boxes explicitly included in an ecosystem model [Note difference from respiration, where the flows represent <u>unusable</u> mass or energy.]

^{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)}	Fisheries biology	Definition and/or remarks
"Steady-state" population	"Average" population	A steady-state population is a theoretical construction, never occurring in reality. It can be approximated by averaging time series data over longer periods if there are no 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 biomasses) in a given ecosystem. A "graph" is "weighted" when the flows linking the boxes are quantified (e.g., in $\text{gCm}^{-2}\text{year}^{-1}$).
Inputs (D_i)	Primary production (if energy as unit); Nutrients (if these are units)	Models of ecosystems must always include an "input", as such systems dissipate energy. In most practical cases, the input will consist of primary production, except some cave and deep sea ecosystems, in which the inputs may consist of detritus.

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

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

The title of Ulanowicz's book ("Growth and Development: Ecosystem Phenomenology") needs some explaining. This is so because the two first words "growth" and "development", as used in that book cannot be interpreted intuitively. Thus, "growth" refers to the *size* of an ecosystem, while "development" refers to the *information contents* embodied in ecosystem structure. This implies that the *time dimension*, an important aspect of standard definition of growth and development, is not an explicit part of the theory leading to Ulanowicz' various key concepts; this again is the reason why it could so easily be incorporated into ECOPATH II.

Also, the last word of the title of Ulanowicz's book 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 *explain*, i.e., to identify the causes of phenomena. The use of this term by R.E. Ulanowicz is to emphasize his contention that the flows between the components of ecosystems are sufficient for a "complete" description of those system - a contention with which many may disagree. However, his indices and the theory from which they were derived are still useful to improve our (partial) descriptions of ecosystems.

Index (with symbols, dimensions 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 day ⁻¹ , or kcal m ⁻² year ⁻¹)	Sum of all flows into and from the boxes in an ecosystem, i.e., including imports, exports of <u>usable</u> 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 <u>size</u> 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 year ⁻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 <u>throughput</u> (T) <u>times</u> an index of the "average mutual information", or <u>information</u> content of an ecosystem. An ecosystem may seek to increase its ascendency as it matures. This can be done by decreasing the overheads, F (see below), which means decreasing the size or redundancy of imports, exports, or respiration. In practice this is only possible to a certain system-specific level. Going beyond this would render the system vulnerable to perturbations.

Index (with symbols, dimensions and units)	Definition and remarks with page and equation no.
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 $\Phi = C - A$; Φ is the sum of four components ($\Phi_o + \Phi_e + \Phi_r + \Phi_j$, defined (on p. 107, eq. 6.18 and further below). Overheads provide limits on the increase in ascendency and reflect the system's "Strength in reserve" from which it can draw to meet unexpected perturbations (Ulanowicz and Norden 1990).
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_r)	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_r increase with respiration and must always be > 0 .

Index (with symbols, dimensions and units)	Definition and remarks with page and equation no.
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_i), exports (A_e) and respiration (A_r). Note that $A_i = C_i - (E + S + R)$ with E and S defined below and $R = \Phi_r$.
Tribute to other (E)	The sum of $\Phi_o + A_e$, i.e., of the system's contributions of the exports from a system to the overheads (Φ_o) and to Ascendency (A_e) (p. 114-115).
Dissipation (S)	The sum of Φ_r and A_r , i.e., of the contributions of respiration to the overhead of a system (Φ_r) and to its ascendency (A_r).
Ascendency/development capacity (A/C)	A measure of ecosystem network efficiency (see p. 111).

Appendix 3. Definitions and symbols of variables used in Appendix 4.

Symbol	Equations	Definitions	Dimensions
B_i	-	Biomass of group (i).	UNIT
C_i		Catch of group (i)	UNIT time ⁻¹
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.	UNIT time ⁻¹
DC (N1,i)	DET_i/DT	Diet composition of detritus box	Dimensionless
DET_i		Flow from group i to detritus	UNIT time ⁻¹
DT	$\sum_i DET_i$	Sum of all flows to detritus	UNIT time ⁻¹
DIFF	TOTPP-PPROD	The difference between input and calculated total primary production 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 <u>flow</u> from the primary producers to the detritus.	UNIT time ⁻¹
DTPP	$\sum_{(PP>0)} DET_i$	Sum of all flows to detritus from producers	UNIT time ⁻¹
Ecosystem		A system where input balances output, and where total production $>$ EXPORT + IMPORT	Dimensionless
EE_i	Appendix 4, Algorithm 2, $EE_i * P_i = EX_i + M2_i * B_i$	Ecotrophic Efficiency is that part of production that goes to predation <u>and</u> catches (including exports); same as (1 - other mortality)	Dimensionless
EX_i		Exports (including catches) out of the system.	UNIT time ⁻¹
GE_i	PB_i/QB_i	Gross efficiency (of food conversion).	Dimensionless
F_i	C_i/B_i	Fishing mortality coefficient	time ⁻¹

Symbol	Equations	Definitions	Dimensions
E_i	$(EX_i - C_i)/B_i$	The coefficient for other exports than fishery	time ⁻¹
GS		Proportion of food that is not assimilated. A required input; the default value used is 0.20 for all consumers (Winberg 1956). Nonassimilated food goes to the detritus.	dimensionless
$M0_i$	$(1 - EE_i) * PB_i$	Other mortality coefficient	time ⁻¹
$M2_i$	$(\sum_j B_j QB_j DC_{ji})/B_i$	Predation mortality of (i)	time ⁻¹
N		Number of living groups	dimensionless
N1	$N + 1$	Total number of boxes including detritus group	dimensionless
NE	$PB/(QB*(1-GS))$	Net efficiency	dimensionless
OI_i	$\sum_j (TL_j - (TL_i - 1))^2 * DC_{ij}$	Omnivory index of group i	dimensionless
PARTM2	$M2_i - B_i QB_i DC_{ii}$ (Equation 10)	Partial predation mortality of (i) excludes "cannibalism"	time ⁻¹
PB_i	(Equation 8) P_i/B_i	Production/biomass ratio of (i). Equals the total mortality	time ⁻¹
P_i	$B_i * PB_i$	Production rate of (i).	UNIT time ⁻¹
PP		Total primary production in the system	UNIT time ⁻¹
PP_i		Proportion of production of (i) that is attributed to primary production $0 \leq PP \leq 1$	dimensionless
PPROD	$\sum_i B_i PB_i PP_i$	Calculated total primary production	UNIT time ⁻¹
Primary Producers	$PP_i > 0$	All groups (i) for which $PP_i > 0$	
R	$\sum_i RESP_i$	Total respiration in the system	UNIT time ⁻¹
QB_i	Q_i/B_i	Consumption/biomass ratio of (i). $QB_i > 0$ for consumers.	time ⁻¹

Symbol	Equations	Definitions	Dimensions
Q_i	$B_i + QB_i$	Consumption rate of (i).	UNIT time ⁻¹
RESP _i	$(1-GS_i)*Q_i-(1-PP_i)*P_i$	Respiration of group i. If the unit is a nutrient PP _i is set equal to zero, irrespective of if the group is an autotroph or not (as nutrients are not produced)	UNIT time ⁻¹
time		Any time period found useful for the model	e.g., year
TOTPP		Total net primary production of all producers. TOTPP is not a required input.	UNIT time ⁻¹
TRPUT		Total system throughput, i.e., the sum of all production, catches im- and exports, respiratory flows and flows to the detritus	UNIT time ⁻¹
TL _i	Appendix 4, Algorithm 6	Trophic level of (i)	Dimensionless
UNIT		Units used for nutrients/energy;	e.g., t km ⁻²

Appendix 4. Description of algorithms.

Algorithm 1 Estimation of PB

From equation (2), we have

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

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).

Problem: How to deal with top predators

It should be noted that for a fished top predator i that is not preyed upon, ($M2_i$ is zero), the production/biomass ratio can be estimated from knowledge of group i alone.

For a top predator i on which no fishing takes place, i.e. where the ecotrophic efficiency, $EE_i = 0$, it is necessary to have independent estimates of PB_i . This parameter cannot be estimated from equation (9) as EE_i , C_i and $\sum_j B_j QB_j DC_{ji}$ 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 Appendix 1) for top predators can be readily estimated from the age/size structure of the population or from their growth parameters.

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, 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

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

The data requirements are as mentioned for Algorithm 1.

This equation also defines EE , i.e., the ecotrophic efficiency is that part of the production that is exported or consumed by predators.

* 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 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

$$B_i * PB_i * EE_i = EX_i + \sum_j B_j QB_j DC_{ji} \quad \dots 8)$$

If $EE_i > 0$, then

$$B_i * PB_i = (EX_i + \sum_j B_j QB_j DC_{ji}) / EE_i \quad \dots 9)$$

Total predation mortality $B_i * M2_i$ is,

$$\begin{aligned} B_i * M2_i = \sum_j B_j * QB_j * DC_{ji} &= \sum_{j(G < > i)} B_j * QB_j * DC_{ji} + B_i * QB_i * DC_{ii} \\ &= PARTM2_i + B_i * QB_i * DC_{ii} \end{aligned} \quad \dots 10)$$

Further, since

$$\begin{aligned} B_k * PB_k * EE_k &= EX_k + \sum_j B_j * QB_j * DC_{jk} \\ &= EX_k + \sum_{j(G < > i)} B_j * QB_j * DC_{jk} + B_i * QB_i * DC_{ik} \end{aligned}$$

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

$$B_i * QB_i = (B_k * PB_k * EE_k - EX_k - \sum_{j(G < > i)} B_j * QB_j * DC_{jk}) / DC_{ik} \quad \dots 11)$$

or

$$QB_i = (B_k * PB_k * EE_k - EX_k - \sum_{j(G < > i)} B_j * QB_j * DC_{jk}) / (DC_{jk} * B_i) \quad \dots 12)$$

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

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

Finally QB_i can be found using equation (12).

Algorithm 4 Estimating biomasses (B_i) only

Generally it is not possible to estimate biomasses for top-predator groups from which there are no exports.

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

$$\begin{aligned} B_i PB_i EE_i &= EX_i + M2_i * B_i \\ &= EX_i + PARTM2_i + B_i QB_j DC_{ji} \end{aligned}$$

and thus

$$B_i = \frac{EX_i + PARTM2_i}{(PB_i EE_i - QB_j DC_{ji})} \quad \dots 14)$$

if $PB_i EE_i = QB_j DC_{ji}$, 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,

$$PB_i * EE_i < QB_j DC_{ji}$$

(that is if "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 there are no exports (including fishery) for any of the groups, it is necessary to enter an estimate of the biomasses of all top predators, i.e. for all group that is not preyed upon by any other group.

Algorithm 5 The Generalized Inverse

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

$$B_1 PB_1 EE_1 - B_1 QB_1 DC_{11} - B_2 QB_2 DC_{21} - \dots - B_n QB_n DC_{n1} - EX_1 = 0 \quad \dots 3.1)$$

$$B_2 PB_2 EE_2 - B_1 QB_1 DC_{12} - B_2 QB_2 DC_{22} - \dots - B_n QB_n DC_{n2} - EX_2 = 0 \quad \dots 3.2)$$

:

:

$$B_n PB_n EE_n - B_1 QB_1 DC_{1n} - B_2 QB_2 DC_{2n} - \dots - B_n QB_n DC_{nn} - EX_n = 0 \quad \dots 3.n)$$

This can be reexpressed as

$$a_{11} X_1 + a_{12} X_2 + \dots + a_{1m} X_m = Q_1 \quad \dots 4.1)$$

$$a_{21} X_1 + a_{22} X_2 + \dots + a_{2m} X_m = Q_2 \quad \dots 4.2)$$

:

:

$$a_{p1} X_1 + a_{p2} X_2 + \dots + a_{pm} X_m = Q_p \quad \dots 4.n)$$

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

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_j is estimated from the other equations, and PB_j or EE_j is calculated from algorithm 1 or 2.

b. **Both B_j and QB_j unknown**

If it has not been possible to estimate B_j and QB_j 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 unknown**

If $i \neq j$, 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 unknown**

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

e. **The X matrix**

The i^{th} element of the x-matrix will be either B_j or QB_j 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

$$q_{ij} = \begin{cases} 0 & \text{if } B_j \text{ is unknown} \\ + B_j * QB_j * EE_j & \text{if } QB_j \text{ is unknown} \\ B_j * QB_j * DC_{ji} & \text{if } B_j \text{ and } QB_j \text{ are known} \\ & \text{and } B_j \text{ is unknown} \\ B_i * QB_j * DC_{ii} - B_i * PB_j * EE_i & \text{if } B_i \text{ and } QB_j \text{ are} \\ & \text{known and } i = j. \end{cases}$$

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 $\sum DC_{jm} = 0$ (i.e. none of the possible predators eats m) it is not possible to estimate QB_m .

Algorithm 6 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 (TL) 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).

$$TL_i = 1 + \sum_j DC_{ij} * TL_j \quad \dots 15)$$

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 (TL_D) poses a small problem discussed at length in the draft version (1.0) of this manual; we have in later versions resolved the problem by defining TL_D as being equal to 1, i.e. the same as for primary producers. This is in accordance with what was done in the International Biological Program (IBP).

The trophic levels of groups other than primary producer or detritus may be expressed as a system of equations in the form:

$$\begin{array}{rcl}
 1 & = & TL_1(1-DC_{11}) \quad -TL_2DC_{12} \quad -TL_3DC_{13} \quad \dots -TL_nDC_{1n} \\
 1 & = & -TL_1DC_{21} \quad +TL_2(1-DC_{22}) \quad -TL_3DC_{23} \quad \dots -TL_nDC_{2n} \\
 \vdots & & \vdots \quad \vdots \quad \vdots \quad \vdots \\
 \vdots & & \vdots \quad \vdots \quad \vdots \quad \vdots \\
 \vdots & & \vdots \quad \vdots \quad \vdots \quad \vdots \\
 1 & = & -TL_1DC_{n1} \quad -TL_2DC_{n2} \quad -TL_3DC_{n3} \quad \dots +TL_n(1-DC_{nn})
 \end{array}$$

Putting the above in matrix form:

$$\begin{bmatrix} 1 \\ 1 \\ \vdots \\ \vdots \\ 1 \end{bmatrix} = \begin{bmatrix} (1-DC_{11}) & -DC_{12} & \dots -DC_{1n} \\ -DC_{21} & (1-DC_{22}) & \dots -DC_{2n} \\ \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots \\ -DC_{n1} & -DC_{n2} & \dots (1-DC_{nn}) \end{bmatrix} * \begin{bmatrix} t_1 \\ t_2 \\ \vdots \\ \vdots \\ t_n \end{bmatrix}$$

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 a standard inverse method.

Algorithm 7 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.

$$OI_i = \sum_j (T_j - T)^2 * DC_{ij} \quad \dots 16)$$

where: T_j is the trophic level of prey j, and

T is the average trophic levels of the prey, i.e. one less than the trophic level of the predator i.

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

If a predator only has one prey on one trophic level, its omnivory index will equal zero.

TITLES IN THIS SERIES

- User's manual for the fish population dynamics plug-in module for HP41CV calculators. M.L. Palomares and D. Pauly. 1987. ICLARM Software 1, 5 p. Distributed with a custom-made plug-in module for HP41CV calculators for US\$150 (airmail). [no longer distributed]
- A draft guide to the Compleat ELEFAN. F.C. Gayanilo, Jr., M. Soriano and D. Pauly. 1989. ICLARM Software 2, 70 p. Distributed with a 12-diskette (5-1/4") Compleat ELEFAN package for US\$75 (airmail).
- Estimation and comparison of fish growth parameters from pond experiments: a spreadsheet solution. J.M. Vakily. 1988. ICLARM Software 3, 12 p. Distributed with one 5-1/4" diskette for US\$15 (airmail).
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- CDS ASSISTANT. F.C. Gayanilo, Jr. 1990. ICLARM Software 5, 19 p. Distributed with one 5-1/4" diskette for US\$15 (airmail).
- A guide to the ECOPATH II software system (ver. 2.1). V. Christensen and D. Pauly. 1992. ICLARM Software 6, 72 p. Distributed with one 5-1/4" MS-DOS diskette for US\$20 (airmail). Software 6 is available free of cost for cooperators of the ICLARM/DANIDA project "Global Comparisons of Aquatic Ecosystems". Please contact V. Christensen for further details.

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