

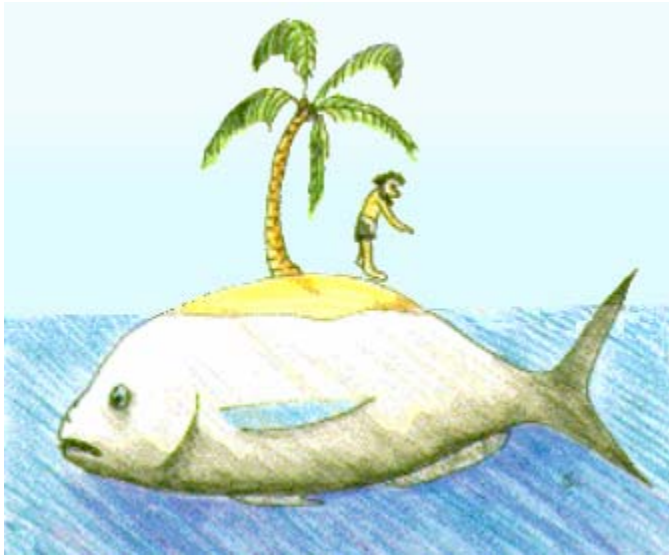
ECOPATH WITH ECOSIM: A USER'S GUIDE

by

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No fish is an island...

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1. Abstract

Ecopath with Ecosim is designed for straightforward construction, parameterization and analysis of mass-balance trophic models of aquatic and terrestrial ecosystems. Focus is on using the models for fisheries management, and a suite of tools are included for this aim. This help system describes how to obtain, install and use the Ecopath software system written for personal computers using the Windows environment. Brief accounts are given of the theory behind the models developed using Ecopath with Ecosim.

The Ecopath mass-balance modeling system is built on an approach initially presented by J.J. Polovina for estimating biomass and food consumption of the elements (species or groups of species) of an aquatic ecosystem. Subsequently it was combined with various approaches from theoretical ecology, notably those proposed by R.E. Ulanowicz, for the analysis of flows between the elements of ecosystems. However, the system has been optimized for direct use in fisheries assessment as well as for addressing environmental questions through the inclusion of the temporal dynamic model, Ecosim, and the spatial dynamic model, Ecospace.

Since its initial development in the early 1980s, the mass-balance approach incorporated in the Ecopath software has been widely used for constructing food web models of marine and other ecosystems. This has led to a number of generalizations on the structure and functioning of such ecosystems, relevant to the issue of fisheries impacts. Some of these generalizations have revisited older themes, while others were new. Both sets of generalizations have impacted on the development of the Ecopath approach itself. Herein, the description of the average state of an ecosystem, using Ecopath proper, also serves to parameterize systems of coupled difference and differential equations, used to depict changes in biomasses and trophic interactions in time (Ecosim) and space (Ecospace).

The results of these simulations can then be used to modify the initial Ecopath parameterization, and the simulations rerun until external validation is achieved. This reconceptualization of the Ecopath approach as an iterative process, which helps address issues of structural uncertainty, does not, however, markedly increase its input requirements. Rather, it has become possible, through a semi-Bayesian resampling routine to explicitly consider the numerical uncertainty associated with these inputs.

Real ecosystems are more complicated than the mass-balance fluxes of biomass in Ecopath, however large the number of functional groups we include in our models. Real ecosystems also have dynamics far more complex than represented in Ecosim. The issue to consider, when evaluating the realism of simulation software, is, however, not how complex the software and the processes are that are represented therein. Rather, the question is which structure allows a representation of the basic features of an ecosystem, given a limited amount of inputs. On such criterion, it was obvious that a major deficiency of the Ecopath with Ecosim approach was its assumption of homogenous spatial behavior. This has been remedied through the development of Ecospace (Note that in Walters *et al.*, 1999 Equation 13, the sign for the T' factor was reversed by mistake.), a dynamic, spatial version of Ecopath, incorporating all key elements of Ecosim.

The Ecopath with Ecosim software has been distributed to more than 3000 registered users in 124 countries, and more than 200 publications utilizing it have appeared in the scientific literature. See www.ecopath.org for an update.

2. Introduction

The software described in the present guide is designed to help you construct a (simple or complex) model of the trophic flows in an ecosystem. Once the model is constructed you will have an overview of the feeding interactions in the ecosystem, and of the resources it contains. You will be able to analyze the ecosystem in details, and through Ecosim you can simulate effects of changes in fishing pressure, and, given time series data, evaluate the relative impact of fisheries and environment. Further, spatially explicit research or policy question can be addressed using the spatial simulation module Ecospace, also included in EwE. Aquatic ecosystems will be emphasized because the approach presented here was initially applied to marine and freshwater ecosystems, but it can also be applied to terrestrial ecosystems, such as, e.g., farming systems (Dalsgaard *et al.*, 1995).

The Ecopath system is built on an approach presented by Polovina (1984a; 1984b) for the estimation of the biomass of the various elements (species or groups of species) of an aquatic ecosystem. It was subsequently combined with various approaches from theoretical ecology, notably those proposed by R.E. Ulanowicz (1986), for the analysis of flows between the elements of ecosystems.

In many cases, the period considered will be a given 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.*, 1991b). Several other examples for this may be found in Christensen and Pauly (1993b). We emphasize though that as time series analysis are becoming increasingly important for EwE simulations, it may be advantageous to model a specific year early at the beginning of the time series, and let Ecosim handle development over time, rather than average the model over time periods.

Once a model of the type discussed here has been built it can be used directly for simulation modeling using Ecosim. This approach is fully integrated with Ecopath, and is a complex simulation model for evaluating the impact of different fishing regimes on the biological components of ecosystems. Real ecosystems are more complicated than the mass-balance fluxes of biomass in Ecopath, however large the number of functional groups we include in our models. Real ecosystems also have dynamics far more complex than represented in Ecosim. The issue to consider, when evaluating the realism of simulation software is, however, not how complex the software and the processes are that is represented therein. Rather, the question is which structure allows a representation of the basic features of an ecosystem, given a limited amount of input variables. On such criterion, it was obvious that a major deficiency of the Ecopath with Ecosim approach was its lack of an explicit capability for addressing spatial policy questions. This has been remedied through the development of Ecospace (Walters *et al.*, 1999), a dynamic, spatial module incorporating key elements of Ecosim simulations.

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 Appendix 3 and Appendix 4.

This guide does not give full descriptions of all aspects of the methodology incorporated in Ecopath with Ecosim. Indeed, the Help file of the software contains more information than this guide! Choose Help at any time in the software by pressing F1.

2.1 General conventions

The following terms and phrases have defined meaning in this Guide:

- Choose: Carry out a menu command by clicking on it with the mouse or by pressing the menu keys;
- Select: Highlight text, e.g., in data input forms;
- **Bold** type indicates words or characters you type. Lowercase or uppercase characters can be used at will;
- *Italic* type refer to either important terms, e.g. menu items, (or to the scientific names of organisms);
- Bulleted lists (such as this one) provide information, but may also be used to indicate alternatives in procedural steps;
- Numbered lists (1, 2, ...) indicate procedures with steps to be carried out sequentially. A single bullet indicates a procedure with only one step;
- Unless otherwise specified ‘mouse button’ means left mouse button;
- *Click* means point on a specified item with the mouse and press and release the mouse button once;
- *Double Click* means point with the mouse and press and release the mouse button twice in quick succession;

- Key names are given in small capital letters, and are referred to without the work ‘key’. As an example ‘Hold down ALT’ mean hold down the ALT key;
- A plus sign (+) between two key names means you are to hold down the first key while pressing the second key;
- A comma (,) between two key names means you can press and release the first key, and then press and release the second key;
- *Option buttons* are part of an option group from which only one option can be selected;
- *List boxes* displays a list of items from which none, one or many items may be selected depending on the context.

2.2 How to obtain the Ecopath with Ecosim software

The Ecopath software for construction of trophic ecosystem models can be obtained in three different versions:

- Ecopath with Ecosim (32-bit Windows operating system)
- Ecopath 3.1 for Windows (16 bit Windows operating system)
- Ecopath II, Version 2.2. (for DOS)

The different versions can be downloaded from www.ecopath.org. Alternatively (write, fax or) email us and we will send you a CD with the software. We strongly encourage all users to register with us (with email address) so that we can keep you informed of new releases, bugs, etc.

So far more than 200 Ecopath models have been published. References to many of these are included in this guide. We are collecting manuscripts and publications with includes Ecopath applications, and would appreciate being notified (or even better to receive copies) of such work. Published Ecopath models can be downloaded from www.ecopath.org.

2.3 Software support, copyright and liability

We expect that the Ecopath software, i.e. the 32-bit Windows versions including Ecosim and Ecospace will be maintained and supported for a number of years, even though we don’t have dedicated funding for the development. The DOS version (2.2+) and the 16-bit Windows versions (3.1+), are still available, but will not be updated further. Distribution, registration and support are free-of-charge.

The software is copyrighted but not copy-protected. You may freely copy and distribute the program and the documentation as long as this is not done commercially. Please inform us when you copy the software to anyone, or if you received it from someone else. This will enable new users to be registered (free of charge), and thus to be informed of new developments, bugs, etc. At the same time, you are invited to send brief descriptions of your ecosystem models to the authors, initially for inclusion on www.ecopath.org.

2.4 Installing and running Ecopath with Ecosim

Installation is done via a customized third-party setup program. The Setup program will suggest installing the program in a default directory but another directory may be chosen. Setup programs are notoriously difficult to get to function properly, and we encourage you to inform Villy Christensen if you encounter problems with installation.

Some test data sets are included for the initial testing of the software. You can open these from the File menu.

2.5 Previous versions

Ecopath releases:

- **Ecopath with Ecosim Vers 4.** Version 5 has a number of new features added. EwE is for PC’s only.

- **Ecopath with Ecosim.** Ecopath with Ecosim can only be run on PCs with a 32-bit operating system, such as Windows 95/98/Me/XP or Windows NT4/2000.

The previous versions (which do not include Ecosim and Ecospace) can be used in DOS-mode or with Windows 3.1:

- **Ecopath for Windows**, versions 3.0 and 3.1; released 1996-1997.
- **ECOPATH II**, versions 2.0 and 2.1; released 1991-1993.
- **ECOPATH II**, versions 1.0; released 1990.

To update from test versions (and previous versions) of Ecopath with Ecosim: You will need to use the database that came with the released version if your database is prior to Database version 1.50 (See Ecopath About from the Help menu). Later database versions, i.e. from September 1999 onwards can be updated programmatically by EwE.

If you have data in a previous database (a file with the extension ‘.mdb’) you can import your models to the new database as follows: Select ‘Transfer’ from the File-menu. An ‘Import/export model’ form will pop up, and you now select ‘Import a model’. See the file menu for a more thorough description.

Files from Versions 2 and 3 are text files with the file extension ‘.eii’. Such files can be imported to the new version using the ‘import text file’ option from the File menu. Notice that remarks entered in Version 3.0+ will not be included, nor will scenarios from routines such as Ecosim and Ecospace.

3. Ecopath: mass balance modeling

3.1 About Ecopath

EwE is an ecological software suite for personal computers that has been under development for more than a decade. The development is now centered at the University of British Columbia’s Fishery Centre, while applications are widespread throughout the world. The software has more than 2500 registered users in 124 countries, and more than two hundred publications based on the software have appeared, see www.ecopath.org. The approach is thoroughly documented in the scientific literature, and key references are mentioned below. EwE has three main components: Ecopath – a static, mass-balanced snapshot of the system; Ecosim – a time dynamic simulation module for policy exploration; and Ecospace – a spatial and temporal dynamic module primarily designed for exploring impact and placement of protected areas. The Ecopath software package can be used to

- Address ecological questions;
- Evaluate ecosystem effects of fishing;
- Explore management policy options;
- Evaluate impact and placement of marine protected areas;
- Evaluate effect of environmental changes.

The foundation of the EwE suite is an Ecopath model (Christensen and Pauly, 1992; Pauly *et al.*, 2000), which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by trophically linked biomass ‘pools’. The biomass pools consist of a single species, or species groups representing ecological guilds. Pools may be further split into ontogenetic linked groups; a group may as an example be split in larvae, juvenile, age 1-2, and spawners (age 3+). Ecopath data requirements are relatively simple, and generally already available from stock assessment, ecological studies, or the literature: biomass estimates, total mortality estimates, consumption estimates, diet compositions, and fishery catches.

The process of constructing an Ecopath model provides a valuable end product in itself through explicit synthesis of work from many researchers. Several EwE models illustrate this, e.g., for the Prince William Sound (Okey and Pauly, 1998; 1999), the Strait of Georgia (Pauly *et al.*, 1998b) and several North Atlantic models created as part of the Sea Around Us project activities at the UBC Fisheries Centre, (Guénette and Diallo, 2002). The model construction process has brought together scientists, researchers and data from state and federal levels of government, international research organizations, universities, public interest groups and private contractors. Key

results include the identification of data gaps as well as common goals between collaborating parties that previously were hidden or less obvious. We find the process especially important for enabling the interest groups to take ownership of the model that is derived; this is especially required when operating at the ecosystem level, where multi-faceted policy goals have to be discussed widely as part of the management process. This is facilitated by the policy exploration methods included in the Ecosim model discussed further below.

3.2 *On modeling*

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 that follow, through time, the interactive behavior of the (major) components of an ecosystem.

Traditional simulation models are difficult to build, and even more difficult to get to realistically simulate, without ‘crashing’, the behavior of a system over a long period of time. This is one reason why many biologists shied away from constructing such models, or even interacting with ‘modelers’ (who, traditionally being non-biologists, may have had scant knowledge of the intricate interactions between living organisms). However, ‘modeling’ does not necessarily imply ‘simulation modeling’. There are various ways of constructing quantitative models of ecosystems which avoid the intricacies of traditional simulation modeling, yet still give most of the benefits that can be expected from such exercise viz:

- requiring the biologist/ecologist to review and standardize all available data on a given ecosystem, and identify information gaps;
- requiring the would-be modeler to identify estimates (of states, or rates) that are mutually incompatible, and which would prevent the system from functioning (e.g., the production of a prey being lower than the food requirements of its predators);
- requiring the same would-be modeler to interact with disciplines other than her/his own, e.g., a plankton specialist will in order to model a lake ecosystem have to either cooperate with fish biologists and other colleagues working on the various consumer groups in the lake, or at least read the literature they produced.

To avail of these and other related advantages, one's models should be limited to describing the situation prevailing during a certain ‘average’ period. This limitation 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 represent ‘averages’, applying to a certain period (although this generally is not stated). It is also consistent with the practice common in traditional simulation modeling of using the mass-balance assumption to estimate the parameters of simulation model. This justifies the approach proposed here, to use state and rate estimates for single species in a multispecies context for describing trophic flows in 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 a typical season, or a typical 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 for this may be found in Christensen and Pauly (1993b).

When it is seasonal changes which must be emphasized, different models may be constructed for each month, 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 an ‘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 (1993b).

Judicious identification of periods long enough for sufficient data to be available, but short enough for massive changes of biomass not to have occurred, will thus solve most problems associated with the lack of an explicit time dimension. Moreover, when a build-up of biomass is known to have occurred, this can be considered explicitly as ‘accumulated biomass’, a component of biological production.

The Ecopath system is built on an approach presented by Polovina (1984a; 1984b) for the estimation of the biomass and food consumption of the various elements (species or groups of species) of an aquatic ecosystem, and subsequently combined with various approaches from theoretical ecology, notably those proposed by R.E. Ulanowicz (1986), for the analysis of flows between the elements of ecosystems.

Once a model of the type discussed here has been built, it can be used directly for simulation modeling thanks to the time dynamic model, Ecosim, and the spatial dynamic model, Ecospace, both fully integrated with Ecopath in the present software.

3.3 The Ecopath model

The core routine of Ecopath is derived from the Ecopath program of Polovina (1984a; 1984b) modified to render superfluous its original assumption of steady state. Ecopath no longer assumes steady state but instead bases the parameterization on an assumption of mass balance over an arbitrary period, usually a year (but also see discussion about seasonal modeling). In its present implementation Ecopath parameterizes models based on two master equations, one to describe the production term and one for the energy balance of each group.

3.3.1 Mortality for a prey is consumption for a predator

The first Ecopath equation describes how the production term for each group (i) can be split in components. This is implemented with the equation,

Production = catches + predation mortality + biomass accumulation + net migration + other mortality;

Eq. 1

or, more formally,

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$

Eq. 2

where P_i is the total production rate of (i), Y_i is the total fishery catch rate of (i), $M2_i$ is the total predation rate for group (i), B_i the biomass of the group, E_i the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate for (i), while $M0_i = P_i \cdot (1 - EE_i)$ is the ‘other mortality’ rate for (i).

This formulation incorporates most of the production (or mortality) components in common use, perhaps with the exception of gonadal products. Gonadal products however nearly always end up being eaten by other groups, and can be included in either predation or other mortality.

Eq. 2 can be re-expressed as

$$B_i \cdot (P/B)_i - \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} - (P/B)_i \cdot B_i \cdot (1 - EE_i) - Y_i - E_i - BA_i = 0$$

Eq. 3

or

$$B_i \cdot (P/B)_i \cdot EE_i - \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0$$

Eq. 4

where: P/B_i is the production/biomass ratio, Q/B_i is the consumption / biomass ratio, and $DC_{j,i}$ is the fraction of prey (i) in the average diet of predator (j).

Based on Eq. 3, for a system with n groups, n linear equations can be given, in explicit terms,

$$\begin{aligned} B_1 \cdot (P/B)_1 \cdot EE_1 - B_1 \cdot (Q/B)_1 \cdot DC_{11} - B_2 \cdot (Q/B)_2 \cdot DC_{21} \dots - B_n \cdot (Q/B)_n \cdot DC_{n1} - Y_1 - E_1 - BA_1 &= 0 \\ B_2 \cdot (P/B)_2 \cdot EE_2 - B_1 \cdot (Q/B)_1 \cdot DC_{12} - B_2 \cdot (Q/B)_2 \cdot DC_{22} \dots - B_n \cdot (Q/B)_n \cdot DC_{n2} - Y_2 - E_2 - BA_2 &= 0 \\ \vdots & \\ \vdots & \\ B_n \cdot (P/B)_n \cdot EE_n - B_1 \cdot (Q/B)_1 \cdot DC_{1n} - B_2 \cdot (Q/B)_2 \cdot DC_{2n} \dots - B_n \cdot (Q/B)_n \cdot DC_{nn} - Y_n - E_n - BA_n &= 0 \end{aligned}$$

Eq. 5

This system of simultaneous linear equations can be re-expressed

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

Eq. 6

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

This can be written in matrix notation as

$$[A]_{nm} \cdot [X]_m = [Q]_m$$

Eq. 7

Given the inverse A^{-1} of the matrix A , this provides

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

Eq. 8

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 model, the approach of Mackay (1981) is used to estimate the generalized inverse.

If the set of equations is over-determined (more equations than unknowns), and the equations are not consistent with each other, the generalized inverse method provides least squares estimates, which minimizes 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. However, it will not be a *unique* answer.

Of the terms Eq. 3 the production rate, P_i , is calculated as the product of B_i , the biomass of (i) and P_i/B_i , the production/biomass ratio for group (i). The P_i/B_i rate under most conditions corresponds to the total mortality rate, Z , see Allen (1971), commonly estimated as part of fishery stock assessments. The ‘other mortality’ is a catch-all term including all mortality not elsewhere included, e.g., mortality due to diseases or old age, and is internally computed from,

$$M0_i = P_i \cdot (1 - EE_i)$$

Eq. 9

where EE_i is called the ‘ecotrophic efficiency’ of (i), and can be described as the proportion of the production that is utilized in the system. The production term describing predation mortality, $M2$, serves to link predators and prey as,

$$M2_i = \sum_{j=1}^n Q_j \cdot DC_{ji}$$

Eq. 10

where the summation is over all (n) predator groups (j) feeding on group (i), Q_j is the total consumption rate for group (j), and DC_{ji} is the fraction of predator (j)’s diet contributed by prey (i). Q_j is calculated as the product of B_j , the biomass of group (j) and Q_j/B_j , the consumption/biomass ratio for group (j).

An important implication of the equation above is that information about predator consumption rates and diets concerning a given prey can be used to estimate the predation mortality term for the group, or, alternatively, that if the predation mortality for a given prey is known the equation can be used to estimate the consumption rates for one or more predators instead.

For parameterization Ecopath sets up a system with (at least in principle) as many linear equations as there are groups in a system, and it solves the set for one of the following parameters for each group:

- biomass;
- production/biomass ratio;
- consumption/biomass ratio; or
- ecotrophic efficiency.

If, and only if, all four of these parameters are entered, the program will prompt you during basic parameterization whether to estimate the biomass accumulation, or, alternatively, to estimate the net migration rate. If a positive response is given, the program will use all the four basic parameters and it will establish mass-balance by calculating one of the two other parameters. If only three of the basic parameters are entered the following parameters must be entered for all groups:

- catch rate;
- net migration rate;
- biomass accumulation rate;
- assimilation rate; and
- diet compositions.

It was indicated above that Ecopath does not rely on solving a full set of linear equations, i.e., there may be less equations than there are groups in the system. This is due to a number of algorithms included in the parameterization routine that will try to estimate iteratively as many ‘missing’ parameters as possible before setting up the set of linear equations. The following loop is carried out until no additional parameters can be estimated.

The gross food conversion efficiency, g_i , is estimated using

$$g_i = (P_i/B_i) / (Q_i/B_i)$$

Eq. 11

while P_i/B_i and Q_i/B_i are attempted solved by inverting the same equation. The P/B ratio is then estimated (if possible) from

$$\frac{P_i}{B_i} = \frac{Y_i + E_i + BA_i + \sum_j Q_j \cdot DC_{ji}}{B_i \cdot EE_i}$$

Eq. 12

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). The catch, net migration and biomass accumulation rates are required input, and hence always known;

The EE is sought estimated from

$$EE_i = \frac{Y_i + E_i + BA_i + M2_i \cdot B_i}{P_i},$$

Eq. 13

where the predation mortality $M2$ is estimated from Eq. 10.

In cases where all input parameters have been estimated for all prey for a given predator group it is possible to estimate both the biomass and consumption/biomass ratio for such a predator. The details of this are described in Appendix 4, Algorithm 3.

If for a group the total predation can be estimated it is possible to calculate the biomass for the group as described in detail in Appendix 4, Algorithm 4.

In cases where for a given predator j the P/B , B , and EE are known for all prey, and where all predation on these prey apart from that caused by predator j is known the B or Q/B for the predator may be estimated directly.

In cases where for a given prey the P/B , B , EE are known and where the only unknown predation is due to one predator whose B or Q/B is unknown, it may be possible to estimate the B or Q/B of the prey in question.

After the loop no longer results in estimate of any ‘missing’ parameters a set of linear equations is set up including the groups for which parameters are still ‘missing’. The set of linear equations is then solved using a generalized inverse method for matrix inversion described by Mackay (1981). It is usually possible to estimate P/B and EE values for groups without resorting to including such groups in the set of linear equations.

The loop above serves to minimize the computations associated with establishing mass-balance in Ecopath. The desired situation is, however, that the biomasses, production/biomass and consumption/biomass ratios are entered for all groups and that only the ecotrophic efficiency is estimated, given that no procedure exists for its field estimation.

3.3.2 The energy balance of a box

A box (group) in an Ecopath 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. The basic Ecopath Eq. 1 includes only the production of a box. Here production equals predation + catches + net migration + accumulated biomass + other mortality. When balancing the energy balance of a box, other flows should be considered. After the ‘missing’ parameters have been estimated so as to ensure mass balance between groups energy balance is ensured within each group using the equation

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food}$$

Eq. 14

This equation is in line with Winberg (1956) who defined consumption as the sum of somatic and gonadal growth, metabolic costs and waste products. The main differences are that Winberg (along with many other bioenergeticists, see Ney, 1990) focused on measuring growth, where we focus on estimating losses, and that the Ecopath formulation does not explicitly include gonadal growth. The Ecopath equation treats this as included in the predation term (where nearly all gonadal products end up in any case). This may be a shortcoming, but it is one that can be remedied fairly easily, and actually is in Ecosim (see section 9.5.20, ‘Food allocation between growth and reproduction’ on page 104).

We have chosen to perform the energy balance so as to estimate respiration from the difference between consumption and the production and unassimilated food terms. This mainly reflects our focus on application for

fisheries analysis, where respiration rarely is measured while the other terms are more readily available. To facilitate computations we have, however, included a routine ('alternative input') where the energy balance can be estimated using any given combination (including ratios) of the terms in the equation above.

Ecopath can work with energy- as well as with nutrient-related currencies (while Ecosim and Ecospace only work with energy related currencies). If a nutrient based currency is used in Ecopath the respiration term is excluded from the above equation, and the unassimilated food term is estimated as the difference between consumption and production.

From Eq. 14 respiration can be estimated as a difference, and replace another parameter in model construction (see Help System, 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.

The mass balance constraint implemented in the two master equations of Ecopath (Eq. 1 and Eq. 14) should not be seen as questionable assumptions but rather as filters for mutually incompatible estimates of flow. One gathers all possible information about the components of an ecosystem, of their exploitation and interaction and passes them through the 'mass balance filter' of Ecopath. The result is a possible picture of the energetic flows, the biomasses and their utilization. The more information used in the process and the more reliable the information, the more constrained and realistic the outcome will be.

3.4 Defining the system

The ecosystems that can be modeled using Ecopath can be of nearly any kind: the modeler sets the limits. However, each system should be defined such that the interactions within add up to a larger flow than the interactions between it and the adjacent system(s). 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 originally left 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, i.e., they must correspond to what is generally known as 'functional groups'. Using single species as the basic units has clear advantages, especially as one then can use estimated or published consumption and mortality rates without having to average between species. On the other hand, averaging is straightforward and should lead 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 means of the component parameters, weighted by the relative biomass of the components. Often one does not, however, have all the data needed for weighting the means. In such cases, try to aggregate species that have similar sizes, growth and mortality rates, and which have similar diet compositions.

A procedure has been incorporated in FishBase (www.fishbase.org) which assembles, for any country, a list of the freshwater and marine fish occurring in different habitat types, and other information useful for Ecopath models (maximum size, growth parameters, diet compositions, etc.)

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 provide specific guidelines on how to make the groupings, as this may differ among ecosystems. Generally however, one should consider the whole ecosystem, e.g., for an aquatic model, one or two types of detritus (e.g., one to include mainly marine snow, the other discarded bycatch, if any), phytoplankton, benthic producers, herbivorous and carnivorous zooplankton, meio- and macrobenthos, herbivorous fish, planktivorous fish, predatory fish, etc., and that at least 12 groups are included, including the fishery (any number of fleets/gears), if any. But most important is the personal judgment of what is appropriate for your system.

Special consideration needs to be given to the bacteria associated with the detritus. One option, applicable in cases where no special emphasis needs to be given to bacterial biomass, production and respiration, is to disregard the flows associated with these processes, which are, in any case, hard to estimate reliably (see contributions in Moriarty and Pullin, 1987), and which tend to completely overshadow the other flows in a system. (In such cases, one assumes that the bacteria belong to a different, adjacent ecosystem linked to yours only through detritus export). Alternatively, bacteria can be attached to one or all of the detritus boxes included in a system. To do this, create a 'box' for the bacteria, and have them feed on one or several of the detritus boxes. (This is required because detritus, in the Ecopath model is assumed not to respire). Consider, finally, that there is no point including bacteria in your model if nothing feeds on them.

For an overview of the ecosystem concept in ecology, we suggest that you consult the book by Golley (1993).

3.5 Dealing with open system problems (species and fisheries that cross system boundaries)

For almost every defined Ecopath study area, there will be some species that have life cycles that take them outside the defined area for at least part of each year. Movements (exchange) of biomass across the area boundary can be of two types: dispersal, involving unidirectional movement of organisms to and from sink and source populations outside the study area; and migration, involving regular, repeated movements into and out of the area by the same individuals. These are fundamentally different processes, with very different policy consequences. Dispersal acts as an extra mortality agent and recruitment source independent of fisheries and other impacts in the study area, while migration exposes organisms from the study area to particular risks and opportunities for part of the time, without acting as a ‘permanent’ drain or source of those organisms. Dispersal can be represented in both Ecopath and Ecosim by setting immigration and emigration rates in the ‘migration’ tab in Ecopath; these rates are used in the Ecopath mass balance and are treated in Ecosim as unidirectional (non-migratory) dispersal rates. True migration is more complex to deal with, and Ecosim will give misleading answers if migration is represented only by immigration/emigration rates from Ecopath.

There are two broad options for dealing with directed migration to and from the Ecopath study area so as to avoid misleading predictions in Ecosim:

- (1) ‘diet import’ approach: for species that migrate to/from the study area for part of each year, include all fisheries/catches that impact the species, independent of whether these are taken within the study area. But set the diet import proportion to the proportion of time spent outside the system, and set remaining diet proportions to the diet proportions while in the system times the proportion of time spent in the system. Using this convention, Ecosim then will allow policy exploration of all fisheries that may impact the migratory species, and will treat the food intake rate (per biomass) as constant over time for the time spent feeding outside the system. Ecopath and Ecosim will ‘automatically’ account for reductions in prey impacts caused by the species for the proportion of time that the species spends feeding in outside areas. Note that the list of fisheries impacting migratory species can involve splitting fleets into ‘inside’ and ‘outside’ fishing components (which can be varied or ‘managed’ separately in Ecosim), to represent possible policy changes in where/when the migratory fish are harvested.
- (2) ‘model expansion’ approach: If it is considered unsafe to assume that food consumption rates obtained while outside the system (by migratory species) will remain constant in the future, then Ecosim must be provided information on possible changes in food organism populations in those outside areas. That is, the outside areas must be ‘internalized’ as part of the modeled system, by adding functional groups representing the outside food web structure. Often, adding such groups may simply mean replicating the initial Ecopath group structure, with the second set of groups labeled ‘outside species X’ and with diet matrix entries set so that the added groups feed on one another but not on the ‘inside’ groups.

A good modeling tactic is to try both approaches and see whether they give different answers. However, note that the first approach can lead to misleading answers upon entry to Ecospace, if the Ecospace mapped area includes the ‘outside’ system: in that case, the model will continue to ‘import’ part of the diet and food consumption of migratory species. Thus when the model development plan includes use of Ecospace to represent a larger spatial system, the functional group organization for that larger system needs to be included in the initial Ecopath/Ecosim model definition (approach 2).

It is possible to incorporate migration in Ecospace by defining which groups migrate and where their concentration is by month, see ‘Representing seasonal migration in Ecospace’ on page 129 for further information.

4. Using Ecopath

Constructing an Ecopath model is like taking a refresher course in ecology. In the construction, main emphasis is on ecological relationships, not on the ‘modeling’ *per se*. This feature has been made very clear by the many courses and workshops conducted up to now, (see www.ecopath.org).

At a number of universities, (e.g., at the Fisheries Centre, University of British Columbia, Canada) Ecopath with Ecosim is being used as a part of the curriculum. For instance by letting students work with test data sets, or as

teamwork where the students are assigned different parts of an ecosystem, each group securing input parameters from fieldwork or the literature, while the final model construction is done *in plenum*. Construction of Ecopath models have also shown very useful for graduate studies, and to date more than a dozen MS and Ph.D. theses have been completed using Ecopath as a structuring tool with many more underway.

When constructing a model, information is needed of the trophic interactions of the entire ecosystem and this encourages cooperation between, e.g., university researchers working on different ecological groups. As an example, production of prey must be sufficient to meet the requirements of the consumers. Therefore researchers who may perhaps otherwise remain focused on ‘their’ groups of organisms must communicate, which may lead to cooperation, hypothesis testing, and other good things such as, publications presenting overviews of the important trophic flows in the system around a university field station.

4.1 Getting help

Pressing F1 at any time while running the Ecopath program will open the Ecopath help file and give you context-sensitive help. Should you have problems not easily solved using the help file or this guide we encourage you to contact us for support.

4.2 File handling

The basic concept for file management is: All data pertaining to a given Ecopath model (including its Ecoranger, Ecosim and Ecospace scenarios, its remarks, references, etc.) are saved in a Microsoft Access database (a standard type file with extension .mdb). When you install Ecopath with Ecosim the database will be saved in the ‘Program files\Ecopath with Ecosim\Database’ on your hard disk, assuming you have used the default folder setting for your Ecopath with Ecosim installation. The default name of the database is ‘Ecopath.mdb’, but you can change the location of the database and also use a database of a different name (as long as it is version 1.5 or later). You may want to do this if you for instance transfer a model to a new database. You can then open this other database and use it as your default database.

New: Select from the File menu or use the ‘blank sheet of paper’ icon on the main button bar. Use this option to create a new Ecopath model from scratch. When doing so, start by entering a unique title of the model you want to create. There will be a remark for the model indicating the date and time of model creation, and you may modify the remark at will (now or later).

Click OK, and the new model will be created. There will be one group initially, ‘Detritus’. You should keep this detritus group. YOUR MODEL MUST HAVE AT LEAST ONE DETRITUS GROUP. You can however rename the group if you so desire. This can be done by clicking the group name, or by selecting ‘Group information’ from the Edit menu. See the Edit menu for how to continue with creation of a model from scratch.

Open: Select Open to open an existing Ecopath model (with its associated Ecosim and Ecospace scenarios). You must create and mass-balance an Ecopath model before you can use Ecosim and Ecospace. After clicking Open, a sub-menu with the following options is available

- Open in Ecopath: Open an existing Ecopath model. You have to create and balance your Ecopath model before you can use Ecosim and Ecospace
- Open in Ecosim (and Ecospace): Choose this option only after you have balanced your Ecopath model. Ecosim and Ecospace build on the Ecopath model. If you want to use Ecospace you have to pass via Ecosim – Ecospace builds on and uses Ecosim routines. Also, if you change fishing pattern in Ecosim the changes will be carried over to Ecospace
- Change database: You can point to another Ecopath database. The database need not be named Ecopath.mdb, but must have the structure of this file; i.e. you cannot use any Access database as your Ecopath database. Only files that are created by Ecopath with Ecosim (newest version) can be used. When you select ‘Change database’ you will be prompted to either enter the path and name of the database you want to change to, or (recommended) you can browse to find the database you want. If you choose a version, which is not current or of a format that cannot be used you will be warned of this.

Transfer: You can transfer model to and from your existing Ecopath database. To do so select ‘Transfer’ from the file menu. A pop-up form will give you a choice between model import and export

- **Import a model:** Select to import a model from an existing Ecopath database.
 1. A pop-up form will then ask you to locate the Source database (Ecopath database with ‘.mdb’ extension).
 2. Once done the source will be displayed on the Import/Export model form. The field below will give the destination database, i.e., your default Ecopath database. The destination field is not enabled as you can import to your default database only.
 3. Next, click the arrow at the right hand side of the Model field, to display a drop-down list of the models in the source database. Select one model from this list and the importing will start.
 4. If some of the ‘short references’, (e.g., ‘Pongase 1993’) are found in both the source and destination database, a pop-up form will give you a choice of options as follows¹:
 - Change short reference: If you are for instance importing ‘Pongase 1993’, and you have another reference to a *different* paper with the same short reference, then use this option to change the short reference to, e.g., ‘Pongase 1993b’;
 - Use reference already in database: link the reference in your destination database to the short reference in your source database if the two short references refer to the same paper;
 - Always use existing reference: If you know you have all duplicate references in your database already select the option to ‘always use existing reference’;
 - Cancel.
- **Export a model:** Select to export *one* model (with all its scenarios, remarks and references) from your default database. You can only export one model to each new database, but once you have done so, you can change your Ecopath default database to the database you have just exported a model to, and then you can import as many models as you please to this database.
 1. A pop-up form will ask you to select the path and give the name of the database you want to export to. This should be a new and empty database that you create, not an existing database. If you select an existing file you will be warned that the existing file will be overwritten.
 2. The source mdb (your default Ecopath database) will now be displayed on the ‘Source’ line of the Import/Export model pop-up form. The Source field is not enabled and you cannot change the source. It must be your default database (which you however may change). The ‘Destination’ line of the form will show the database you selected above. Now, click the arrow at the right hand side of the ‘Model’ field, and select a model to export to the destination database from the list of models presented

Import text (.eii): You can import a text file with the ‘.eii’ (named after **E**copath **I**I) extension. If the ‘.eii’ has been exported from Ecopath with Ecosim it will include multiple fleet landings and discards, migration, and other input data. If from Version 3 or earlier it will only hold the raw Ecopath data as were used for those versions.

Locate the ‘.eii’ file you want to import and select ‘**O**pen’

A pop-up form will then show you a list of the existing model titles in your default database. Enter a title for your new model or simply accept the suggested title, which is based on the ‘.eii’ file name.

Select ‘**O**K’ to perform the import, or ‘**C**ancel’ to abort import.

Export text (.eii): Export a text file with .eii extension that will hold all input data for Ecopath. It will not include remarks, Ecosim and Ecosim scenarios and data.

Save: Saves the currently opened model to the database. It works like this: when you open a model it will actually be exported to a temporary database. This database will be located in your default temporary directory, which typically will be c:\windows\temp in a folder called Ecopath. It will have the name temp.mdb. Hence, the

¹ The reference system is presently disabled while we are working on a new system.

typical path is: c:\windows\temp\Ecopath\temp.mdb. As you edit your model the changes will be saved as you type along to the temporary database. When you save the model the temporary database will be transferred to replace the model that is in the database already.

If you exit without saving (you will be prompted to save if you have edited any data) the temporary database will not be transferred, and hence you will keep your model as it was when last saved.

You will need to save your model before using Ecoranger, Ecosim or Ecospace. If you are exploring options ('playing'), you can use 'Save as' from the file menu to work on a copy of your original model.

Save as: Save your model under a new name, i.e., create a new copy. If you enter the same name as previously a copy will not be made.

Rename: rename the model. This will not invoke any saving, and if you later exit without saving the original name will be maintained. The option is faster than a full saving as is invoked by 'Save' and 'Save as'.

Delete: Use to delete models. Will delete all information pertaining to a model, i.e. also the Ecoranger, Ecosim and Ecospace scenarios belonging to the model. References entered in connection with a model will not be deleted.

Print: From here you can select printer etc. If you use the 'Save' button on the button bar it will print using the default printer.

Close: Close the open model. You will be prompted to save if the model has been edited since last save operation.

Exit: Leave Ecopath with Ecosim

4.3 Edit menu

The edit menu is for editing of Ecopath input information for the model you have opened. The menu items are:

Units and model description: Define the units and enter a remark and reference describing the model. See 'Units and remarks'.

Group information: Can be assessed in two ways: either from the Edit menu or by clicking on a group name or by clicking on the 'Trophic mode' for a group. See 'Group information' for more details

Insert group, add multi stanza: You can add a new group by selecting 'Edit', then 'Insert Group' from the menu. You will be given an option where you want to insert the group. Remember that detritus groups must be placed after living groups. You can also use this interface to define multi stanza groups. When doing so make sure that the stanzas belonging to a given group get exactly the same group name.

Delete group: You can delete a group by selecting 'Edit', then 'Delete Group' from the menu. You will be given a list from which to select the group(s) you want to delete. Do not delete all detritus groups.

Sort groups: For rearranging the order of groups. You may do this manually, or (if you have performed basic parameterization, i.e. estimated the 'missing' parameters) you have the option of an automatic sorting after trophic levels, (with top predators listed first, primary producers as the last living groups followed by detritus groups). If you sort manually please take note that living groups must be placed before detritus groups.

Sorting after trophic level can facilitate identification of structures in the model. An example can be that you may see patterns in the mixed trophic impact analysis indicating cascading more clearly if the groups are sorted in this way

Aggregation: the number of groups included in the description affects a number of features of an ecosystem. 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. An 'automatic aggregation' routine was included in Ecopath 3 based on this suggestion, but has not yet been constructed for the new version.

Selecting 'aggregation' will lead you to a pop-up window, where you can choose pairs of groups to be aggregated. The aggregation itself involves calculation of a new biomass, production, consumption, trophic level, diet

composition, etc., and the new group resulting from the aggregation also gets a new group name. The first group resulting from an aggregation is called 'Aggregate 1', the second 'Aggregate 2', etc.

Aggregation may not aggregate all group specific information in Ecoranger, Ecosim and Ecospace scenarios. Check this carefully if you have existing scenarios in a model being aggregated.

It is advisable to save the aggregated model under a new name using 'Save as'.



Add fleet: See the fishery input forms.



Delete fleet: See the fishery input forms.

Alternative input: see section on 'Alternative input'

Ecotracer input: see description of the 'Ecotracer' module

Use prey preference from another model: If a model has been constructed (for a given, typically recent time period), and one wants to construct another model, (e.g., for an earlier time period) with the same ecosystem groupings this can be done by modifying the original model. Typically one would change the biomasses, catches, mortality rates, etc. Often however, diets are not known for earlier time periods. One may, however, hypothesize that prey preference will remain constant, even if prey abundance changes, i.e. that switching is not a dominant factor. If so, it is possible to let the program estimate diets for the new model through this menu option. The estimation is done using an iterative process that will ensure food preference is the same for all groups in the two models.

Group taxonomy: not yet fully implemented; will be used for database-driven model construction.

Catch codes: Used for allocating catches to the catch categories used in the Sea Around Us global catch database (www.seaaroundus.org).

Import group taxonomy from another model

Remarks: Remarks may be entered for the file as a whole, on the Units/remarks menu; for the Group names on the Group Info screen; and separately for most parameters and output forms.

You enter remarks by double-clicking the left mouse button while pointing to the cell on the spreadsheet for which you want to enter a remark, or by pressing <Enter> while the cursor is placed in the cell in question. For output forms select the Remark icon on the sub-toolbar.

You may enter a reference in addition to the remark. Remarks as well as references are extracted when you use the Ecowrite tool, and you can edit the remarks using Notepad (link provided) or other Windows text editors or word processors.

Entering of remarks is optional, but recommended, as it is an important part of the model documentation.

4.4 Units

There are two basic choices for the 'currency' of your model: energy-related units (which imply a respiration term), and nutrient-related units (which imply no respiration term). Only models constructed using an energy-related currency ($t \cdot km^2 \cdot year^{-1}$) can be run under Ecosim and Ecospace.

Selection of time unit does not influence any of the calculations in the software (except for determining whether Ecosim / Ecospace can be assessed or not, see above). It affects only the labels on tops of the output forms, etc.

The Remarks on this page are meant to refer to the entire model and/or ecosystem. These and the other remarks documenting most input and some output forms can be extracted and edited using the Ecowrite of Ecopath.

4.5 Group information

If you click the group name on the basic input form or select 'Group information' from the Edit menu, you will see a group information form where you can enter the information described below.

Required information is shown in **blue**, other information is recommended as it is relevant for model description and interpretation

Group name: you can enter up to 50 alphanumeric (letter or number) characters to describe the group. The name can be changed later if desired

Dead/Living: Specify if the group is a dead (detritus) or living group. Remember that detritus groups can only be placed after (i.e., below on the input form) living groups (higher group number).

In this version of Ecopath you must enter at least one detritus group. You can have as many detritus groups as you please. This is different from the DOS-versions, where only one all-encompassing detritus box, generated by the program, could be included. Includes non-living groups. It is possible to include several detritus groups, but all detritus groups must appear after the living groups.

It must be specified where the surplus detritus (that left after feeding by detritivores) will go to, see 'detritus fate'.

Proportion of production due to primary production (or trophic mode): Use the scroll-bar below the field to inform Ecopath of how much of the production that is due to primary production, (and hence need to be accounted for as part of the mass balancing). The proportion entered is transferred to the first column of the [input form](#).

Three different trophic modes may be distinguished: organisms completely dependent on external food intake (heterotrophs), organisms generating their own 'food' (autotrophs), generally through photosynthesis, and facultative consumers, capturing a part, and photosynthesizing the other part of their food, (e.g., corals, or tridacnid clams). In Ecopath, these three trophic modes (*TM*) are described by a range (of *TM* values), from 0 in autotrophs, to 1 in heterotrophs, and all facultative consumers in between, the *TM* value itself expressing the degree of heterotrophy. Thus for example, if $TM = 0.20$ and consumption $Q = Q/B * B = 2$ then the net energy or nutrient uptake is $Q / TM = 2 / 0.2 = 10$.

Primary producers are groups that capture energy through photosynthesis (when an energy-based currency is used) or 'capture' a nutrient, e.g., through nitrogen fixation. If the model currency is a nutrient, all plants, except those that capture the nutrient, will be treated as 'consumers'. The *TM* value will be 1 only for groups that introduce the nutrient into the ecosystem, e.g. through fixation by blue-green algae in the case of nitrogen.

Commercial fish/invertebrate: Specify whether the group is an exploitable fish or an exploitable invertebrate. This can be used in Ecosim to show how the total biomasses of these groups react to management options.

The screenshot shows the 'Group Information' dialog box. At the top, the 'Group name' is 'Epipelagics (mackerel, flyingfish)'. Below it, there are radio buttons for 'Dead' and 'Living' (selected), and a scroll bar for 'Prop. of production due to primary production' set to 0.00. There are checkboxes for 'Commercial fish' (checked), 'Commercial invertebrate', and 'Primary producer' (set to 1). A 'Remarks' field contains 'Just an example to illustrate group information' and a 'Reference' field contains 'Opitz 1993'. At the bottom, there is a table with three columns: 'Genus', 'Species', and 'Proportion of group'. The table contains the following data:

Genus	Species	Proportion of group
Chellopogon	atriisignis	.1
Hirundichthys	speculiger	.1
Cypselurus	simus	.05
Rastrelliger	kanagurta	.3

Buttons for 'Add' and 'Delete' are next to the table. At the bottom of the dialog are 'OK', 'Cancel', and 'Ref. details' buttons.

Exhibit 1. Group information form, click the 'Ref. details' to see the reference details, see Exhibit below.

Remark/reference: Enter a remark that describes the group. This information can be extracted later using Ecowrite – you can in essence write the manuscript that documents and discusses your Ecopath model from within Ecopath. Also give a reference to the source for the information for the group in question. There is a built in reference system in the Ecopath database, which already contains hundreds of references related to Ecopath².

Genus/species: Enter the scientific name along with the proportion of the biomass (or throughput) contributed by the species. The scientific name is the link to FishBase (Froese and Pauly, 2000), (www.fishbase.org); we are presently building a bi-directional bridge between FishBase and Ecopath. At present the first lane has been through a few generations, and it is available at the FishBase web site. The lane in the other direction has been operative for a long time, and is being used intensively by the FishBase team: you can see the result of this if you check out FishBase, there is a lot of information derived from Ecopath models that is now in FishBase. FishBase 2000 (and the web-version) has a facility for supplying Ecopath relevant information at the push of a few buttons.

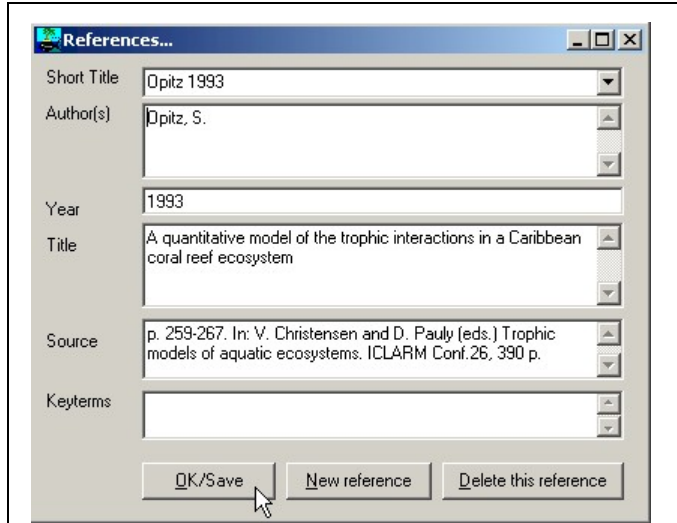


Exhibit 2. The EwE software comes with a large collection of references used for documenting previous applications, and new can be added by typing a new ‘short title’ on a remarks form. *The reference system is currently not activated.*

Ecopath with Ecosim: insert groups

	Group	Consumer	Producer	Detritus	Multistanza group name	Stanza no. (youngest=1)
1	Piscivorous birds	+				
2	Non-piscivorous seabirds	+				
3	Spot	+				
4	Striped bass YOY	+			Striped bass	1
5	Striped bass resident	+			Striped bass	2
6	Striped bass migratory	+			Striped bass	3
7	reef assoc. fish	+				
8	Bluefish YOY	+			Bluefish YOY	1
9	Bluefish adult	+			Bluefish YOY	2
10	Weakfish YOY	+			Weakfish YOY	1
11	Weakfish Adult	+			Weakfish YOY	2
12	Summer flounder	+				
13	Atl. croaker	+				
14	Menhaden YOY	+			Menhaden	1
15	Menhaden adult	+			Menhaden	2

Exhibit 3. Form for addition of new groups and definition of multi-stanza groups. Click the row number to insert a new group. Then enter a group name in the column marked ‘Group’, further click to indicate if the group is a consumer, producer, or a detritus group. The multi-stanza group name should be entered taking care to use the same spelling for all stanza. For mixed consumer/producers it is necessary to use the ‘Group information’ form (**Exhibit 1**) subsequently to specify a proper setting.

² We are currently updating the reference system, and it is currently not accessible. We hope to have a new version

Add/delete: Use these buttons to add or delete species.

Reference details: If a short reference has been entered or selected this button lead to the full reference information.

4.6 Other group manipulations (Edit menu)

4.6.1 Insert groups, add multi stanza

If you choose *Edit, Insert group, add multi stanza* (or press Ctrl + I) a form will appear where you can add new groups (click the row number) and also change the name of existing groups. If you insert a series a blank rows it is possible to cut and paste (use Ctrl + C and Ctrl + V, respectively), group names from, e.g., an Excel spreadsheet.

This form is also used to add and define multi stanza groups.

4.6.2 Delete groups

Groups can be deleted at any time by choosing *Edit, Delete Group* from the main menu. A form (Exhibit 4) will then be displayed, and the group(s) to be deleted can be chosen. The model will be closed after deletion to make sure that input forms are updated properly

4.7 Basic input

4.7.1 On the need for input parameters

Not all parameters used to construct a model need to be entered. The Ecopath model ‘links’ the production of each group with the consumption of all groups, and uses the linkages to estimate missing parameters, based on the mass-balance requirement of equation (1) that production from any of the groups has to end somewhere else in the system. This can be expressed, where there is not accumulation of biomass as

Production = Catch + biomass accumulation + predation mortality + net migration + other mortality

where the predation mortality term is the parameter that links the groups with each other. 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.,

$$\begin{aligned}
 P_1 &= Y_1 + E_1 + BA_1 + B_1 \cdot Q/B_1 \cdot DC_{11} + B_2 \cdot Q/B_2 \cdot DC_{21} + B_3 \cdot Q/B_3 \cdot DC_{31} + B_1 \cdot P/B_1 \cdot (1 - EE_1) \\
 P_2 &= Y_2 + E_2 + BA_2 + B_1 \cdot Q/B_1 \cdot DC_{12} + B_2 \cdot Q/B_2 \cdot DC_{22} + B_3 \cdot Q/B_3 \cdot DC_{32} + B_2 \cdot P/B_2 \cdot (1 - EE_2) \\
 P_3 &= Y_3 + E_3 + BA_3 + B_1 \cdot Q/B_1 \cdot DC_{13} + B_2 \cdot Q/B_2 \cdot DC_{23} + B_3 \cdot Q/B_3 \cdot DC_{33} + B_3 \cdot P/B_3 \cdot (1 - EE_3)
 \end{aligned}$$

Eq. 15

where, P_i is the total production of group i ; Y_i is the catches of group i , E_i is the net migration of i , and BA_i the biomass accumulation. DC_{ij} is the proportion of the diet predator group i obtains from prey group j . B_i is the biomass of group i ; Q/B_i is the consumption/biomass ratio of group i . P/B_i is the production/biomass ratio of group i ; EE_i is the ecotrophic efficiency, i.e. (1 - other mortality), of group i .

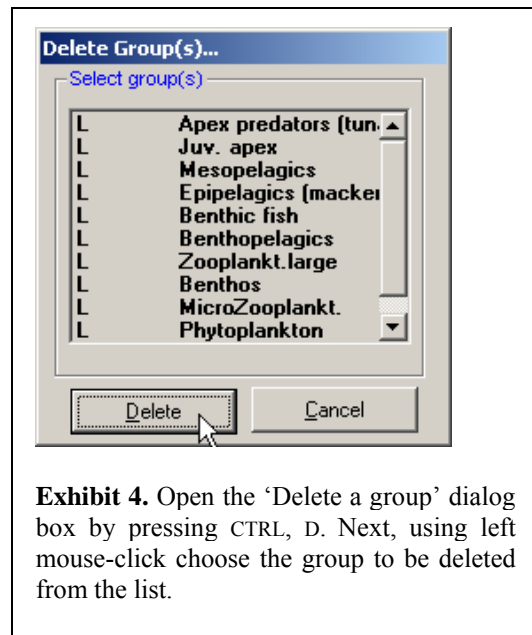




Exhibit 4. Open the ‘Delete a group’ dialog box by pressing CTRL, D. Next, using left mouse-click choose the group to be deleted from the list.

ready soon.

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

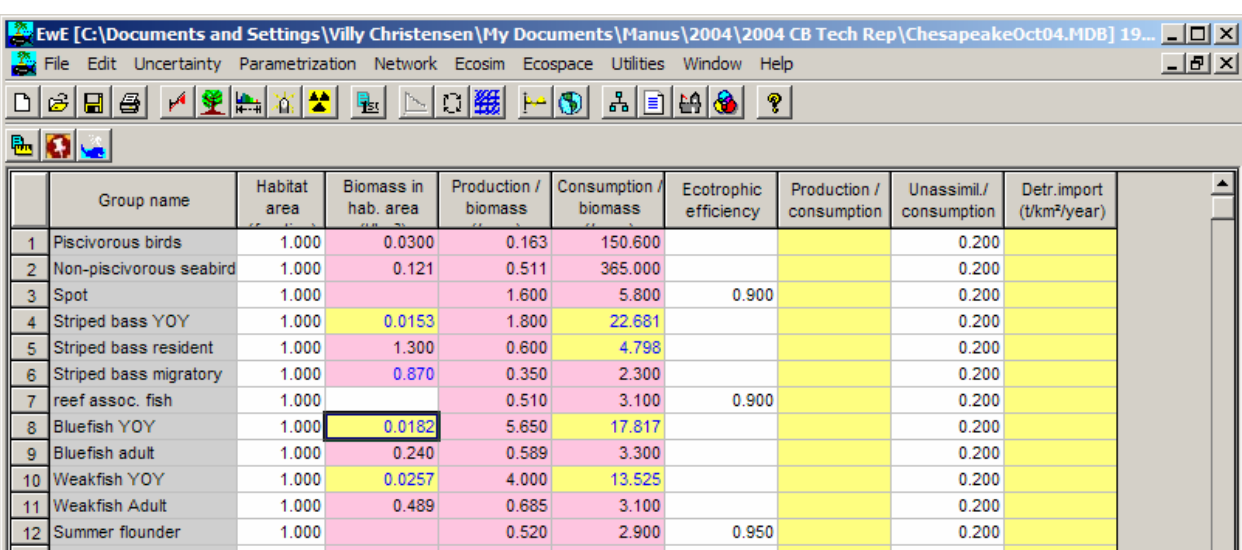
However, it is generally not possible to estimate the biomasses or P/B of apex predators from which there is no exports, or more specifically no fishery catches. Moreover, if too many input parameters are missing when estimating the basic parameters, a message to this effect will be displayed and the program will be aborted. In such cases, the data set will need to be complemented with additional inputs.

4.7.2 Basic input menu

The basic input menu is accessible from the Edit menu, or by pressing the input button on the first button toolbar . After you have entered all data continue with 'Parameterization' and 'Basic Estimates' from menu – or press  on main toolbar.

Click once with the left mouse key in the group name column to enter group information and remarks.

Of the four basic input parameters, Biomass, Production/Biomass ratio, Consumption/Biomass ratio and Ecotrophic Efficiency, the three must as a rule be entered. If all four are entered the program will assume that the ecotrophic efficiency is the most uncertain, and it will be recalculated.



	Group name	Habitat area	Biomass in hab. area	Production / biomass	Consumption / biomass	Ecotrophic efficiency	Production / consumption	Unassimil./ consumption	Detr.import (t/km ² /year)
1	Piscivorous birds	1.000	0.0300	0.163	150.600			0.200	
2	Non-piscivorous seabird	1.000	0.121	0.511	365.000			0.200	
3	Spot	1.000		1.600	5.800	0.900		0.200	
4	Striped bass YOY	1.000	0.0153	1.800	22.681			0.200	
5	Striped bass resident	1.000	1.300	0.600	4.798			0.200	
6	Striped bass migratory	1.000	0.870	0.350	2.300			0.200	
7	reef assoc. fish	1.000		0.510	3.100	0.900		0.200	
8	Bluefish YOY	1.000	0.0182	5.650	17.817			0.200	
9	Bluefish adult	1.000	0.240	0.589	3.300			0.200	
10	Weakfish YOY	1.000	0.0257	4.000	13.525			0.200	
11	Weakfish Adult	1.000	0.489	0.685	3.100			0.200	
12	Summer flounder	1.000		0.520	2.900	0.950		0.200	

Exhibit 5. Basic input form for an Ecopath model. The name of the current database is displayed at the title bar at the top. The pink coloring indicates the presence of a remark (accessible by double-clicking the cell). The cells with yellow background are blocked for entry. Multi-stanza groups (4-6, 8-9, 10-11) are blocked for direct entry, clicking them will open an input box where you can choose to enter a remark or edit multi-stanza parameters.

Habitat area (fraction): The fraction of the total area in which the group occurs, that is, the fraction of the total area to which the **biomass in habitat area** pertains. Default is that the habitat area is 1, i.e. that the group occurs in the total area

Biomass in habitat area (B): The average biomass per unit area in the **habitat area** where the group occurs. It is assumed that an average value can be used to represent the biomass of each group (this applies even if the biomasses, due to accumulation (or depletion, i.e. negative accumulation) do change during the time period covered by the model). Appropriate units should be used, (e.g., t/km²) for the biomasses. Entry of biomasses is optional for living groups but biomass(es) should be entered for the detritus group(s). However, if biomasses are unknown for all living groups and there are no exports from any of the groups, it is necessary to enter at least one biomass estimate, preferably of a top predator.

Biomasses should be entered relative to the habitat area where the group occurs. An example: assume a species for instance has a biomass of 1 t/km² in its habitat area, and the habitat area is 100 km², while the total area in your model is 1000 km². You should then enter a **habitat area** of 0.1 and a **biomass in habitat area** of 1 t/km² as the biomass for the group in your model.

Note that this 'new' parameter does not invalidate the entries of earlier models, whose biomasses were adjusted to overall area. Ecopath, in any case use the overall production and consumption values for the entire area.

Production/biomass ratio (P/B): Enter the P/B ratio for each group using consistent units, e.g., per year. The P/B ratio is equivalent to the instantaneous rate of total mortality ('Z') used by fisheries biologists (Allen 1971). Entry of P/B ratios is optional. Production itself is described in more detail elsewhere. Production includes fishery yield plus predation plus net migration plus biomass change plus other mortality; or $P/B = Z = F + M2 + NM + BA + M0$.

Consumption/biomass ratio (Q/B): Consumption/biomass ratios are entered using the same units as for P/B. Entry of consumption/biomass ratios is optional. Consumption is described in more detail elsewhere. The Q/B input box will be blocked (yellow color) for primary producers. If your model unit is carbon, you can however, click the yellow input box, and enter a Q/B value, which will be used to calculate respiration for the group.

Ecotrophic Efficiency (EE): The ecotrophic efficiency (EE) is the fraction of the production that is used in the system, i.e. either passed up the food web, used for biomass accumulation, migration or export. Ecotrophic efficiency is difficult to measure directly; it varies between 0 and 1, and can be expected to approach 1 for groups with considerable predation pressure. The part of the production that is not included in the EE is often called 'other mortality'. EE is dimensionless, and the entry of EE values is optional.

The ecotrophic efficiency, EE, of a detritus group is defined as the ratio between the flow out of a detritus box, and the flow into the same box. EE for detritus cannot be entered, it is always calculated.

Production/consumption (P/Q): expresses the ratio between production (P) and consumption (Q), and corresponds to what was called the gross food conversion efficiency (GE in the basic input screen of Ecopath versions 2 and 3). P/Q is thus a dimensionless parameter.

In normal cases, P/Q values will range from 0.05 to 0.3, i.e., the consumption of most groups is about 3-10 times higher than their production. Exceptions are top predators, e.g., marine mammals, which can have lower P/Q values, and small fast-growing fish larvae or nauplii or bacteria, which can have higher P/Q's. The value of the ratio is checked, in Ecopath, and warnings are given if production exceeds consumption (as it occur in corals and giant clams), or if the production exceeds half the consumption (which may be acceptable for bacteria, small nauplii and fish larvae, but usually not for other groups).

P/Q can only be entered if the production/biomass and/or the consumption/biomass ratio is left blank. If the production/consumption ratio is entered along with, e.g., the production/biomass ratio, then the consumption/biomass will be calculated as,

Consumption/biomass = (production/biomass) / (production/consumption).

Biomass accumulation (BA): Ecopath is not a steady-state model. If the biomass for a group is known, e.g., at the beginning of the year and at the beginning of the next year, the BA can be calculated as the difference between these biomasses. BA is a production term that can be entered for all living groups (default is 0), but is calculated for all detritus groups (see detritus fate). It is a flow term, with a rate unit of, e.g., t / km² / year. The default value for BA is zero indicating no biomass accumulation. A negative value signifies biomass depletion (biomass decreased during period modeled).

If B, P/B, Q/B and EE is entered for a group a prompt will ask during parameterization if you want to estimate BA. If you answer yes to this question the BA will be calculated, overruling any BA you may have entered.

Unassimilated/consumption (GS): Information of the fraction of the food that is not assimilated must be entered if the currency of your model is energy-related. Following Winberg (1956), a default value of 0.2 is suggested 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 (consisting of urine and feces) is directed to the detritus. For herbivores, the proportion not assimilated may be considerably higher, e.g. up to 0.4 in zooplankton.

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

The parameter for non-assimilated food is dimension-less, it is entered as a proportion. A routine checks whether the sum of gross efficiency plus proportion of food not assimilated exceeds 1, and displays a warning if so. Then, a new and consistent proportion for the non-assimilated food must be entered.

Detritus import: If there is import of detritus to the system, enter the quantity as a rate with a unit of, e.g., t / km² / year.

Generally, leaving an input blank on a data entry form implies it is unknown. This can also be made explicit by entering a negative value, (which will subsequently be blanked). For some required parameters defaults (usually of zero) are supplied; skipping over these means accepting the default values. This is the case for biomass accumulation, detritus import, landings, discards, migrations, and prices.

4.7.3 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, under the condition assumed for the construction of mass-balance models, equal to production over biomass (Allen, 1971). Therefore, one can use estimates of total mortality (Z) as input values for the production over biomass ratio (P/B) in Ecopath models. Some examples of how to obtain P/B values is given below.

Even if the parameter is labeled ‘production/biomass’ in EwE, what should be entered is actually the mortality rate. An example, if you have a juvenile group and use a bioenergetic model to calculate the production, you should subtract the amount that is recruited to the adult group from the production in order to the actual mortality, which is what Ecosim needs to work with.

4.7.3.1 Total mortality catch curves

Total mortalities can be estimated from catch curves, i.e., from catch composition data, either in terms of age-structured catch curves; (Robson and Chapman, 1961), or of length-converted catch curves (Pauly *et al.*, 1995). The estimation can be carried out using appropriate software for analysis, such as the FiSAT package (Gayaniilo *et al.*, 1996).

4.7.3.2 Total mortality from sum of components

Production rate is the sum of natural mortality ($M = M0 + M2$) and fishing mortality (F), i.e., $Z = M + F$. 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 , two parameters of the von Bertalanffy Growth Function (VBGF) and mean environmental temperature, i.e.,

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

Eq. 16

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

In equilibrium situations, fishing mortality can be estimated directly from the catch (or more precisely from the ‘yield’, which expresses catches (including discards) *in weight*):

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

where the yield is a rate, (e.g., t/km²/year), the biomass lacks a time dimension, (i.e., is expressed as t/km²), and thus the fishing mortality is an instantaneous rate, (e.g., per year).

4.7.3.3 Total mortality from average length

Beverton and Holt (1957) showed that total mortality ($Z = P/B$), in fish population whose individuals grow according to the von Bertalanffy Growth Function (VBGF), can be expressed by:

$$Z = P/B = \frac{K \cdot (L_{\infty} - \bar{L})}{\bar{L} - L'}$$

where L_{∞} is the asymptotic length, i.e., the mean size the individuals in the population would reach if they were to live and grow indefinitely, K is the VBGF curvature parameter (expressing the rate at which L_{∞} is approached), \bar{L} is the mean length in the population, computed from L' upward. Here, L' represents the mean length at entry into the fishery, assuming knife-edge selection. Note that \bar{L} must be $> L'$.

4.7.3.4 Production from empirical relationships

Production/biomass ratios for invertebrates based on empirical relationships is available in the 'Ecoempire' routine of Ecopath with Ecosim based on the relationships derived by T. Brey, Alfred Wegener Institute, Bremerhaven, Germany (Brey, 1999).

4.7.4 Consumption

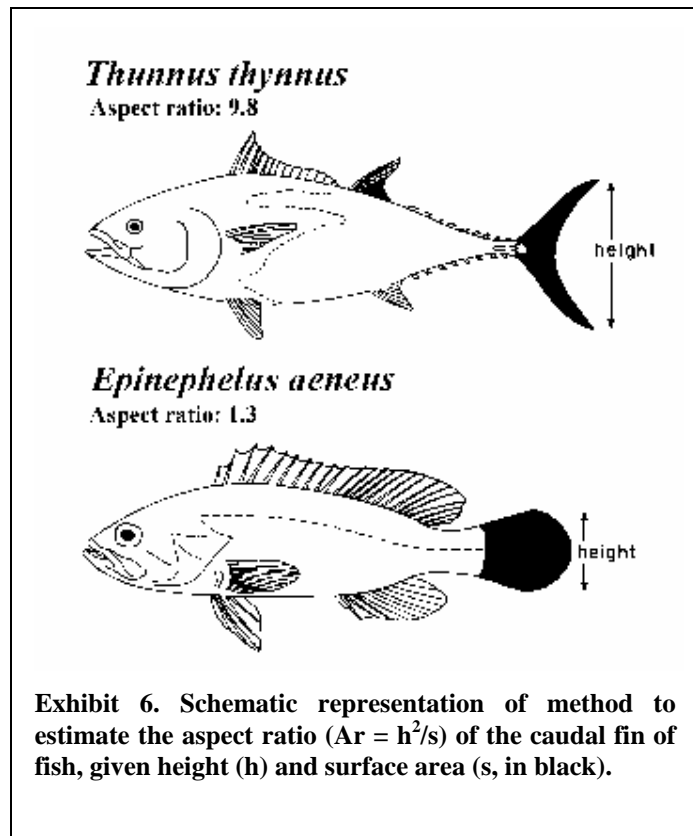
Consumption is the intake of food by a group over the time period considered. It is entered as the ratio of consumption over biomass (Q/B). Absolute consumption computed by Ecopath is a flow expressed, e.g., in t/km²/year, while the corresponding Q/B would be /year.

There are various approaches for obtaining estimates of the consumption/ biomass ratio (Q/B). They may be split 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.*, 1991c), or by combining laboratory and field data (Pauly, 1986).

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



Palomares and Pauly (1989; 1998) described based on a data set of relative food-consumption estimates (Q/B , per year) of marine and freshwater population ($n=108$ populations, 38 species) a predictive model for Q/B using

asymptotic weight, habitat temperature, a morphological variable and food type as independent variables. Salinity was not found to effect Q/B in fish well adapted to fresh or saltwater (other things being equal). In contrast the total mortality (Z, per year) showed a strong, positive effect on Q/B and also on the gross food-conversion efficiency (defined by $GE = Z / (Q/B)$), by affecting the ratio of small to large fish.

The authors present three related models (see Ecoempire for implementation in EwE):

$$\log(Q/B) = 7.964 - 0.204 \cdot \log W_{\infty} - 1.965 \cdot T' + 0.083 \cdot A + 0.532 \cdot h + 0.398 \cdot d$$

Eq. 17

($R^2=0.53$, 98 df), where, W_{∞} is the asymptotic weight (g), T' is an expression for the mean annual temperature of the water body, expressed using $T' = 1000/\text{Kelvin}$ (Kelvin = $^{\circ}\text{C} + 273.15$), A is the aspect ratio (see Exhibit 6), h is a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores), and d is a dummy variable also expressing food type (1 for detritivores, and 0 for herbivores and carnivores)

The equation was modified to investigate the effect on mortality on Q/B, and to derive predictive models of Q/B taking explicit account of different mortalities, values of Q/B were calculated using the equation above for mortalities corresponding to $f \cdot M$, where f is a multiplicative factor with value of 0.5, 1, 2 or 4, and M is the natural mortality rate that is estimated from Pauly's (1980) empirical relationship, (included in the Ecoempire relationships)

$$\log(Q/B) = 8.056 + 0.300 \log f - 0.201 \cdot \log W_{\infty} - 1.989 \cdot T' + 0.081 \cdot A + 0.522 \cdot h + 0.393 \cdot d$$

Eq. 18

($R^2=0.52$, 102 df), where f is the multiplicative factor introduces above, and the rest of the variables are as defined earlier. Note that in Palomares and Pauly (1998) Equation 12, the sign for the T' factor was reversed by mistake.

For cases where an estimate of total mortality, Z , (per year) is available the following relation may be used:

$$\log(Q/B) = 5.847 + 0.280 \log Z - 0.152 \cdot \log W_{\infty} - 1.360 \cdot T' + 0.062 \cdot A + 0.510 \cdot h + 0.390 \cdot d$$

Eq. 19

The models presented here updates the models derived from 33 empirical estimates of the consumption/biomass ratio (Q/B) for marine fishes, and published by the same authors in 1989.

This relationship can be used only for fish groups that use their caudal fin as the (main) organ of propulsion.

4.7.5 Other mortality

'Other mortality' is the difference between total production and the sum of export, biomass accumulation, net migration, and predation mortality. 'Other mortality' is called 'M0' in some other models. These may also include a term for mortality called 'M1', referring to the mortality caused by predator groups not explicitly included in the model. This kind of mortality can, in Ecopath, be considered a part of the net migration rate (the prey 'migrates' out of the system, and may then be eaten.) This normally should not cause problems if the recommendation is heeded to include, in Ecopath models, *all* the groups that occur in an ecosystem, not just some of them.

Other mortality consists of organisms dying due to diseases, starvation, etc., and the animals or plants concerned end up as part of the detritus. This mortality can be entered in Ecopath in form of the ecotrophic efficiency (EE), i.e., as (1 - other mortality). The ecotrophic efficiency is, thus, the proportion of the production that is used within the system. It is what is accounted for in Ecopath.


It is difficult to estimate EE independently, and few, if any, direct estimates appear to exist. Intuitively one would expect EE to be very close to 1 for small prey organisms, diseases and starvation probably being, for such groups, much less frequent than predation. For some groups, EE, may however, be low. It is often seen that phytoplankton simply die off in systems where blooms occur (EE of 0.5 or less). Also, kelps and seagrasses are hardly consumed when alive (EE of 0.1 or so), and apex predators have very low EE s when fishing intensity is low: many incidences of tunas or cetaceans simply dying and sinking have been reported from open oceans, and there are indeed abyssal organisms (such as ratfishes) specialized in feeding on such carcasses.

An *EE* of 0.95, based on Ricker (1968) was used for many groups in Polovina's original model (Polovina, 1984a) and in other, later models.

4.7.6 Alternative input

Following the second Ecopath master equation (Eq. 14):

Consumption = production + respiration + unassimilated food

Here, the standard operation in Ecopath is to enter consumption, production and unassimilated food, and then calculate the respiration. If desired, an alternative form for entry has been added in the data entry form. The alternative form can be selected from the Edit menu or by clicking the icon with the blowing whale  (respiring!). Respiration for primary producers and detritus can be included through this form only.

Using the 'Alternative Input' (AI) form you can choose to enter any of a wide array of input parameters for the selected group:

- Biomass
- Production/biomass
- Consumption/biomass
- Unassimilated/consumption
- Production/respiration
- Respiration/consumption
- Respiration/biomass
- Total consumption
- Total respiration
- Total production
- Total amount of unassimilated food

When you open the AI form information for the first group in your model will be displayed. Using the Up and Down arrows at the top of the form you can change to edit information for other groups.

The spreadsheet will initially show the input data that has been entered in your standard Ecopath input data form, if any. These are on the first five rows and are shown in blue. Further, variables that can be estimated based on the Ecopath input data will be displayed. If, for instance, for a group the biomass, production/biomass and unassimilated/consumption has been entered, the AI form will display biomass, production/biomass, unassimilated/consumption, production, and unassimilated food.

As you enter information a routine will check if more parameters can be estimated, and if so it will show the values for these in the spreadsheet.

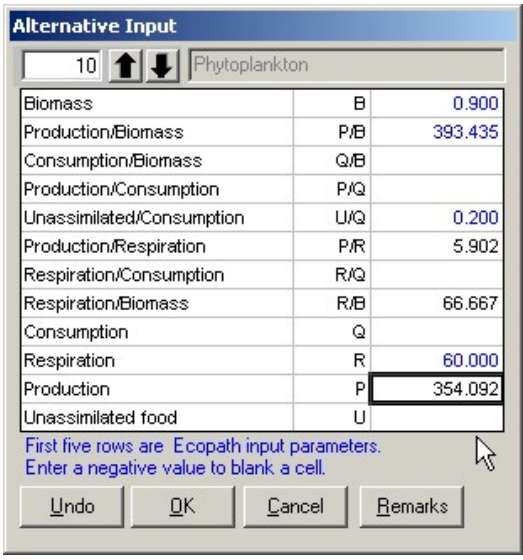
At the bottom of the AI form are a number of control buttons:

Undo: Undo entries and calculations

OK: Return to Ecopath input forms carrying over the information from the first five rows for all groups

Cancel: Return to Ecopath input forms without updating

Remarks: You can enter a remark, which will be part of the group information remark.



Alternative Input		
10		Phytoplankton
Biomass	B	0.900
Production/Biomass	P/B	393.435
Consumption/Biomass	Q/B	
Production/Consumption	P/Q	
Unassimilated/Consumption	U/Q	0.200
Production/Respiration	P/R	5.902
Respiration/Consumption	R/Q	
Respiration/Biomass	R/B	66.667
Consumption	Q	
Respiration	R	60.000
Production	P	354.092
Unassimilated food	U	

First five rows are Ecopath input parameters.
Enter a negative value to blank a cell.

Undo OK Cancel Remarks

Exhibit 7. Alternative input' form. Respiration for phytoplankton and for detritus can only be entered through this form.

4.7.7 Representation of multi-stanza life histories in Ecopath and Ecosim

EwE users can create a set of biomass groups representing life history stages or stanzas for species that have complex trophic ontogeny. Mortality rates (M_0 , predation, fishing) and diet composition are assumed to be similar for individuals within each stanza (e.g. larvae having high mortality and feed on zooplankton, juveniles having lower mortality and feed on benthic insects, adults having still lower mortality and feed on fish). Users of this feature must enter baseline estimates of total mortality rate Z and diet composition for each stanza, then biomass, QB, and BA for one “leading” stanza only.

For Ecopath mass balance calculations, the total mortality rate Z entered for each stanza-group is used to replace the Ecopath P/B for that group. That is, the Ecopath master equation is interpreted as mass balance accounting for the mortality rate for the group ($EE \times Z = \text{sum of predation mortality rates}$, EE calculated for the group). Further, the B and Q/B for all stanza-groups besides the leading (entry) stanza are calculated before entry to Ecopath, using the assumptions that (1) body growth for the species as a whole follows a von Bertalanffy growth curve with weight proportional to length-cubed; and (2) the species population as a whole has had relatively stable mortality and relative recruitment rate for at least a few years, and so has reached a stable age-size distribution.

Edit groups representing stanzas of a species (or functional group)

Specify only one biomass and one consumption/biomass ratio
Mortality rates, $Z (=P/B)$, must be entered for all stanza

Name of species/functional group:

Calculate

Close

Cancel

Forcing function number for hatchery stocking:

Youngest stanza first, etc.

Biomass and numbers

Red: number
Blue: indiv. weight
Black: pop. biomass
Green: stanza separation

	Name	Age, start (months)	Biomass (t/km ²)	Z (/year)	Cons./biomass (/year)	
1	Striped bass YOY	0	0.013	1.8	23.077	Fishbase: median record L inf = 95.5 cm TL K = 0.2
2	Striped bass resident	12	1.300	0.6	4.792	QB from FB, W _{inf} 115760 g., carnivore
3	Striped bass migratory	84	1.157	0.35	2.300	t=10C (mostly offshore), carnivore

Exhibit 8. Multi-stanza input form. Three stanza are defined with the second being the leading stanza for input of biomass, and the third the leading for input of Q/B. Total mortality, Z or P/B, needs to be entered for all stanza.

Under the stable age distribution assumption, the relative number of age “a” animals is given by $l_a / \sum l_a$ where the sum is over all ages, and l_a is the population growth rate-corrected survivorship $l_a = \exp(-\sum Z_a - aBA/B)$ where the sum of Z 's is over all ages up to “a” and the BA/B term represents effect on the numbers at age of the population growth rate (e.g. the cohort born one year ago should be smaller by the factor $\exp(-aBA/B)$ than the cohort born “a” years ago, if the relative population growth rate has been BA/B for at least “a” years). Further, the relative biomass of animals in stanza s should be $b_s = (\sum_{a \text{ in } s} l_a W_a) / (\sum_{\text{all } a} l_a W_a)$, where $w_a = (1 - \exp(-Ka))^3$ is the von Bertalanffy prediction of relative body weight at age a.

Knowing the B for one leading stanza, and the b_s for each stanza s, the biomasses for the other stanzas can be calculated by first calculating population biomass $B = B_{\text{leading } s} / b_{\text{leading } s}$, then setting $B_s = b_s B$ for the other stanzas. QB estimates for non-leading stanzas are calculated with a similar approach, assuming that feeding rates vary with age as the 2/3 power of body weight (a “hidden” assumption in the von Bertalanffy growth model). This method for ‘extending’ biomass and QB estimates over stanzas avoids a problem encountered in earlier ‘split-group’ EwE representations, where users could enter juvenile biomasses and feeding rates quite inconsistent with the adult biomasses and feeding rates that they had entered. The internal calculations of survivorship and biomass are actually done in monthly age steps, so as to allow finer resolution than one year in the stanza biomass and mortality structure (e.g. larval and juvenile stanzas that last only one or a few months).

Multi-stanza groups are defined, and basic input information (Z , B , Q/B , BA) provided for the stanzas, by an editing interface in Ecopath. For initial definition of a multi-stanza population, select “insert/edit split group” under the edit menu. To edit the basic information for a multi-stanza group already in the Ecopath model, display the basic estimates tab (multi-stanza input information will be colored in yellow) and click on any input cell for that group. The editing interface has a “calculate” button that allows you to vary the Z , B , Q/B , and stanza age limit information, then re-calculate biomasses and Q/B s implied by stable age distribution assumption. Once an acceptable calculation is found, closing the editing interface causes an Ecopath input information update, and the model is closed (so as to facilitate reorganization of group code information in the access database).

In Ecoranger runs, biomasses and Q/B s for non-leading stanzas are recalculated using the stable age distribution method, overriding any random variation in these inputs that you might try to assign using the Ecoranger interface. That is, random variation is applied only to the Z and diet composition parameters for all stanzas, and to the B , Q/B , BA values for the leading stanza. This just means that Ecoranger does not recognize possible variation due to multi-stanza populations not being in a stable distribution state at the Ecopath reference time; this is not a particularly restrictive assumption considering the larger uncertainties in most models about the other basic input parameters.

On entry to Ecosim from Ecopath, the stanza age-size distribution information (l_a , w_a) is passed along and is used to initialize a fully size-age structured simulation for the multi-stanza populations. That is, for each monthly time step in Ecosim, numbers at monthly ages $N_{a,t}$ and body weights $w_{a,t}$ are updated for ages up to the 90% maximum body weight age (older, slow growing animals are accounted in an ‘accumulator’ age group). The body growth $w_{a,t}$ calculations are parameterized so as to follow von Bertalanffy growth curves, with growth rates dependent on body size and (size- and time-varying) food consumption rates. Fecundity is assumed proportional to body weight above a weight at maturity, and size-numbers dependent monthly egg production is used to predict changes in recruitment rates of age 0 fish. Compensatory juvenile mortality is represented through changes in Z for juvenile stanzas associated with changes in foraging time and predator abundances, as in previous split-group (Ecosim II) calculations.

In Ecospace, it is not practical to dynamically update the full multi-stanza age structures for every spatial cell (computer time and memory limits). The multi-stanza dynamics are retained, but the population numbers at age are assumed to remain close to equilibrium (changes in numbers at age associated with changes in mortality rates, foraging times, etc. are assumed to ‘immediately’ move the numbers-at-age composition to a new equilibrium). In practice, we have found that this moving-equilibrium representation of population numbers generally gives results quite close to those obtained when full age-size accounting is done dynamically, provided feeding and mortality rates do not change too rapidly. This is similar to the general finding with Ecospace that time predictions of overall abundance change are quite similar to those obtained with Ecosim, despite how the “dynamic” calculation in Ecospace is really just a stepwise movement toward predicted spatial equilibrium values for all variables.

Here are a few implementation issues that users of the multi-stanza capability should consider:

- (1) *How many stanzas?* The main computational burden of the full representation is in Ecosim, and this burden depends on the number of age classes accounted (calculated from K , Z for adult stanza) rather than the number of stanzas with distinct mortality/feeding patterns within the age structure. So the best advice we can give is to err on the high side. Add stanzas for each major ontogenetic shift in habitat use and diet (though larval stages can often be ignored due to low biomass, low impact on prey, and unlikely to show density-dependent effects). If necessary additional stanzas for size-age ranges that are subject to selective fishing impacts that might cause growth overfishing under some policy scenarios (growth overfishing can be a problem whenever juvenile fish are harvested over age ranges where they display accelerating growth in body weight, so cohort biomass is still increasing over the age range being fished).
- (2) *Representation of seasonality?* It is common for early juvenile stanzas to be completed within a short season each year. Yet Ecopath mass balance is based on annual average mass transfers. The initialization described above is based on “spreading” the seasonal effects evenly over the annual cycle (in monthly steps), and in practice this does not cause serious problems for the mass-balance calculation/Ecopath estimation. On entry to Ecosim, users can specify seasonal recruitment patterns and represent seasonal interaction dynamics in detail, but this generally forces care in all aspects of seasonality, (e.g., in prey productivity and availability as well as juvenile abundance). Generally we find that these more detailed calculations give about the same long term population dynamics as when recruitment is treated as aseasonal, except in scenarios that involve match-mismatch variation from year to year in the timing of

food availability relative to the timing of recruitment (so unless you specifically want to examine match-mismatch hypotheses, consider not bothering to include seasonality in the simulations).

- (3) *Representation of stanzas that occur outside the modeled system.* It is common, especially in models for coastal ecosystems, to have species that spend only part (or none) of their time in the system. For example, juvenile rearing may be in the modeled ecosystem, but adult foraging and harvest impacts may occur in outside areas. The preferred way to handle trophic/fishery impacts for such species in EwE is to treat part (or all) of the diet for outside-migrant stanzas as imported, rather than to model the movement into and out of the system as immigration/emigration rates. With the diet import convention, EwE will still handle overall fishery impacts at the population scale whether or not these impacts occur within the modeled system; all that will be “lost” is dynamic change in food availability (and feeding rates) and predation mortality of organisms during times when they are outside the modeled system (outside world treated as having constant trophic conditions). Most often, the stanzas that reside outside the modeled system are older fish, for which the assumption of constant resource availability and natural mortality risk may be quite reasonable. When it appears that using the diet-import convention is inappropriate due to changing trophic conditions outside the modeled system, then the modeled system should be extended to include the ‘outside’ trophic interactions of concern.

The multi-stanza representation is quite flexible, and users may find other ways to use it for effectively representing ‘problem processes’ in ecological systems. Such findings can be reported to www.ecopath.org for use by others.

4.7.8 Hatchery populations in Ecosim

Multi-stanza populations can be designated as hatchery populations, and hatchery production can be varied over time using time forcing functions. To turn off natural reproduction and replace it with a time series of hatchery stocking rates, open the multi-stanza editing interface for a population (click on any stanza parameter on Ecopath input form), and enter a nonzero value for the hatchery forcing function number (remember that forcing functions 4 and higher are for long-term, multiyear forcing).

Then at each simulation time step, the base recruitment for the population (calculated from Ecopath input parameters) will be multiplied by the current time value for the designated forcing function. A forcing function value of 1.0 corresponds to the stocking rate that would result in the Ecopath base abundance (biomass) entered by the user.

Note that forcing functions to represent historical changes in stocking rates can be entered via the same csv files as used to set up historical fishing and model fitting scenarios. Enter stocking rates as values relative to the stocking rate of 1.0 assumed for the Ecopath base year.

Note also that if it is desired to simulate stocking of older fish at some age like 18 months, the first stanza for the population should be set to have this duration, the mortality rate (Z or PB) for the stanza should be set to .001, and the diet for the stanza should be set to 1.0 imported (ie, do not have fish in the stanza feeding in the modeled ecosystem).

4.7.9 Diet composition

Must be entered. Enter diet composition, for all consumers, column by column. As you move the cursor across columns the name of the current consumer is indicated in a box at the bottom status bar. The diet should be expressed as the fraction each prey contributes (on a weight, energy, or volume basis) to the overall diet.

In Ecopath ‘import’ to a system is the consumption of preys that are not a part of the system as it is defined. Import is thus different from migration, which is a production term. Import is treated as a ‘prey’ in the diet composition, and should be entered as a fraction of the total diet. Import is entered as the last food item.



The diet compositions of each group should sum to 1, however it is possible to do the raising of diet compositions to 1 automatically. For guidance, the current sum of the fractions representing the food composition is summed at the last row. You can use the ‘raise to 1’ button () to raise a diet to unity. If diets do not sum to unity when you start basic estimation () you will be given the option of having the software do the raising for you, or to return to the diet to do it yourself.

Exhibit 9. Diet composition form, diets for consumers (in columns) are entered so as to sum to 1, this can also be achieved by pressing the ‘raise to 1’ button on the lower button bar.

In a trophic model such as constructed using the Ecopath approach and software, it is predation that links together the different groups in a system. What is consumption for one group is mortality for another. Therefore, information on predation is important for understanding the dynamics of ecosystems. Unfortunately, quantitative 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 ‘percent occurrence’ basis or as ‘dominance’, both of which are of little use for quantification of diets. What are needed are measures based on weight, volume or energy content of the preys, which are all equivalent (MacDonald and Green, 1983).

A warning about zero order cycles, i.e. boxes that feed on themselves (‘cannibalism’): avoid situations where the fraction of the food of a box taken from that same box exceeds 0.10. In such cases, it is advised to split the box into groups representing predator and prey stanza, e.g. adults and juveniles. This will not only reduce or eliminate a zero-order cycle, and the bothersome computational problems usually associated with such cycles, but also lead to boxes with better-defined characteristics (because adults usually have P/B ratios lower than those of juveniles). For Ecosim and Ecospace it is in any case advised to split top predators in multi-stanza groups as this makes their dynamic more realistic, provides insights on stock-recruitment relationship, and allows consideration of stage-specific habitat use.

4.7.10 Detritus fate

If there is more than one detritus group in the system, you must specify where the detritus left over after the detritivores have covered their food intake is to be directed. This can be specified on the ‘detritus fate’ form.

Surplus detritus can be directed to the same detritus group (as ‘biomass accumulation’) or to other groups, by entering the appropriate fractions directed to each detritus groups. If these fractions sum to less than 1, the remaining part of the surplus detritus will be exported out of the system.

4.7.11 Migration

Immigration: Migration into the area covered by the model. Must be entered as a non-negative value. Unit is a flow, e.g., t / km² / year.

Emigration: Migration out of the area.

The net migration is calculated as immigration less emigration. This means that net migration will be negative if there is more coming into the system than leaving it. This may seem contradictory but it should be remembered that a negative mortality yields an increase in population.

If B, P/B, Q/B and EE are entered for a group, a prompt will appear during parameterization asking if you want to estimate biomass accumulation. If you answer no to this, a new prompt will ask if you want to estimate net migration. If you answer yes, the program will estimate net migration, and you this estimated net migration for the further analysis.

Migration is not the same as import – emigration and immigration are production factors, while import is food consumption. See the section below on ‘Representing movement of organisms across modeled area boundaries due to migration and ontogenetic habitat shifts’ for more information on how to treat groups that moves in and out of the modeled area.

Fisheries biologists rarely consider migration, at least in biomass terms, and even more rarely quantify it. If the net migration is positive (immigration > emigration), but not included, the main effect will depend on the previous entries,

- if the production had been entered, the fraction of production directed toward the detritus will be overestimated, or
- if production was to be estimated, this estimate will be biased downwards.

4.7.12 Representing movement of organisms across modeled area boundaries due to migration and ontogenetic habitat shifts

We often want to model interaction dynamics in relatively small areas, that some species use only seasonally or for only parts of their life cycles. For example, models of Pacific coastal ecosystems usually need to include Pacific salmon that pass through coastal areas on their way from freshwater natal streams to high seas rearing areas. Marine birds often undertake hemisphere-scale migrations, and use any particular oceanic region for one season of the year.

There are two ways to represent such spatial biomass ‘flows’ across the model boundaries:

- (1) treat the migratory organism as part of the ‘system’ all the time in terms of some calculated impacts like fishing, but represent part of the feeding ecology of the species as occurring outside the system (by setting a high Ecopath diet proportion as ‘Import’ in the Ecopath diet composition matrix); or
- (2) treat the migratory flows as dispersal (immigration/emigration) rates across the system boundaries.

We strongly recommend that you avoid the second of these approaches, since Ecosim will treat immigration flows as purely ‘density independent’ (immigration biomass/time independent of abundance, emigration a constant proportion of abundance per time) rather than as part of the life cycle of organisms. In other words, the second approach effectively breaks any life cycle linkages or dependencies that you may want to represent. If you take the first approach, you will maintain life cycle dependencies, e.g. life-stage linkages (stock-recruitment linkages) for multi-stanza groups, and you will ‘oversimplify’ the model only to the degree of assuming that trophic relationships for individuals that migrate outside the modeled system are stable over time. Ecosim assumes that the ‘Import’ of food intake per biomass remains stable over time, no matter how much biomass may increase or decrease.

When you set a value, e.g. 0.4, for ‘Import’ in the diet matrix, you are in effect assuming that the predator for which you set this value obtains that proportion of its total food consumption from sources outside the system, (e.g., spends 40% of its feeding time outside the modeled system). Impact of fisheries (fishing rates F calculated from Ecopath catch inputs and modified in various ways for Ecosim scenarios) will be correctly accounted for no matter where you assume such fisheries actually take place, (e.g., at river mouths after maturing adult salmon have left your modeled oceanic feeding area), except possibly impacts associated with discarding (you need to be careful not to have the model make discards that actually occur outside the system available to organisms within the system as food).

For organisms that you want to represent as spending a high proportion of their time outside the modeled system, you need to be careful about a few other parameter settings:

- (1) make sure you do not set or calculate EE too high, if a high proportion of the organism's mortality actually occurs outside the system (M0 should be a relatively high proportion of total natural mortality if most mortality occurs 'elsewhere').
- (2) Make sure the Ecosim Group Info tab has reasonable settings for 'Fraction of other mortality sensitive to feeding time' (low setting for this if most of Mo occurs outside the system)
- (3) For multi-stanza groups, you may need to edit parameters on the Ecopath input form for multi-stanza groups to set a low value, (e.g., 0.1-0.5) for the 'recruitment power parameter' if the juveniles for a group spend some time 'outside' the system in a nursery area where they are subject to density-dependent juvenile mortality rate, (e.g., juvenile Pacific salmon abundance may be limited by freshwater nursery habitat, so that numbers recruiting to a coastal oceanic area can be practically independent of adult abundance in the oceanic area, especially if juvenile production is 'enhanced' by hatchery systems).
- (4) Migrations (Ecopath data input tab) into and out of the system should be set to zero unless there is real, 'permanent' addition of organisms from other populations and/or permanent dispersal out of the system.

Note that you should not need to change other basic parameters defining trophic ontogeny for split groups. When it is the very early juvenile stage that is spent in some rearing habitat outside your modeled area (e.g. a stream or coastal lagoon), you may model the effect of limiting factors within that rearing habitat just by adjusting the recruitment power parameter, without bothering to account factors such as 'Import' of food to the juvenile biomass while juveniles are in the rearing area (cumulative effect of such trophic development are automatically calculated when scaling the juvenile body sizes within Ecosim based on Ecopath juvenile pool biomass). You can also use a low recruitment power parameter to make juvenile recruitment 'flat' with respect to modeled adult biomass due to recruitment of juveniles from some adult population 'egg source' outside the modeled area.

4.7.13 Fishery information and non-market value

Ecopath with Ecosim is intended to lead to policy exploration for ecosystem-based fisheries management. To facilitate this, the routines have been designed to include biological and economical information for use in a rather simple bio-economical model.

To enter fishery related information click the fishery tab on the input forms. This will place a sub toolbar with three buttons and a drop-down list:

Sub-toolbar:



Add fleet: Select this to add a fleet/gear. Fleets may in this context be gears or other type of fishing units. Two different fishing villages may for instance be different fleets; or hook and line fishery may be one fleet, and gill nets another. You have to add fleets in order to enter catches. Add a fleet by pressing the icon with the boat



Delete fleet: To delete a fleet you should press the boat icon with a red X across. You will be prompted to enter the number of the fleet to be deleted, and again to confirm deletion.

Monetary unit: Used for display only. Select a currency from the drop-down list, or enter a new one.

The following tabs for entry of fishery information are now available:

Definitions of fleets: Use this to enter:

Name of fleet: The default names of fleets are 'Fleet1', 'Fleet2', etc. You can change the names by typing new names instead in the first column

Fixed cost (%): Cost of operating a fleet unit in the unit time defined in Ecopath (typically on annual basis). Enter this as a percentage of the total value of the fishery in the given year. The fixed costs are used for cost calculations in Ecosim and Ecospace simulations in combination with the entry of the next items. The definition of 'fixed' costs depends on the actual situation being modeled. To illustrate this consider some examples:

A new module of Ecospace, Ecosed, allows for effort reduction to nil in connection with simulating increase in protected areas from 0 to 100% of total area. As the last boats operating in a fleet cannot bear the total 'fixed' costs of the total fleet; they should only bear the 'fixed' costs that are independent of effort. For this type of application use the 'fixed costs' only for costs that are independent of effort at the fleet scale, for instance for the costs of management and monitoring, (and subsidies if there are fixed subsidies to the fleet). Costs that are capacity dependent in this situation be considered effort-related variable costs instead.

Effort can also be changed in Ecosim:

If the changes are relatively small, and intended to represent changes in effort with constant capacity, the fixed costs can be seen to represent all costs that are effort-independent at the boat-level. Examples are costs for management, monitoring, licenses, capitalization, and insurance. In this case the variable costs are costs that are directly related to effort, e.g., fuel costs.

If the changes are major, changing effort for a fleet drastically the procedure outline for Ecosed above should be adopted instead. Hence, consider the fixed costs to be effort-independent at the fleet level.

Effort-related variable costs (%): Represents costs that are a function of effort. The examples above give some guidance to how these should be defined. Enter the costs as a percentage of the total value of the fishery in the given year. Simulation in Ecosim with changes in fishing effort are entered relative to the base effort, hence if the effort is increased with, e.g., 10% the variable costs are assumed to increase 10% as well, whereas the fixed costs are assumed unchanged.

- Ecosim: use this for all variable costs;
- Ecospace: use this for variable costs that depend on effort, e.g., for gear costs (which mainly depends on how many hours the gears is used), but not for costs that depends on spatial effort allocation, e.g., sailing costs.

Spatially related variable costs (%): For Ecospace applications it is recommended to separate two forms for variable costs, effort-related and spatially-related:

Ecosim: does not include spatial considerations, so do not use this option. If it is used the effort- and the spatially related costs are simply added in the Ecosim calculations;

	Name of fleet	Fixed cost (%)	Effort related cost (%)	Sailing related cost (%)	Profit (%)	Total value (%)
1	Longline	0.0	40.0	40.0	20.0	100.0
2	Salmon Fishers	0.0	40.0	40.0	20.0	100.0
3	Herring Gill/Seine	0.0	40.0	40.0	20.0	100.0
4	Seal control	0.0	40.0	40.0	20.0	100.0

Exhibit 10. Fleet definition form where any number of fleets/gears can be define, click the boat on the lower button bar to enter an additional fleet, or the boat with the red X across to delete a fleet/gear. The yellow background on the profit column indicates that the profit is calculated and cannot be entered. The total value is derived by summing the products of the landings and their prices.

Ecospace: costs that depend on spatial effort allocation, e.g., sailing costs.

Profits (%): profits as percentage of value, calculated from total value less all costs. Cannot be entered directly.

Total value (%): the total value is calculated as the value of all landings (as entered on subsequent forms). It is displayed here only to indicate that the '100 %' relates to value, not to total costs.

Grid specific cost (per unit effort): A scaling factor that is multiplied with the cost of fishing entered for individual grids in the basemap of Ecospace. Unit effort is the effort in the Ecopath model (typically effort over one year).

Landings: Landings and catches are not the same, discarding is an integral part of most fishing operations. Ecopath calculates:

$$\text{Catch} = \text{landings} + \text{discards}$$

You should therefore enter only the landings here – while any discards should go onto the following tab. Landings must be expressed as flows, typically in t/km²/year. The area to be used should be the total area of your model, not just a habitat area, or the area in which the fleet operates. If you for instance are entering information for a coastal shrimp fishery, the landings (and discards) should be calculated relative to the total area of the model – even if most of it is too deep for trawling.

In a model of an ecosystem exploited by a fishery, the catch is the total withdrawals over the time period considered in the model, (e.g., a year), for each of the groups modeled. Similarly, in an aquaculture system the 'catch' is the harvest from each group over the time period considered, (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 when defining the system to be modeled, either as a geographical/political region or as an ecosystem. It is necessary to consider the availability of appropriate catch data when taking such decisions. The origin of data can be specified using the 'Pedigree' routine of Ecopath.

The catches together with other export sum up to the total export. Catches are also used to estimate the fraction of primary production that is utilized in the system (i.e., the 'gross efficiency of the fishery').

Discards: Discarding is a normal practice in most fisheries. If you do not enter any information, you are in essence stating that discarding does not take place. If discarding does take place this is worse than guessing! Thus, it is better to use information from similar fisheries in other areas or based on for instance interviews with fishers in your area. Discarding is important for ecosystem models, which do not treat the target species as if they existed in a vacuum. An example may be shrimp fisheries where the discards include predators on shrimps that may be turned into food for shrimps. A trophic ecosystem model can be used to quantify the role of discarding in such systems.

Discard fate: Ecopath needs to be told what to do with the discards you enter as part of the catches. Discard can either go to a detritus group or be exported. Discard fate is entered as a proportion, i.e., a value between and including 0 and 1, representing the fraction of the discards that is directed to a given detritus group. If you are interested in quantifying the ecological impact of discarding it is recommended that you make a special detritus group called, e.g., 'Discarded fish' and direct the discards to this group.

Market price: Enter the market value (in the specified monetary unit per unit catch) for each group for each gear (fleet). It is not important whether the market values are entered in, e.g., Euro/kg or Euro/tonnes, as long as the entries are consistent between groups. The market prices are fleet-specific on the entry forms as quality and hence price varies more between fleets than within fleets.

Non-market price: Shadow price or non-market price represents the value of a resource in the ecosystem, e.g., for non-exploitative uses. Values should be expressed in monetary units per unit biomass. At present it is assumed that there is a linear relationship between the biomass of a resource and its non-market price (if there is any). Hence, for groups with a non-market price it is assumed that a doubling in biomass will lead to a doubling of the resource's non-market value.

Fleet size dynamics: see section 9.5.9, 'Fleet and effort dynamics' on page 96.

4.7.14 Growth

Given information about growth and mortality rates the size (or rather the weight distribution) for all components of a system can be straightforwardly computed. This lead to a system weight distribution, or a Particle Size Distribution (PSD) as it has been labeled since it was described by Sheldon et al. (1977) based mainly on planktonic

	Group	a in LW	b in LW	Loo (cm)	Woo (g)	K in VBGF (1/year)	t ₀ in VBGF (year)	Age first capture (year)	Max. age (year)
1	Transient orca	0.010	3.000						183.511
2	Toothed whales	0.010	3.000						64.452
3	Baleen whales	0.010	3.000						45.786
4	SSL embryo	0.010	3.000						0.500
5	SSL pups	0.010	3.000						1.583
6	SSL juveniles	0.010	3.000						4.667

Exhibit 11. Form for entry of growth and related statistics for use in deriving particle size distributions (PSD). Input is not required for Ecopath and Ecosim runs in general.

size counters. The information required for this is described below while the calculations are outlined in the Parameter Estimation section.

The information for calculation of the PSD is accessible through a spreadsheet on the basic input form. They are:

a in LW: the scaling factor in the standard length-weight (LW) relationship, $W = a \cdot L^b$. A default value of .01 is supplied (for commonly shaped (fusiform) fishes, which assumes length to be in cm and weight in g);

b in LW: the exponent in the LW relationship. A default value of 3 is supplied;

Loo: the asymptotic length (in cm). If L_{inf} is entered the asymptotic weight (W_{inf}) will be calculated from the LW relationship. If so, the calculated value will be highlighted.

Woo: the asymptotic weight (in g). See L_{inf} above;

K in VBGF: the curvature parameter of the von Bertalanffy Growth Function (VBGF).

t₀ in VBGF (year): the time at which length is zero in the VBGF. A default value of -0.1 year is supplied;

Age at first capture (year): time at first capture. Up to this age only the non-fishery related mortalities are used to calculate survival, from then on the total mortality rate is applied;

Max age (year): defaults are calculated using the empirical relationship of Hoenig (1983), derived based on a large number of aquatic animals (mollusks, fish and cetaceans), see Pauly (1984): $t_{max} = \exp[(\ln Z) - 1.44]/(-.984)$; where Z is the P/B ratio. For multi-stanza groups this is the age at transition from one stanza to the next.

5. Addressing uncertainty

Most, if not all, Ecopath models constructed so far have initially been based on a single set of input parameters representing the mean for the model period, typically for a given year. The model constructor typically modifies the input parameters so as to obtain mass balance, and the outcome is a possible model of how the trophic model in the system may have been during the given year. 'Possible' in this context means that basic physiological and thermodynamic constraints are considered, but also that it is just one of many possible representations of the flows in the ecosystem.

A procedure as described above has heuristic value as the model constructor may gain knowledge of how ecosystem resources interact and also of the implications of changes in input parameters (something made explicit in Ecopath through a formal sensitivity routine quantifying the impact on all estimated parameters of changes in any of the input parameters). The procedure does, however, ignore the inherent uncertainty of input parameters. To account for this a resampling routine, Ecoranger, has been designed to accept input probability distributions for the biomasses, consumption and production rates, ecotrophic efficiencies, catch rates, and diet compositions.

5.1 Ecoranger

The Ecoranger module allows entry of a range – hence the name – and mean/mode values for all the basic parameters, i.e., for the biomasses, consumption rates, production rates, ecotrophic efficiencies, and all elements of the diet compositions. Alternatively, default values for the ranges may be used (see below).

Random input variables are then drawn using user-selected frequency distributions (uniform, triangular, or normal) for each parameter type, and the resulting model is then evaluated (based on user-defined criteria such as least sum of squared residuals (the default setting, see Exhibit 12) and physiological and mass-balance constraints).

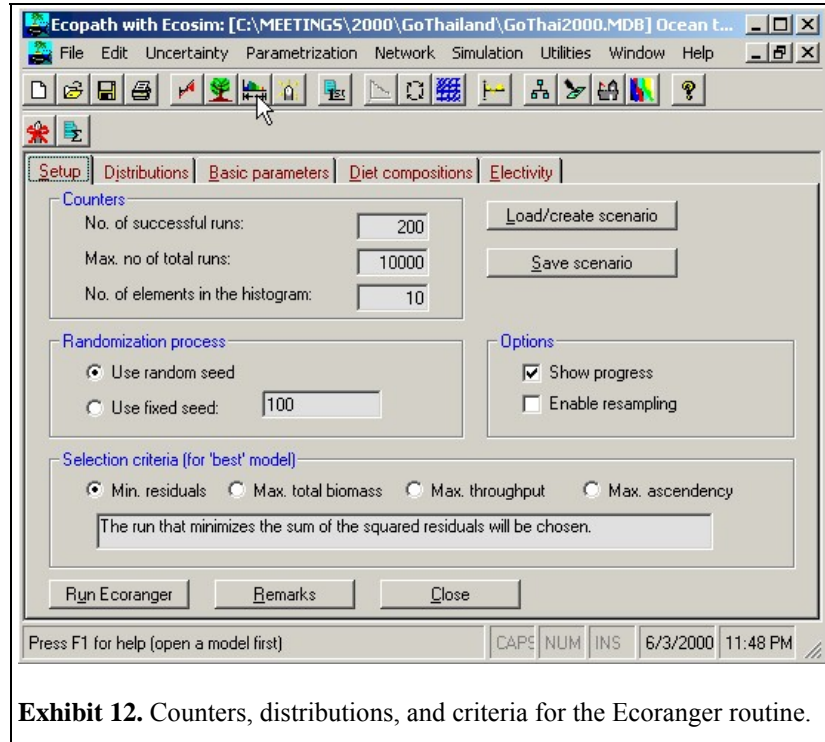


Exhibit 12. Counters, distributions, and criteria for the Ecoranger routine.

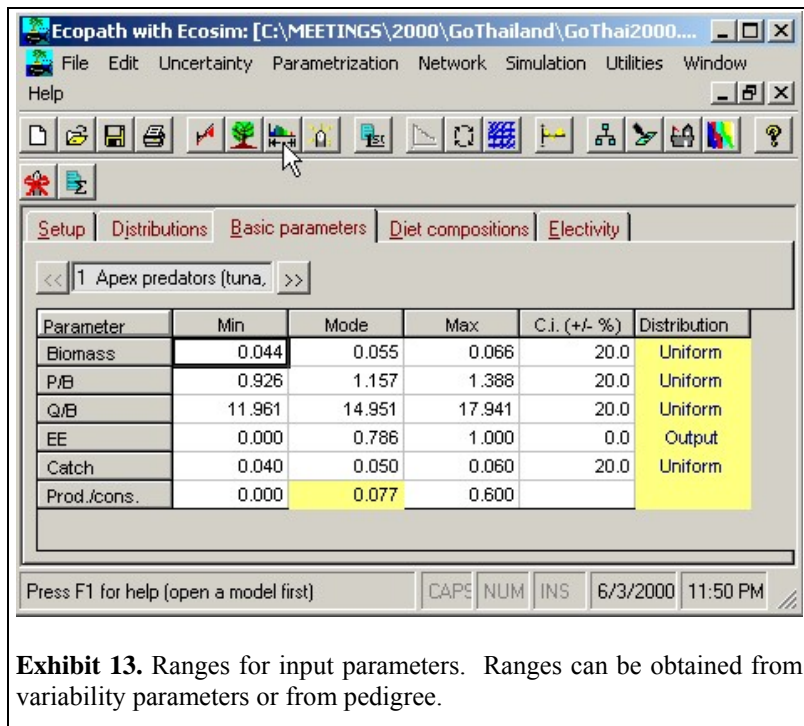


Exhibit 13. Ranges for input parameters. Ranges can be obtained from variability parameters or from pedigree.

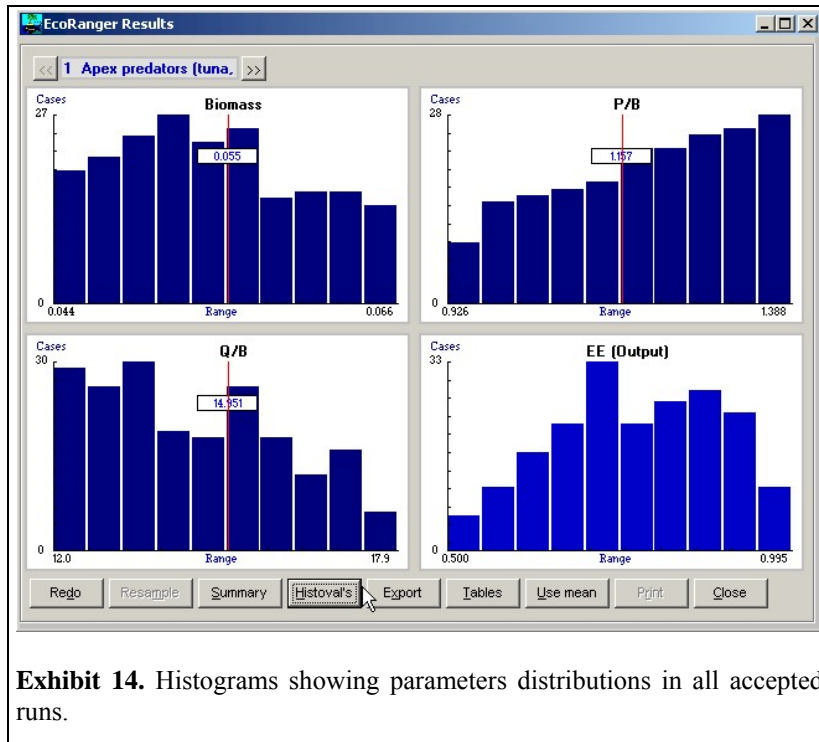


Exhibit 14. Histograms showing parameters distributions in all accepted runs.

The process is repeated in a Monte-Carlo fashion, and of the model runs that pass the selection criteria, the best-fitting one is chosen using a least square criterion. If the 'Min. residual' option is chosen, this results in a 'best' model in the least square sense, which can then be used for further analysis, and whose characteristics can be studied. Notably, a global goodness-of-fit (R_E), is calculated along with parameter-specific indices (r_e) for each of the model inputs. Further applying a Sampling-Importance-Resampling, SIR scheme it is possible to derive what may be called 'Bayes' marginal posterior distribution' (see Section 5.1.1). The SIR scheme was developed by McAllister et al. (1994). A summary is also given of the parameters in all the accepted runs.

The Ecoranger module thus introduces a statistically based

approach to fitting of Ecopath models, and most importantly, it helps you select the model that best fits a given set of constraints. Alternatively it is also possible to select a best fitting model that will either have the maximum total system biomass, maximum ascendancy or maximum throughput giving constraints.

The Ecoranger can be a help to parameterization even when the models do not balance by producing a summary of what went wrong in the rejected run. This aspect is discussed on page 48.

5.1.1 Labeling probability distributions for Ecoranger

Ecopath computes values of some 'output' flow/biomass variables needed to provide mass balance (equilibrium in flows and biomasses) given 'input' values for other variables. Ecoranger allows the Ecopath user to specify probability distributions for the input variables, and uses a Monte Carlo procedure to sample from these input distributions so as to generate probability distributions of the output variables. Such Monte Carlo simulation procedures are perfectly acceptable (and indeed probably the most efficient) as a method for numerical assessment of probability distributions that are complicated functions of probabilistic inputs. A question has arisen about whether the Ecoranger output distributions can properly be labeled 'Bayes posterior distributions.'

Put in purely technical terms, the answer should be no, since strictly speaking, the Bayes posterior distribution for a parameter is the conditional distribution for the parameter given the data. The Bayes posterior probability assigned to parameter value b given a data set Y is the ratio $p_{(b|Y)} = p_{(Y|b)}pN_b / p_Y$, where pN is a prior probability assigned to b and p_Y is the total probability of obtaining Y (integrated over all possible values of the parameters, i.e. integral of $p_{(Y|b)}pN_b$ over all b values). If one thinks of the Ecopath inputs as Y and the Ecoranger probability specifications for Y as $p_{(Y|b)}$, there is an apparent resemblance to the Bayes posterior distribution since the Ecoranger simulation procedure also maps $p_{(b|Y)}$ from $p_{(Y|b)}$. But the mapping is not as simple as in Bayes formula above.

The Ecopath model structure provides a unique value of b for each input combination Y that is biologically feasible, and also defines combinations Y that would imply biologically impossible b values. Thus what Ecoranger does is generate the probability distribution for a transformation or function (b) of the input variables Y . That is, it finds the marginal distributions p_b of functions b_Y , given the distributions p_Y from which these functions b_Y are calculated. This is a perfectly valid probabilistic calculation, [a textbook case is find p_u given p_y and assuming $u = f_y$] whether or not a Bayesian interpretation is given to the p_b by viewing the p_Y 's as 'priors'. If the p_Y 's are viewed as Bayes prior credibility measures, then strictly speaking the p_b distributions generated by Ecoranger should be termed 'derived Bayes prior distributions for output parameters b '. Here, 'derived' means that p_b is derived from p_Y by using the fact that each Y value implies a unique b value, which has non-zero probability only if it is biologically feasible.

The screenshot shows the 'EcoRanger : Summary' window. The title bar reads 'EcoRanger : Summary'. Below the title bar, it says 'For first 50 failed runs: parameter causing failure'. The main content is a table with columns 'Criterion', 'Group', and 'Value'. The table lists 14 rows of data. To the right of the table is a 'Criteria' list with 5 items. Below the criteria is an 'Overall summary' section with statistics: Accepted runs: 200, Total runs: 806, Accepted (%): 24.81, and Min. residuals: 80.604. At the bottom of the window are 'Copy' and 'Close' buttons.

	Criterion	Group	Value
1	1	4	1.272
2	1	4	1.215
3	1	4	1.111
4	1	3	1.013
5	1	4	1.064
6	1	4	1.027
7	1	4	1.335
8	1	3	1.088
9	1	4	1.362
10	1	7	1.111
11	1	7	1.082
12	1	7	1.062
13	1	1	1.422
14	1	4	1.012

Criteria

1. $EE > 1$
2. Prod./cons. too high
3. $EE < EE_{min}$ or $EE > EE_{max}$
EE may have been recalculated, and thus can have changed
4. Output parameter is outside range
5. Electivity outside range

Overall summary

Accepted runs: 200
Total runs: 806
Accepted (%): 24.81
Min. residuals: 80.604

Exhibit 15. Summary of the first 50 failed runs in the Ecoranger can be used to pinpoint problematic parameter values. In this example the problem is the EE (criteria 1 and 3) of groups 3, 4, and 7.

This is a bit more than haggling over terminology. Suppose you provide a prior distribution for the b , pN_b , then compare this to the 'tighter' distribution p_b that is produced by the Ecoranger Monte Carlo process. You have clearly gained information about b . But this information did not come from gathering 'data' in the classical statistical sense. Rather, it comes from recognition of the structural relationship $b = f_Y$ that is defined in the Ecopath model. Combining this structural information with prior probabilities p_Y to generate p_b is like combining data with priors to generate posteriors in Bayesian statistics. But there are those who would argue that combining structural knowledge with prior probabilities should not be termed the same as combining data with priors.

To be safe and avoid silly arguments about Bayesian analysis and the nature of 'real data', Bayesian terminology should be avoided unless b values are to be predicted for which there are (1) particular observed values, and (2) likelihood functions for these observed values derived by analysis of the sampling process leading to the observed values. At least some Ecopath biomass assessments and their corresponding field estimates may be regarded in this way in the future. In this case, it will be necessary to be careful about the distribution form and distribution parameters specified in Ecoranger for such b values, since these distributions have to be regarded as likelihood functions $p(b_{measured} \cdot b_{true})$ rather than as specifications of prior belief about the true value.

Another Ecopath development that would move the methodology more directly into the traditional Bayesian approach would be the inclusion of Ecopath estimates of derived quantities not required for the mass balance solutions, but for which there are observed data or 'likelihood' expectations. For example, Ecopath could be used to predict rates of effective search for predators i on prey types j , as $a_{ij} = (Q_{i,j}) / (B_i B_j)$. If likelihood functions for the observed input values of such derived quantities are specified, then the product of such likelihood for any specific Ecopath input parameter combination Y is an additional measure of the credibility of that combination Y beyond the p_Y measures included using Ecoranger).

5.1.2 Sampling/Importance resampling

To include, as suggested above, likelihood functions for some b and derived quantities in the Ecoranger calculations, the Monte Carlo sampling procedure incorporated in Ecopath was made to include a

‘Sampling/Importance Resampling’ (SIR) scheme (see McAllister *et al.*, 1994). This procedure is very simple. The Monte Carlo simulations initially run; for each of the $k=1\dots n$ sampled parameter combinations $(Y,b)_k$, the $(Y,b)_k$ value and the likelihood function value (product of probabilities of observed values $b_{i,j}$, etc. given Y) L_k for the sampled combination are stored. Then by selecting the ‘Resample’ option (second *Command button* on Exhibit 14), the results from a subsample m of the trials, where the probability of each sample k being included in this subsample (resample) be just the sample ‘importance weight’ w_k , which is simply L_k divided by the sum of the L_k values over all n samples. There are more elaborate procedures for obtaining the w_k weights, but these only apply when the Y input samples are chosen from other distributions or criteria than the Ecoranger priors for these Y .

Suppose specified prior distributions p_b have been specified for the Ecopath derived variables (computed from Y variables), and that the product of these p_b values over b is treated as though it were the likelihood L_k in setting up an SIR algorithm. Then examine the (Y,b) subsample from the resampling process, you will generally find the sample distributions p_Y for the inputs to be different than originally specified; that is, including p_b information in the resampling process leads to the appearance that some information has been gained about the inputs Y as well as the outputs b . This information arises not from data in the traditional Bayesian sense, but rather from applying the relations between Y and b implied by the Ecopath functional structure. So what has been done, technically is finding the joint distribution for (Y,b) implied by the marginal priors p_Y and p_b under the relational constraints on (Y,b) implied by Ecopath structure. Describing this joint distribution using a standard technical term is not straightforward. One could call it a ‘joint prior’ or just the ‘joint distribution given Ecopath relations and constraints’. When the sample frequency distributions are plotted for individual Y and b parameters selected by the resampling process, each of these individual frequency patterns should be referred as the ‘marginal distribution under Ecopath’, and each distribution should only be referred to as a ‘Bayes marginal posterior distribution’ if the p_b has been structured explicitly as a likelihood function $p_b(\text{observed } b)$ for some particular observed values(s).

5.2 Pedigree: categorizing data sources

The Ecoranger module has been available for several years but only a few examples of its use have been published, and so far none has fully exploited its Bayesian capabilities. A major reason for this is that it was a very data intensive task to describe the probability distributions for all input parameters (including the diet compositions matrices). To facilitate this task and to make the process more transparent we have implemented a ‘pedigree’ (Funtowicz and Ravetz, 1990) routine that serves a dual purpose by describing data origin, and by assigning confidence intervals to data based on their origin (Pauly *et al.*, 2000).

The pedigree of an Ecopath input is here understood as a coded statement categorizing the origin a given input (i.e., the type of data on which it is based), and by the same token, specifying the likely uncertainty associated with the input.

The pedigree routine allows you to mark the data origin using a pre-defined table for each type of input parameters. An example pertaining to both production/biomass and consumption/biomass ratios is given in Table 1. The Ecoranger module can subsequently pick up the confidence intervals from the pedigree tables and use these as prior probability distributions for all input data.

The key criterion used here is that input estimated from local data (i.e., from the area covered by the model is question) as a rule is better than data from elsewhere, be it a guesstimate, derived from empirical relationships (see Ecoempire) or derived from other Ecopath models.

Specifying the pedigree of data used to generate Ecopath input is useful, for these reasons:

- to make users aware of the danger of constructing an Ecopath model mainly from input taken from other Ecopath models, pertaining to different areas or periods;
- to provide defaults for the Ecoranger routine of Ecopath, and thus allow explicit consideration of uncertainties in the input; and
- to provide a basis for the computation of an overall index of model ‘quality’, a model being of high quality when it is constructed mainly using precise estimates of various parameters, based on data from the system to be represented by the model.

These requirements are met here by three scales, one for biomass, one for P/B and Q/B estimates, and one for diet composition. Specific comments follow on each of these scales. Note that all the default values for the pedigree options suggested below can be changed on the 'Definitions' tab on the Pedigree form. On this tab an approximate 95% confidence interval is suggested for each

- Biomass
- P/B and Q/B
- Diet composition
- Catches

Biomass: This scale is based on the observation that biomasses are very hard to estimate accurately, and that guesses may easily be off by orders of magnitude. This also apply to biomasses estimates taken over from other models, where local conditions for a (group of) species may be different, and lead to biomasses differing by orders of magnitudes form these or one's system.

This scale also accounts for the fact that even the best stratified random trawl surveys estimate biomass with a precision of at best 70%, not to speak of the accuracy issues related to the catchability of the gear. Similarly, Virtual Population Analysis cannot be expected to perform any better.

#	Parameter	Index	Default c.i. (+/- %)
1	'Missing' parameter (estimated by Ecopath)	0.0	n.a.
2	From other model	0.0	80
3	Guesstimates	0.0	80
4	Approximate or indirect method	0.4	50-80
5	Sampling based, low precision	0.7	40
6	Sampling based, high precision	1.0	10

Production/biomass (P/B) and consumption biomass ratios (Q/B): This scale is based on the observation that P/B and QB are highly conservative parameters, which have characteristic values of different (group of) species. Thus, the output of empirical models (as incorporated on Ecoempire) will tend to be more reliable than guesstimates, and as well, than estimates from other models (which tend to have uncertain pedigrees).

#	Parameter	Index	Default c.i. (+/- %)
1	'Missing' parameter (estimated by Ecopath)	0.0	n.a.
2	Guesstimates	0.1	90
3	From other model	0.2	80
4	Empirical relationships	0.5	50
5	Similar group/species, similar system	0.6	40
6	Similar group/species, same system	0.7	30
7	Same group/species, similar system	0.8	20
8	Same group/species, same system	1.0	10

Diets: This scale is based on the observation that diet composition, even in the same species is highly variable between systems, and hence that locally observed diet composition –even if quantitative – are always better than observations from other systems, and/or species groups. However, even the best, most detailed local studies will generally fail to be weighted each as required in Ecopath, hence the need for subsequent adjustments.

#	Parameter	Index	Default c.i. (+/- %)
1	General knowledge of related group/species	0.0	80
2	From other model	0.0	80
3	General knowledge for same group/species	0.2	80
4	Qualitative diet composition study,	0.5	50
5	Quantitative but limited diet composition study,	0.7	40
6	Quantitative, detailed, diet composition study,	1.0	30

Catches: Accurate fishing catches are essential to an Ecopath model, and even guesstimates are better than leaving the catch field blank (and thus assuming catches of precisely zero).

However, here again, locally catch figures will be better than catches extracted from a global (FAO), or national database. There are catches that are complete, i.e., which include estimates for categories often neglected (sport, artisanal catches), for hard-to-estimate quantities (illegal catches) and for discarded by-catch, which is too often neglected.

The scales provided with each type of inputs are evoked when entering the data defining a new model. To assist users in completing this important step, the parameterization routine of Ecopath checks that pedigree indicators have been selected for all inputs of a model, and a message is displayed which lists, when appropriate, the group(s) for which pedigree indicators must still be clicked.

#	Parameter	Index	Default c.i. (+/- %)
1	Guesstimates	0.0	>80
2	From other model	0.0	>80
3	FAO statistics	0.2	80
4	National statistics	0.5	50
5	Local study, low precision/incomplete	0.7	30
6	Local study, high precision/complete	1.0	10

Thus, any Ecopath model for which basic parameters have been estimated will also have complete pedigree indicators for all the underlying inputs. These indicators are then used in two different fashions:

1. the approximate 95% confidence intervals associated with the indicators are passed on to Ecoranger, for which they provide the default, thus making this routine immediately accessible; and
2. the pedigree indicator scores (ranging from 0.0 to 1.0) are averaged over all parameters and functional groups of a model to provide an index of that model's 'quality'.

The reasoning behind (2) is that a model based on locally, well-sampled high-precision data. is of higher quality than a model whose input values were guessed, or taken over from other models (see contrasts in above scales).

We follow herein the logic of Funtowicz and Ravetz (1990) who closely linked the pedigree of estimates with the quality of models based thereon, (more details are available at www.alba.jrc.it/tahome/research/post_normal.html).

The pedigree index: Based on the options selected for each parameter for each group a pedigree index, P, can be calculated (once all entries have been made – the routine checks for this) as the product of all the pedigree parameter specific indices. The P scales between 0 and 1 (inclusive). It is calculated when the ‘Index’ command button on the Pedigree form is pressed, along with a measure of fit, see below.

Measure of fit: The pedigree index, P, will be, among other things, a function of the number of groups in the system. We are therefore also using a measure of fit, t*:

$$t^* = P \cdot \sqrt{(N - 2) / \sqrt{1 - P^2}}$$

where N is the number of living groups in the given model.

The pedigree index values are also used to calculate an overall pedigree index for a given model. The index values for input data scale from 0 for data that is not rooted in local data up to a value of 1 for data that are fully rooted in local data. Based on the individual index value an overall ‘pedigree index’ P is calculated based on

$$P = \sum_{i=1}^n \frac{I_{ij}}{n}$$

Eq. 20

where I_{ij} is the pedigree index value for group i and parameter j for each of the n living groups in the ecosystem; j can represent either B, P/B, Q/B, Y or the diet. To scale based on the number of living groups in the system, an overall measure of fit, t^* is calculated as,

$$t^* = P \cdot \frac{\sqrt{(n - 2)}}{\sqrt{1 - P^2}}$$

Eq. 21

	Group	Input parameter	Group	Estimated parameter	-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
1	1	Biom	1	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
2	1	Biom	2	EE	-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
3	1	Biom	4	EE	-0.311	-0.248	-0.186	-0.124	-0.062	0	0.062	0.124	0.186	0.248	0.311
4	1	Prod/biom	1	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
5	1	Cons/biom	2	EE	-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
6	1	Cons/biom	4	EE	-0.311	-0.248	-0.186	-0.124	-0.062	0	0.062	0.124	0.186	0.248	0.311
7	2	Biom	2	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
8	2	Biom	7	EE	-0.060	-0.048	-0.036	-0.024	-0.012	0	0.012	0.024	0.036	0.048	0.060
9	2	Prod/biom	2	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333

Exhibit 16. Results from sensitivity analysis. First line shows the impact changing biomass for group 1 has on ecotrophic efficiency for the same group.

The measure of fit is seen to describe how well rooted a given model is in local data. It addresses an often-aided concern of to which degree ‘models feed on models’, i.e., whether models are based on data from other models,

which again are based on data from other models, etc. We are presently in the process of describing the pedigrees of all published Ecopath models for which we have access to the model descriptions (over 100 cases).

5.3 Sensitivity

A simple sensitivity routine (sensu Majkowski, 1982) is included in Ecopath, see Exhibit 16. The routine varies all basic input parameters in steps from -50% to +50% and checks what effect each of these steps has for each of the input parameters on all of the ‘missing’ basic parameters for each group in the system. The output is given as:

(Estimated parameter - original parameter) / original parameter.

Some aspects of the mixed trophic impact routine resemble a sensitivity routine. Also, the Ecoranger can be seen as a form of a complex sensitivity analysis.

	Group name	Trophic level	Habitat area	Biomass in habitat area (t/km ²)	Biomass (t/km ²)	Prod./biom. (/year)	Cons./biom. (/year)	Ecotrophic efficiency	Production / consumption
1	Transient Orcas	5.36	1.000	0.00300	0.00300	0.020	7.400	0.000	0.003
2	Dolphins (Res. Orca)	4.11	1.000	0.0600	0.0600	0.040	7.300	0.602	0.005
3	Seals Sealions	4.38	1.000	0.400	0.400	0.160	8.100	0.960	0.020
4	Halibut	4.15	1.000	0.00400	0.00400	0.440	1.700	0.818	0.259
5	Lingcod	4.18	1.000	5.591	5.591	0.390	1.200	0.169	0.325

Basic estimates | Key indices | Mortalities | Consumption | Respiration | Niche overlap | Electivity | Search rates | Fishery

Press F1 for help (open a model first) | CAPS | NUM | INS | 28-Nov-01 | 13:00

Exhibit 17. Missing parameters (in blue on screen) have been estimated such that mass-balance is maintained. Red font calls for attention; in the example here it indicates that there are no groups eating transient killerwhales, more commonly read cells indicate values > 1, i.e. cases where demand exceeds production. Notice that the results forms have red cell borders to make output forms easier to distinguish from input forms (grey borders).

6. Parameter estimation, evaluation, and basic analysis

Once the basic input parameters have been entered as described in the previous section you may estimate the basic parameters by choosing *Parameterization*, *Basic estimates* from the main menu. The missing parameters will be estimated so that mass balance is ensured. Both input and **calculated** (with red font) parameters are displayed on the *Basic Estimates* form.

Problems in parameter estimation will be shown on message forms. If the parameter estimation was successful all tabs on the main Ecopath form will be enabled, along with all menu headings. It is now possible to proceed with all other analyses.

The parameter estimation program outputs a number of indices that may be of use for assessing the status of the overall ecosystem and of its constituent groups.

6.1 The estimation procedure

The estimation is performed using a number of algorithms and a routine for matrix inversion described in Section 3.3, on page 12 in general terms. (See also Appendix 4 in the Help system for computational aspects).

Once the program has estimated the parameters, the system balances the input and output of each group, using respiration for adjustments. The relationship used is:

$$\text{Consumption} = \text{Production} + \text{Respiration} + \text{Non-assimilated food}$$

where, Consumption is the total consumption of a group, i.e., $\text{biomass} \cdot (\text{consumption} / \text{biomass})$; Production excludes primary production, i.e., is defined by $\text{biomass} \cdot (\text{production} / \text{biomass}) \cdot (1 - \text{PP})$, where PP is the proportion of total production that can be attributed to primary production (thus $(1 - \text{PP}) = 0$ in plants, 1 in heterotrophic consumers, and intermediate in e.g. corals or tridacnid clams); Respiration is the part of the consumption that is not used for production or recycled as feces or urine. Respiration is nonusable currency, i.e., it cannot be used by the other groups in the system. Autotrophs with $Q/B = 0$ and detritus have zero respiration; Nonassimilated food is an input parameter expressing the fraction of food that is not assimilated, (i.e., is egested or excreted). For models whose currency is energy, the default is 0.20, i.e. 20% of consumption for all groups, though this is most applicable for finfish groups (Winberg, 1956). The non-assimilated food is directed to the detritus;

If the model currency is a nutrient, there is no respiration. Instead, the model is balanced such that the non-assimilated food equals the difference between consumption and production.

6.2 Parameter evaluation

The program estimates the missing parameters and a number of indices without further input. 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 forms. In the more serious cases, the parameter estimation 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 sections below may help you evaluate the results of a run.

Ecoranger, the Monte Carlo routine described above will help you identify problematic parameter values by pointing out what made runs fail.

6.2.1 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 (which are usually calculated). The values should be between 0 and 1 (inclusive). Here, a value of zero indicates that any other group does not consume the group in the system, and neither is it exported. Conversely, a value near or equal to 1 indicates that the group is being heavily preyed upon or grazed and/or that fishing pressure is high, leaving no individuals to die of old age. The whole range of ecotrophic efficiencies can be found in nature.

However, a generalization has emerged from previous modeling: for most groups, the *EE* should be close to one, the exceptions being top predators and primary producers (see the other sections on mortality for a discussion of these).

If, in a first run, any of the *EE* values are larger than 1, something is wrong: it is not possible that more of something to be eaten and/or caught than is produced. The problem can of course be due to the equilibrium assumption not being met, e.g., when the model includes a new fishery on a previously unexploited stock. Unless this is known to be the case, you should 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 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 into juveniles and adults, with the adults acting as predator on the juveniles. The juveniles must then have a higher production rate than the adults, as production is almost always inversely related to size. Splitting groups into juveniles and adults is also useful for the Ecosim discussed later.

It is advisable to make one change at the time when editing input parameters. Make that one change, rerun the *Basic estimates* routine, re-examine the run, and if necessary re-edit the data, etc. Continue with one change at a time until you get a run you consider acceptable. Make sure through the entry of remarks to record en route what you do and why.

An alternative routine for balancing is to use Ecoranger. This routine will use randomly selected parameter combinations to find possible models. Note that even Ecoranger will fail to balance a model if the initial set of basic input is very far away from a possible configuration, in such cases, Ecoranger will abort and display a list of the first 50 failed runs. By examining the list and checking what went run it is usually possible to pinpoint the most problematic input.

6.2.2 Ecotrophic efficiency of detritus

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

The fate of the detritus (*DF*) can be entered (Detritus fate form). If all detritus from a detritus group is directed to other detritus boxes the *EE* of the group will be 1.

Estimates of *EE* of less than 1 indicate that more is entering a detritus group than is leaving it.

Estimates of *EE* of more than 1 for a detritus group 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 consumption from that group. It will be necessary to examine the basic inputs that define production and consumption of the lower parts of the food web closely, and to examine whether more detritus should be directed to the detritus group.

Of importance for the flow to detritus is the parameter for non-assimilated food. The default value of 0.2 often underestimates egestion, especially for herbivores and detritivores. For instance that a value of 0.4 for zooplankton often leads to more reasonable respiration/biomass ratios than 0.2. Higher parameter values means that a greater flow is directed to detritus and less to respiration for a given group.

6.2.3 Are the 'efficiencies' possible?

Recall that the gross food conversion efficiency, *GE*, is defined as the ratio between production and consumption. In most cases, production/consumption ratios will range from 0.1 to 0.3, but exceptions may occur, (e.g., bacteria, nauplii, fish larvae and other small, fast-growing organisms). If the *GE* values are unrealistic, check the input parameters, especially for groups whose production has been estimated. In such cases, carefully editing the diet composition of the predators of the problem groups will generally help.

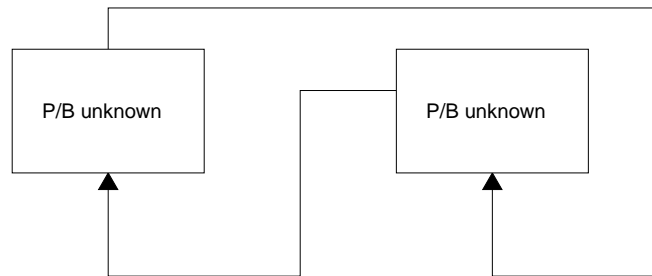
6.3 Balancing a model

An exhaustive set of guidelines for how a model should be balanced cannot be given. However, if it existed, such a set would include the following general guidelines:

- Make sure to document what is done in the balancing process by entering remarks for all parameters and to extract these subsequently. A model where the balancing process is not appropriately documented is not likely to be publishable;
- Remember which data are the more reliable and avoid changing these;
- Formulate assumptions and argumentation for changes: the ones easy to explain are likely to be the better assumptions;
- Start by looking at the estimated values. Are the EE values possible (less than 1)? Are the GE (= P/Q) values physiologically realistic (0.1-0.3 for most groups, perhaps lower for top predators and higher for very small organisms, (e.g., up to 0.5 for bacteria). If not decide from where the problem is the biggest if you want to balance your model starting from the bottom (producers) or from the top down;

Box 1. Problem: Loops

In cases where P/B is to be estimated for groups that feed on each others (cycles) the program may first estimate a P/B for one groups based on the consumption by the other groups. Subsequently it may estimate the P/B for the second group based on the consumption by the first, and then it may continue with the P/B for the first again, and so on in a loop. The result may be completely unrealistic parameter estimates.



It is necessary to break such loops, e.g., by entering the P/B for one of the groups.

If all ecotrophic efficiencies are low it indicates that the trophic transfer efficiencies are low. This may be OK for a system with high production and low abundance of organisms. It may however also indicate that the estimates of the biomasses in the system are too low.

Box 2. Problem: Cannibalism (0-order cycles)

Groups where 0-order cycles (cannibalism) are important should be broken into two or more groups. Such cases occur, for example, when a predatory fish feeds on fish of the same species or grouping. The prey fish will, however, be smaller fish, and often the P/B value for the group is based on the recruited part of the population only, and thus does not cover the dynamics of the juveniles, (which generally have much higher P/B values than the recruited part of the population). The solution may be to split the group in an adult and a juvenile fish group. This will also be an advantage for subsequent Ecosim simulations.

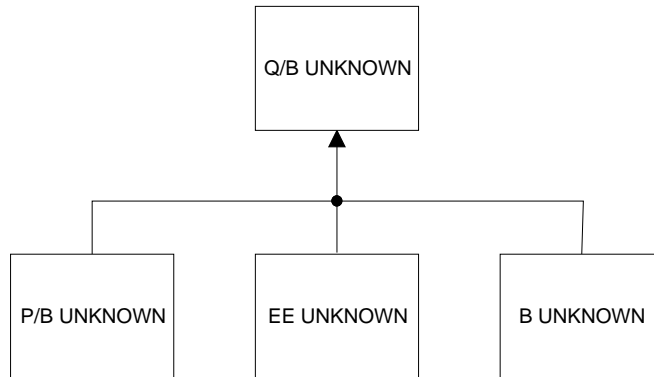
Remember that the gross food conversion efficiency or GE is the P/Q ratio. Typically this ratio is in the range of 10-30%. If the proportion of the 0-order cycle is in the same range there may not be any production left over for other purposes (predation and export). As a guideline if a 0-order cycle includes more than say 5% of the diet composition it is necessary to consider if it would be better to split the group in two.

- Search out one group with a bigger problem and try to solve this. Are the P/B, Q/B and B values appropriate for this group? What would happen to, e.g., the GE and the EE if you changed the parameters? If the problem is the consumption by predators, look at the predation mortality estimate form (Section 6.5.1 on page 56), and identify the quantitatively most important predators. Check the diet compositions and B and Q/B values for these predators;

- Continue for as long as necessary, documenting carefully what changes are made. It may be a good idea to save the data file under a new name each time changes are made (e.g. starting with 'Model_1', on to 'Model_2' etc.;

- You may get warnings that the 'Respiration cannot be negative'. If this happens the second master equation of Ecopath has been violated. We have: Consumption = production + respiration + unassimilated food, or $Q = P + R + U$. Expressing this relative to consumption we have: $P/Q + R/Q + U/Q = 1$. Of these P/Q is entered as GE or the gross food conversion efficiency and U/Q is the proportion of food that is not assimilated. If $GE + U/Q$ exceeds unity then R/Q and hence the respiration, R , has to be negative. You will need to reduce the production/consumption (GE)

Box 3. Problem: Estimation of predator consumption and prey production



In this example it is assumed that the consumption is unknown for the predator and the (used part of the) production, (i.e., the B, P/B or EE) unknown for all of the prey groups. In this case, it will not be possible for the program to calculate meaningful parameters and it will (probably) resort to the trivial solution: set the Q/B for the predator to zero, and see what can be estimated for the other groups. The problem is easily identified from an examination of the estimated parameters and statistics. The solution may well be to either input a gross efficiency for the predator or one of the missing input parameters for one of the prey groups.

ratio by lowering the production/biomass (P/B) ratio or increasing the consumption/biomass (Q/B) ratio, and/or reduce the proportion of unassimilated food;

- Examine the respiration/biomass (R/B) ratios for each group. Generally this ratio reflects activity level. For fish it should as a rule be in the range 1-10 year⁻¹, for copepods perhaps around 50-100. Please consult physiology handbooks for more information. If the ratio seems high it may be necessary to change the (assumed) proportion of the food that is not assimilated on the basic input form;
- Examine the Electivity (selection) tab on the Basis Parameter form. Do the preferences seem reasonable?
- Examine the predation mortalities on the mortality tab on the Basic Parameter form. The predation mortality spreadsheet will show you how important the various predators are for any group. Does this show what you expect? Are the predators shown to be the most important predators in accordance with what you expect? If not, reevaluate your model's diet compositions.
- Noting how the energy balance of a group is formulated, it is clear that, for instance, increasing the proportion of the consumption that is not assimilated will leave less energy to respiration (production being unaffected). This will result in a lower R/B ratio, and to a larger flow to the detritus. The latter may be necessary to balance the model if there is little system surplus production.

6.4 Basic analysis

6.4.1 Flow 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., (i.e., of sources of 'other mortality', expressed by $1 - EE$). The flow to the detritus, expressed, e.g., in $t \cdot km^{-2} \cdot year^{-1}$, should be positive for all groups.

Box 4. Problem: Estimation of Q/B for detritivores

It is not possible to estimate the consumption/biomass ratio for groups that feed exclusively on detritus. For detritus the production is not defined, and it will be necessary for such detritivores to input an estimate of Q/B (or P/B and an estimate for GE, gross food conversion efficiency).

6.4.2 Amounts exported or eaten

The ecotrophic efficiency, EE is the part of the production ($PB \cdot B$) of a group that is exported from or consumed by consumers included in the model. Thus, $PB_i \cdot B_i \cdot EE_i$ is the total amount of group (i) that is exported from or is eaten within the system. This amount is a rate expressed, e.g., as $t \cdot km^{-2} \cdot year^{-1}$.

6.4.3 Net efficiency

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

$$\text{Net efficiency} = P/B / (Q/B \cdot (1 - GS))$$

where P/B is the production / biomass ratio, Q/B is the consumption / biomass ratio, and GS is the proportion of the food that is not assimilated.

The net efficiency can also be expressed

$$\text{Net efficiency} = \text{Production} / (\text{production} + \text{respiration})$$

The net efficiency is a dimensionless fraction. It is positive and, in nearly all cases, less than 1, the exceptions being groups with intermediate trophic modes, e.g., groups with symbiotic algae. The net efficiency cannot be lower than the gross food conversion efficiency, GE .

6.4.4 Trophic levels

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

Following this approach, a consumer eating 40% plants (with $TL = 1$) and 60% herbivores (with $TL = 2$) will have a trophic level of $1 + [0.4 \cdot 1 + 0.6 \cdot 2] = 2.6$. The fishery is assigned a trophic level corresponding to the average trophic level of the catch, i.e. without adding 1 as is done for 'ordinary' predators.

The trophic level is a dimensionless index.

6.4.5 The omnivory index

The 'omnivory index' was introduced in 1987 (Pauly *et al.*, 1993a) in the initial version of the Ecopath II software. This index (OI) is calculated as the variance of the trophic level of a consumer's prey groups. Thus

$$OI_i = \sum_{j=1}^n (TL_j - (TL_i - 1))^2 \cdot DC_{ij}$$

Eq. 22

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 is dimensionless.

The square root of the omnivory index is the standard error of the trophic level, and a measure of the uncertainty about its precise value due to both omnivory and sampling variability.

6.4.6 Respiration

Respiration includes all non-usable ‘model currency’ that leaves the box representing a group.

When the currency is energy or carbon, the bulk of the assimilated food will end up as respiration. If, however, a nutrient (e.g. phosphorus or nitrogen) is used as currency, all nutrients that leave the box is re-utilized; in this case, respiration is nil.

Primary producers will not have respiration if the unit is energy based. Note, however, that for Carbon models you can enter a Q/B for producers (the input box will be colored yellow, but click it and you can enter a Q/B value nevertheless), and respiration values will be calculated for the producers.

Since assimilated food ends up as either production or respiration, only one of these two quantities needs to be estimated, as the other - here respiration - can be calculated as a difference. In Ecopath, this is calculated as the difference between the assimilated part of the consumption and that part of production that is not attributable to primary production (i.e., $1 - TM$). Thus, for groups with intermediate values of TM , i.e., for mixed producers/consumers, only that part of the production that is not attributable to primary production is subtracted. For reasons of consistency, in Ecopath, detritus is assumed not to respire, although it would if bacteria were considered part of the detritus (which is one reason why it is better to create one or more separate groups for the detritus-feeding bacteria if this difficult group is to be included at all).

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

$$Resp_i = (1 - GS_i) \cdot Q_i - (1 - TM_i) \cdot P_i$$

Eq. 23

where $Resp_i$ is the respiration of group i , GS_i is the fraction of i 's consumption that is not assimilated, Q_i is the consumption of i , and TM_i is the proportion of the production that can be attributed to primary production. If the unit is a nutrient TM_i is equal to zero, irrespective of whether the group is an autotroph or not (nutrients are not ‘produced’), and, P_i is the total production of group i .

Respiration is used, in Ecopath, only for balancing the flows between groups. Thus, it is not possible to enter respiration data. However, known respiration values (i.e., the metabolic rate) of a group can be compared with the output, and the input parameters adjusted to achieve the desired respiration. (For an application of this approach, see Browder, 1993)

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

6.4.7 Assimilation

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

$$B_i \cdot (Q/B)_i \cdot (1 - GS_i)$$

Eq. 24

where B_i is the biomass of group i ; Q/B_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 $t \cdot km^{-2} \cdot year^{-1}$.

6.4.8 Respiration/assimilation

The (dimensionless) ratio of respiration to assimilation cannot exceed 1, because respiration cannot exceed assimilation. For top predators, whose production is relatively low, the respiration/assimilation ratio can be expected to be close to 1, while it will tend to be lower, but still positive, for organisms at lower trophic levels.

6.4.9 Production/respiration

The (dimensionless) ratio production / respiration express the fate of the assimilated food. Computationally, this ratio can take any positive value, though thermodynamic constraints limit the realized range of this ratio to values lower than 1.

6.4.10 Respiration/biomass

The R/B ratio can be seen as an expression of the activity of the group. The higher the activity-level is for a given group, the higher the ratio. The R/B ratio is strongly impacted by the assumed fraction of the food that is not assimilated, see the basic input form. If the ratio is too high, this may be due to GS being too low.

The ratio respiration / biomass can take any positive value, and has the dimension $time^{-1}$.

6.5 Mortality coefficients

Under equilibrium, each group can be represented by an average organism, with an average weight. This makes it possible to use equations for estimating mortality in numbers, even when dealing with biomass. One such equation is

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

Eq. 25

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 , it turns out that, for a large number of growth functions (including the von Bertalanffy Growth Function, or VBGF):

$$Z_i = (production / biomass)_i = P/B_i$$

Eq. 26

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.,

$$Z_i = P/B_i = \text{other mortality} + \text{predation mortality} + \text{catches} + \text{net migration} + \text{biomass accumulation}$$

or

$$P/B_i = M0_i + M2_i + F_i + E_i + BA_i$$

Results form: displays mass-balance solution

	Group name	Prod./biom (=Z)	= Fishing mort. rate	+ Predat.mort. rate	+ Biom.accum. rate	+ Net migration rate	+ Other mort. rate
1	Transient Orcas	0.020	0.000	0.000	0.000	0.000	0.020
2	Dolphins (Res. Orca)	0.040	0.000	0.007	0.017	0.000	0.016
3	Seals Sealions	0.160	0.100	0.054	0.000	0.000	0.006
4	Halibut	0.440	0.250	0.110	0.000	0.000	0.080
5	Lingcod	0.390	0.049	0.017	0.000	0.000	0.324
6	Dogfish Shark	0.100	0.000	0.003	0.000	0.000	0.097
7	A. Hake	0.500	0.000	0.434	0.000	0.000	0.066
8	J. Hake	2.480	0.000	1.478	0.000	0.000	1.002

Basic estimates | Key indices | Mortalities | Consumption | Respiration | Niche overlap | Electivity | Search rates | Fishery

Press F1 for help (open a mode) CAPS NUM INS 28-Nov-01 13:04

Exhibit 18. Mortality rates. Z is total mortality; F is fishing mortality; M_0 other mortality; and M_2 predation mortality. $Z = P/B = F + E + M_0 + M_2$. The mortality tab is probably the most important tab on the basic parameter screen, and it is as a rule the first one that should be checked when balancing a model. The Mortality coefficient tab will tell you what the problem with balancing is (e.g., if its fishing or predation mortality that is too high). If its predation then see the Predation mortality tab (Exhibit 19).

In some models, (e.g., the Multispecies Virtual Population Analysis model of the North Sea, Sparre, 1991), the ‘other mortality’ component is split between M_{1i} , i.e., predation by predators not included in the model, and M_{0i} , ‘other mortality’, caused by diseases, senescence, etc. In Ecopath, M_1 is not included, as all predation mortality should be described explicitly. Further, M_{0i} is not entered directly, but is computed from the ecotrophic efficiency, EE_i . Thus:

M_{2i} is the predation mortality coefficient;

F_i is the fishing mortality coefficient;

E_i is the net migration (immigration less emigration).

The mortality coefficients are estimated from the following equations:

$$Z_i = P/B_i$$

$$M_{0i} = (1-EE_i) \cdot P/B_i$$

$$M_{2i} = (\sum B_j \cdot Q/B_j \cdot DC_{ji}) / B_i$$

$$F_i = Y_i/B_i$$

where Q/B_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 . The biomass accumulation term, BA_i , is a basic input term.

If any component of the system is harvested, a summary of the mortality coefficients can be displayed, which presents total mortality ($Z = P/B$) and its component: fishing mortality (F), other exports (E), other mortality ($M0$), and predation mortality ($M2$). Predation mortality is further broken down to show the contribution of each consumer groups to the total predation mortality of each prey group.

6.5.1 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). Predation mortality is calculated in the program, i.e., it is not an input parameter. Predation mortality corresponds to what is called ‘ $M2$ ’ in some other models.

6.6 Other mortality

‘Other mortality’ is the difference between total production and the sum of export and predation mortality. Other mortality is called ‘ $M0$ ’ in some other models. These may also include a term for mortality called ‘ $M1$ ’, referring to the mortality caused by predator groups not explicitly included in the model. This kind of mortality is, in Ecopath, considered a part of emigration (the prey ‘migrates’ out of the system, and may then be eaten). $M1$ should be negligible if the rule is followed to include, in Ecopath models, *all* the groups that occur in an ecosystem, not just some of them.

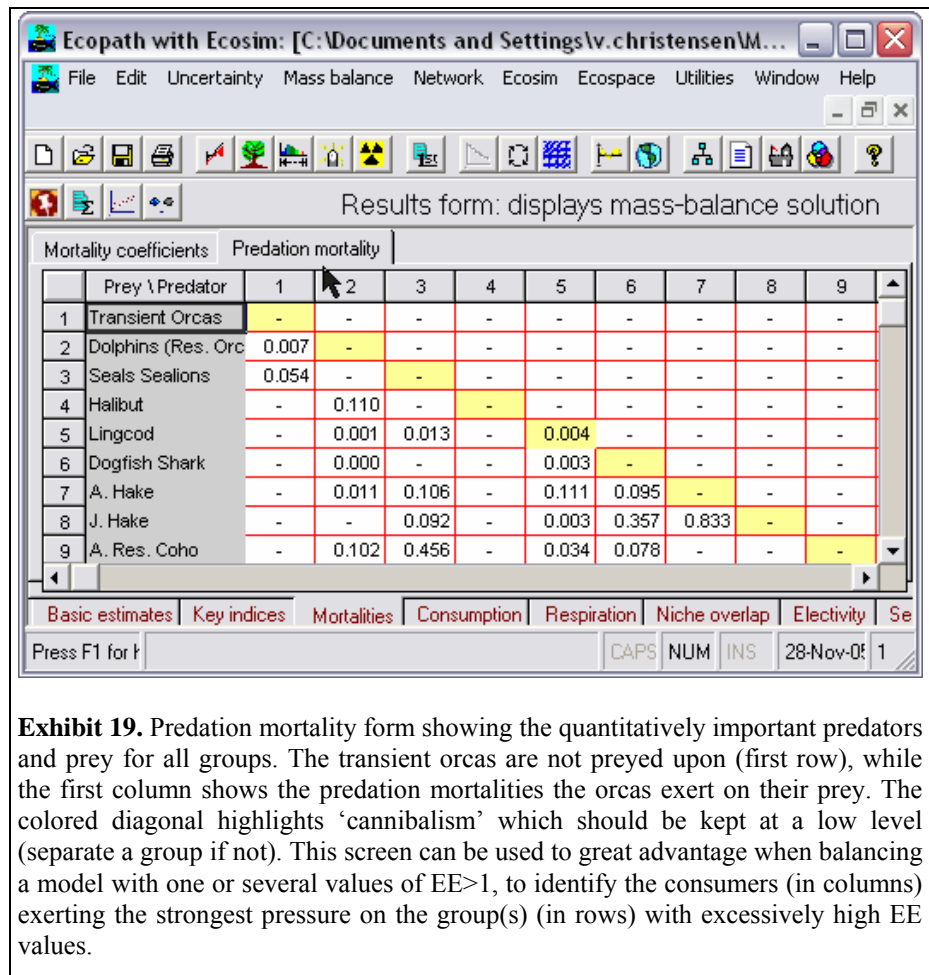


Exhibit 19. Predation mortality form showing the quantitatively important predators and prey for all groups. The transient orcas are not preyed upon (first row), while the first column shows the predation mortalities the orcas exert on their prey. The colored diagonal highlights ‘cannibalism’ which should be kept at a low level (separate a group if not). This screen can be used to great advantage when balancing a model with one or several values of $EE > 1$, to identify the consumers (in columns) exerting the strongest pressure on the group(s) (in rows) with excessively high EE values.

Other mortality consists of organisms dying due to diseases, starvation, breakage in the case of plants, etc., with the animals or plants concerned ending up as part of the detritus. This mortality is entered in Ecopath in form of the ecotrophic efficiency, EE , i.e., as $1 - \text{other mortality}$. The ecotrophic efficiency is, thus, the proportion of the production that is consumed within or exported out of the system.

It is difficult to estimate EE independently, and few, if any, direct estimates of this parameter appear to exist. Intuitively one would expect EE to be very close to 1 for small prey organisms, diseases and starvation probably being, for such groups, much less frequent than predation. For some groups, EE , may however, be low. It is often seen that phytoplankton simply die off in systems where blooms occur (EE of 0.5 or less). Also, kelps, seagrasses and other macrophytes are hardly consumed when alive (EE of 0.1 or so), and apex predators have very low EE s when fishing intensity is low: incidences of tunas or cetaceans simply dying and sinking have been reported from open oceans.

Settings of $EE = 0.95$, based on Ricker (1968) were used for many groups in Polovina's original model (Polovina 1984a) and in other, later models.

6.7 Summary statistics

A number of statistics describing an ecosystem as a whole have been included into Ecopath. 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).

6.7.1 Total system throughput

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

- Total consumption
 + Total export
 + Total respiration
 + Total flows to detritus
 = Total system throughput.

Total system throughput represents the 'size of the entire system in terms of flow' (Ulanowicz, 1986). As such, it is an important parameter for comparisons of flow networks.

6.7.2 Total primary production

Total net primary production is calculated as the summed primary production from all producers. Primary production is a flow expressed, e.g., in $t \cdot km^{-2} \cdot year^{-1}$.

6.7.3 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 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.

6.7.4 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. In immature systems, production exceeds respiration for most groups, and as a consequence, one can expect the biomass to accumulate over time. This, in turn, will influence the system ratio, which can be expected to decline. The system ratio behaves like that of individual groups; its dimension is $time^{-1}$ and it can take any positive value

6.7.5 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, total system throughput is used as a measure consistent with other Ecopath outputs (E.P. Odum originally used the sum of total

Parameter	Value	Units
Sum of all consumption	276.892	t/km ² /year
Sum of all exports	188.779	t/km ² /year
Sum of all respiratory flows	165.312	t/km ² /year
Sum of all flows into detritus	190.669	t/km ² /year
Total system throughput	822.000	t/km ² /year
Sum of all production	411.000	t/km ² /year
Mean trophic level of the catch	4.23	
Gross efficiency (catch/het p.p.)	0.000141	
Calculated total net primary production	354.092	t/km ² /year
Total primary production/total respiration	2.142	
Net system production	188.779	t/km ² /year
Total primary production/total biomass	15.710	
Total biomass/total throughput	0.027	
Total biomass (excluding detritus)	22.539	t/km ²
Total catches	0.050	t/km ² /year
Connectance Index	0.270	
System Omnivory Index	0.163	
Total market value	0.00	Euro
Total shadow value	0.00	Euro
Total value	0.00	Euro
Total fixed cost	0.00	Euro
Total variable cost	0.00	Euro
Total cost	0.00	Euro
Profit	0.00	Euro

Exhibit 20. Summary statistics giving a number of indices that may be of use for assessing the status of an ecosystem.

primary production and total system respiration). The system biomass / throughput ratio can take any positive value, and has time as dimension.

6.7.6 Net system production

Net system production is the difference between total primary production and total respiration. As can be inferred from the discussion of ecosystem maturity, 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., $t \cdot km^{-2} \cdot year^{-1}$.

6.7.7 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 calls it the 'Schrödinger ratio', after the physicist E. Schrödinger who showed that biological systems, in the presence of thermal vibrations, must continuously pump out 'disorder' if they are to maintain their internal 'order'. Thus, the larger the biomass, the greater the maintenance cost. Whether biological systems (individual organisms, or ecosystems) tend to maximize their R/B ratio over evolutionary time or not is a matter of debate. The ratio has the dimension $year^{-1}$, and can take any positive value.

6.7.8 The efficiency of the fishery

Correlations between primary production and realized on potential fishery yields have been presented by various authors, (see, e.g., Polovina and Marten, 1982). To encourage future comparative work along these lines, an index of the efficiency of a fishery was added to the outputs of Ecopath. This is computed as the sum of all realized fisheries catches relative to 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 web, (e.g., an 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).

The index is the ratio between two flows, and is thus dimensionless. It is generally much lower than 1.0 (the weighted global average is about 0.0002).

6.7.9 Total system biomass and catches/harvests

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., $t \cdot km^{-2}$ and $t \cdot km^{-2} \cdot year^{-1}$, respectively.

The production of a group in a system is size-specific, and it has been demonstrated that the inverse of a group's production / biomass ratio is a measure of size (see, e.g., Christensen and Pauly, 1993a). This, presumably, is also the case on a system level, which enables the use of the ratio between total biomass and total production as an index of the average size of the organisms in a system.

6.7.10 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. 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 model can be estimated as $(N-1)^2$, where N is the number of living groups.

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

$$CI \approx N / (N - 1)^2 \approx 1 / (N - 1), \quad \text{Eq. 28}$$

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

The value of the connectance index is - at least in aquatic systems - largely determined by the level of taxonomic detail used to represent prey groups, and this preclude meaningful intersystem comparisons. The System omnivory index is suggested as an alternative.

6.7.11 System omnivory index

The system omnivory index is 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). The logarithms is used as weighting factors because it can be expected that the intake rates are approximately log normally distributed within the system.

The system omnivory index is a measure of how the feeding interactions are distributed between trophic levels. (See the discussion of the omnivory index for a further description of the component omnivory indices). The idea of system omnivory index was inspired by drawbacks of the connectance index (Pauly *et al.*, 1993b). 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. The use of the latter index is recommended to characterize the extent to which a system displays web-like features.

6.8 Food intake

Food intake is displayed as a form on the main Ecopath form selected by clicking the *Food Intake* tab with the mouse button.

The food intake of a living group is the product of its biomass (*B*) times its consumption/biomass ratio (*Q/B*). The food intake is a rate expressed, e.g., as $t \cdot km^{-2} \cdot year^{-1}$. The food intake table also displays all flows to the detritus group(s).

6.9 Niche overlap

Numerous overlap indices have been suggested for quantification of how species overlap. Hurlbert (1978) and Loman (1986) summarized different types of indices, and described their properties based on a number of hypothetical examples.

Here a simple niche overlap index is adopted and it is shown how it can serve as a starting point for the development of a new (predator) niche overlap index incorporating predation. The procedure involved in deriving a predator niche overlap index (from a prey niche overlap index) should be generally applicable, i.e., not limited to the type of index presented below.

Pianka (1973) suggested the use of an overlap index derived from the competition coefficients of the Lotka-Volterra equations. This index, O_{jk} , which has been used for many descriptions of niche overlap, can be estimated, for two species/groups (j) and (k), from

$$O_{jk} = \frac{\sum_{i=1}^n (p_{ji} \cdot p_{ki})}{\sqrt{(\sum_{i=1}^n p_{ji}^2 p_{ki}^2)}}$$

Eq. 29

where P_{ji} and P_{ki} are the proportions of the resource (i) used by species (j) and (k), respectively. The index is symmetrical and assumes values between 0 and 1.

A value of 0 suggests that the two species do not share resources, 1 indicates complete overlap, and intermediate values show partial overlap in resource utilization.

Closer examination of the Pianka overlap index shows it to have an unwanted characteristic, and it is therefore slightly modified here. If one of the groups (say j) only overlaps with one other group (k) then P_{ji} will be zero for all values of (i) but ($i = k$), where it will reach a value of 1. In such a case, the denominator of Equation (1) will

always be 1, and the overlap index will equal P_{ki} , whereas a value between P_{ki} and P_{ji} would be more reasonable. This behavior is caused by the geometric mean implied in the denominator of (1), and can be circumvented by the use of an arithmetic mean. For this (1) is changed to

$$O_{jk} = \frac{\sum_{i=1}^n (p_{ji} \cdot p_{ki})}{(\sum_{i=1}^n (p_{ji}^2 + p_{ki}^2) / 2)}$$

Eq. 30

where the index and all of its terms can be interpreted as above. This version of the Pianka overlap index is used in the subsequent calculations.

The niche overlap index can be used to describe various kinds of niche partitioning. Here attention will be focused on the trophic aspects. In this case, the P_{ki} and P_{ji} in (2) can be interpreted as the fraction prey (i) contributes to the diets of (j) and (k), respectively.

Using an approach similar to that above, it is possible to quantify the predation on all preys (m) and (n) by all predators (l), and to derive a

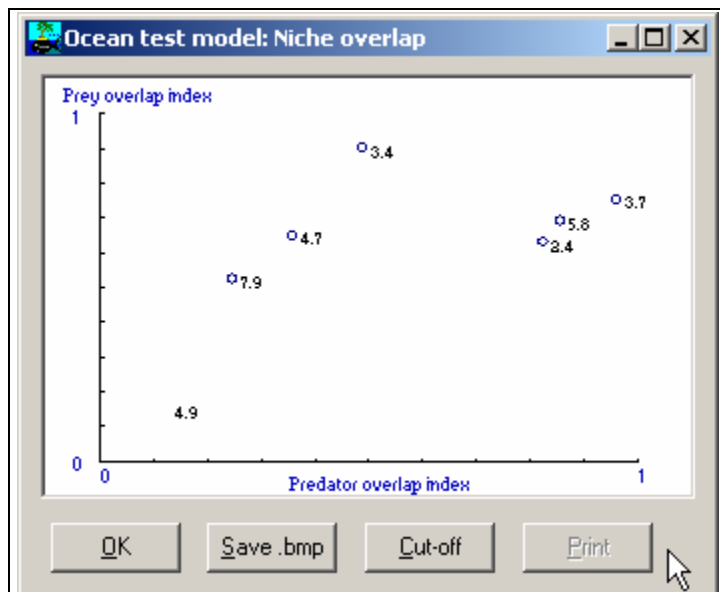


Exhibit 21. Prey versus predator niche overlap index plot. Group 3 and 7 (shown in the upper right corner) have a very high overlap of both predators and prey, and could be candidates for aggregation into a single group. The plot is available from the niche overlap form (button on lower button bar).

‘predator’ composition, estimated from

$$X_{ml} = Q_i P_{lm} / \sum_{l=1}^n (Q_l \cdot P_{lm})$$

Eq. 31

and

$$X_{nl} = Q_i P_{ln} / \sum_{l=1}^n (Q_l \cdot P_{ln})$$

Eq. 32

Here X_{ml} can be interpreted as the fraction the predation by (l) contributes to the total predation on (m), while Q_l is the total consumption for predator (l). The predator compositions given above correspond to what Augoustinovics (1970) defined, in the context of input-output analysis, as ‘technical coefficients’.

Based on the predator composition a ‘predator overlap index’ (P) can be derived as

$$P_{mn} = \frac{\sum_{l=1}^n (X_{ml} \cdot X_{nl})}{(\sum_{l=1}^n (x_{ml}^2 + x_{nl}^2) / 2)}$$

Eq. 33

the values of this predator overlap index range between 0 and 1 and can be interpreted in the same way as those of the prey overlap index, given in (2).

In the present version, only one type of niche overlap index is incorporated, but both predator and prey niche overlap is given for this index. Given users' interest, more indices may be included in later versions of EwE.

6.10 Particle size distributions

Based on growth and mortality information (see input data) the particle size distribution, (PSD, Sheldon *et al.*, 1972) for a model can be calculated. A routine for this is included in EwE, where for each living group the following steps are performed:

The time spent in each of a user-defined number of weight class is calculated starting at time 0, is calculated from the age corresponding to the lower limit of each weight class, i.e.,

$$t = \ln\left(1 - \left(\frac{W_t}{W_\infty}\right)^{-b}\right) / (-K) + t_0$$

Eq. 34

where W_t is the lower limit of the weight interval, W_∞ is the asymptotic weight, b the exponent in the Length-Weight relationship of the form $W = a \cdot L^b$, K the curvature parameter of the von Bertalanffy Growth Function (VBGF), and t_0 is the usually negative 'age' at which the weight is estimated to be zero in the VBGF. Once the time spent to reach each weight class limit is available, the time spent in each weight class (Δt) is calculated by subtraction.

The survival is calculated as,

$$N_t = N_{t-\Delta t} \cdot e^{-Z \cdot \Delta t}$$

Eq. 35

where N_t is the number alive at time t , $N_{t-\Delta t}$ the number alive at the previous time step, and Z is the total mortality rate, equivalent to the production/biomass ratio for the group.

The biomass contribution for the group to each weight class is calculated as,

$$B_t = N_t \cdot W_t \cdot \Delta t$$

Eq. 36

where B_t is the biomass contribution, Δt is the time the groups spends to grow through the given weight class, and the rest as defined above. B_t is scaled over all weight classes so as to sum up to the total biomass of the group.

The system PSD is calculated, finally, by summing up over all groups within each weight class.

7. Network analysis

The Ecopath software links concepts developed by theoretical ecologists, especially the theory of Ulanowicz (1986), with those used by biologists involved with fisheries, aquaculture and farming systems research. The following

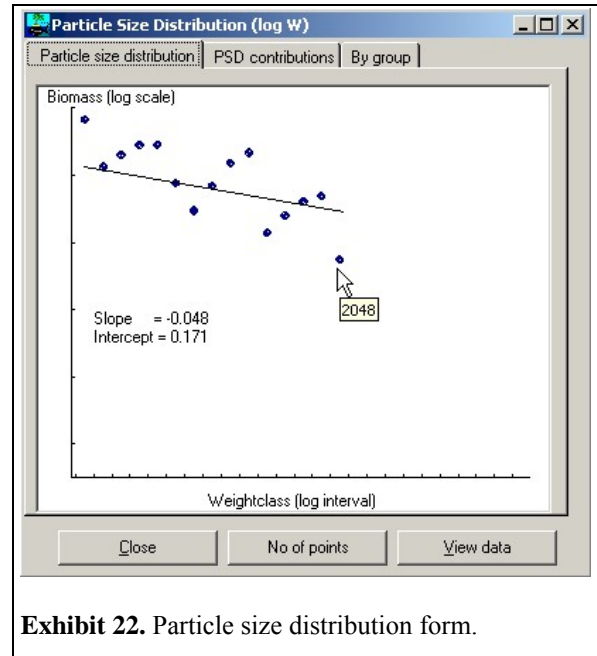


Exhibit 22. Particle size distribution form.

sections gives only brief accounts of the concepts from theoretical ecology included in Ecopath. (See also Appendix 2 in the Help system). For complete descriptions, we refer to the literature cited in the respective sections.

7.1 Flow indices

A large number of flow indices are included, see below.

7.1.1 The ascendancy measure

Ascendancy is a measure of the average mutual information in a system, scaled by system throughput, and is derived from information theory (see Ulanowicz and Norden, 1990). If one know the location of a unit of energy the uncertainty about where it will next flow to is reduced by an amount known as the average mutual information',

$$I = \sum_{i=1, j=1}^n f_{ij} Q_i \log \left(f_{ij} / \sum_{k=1}^n f_{kj} Q_k \right)$$

Eq. 37

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,

$$f_{ij} = T_{ij} / \sum_{k=1}^n T_{kj} .$$

Eq. 38

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

$$Q_i = \sum_{k=1}^n T_{ki} / \sum_{l=1, m=1}^n T_{lm} .$$

Eq. 39

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

$$T = \sum_{i=1, j=1}^n T_{ij} .$$

Eq. 40

Further

$$A = T \cdot I$$

Eq. 41

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

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

$$C = H \cdot T ,$$

Eq. 42

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

$$H \sum_{i=1}^n Q_i \log Q_i .$$

The difference between the capacity and the ascendancy is called ‘system overhead’. The overheads provide limits on how much the ascendancy 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 ascendancy that is due to imports, A_0 , can increase at the expense of the overheads due to imports, Q_0 . 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_0 below a certain system-specific critical level (Ulanowicz and Norden, 1990).

The ascendancy, overheads and capacity can all be split into contributions from imports, internal flow, exports and dissipation (respiration). These contributions are additive.

The unit for these measures is ‘flowbits’, or the product of flow (e.g., $\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$) and bits. Here the ‘bits’ is an information unit, corresponding to the amount of uncertainty associated with a single binary decision.

The overheads on imports and internal flows (redundancy) may be seen as a measure of system stability *sensu* Odum, and the ascendancy / system throughput ratio as a measure of information, as included in Odum's attributes of ecosystem maturity. For a study of ecosystem maturity using Ecopath see Christensen (1995a).

7.1.2 System throughput

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

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

Total system throughput represents the “size of the entire system in terms of flow” (Ulanowicz 1986). As such, it is an important parameter for comparisons of flow networks.

Ascendancy (Section 7.1.1 on page 62) is calculated as

$$\text{Ascendancy} = \text{Total system throughput} \cdot \text{Information content of flows.}$$

Both of these factors are given on the total throughput form.

7.1.3 Cycling and path length

The ‘cycling index’ is the fraction of an ecosystem's throughput that is recycled. This index, developed by Finn (1976), is expressed here (Exhibit 23) as a percentage, and quantifies one of Odum's (1969) 24 properties of system maturity (Christensen 1995). Recent work shows this index to strongly correlate with system maturity, resilience and stability.

In addition to Finn's cycling index, Ecopath includes a slightly modified ‘predatory cycling index’, computed after cycles involving detritus groups have been removed.

Cycling and path length: Ocean test model		
Parameter	Value	
Throughput cycled (excluding detritus)	0.94	t/km ² /year
Predatory cycling index	0.21	% of throughput w/o detritus
Throughput cycled (including detritus)	56.40	t/km ² /year
Finn's cycling index	0.20	% of total throughput
Finn's mean path length	2.320	-
Finn's straight-through path length	2.657	without detritus
Finn's straight-through path length	2.316	with detritus

Exhibit 23. Measures of cycling efficiency and system path lengths.

The path length is defined as the average number of groups that an inflow or outflow passes through (Finn 1980). It is calculated as

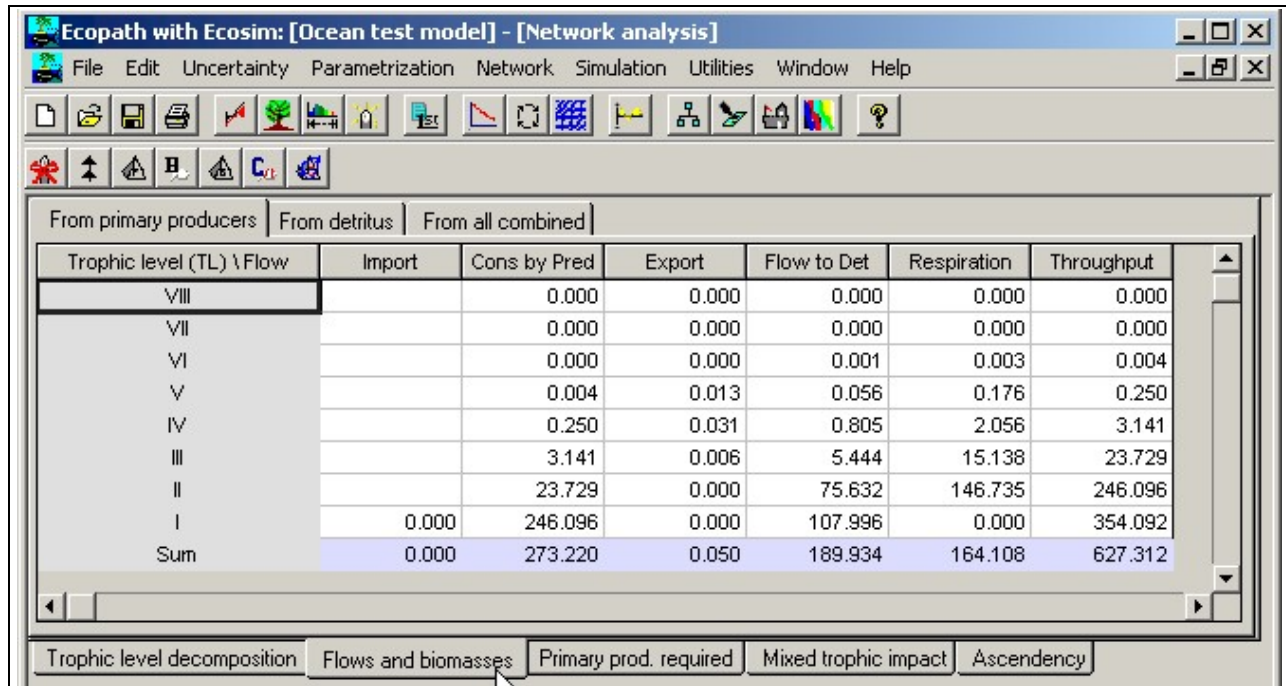


Exhibit 24. Flows by trophic levels. The trophic levels are not pre-defined but calculated based on diet compositions. Flows can be broken down to components originating from primary producers (first tab), and components originating from detritus (second tab). Trophic level I is the level of primary producers and detritus.

Path length = Total System Throughput / (\sum Export + \sum Respiration).

As diversity of flows and recycling is expected to increase with maturity, so is the path length.

7.2 Trophic aggregation

In addition to the routine for calculation of fractional trophic levels, a routine is included in Ecopath which aggregates the entire system into discrete trophic levels *sensu* Lindeman. This routine, based on an approach suggested by Ulanowicz (1995), reverses the routine for calculation of fractional trophic levels. Thus, for the example when a group obtains 40% of its food as a herbivore and 60% as a first-order carnivore, the corresponding fractions of the flow through the group are attributed to the herbivore level and the first consumer level.

The result of these analyses is presented in five tables, where the import (on Trophic Level I

Transfer efficiency: Ocean test model							
Source \ TL	II	III	IV	V	VI	VII	
Producer	9.6	13.3	8.9	6.9	6.1		
Detritus	9.3						
All flows	9.6	13.2	8.9	6.9	6.1	6.1	
Proportion of total flow originating from detritus: 0.24							
Transfer efficiencies (calc. as geometric mean for TL II-IV)							
From primary producers: 10.4%							
Total:	10.4%						

Exhibit 25. Trophic transfer efficiencies (%) expressing how efficiently transfers are from one trophic level to the next.

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 fourth table with transfer efficiencies can be used for constructing a figure presenting the trophic flows in form of a pyramid using a built-in graphic routine run by clicking the *Pyramid* button at the form bottom with the mouse. Here, the traditional two-dimensional Lindeman pyramids, consisting of a number of rectangles placed on top of each other, are replaced by a three-dimensional, Egyptian-style, solid pyramid.

These pyramids are drawn such that the volume of each compartment representing a trophic level is proportional to the total throughput of that level. In addition, to enable various comparisons, the top-angle of the pyramids was made inversely proportional to the geometric mean of the transfer efficiencies between trophic levels observed in the system.

Based on the three tables discussed above, the transfer efficiencies between successive discrete trophic levels can be calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from trophic level to the next, and the throughput on the trophic level. This is presented in a table with transfer efficiencies (%) by trophic levels (Exhibit 25).

The efficiency of detritus transfer is not defined. On the other hand, the outputs include the ratio of total flow originating from the detritus to the total flow originating from both primary producers and detritus. This ratio, which may be viewed as an index of the importance of detritus in a system, is the quantitative form of yet another of Odum's (1969) measures of ecosystem maturity. The index is complementary, i.e., it sums to 1 with the proportion of the total flow that originates from the primary producers.

Biomass pyramids can be constructed based on biomasses by trophic level. For calculation of this the biomass of each group in the system is distributed onto trophic levels in proportion to the flows by trophic levels for the groups.

Two forms are available, after choosing *Network*, *Trophic aggregation*, *Transformation matrix* from the main menu, to display relative and absolute flows. They show how the flows for each group are distributed on trophic levels. An example giving the relative flows is displayed in Exhibit 27.

7.3 Primary production required

For terrestrial systems, it has been shown by Vitousek et al. (1986), based on a detailed analysis of agriculture, industry and other activities, that nearly 40% of potential net primary production is used directly or indirectly by these activities. Comparable estimates for aquatic systems were not available until recently, though a rough estimate, of 2% was presented in the same publication. This figure, much lower than that for terrestrial systems, was based on the assumptions that an 'average fish' feeds two trophic levels above the primary producers, and has been since revised upward (Pauly and Christensen, 1995).

The crudeness of Vitousek et al.'s approach for the aquatic systems was due mainly to lack of information on marine food webs, especially on the trophic positions of the various organisms harvested by humans. Models of trophic interactions may however help overcome this situation, and an alternative approach, based on network

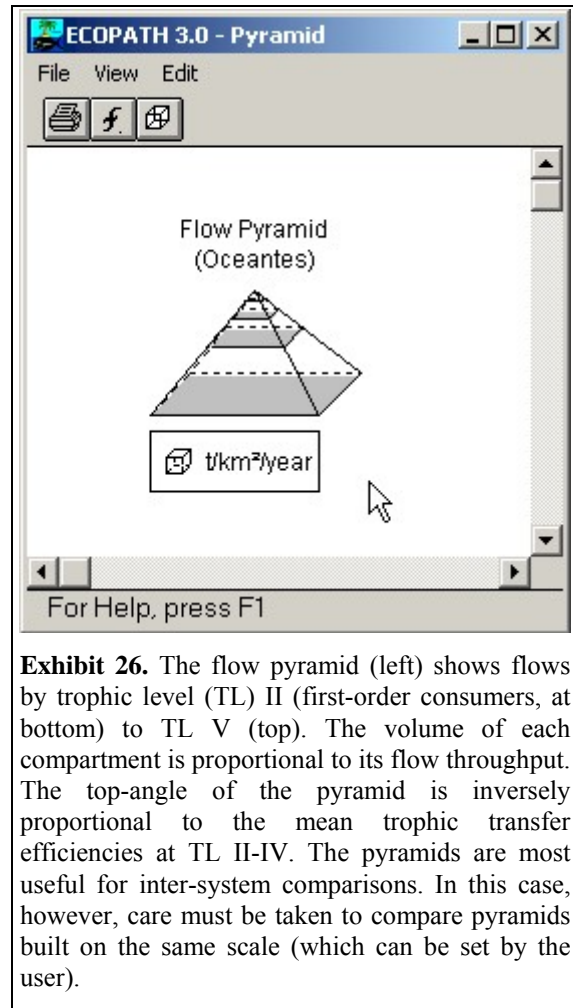


Exhibit 26. The flow pyramid (left) shows flows by trophic level (TL) II (first-order consumers, at bottom) to TL V (top). The volume of each compartment is proportional to its flow throughput. The top-angle of the pyramid is inversely proportional to the mean trophic transfer efficiencies at TL II-IV. The pyramids are most useful for inter-system comparisons. In this case, however, care must be taken to compare pyramids built on the same scale (which can be set by the user).

The screenshot shows the 'Ecopath with Ecosim' software window. The main window displays a table titled 'Absolute flow (t/km²/year)'. The table has columns for Trophic levels I through VII and a 'Total' column. The rows represent different trophic groups. The 'Total' row is highlighted in blue.

Group\Trophic level	I	II	III	IV	V	VI	VII
22 Grazing Invertebrates	0.000	8420.104	713.248	61.422	4.829	0.380	0.017
23 C. Zooplankton	0.000	310.905	207.270	0.000	0.000	0.000	0.000
24 H. Zooplankton	0.000	4526.451	0.000	0.000	0.000	0.000	0.000
25 Kelp/Sea Grass	75.750	0.000	0.000	0.000	0.000	0.000	0.000
26 Phytoplankton	5217.189	0.000	0.000	0.000	0.000	0.000	0.000
27 Detritus	2672.256	0.000	0.000	0.000	0.000	0.000	0.000
28 Total	7965.195	14427.580	1494.847	168.876	14.320	1.022	0.042

Exhibit 27. Breakdown of (absolute) flows by trophic level based on diet compositions. Breakdown by proportions (unit-less) is also available.

analysis, may be suggested for quantification of the primary productivity required to sustain harvest by humans (or by analogy by any other group that extracts production from an ecosystem).

To estimate the primary production required (PPR, Christensen and Pauly, 1993a) to sustain the catches and the consumption by the trophic groups in an ecosystem, the following procedure has been implemented in Ecopath: First, all cycles are removed from the diet compositions, and all paths in the flow network are identified using the method suggested by Ulanowicz (1995). For each path, the flows are then raised to primary production equivalents using the product of the catch, the consumption/production ratio of each path element times the proportion the next element of the path contributes to the diet of the given path element. For a simple path from trophic level (TL) I (primary producers and detritus), over TL II and III, and on to the fishery,

$$TL_I \xrightarrow{Q_{II}} TL_{II} \xrightarrow{Q_{III}} TL_{III} \xrightarrow{Y} Fishery$$

the primary production (or detritus) equivalents, PPR_c , corresponding to the catch of Y is:

$$PPR_c = Y \cdot \frac{Q_{III}}{Y} \cdot \frac{Q_{II}}{Q_{III}} = Q_{II}$$

For the general (and more realistic) case where the pathways includes branching the PPR corresponding to a catch Y of a given group can be quantified by summing over all pathways leading to the given group the PPR_c 's

$$PPR_c = \sum_{Paths} [Y \cdot \prod_{Pred,prey} \frac{Q_{Pred}}{P_{Pred}} \cdot DC'_{Pred,prey}]$$

Eq. 44

where P is production, Q consumption, and DC' is the diet composition for each predator/prey constellation in each path (with cycles removed from the diet compositions).

The PPR required to sustain the catch is presented as a page on the PPR form.

Further, the PPR for sustaining the consumption of each trophic group in a system can be estimated from the same equation as above by substituting the catch, Y , with the production term, P , calculated as the production/biomass ration, P/B , times the biomass, B . This is presented on a separate page on the PPR form.

PPR should actually be interpreted as flow from Trophic Level I as it includes primary production as well as detritus uptake. The denominator, PP , thus actually includes all 'new' flow to the detritus groups, i.e. flow from primary

	Group Name	No. of paths	TL	PPR (PP)	PPR (Det)	PPR	Catch	PPR/catch	PPR/TotPP	PPR/u.catch
3	Seals Sealions	10291	4.38	418.38	136.74	555.12	0.04	13878.01	2.48	0.62
4	Hallbut	1106	4.15	0.32	0.10	0.42	0.00	424.33	0.00	0.02
5	Lingcod	5997	4.18	184.75	63.05	247.80	0.27	907.69	1.11	0.04
9	A. Res. Coho	1230	3.76	15.51	3.50	19.01	0.12	158.41	0.08	0.01
11	A. Res. Chinook	1283	3.80	69.28	13.84	83.11	0.30	280.79	0.37	0.01
17	A. Herring	524	3.18	489.86	92.96	582.83	7.22	80.72	2.60	0.00
27	Total	20431	3.25	1178.10	310.19	1488.29	7.95	187.21	6.65	-

Exhibit 28. Primary production required (PPR) to sustain the fishery, calculated based on all food pathways in the system. In this system the fishery is appropriating 6.65% of the primary production, all indirectly.

producers and import of detritus.

The PPR is closely related to the emergy concept of H. T. Odum (1988), and is proportional to the ecological footprint of Wackernagel and Rees (1996).

7.4 Mixed trophic impact

Leontief (1951) developed a method to assess the direct and indirect interactions in the economy of the USA, using what has since been called the Leontief matrix. This approach was introduced to ecology by Hannon (1973) and Hannon and Joiris (1989). Using this, 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 system. The example given represents the open ocean, central part of the South China Sea ecosystem (Pauly and Christensen, 1993).

The MTI for living groups is calculated by constructing an $n \times n$ matrix, where the i,j^{th} element representing the interaction between the impacting group i and the impacted group j is

$$MTI_{i,j} = DC_{i,j} - FC_{j,i},$$

Eq. 45

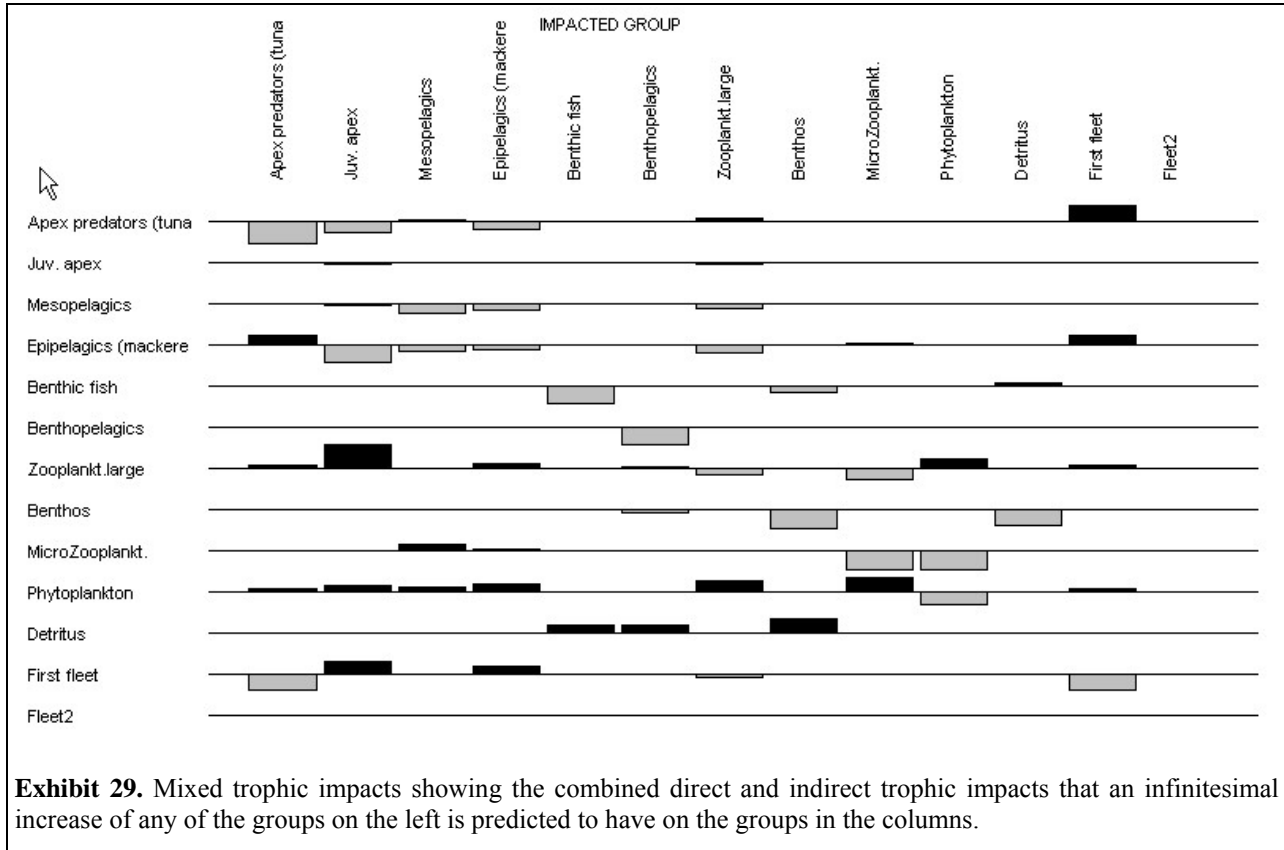
where $DC_{i,j}$ is the diet composition term expressing how much j contributes to the diet of i , and $FC_{j,i}$ is a host composition term giving the proportion of the predation on j that is due to i as a predator. When calculating the host compositions the fishing fleets are included as 'predators'.

For detritus groups the $DC_{i,j}$ terms are set to 0. For each fishing fleet a ‘diet compositions’ is calculated representing how much each group contributes to the catches, while the host composition term as mentioned above includes both predation and catches.

The diagonal elements of the MTI are further increased by 1, i.e.

$$MTI_{i,i} = 1 + MTI_{i,i}$$

Eq. 46



The matrix is inverted using a standard matrix inversion routine.

The mixed trophic impact graph can be opened using a button () on the second button bar. The number of group included in the mixed trophic impact graph can be limited by pressing the following button () on the second button bar.

Exhibit 29 shows the direct and indirect impact that the very small increase of the biomass of groups mentioned to the left of the histograms (rows) have on the biomass of the other groups mentioned above the histograms (columns). The bars pointing upwards indicate positive impacts, while the bars pointing downwards show negative impacts. The bars should not be interpreted in an absolute sense: the impacts are relative, but comparable between groups.

In this example, the apex predators will have a negative impact on their preferred prey, epipelagic nekton, and an indirect, if slight (0.03, not visible on Exhibit 29 but available on the mixed trophic impact table output by the program) positive impact on the prey of their prey, the larger zooplankton (this effect is known as a ‘cascade’). Further, the impact of the epipelagic nekton on the microzooplankton is slightly positive (0.01), even though the former feeds on microzooplankton directly. This is because the epipelagics also feed on the large zooplankton, and this overrules the direct impact.

Most groups have a negative impact on themselves, interpreted here as reflecting increased within-group competition for resources. Exceptions exist; thus, if a group cannibalizes itself (0-order cycle), the impact of a group on itself may be positive.

The mixed trophic impact routine can also be regarded as a form of ‘ordinary’ sensitivity analysis (Majkowski, 1982). In this system, it can be concluded, e.g., that the impact of the bathypelagics on any other group is negligible: these fishes are too scarce to have any quantitative impacts. This can be seen to indicate that one need not allocate much effort in refining one’s parameter estimates for this group; it may be better to concentrate on other groups.

One should regard the mixed trophic 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 of what will happen in the future if certain interaction terms are changed. The major reason for this is that changes in abundance may lead to changes in diet compositions, and this cannot be accommodated with the mixed trophic impact analysis. We suggest the use of Ecoranger (see Section 9.3 on page 75 to explore the ecosystem impact of moderate changes in biomasses, and especially the Ecosim model, which was developed with this purpose in mind.

This version of Ecopath includes two additional diagnostic tools: an explicit sensitivity routine (Section 5.3 on page 40) and, the Ecoranger routine for dealing with distributions of input and output parameters, and Ecopath’s sensitivity to them.

7.4.1 Keystone species (by Simone Libralatto)

Keystones are defined as relatively low biomass species with a structuring role in their food webs. Thus, identifying keystone species in a given ecosystem may be formulated as: (1) estimating the impact on the different elements of an ecosystem resulting from a small change to the biomass of the species to be evaluated for its ‘keystoneness’; and (2) deciding on the keystoneness of a given species as a function of both the impact estimated in (1) and its own biomass. Experimental quantification of interaction strength, necessarily focus on few species, and they require a priori assumptions on the importance of the interactions, which can bias the identification of keystone species. Moreover, empirical measurements, although very important, are expensive and time consuming and, owing to the spatio-temporal heterogeneity of habitats, physical conditions, and densities of organisms, published results tend to be case-specific and context-dependent. Although models can only represent but a caricature of the complexity of the real world, the modelling approach can be helpful since it allows overcoming some of the difficulties mentioned. Here we present an approach for estimating the keystoneness of the functional groups (species or group of species) of food web models. Network mixed trophic impact analysis, based on Leontief’s economic input-output analysis, allows us to express the relative change of biomasses in the food web that would result from an infinitesimal increase of the biomass of the observed group, thus identifying its total impact. The analysis of the mixed trophic impacts presented here was applied to a suite of mass-balance models, and the results allow us to rank functional groups by their keystoneness. Overall, we concluded that the straightforward methodology proposed here and the broad use of Ecopath with Ecosim (where mixed trophic impact analysis is implemented) together give a solid empirical basis for identification of keystone functional groups (Libralatto *et al.*, 2006).

We will implement identification of keystoneness based on MTI in a coming release of EwE.

7.5 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 by the food web representing an ecosystem. For a further description see Ulanowicz (1986, his examples 4.4 and 4.5, page 65f.)

7.5.1 To consumers from Trophic Level I

This routine lists all pathways leading from all groups on Trophic Level I (primary producers and detritus) to any selected consumer. A list of all consumers in the system will be displayed, and one can select from this. The program then searches through the diet compositions, finds all the pathways from the primary producers to the specified consumer, and then presents these pathways. Further, a summary presents the total number of pathways and the mean length of the pathways. The latter is calculated as the total number of trophic links divided by the number of pathways.

7.5.2 From Trophic Level I to consumers via specified prey

This routine lists all pathways leading from all groups on Trophic Level I (primary producers and detritus) to any selected consumer via a selected prey. A list of all consumers in the system will be displayed, and one can select from this. Then, a specific prey is chosen. The program searches through the diet compositions, finds all the pathways from the primary producers, via the selected prey, to the specified consumer, and then presents the pathways. Further, a summary presents the total number of pathways and the mean length of the pathways.

7.5.3 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 presents the total number of pathways and the mean length of the pathways.

7.5.4 All cycles

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

7.5.5 From Trophic Level I to all top predators

This routine counts the number of all pathways leading from Trophic Level I (primary producers and detritus) to the top predators. (These pathways will not be displayed automatically; for this, use the routine repetitively the routine which list all pathways from Trophic Level I to a given top predator). The mean path length will be calculated and displayed. This mean path length is calculated as the total number of trophic links divided by the number of pathways.

The screenshot shows a software window titled 'Pathways leading to: Juv. apex'. It contains a table with 16 rows, each representing a pathway from primary producers or detritus to a selected consumer. The pathways are listed as sequences of numbers connected by double arrows (e.g., 2<-3<-4<-7<-9<-10). A tooltip for pathway 14 explains that '1<-2' shows a pathway from group 2 to group 1, etc. Below the table are four buttons: 'TL1 --> Consumer', 'TL1 --> Prey --> Consumer', 'Prey --> Top predator', and 'Cycles (excl. detritus)'.

Pathway #	Pathways from primary producer or detritus groups to a selected consumer
1	2<-3<-4<-7<-9<-10
2	2<-3<-4<-7<-10
3	2<-3<-4<-9<-10
4	2<-3<-4<-10
5	2<-3<-7<-9<-10
6	2<-3<-7<-10
7	2<-3<-9<-10
8	2<-4<-3<-7<-9<-10
9	2<-4<-3<-7<-10
10	2<-4<-3<-9<-10
11	2<-4<-7<-9<-10
12	2<-4<-7<-10
13	2<-4<-9<-10
14	2<-4<-10
15	2<-7<-9<-10
16	2<-7<-10

Here, 1<-2 shows a pathway from group 2 to group 1, etc.

TL1 --> Consumer TL1 --> Prey --> Consumer Prey --> Top predator Cycles (excl. detritus)

Exhibit 30. All (16) pathways in the food web leading from primary producers and detritus to the juvenile apex predators have been identified. Similar pages are displayed for the other routines in this section.

8. Utilities

8.1 Flow diagram

One of the characteristics of network 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 changes feel that such models resemble cemeteries, with the boxes as tombs and the flows as walkways. No matter how the interpretation may be, the output, to be interpretable, should be presented in form of a graph

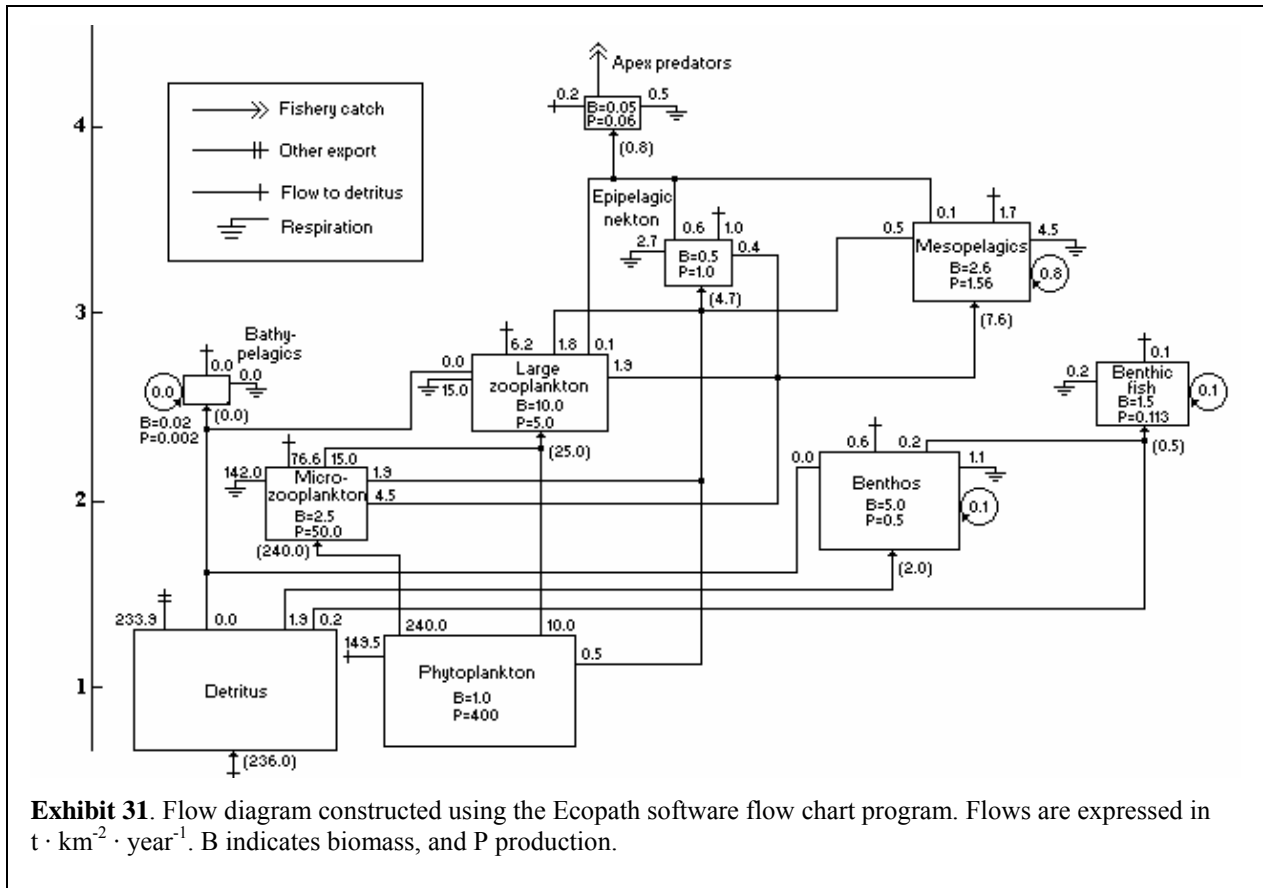
The traditional method of representing trophic flow ecosystem models, usually by scattering interconnected boxes across a page, both under-utilizes the potential descriptive and explanatory power of graphical representations and makes it difficult to compare different system representations.

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.

In the flow chart incorporated in Ecopath, explicit use is made 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.

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:

- 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,
- arranging the boxes such that the arrows linking the boxes cross each other as little as possible, hence



maximizing clarity of the graph.

You might consider (i) and (ii) when constructing flow charts using the graphing routine incorporated in this version of Ecopath. The boxes are assumed to be three dimensional, with their depth (not shown) equal to their height, and the implied volume of each box proportional to the biomass it represents. This trick is 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 surfaces directly proportional to biomass fail to do as well.

Another rule of construction was incorporated in the flow chart design of Ecopath. 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 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 an incomplete circle before entering the lower half. The flow chart routine of Ecopath will label all connecting arrows with their respective flows.

On the other hand, flows are not represented through arrows of different sizes, (e.g., with thickness proportional to the flow). This would clutter up the graphs. Indeed, it is often necessary to omit, for clarity's sake, lesser flows from graphs representing highly interconnected systems. This can be done from within the flow chart program.

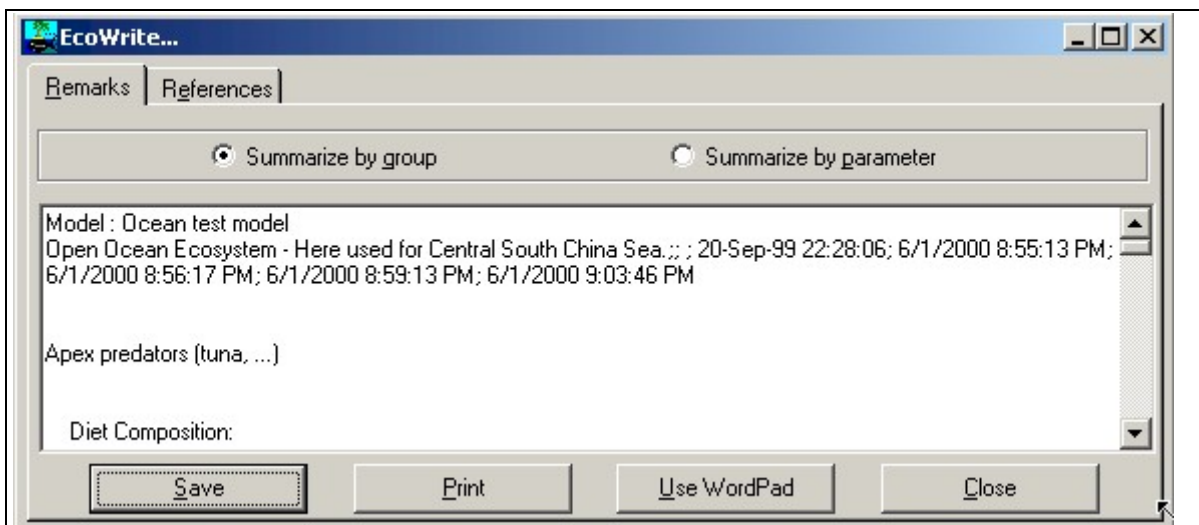


Exhibit 32. Ecowrite – the built-in word processor of Ecopath can be used for model documentation. The result can be saved in a format (.rtf) easily accessible from virtually any word processor.

8.2 Ecowrite

It is possible to enter a remark for each input parameter and for most of the output forms at the press of a button. Such remarks may indicate the sources of estimates, describe how they were standardized, etc. Once the model is constructed, a reporting facility extracts the remarks. How the extracting is done through can be controlled by including (or excluding) complete sections by enabling/disabling the check boxes. Further, an option is given to arrange remarks on parameters by functional groups, or parameter by parameter. The references will be sorted alphabetically.

Clicking on the OK *command button* will open a built-in word processor (Exhibit 32). The text may then be edited or saved in a form (.rtf) accessible from any Windows-based word processor.

8.3 Ecoempire

Often system-specific estimates of input parameters are not available for all groups to be included in a model. In such cases it can be useful to use one of the many published empirical relationships (e.g., in Calder, 1984),

especially where there are physiological constraints likely to overrule local conditions, e.g., in the case of the consumption/biomass ratio of fish (see Pauly, 1989). To facilitate parameterization, a number of these relationships have been included in an interactive routine (*'Ecoempire'*). Successive versions of Ecopath will include increasing numbers of such relationships, and colleagues are welcome to submit relationships that should be considered for

9. Time-dynamic simulation: Ecosim

9.1 On overview of Ecosim

Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model. The key computational aspects are in summary form:

- Use of mass-balance results (from Ecopath) for parameter estimation;
- Variable speed splitting enables efficient modeling of the dynamics of both 'fast' (phytoplankton) and 'slow' groups (whales);
- Effects of micro-scale behaviors on macro-scale rates: top-down vs. bottom-up control incorporated explicitly.
- Includes biomass and size structure dynamics for key ecosystem groups, using a mix of differential and difference equations. As part of this EwE incorporates:
 - Multi-stanza life stage structure by monthly cohorts, density- and risk-dependent growth;
 - Adult numbers, biomass, mean size accounting via delay-difference equations;
 - Stock-recruitment relationship as 'emergent' property of competition/predation interactions of juveniles.

Ecosim uses a system of differential equations that express biomass flux rates among pools as a function of time varying biomass and harvest rates, (for equations see Walters *et al.*, 1997; Walters *et al.*, 2000; Christensen and Walters, 2004). Predator prey interactions are moderated by prey behavior to limit exposure to predation, such that biomass flux patterns can show either bottom-up or top down (trophic cascade) control (Walters *et al.*, 2000). By doing repeated simulations Ecosim allows for the fitting of predicted biomasses to time series data.

9.1.1 Time series fitting in Ecosim: evaluating fisheries and environmental effects

Ecosim can thus incorporate (and indeed benefits from) time series data. For many of the groups to be incorporated in the model the time series data will be available from single species stock assessments. EwE thus builds on the more traditional stock assessment, using much of the information available from these, while integrating to the ecosystem level.

The time series fitting use either fishing effort or fishing mortality data as driving factors for the Ecosim model runs. A statistical measure of goodness of fit to the time series data outlined above is generated each time Ecosim is run. The model allows four types of analysis with the SS measure:

1. determine sensitivity of SS to the critical Ecosim vulnerability parameters by changing each one slightly (1%) then rerunning the model to see how much SS is changed, (i.e., how sensitive the time series predictions 'supported' by data are to the vulnerabilities);
2. search for vulnerability estimates that give better 'fits' of Ecosim to the time series data (lower SS), with vulnerabilities 'blocked' by the user into sets that are expected to be similar;
3. search for time series values of annual relative primary productivity that may represent historical productivity 'regime shifts' impacting biomasses throughout the ecosystem;
4. estimate a probability distribution for the null hypothesis that all of the deviations between model and predicted abundances are due to chance alone, i.e. under the hypothesis that there are no real productivity anomalies.

In addition to the nonlinear optimization routines described above the fit to data can also be improved in a feedback-process by examining some of the crucial ecological parameters in the EwE model (notably total mortality rates and the settings for top-down/bottom-up control). It is important to note here that such fitting does not include any ‘fiddling-factors’ internal to the model, instead the type of question that is addressed after each run is “which species parameters or ecological settings are not set such that the model captures the observed trends over time adequately?”

The inclusion of time series data in EwE facilitates its use for exploring policy options for ecosystem-based management of fisheries. An important preliminary conclusion from applications to various ecosystems is that the model is capable of producing a reasonable fit, (i.e. fits that can be compared to those obtained using single species models) for all available time series related to the ecological resources of an ecosystem in one go. This indicates a capability or at least a potential to replicate the known history of the ecosystems. In turn this lends some confidence to how the model can be used for policy exploration. It is also indicated that the fitting of time series in Ecosim may be used not just for identification of ecosystem effects of fishing but also to address questions of environmental impact at the ecosystem level (as well as for individual groups of course).

9.1.2 Using Ecosim for policy exploration

A central aim of fisheries management is to regulate fishing mortality rates over time so as to achieve economic, social and ecological sustainability objectives. An important dynamic modeling and assessment objective is thus to provide insight about how high these mortality rates should be, and how they should be varied over time (at least during development or recovery from past overfishing). We cannot expect models to provide very precise estimates of optimum fishing mortality rates, but we should at least be able to define reasonable and prudent ranges for the rates.

The Ecosim module of EwE provides two ways to explore impacts of alternative fishing policies:

1. Fishing rates can be ‘sketched’ over time and results (catches, economic performance indicators, biomass changes) examined for each sketch. This is using Ecosim in a ‘gaming’ mode, where the aim is to encourage rapid exploration of options.
2. Formal optimization methods can be used to search for fishing policies that would maximize a particular policy goal or ‘objective function’ for management.

The first of these approaches has been implemented in Ecosim since its first version, and has been widely applied for exploring ecosystem effects of changes in fishing effort. The second is ‘open loop’ policy exploration simulation that acknowledges that policy may be defined as an approach towards reaching a broadly defined goal, that fisheries policies are often implemented via TACs that are recalculated annually, and through regulation that affects fleet structure and deployment.

The goal function for policy optimization is defined by the user in Ecosim, based on an evaluation of four weighted policy objectives:

1. Maximize fisheries rent;
2. Maximize social benefits;
3. Maximize mandated rebuilding of species;
4. Maximize ecosystem structure or ‘health’.

The first of these, maximizing profits, is based on calculating profits as the value of the catch (catch · price, by species) less the cost of fishing (fixed + variable costs). Giving a high weight to this objective often results in phasing out most fleets except the most profitable ones, and the wiping out of ecosystems groups competing with or preying on the more valuable target species.

The second objective, maximizing social benefits, is expressed through the employment supported by each fleet. The benefits are calculated as number of jobs relative to the catch value, and are fleet specific. Therefore social benefits are largely proportional to fishing effort. Optimizing efforts often leads to even more extreme (with regards to overfishing) fishing scenarios than optimizing for profit.

The maximization of mandated rebuilding of species (or guilds) is incorporated to capture that external pressure (or legal decisions) may force policy makers to concentrate on preserving or rebuilding the population of a given species in a given area. In Ecosim this corresponds to setting a threshold biomass (relative to the biomass in Ecopath) for the species or group, and optimizing towards the fleet effort structure that will most effectively ensure this objective. The implications of this are case-specific: we are finding that the optimization routine may rigorously hammer (through increased fishing) competitors and predators of the species in question; or at the other extreme that fisheries may be shut down without social or economic consideration (as is indeed often the case when legal considerations take over).

The last objective included, maximizing ecosystem structure (or 'health') is inspired by E.P. Odum's description of ecosystem 'maturity', wherein mature ecosystems are dominated by large, long-lived organisms, (see Christensen, 1995a). The default setting we have incorporated for ecosystem structure is therefore the group-specific biomass/production ratio as this measure is indicative of the longevity of the groups. The ecosystem structure optimization often implies reduction of fishing effort for all fleets except those targeting species with low weighting factors.

The fishing policy search routine described above estimates time series of relative fleet sizes that would maximize a multi-criterion objective function. In Ecosim, the relative fleet sizes are used to calculate relative fishing mortality rates by each fleet type, assuming the mix of fishing rates over biomass groups remains constant for each fleet type, (i.e., reducing a fleet type by some percentage results in the same percentage decrease in the fishing rates that it causes on all the groups that it catches). However, density-dependent catchability effects can be entered, and if so reductions in biomass for a group may result in fishing rate remaining high despite reductions in total effort by any/all fleets that harvest it. Despite this caveat, the basic philosophy in the fishing policy search is that future management will be based on control of relative fishing efforts by fleet type, rather than on multispecies quota systems. It is not yet clear that there is any way to implement multispecies quotas safely anyway, without either using some arbitrary conservative rule like closing the fleet when it reaches the quota for the first (weakest) species taken or else allowing wasteful discarding of species once their quotas are reached.

If future multispecies management is indeed implemented by regulation of fleet fishing efforts so as to track time-varying fishing mortality rate targets as closely as possible, then a key practical issue is how to monitor changes in gear efficiency (catchability coefficients) so as to set effort limits each year that account for such changes in efficiency. Such monitoring is particularly important for fisheries that can show strong density-dependence in catchability, such that a unit of fishing effort takes a much higher proportion of some stocks (exerts a higher fishing mortality rate per unit of effort) when their stock sizes are small.

Ecosim also incorporates a 'closed loop policy simulations' to evaluate monitoring alternatives in terms of their implications for temporal variation in biomasses and also the objective function value components used in searches for optimum long-term fishing rate plans. The idea in the closed loop simulation is to model not only the ecological dynamics over time, but also the dynamics of the stock assessment and regulatory process. That is, a closed loop simulation includes 'submodels' for the dynamics of assessment (data gathering, random and systematic errors in biomass and fishing rate estimates) and for the implementation of assessment results through limitation of annual fishing efforts.

The closed loop simulation module includes options to:

1. decide how many closed loop stochastic simulation trials to do;
2. set the type of annual assessment to be used ($F=C/B$ versus F directly from tags);
3. set the accuracy of the annual assessment procedures (coefficient of variation of annual biomass or F estimates, by stock);
4. set value or importance weights for the F 's caused on various species by each fishing fleet; and
5. do the simulation trials and display time series and mean value results.

The value weights are used for each fleet/species combination to calculate a weighted average catchability q_t for each fleet type, recognizing that some species may be more important than others in terms of the effect that they might be allowed to have on effort reduction should q increase over time.

Closed loop policy simulations could obviously include a wide range of complications related to the details of annual stock assessment procedures, survey designs, and methods for direct F estimation. We suggest using other assessment modeling tools to examine these details, and so need only consider overall performance information (coefficients of variation in estimates) for the ecosystem-scale analysis performed using Ecosim.

9.2 Ecosim basic

The basics of Ecosim consist of biomass dynamics expressed through a series of coupled differential equations. The equations are derived from the Ecopath master equation (Eq. 1), and take the form

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i$$

Eq. 47

where dB_i/dt represents the growth rate during the time interval dt of group (i) in terms of its biomass, B_i , g_i is the net growth efficiency (production/consumption ratio), M_i the non-predation ('other') natural mortality rate, F_i is fishing mortality rate, e_i is emigration rate, I_i is immigration rate, (and $e_i \cdot B_i - I_i$ is the net migration rate). The two summations estimates consumption rates, the first expressing the total consumption by group (i), and the second the predation by all predators on the same group (i). The consumption rates, Q_{ji} , are calculated based on the 'foraging arena' concept, where B_i 's are divided into vulnerable and invulnerable components (Walters *et al.*, 1997 Figure 1), and it is the transfer rate (v_{ij}) between these two components that determines if control is top-down (i.e., Lotka-Volterra), bottom-up (i.e., donor-driven), or of an intermediate type.

The set of differential equations is solved in Ecosim using (by default) an Adams-Bashford integration routine or (if selected) a Runge-Kutta 4th order routine.

9.3 Nutrient cycling and nutrient limitation in Ecosim

Ecosim uses a very simple strategy to represent nutrient cycling and potential nutrient limitation of primary production rates. It is assumed that at any instant in time the system has a total nutrient concentration N_T , which is partitioned between nutrient 'bound' in biomass versus free in the environment (accessible to plants for nutrient uptake). That is, T is represented as the sum $N_T = \sum_i \eta_i B_i + N_f$, where η_i is (fixed) nutrient content per unit of pool i biomass, and N_f is free nutrient concentration. Then assuming that N_T varies as $dN_T/dt = I - vN_T$, where I is total inflow rate to the system from all nutrient loading sources and v is total loss rate from the system due to all loss agents (volume exchange, sedimentation, export in harvests, etc.), and that v is relatively large, N_T is approximated in Ecosim by the (possibly moving) equilibrium value $N_T = I/v$.

Changes in nutrient loading can be simulated by assigning a time forcing function number to N_T , in which case N_T is calculated as $N_T = f_t N_T^o$ where N_T^o is the Ecopath base estimate of N_T (at the start of each simulation) and f_t is a time multiplier ($f_t = 1$ implies Ecopath base value of N_T) supplied by the user the same as any other time forcing function. Note that under the moving equilibrium assumption, changes in f_t can be viewed as caused by either changes in input rate I or nutrient loss rate v . The Ecopath base estimate N_T^o of total nutrient is entered by specifying the base free nutrient proportion $p_f = N_f / N_T^o$ on entry to Ecosim, from which the Ecosim initialization can calculate N_T^o as simply $N_T^o = \sum_i \eta_i B_i / (1 - p_f)$. Note here that the units of nutrient concentration are contained in the per-biomass relative nutrient concentrations η_i , and these need not be specified in any particular absolute units. During each simulation, N_f is varied dynamically by setting it equal at any time to $N_T - \sum_i \eta_i B_i$, so that accumulation of nutrient in any biomass pool(s) can reduce free nutrient available to promote primary production.

Primary production rates for producer pools j are linked to free nutrient concentration during each simulation through assumed Michaelis-Menten uptake relationships of the form $PB_j = PB_{max,j} N_f / (K_j + N_f)$, where the parameters $PB_{max,j}$ and K_j are calculated as part of the Ecosim initialization using input estimates by the user of the ratios $PB_{max,j} / PB_{Ecopath,j}$ (Ecosim Group Info interface). The Michaelis constant K_j is set so that $PB_j = PB_{Ecopath,j}$ when N_f is at the initial concentration determined by $N_T - \sum_i \eta_i B_i$ when all B_i are at Ecopath base values). The user can increase sensitivity to changes in nutrient concentration (make PB_j more variable with changes in N_T and N_f) by increasing the input $PB_{max,j} / PB_{Ecopath,j}$ ratio.

To insure that Ecosim (5) results are compatible with earlier Ecosim versions for saved simulations, the default free nutrient proportion p_f is set very high (0.9999), which causes N_f to be virtually constant over time (and hence PB_j 's to be virtually independent of nutrient concentration changes). Thus to “turn on” nutrient limitation effects, the Ecosim user must set a lower value for p_f , (e.g., 0.3) in the Ecosim general parameters (startup tab) interface.

Users should be aware that this simple approach to accounting for nutrient limitation can interact with the numerical method used to simulate very fast phytoplankton dynamics over time, to cause numerical instability or “chattering” in the values of phytoplankton biomass. This happens mainly in cases where p_f is low, so that N_f is initially small. Then any biomass decline in the system (e.g. due to decline in zooplankton biomass) results in a relatively large increase in N_f , which can cause an over-response in the calculated phytoplankton biomass(es) B_j , which then drives N_f to near zero, which in turn causes too large a decrease in calculated B_j for the next monthly Ecosim time step.

Chattering can be reduced by using the Runge-Kutta integration option and/or higher p_f settings. Improved numerical integration procedures should allow us to avoid the problem entirely in future Ecosim versions, but at present the computational cost of avoiding the problem by ‘brute force’ (shorter simulation time steps) would be prohibitively expensive of computer time.

Note further that the single free nutrient concentration N_f is linked to all primary producer groups in the model (through the uptake kinetics- PB relationships), implying competition among all plant types in the model for free nutrients. This can cause major shifts in primary production structure over time, e.g. between benthic and pelagic primary production and between grazeable and non-grazeable algal types.

9.4 Predicting movement and accumulation of contaminants and tracers in food webs

Ecosim predicts temporal changes in flows of biomass among living and detritus pools using nonlinear functional relationships between flow rates and abundances of the interacting species. These flow rates (along with auxiliary information about factors such as isotope decay rate and physical exchange rates) can be used to predict changes in concentrations (and per-biomass burdens) of chemicals like organic contaminants and isotope tracers that ‘flow’ passively along with the biomass flows. The dynamic equations for such passive flow (and accumulation, e.g., ‘bioamplification’) are not the same as the biomass flow rate equations, and in fact are generally linear dynamical equations with time-varying rate coefficients that depend on the biomass flow rates; these linear equations are relatively easy to solve in parallel with the Ecosim biomass dynamics equations.

In Ecosim we allow parallel simulation of one tracer or contaminant type while the biomass dynamics equations are being solved. Tracer molecules are assumed to be either in the ‘environment’ or in the biota (in biomass and detritus pools) at any moment. Molecules are assumed to flow between pools at instantaneous rates (i.e. to be sampled along with biomass during biomass flows at rates) equal to the probabilities of being ‘sampled’ as part of the biomass flow: instantaneous rate = (flow) / (biomass in prey pool). We also allow for direct flows from the environment into pools, representing direct uptake or absorption of the tracer material, and for differential decomposition/decay/export rates by pool and from the environmental pool. Schematically, the flow of tracer molecules through any biomass pool is represented by the components shown below:

In the rate equation for time changes in contaminant concentration in pool i , these components are represented as follows:

- 1) Uptake from food: $C_j \cdot GC_i \cdot Q_{ji} / B_j$ where C_j = conc in food j , GC_i = proportion of food assimilated by type i organisms; Q_{ji} = biomass flow rate from j to i (estimated in Ecopath as $B_i \cdot (Q/B)_i \cdot DC_{ij}$), B_j = food j biomass;
- 2) Direct uptake from environment: $u_i \cdot B_i \cdot C_o$, where u_i = parameter representing uptake per biomass per time, per unit environmental concentration, B_i = biomass, C_o = environmental concentration;
- 3) Concentration in immigrating organisms: $c_i \cdot I_i$, where c_i = parameter (tracer per unit biomass in immigrating biomass), I_i = biomass of pool i immigrants per time;
- 4) Predation: $C_i \cdot Q_{ij} / B_i$, where C_i = concentration in pool i , Q_{ij} = consumption rate of type i organisms by predator type j , B_i = biomass in pool i ;
- 5) Detritus: $C_i \cdot MO_i + (1-GC_i) \cdot S_j \cdot C_j \cdot Q_{ji} / B_j$, where MO_i = non-predation death rate of type i (per year), GC_i = fraction of food intake assimilated, Q_{ji} = intake rate of type j biomass by type i ;
- 6) Emigration: $e_i \cdot C_i$, where e_i = emigration rate (per year);

7) Metabolism: $d_i \cdot C_i$, where d_i = metabolism + decay rate for the material while in pool i .

Hence, users must specify some parameters (using the Ecotracer input form) besides those needed for Ecopath/Ecosim mass balance and biomass dynamics calculations:

- a. initial pool concentrations C_i , including environmental concentration C_o ;
- b. direct uptake rate parameters u_i as rates per time per biomass per unit C_o ;
- c. concentrations per biomass c_i in immigrating organisms;
- d. metabolism/decay rates d_i .

The other parameters (GC_i , MO_i) are already entered or calculated in Ecopath, and the Q_{ij} flows are calculated dynamically in Ecosim. Ecotracer users can also enter inflow, outflow (dispersal/advection exchange to outside systems), and decay rates for the 'environmental' (abiotic) concentration C_o .

When the Ecotracer simulation component is enabled (check box on Ecotracer entry form), Ecosim integrates the rate components listed above to generate time concentration patterns C_i ($i = 0$ to number of biomass pools), and time patterns of concentration per biomass C_i / B_i for all Ecopath/Ecosim biomass pools. These results can be compared to data on bioaccumulation or tracer movement. Discrepancies between model and data may help identify weaknesses in the Ecopath/Ecosim trophic flow rate (Q_{ij}) estimates, and/or in the Ecotracer rate parameters (u_i , e_i , d_i).

9.5 Prepare Ecosim simulations

The first Ecosim screen is designed to enter and store key information on the current Ecosim simulation, equilibrium analysis and Ecospace simulation.

- **Duration of simulation:** Default is 20 years, while the maximum is 999 years. It is possible to save the end state of a simulation, and continue a new simulation from the end point, thus enabling even-longer term simulations;
- **Integration steps** (per year): the step size for the integration of biomass in the 'fast' groups (the default is 100 steps per year and it is recommended to stick to it, unless a study of step size effects is to be conducted). Integration step size is used relative to the highest turnover rate;
- **Relaxation parameter:** Biomasses change for each integration step. Range for relaxation parameter is [0, 1]. Low value causes slow changes in biomass, a high value fast changes;
- **Discount rate:** Annual rate (entered in %) applied to discount the present value of future catches; displayed on simulation relative to present base value;
- **Equilibrium step size:** Step size (year) used for the equilibrium analysis;
- **Equilibrium max. fishing rate:** Max fishing rate in equilibrium analysis expressed relative to the fishing rate in Ecopath for the group on which fishing is changed;
- **Number of time steps for averaging results:** You can define how many time steps should be used for averaging results in Ecosim and Ecospace. Averaging will start at the vertical red line displayed in the time plot scales of the two routines (use left-mouse click to set the first time, and right-mouse click to send the second time), and will continue over the number of time steps entered here.
- **Prepare pulse fishing (nudging):** A measure of persistence to perturbation. Checking the command button opens for entry of:
- **Multiplicative factor for nudging:** Toggle whether the nudging is done with a factor, e.g., +20%, or by adding an amount, e.g., +0.20, to the instantaneous fishing mortalities
- **Start nudge:** When to start nudging (year)
- **End nudge:** When to end nudging (year)
- **Use amount/factor for nudging:**

- **System recovery (+/- %):** When 'nudging' it is checked when all biomass have returned to within this percentage of their original value;

The nudging is done on the 'temporal simulation tab (Ecosim)'

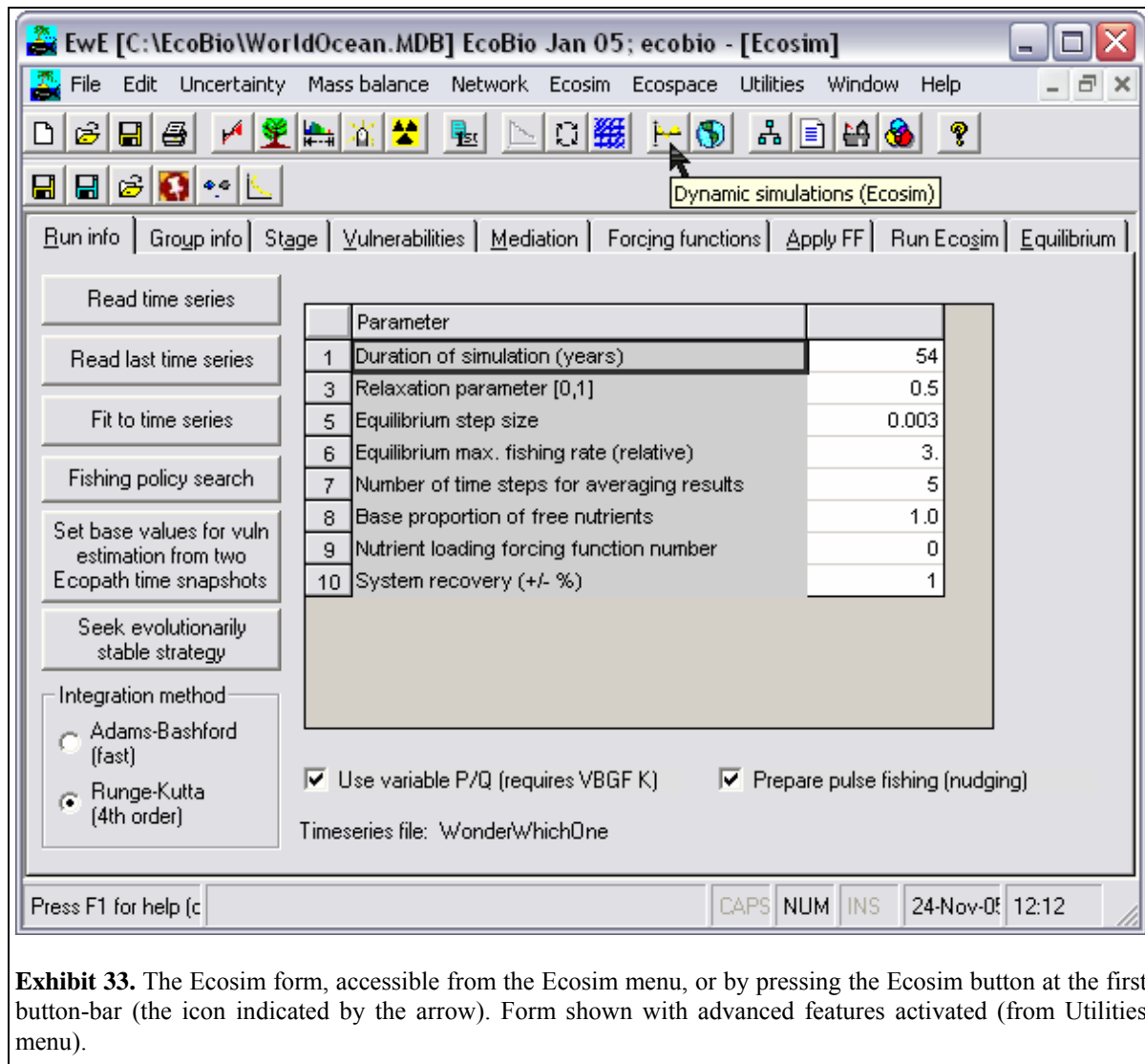


Exhibit 33. The Ecosim form, accessible from the Ecosim menu, or by pressing the Ecosim button at the first button-bar (the icon indicated by the arrow). Form shown with advanced features activated (from Utilities menu).

When working in Ecosim or Ecospace you work within a 'scenario'. A given Ecopath model can have any number of Ecosim and Ecospace scenarios attached, and they all inherit their basic parameters (such a number of groups, group names, diets and other parameters) from the parent Ecopath model. If you change a group name or delete a group in Ecopath the changes will be carried over to existing (and new) Ecosim and Ecospace scenarios. A scenario keeps track of all the information that is needed to store and later duplicate a simulation. Handling of Ecosim scenarios is carried out through a series of commands accessible from the Ecosim menu and from the second button bar:

- **Save scenario:** Save the current scenario under its current name;
- **Save as:** Save the current scenario under a new (or the existing) name;
- **Load scenario:** Load a new scenario. You will be prompted whether you want to save the current scenario before loading another;
- **Reset to defaults:** Use Ecosim default values for the current scenario;

- **Remarks:** Enter a remark for the current Ecosim scenario;

In addition the first tab on the Ecosim form includes the following series of command buttons:

- **Read time series data:** Use this control button to load historical comparison data stored in CSV (comma delimited DOS text) format from an Excel spreadsheet. The data will be saved with the current model upon loading. Additional help for time series data is available below;
- **Fit to time series:** See the section ‘Fitting Ecosim to time series data: the Parameter search interface’ below;
- **Change colors:** Opens the form for change of colors used for, e.g., the groups in Ecosim and Ecospace;
- **Set base values for vulnerability estimation from two Ecopath time snapshots;**
- **Seek evolutionary stable strategy;**
- **Integration method:** Choose between using an Adams-Bashford or a Range-Kutta 4th Order method. The default choice is the Adams-Bashford method, which is faster, and which we have found to be stable. The Adams-Bashford method is programmed from algorithms 5-6 of Nash (1979). The Runge-Kutta integration is based on Press *et al.* (1992 edition, p 707).

9.5.1 Read time series data

Use the ‘read time series’ interface to load historical comparison data stored in CSV (comma delimited DOS text) format from an Excel spreadsheet such as that shown in Exhibit 34. For each data series (column) you need to enter the EwE pool number (pool code) and specify the data type (0=relative biomass (e.g. CPUE), 1=absolute abundance). You can leave cells blank for which you have no data. Ecosim will assume that the first calendar year for which you enter a data row (e.g., 1955) is to be the simulation start year. Absolute biomasses will be displayed as Ecosim passes the year for which they have been entered; relative abundances are scaled and displayed at the end of simulation runs. You can have as many data rows (years) and abundance indices as you like.

title	shark CPUE	shark B	Tuna CPUE
pool code	1	1	11
type	0	1	0
1955	0.33		3.7
1956	0.4	0.06	3.5
1957	0.26		3.6
1958	0.27		2.9
1959	0.21		4.1
1960	0.22		3.8
1961	0.25		2.6
1962	0.27		2.7

Exhibit 34. Time series file for use in Ecosim, should be saved as ‘comma separated values’, e.g., using Excel and saving as a ‘.csv’ file.

You can also use the file to load time forcing, relative fishing rate by gear, or fishing rates by pool for the same years. For time forcing, set row 2 (pool code) value to the forcing function number (4, 5, 6) and the row 3 value (type) to 2. For effort by gear forcing, set row 2 value to the fleet number, and row 3 value to 3. Note that relative fishing rate by gear type must be scaled so relative value is 1.0 for the Ecopath base year (year for which catches are provided to Ecopath). For F by pool, set the pool code to the pool number and the type code to 4.

Overview of data types:	-1	Force biomass
	0	Relative biomass
	1	Absolute biomass
	2	Time forcing data
	3	Effort data by gear type
	4	Fishing mortality, (F) by pool
	5	Total mortality, (Z) by pool
	-5	Forced total mortality (Z)

6	Catches
-6	Forced catches
7	Average weight (stanza/split groups only)

Note: The data must be formatted with a maximum of 4 digits before and 4 digits after the decimal. Rescale your data correspondingly, and do not use scientific notation.

In order to enable reading of csv-files with varying international notation the content of the csv-file will be checked on reading. You will have the chance to specify what symbol is used for decimal sign etc. This is necessary due to an Excel problem with reading international character sets.

Read data file: Use this command button to open a file dialog where you can browse to find and load a '.CSV' file (constructed as described above)

Read from database: Click this button if you want to read a data set that has already been read (and hence stored with the current model in the database). Clicking the button will make visible some additional controls for reading: the combo-box and the 'Load', 'Rename' and 'Delete' buttons described below.

Read from clipboard

Read forcing (monthly)

Cancel: Return to Ecosim without updating time series.

- **Combo-box:** All data sets that have been stored with the current model in the database will be listed in a combo-box. You can click the arrow at the right hand side and move down to highlight the data set you want to read.
- **Load:** Once a data set name has been highlighted in the combo-box click the 'Load' button to read the data set.
- **Rename:** When data sets are read from '.CSV' files using the 'Read data file' button they will be named automatically using the first part of the filename. As an example, a file with path and name 'c:/My files/GoodData.CSV' will be stored in the database as 'GoodData'. You can use the Rename button to change the name of data set.
- **Delete:** Will delete the data set that is highlighted.

As soon as a data set has been read (be it from a '.CSV' file or from the database) the '**Time series**' button on the 'Run model' tab of Ecosim will be enabled.

9.5.2 Fitting Ecosim to time series data: Parameter search interface

When an Ecosim model is loaded, you can load time series 'reference' data on relative and absolute biomasses of various pools over a particular historical period, along with estimates of changes in fishing impacts over that period. After such data have been loaded ('read reference data' button on Run Info tab), a statistical measure of goodness of fit to these data is generated each time Ecosim is run. This goodness of fit measure is a weighted sum of squared deviations (*SS*) of log biomasses from log predicted biomasses, scaled in the case of relative abundance data by the maximum likelihood estimate of the relative abundance scaling factor q in the equation $y = qB$ (y = relative abundance, B = absolute abundance). Each reference data series can be assigned a relative weight using a simple spreadsheet in the search interface, representing a prior assessment by the user about relatively how variable or reliable that type of data is compared to the other reference time series (low weights imply relatively high variance, unreliable data).

The search interface allows users to do four types of analysis with the *SS* measure:

- (1) determine sensitivity of *SS* to the critical Ecosim vulnerability parameters (Flow control tab), by changing each one slightly (1%) then rerunning the model to see how much *SS* is changed (i.e., how sensitive the time series predictions 'supported' by data are to the vulnerabilities);

Reference data load

Data Source

Read data file

Read from database

Read from clipboard

Read forcing (monthly)

Cancel

Help info

Use this interface to load historical comparison and driver data stored in CSV (comma delimited DOS text) format from an Excel spreadsheet (see spreadsheet example for formatting -- which must be followed).

For each data series (column) you need to enter the EwE group/pool number (pool code) and specify the data type.

Ecosim will assume that the first calendar year for which you enter a data row (e.g. 1955 in the spreadsheet example) is to be the simulation start year. You can have as many data rows (years) and data series as you like. Time series will be saved in the database once read from the CSV file. To accommodate international character sets it is necessary to load the data to a temporary spreadsheet first. You will then need to check that the delimiters are properly specified, and subsequently load the spreadsheet data

	A	B	C	D
1	Title	Shark CPUE	Shark B	Tuna CPUE
2	Pool code	1	1	11
3	Type	0	1	0
4	1955	0.33		3.7
5	1956	0.36	0.06	3.5
6	1957	0.31		3.2
7	1958	0.27		3.4
8	1959	0.26		3.6

Types of time series: (click for comments)

Type = 0. Relative biomass

Type = 1. Absolute biomass

Type = 1. Force biomass

Type = 2. Time forcing data

Type = 3. Fleet/gear effort

Type = 4. F (Fishing mortality)

Type = 5. Z (Total mortality)

Type = 5. Constant total mortality (Z)

Type = 6. Catches

Type = 6. Force catches

Type = 7. Average weight

Set:
Row 2 (pool) to the fleet number, and
Row 3 (type) to 3.
The relative fishing rate by gear must be scale so that the relative value is 1 for the Ecopath base year. Time series should include all years

If you are reading monthly forcing functions your csv file needs to be organized with:

First line: Dummy, one col for each series with the name of the series.

Second line: Dummy, one col for each series with the number of the series (the number to be used on the Forcing Function tab of Ecosim).

Third and following lines (one line per month) has first a Dummy (e.g., month number), then one col for each series with the forcing function value

Exhibit 35. Form used for reading historical data into Ecosim. Time series data can be entered in formatted spreadsheet files (saved as text files with .csv extension), or read from memory. Time series data is subsequently stored in the Ecopath database with the current model.

- (2) search for vulnerability estimates that give better 'fits' of Ecosim to the time series data (lower SS), with vulnerabilities 'blocked' by the user into sets that are expected to be similar, (i.e., user can search for just one best overall vulnerability, or for better estimates for up to 15 'blocks' of predator-prey vulnerabilities);
- (3) search for time series values of annual relative primary productivity that may represent historical productivity 'regime shifts' impacting biomasses throughout the ecosystem (for this search, user must have linked time forcing function #4 to primary production using the apply FF tab and setting the i,i element of the forcing table for i = primary producers to 4);
- (4) estimate a probability distribution for the null hypothesis that all of the deviations between model and predicted abundances are due to chance alone, i.e. under the hypothesis that there are no real productivity anomalies, see 'Time series random effects' below.

Option (1) is invoked by clicking the button labeled 'Sensitivities of SS to v 's'. Progress in this assessment is shown by placing an X in the vulnerability grid picture (right part of the interface) as the sensitivity to each vulnerability is computed. When all tests are completed or the testing is stopped by clicking the red box above the vulnerability grid, relative sensitivities are shown on a color code scale on the vulnerability grid. A grid cell shown in red (for prey type in row i , predator type in column j of the grid) is one for which SS was most sensitive (among those tested) to changing that vulnerability, while a grid cell shown in blue is one for which SS was not sensitive to changing that vulnerability. Note that the colors shown on the vulnerability grid after this search are purely to help the user identify vulnerability blocks for the parameter search, and are NOT used by the interface to define vulnerability blocks for estimation.

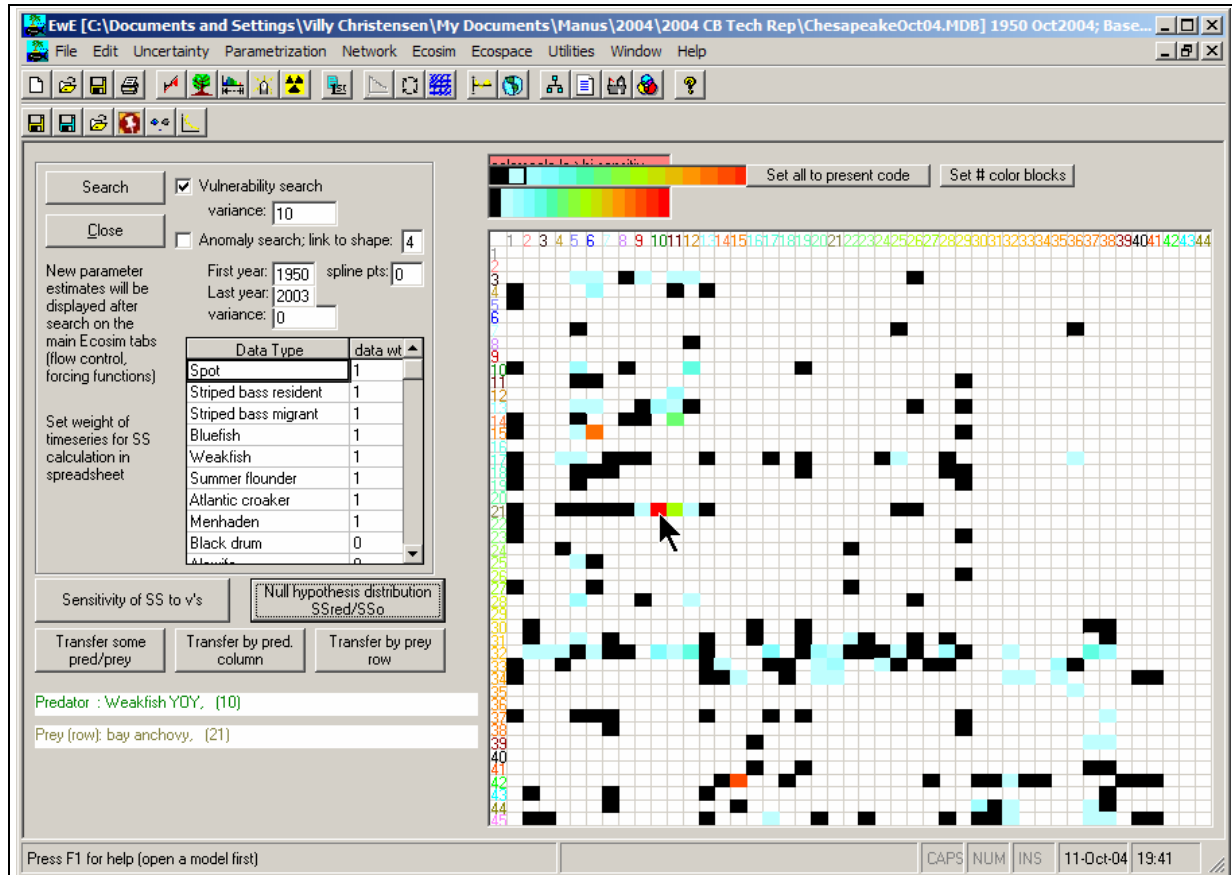


Exhibit 36. Ecosim: fitting to time series data. Results from checking “sensitivity of SS to v’s”. The search procedure has determined the most sensitive interactions, the most sensitive being the interaction between weakfish YOU and bay anchovy (cursor). The most sensitive interactions can subsequently be used for the vulnerability search by choosing one of the three ‘transfer’ buttons (though avoid the option to transfer by prey row). Next click ‘Search’ or if desired, check the ‘Anomaly search’ first (if so link primary producers to the shape file listed). See text for further explanation.

It is, however, possible to transfer the information from the sensitivity table to the search table using one of the three transfer buttons on the form. We recommend that you use the ‘transfer some pred/prey’ or ‘transfer by pred column’ rather than the ‘transfer by prey column,’ which biologically makes less sense.

Options (2) and/or (3) are invoked by pressing the ‘Search’ button on the search interface, after deciding which parameters to include in the search by setting nonzero variance values in one or both of the frames below the search button. Setting variance > 0 in the primary production frame causes the search to include *PP* parameters for the year range set in that frame, and setting variance > 0 in the vulnerability frame causes search to include parameter blocks that have been sketched as non-black in the vulnerability layout grid on the right side of the search interface. The variance values set by the user are treated as Bayesian ‘prior’ variances for the parameters included in the search. Large variance values ‘allow’ the search procedure to vary the parameters more widely in search of lower *SS* parameter combinations.

When the search button is pressed, a frame appears at the left of the interface to show progress of the *SS* minimization procedure (a Marquardt nonlinear search algorithm with trust region modification of the Marquardt steps). For each step in the search, the algorithm must run the Ecosim model at least $N + 1$ times, where N is the number of parameters with nonzero variances (N can be up to $Last\ year - First\ year + 16$). A dot is written in the frame for each Ecosim run. For most of these runs, what the algorithm is doing is to increment one *PP* annual value

or one vulnerability block value slightly, so as to calculate the ‘Jacobian matrix’ of sensitivities of each of the predicted time series observations to each of the parameters. After $N+1$ such checks, the Jacobian matrix is used to estimate an initial best step change for each parameter, and a few more runs are used to further improve the step. The algorithm stops when these changes become very small (or a numerical error occurs in the search calculations, if the search results in unrealistic values for some parameters). If no numerical error occurs during the search, the best estimates found during the search will be displayed in the Forcing functions tab (for *PP* time series) and/or the Flow control tab (for vulnerabilities). These new values will be saved with the Ecosim scenario if the user answers yes to the save scenario message on exit from Ecosim.

For users familiar with nonlinear estimation procedures used in single-species stock assessment, e.g., for fitting production models to time series CPUE data, searches on the vulnerability parameters should look quite familiar. In essence, the Ecosim search procedure for vulnerabilities is just an ‘observation error’ fitting procedure where vulnerability changes usually have effects quite similar to changes in population ‘*r*’ parameters in single-species models. Allowing the search to also include historical *PP* ‘anomalies’ corresponds to searching also for ‘nuisance parameter’ estimates of what we usually call the ‘process errors’ in single species assessment.

Ecosim users are cautioned that the search procedure in no way guarantees finding ‘better’ Ecosim parameter estimates. Better fits to data can easily be obtained for the wrong reasons (some time series, particularly *CPUE* data, can be misleading in the first place, as can historical estimates of changes in fishing mortality rates; many parameter combinations may equally well ‘explain’ patterns in the data). Nonlinear search procedures can become lost or ‘trapped’ at local parameter combinations where there are local minima in the *SS* function far from the combinations that would actually fit the data best. The best way to insure against the technical problems of searching a complex *SS* function is to use ‘multiple shooting’: start the search from a variety of initial parameter combinations (patterns sketched in time forcing function #4, vulnerability settings in flow control interface), and see if it keeps coming back to the same final estimates. Look very closely at the time series data for possible violations of the assumption that $y = qB$, due to progressive changes in the methods of measuring relative abundance (*y*) or nonlinearities caused by factors such as density-dependent catchability. If *y* is a biomass reconstruction from methods such as VPA that assume constant natural mortality rate *M*, watch out for spurious trends in *y* caused by the sort of changes in *M* that Ecosim predicts, particularly for younger animals. Look for alternative combinations of Ecosim parameters that appear to fit the data equally well but would imply quite different responses to policy changes such as increases in fishing rates.

Search procedures are most useful in diagnosing problems with both the model and data. That is, the greatest value of doing some formal estimation is while it seems not to be working, when it cannot find good fits to data. Poor fits can be informative about both the model and the data. For example, in a study on impact of lobster fishing on Hawaiian monk seals, it seemed initially that Ecosim could ‘explain’ monk seal decline as a consequence of fishing down one of their foods, the lobster. But this hypothesis never really fit the monk seal population trend data well: Ecosim predicted a monk seal decline with development of the lobster fishery, but nowhere as severe or persistent as the observed decline. This lack of fit told us we needed to look for some other factor that hit the monk seals well after the lobster fishery had its impacts, and this factor turned out to be an oceanographic regime shift (decrease in primary productivity) that apparently impacted the availability of fish prey as well as lobsters. As an example of learning things about the data as well as the model, attempts to fit Ecosim to historical abundance estimates (from VPA) for Pacific herring in the Georgia Strait, British Columbia, Canada, have consistently led to Ecosim predicting lower juvenile herring abundances than observed during peak periods of historical fishing, and lower recent biomass of adult herring than observed. It looks in this case like the problem is with the data, not Ecosim: VPA likely resulted in overestimates of juvenile herring abundance during a period when we would expect juvenile herring to have had higher natural mortality rate than assumed in the VPA, and overestimates of adult biomass due to not correcting the VPA estimates for observed changes in growth rates (lower conditions factors observed) during the period where Ecosim predicts lower biomass.

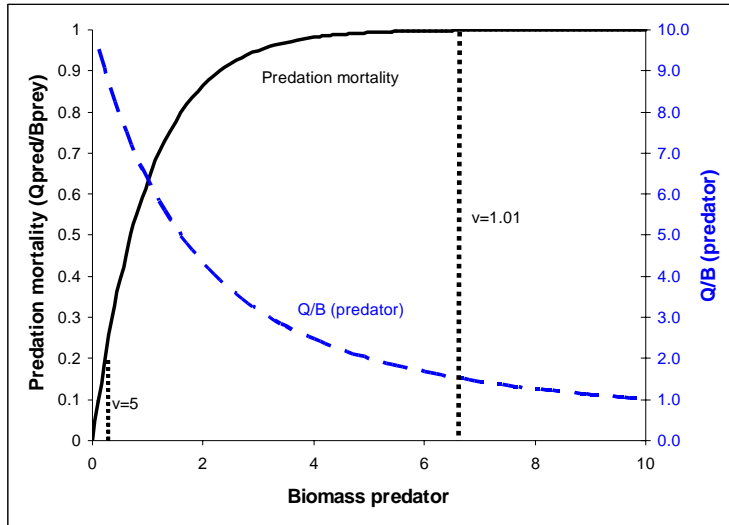


Exhibit 37. Relationship between biomass of a predator and the predation mortality it causes on a given prey, as well as the corresponding Q/B for the given predator and prey (assuming that the predator does not reduce prey biomass substantially). Vulnerability, v , is estimated as $\text{max. predation mortality}/\text{baseline predation mortality}$, (e.g., 5 at the leftmost stippled line). Baseline mortality is the mortality caused by the predator in the underlying Ecopath model.

If we to illustrate the relationship between predator biomass and Q/B, (this is not an assumption in the actual Ecosim calculations) assume that the predator in question does not cause any substantial (actually no) change in the prey biomass we can calculate the relative Q/B for the predator; see Exhibit 37. For higher predator biomass a change will result in relatively stable predation mortality; hence, if biomass is impacted so as to cause a reduction, the individual predators will get more, their Q/B increase and this will largely compensate for the reduction in their abundance, bringing the biomass back up again. At lower biomass Q/B will also increase, but to a lower degree. This is illustrated in Exhibit 38 showing how halving or doubling the predator biomass will impact the relative Q/B. At high biomasses halving biomass results in close to a doubling in Q/B, which will tend to bring biomass back up again. There is, however, less and less relative surplus production as we move to the left on the curve. If biomasses are doubled instead, the Q/B will be decreased when biomasses are high, resulting in a decrease in biomass back toward the original level,

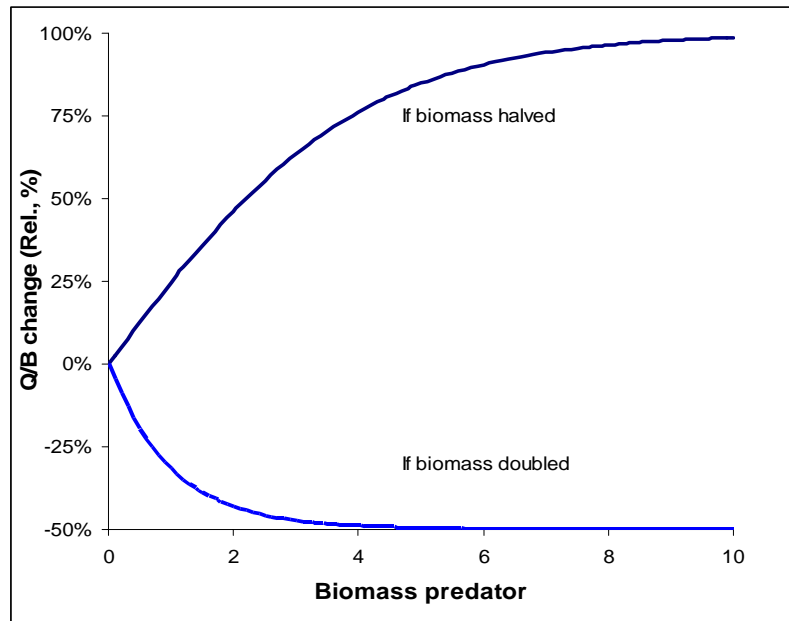
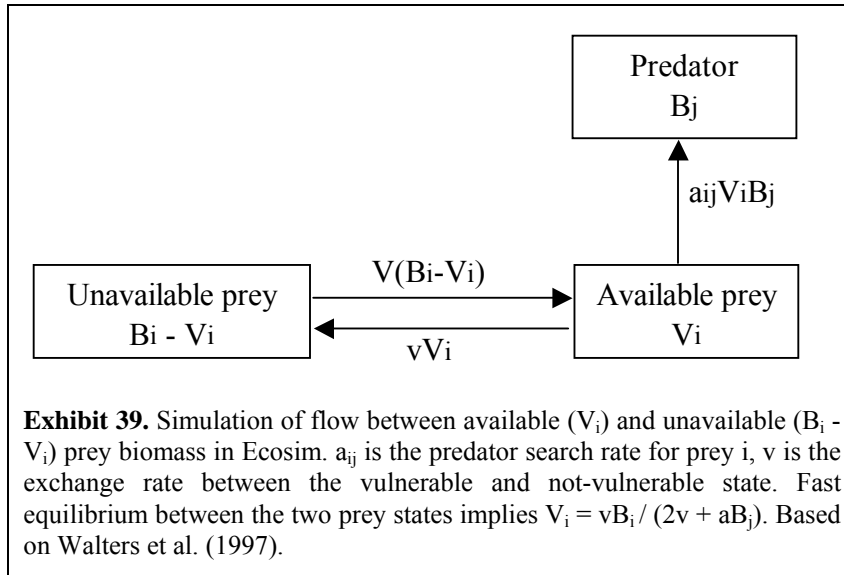


Exhibit 38. Relative increase in Q/B (%) as a function of predator biomass resulting from the predator biomass being halved or doubled. At high predator biomasses (i.e. near the carrying capacity for the given predator-prey interaction) a halving of predator biomass will result in nearly a doubling in the Q/B for the predator. The resulting surplus production will tend to bring the predator biomass back to the original level, and the overall effect is that the predator biomass will change only little. Conversely, a doubling of predators will cause the Q/B to be halved at high predator biomasses (resulting in very little effective change in biomass), while a doubling at low biomasses will result in only a very small reduction in Q/B.

9.5.3 Flow control: foraging arena parameter (vulnerabilities)

One key feature of Ecosim is its ability to allow exploring the implications on system dynamics of different views of how the biomass of different groups in ecosystem is controlled. The two extreme views are ‘predator’ control’ (also called top-down control) and ‘prey (or bottom-up) control’. We model this using ‘vulnerabilities,’ which represent the factor that a large increase in predator biomass will cause in predation mortality for a given prey. Low vulnerability (close to 1) means that an increase in predator biomass will not cause any noticeable increase in the predation mortality the predator may cause on the given prey; see Exhibit 37. A high vulnerability, e.g., of 100, indicates that if the predator biomass is for instance doubled, it will cause close to a doubling in the predation mortality it causes for a given prey.

i.e., the biomasses will be stable when close to carrying capacity (where v 's are low), and unstable when far below carrying capacity (where v 's are high).



If vulnerabilities are high, the amount of prey consumed by the predator is the product of predator \times prey biomass, i.e., the predator biomass impact how much of the prey is consumed. Such situation may occur in situation where the prey has no refuge, and is thus always taken upon being encountered by a predator.

Top-down control, also known as Lotka-Volterra dynamics, easily leads to rapid oscillations of prey and predator biomasses and/or unpredictable behavior.

The converse (bottom-up control) is the situation that occurs when a prey is protected most of the time, (e.g., by hiding in crevices) and

The screenshot shows the Ecosim software interface with a vulnerability matrix. The matrix has 26 rows representing prey species and 24 columns representing predator types. The values in the matrix represent vulnerability settings. The interface includes a menu bar, a toolbar, and a status bar.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1 Piscivorous birds																								
2 Non-piscivorous se																								
3 Spot					2	5.18		20.0	2		2	2												
4 Striped bass YOY	2					5.18					2		1.23											
5 Striped bass reside	2																							
6 Striped bass migrat																								
7 reef assoc. fish					5.18																			
8 Bluefish YOY												2												
9 Bluefish adult													2											
10 Weakfish YOY	2																		2					
11 Weakfish Adult					2	5.18																		
12 Summer flounder												2												
13 Atl. croaker					5.18	5.18			2	2	2	2												
14 Menhaden YOY	2				5.18			20.0	2		2													
15 Menhaden adult	2				5.18	5.18																		
16 black drum																								
17 Littoral forage fish	2				5.18	5.18		2	20.0	2			1.23				2		2					2
18 Alewife and herring	2				2	5.18	2																	
19 American eel	2				2																			
20 American shad																								
21 bay anchovy	2				5.18	5.18	5.18	2	20.0	2	2	2	2	1.23										
22 Catfish	2																							
23 Other flatfish	2																							
24 White perch YOY					5.18																	2		
25 White perch adult						2	5.18																	
26 other elasmobranch																								

Exhibit 40. Ecosim vulnerability settings reflecting how far a consumer is from its carrying capacity with regards to a prey.

becomes available to predators only when it leaves the feature that protects it. Here being caught is a function of the prey's behavior. Bottom-up control usually leads to unrealistically little biomass changes in the prey and predator(s) concerned, but which usually do not propagate through the other elements of a food web.

To model this aspect of predator-prey interactions, the group biomasses (B) on the underlying Ecopath model were reconceived in Ecosim as consisting of two components, one vulnerable, the other invulnerable to predation (B' and V , respectively in Exhibit 39). Further, it is assumed that there is a flow (v_{ij}) of organisms from the invulnerable to the vulnerable stage, and conversely (v_{ji}), with the assumption $v = v_{ij} = v_{ji}$.

As might be seen in Exhibit 39, when v is high, the rapid replenishment of vulnerable biomass depleted by predator will rapidly drain the invulnerable part of the biomass. Thus, with v set high, predation control will be top down.

Conversely, if v is low, replacement of depleted biomass from the invulnerable to the vulnerable part of the population will be slow, and the amount that the predators consume will be largely determined by the low value of v , rather than by their own biomass. Thus, when v is low, control is bottom up.

Vulnerabilities are entered on (or transferred from the time series fitting routine to) an input tab on the Ecosim form, see Exhibit 40). Here, the vulnerabilities can be set for the entire system (upper left panel), or for the interactions of different groups (on the vertical axis) with their own predator (horizontal axis). Also, individual values can be entered to characterize e.g., the interactions of one (or several) predator/prey pair(s) under special conditions.

9.5.3.1 Predicting consumption

Ecosim bases the crucial assumption for prediction of consumption rates on a simple Lotka-Volterra or 'mass action' assumption, modified to consider 'foraging arena' properties. Following this, prey can be states that are or are not vulnerable to predation, for instance by hiding, (e.g., in crevices of coral reefs or inside a school) when not feeding, and only being subject to predation when having left their shelter to feed, (see Exhibit 39). In the original Ecosim formulations (Walters et al 1997, 2000) the consumption rate for a given predator i feeding on a prey j was thus predicted from,

$$C_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot P_j}{2v_{ij} + a_{ij} \cdot P_j}$$

Eq. 48

where, a_{ij} is the effective search rate for predator i feeding on a prey j , v_{ij} base vulnerability expressing the rate with which prey move between being vulnerable and not vulnerable, B_i prey biomass, P_j predator abundance (N_j for split pool groups discussed later, and B_j for other groups).

The model as implemented argues that 'top-down vs. bottom-up' control is in fact a continuum, where low v 's implies bottom-up and high v 's top-down control.

Early experience with Ecosim has led to a more elaborate expression to describe the consumption:

$$C_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot P_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij} / D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot P_j \cdot S_{ij} \cdot T_j / D_j}$$

Eq. 49

where, T_i represents prey relative feeding time, T_j predator relative feeding time, S_{ij} user-defined seasonal or long term forcing effects, M_{ij} mediation forcing effects, and D_j represents effects of handling time as a limit to consumption rate,

$$D_j = \frac{h_j \cdot T_j}{1 + \sum_k a_{kj} \cdot B_k \cdot T_k \cdot M_{kj}}$$

Eq. 50

where h_j is the predator handling time. The feeding time factors are discussed further below, (see Eq. 62). A vulnerability setting of 0 will result in consumption being estimated using bottom-up conditions only through

$$C_{ij} = a_{ij} \cdot B_i \cdot T_j \cdot S_{ij}$$

Eq. 51

9.5.4 Hints about fitting models to time series reference data

A critical step in development of credible models for policy analysis is to show that they can at least reproduce observed historical responses to disturbances such as fishing. This demonstration necessarily involves an iterative exercise in ‘fitting’ the model to data, by correcting parameter estimates and time series forcing information so as to show what values (or ranges of values, or alternative hypotheses about key processes) could explain the observed historical patterns. For any such fitting exercise, it is critical to have as long a reference period, with as many different disturbance patterns, as is possible to assemble. Note though, that only where a time is used to ‘drive’ the model, (i.e. fishing mortalities and effort series) is it necessary to have information for all years in the time series. Estimates of relative abundance, catches, etc. are not required for all years. Short reference data series carry little information about responses to some disturbances, and hence ability of a model to fit such short series is no test at all of its ability to make useful predictions about disturbances not represented in the reference data. In more vivid terms, many model errors (structure and parameter values) will only reveal themselves (make themselves evident through strong departures of predicted from observed patterns) when the model is challenged to reproduce very long time series of responses.

Here we recommend an iterative, stepwise procedure for model fitting. It is generally not possible, or even wise, to try fitting a large ecosystem model using one big nonlinear estimation scheme that simultaneously varies all uncertain model parameters and inputs.

There are simply too many inputs, some of the parameters are constrained in complex ways by mass balance considerations, and many model errors involve qualitative omissions of interaction terms (or processes, or disturbing inputs) entirely. Such possible omissions are most productively viewed as ‘alternative hypotheses’ about what processes and inputs have been important in shaping historical ecosystem behavior.

The basic idea in this procedure is as follows. Set up an Ecosim model and reference time series (of forcing inputs like fishing rates, and indices of temporal system response like relative biomasses and estimated total mortality rates). Examine the simulated and observed time patterns of response indices, look for groups that show large discrepancies in time pattern (trend), with particular emphasis on groups that have high biomass and are important prey or predator for other groups. As an example, sardines and anchovy in a Benguela model (Shannon *et al.*, 2004) showed upward trend in data but not in initial simulation results. Focus in turn on each such group, and examine alternative hypotheses for the discrepancy (by varying appropriate parameters to see

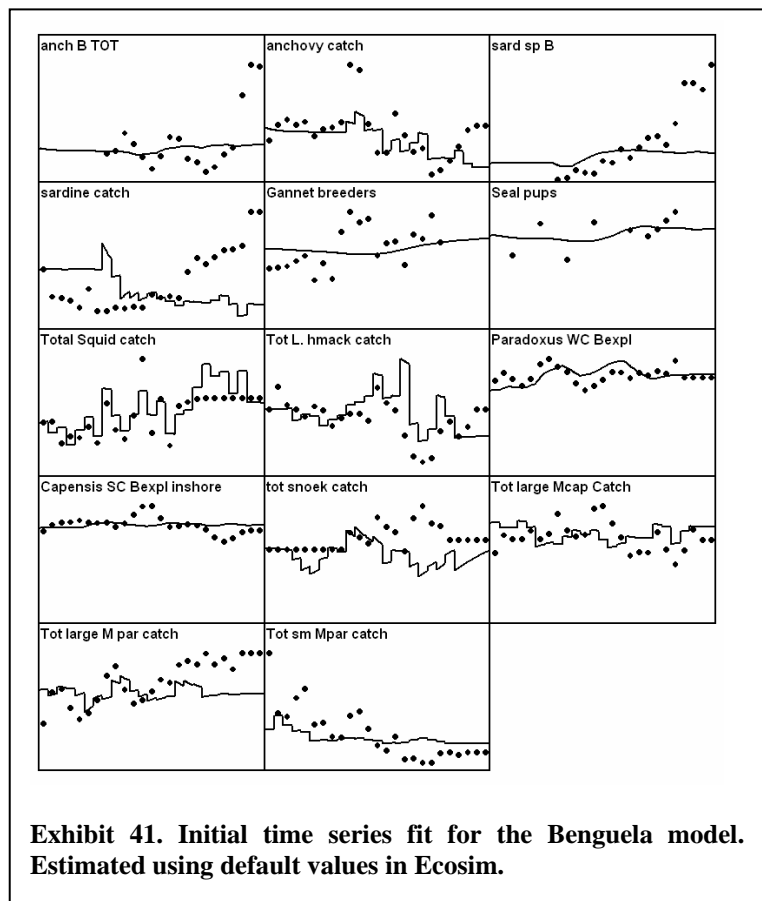


Exhibit 41. Initial time series fit for the Benguela model. Estimated using default values in Ecosim.

if the model fit is improved). The following are common hypotheses that should be examined in roughly the order listed:

(1) Bad trend data — it is possible that the model predictions are sound, but that the trend data are misleading for some reason, (e.g., increasing catchability in CPUE indices).

(2) Incomplete or incorrect forcing data, especially for fishing mortality rates—Ecosim simulated patterns for exploited species will obviously not track observed patterns if those patterns have been caused by fishing, but no good time pattern of fishing mortalities (or at least fishing efforts) have been provided.

(3) Inappropriate vulnerability parameters for the group’s prey — low vulnerability settings (e.g., the 2.0 default) for a group’s column in the vulnerability matrix (of its prey to it) can cause two errors: failure of the group to increase following reductions in mortality (due to preventing the group from increasing its total food intake), and/or failure of the group to decrease following increases in mortality, due to overestimates of compensatory Q/B responses to decreased intraspecific competition. Check this by clicking the ‘sensitivity of SS to vulnerabilities’ button in the ‘fit to time series’ interface to determine whether vulnerability changes would cause changes in goodness of fit, and consider using the fitting interface to search for improved vulnerability estimates.

(4) Incorrect P/B (Z) setting in Ecopath for the group—it is common to see P/B, i.e. Z values set far too large in the Ecopath inputs, resulting in low EE and hence low sensitivity of a group to changes in mortality agents. Check the simulated time plot of total, fishing, and predation mortality rate components on the Ecosim run tab to see if the total mortality rate and its partitioning among factors are reasonable.

(5) Changes in system productivity—in some systems we have seen correlated declines or increases across a variety of species, despite differences among species in harvesting impacts, which might be explained by changes in basic productivity due to factors like upwelling. The Ecosim time series fitting interface can be used to ‘reconstruct’ an apparent temporal pattern in primary productivity, by fitting the model to time series for all groups while varying a time series of productivity ‘anomalies’.

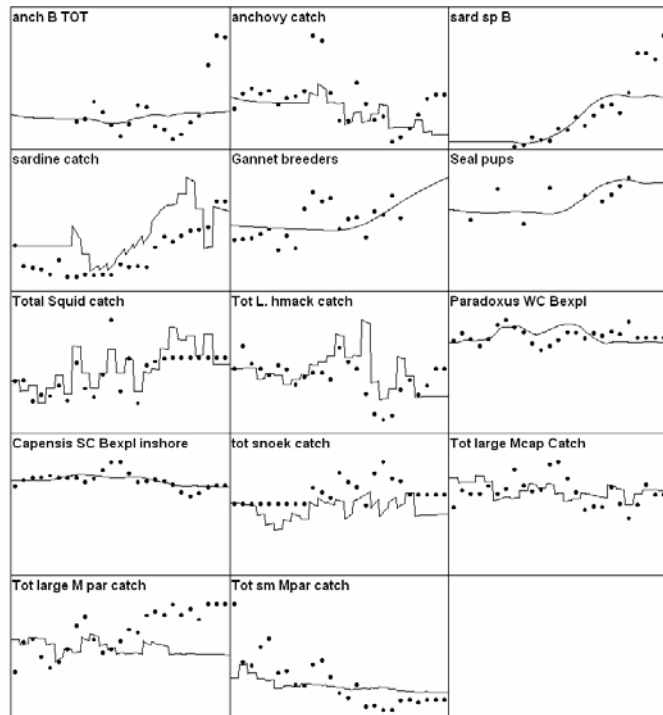


Exhibit 42. Time series fit for Benguela model after estimating vulnerabilities (for 15 groups of consumers).

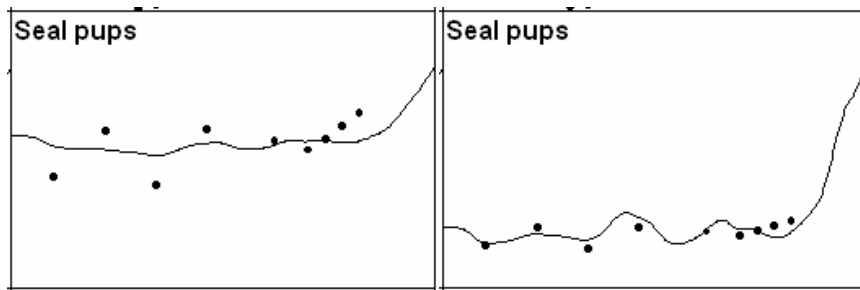
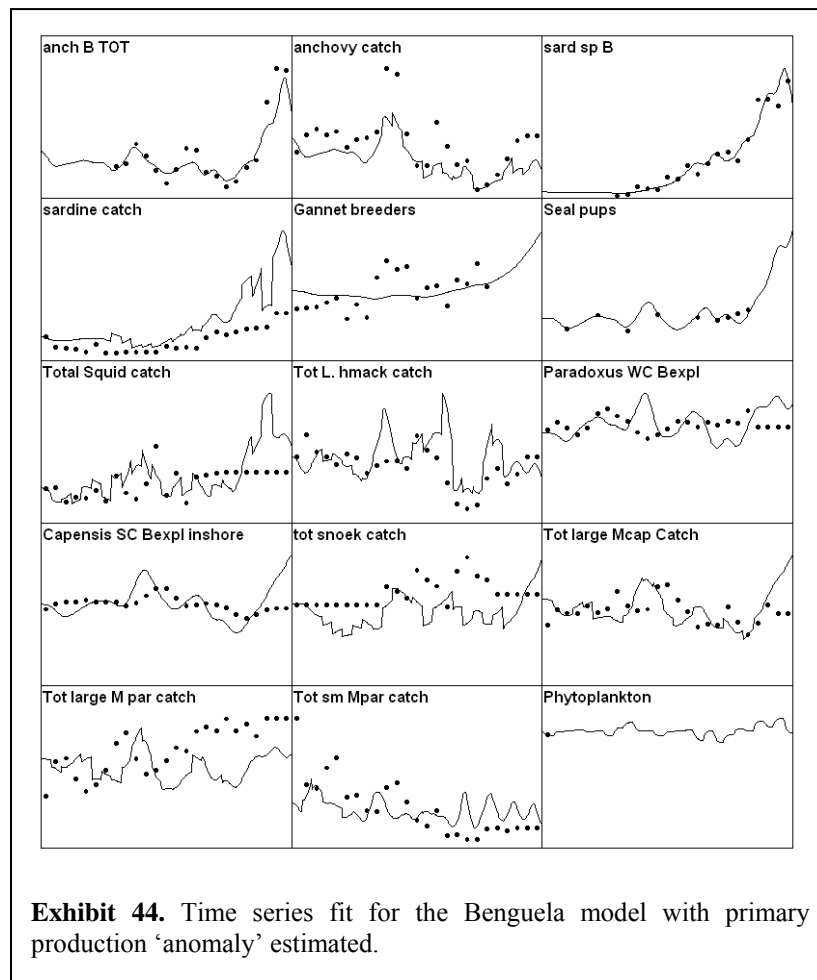


Exhibit 43. Effect of P/B rate on time series fitting for seals in the Benguela model. Left figure is with a P/B of 0.95 year⁻¹ for seals, while right-hand one is with a more realistic value of 0.15 year⁻¹.

(6) Trophic mediation effects—evaluate the possibility that changes in consumption and mortality have been caused by ‘indirect’ or ‘mediation’ effects, such as groups providing hiding places for other groups or driving behavior of groups so as to make those groups more or less vulnerable to other predators. In systems that have benthic and pelagic primary producers, note that shading effects by phytoplankton on benthic plants are not represented explicitly in Ecosim, and must be modeled as mediation effects (by setting up a mediation function that causes negative effects on benthic plant production as phytoplankton biomass increases). This is also the case with turbidity and decreased foraging efficiency of visual predators that can be caused by phytoplankton.

If none of these hypotheses produces predicted patterns similar to the data, look closely at the Ecosim predicted patterns of change in consumption, growth, and mortality rates, and try to evaluate how these rates would have to change in order to produce observed trend patterns. Examine the observed time series for other groups, particularly prey and predators of the group under study, to see if those time series suggest changes in trophic conditions (growth, mortality) that have not yet been captured by the model due to inappropriate parameter settings for the other groups.

Repeat the multiple hypothesis evaluation steps above for each group, with initial emphasis on those groups for



which the model predictions depart strongly from the data. Note that ‘correcting’ the parameters and time inputs for any one group can either improve or degrade the model fits for other groups, including groups for which good fits have already been obtained. This means that the fitting/evaluation process is necessarily iterative, requiring several passes or tries to obtain an overall valid model. For example, in the Benguela model example, obtaining good fits to strong time trends in sardine and anchovy biomass (using hypotheses (3) and/or (5) above) resulted in predicted increases in several predator populations, particularly hakes, for which the data do not indicate such increase. An interesting question then arose about why the predators did not show responses to the apparently large prey increases, and this question led to examination of a variety of hypotheses about why the response did not occur (limitation of recruitment due to cannibalism, undetected increases in fishing impact as responses started to occur so as to prevent those responses from being expressed, errors in initial

estimates of diet composition and dependency on sardines and anchovy by the predators, etc.).

It is possible for the step-wise, iterative process of hypothesis evaluation and model testing/fitting described above to fail completely, in at least two basic ways. First, it may result in an apparently endless cycle back and forth between groups, with each step in the cycle resulting in improvement in fit to one group at the expense of poor fit to others. Such cycles have not yet been seen in case studies, but would indicate either ‘contradictory data’, where the model structure is valid but one or more trend data sets are misleading and apparently contradict the others, or a fundamental failure of the model structure to represent some important interactions or processes.

Second, the model may fail to capture (due to lack of correct input data or structural error) the dynamics of some particular, important group that has driven the dynamics of several others, and inability to simulate this one group may contaminate a variety of model predictions. For example, in models of the Bering Sea ecosystem, we have had trouble simulating (explaining) declines that apparently occurred in small, inshore pelagic fish species in the late 1970s and early 1980s. These declines were associated with onset of a rapid decline in Stellar Sea Lion, and onset of a strong upward trend in jellyfish (which compete with small pelagic fish for zooplankton). In that model, simply forcing the small pelagics to decline (with an arbitrary fake fishery) results in considerably better fits to the data for the other groups. In several models of relatively small oceanic regions (North Sea, West Coast of Vancouver Island), we have had to deal with apparently unpredictable biomass dynamics of species (especially mackerels) that have apparently invaded the regions in conjunction with changing ocean climate regimes. In fact, it is probably a general principle that for any region that might be arbitrarily defined for analysis, there are at least some species that have potentially important impact (on predator-prey relationships) within the region but display changes that can only be explained by examining their dynamics (production, fishing impacts) over some much larger spatial domain. With respect to any small study region, it is appropriate to treat the abundances of such species as forcing functions provided policy choices made within the region are unlikely to affect the larger scale dynamics of those species.

In most early Ecosim fitting exercises, the goal has been to find even one reasonably good fit to the data, i.e. to simply demonstrate whether the model is capable (flexible) of describing historical patterns. During such exercises, interesting alternative hypotheses and parameter changes that might have provided equally good explanations have not been thoroughly documented and pursued, nor have users typically even recorded the often simple research studies and auxiliary measurements that would be needed to test among alternatives (e.g. diet composition studies to detect rare prey in cases where an abundant predator may have big impacts on such prey despite such prey not being important to support of the predator). This failure to document the 'brainstorming' process involved in model fitting/testing can be costly for people who then try to use the model for policy analysis: (1) clear articulation of alternative hypotheses that could equally well explain historical changes is a critical part of adaptive policy design involving planned experimental comparisons of policy options; (2) analyses based on the model are left open to attack by stakeholders who have vested interest in presuming some particular hypothesis to be true (e.g. people who want to blame stock declines on environmental factors so as to avoid restrictions in fishing); (3) potential value of the modeling to help guide and prioritize research projects is lost, and this is a very big issue indeed in situations where very limited scientific resources are expected to provide useful information for complex ecosystem management planning.

Documentation of alternative hypotheses and parameter changes during the sequential fitting process would appear at first glance to be an exceedingly complex process, involving geometric increase in number of hypothesis combinations as more time series and groups are examined (e.g. if there are two ways to explain changes in group 1, and two ways to explain changes in group 2, there are 4 possible ways to explain the joint dynamics). This 'explosion' in hypotheses is not that serious a problem in practice, for at least two reasons: (1) uncertainty about why a group has responded or not may be independent of uncertainty about why other groups have responded, e.g. we can examine hypotheses (and policy implications) about failure of hake to increase following sardine-anchovy increases in the Benguela system, without regard to what drove those increases in the first place; and (2) typically the alternative hypotheses involve 'environmental forcing' versus fishing effects, and the environmental forcing hypotheses are not independent for each group (i.e. hypotheses about increases or decreases in productivity due to factors like upwelling are expected to apply to a variety of groups). The main implication of point (2) is that we can generally identify just a few overall hypotheses for why an ecosystem has behaved as it has, each with very different policy implications. For example, in the Georgia Strait, B.C. models, two main hypotheses have emerged (can be made to fit the data using Ecosim) about why a whole suite of fish species has declined: either the system as a whole has experienced major decreases in primary production, or the observed dramatic growth in marine mammal populations (harbour seal) has had devastating impacts not reflected in the relatively crude diet information available from historical studies (in conjunction with modest declines in primary production).

9.5.5 Effect of P/B (Z) and vulnerability for time series fitting

For the balancing it is useful to think of how growth and mortality is modeled in Ecosim. Mortality is considered a linear function of biomass (solid line in Exhibit 45), while the population increase will be a non-linear function of the biomass (dotted line in Exhibit 45). This non-linear function corresponds to the consumption times the gross food conversion efficiency (from Ecopath, where it is estimated as base production over base consumption). For a given biomass, the population will increase or decrease depending on the area between the lines. The growth/decline of a given population can hence be modified by changing either the mortality rate, or food consumption. Food consumption, in turn, is a function of complex predator-prey relationships modeled using a variable 'vulnerability' setting for top-down vs. bottom-up control.

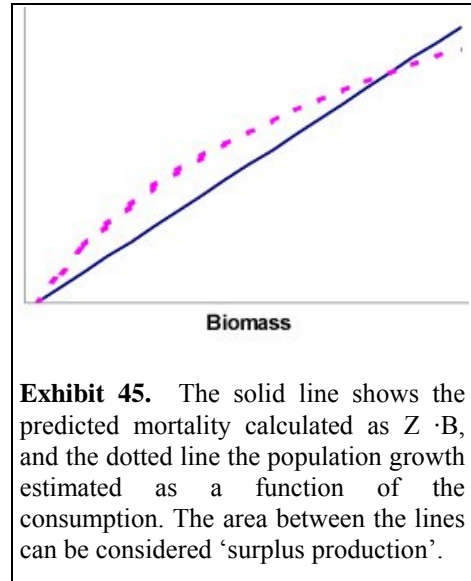


Exhibit 45. The solid line shows the predicted mortality calculated as $Z \cdot B$, and the dotted line the population growth estimated as a function of the consumption. The area between the lines can be considered 'surplus production'.

This can be illustrated using a model of the Gulf of Thailand (Christensen, 1998) along with time series data from research vessel surveys in the Gulf, an initial simulation using default settings throughout (most notably a default vulnerability setting of 2 for all predator-prey interactions) produces the fit shown in Exhibit 46A for the 'large piscivores' group. During the time period included the fishing intensity increased with more than an order of magnitude. The model (solid line) shows a clear decline in biomass over the time, while the CPUE from the surveys (dots) indicates much less decline over time. As described above we have some handles that can be used to manipulate how Ecosim models the growth of the population. Panel B thus shows the effect of raising the groups total mortality rate from 0.8 year^{-1} to 1.2 year^{-1} . The effect of this is to make the group much better able to tolerate the grossly increased fishing intensity over time, but it is also clear that a 50% increase in the initial mortality rate setting is insufficient to optimize the fit over time. A second handle is therefore invoked. The vulnerability setting affects how the consumption is influenced by changes in predator and prey abundance. Using the default setting of 2 (panels A and B) corresponds to assuming that if the biomass of large piscivores was increased drastically they would be able to double the predation mortality they are causing their prey. Changing the value to 1.01 for all prey of the large piscivores makes prey availability largely independent of changes in the predator abundance. As the increased fishery leads to a reduction in the biomass of large piscivores, those remaining will have a good time (from a food perspective: their consumption rate will increase, and this will tend to counterbalance the increased fishing pressure). The result is increased resilience as can be seen from panels

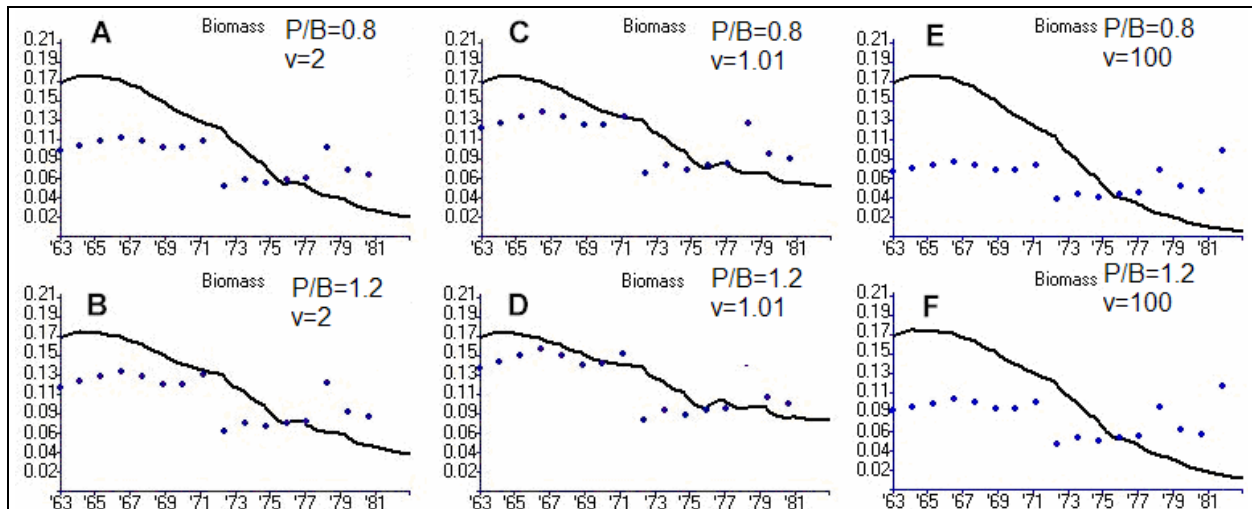


Exhibit 46. Biomass over time (lines) for 'large piscivores' in the Gulf of Thailand. P/B is the production/biomass ratio (equals Z , the total mortality) for the group, while v is the vulnerability setting describing how the group interacts with each of its prey groups. Dots represent CPUE from surveys.

C and D in Exhibit 46. Comparing panels B and C shows that the fit is better through incorporating bottom-up control, while panel D shows the best fit overall.

For illustration the panels E and F are included in Exhibit 46 to show the effect of using a high vulnerability ($v=100$) for the interactions between the large piscivores and each of its prey groups. It is apparent that this does not result in any improvement in fit between model and CPUE, but in fact in the opposite. The best fit in the example is thus obtained using the parameter settings of panel D.

9.5.6 Using evolutionary criteria to estimate trophic flow vulnerabilities⁴

In Ecosim, we assume that predation rates are potentially limited by the flow of organisms between “vulnerable” and “invulnerable” behavioral states. It may often be reasonable to assume that these flows are dependent on how much time organisms spend feeding, such that increasing the proportion of time spent feeding implies increased vulnerability of prey to the organism, but also increased time spent exposed to predation. That is, there may be a fundamental link between acquiring food resources and exposure to being a food resource, such that natural selection has acted to “balance” the benefits of increased foraging time against the predation risk costs. The Ecosim vulnerability parameters are in fact assumed proportional to relative feeding time: consumption rate increases proportionally as feeding time increases, but so also does vulnerability to predators.

The Ecosim biomass rate equations provide a fitness measure. If $dB/dt = \text{net food consumption} - \text{predation mortality} - \text{other mortality}$, and if consumption and mortality depend on feeding time, then $f = (dB/dt)/B$ (the per-biomass or per capita rate of biomass change) is a relative fitness measure. It is easy to calculate how this relative rate would change for each biomass pool, as a function of the relative time spent feeding (see Ecosim equations relating consumption and predation rate to time spent feeding). The routines invoked under the “Seek evolutionarily stable strategy” button in the Ecosim Run Info interface allow two explorations of the effect of feeding time (or vulnerability parameters) on the fitness measure f . (1) One routine sets *all* vulnerability parameters (relative v 's) for trophic flows to the same value, then increases this value to see which value for the system as a whole would be closest to an “evolutionarily stable” value (where the derivatives of f with respect to feeding time are near zero, i.e. no organism could improve fitness much by increasing or decreasing its feeding time). (2) A more routine “searches” randomly for relative feeding times for each functional group that would give the lowest derivative of f with respect to feeding time. The second procedure amounts to trying to find the stable point of the co-evolutionary “game” implied when selection acts on feeding time for prey and predators simultaneously: if selection would favor increased predator feeding time (increased v of prey to that predator, $df/d\text{feeding time} > 0$ for predator), then such selection would also change the optimum feeding time for the prey (would generally make it smaller).

These routines are not meant to be used for precise estimation of vulnerability parameters, but rather to give a general feeling for ranges of vulnerability values that might make sense in evolutionary terms, i.e. would imply feeding/predation rate parameter values such that natural selection would not be driving organisms toward spending much more or much less time feeding. Interestingly, the “Overall v ” routine (single vulnerability parameter for all trophic linkages) usually

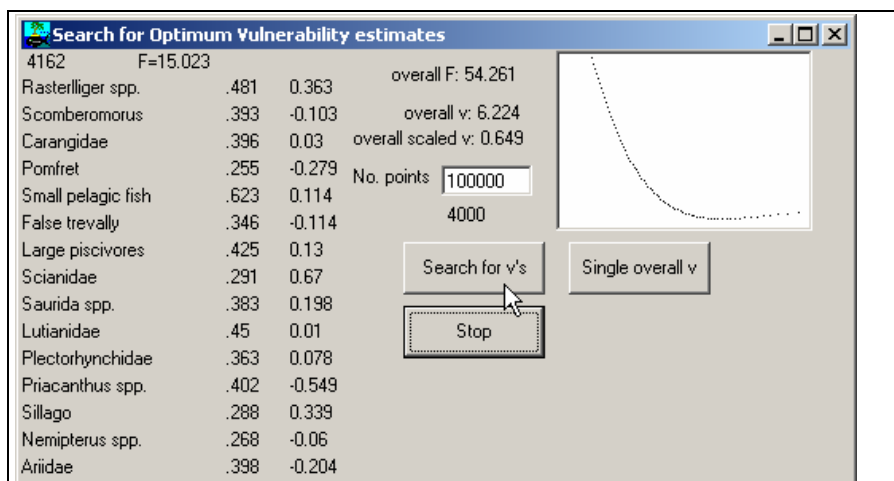


Exhibit 47. Ecosim procedure for estimating flow vulnerabilities.

⁴ Our experience with this option has not been encouraging and we caution against its use.

produces scaled values in the range 0.3-0.5, which is the same range that we most often give “reasonable” ecosystem behavior in time simulations (species unlikely to drop out due to predation or competition, predator-prey cycles rare or absent, recruitment relationships with realistic compensatory responses).

9.5.7 Time series random effects

When you use the search interface to estimate time series values of forcing function 4, e.g., to obtain a temporal pattern of apparent primary production ‘anomalies’ for the ecosystem, you need to be careful about the risk of obtaining a spurious anomaly sequence that just represents measurement errors in the fitting data. Generally, if you are fitting the data to n independent time series of relative abundance, (i.e., for n of the groups), you can expect the fitting procedure to reduce the sum of squares (SS) by the proportion $(n-1)/n$ by varying time forcing values even if there is no real time forcing effect. So if $n=1$, the fitting procedure can usually find a sequence of forcing values that make $SS=0$, but this sequence is meaningless (could be either real productivity anomalies or just spurious way of explaining measurement errors in the single abundance time series). A command button on the search interface allows you to estimate a probability distribution for the F statistic $SS_{\text{reduced}}/SS_{\text{base}}$ under the null hypothesis that all of the deviations between model and predicted abundances are due to chance alone, i.e. under the hypothesis that there are no real productivity anomalies. The calculation of this F statistic requires a Monte-Carlo simulation procedure in order to account for autocorrelation in the model residuals that is expected even under the null hypothesis. Be warned that even if you do find a statistically significant reduction in SS by using the search procedure, this does not mean that the estimated sequence of relative primary production values is in fact ‘real’; all that you can say is this: “assuming that primary production was in fact variable and that this did cause changes in relative abundance throughout the food web, then our best estimate of the historical pattern of variation is the one obtained by the fitting procedure”.

	Group	Max rel. P/B	Max rel. feeding time	Feeding time adjust rate [0,1]	Fraction of 'other' mortality sens. to changes in feeding time	Predator effect on feeding time [0,1]	Density-dep. catchability: Qmax/Qo [≥=1]	QBmax/QBo (for handling time) [≥1]	Switching power parameter [0,2]
1	Transient Orcas		2.0	0.5	0.50	0.00	1.00	1000.00	0.0
2	Dolphins (Res. Orca)		10.0	0.5	0.50	0.00	1.00	1000.00	0.0
3	Seals Sealion		10.0	0.5	1.00	0.00	1.00	1000.00	0.0
4	Halibut		2.0	0.5	0.50	0.00	1.00	1000.00	0.0
5	Lingcod		2.0	0.5	0.50	0.00	1.00	1000.00	0.0

Exhibit 48. Ecosim group information form.

9.5.8 Ecosim group information

Max. rel. P/B: In Ecosim, the simulated biomass of some prey group may increase such that their predators, if not somehow constrained, would be able to consume huge amounts of prey, with their own biomass growing accordingly.

To constrain this, the option is provided to limit, via a multiplier, the increase of P/B that results from abundant prey being available.

Max. relative feeding time: If prey becomes more scarce, (e.g., because predator abundance increases), their predators will have to spend more time feeding (and hence be at a greater risk to predation themselves). Use this variable to limit how much the feeding time may increase. The default is that the feeding time may

at the most double, i.e., a value of 2.0. There is empirical evidence showing limits to how great a predation risk organisms are willing to take. Juveniles may for instance be found hiding at food-deprived shorelines even though suitable prey is more abundant in the pelagic zone close by. Going out to there for prey would however place the juveniles at a considerable risk of predation, and they may choose not to do so, or at least to lower the risk by limiting the time spent feeding.

Feeding time factor: This factor determines how fast organisms adjust feeding times so as to stabilize consumption rate per biomass. Setting the value to 0.0 causes feeding time (and hence time exposed to predation risk) to remain constant, all changes in consumption per biomass then result in growth rate changes. Setting it to 1.0 results in fast time response, which causes reduction in vulnerability to predation rather than increased growth rate when/if food density increases. In general we recommend that you set the feeding time to 0 for all groups, apart from, e.g., marine mammals where a value of 0.5 often seems reasonable. Explore the consequences of changing this factor.

Unexplained predation (Range: [0,1]): This is the proportion of the unexplained natural mortality rate (M_0 , $1-EE \times$ total mortality rate) that is assumed to be sensitive to changes in feeding time. Setting it to 0.0 causes M_0 to remain constant. Setting it to a higher value causes that proportion of M_0 to vary in proportion to relative time spent feeding (see feeding time factor above). Setting nonzero value along with nonzero feeding time factor generally results in density-dependent M : as density increases, feeding time usually has to increase to maintain food consumption rate, and this increased feeding time leads to higher mortality rate.

Predator effect on feeding time [0,1]: Setting a nonzero value for this parameter allows you to simulate direct response of feeding time and food consumption rate to changes in predator abundance, i.e. 'risk sensitive foraging behavior'. If the value is high, it is assumed that a high proportion of the food consumption rate per biomass is 'discretionary', i.e., the organism will reduce target food consumption rate (and hence time exposed to predation risk) by up to this fraction if predator abundance increases, and will correspondingly increase food consumption rate if predator abundance falls below the Ecopath baseline. Note that the feeding time adjustment rate (see above) has to be greater than zero in order to see effects from nonzero values of this parameter (effect is expressed in calculations as changes in time spent feeding with changes in predator abundance, and such changes are not implemented unless adjustment rate is greater than zero)..

Density-dependent catchability: (≥ 1): see section 9.5.10, below.

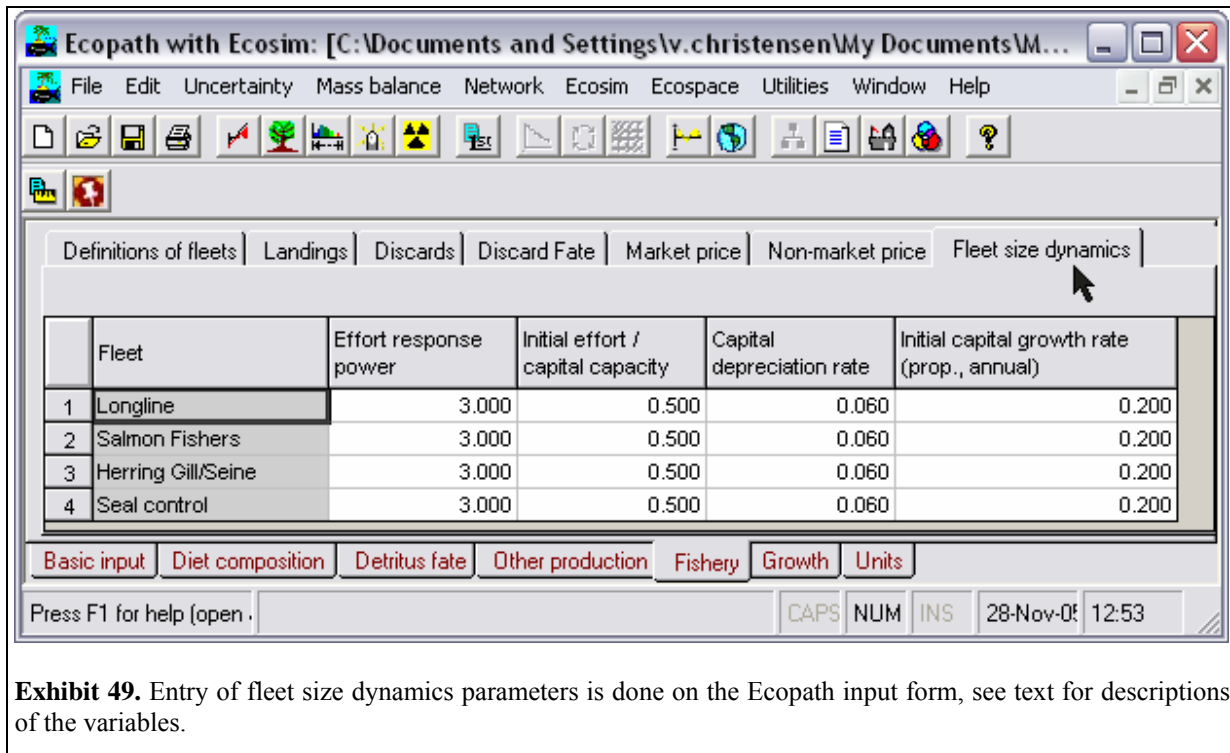


Exhibit 49. Entry of fleet size dynamics parameters is done on the Ecopath input form, see text for descriptions of the variables.

QBmax/QBo (for handling time): (>1): see section on predator satiation and handling time below

Switching factor [0-2]: Default 0 is no switching. See switching section 9.5.12.

See separate section about compensatory mechanisms.

9.5.9 Fleet and effort dynamics

Ecosim users can specify temporal changes in fishing fleet sizes and fishing effort in three ways: (1) by sketching temporal patterns of effort in the model run interface; (2) by entering annual patterns via reference “csv” files along with historical ecological response data; and (3) by treating dynamics of fleet sizes and resulting fishing effort as unregulated and subject to fisher investment and operating decisions (“bionomic” dynamics, fishers as dynamic predators). To facilitate exploration of alternative harvest regulation policies, the Ecosim default options are (1) or (2). However, users can invoke the fleet/effort dynamics model in order to explore consequences of unregulated economic response dynamics, by clicking the “fleet/effort response” check box on the Ecosim Run tab.

When the fleet/effort response option is invoked (for entry of input parameters see exhibit Exhibit 49), Ecosim erases all previously entered time patterns for fishing efforts and fishing rates, and replaces these with simulated values generated as each simulation proceeds. The fleet/effort dynamics simulation model uses the idea that there are two time scales of fisher response: (1) a short time response of fishing effort to potential income from fishing, within the constraints imposed by current fleet size, and (2) a longer time investment/depreciation ‘population dynamics’ for capital capacity to fish (fleet size, vessel characteristics). These response scales are represented in Ecosim by two ‘state variables’ for each gear type g : $E_{g,t}$ is the current amount of active, searching gear (scaled to 1.0 at the Ecopath base fishing mortality rates), and $K_{g,t}$ is the fleet effort capacity ($E_{g,t} < K_{g,t}$). At each time step, a mean income per effort index $I_{g,t}$ is calculated as $I_{g,t} = \sum_i q_{g,i} B_i P_{g,i}$ where i =ecological species or biomass group, $q_{g,i}$ is the catchability coefficient (possibly dependent on B_i) for species i by gear g , and $P_{g,i}$ is the market price obtained per biomass of i by gear g fishers. Also, mean fleet profit rates $PR_{g,t}$ for fishing are calculated, equal to $(I_{g,t} - c_g) E_{g,t}$ where c_g is the cost of a unit of fishing effort for gear g (cost and price factors are entered via the Ecopath interface, Fishery tab). For each time step, the “fast” effort response for the next (monthly) time step is predicted by a sigmoid function of income per effort and current fleet capacity:

$$E_{g,t+1} = K_{g,t} I_{g,t}^p / (I_{h_g}^p + I_{g,t}^p)$$

Here, I_{h_g} and p are fleet-specific response parameters, where the income level needed for $\frac{1}{2}$ maximum effort is I_{h_g} and p represents a “heterogeneity” parameter for fishers: high p values imply all fishers “see” income opportunity similarly, while low p values imply fishers “turn on” their effort over a wide range of mean incomes, as shown in Exhibit 50.

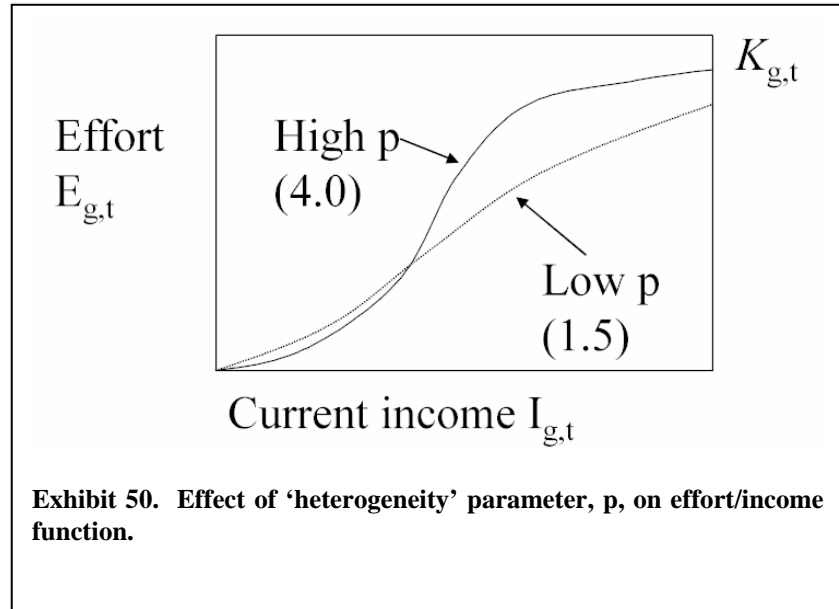
9.5.10 Density-dependent changes in catchability

In fisheries modeling we usually represent the fishing mortality rate F as a product of catchability q times fishing effort f : $F = qf$. Here the catchability q represents the mortality rate caused by a unit of fishing effort, or in intuitive terms the proportion of the stock harvested by a unit of fishing effort. A useful way to think about q is in terms of the spatial organization of fishing: if each unit of effort ‘sweeps’ an area ‘ a ’ while the stock is distributed over a total area A , and if effort is randomly distributed within A , then $q = a/A$. There are two problems with this formulation:

1. A is generally seen by both fish and fishers as a much smaller area than the map area over which you might display a stock’s range (neither fish nor fishing are randomly distributed, so A is generally much smaller than the map range area for a stock), so we usually cannot predict q from simple analysis of gear swept area and total range area; and
2. almost always, the actual area A occupied by fish and fishers decreases with decreasing fish abundance, (i.e., the occupied range ‘collapses’ as stock size decreases) due to fish behaviors like shoaling and also cumulative effects of localized stock depletion events. The second problem is particularly important for fisheries analysis, since it implies that q increases, sometimes grossly, as A decreases ($q = a/A$ increases when A decreases) whether or not there is a change in fishing technology as represented in the area swept per unit effort.

On entry to Ecosim, Ecopath has provided a base fishing rate $F_o = Catch / (Ecopath\ biomass)$. You can specify time scenarios for F ($F_t, t > 0$) relative to this F_o by using either the fishing rate ‘sketch pad’ interface (Ecosim ‘Temporal simulation’ tab) or time reference data files (csv files). The Ecosim default is to treat your time series values as relative or absolute fishing rates without reference to changes in q . But you can also treat the time input values as relative fishing efforts f_t , where $f_o = F_o$ (efforts scaled so base $q_o = 1$). Then to create density-dependent catchability effects, set a value greater than 1.0 for the q_{max}/q_o ratio(s) in the Ecosim Group Info tab. For example, setting a value of 5.0 represents assuming that q can be as much as 5 times higher than the q that led to the Ecopath base F_o , if stock size is very low. That is, suppose you set $q_{max}/q_o = 5$, then run a scenario where you shape the relative fishing rate over time (now treated as relative effort) so as to cause a gross stock depletion followed by a return to $f_t = f_o$; in this scenario, the ‘realized’ fishing rate F_t can be as much as 5 times F_o even for $f_t = f_o$, due to density-dependent decrease in the effective area A occupied by the depleted stock.

Internally, Ecosim represents the density-dependent effect by calculating time dependent fishing rate F_t using the equation $F_t = f_t QR_o / [1 + (QR_o - 1) B_t / B_o]$ where $QR_o = q_{max}/q_o$ is your specified catchability increase ratio, B_t is stock biomass, and B_o is Ecopath base biomass. Note that this dependence is applied to the individual group fishing rates rather than the relative efforts by fishing fleets, to represent the idea that decreases in area occupied by a stock (A) when biomass B_t is less than the Ecopath base biomass B_o are likely to result in concentration of efforts by fishers in general. If you need to represent a differential change in availability of fish to some particular fleet(s) but



not others, you will need to develop an Ecospace model that explicitly represents spatial distinctions in where particular gears can operate. Note further that the QR parameter is not used in Ecospace; we assume random distribution of effort within each Ecospace cell, recognizing that Ecospace can already represent larger-scale range changes and associated changes in the spatial concentration of fishing effort.

In Ecosim scenarios where you do choose to treat the time input fishing information as relative fishing efforts f_t rather than absolute fishing rates F_t , you should be quite careful to recognize that catchability often increases quite dramatically for low values of B_t/B_o . QR values (q_{max}/q_o) of 5 to 10 are not uncommon in the fishery literature, especially for shoaling fishes like herring, sardine, and spawning cod. Further, modern fishing technologies like side-scan sonar and GPS are making fishers ever better at concentrating their swept areas 'a' within the actual areas A where fish are concentrated (probability of a sweep of area 'a' not being within the occupied area A has decreased dramatically). Even where there are not such technological changes, fishers are generally capable of making very good assessments of A just by combining their own search information with observation of where other fishers are doing well.

Note that you generally do not want to set $QR > 1$ for 'reconstruction' scenarios where you have provided historical F_t estimates based on single-species assessment methods such as virtual population analysis (VPA) or stock synthesis. Presumably these methods have already accounted for density dependent effects on q , by calculating $F_t = (\text{historical catch}) / (\text{estimated stock biomass})$ without regard to whether the historical catch was high relative to biomass because of catchability changes or changes in total fishing effort. But you should check the single species assessment method carefully, to insure that the method did not make an inappropriate assumption about stability of q in its reconstruction of historical biomass, (e.g., was fitted to the data using historical effort data under a constant q assumption, or was 'tuned' to historical catch per effort data uncorrected for temporal/stock dependent changes in q).

9.5.11 Predator satiation and handling time effects

Ecosim/Ecospace allows you to represent two factors that may limit prey consumption rates per predator (Q/B): foraging time adjustments related to predation risk and/or satiation, and handling time effects. Parameters for both are specified via the Ecosim Group Info tab.

Satiation and/or choices to forage for short times in order to avoid higher predation risk are represented by setting nonzero values for the 'feeding time adjustment rate' of a group; larger values of this rate represent more rapid adjustment of foraging time. Nonzero foraging time adjustment rates cause Ecosim/Ecospace to update relative foraging time during each simulation so as to represent predators as trying to maintain Q/B near the Ecopath input base rate. For some organisms (particularly marine mammals) this foraging time adjustment may represent animals always trying to feed to satiation (Q/B from Ecopath the satiation feeding rate) and taking more or less time to reach satiation depending on prey densities (and possibly also facing higher predation risk when foraging times are longer). For other organisms, the Ecopath base Q/B may represent a much lower feeding rate than the animal could achieve under 'safe' laboratory conditions, and in this case we view the base Q/B as an evolutionary 'target' rate representing results of natural selection for balancing benefits from feeding with predation risk costs of spending more time feeding.

Handling time effects represent the notion that predators have limited time available for foraging, and this time can be used up by 'handling time' (pursuit/manipulation/ingestion time per prey captured) rather than searching for prey, when prey densities are high. The Ecosim Group Info tab allows you to set ratios of maximum to Ecopath base food consumption rates per individual (or per biomass). These ratios are set to large values (1000) by default, which allows predators to increase their feeding rates without limit as prey densities increase (i.e. not limited by time required to handle each prey). In most scenarios, limitation of prey vulnerability prevents this unreasonable assumption from having noticeable effect. But in scenarios where vulnerable prey densities of at least one type do increase greatly, setting a low value (e.g. 2 or 3) for the predator's maximum/base feeding rate ratio allows you to represent limits on feeding rate associated with time needed to handle each prey. Without such limits, your predictions of increase in predator Q/B , and hence productivity, at low predator density (or high prey density) might be too optimistic and lead you to errors like overestimating sustainable harvest rate for the predator. Also, ignoring handling time effects when one prey type increases greatly can cause an underestimate of the 'buffering' effect that such increases can have on predation rates felt by other prey: if the predator consumes more of the abundant prey, and spends more time handling/resting because of this, predation rates on other prey species should decrease.

Ecosim/Ecospace calculates feeding rates of predators using the ‘multispecies disc equation’, a generalization of Holling’s type II functional response model for multiple prey types. Using the maximum/base ratio from the Group Info tab along with the Ecopath base food consumption rate per predator, the program calculates a maximum ration and effective handling time per prey biomass eaten (handling time = $1 / (\text{maximum prey biomass eaten per time})$). This handling time (Holling’s ‘ h ’ parameter) is used to calculate the denominator in the disc equation formulation $Q/B_{ij} = \text{biomass of prey type } i \text{ consumed per time per predator } j, Qb_{ij} = a_{ij} V_{ij} / (1 + h_j S_i a_{ij} V_{ij})$ where a_{ij} is the rate of effective search by predator j for type i prey, h_j is the predator handling time parameter, and V_{ij} is the instantaneous density of prey type i vulnerable to predator j . V_{ij} is calculated by solving the ‘fast dynamics’ equation $dV_{ij}/dt = v(B_i - V_{ij}) - v'V_{ij} - a_{ij}P_j V_{ij} / (1 + h_j S_i a_{ij} V_{ij})$ for V_{ij} , while assuming the vulnerability-exploitation dynamics are fast enough to keep dV/dt near zero (vulnerability exchange rates v, v' large). The solution for V_{ij} over time involves a numerical procedure that can sometimes cause annoying ‘chatter’ in the Ecosim results when handling times are large (ratio of maximum/base consumption rate small): at each simulation time step the program updates an estimate of the ratio of predator search time to total time (this ratio is given by $Ps_j = 1 / (1 + h_j S_i a_{ij} V_{ij})$ in the Holling formulation), using this update to provide an improved estimate of the V_{ij} . We do this because providing an exact value for the V_{ij} (exact solution for the nonlinear equation solutions for all the V_{ij} at the condition $dV_{ij} / dt=0$) at each simulation time step would require excessive computer time.

An interesting and useful feature of the algebra of multispecies disc equations is that the initial (starting simulation time) value for the Ps_j ratio (of search time to handling time, i.e. the denominator of the disc equation) for each predator type is given just by $Ps_j = R_j / (R_j - 1)$, where R_j is the Group Info tab ratio of maximum to Ecopath base consumption rate per predator. Ps_j is updated at each Ecosim/Ecospace time step by first calculating starting estimates of the V_{ij} using the Ps_j from the previous (or initial) time step, then using these estimates in the sums $S_i a_{ij} V_{ij}$ that define Ps_j .

Bioenergetics models for fish most often indicate that feeding rates are low compared to maximum ration; typical ratios of estimated to maximum ration (Hewett-Johnson ‘ P ’ parameter) are around 0.3-0.4. These estimates imply R_j (maximum/Ecopath base ration) values of at least 2-4. If you choose to use such realistic values instead of the default 1000, and if this causes Ecosim/Ecospace to exhibit oscillatory behavior, you need to consider two possibilities:

- (1) the oscillatory behavior may be a numerical artifact of the procedure used to update Ps_j ; or
- (2) the model’s ‘correct’ behavior for the parameter combinations you have provided is indeed a predator-prey cycle.

If the oscillation has a period of several time steps (months), it is very likely a predator-prey cycle. Persistent predator-prey cycles are commonly predicted by models that include handling time, along with strong top-down control (high vulnerabilities v_{ij} of prey to predators). If you think the cycle is unrealistic, you should adjust the prey vulnerabilities (Ecosim Flow Control Tab) to lower values (toward ‘bottom up’, prey vulnerability control) rather than just setting high R_j values. If you see very short cycles indicating numerical instability in the Ps_j adjustment procedure (usually happens for fast turnover groups like microzooplankton), you should set higher R_j values for the offending groups; this amounts to admitting that Ecosim is limited in its ability to represent very fast dynamic changes in groups that turn over very rapidly.

9.5.12 Modeling switching behavior in Ecosim

Predators are said to ‘switch’ from one prey to another when predator diet proportion of each type changes more rapidly than the relative abundance of that type in the environment. Eating more of something when it becomes abundant does NOT imply switching, but rather just more frequent encounters with that type; the predator is said to switch if it takes disproportionately more of the thing as it becomes more abundant.

Three mechanisms that can lead to switching patterns in diet composition and prey mortality are represented in Ecosim:

- 1) Apparent switching away from prey that are declining in abundance, due to those prey seeing less intraspecific competition and hence spending less time at risk to predation; this effect occurs for any prey species (and impacts feeding on it by all of its predators) whenever Ecosim foraging time adjustment is set >0 in Group Info interface.

2) Apparent switching in Ecospace, caused by fitness-sensitive movement; when Ecospace parameters are set to cause increased (and/or directional) movement from cells where ‘fitness’ (per capita food intake minus instantaneous mortality rate) is lower, predators will appear (for the system as a whole) to switch to more abundant prey, and prey that are declining in abundance will see lower predation rates in the cells where they remain concentrated.

3) Explicit changes in Ecosim rates of effective search, representing fine-scale behavioral choices by predators to spend more or less foraging time in the arenas where specific prey are concentrated, where the behavioral choice among arenas is predicted from Ideal Free Distribution (IFD) arguments that predators should allocate foraging time so as to minimize time needed to obtain normal food consumption rates.

In the third of these approaches, the Ecosim rate of effective search a_{ij} for predator type j on prey type i is modified at each simulation time step in relation to changes in abundance of all prey types, using a ‘gravity model’ approximation for the IFD allocation of predator foraging time among prey-specific foraging arenas. The equation used for this modification is

$$a_{ij}(t) = K_{ij}a_{ij}B_i(t)^{P_j} / \sum_i a_{ij}B_i(t)^{P_j}$$

Eq. 52

Here, a_{ij} is the base rate of effective search calculated from Ecopath and vulnerability exchange parameters, K_{ij} is a scaling constant that makes the time-specific $a_{ij}(t)$ equal a_{ij} when all prey biomasses B_i are at Ecopath base values, and the ‘switching power parameter’ P_j is a user-supplied (empirical, to be estimated from field data or model fitting) power parameter representing how strongly the predator responds to changes in prey availability. In particular:

- $P_j = 0$, no switching
- $P_j \ll 1$, prey must become very rare before predator j stops searching for them
- $P_j \gg 1$, predator switches violently when any prey increases or decreases.

P_j is limited to the range [0,2]. While Eq. 52 is derived by pretending that predators must allocate time among mutually exclusive foraging arenas for each of their prey types (a typically unrealistic assumption), it can still be used (with $P_j \ll 1$ values) to represent more general ideas about why and how predators switch among prey, e.g. formation and loss of search images for finding them.

Impact of setting a positive switching power parameter can be exemplified based on migratory striped bass. In this example switching results in much more variable for the predator – which simulation is the more appropriate can only be determined from empirical information.

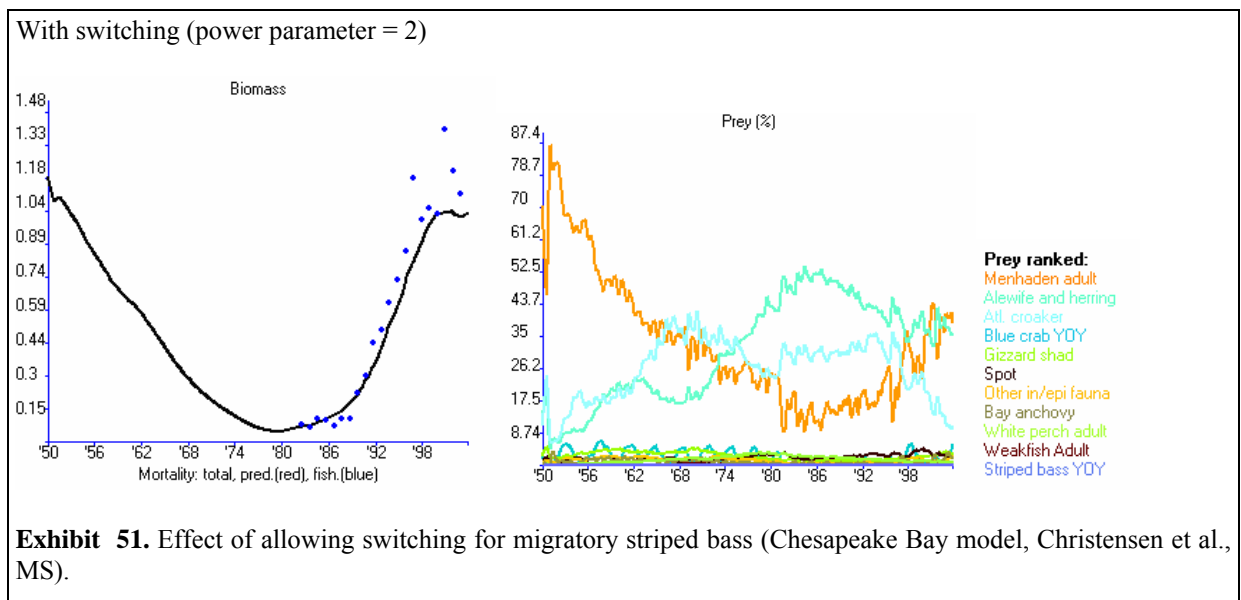
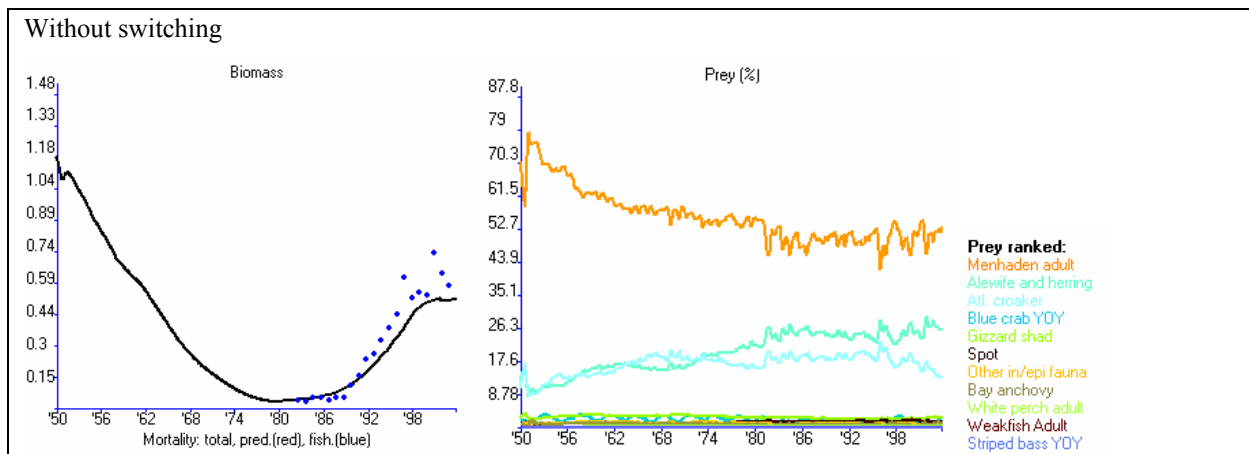


Exhibit 51. Effect of allowing switching for migratory striped bass (Chesapeake Bay model, Christensen et al., MS).

9.5.13 Compensatory mechanisms

Sustaining fisheries yield when fishing reduces stock size depends on the existence of compensatory improvements in per capita recruitment, growth, and/or natural mortality rates. Ecosim allows users to represent a variety of specific hypotheses about compensatory mechanisms. Broadly, these mechanisms fall in two categories:

1. *direct* - changes caused over short time scales (order one year) by changes in behavior of organisms, whether or not there is an ecosystem-scale change due to fishing; and
2. *indirect* - changes over longer time scales due to ecosystem-scale responses such as increased prey densities and/or reduced predator densities. Usually we find the direct effects to be most important in explaining historical response data. Here we describe how to generate alternative models or hypotheses about direct compensatory responses; these hypotheses fall in three obvious categories: recruitment, growth, and natural mortality.

9.5.14 Compensatory recruitment (models with split pools only)

Compensatory recruitment effects are usually expressed as a flat or dome-shaped relationship between numbers of juveniles recruiting to the adult pool versus parental abundance (stock recruit relation). There are two main ways to create such effects in Ecosim:

- a. non-zero feeding time adjustment for the juvenile pool combined with fixed time in juvenile stage and high EE , or high proportion of the ‘other’ mortality (the mortality not accounted for) being sensitive to changes in predator feeding time; and
- b. zero feeding time adjustment combined with variable time in juvenile stage.

Mechanism (a) represents density-dependent changes in juvenile mortality rate associated with changes in feeding time and predation risk, while (b) represents density-dependent changes in juvenile growth rate and hence total time spent exposed to high predation rates over the juvenile life stage. Other, generally weaker compensatory responses can also be caused by changes in adult energy allocation to reproduction. For mechanisms (a) and (b), it is usually also important that the vulnerabilities of prey to the juvenile group (Flow control tab) also be relatively low.

9.5.15 Compensatory growth (overall P/B)

Compensatory growth rate responses are modeled by setting the feeding time adjustment rate (‘Group Info’ tab) to zero, so that simulated Q/B is allowed to vary with pool biomass (nonzero feeding time adjustment results in simulated organisms trying to maintain Ecopath base Q/B by varying relative feeding time). Net production is assumed proportional (growth efficiency) to Q/B , whether or not this production is due to recruitment (split pools) or growth. The Q/B increase with decreasing pool biomass is increased by decreasing vulnerability of prey to the pool (Flow control tab). In the extreme as vulnerability approaches zero (donor or bottom up control), total food consumption rate Q approaches a constant (Ecopath base consumption), so Q/B becomes inversely proportional to B .

9.5.16 Compensatory natural mortality

Compensatory changes in natural mortality rate (M) can be simulated by combining two effects in the ‘Group Info’ tab: nonzero feeding time adjustment, and either high EE from Ecopath or high proportion of Mo due to predation (unexplained predation > 0). With these settings, especially when vulnerabilities of prey to a group are low, decreases in biomass lead to reduced feeding time, which leads to proportional reduction in natural mortality rate.

9.5.17 Compensation in recruitment

The ‘split pool’ representation of juvenile and adult biomasses was originally included in Ecosim to allow representation of trophic ontogeny (differential diets for juveniles and adults). To implement this representation it was necessary to include population numbers and age structure, at least for juveniles, so as to prevent unrealistic dynamics such as elimination of juvenile biomass by competition/predation or fishing without attendant impact on adult abundance (graduation from juvenile to adult pools cannot be well represented just as a biomass ‘flow’).

When we elected to include age structure dynamics, we in effect created a requirement for model users to think carefully about the dynamics of compensatory processes that have traditionally been studied in terms of the ‘stock-recruitment’ concept and relationships. To credibly describe the dynamics of split-pool populations, Ecosim parameters for split pools usually need to be set so as to produce an ‘emergent’ stock-recruitment relationship that is at least qualitatively similar to the many, many relationships for which we now have empirical data (see data summary in www.mscs.dal.ca/~myers/data.html). In most cases, these relationships are ‘flat’ over a wide range of spawning stock size, implying there must generally be strong compensatory increase in juvenile survival rate as spawning stock declines (otherwise less eggs would mean less recruits on average, no matter how variable the survival rate might be).

When creating split pool dynamics care must be exerted in setting model parameters that define or create compensatory effects. This begins with the Ecopath input parameters; in order for the juvenile dynamics to exhibit compensatory mortality changes, at least two conditions are needed or helpful:

1. the juvenile group must have relatively high total mortality rate;
2. the juvenile group must have most mortality accounted for as predation or fishery effects within the model, or the user must specify that the ‘other’ mortality (the mortality not accounted for) is very sensitive to changes in predator feeding time.

Given these Ecopath conditions, Ecosim can then generate direct (as opposed to just predator-prey) compensatory changes in juvenile recruitment via at least three alternative mechanisms or hypotheses:

1. simple density-dependence in juvenile production rate by adults, due to changes in adult feeding rates and fecundity (not a likely mechanism);
2. changes in duration of the juvenile stage and hence in total time exposed to relatively high predation risk;
3. changes in juvenile foraging time (and hence exposure to predation risk) with changes in juvenile feeding rates.

For all of these mechanisms, compensatory effects are increased (recruitment relationship flat over a wider range of adult stock size, steeper slope of recruitment curve near the origin) by

1. limiting availability of prey to juveniles by forcing juveniles to use small ‘foraging arenas’ for feeding;
2. make effective time exposed to predation while feeding drop directly with decreasing juvenile abundance (simulates possibility that when juveniles are less abundant, remaining ones may be able to forage ‘safely’ only in refuge sites without exposing themselves to predation risk). This option should be used only if field natural history observation indicates that the juveniles do in fact restrict their distribution to safe habitats when at very low abundance.

9.5.18 Life history handling

Version 4 of Ecosim included split adult/juvenile groupings to incorporate ontogenetic shifts as described in more detail below. From Version 5 on we also include multi-stanza groupings where any number (≥ 2) of stanza’s can be invoked. We recommend the use of multi-stanza rather than the adult/juvenile split (as this does not ensure consistent biomasses and mortalities across stanza), but have kept the option of using adult/juvenile split in order to ensure compatibility for existing models.

To better represent ontogenetic shifts in Ecosim groups can be split in juvenile and adult components, and Ecosim then applies a Deriso-Schnute delay-difference model (Deriso, 1980; Schnute, 1987) to keep track of the number that recruits from juvenile to adult stages, and the number at age/size in the adult groups (Walters et al 2000).

Denoting the pool index for adults as A , and for juveniles as J , the basic model structure is,

$$B_{A,t+1} = e^{-Z_{A,t}} [\alpha_{A,t}(C_{A,t})N_{A,t} + \rho_A B_{A,t}] + I_A + w_{J,k,t} N_{J,k,t} \quad \text{Eq. 53}$$

$$N_{A,t+1} = N_{A,t} e^{-Z_{A,t}} + N_{J,k,t} \quad \text{Eq. 54}$$

$$N_{J,1,t+1} = R(B_{A,b}, N_{A,b}, C_{A,t}) \quad \text{Eq. 55}$$

$$N_{j,a,t+1} = e^{-Z_{J,t}} N_{j,a-1,t} \quad a=1, \dots, k \quad \text{Eq. 56}$$

$$w_{J,a,t+1} = w_{J,a-1,t} + g^a C_{J,t} / N_{J,t} \quad \text{Eq. 57}$$

where t = time, (in months to increase flexibility to represent seasonality, short lives);

$Z_{A,t}$ = adult pool total mortality rate $M_{A,o} + e_{A,o} + F_{A,t} + \sum C_{A,j} / B_{A,t}$;

$Z_{J,t}$ = juvenile pool total mortality rate $M_{J,o} + e_{J,o} + F_{J,t} + \sum C_{J,j} / B_{J,t}$;

$N_{J,a,t}$ = Number of age (months) a juveniles at time t ;

$R(B_{A,b}, N_{A,b}, C_{A,t})$ = recruitment function predicting the number of age (month) 0 juveniles produced in month t , from adult numbers, biomass, and food consumption $C_{A,t}$;

k = age (months) at recruitment to the adult pool;

$w_{J,a,t}$ = body weight of an age a juvenile at time t ;

$C_{J,t}$ = total food consumption by juveniles J in month t ;

$N_{J,t}$ = total number of juveniles at start of month t (summed over ages a);

g' = juvenile growth efficiency;

$\alpha_{A,t}(C_{A,t})$ = Ford-Brody growth model intercept, assumed to depend on adult food consumption $C_{A,t}$ in month t ;

ρ = Ford-Brody growth model slope, i.e., partly linearized version of VBGF for weight growth, representing metabolism.

The delay-difference representation of population age and size structure permits explicit representation of changes in growth, mortality, and recruitment processes with changing feeding conditions. It also makes it straightforward to include,

1. changes in how food intake is allocated between growth and reproduction as food conditions varies;
2. changes in vulnerability to predation associated with changes in feeding behavior as prey densities vary; and
3. recruitment constraints related to juvenile size and fecundity.

These aspects will be described further in the next sections.

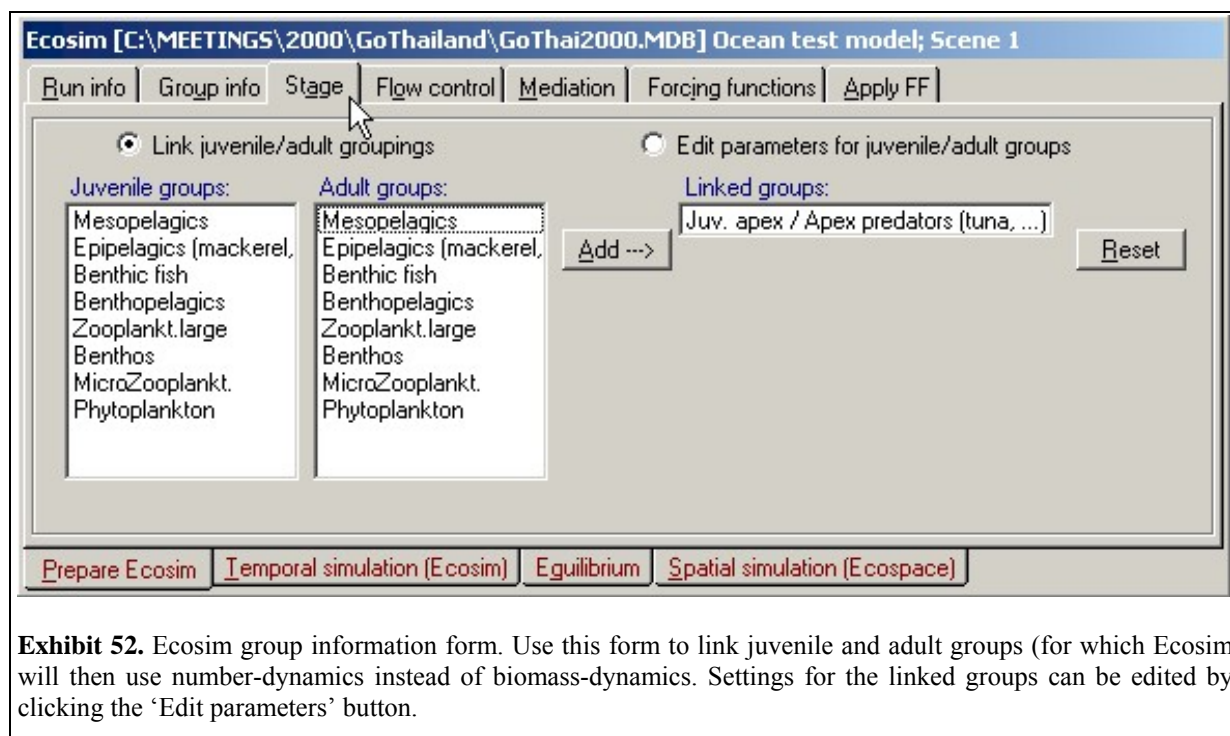


Exhibit 52. Ecosim group information form. Use this form to link juvenile and adult groups (for which Ecosim will then use number-dynamics instead of biomass-dynamics). Settings for the linked groups can be edited by clicking the 'Edit parameters' button.

9.5.19 Handling life histories: Ecosim stage information

As discussed above, we recommend that you use multi-stanza (see 'Representation of multi-stanza life histories in Ecopath and Ecosim' on page 31) to model groups where ontogenetic shifts are of importance for the modeling. The Ecosim 'stage' screen (Exhibit 52) is to:

- Link juvenile and adults of split pools: Identify which of the groups of the underlying Ecopath file that are the juveniles and the adults, respectively of a given split pool. This step requires clicking a juvenile group, the corresponding adult group, then add(ing) the pair to the frame headed 'Linked groups'. More than one split pool may be created, and an 'Unlink' button is provided to restart the procedure.
- Once one or several split pools have been identified, clicking the 'Edit' parameters to edit the default parameters defining the modalities of the juvenile-to-adult transition. Here, the following information is available:
 - Juvenile group: Name of juvenile group of selected group pair. For information only, group name can only be changed from within Ecopath proper;
 - Adult group: Name of adult group of selected group pair;
 - Minimum time as juvenile: If food is abundant growth rates will increase, and the juvenile stage will take less time to grow through, reducing the time they are susceptible to the higher mortalities caused by their small sizes. Use this entry to limit how short the juvenile stage may be relative to the default duration. Ecosim simulations are very sensitive to this parameter, and we recommend that you use 1 as minimum time;
 - Maximum time as juvenile: If food is limited growth rates will decrease, and the juvenile stage will take longer time to grow through. Use this entry to limit how long the juvenile stage may be relative to the default duration. Ecosim simulations are very sensitive to this parameter, and we recommend that you use 1.0001 as maximum time multiplier;
 - Age at transition to adult group: Ecosim simulations are not very sensitive to this parameter;
 - Average weight of adult individual relative to weight at transition to adult group. Value has to exceed unity; default value is 3.
 - Curvature parameter, K , of the von Bertalanffy Growth Function, VBGF:
 - Base proportion of food intake used for reproduction: This entry (default 0.5), together with the next line, for entering the 'Proportion of increase in food intake used for growth' (default 0.8) jointly define how food intake is turned into reproductive products [eggs/larvae; see S/R relationship], as implied from the theory in Walters et al. 1999]
 - Proportion of increase in food intake used for growth: see entry above.

9.5.20 Food allocation between growth and reproduction

The net (of assimilation and SDA losses) food intake $g'Q_{A,t}$ (see Eq. 47 on page 76) by an adult pool can be distributed between food used for growth,

$$F_g = P_g \cdot g' \cdot Q_{A,t} \quad \text{Eq. 58}$$

where P_g is the proportion of net intake allocated to growth, and food used for reproduction,

$$F_r = g' \cdot Q_{A,t} - F_g \quad \text{Eq. 59}$$

Assume that $Q_{A,t}$ is allowed to vary with feeding opportunities as predicted from Eq. 49. In order for the growth curve α to remain constant at some value α_0 , where $\alpha = F_g / N_{A,t}$ (the per capita allocation of food to growth), the allocation proportion P_g must vary as,

$$P_g^{\text{constant growth}} = \frac{\alpha_0}{g' \cdot Q_{A,t} / N_{A,t}} \quad \text{Eq. 60}$$

(subject to $P_g^{constant\ growth} \leq 1.0$). The opposite extreme from this assumption is that a constant proportion P_o of the net food intake is used for growth, which implies that both α and fecundity will be proportional to food intake.

In Ecosim the user can move between these two extreme hypotheses ($\alpha = \alpha_o$ versus α proportional to Q/N) by specifying a life history 'weighting factor' W_g :

$$P_g^{realized} = W_g \cdot P_g^{constant\ growth} + (1 - W_g) \cdot P_o$$

Eq. 61

That is, at every model time step Ecosim calculate the net food intake per animal g' $Q_{A,t} / N_{A,t}$, and uses this to calculate $P_g^{constant\ growth}$. The $P_g^{realized}$ for that time step is then given by the equation above. W_g can be varied freely to generate a range of physiological allocation scenarios.

9.5.21 Foraging time and predation risk

The food consumption prediction relationship in Eq. 49 contains two parameters that directly influence the time spent feeding and the predation risk that feeding may entail: a_{ij} and v'_{ij} . To model possible linked changes in these parameters with changes in food availability as measured by per biomass food intake rate $c_{it} = Q_{it} / B_{it}$ (i =juvenile index J or adult index A), we need to specify how changes in c_{it} will influence at least relative time spent foraging.

Denoting the relative time spent foraging as T_{it} , measured such that the rate of effective search during any model time step can be predicted as $a_{jit} = T_{it} a_{ji}$ for each prey type j that i eats. Further, we assume that time spent vulnerable to predation, as measured by v'_{ijt} for all predators j on i , is inversely related to T_{it} , i.e., $v'_{ijt} = v'_{ij} / T_{it}$. An alternative structure that gives similar results is to leave the a_{ij} constant, while varying the v_{ij} by setting $v_{ijt} = T_{it} \cdot v_{ij}$ in the numerator of Eq. 49, and $v_{ijt} = T_{it} \cdot v_{ij}$ in the denominator.

For convenience in estimating the a_{ij} and v'_{ij} parameters, we scale T_{it} so that $T_{i0} = 1$, and $v'_{ij} = v_{ij}$. Using these scaling conventions, the key issue then becomes how to functionally relate T_{it} to food intake rate c_{it} so as to represent the hypothesis that animals with lots of food available will simply spend less time foraging, rather than increase food intake rates.

In Ecosim a simple functional form for T_{it} is implemented that will result in near constant feeding rates, but changing time at risk to predation, in situations where rate of effective search a_{ji} is the main factor limiting food consumption rather than prey behavior as measured by v_{ji} . This is implemented in form of the relationship:

$$T_{i,t} = T_{i,t-1} \cdot \left(1 - a + \frac{a \cdot c_{i,opt}}{c_{i,t-1}} \right)$$

Eq. 62

where, a is a user-defined feeding time adjustment factor $[0, 1]$, $c_{i,opt}$ is the (internally computed) feeding rate that optimizes feeding rate versus mortality risk for i , $c_{i,t-1}$ is the consumption/biomass ratio in the previous time step for the group. The time spent feeding is constrained by a user-defined value (default of two times the feeding rate in the Ecopath base

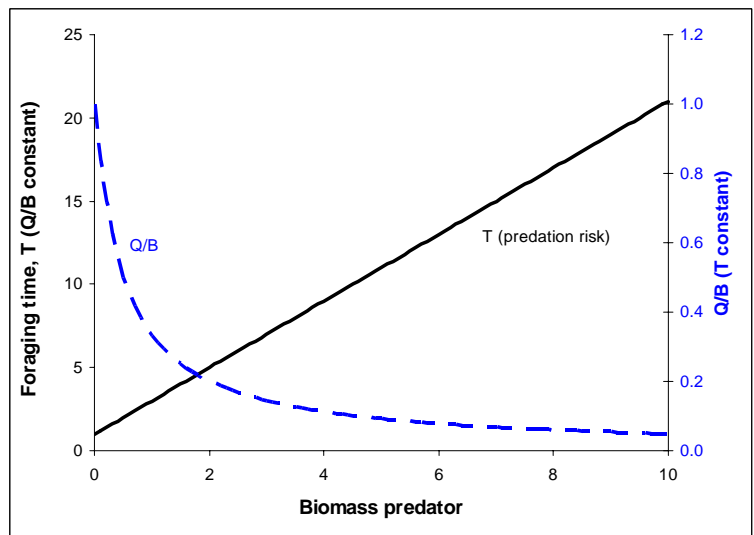


Exhibit 53. Relationship between relative foraging time (T), Q/B and predator biomass. If Q/B is held constant the foraging time (and hence predation risk) is a linear function of the predator biomass (solid line). If T is held constant the Q/B will decrease asymptotically with predator biomass (stippled line).

model).

The relationship between foraging time, consumption and predator biomass is illustrated in **Error! Reference source not found.**

9.5.22 Grow fast, die young?

Ecosim predictions, especially for recruitment dynamics in split-pool cases, are generally quite sensitive to assumptions about how organisms adjust time spent foraging in relation to changes in feeding rates. Foraging time adjustments have two opposing (tradeoff) effects: more time means higher food intake (or less reduction in intake rate during a period of decline in prey abundance), but also possibly higher predation loss rate. There is much interest in evolutionary ecology in how organisms balance these effects, i.e., in how natural selection has ‘optimized’ foraging time.

One type of check of whether the behavioral parameters/assumptions in Ecosim are reasonable is to see if a model would ‘evolve’ toward very different foraging time patterns if the effects of the tradeoff are explicitly recognized. A routine for checking this is included in Ecosim. When applying this routine the normal functions linking foraging time to Q/B are disabled. Instead, Ecosim calls a routine that evaluates the derivative of a fitness measure f with respect to foraging time for each pool, and at each simulated time step Ecosim then adjusts foraging times in a direction that will increase this fitness measure. That is, Ecosim tries to ‘evolve’ foraging times toward values that will maximize fitness. The fitness measure used is simply the per capita biomass derivative, $f = dB/Bdt$, i.e., the biomass derivative divided by biomass.

9.5.23 Stock-recruitment considerations

For split biomass pools, Ecosim estimates a baseline recruitment rate R_0 to each adult pool by assuming equilibrium in Eq. 55 as noted above. Recruitment takes place at age k months, and we can calculate baseline recruitment R^*_o at age 0 months from $R^*_o = R_0 \exp(Z_{j,0} k)$. A basic problem is then to predict how R^* will vary over time with changes in adult abundance, feeding rate, and/or body size (i.e., to define a reasonable recruitment function $R(B_{A,t}, N_{A,t}, Q_{A,t})$). We assume that R^* is limited by recent feeding rate rather than accumulated food intake as reflected in body size, and use the following function to represent this limitation:

$$R(B_{A,t}, N_{A,t}, Q_{A,t}) = R^*_o \cdot \left(\frac{N_{A,t}}{N_{A,0}} \right) \cdot \left[\frac{(1 - P_g^{realized}) \cdot Q_{A,t}}{(1 - P_0) \cdot c_{A,0}} \right]^r$$

Eq. 63

This relationship scales R relative to R^*_o by the ratio of adult abundance at time t to initial ($N_{A,t}/N_{A,0}$), and by the ratio of per biomass food consumption allocated to reproduction $(1 - P_g^{realized})Q_{A,t}$ to the baseline food allocated. The power parameter r can be used to generate nonlinear effects of the food consumption rate on recruitment per adult individual.

If there is immigration of juveniles, this is added to the equation above. Further, egg production is allowed to vary seasonally or over long-term through a user-defined forcing function. If an egg production curve is defined the egg production term is multiplied on the equation above for the first age group of juveniles.

9.5.24 Primary production

For primary producers the production is estimated as a function of the producers’ biomass, B_p , from a simple saturating relationship

$$f(B_i) = \frac{r_i \cdot B_i}{1 + B_i \cdot h_i}$$

Eq. 64

where, r_i is the maximum production/biomass ratio that can be realized (for low B_i 's), and r_i/h_i is the maximum net primary production when the biomass is not limiting to production (high B_i 's). For parameterization it is only necessary to provide an estimate of $r_i / (P_i/B_i)$, i.e., a factor expressing how much primary production can be increased compared to the base model state.

9.6 Parameter sensitivity

Ecosim does not (yet!) include any formal sensitivity analysis. Experience shows, however, that of the extra parameters added to those required by the typical Ecopath models, the most sensitive parameter is the vulnerability setting. This parameter expresses the exchange rate between the prey being in vulnerable and non-vulnerable states (see Exhibit 39).

The vulnerability parameter is in general not subject to direct measurement. There are, however, other ways of estimating it, and Ecosim includes three independent methods of estimation:

1. build Ecopath models for a system covering two different time periods, and use a routine included in Ecosim to search for vulnerability parameter settings that with the given exploitation rates will make it possible to move from the first to the second model state;
2. using the evolutionary optimization model discussed above. Seeks the evolutionary optimum between spending more time feeding and growth faster but at higher mortality risk;
3. through fitting to time series data (see above).

It is possible and indeed recommended to use all of these methods to obtain estimates for the vulnerability parameters.

9.7 Trophic mediation functions

It is not uncommon for some third type of organism to affect the feeding rate of one type of organism j on another i . At least two types of effects are possible:

Facilitation: the third organism type behaves in some way that makes type i prey more available to predator j when the third organism is more abundant. For example, pelagic piscivores like tuna may drive smaller fishes to the surface, where these fishes are then more available to birds. This is a concern of marine mammals and birds in the Eastern Pacific Ocean, at least in areas where heavy fishing has reduced abundances of tunas and billfishes.

Protection: the third organism provides protection for prey type i when the third organism is more abundant. For example, juvenile fishes (as type i prey) may use corals, macrophytes, and/or sponges for protection from predators, and fishing may directly impact these 'cover' types; K. Sainsbury (pers. comm.) has emphasized the possible importance of this effect for evaluating impact of trawling on the Northwest Shelf of Australia. For another example, increases in phytoplankton may reduce water clarity and hence search efficiency of visual predators on small fishes, which would tend to reinforce the 'cascade effect' of increasing abundance of small fishes causing reduced zooplankton abundance and hence increased phytoplankton abundance.

You can define a series of 'trophic mediation functions' that are used to modify vulnerabilities of selected prey types i to their predators j . Each function is defined by

- (1) sketching a functional form for the mediation effect, and
- (2) defining the X variable for the function by specifying weights for each biomass pool, so that X is a weighted sum of third-type organism abundances.

Sketching a function that increases with increasing X represents facilitation effects (prey more vulnerable when X is large), while sketching a function that decreases with X represents protection effects (prey less vulnerable when X is large). The idea behind making X be a weighted sum of third organism biomasses is to allow

- (1) differential protective ‘quality’ for alternative organisms that provide cover for prey, and
- (2) recognize that alternative piscivores may have different tendencies to generate facilitation effects, e.g., some tunas may commonly chase bait fishes to the surface while others may not.

The sketch function approach allows considerable flexibility in specifying the form of the relationship between third organisms and trophic vulnerabilities. Such effects are essentially statistical, and cannot usually be described by any simple functional form. Effects may only occur above/below some threshold abundances, may or may not be large even when third organism abundances are very low, etc. To avoid unnecessary parameter specification, the functions are automatically scaled relative to Ecopath baseline inputs: the X axis of each function is scaled relative to the weighted initial sum of third organism biomasses, and the function is internally scaled so that $Y=1.0$ when $X =$ Ecopath initial weighted sum. The only restriction on the form of the function is that the user must not specify a relative Y value of 0.0 when $X =$ Ecopath base value.

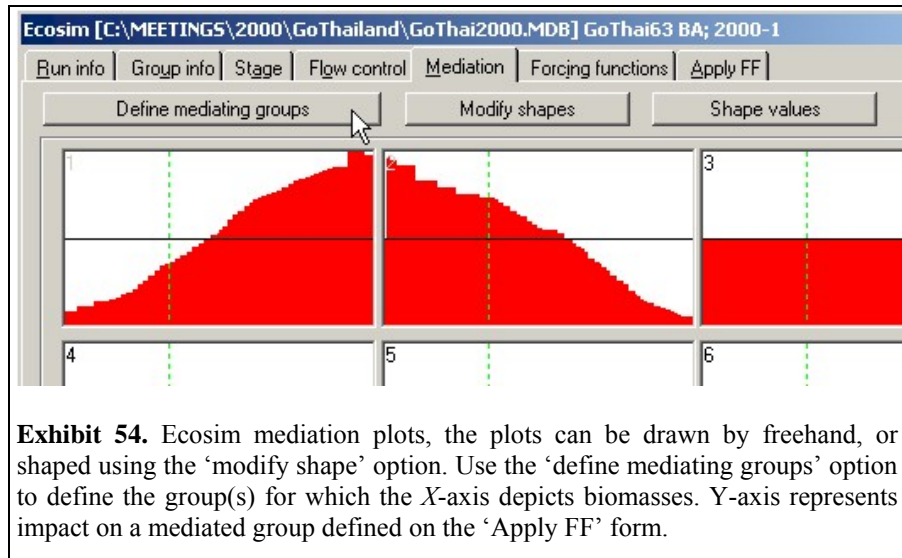


Exhibit 54. Ecosim mediation plots, the plots can be drawn by freehand, or shaped using the ‘modify shape’ option. Use the ‘define mediating groups’ option to define the group(s) for which the X -axis depicts biomasses. Y -axis represents impact on a mediated group defined on the ‘Apply FF’ form.

Internally, Ecosim/space routines use the trophic mediation functions to modify prey vulnerabilities v_{ij} in the basic trophic flow equations. At each simulation time step, any i,j flow that has been defined to be affected by a mediation function is modified to use an effective $v_{ij} = v_{i,j \text{ base}} \cdot Y/Y_o$, where Y is the current value of the mediation function, which depends on the current X of that function, and Y_o is the value of the function when $X =$ Ecopath base weighted sum of mediating biomasses.

Define impacting group: Press this command button to load a form with relative weightings by group. The first line (highlighted in yellow) gives the plot number (numbered from 1 to 9). Below enter group specific weighting factors describing how each groups biomass contribute to the total for a given plot. To illustrate this: If you for, e.g., plot number 3 enter 2 for group 3, 1 for group 4, and 0.5 for group 5, the biomasses on the X -axis of plot 3 will be estimated as $2 \cdot B_3 + 1 \cdot B_4 + 0.5 \cdot B_5$. The vertical line on the mediation plot refers to the Ecopath base line value for these biomasses.

Modify shapes: Click this command button to load a form for shaping the mediation plots. You will need to close the form before continuing with Ecosim simulations.

Shape values: Use to display the values corresponding to the mediation plots. You can paste from the clipboard to the spread displayed. This can for instance be done by opening Excel, highlighting a series of values, click Copy or <Ctrl> + <C>, then place the cursor on the spread in Ecopath where you want to paste, and click the **Paste** command button, or press <Ctrl> + <V>.

After you have defined the mediation shapes: Continue to the tab called ‘Apply forcing functions’. Select the ‘Mediation’ option button, and define the predator-prey relationships that each of the mediation functions impact.

9.8 Ecosim forcing functions

As presently conceived Ecosim does not incorporate the interactions between the components of the food web defined by the underlying Ecopath file, and physical or other environmental factors affecting the ecosystem thus described. Ecosim, like Ecopath, describes only feeding interactions. However, a routine was built to allow ‘forcing function’, which may represent physical or other environmental parameters, to influence these trophic interactions. These forcing functions, which can be used to modify the Q/B ratio of the consumer groups included in an underlying Ecopath file, are of two types:

- Seasonal (i.e. within a year); and
- Longer term (always a 100 hundred year period, irrespective of model run time – however if runtime is shorter only the corresponding time span is used of the forcing function).

There are three seasonal forcing function; their default setting is uniform (no seasonal forcing). However, sinusoid or other shapes can easily be sketched in, with, e.g., a maximum in summer and a minimum in winter, the amplitude of these oscillations being set by the scaling factor (default 2.0) at the upper-left corner of each shape.

Each seasonal shape may be different. It might be appropriate to use highly variable shapes for ‘fast groups’ (usually small organisms) and shapes with low amplitude for slow groups (usually large, long-lived organisms).

The long-term shapes are similar to the seasonal shapes, except that their time scales refer, as the name implies, to a 100 hundred year period. Such shapes may be used to represent e.g., decadal regime shifts, such as occur in the North Pacific. By default only 1 long-term shape is activated but addition long-term shapes can be added using a custom control button.

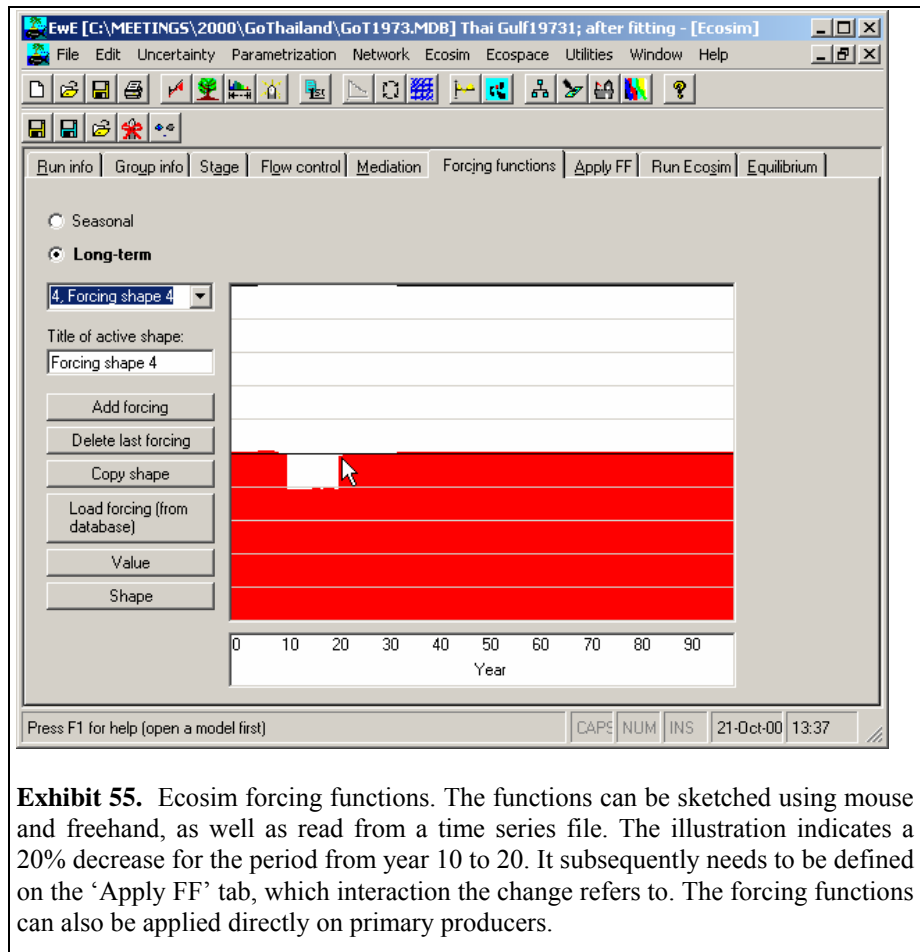


Exhibit 55. Ecosim forcing functions. The functions can be sketched using mouse and freehand, as well as read from a time series file. The illustration indicates a 20% decrease for the period from year 10 to 20. It subsequently needs to be defined on the ‘Apply FF’ tab, which interaction the change refers to. The forcing functions can also be applied directly on primary producers.

9.8.1 Seasonal egg production

Ecosim allows linking a seasonally and long-term oscillating forcing function with the function through which the adults of 'split groups' are made to generate eggs/larvae, i.e., the earliest form of 'juveniles'. Here, it is assumed that a seasonally variable factor (or a set of factors) causes the number of egg/larvae that would be produced, given the adult biomass, to vary as a function of the month. Alternatively, this factor can be interpreted as seasonally modulating the mortality of the eggs/larvae, independently of their density.

This linkage thus allows simulating the effect of abiotic variables, such as, e.g., the effect of wind-induced offshore transport of Peruvian anchoveta, a process which removes eggs/larvae from the (coast-bound) population independently of the density of their food organisms, or of their predators (Mendelssohn, 1989).

Moreover, by shifting the peak(s) of such forcing function relative to the peak(s) of a forcing function for seasonal production of phyto- and/or zooplankton, the match/mismatch hypothesis of Cushing (1975), and related hypotheses, can be tested in an ecosystem context, something previously not achievable.

To link a split pool with a seasonally oscillating forcing function, go to the 'Apply FF' tab, click the 'Egg production' radio button, and a list will display the linked adult/juvenile grouping. Enter the number of the egg production curve.

9.8.2 Apply forcing functions

This form is used to link forcing functions with groups. The three radio buttons opens for entry related to:

Mediation: See the description about 'Trophic mediation functions' on page 108.

Forcing functions: The default screen used here contains zeroes for all interactions between groups for which the underlying Ecopath diet matrix shows some interactions (the other cells are blank).

A number from 1 to 6 can replace each of these zero values, referring to one of the sketched forcing functions. Clicking the row numbers ('preys') adds one to the previous numbers in the row in questions, and conversely for the column (predator numbers), and this facility can be used to quickly enter the same shape for a number of groups.

Note that the consumption of a given prey by a given predator can be modified by only one forcing function, either seasonal or long-term. Thus, when investigating the effect of e.g., seasonal variability, it is not possible to simultaneously evaluate long-term effects, and vice versa. There is some logic in this, though we hope to overcome this constraint in future version of the package.

Egg production: see the section on 'Seasonal egg production' on page 111.

Reset all to shape no: Use to change all shapes. Enter the number of the shape you want to use for all groups.

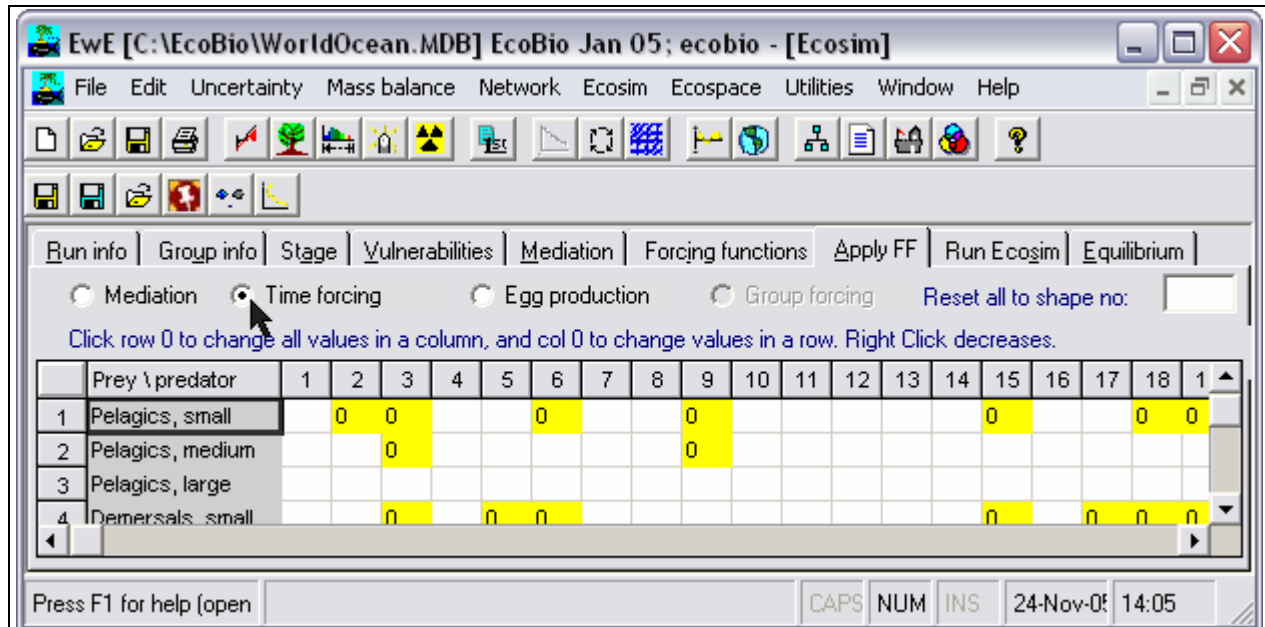


Exhibit 56. Ecosim apply forcing functions. Take care to note which radio-button is selected.

9.9 Searching for optimum fishing strategies for fishery development, recovery and sustainability

Two very different approaches can be taken to the identification of optimum levels of fishing efforts for multiple fleets that may each harvest multiple species from an ecosystem. The first or 'sole owner' approach is to identify a single, overall performance measure for combined value from all fishing operations, then vary the by-fleet efforts so as to try and maximize this performance measure. The sole owner approach has been used extensively in past Ecosim optimization exercises, using performance measures ranging from total profit from fishing (sum over fleets of incomes minus costs) to total employment (sum of catches times employment per catch) to risk-averse utility measures that favor a balanced 'investment portfolio' of fishing activities. A fundamental problem with this approach is the implicit assumption of value and cost pooling; supposedly 'optimum' solutions often involve operating one or more fleets at uneconomic levels, essentially using these fleets to cull some fish species so as to increase production from other, more valued species.

9.9.1 The 'sole owner' of societal approach

Regulating fishing mortality rates over time so as to achieve economic, social and ecological sustainability objectives is indeed a central aim of fisheries management. An important dynamic modeling and assessment objective is to provide insight about how high these mortality rates should be, and how they should be varied over time (at least during development or recovery from past overfishing). We cannot expect models to provide very precise estimates of optimum fishing mortality rates, but we should at least be able to define reasonable and prudent ranges for the rates. Ecosim users now have two ways to explore impacts of alternative time patterns of fishing mortalities:

Exhibit 57. Form used for Ecosim nonlinear search procedure for optimum fishing pattern over time. The form is available by clicking the ‘Fishery policy search’ on the ‘Prepare Ecosim’ tab.

- (1) Fishing rates can be ‘sketched’ over time in the Ecosim simulation interface, and simulated results (catches, economic performance indicators, biomass changes) examined for each sketch. This is using Ecosim in a ‘gaming’ mode, where the aim is to encourage rapid exploration of options.
- (2) Formal optimization methods can be used to search for time patterns of fishing rates (actually, relative fishing efforts by fishing fleet/gear types) that would maximize particular performance measures or ‘objective functions’ for management.

These approaches can be used in combination, e.g. by doing a formal optimization search then ‘reshaping’ the fishing rate estimates from this search in order to meet other objectives besides those recognized during the search process.

The first of these approaches is automatically available to users whenever Ecosim is run: simply click on the Temporal Simulation (Ecosim) tab, select fleet (or biomass group) from drop down menu in the upper left corner of the interface, and sketch fishing rate patterns over time in the lower graph panel (hold mouse down and move it over the panel). Then click the run button to see predicted biomass responses, and the results button to see final performance indicators.

The formal optimization method is invoked by clicking the ‘Fishing policy search’ button on the Ecosim Run Info (startup) tab. Three steps are involved in using the window that then appears:

- (1) Define fleet/year parameter blocking for the search procedure: on the right side of the window, click on a fishing rate color code then sketch the fleet/year cells on the graph below, for which this particular code fishing rate is to be applied (clicking on a fleet name causes the parameter color code to be applied for all years for the fleet). Then select a second color code and sketch the year/fleet combinations for this code. Continue until up

to 16 fleet/year fishing rate blocks have been specified (or increase the number of blocks). Any fleet/year blocks left black will not be modified by the search procedure (i.e. will be left at Ecopath base fishing rate or most recently sketched fishing rate values).

- (2) Define objective function weights for net economic value (total landed value of catch minus total operating cost to take this landed value), employment (a social indicator, assumed proportional to gross landed value of catch for each fleet with a different jobs/landed value ratio for each fleet), and ecological stability (measured by departures of biomasses over time from target biomass levels specified by entering ratios of target to Ecopath base biomasses).
- (3) Invoke the search procedure by clicking the search button.

There are two possible economic optimization criteria. The first is to imagine a 'sole owner' or full cooperation among fishers, where all incomes and costs are pooled and profits shared among fishers. This is the default case for the economic net profit calculation, and the policy interface will seek to maximize total profits totaled over all fleets even if this means operating some fleets unprofitably (to act as controls on less valued species that compete/predate on more valued ones). The second option (invoked by checking the costs < income check box on the search interface) is to seek maximum total profits over all fleets, but subject to the fleet viability constraint that each fleet must earn at least enough to meet its operating costs, i.e. must be economically viable in its own right. This second option is in effect a constrained cooperative economic solution, constrained by the requirement that no fleet be operated at a level that would require public subsidy or transfer payments from other fleets.

When a search has been completed, you can view the resulting 'optimum' fishing rates by year/fleet block by returning to the Ecosim Temporal Simulation tab, where the optimized fishing rates will have replaced the baseline (or previously sketched) relative efforts by fleet/gear type.

Invoking the search option causes Ecosim to use a nonlinear optimization procedure known as the Davidson-Fletcher-Powell (DFP) method to iteratively improve an objective function by changing relative fishing rates, where each color-coded year/fleet block defines one parameter to be varied by the procedure (e.g. setting four color code blocks means a 4-parameter nonlinear search). DFP runs the Ecosim model repeatedly while varying these parameters; in the search output display, each simulation trial is labeled an 'eval' or function evaluation. So if you are running a large model for many years, where each simulation takes several seconds to do, the search may take quite a long time to do enough function evaluations to find a maximum for the objective function. The parameter variation scheme used by DFP is known as a 'conjugate-gradient' method, which involves testing alternative parameter values so as to locally approximate the objective function as a quadratic function of the parameter values, and using this approximation to make parameter update steps. It is one of the more efficient algorithms for complex and highly nonlinear optimization problems like the one of finding a best fishing pattern over time for a nonlinear dynamic model.

It must be understood that nonlinear optimization methods like DFP can be tricky to use and can give grossly misleading results: in particular the method can 'hang up on local maxima', and can give unrealistic, extreme answers due to inappropriate objective functions. To check for false convergence to local maxima, rerun the search at least a few times using the 'random starting F 's' option button on the interface, and check final answers by forcing additional iterations using the 'start at current F 's' option button. To test for sensitivity of the results to objective function parameters, try searches for a variety of values of the objective function weights and parameters accessed through the small spreadsheets on the search interface.

The objective function can be thought of as a 'multi-criterion objective', represented as a weighted sum of three criterion components or indicators: economic, social, and ecological. Assigning alternative weights to these components is a way to see how they conflict or tradeoff with one another in terms of policy choice. For example, placing a high weight on the net economic value component (total fishing profits) typically causes the optimization to favor lower fleet sizes and severe simplification of the simulated ecosystem to maximize production of only those species that are most profitable to harvest. Placing a high weight on the employment (social) indicator typically results in favoring larger fleet sizes, and again often severe ecological simplification in order to maximize production for the fleet that employs the most people. The ecological criterion component is intended to balance these socioeconomic optimization effects: the ecological component is calculated as a sum of squared deviations of biomasses over time from biomasses that the user considers 'desirable' in terms of objectives like maintenance of biodiversity and insurance against ecological instability. The sum of squared deviations of biomasses from

desirable values is treated as a negative value: larger sums of squares result in a decrease in the overall objective function value.

The search procedure results in what control systems analysts call an ‘open loop policy’, i.e. a prescription for what to do at different future times without reference to what the system actually ends up doing along the way to those times. It would obviously be very wrong to just apply an open loop policy blindly over time, each year committing a fishery to fishing rates calculated at some past time from only the data available as of that time. In practice, actual management needs to be implemented using ‘feedback policies’ where harvest goals are adjusted over time as new information becomes available and in response to unpredicted ecological changes due to environmental factors. But this need for feedback in application does not mean that open loop policy calculations are useless: rather, we see the open loop calculations as being done regularly over time as new information becomes available, to keep providing a general blueprint (or directional guidance) for where the system can/should be heading. Also, we can often gain valuable insight about the functional form of better feedback policies (how to relate harvest rates to changes in abundance as these changes occur) by examining how the open loop fishing rates vary with changes in abundance, especially when the open loop calculations are done with Ecosim ‘time forcing’ to represent possible changes in environmental conditions and productivity in the future. For an example of this approach to design of policies for dealing with decadal-scale variation in ocean productivity for single species management, see Walters and Parma (1996).

9.9.2 Multiple fishing rights

The second or ‘multiple fishing rights’ approach is to treat each fishing fleet (and perhaps non-consumptive stakeholder or user groups as well) as a separate economic industry with some legal right or entitlement to harvest, then seek a level for each fleet that optimizes a fleet-specific performance criterion such as total profits or growth until profitability (ratio of profits to income or cost) falls to a typical or reasonable level for economic industries in the economy as a whole. The basic problem in this ‘multiplayer game’ approach is that performances of the fleets are linked through bycatch and trophic interaction effects. Growth of some fleets may enhance fishing opportunities for others (e.g. fishing on piscivores can result in higher net production of planktivores), while growth of other fleets may shunt surplus production away from other fleets (e.g. fishing on planktivores can reduce production of piscivores and abundances of non-target species that are valued for non-consumptive activities like whale-watching).

When filtered through the complex of ecological interactions involved in a food web, the net effect of any fleet on any other can be quite counter-intuitive. For instance, in development of management policy for red snapper (*Lutjanus campechanus*) in the Gulf of Mexico, it has been assumed that large bycatches of this species in shrimp trawls have been deleterious to recruitment, and that sustainable harvests of red snapper would be increased if shrimp trawlers were required to use bycatch reduction devices (BRDs). But in fact there is evidence that recruitment of the snapper may actually have increased since development of the shrimp fishery, and ecosystem modeling exercises suggest that this may be because shrimp trawling has had a larger negative effect on competitors and predators of juvenile red snapper (and shrimp) than its direct mortality effect on the juveniles.

One approach to multispecies optimization would be to promote selective fishery practices by each fleet (minimize wasteful bycatch with no apparent trophic benefits), then encourage each fleet to develop to an optimum economic level (defined by some criterion like profit or profitability). Then as multiple fleets develop in successive moves of the multiplayer game, cross-impacts (both positive and negative) would be exposed in terms of impacts on catches and costs, and the optimum or target level for each fleet would evolve over time in response to changes in the other fleets. Such a system might or might not approach some multi-fleet bionomic equilibrium (they typically do in Ecosim simulations), but that equilibrium would typically involve considerable erosion in ecosystem structure especially at top trophic levels due to shunting of production into fisheries for species of lower trophic levels.

An alternative approach is to explicitly recognize the linkages among fleets in potential production caused by trophic interactions, and to enforce the right of each fleet to a productive existence by charging any other fleet that negatively impacts on its potential production (as an ‘externality’ caused by the impacting fleet) for the losses that the impacting fleet causes. A simple way to assess such costs in a simulation framework is to first find the equilibrium catches, incomes, and costs for all fleets held constant at some starting level, then shut down one simulated fleet and run the simulation to equilibrium with just the other fleets still fishing. The equilibrium gains in income achieved by the other fleets are a direct estimate of the income losses caused by the fleet that has been shut

down. Repeating such shut-down simulations for every fleet results in a cross-impact matrix of costs (or net benefits) to every fleet caused by every other fleet.

The cross-fleet cost assessment method suggests a simple optimization procedure for finding optimum combinations of fleet sizes under the ‘multiple fishing rights’ approach to management. Start at a base size for each of the fleets, and perform the closure simulation test for each fleet to estimate its ‘current’ costs to other fleets. Using those costs, calculate net profits or profitability for each fleet if that fleet were held accountable for all trophic interaction costs (i.e. calculate its income minus direct operating costs minus costs incurred by other fleets in the form of lost production caused by it). Based on that corrected profitability, increment or decrease the fleet size toward a target (economic optimum or socially acceptable) level. Take the resulting set of levels as a new starting point, and repeat the cost, adjusted profitability, and fleet size update calculations. Based on numerical experience with this approach using Ecosim models, the successive moves in this multiplayer game typically result in a unique bionomic equilibrium after a few dozen moves (provided the moves are not so large as to cause instability or chatter in the fleet size solution vector).

Besides explicitly recognizing rights to existence for various fishing fleets or methods, this iterative approach typically produces fleet size solutions that (1) preserve diversity of economic activities and options; (2) avoid loss of biological diversity through deliberate or inadvertent ‘fishing down the food web’ or concentration of ecological production in just a few most valuable species; and (3) allow considerable flexibility among fishing activities in defining alternative performance criteria, e.g. profitability standards can be set quite differently for recreational and artisanal fisheries than would be considered best for typical industrial fisheries. Most importantly, there is no presumption that ‘society’ as a whole can best be served through some particular combination of fleet sizes that maximizes some arbitrary, overall performance criterion.

Implementation of the iterative approach described above for multiple fishing rights optimization is very simple. The model user first resets all fishing efforts to their Ecopath base levels (1.0), then sets the number of simulation years large enough for the simulated ecosystem to reach equilibrium after any fleet is shut down (typically 30-50 yrs). Then the optimization approach is invoked by selecting the ‘Fishing policy search’ button on the Ecosim ‘Run info’ tab. Then click the ‘Set every gear’ button to apply a single effort level over time for each fleet, click the ‘maximize by fleet values’ option button, and click the ‘Search’ button. As each n+1 simulations are completed in the iterative approach (n=number of fleets) and efforts are updated, new effort levels are displayed in tabular form along with values of alternative performance measures for overall system management (total profits, total employment, ecological diversity index). Further, a table is displayed for the current effort levels, with total equilibrium incomes (per model unit area per year) and percentages of these incomes ‘charged’ by other fleets as costs to them in the form of lost incomes due to bycatch and trophic interaction effects.

Note that the multiple fishing rights optimization seeks effort levels that achieve target profitabilities (profit/income), NOT maximum total profits or other measure of total industry performance. Such total industry measures are not typically used in regulation of industries in general, and there has been no convincing argument about why they should be used in fisheries except for the public-ownership possibility that the public could capture rents from public resources (but there is as yet no single instance in the field where such rents have actually been captured by the public; instead the rents in severely limited fisheries go to making vessel owners wealthy).

One useful tactic is to move back and forth between the multiple fishing rights optimization and the Ecosim ‘Equilibrium’ tab. The equilibrium analysis that is conducted when the Run button is selected on that tab is just a very long simulation run (actually two runs each starting from initial Ecopath equilibrium), with gradually increasing effort for the selected fishery (or fishing rate for selected stock). The graphical display then shows the fishery’s ecosystem impact ‘signature’ as expected changes in equilibrium biomass of all functional groups with changes in the fishery’s effort. Typically this signature involves decreases in approximated equilibrium biomass for some species (especially targeted ones) with increasing effort, and increases in other species. Examining these signatures can help to identify reasonable levels of profitability and also why some fleets are penalized more than others.

9.10 Ecosim simulations

The Ecosim simulation form, in addition to enabling run of simulations, opens for a number of settings as described below.

Drop-down list with fleet names: Use this to select which fleets or groups of which you want to change fishing patterns or. By clicking the down-arrow, you can choose between displaying ‘individual groups’, each of the fleets in your model, or ‘combined fleets/gear’. If you select the ‘individual groups’ option, the second list box will be enabled:

Drop-down list with group names: is enabled when ‘individual groups’ is selected in the first list box. Use the down-arrow to select a group for which to change fishing.

Nudge: Control button to the right of the second drop-down list box: Is only visible if the ‘Prepare pulse fishing’ check box has been checked on the ‘Prepare Ecosim’/‘Run info’ form. Clicking the Nudge button (if visible) will generate a pulse fishing (with properties as defined on the ‘Run info’ form). This generates a well-defined perturbation of the system, and may be used to study the resilience of the system. When (if) all biomasses have returned to within a certain percentage of their base values (percentage defined on ‘Run info’ form) a message will be displayed giving the time at return to the base values.

F-value: For entry of a fishing intensity value to be applied to the fleet/group selected

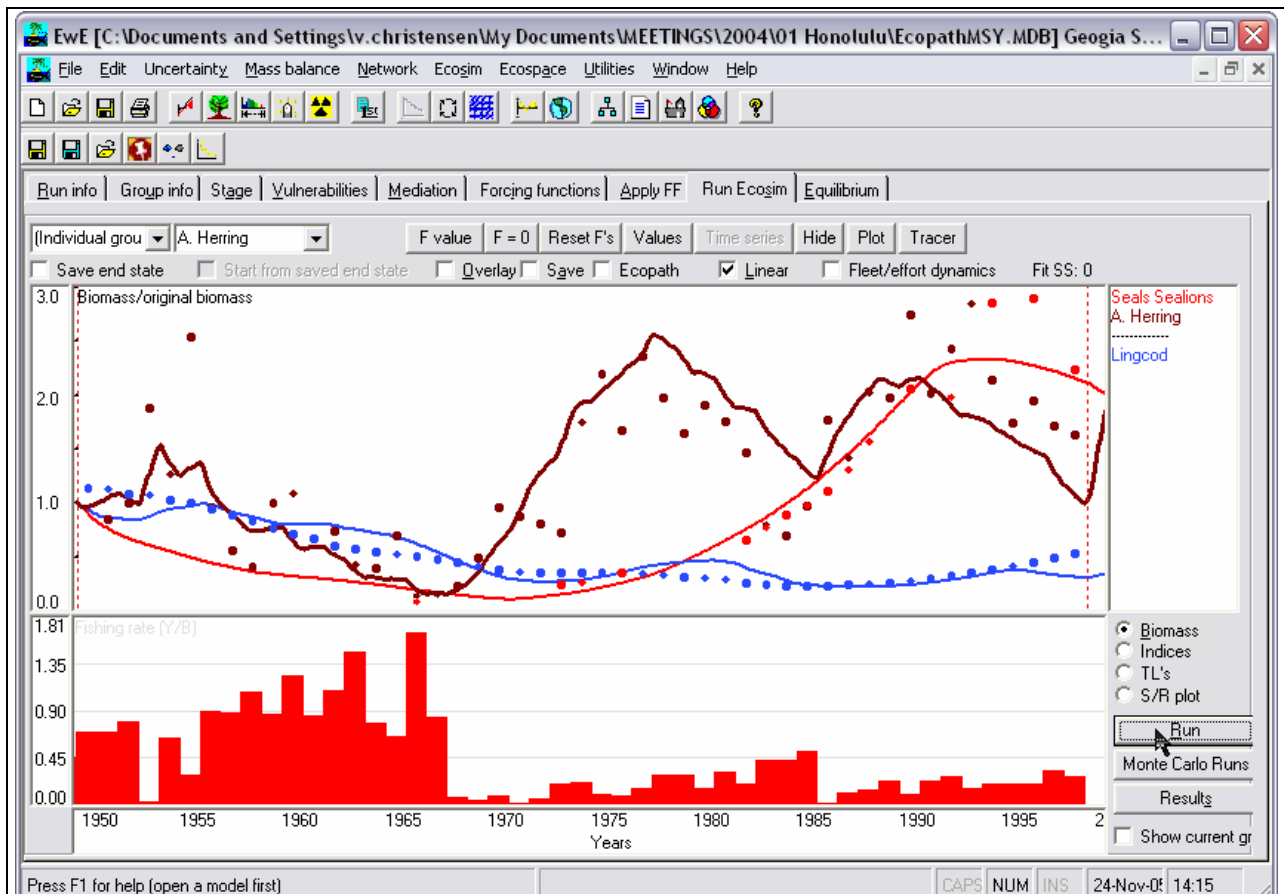


Exhibit 58. Ecosim run form, the gateway to running simulations. Here for a model (with 27 functional groups, not shown) of the Strait of Georgia, B.C., with time series data, 1950-2000. The lines indicate the predicted biomasses for three groups, and the dots the corresponding biomasses from time series data. The lower graph indicates fishing mortalities for adult herring from single-species assessment. Two red-dotted vertical lines (here in 1950 and in 1999) indicates where results (‘Results’ button) will be calculated for comparisons.

F = 0: Set fishing for the fleet/group selected to 0.

Reset fishing: Reset all fishing rates (all groups all fleets) to their Ecosim base values.

Values: Click to see the current fishing rates as values. This will display a spreadsheet where you can change the values or paste in new values from the clipboard. It is possible to enter either monthly or annual fishing rates.

The fishing rates are entered relative to the fishing rates in the underlying Ecopath model, i.e., a value of 2 means twice the fishing rate will be applied for the current fleet or group compared to what it was in the Ecopath base model.

Time series: This button will only be enabled if a data set has been read from either a '.CSV' file, or from the database. Clicking the button (when enabled) opens a spreadsheet for the current fleet or group. The spreadsheet will show the time series that have been read for the current fleet/group. i.e. it may be blank if no data set has been read. A frame will display the following radio option buttons:

- **Relative biomass** (e.g., CPUE). For living groups only.
- **Absolute biomass.** For living groups only.

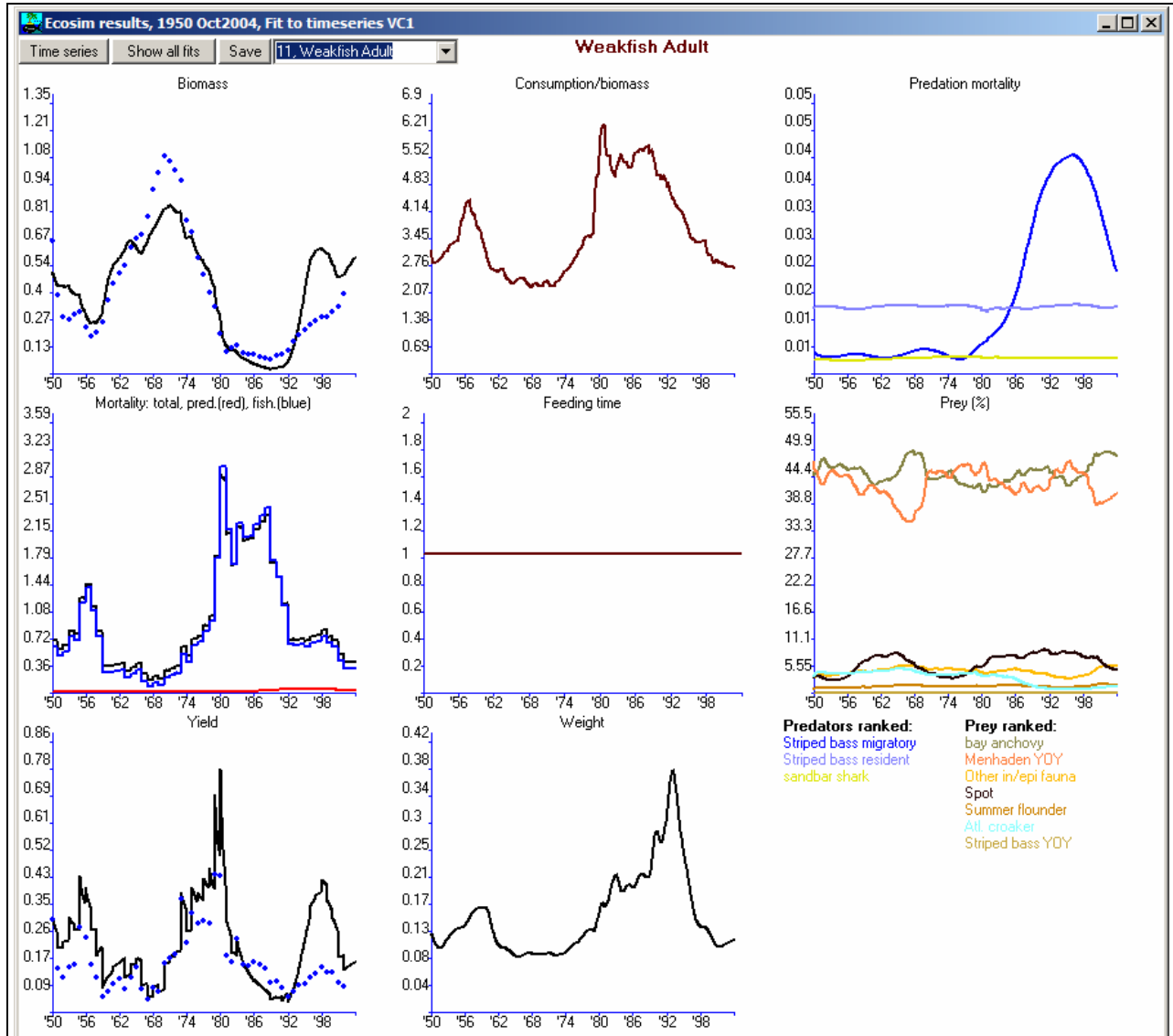


Exhibit 59. Ecosim plot for weakfish in a simulation model of the Chesapeake Bay. The dots on the biomass plots shows a biomass time series from assessments, while those on the Yield plot shows the catches ($t \cdot km^{-2} \cdot year^{-1}$). Clicking the save button will save 6 csv-files, one for each of the plots, storing the data for all groups. The 'Show all fits' will display all fits to time series on a form suitable for printing, see the next exhibit.

- **Effort by gear.** For fleets only
- **Force biomass.** For living groups only. Force the biomass for the current group to the values in the time series during Ecosim runs.

The radio buttons refer to the column where the cursor is placed. You can click a radio button with the mouse to change the data series type

- Add series: Add a new time series. Enter values or paste from clipboard (Use 'Paste' command button or press <Ctrl> + <V>).
- Rename series: Change name of the data series.
- Delete series: Remove the data series where the cursor is placed.

Hide: Opens a form for hiding/displaying groups on forms

Plot: Click this button to display a series of plots of the results of the Ecosim simulations, see Exhibit 59.

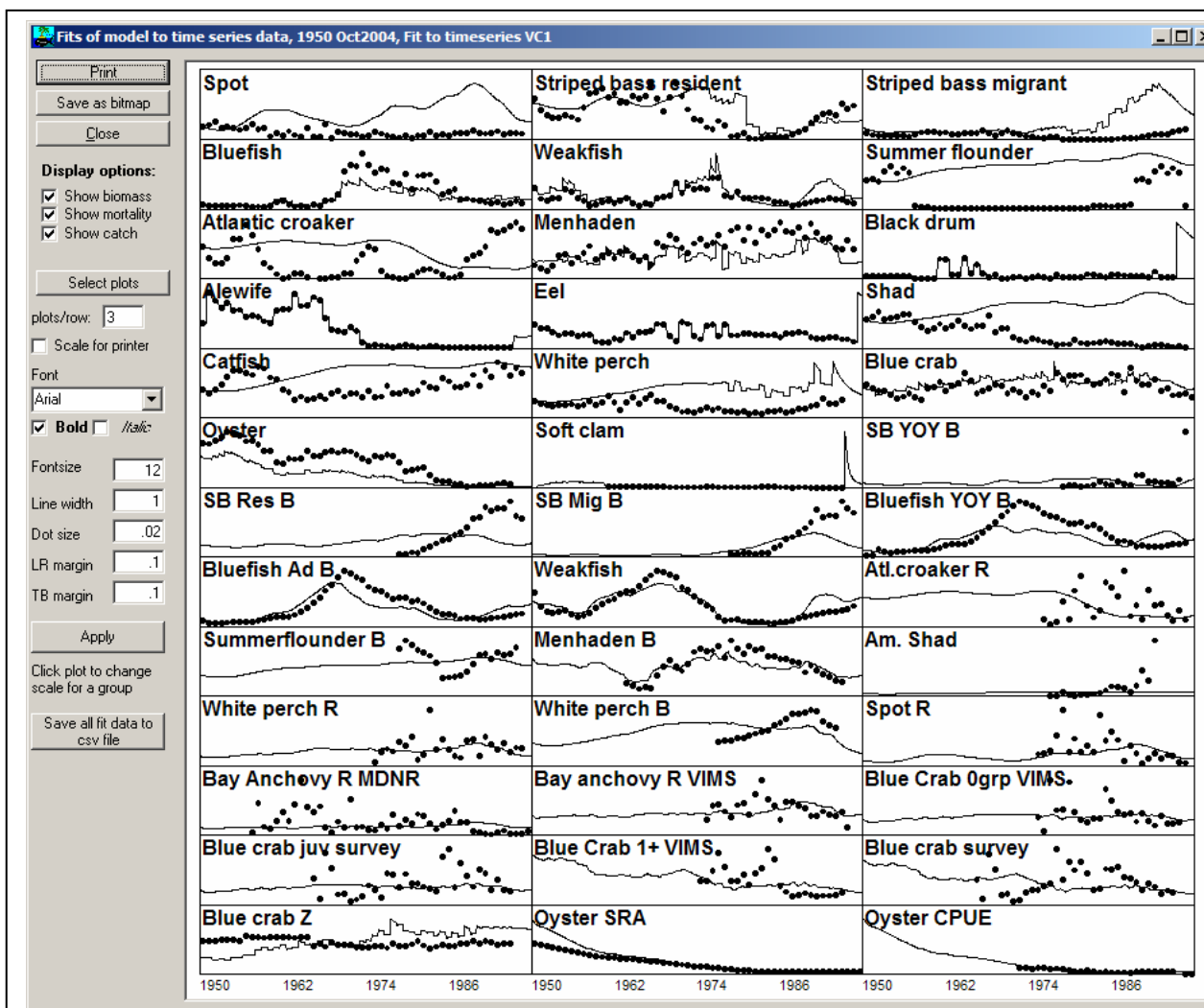


Exhibit 60. 'Show all fits' for a model of the Chesapeake Bay. For publication purposes it may be useful to produce separate graphs for biomass and catches (click checkboxes). Fonts can be manipulated, titles changed ('Select plots'), etc.

Overlay: Display subsequent runs on the same plot (plot not cleared when *Run* button is pressed).

Save: Save biomasses and catches by group and fleet for each time step to a text file (located in the windows\temp\Ecopath directory and named after the modelname.txt). The text file can subsequently be opened in, e.g., Excel and used to produce plots of the results.

Ecopath: Checking this button will make the program stop when it reaches the second red vertical line, and prompt you if you want to save a file with all input parameters for Ecopath. If you accept, an ‘eii’ text file will be saved in the same folder as your database. You can subsequently import this file as a new model in Ecopath using the import text file option from the file menu (see page 18).

Print: Print the main graph.

Linear: Check to make the biomass plot using a linear scale. The alternative is the default logarithmic scaling.

Save end state: Save parameters (in memory) from the end of a run. If so the next button will be enabled

Start from saved end state: Continue the run where the previous run stopped. Together this and the previous option enables study of scenarios that goes beyond 100 years (the maximum simulation period allowed in Ecosim).

The upper y-scale: representing biomass can be either multiplicative (8x, 3x, 1x, 1/3x, 1/8x) or linear (0, 1, 2, etc.), the former being the default. In either case, biomasses are relative, i.e., what is shown on the main panel is biomass/baseline biomass, as specified in the underlying Ecopath model.

The upper, main panel is used to display the evolution over time of the simulation, of those groups that were selected to be shown (see Show/Hide in Prepare Simulations). Biomasses here are shown relative to their baseline values (what they were in the Ecopath model).

- **Vertical red lines:** indicate when to start averaging results for comparisons before/after. Use left-mouse click to set the ‘before’ time, and right-mouse click to set the ‘after’ time. Results will be averaged for the number of time steps after the red lines chosen on the Prepare simulations/Run info form. The default is 5 time steps from the two red lines. The results are displayed using the *Results* button, see Exhibit 61.

To the right of the upper panel, a smaller panel displays the groups’ names, in the same colors as used for the biomass lines, and in the same sequence, from top to bottom. A line will separate groups that are increasing in biomass from groups that are decreasing. [Also note that leaving the mouse for a few seconds on a biomass line in the main panel causes a message (tool-tip) to appear, indicating the group name corresponding to that biomass]. Groups whose biomasses do not deviate more than 10% from their Ecopath base line values will not appear in this panel

The lower y-scale: The scale can be changed by double-clicking on it.

	Gear name	Catch (Start)	Catch (End)	Catch (E/S)	Value (Start)	Value (End)	Value (E/S)	Cost (Start)	Cost (End)	Cost (E/S)	Effort (E/S)
1	Pelagic	0.348	0.082	0.24	1.897	0.433	0.23	2.484	2.762	1.11	1.12
2	Demersal	5.612	5.087	0.91	17.461	16.942	0.97	15.513	17.063	1.10	1.11
	Total	5.960	5.169	0.87	19.358	17.374	0.90	18.00	19.83	1.10	

Exhibit 61. Results form for Ecosim and Ecospace. The ‘begin’ and ‘end’ values indicates the position of the vertical red-dotted lines and when the ‘start’ and ‘end’ values in the tables refer to. Results are available by gear and by groups.

The lower panel is used to display time series of relative fishing rates when the labels in the upper left corner of the Ecosim screen refer to an individual group. When these labels refer to a 'fleet' the y-scale of the lower panel consists of effort multipliers. In either case (individual group or fleet), the uniform series provided (in red) as default can be replaced by a time-varying shape, representing temporal changes on the pattern of fishing, as sketched with a mouse. Note that different fishing patterns can be entered (and saved, see below) when several individual groups are exploited, or different fleets have been entered in the underlying Ecopath model. The fishing rates are expressed relative to the fishing rates in the underlying Ecopath model.

To set linear trend for change in fishing rates: if you first click the start point with the left mouse button, and then the end point with the right mouse button, a line will be drawn between the two points. Use this to enter, e.g., a linear increase over time in relative fishing rates.

Option buttons: Select one of the following:

- **Biomass:** The default selection. If selected the main panel will show biomass relative to baseline biomass;
- **Yield:** Yield relative to baseline yield;
- **Q/B:** Consumption/biomass rates relative to baseline values;
- **Weight:** Average weight relative to baseline weights;
- **Feeding time:** Time spent feeding for each group relative to the time spent feeding in the underlying Ecopath base model;
- **Indices:** Not yet activated;
- **S/R plot:** Will display the emerging Stock-Recruitment plot for the linked groups with adult/juvenile dynamics. See the section 'Using Ecosim to study compensation in recruitment relationships'. If you left-click on the S/R plot a line will be drawn from the origin to the point you selected, and a message box will display the slope of the line.

Run: Generates time series of biomass, whose changes will have different amplitudes, depending on the variability of the fishing regime, and of the vulnerability setting (see 'Prepare simulation', and 'Flow control'). [Note that fishing regimes should generally change gradually from one fishing mortality level to the other, not abruptly. Also, the baseline fishing mortality should be left unchanged for a year or so, such as to allow the biomass changes to be visualized optimally.

Results: Pressing *Results* after a run opens a window, which presents a result summary for the run. See the introduction to the **vertical red lines** above.

Ecopath: Return to Ecopath, e.g., to change parameters. You can move between Ecopath and Ecosim/Ecospace without having to save.

9.10.1 Dealing with dynamic instability in Ecosim/Ecospace

We commonly see several types of dynamic instability following small perturbations in fishing mortality rates (to get away from initial Ecopath equilibrium):

1. predator-prey cycles and related multi-trophic level patterns;
2. system simplification (loss of biomass pools due to competition/predation effects);
3. stock-recruitment instabilities (cyclic or erratic changes in recruitment and stock size for split pool groups);
4. numerical 'chatter' in time solutions (mainly in Ecospace).

Such patterns are not particularly common in fisheries time series, so unless you have data to support a cyclic prediction, you should probably adjust the model parameters to get rid of it.

Predator-prey and simplification effects can usually be eliminated by reducing the predation vulnerability parameters (Ecosim Flow control tab, set values to 0.4 or less). We know of at least four common mechanisms that can decrease the vulnerability parameters so as to create stabilizing and the appearance of 'ratio-dependent' or 'bottom-up' control of consumption rates:

1. *risk-sensitive prey behaviors:*
Prey may spend only a small proportion of their time in foraging arenas where they are subject to predation risk, otherwise taking refuge in schools, deep water, littoral refuge sites, etc.;
2. *risk-sensitive predator behaviors (the 'three to tango' argument):*
Especially if the predator is a small fish, it may severely restrict its own range relative to the range occupied by the prey, so that only a small proportion of the prey move or are mixed into the habitats used by it per unit time; in other words, its predators may drive it to behave in ways that make its own prey less vulnerable to it;
3. *Size-dependent graduation effects:*
Typically a prey pool represents an aggregate of different prey sizes, and a predator can take only some limited range of sizes, limited vulnerability can represent a process of prey graduation into and out of the vulnerable size range due to growth. Size effects may of course be associated with distribution (predator-prey spatial overlap) shifts as well;
4. *Passive, differential spatial depletion effects:*
Even if neither prey or predator shows active behaviors that create foraging arena patches, any physical or behavioral processes that create spatial variation in encounters between i and j will lead to local depletion of i in high risk areas and concentrations of i in partial predation 'refuges' represented by low risk areas. 'Flow' between low and high risk areas (v_{ij}) is then created by any processes that move organisms.

These mechanisms are so ubiquitous that any reader with aquatic natural history experience might wonder why anyone would ever assume a mass-action, random encounter model (vulnerabilities = 1.0 in Flow control interface) in the first place.

Methods for dealing with stock-recruitment instability are discussed in the help section on using Ecosim to study compensation. Generally the simplest solutions are to check (and reduce if needed) cannibalism rates, set higher foraging time adjustment rates (Ecosim Group Info tab) for juvenile pools, reduce vulnerabilities of prey to juvenile fishes (Flow control tab), and reduce proportion of adult food intake used for reproduction (Ecosim Stage tab, adult/juvenile parameters option button).

Numerical instabilities (chatter, oscillations of growing amplitude) occur mainly in Ecospace; they are avoided in Ecosim by only doing time dynamic integration of change for pools that can change relatively slowly. In Ecospace, the only remedy for chatter is to reduce the prediction time step (from 0.25 year default value, sometimes very low values such as 0.05 year are required for stability). In extreme cases, it might be necessary to 'fool' Ecosim/space by implicitly moving to a shorter time step for all dynamics, which you can do by dividing every Ecopath input time rate (P/B, Q/B) with the same factor.

9.10.2 Network analysis indices in Ecosim (by Sheila Heymans)

Some network analysis indices (see the 'Network analysis' section on page 61) have been extended into Ecosim.

To obtain these indices and their changes over time from Ecosim, the "Indices" tab should be selected from the Run Ecosim sheet. If Network Analysis has not been invoked prior to Ecosim, a message stating "Trophic levels not read, do Network Analysis" will be given. It is not necessary to wait for all the cycles to be calculated (which might take 24 hours), but you can press cancel to obtain the Network Analysis indices given in Ecosim.

When the indices tab is invoked and Ecosim is run the FIB, Kempton's Q etc. indices will be shown in Ecosim, and a file named "network.csv" will be saved in the same directory as the Ecopath database. This file should be renamed if you want rerun the network analysis indices, as it will also save results to the same file.

The file (see Table below for example) will give the throughput (Trput), development capacity (Capacity) Ascendency on import (Asc import), flow (Asc flow), export (Asc exp) and respiration (Asc resp), Overhead on import (Ovh import), flow (Ovh flow), export (Ovh exp) and respiration (Ovh resp), predatory cycling index (PCI) and Finn cycling index (FCI) for each monthly time step of the simulation.

Trput	Capacity	Asc import	Asc flow	Asc exp	Asc resp	Ovh import	Ovh flow	Ovh exp	Ovh resp	PCI	FCI
5.85E+17	374912	0	48.71165	7.54E+15	29.01	0	18.024	-7.54E+15	1.4289	7.1697	5.65E-14
5.85E+17	374899	0	48.71222	7.54E+15	29.01	0	18.024	-7.54E+15	1.4286	7.1699	5.65E-14
5.85E+17	374908	0	48.71188	7.54E+15	29.01	0	18.024	-7.54E+15	1.4287	7.1698	5.65E-14

The effects of changes in the ecosystem on the network analysis indices (such as total systems throughput, Finn and predatory cycling indices, ascendancy, overhead and their breakdown into various components) can then be plotted over time and compared for various scenarios of Ecosim.

9.10.3 An Ecosim exercise

Below is a cursory check of Ecosim's behavior, which it is advised that you check out

After opening Ecosim:

- Go straight to 'Temporal Simulation (Ecosim)': Press 'Run'; make sure everything is flat or changing according to the Biomass Accumulation you specified in Ecopath. Crazy cases: discard effects may cause troubles.
- Next: Go to prepare run: set time to 30-50 years. Make a small disturbance for the combined fishery. If everything OK in settings it should come back to initial value eventually. Are all groups reacting at the speed you expect them to do?
- Next take out feeding time dynamics, set to zero
- Set the unexplained predation to 0 throughout
- Remove linkages for adult/juvenile groupings
- Go to flow control (the most important tab in Ecosim); Set to 0.99 top down
- Reset F's
- Run: seems OK
- Create small disturbance
- Run and you will get a chaotic behavior, violent oscillations, there will be groups dropping out completely. Typical Lotka-Volterra behavior
- Put in flow control setting of 0.3 throughout. [Interpretation: curves go through 0, Ecopath value and two times the base (Z_{max}/Z_{base})] Run: it will generally run OK.
- Try to increase vulnerability settings to 0.4, then 0.5, etc. See how far you can go and still get something sensible.
- Do you have a sensible model? What would happen if you had no fishery. Shut the fishing down, set time to 60-70 years to see how it will work for slow group. Reasonable result: should in general maintain all the groups we see today.
- Now check how high you can go with the flow control vulnerability setting. It's harder now because the fishing is gone, so more top predators. This will help you get more reliable vulnerability settings. You got to have reasonable vulnerability settings before you can proceed.
- Turn the feeding time factor back on. This will change feeding time, 1 can cause numerical instability. If this happens it will create violent oscillations right away, and more groups may drop out. Try, e.g., 0.2 they will

change feeding behavior with some 20% per months. If still groups dropping out. Foraging behavior just slowing things down, so not enough. It tries to maintain the Q/B by changing foraging time.

- Group info: predator effective feeding time. The target feeding time is set according to predator abundance. Setting the value to 1 means it willing to give up feeding if predation risk is high only. 0 means they are ignoring predation risk but feed independently. Top predators may be reducing feeding due to parasite risk, (often ignored predators). Try an intermediate value, e.g., 0.5.
- Initially you may not have any idea of what values to use, so play, try it out.
- What we have been doing: Try to rescue the mass interaction model by adding behavior to equation.
- Go to stage: link juveniles and adults. [This will cause deep qualitative change in Ecosim; simple biomass dynamics are discarded for these group, using delay-difference model, now using age-structure model with juveniles in numbers by month and age; the model must produce a S/R relationship; how is the relationship between S/R between – to check the results you need to know to interpret the results]
- Next, go edit parameters for juv/adult groups. Enter age at recruitment and K of the VBGF.
- Increase fishing heavily for 5-10 years, and then shut fishery down. Juvenile group should be hammered,
- Click SR plot: often erratic behavior for short to medium lived group, and Beverton-Holt curves for long lived ones. If you don't see BH curves for long lived groups something is likely to be wrong with your parameters.
- Next use the forcing functions. Here's an experiment: change primary productivity over time using a forcing function and apply to algae/algae interaction, and see how it propagates up through the food web
- Use 'Overlay' for an easy (sensitivity) check of how parameter values impacts the results.

9.11 Equilibrium analysis

This analysis takes the partial derivatives of the differential equations which define Ecosim ($dB/dt = f(\text{fishing rate, predation rate, etc.})$) with regard to fishing mortality ($\partial B/\partial F$), and sets these equal zero to identify the biomass values that would result from the continued application of the different levels of fishing mortality (F).

The analysis can be performed by varying F for different fleet (in which case the x-axis is a multiplier of its effort) or for different groups (in which case the x-axis has the dimension /year).

The results consist of a plot, centered about the Ecopath baseline value of F with, on the left, the biomasses of different groups resulting from low F (including $F = 0$ at the leftmost side of the graph), and on the right, the biomasses resulting from

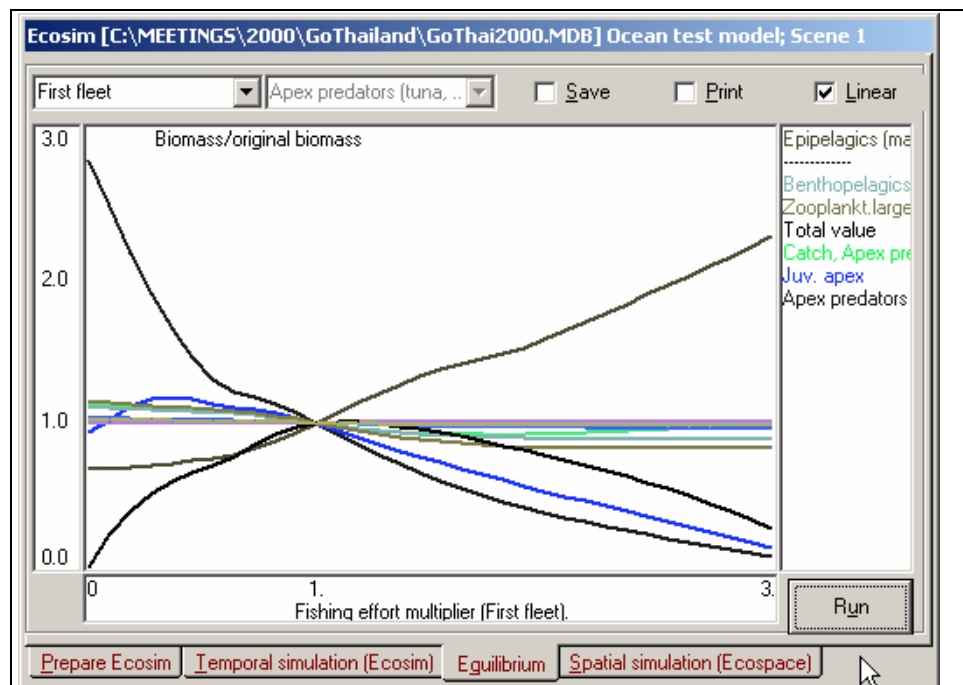


Exhibit 62. Ecosim equilibrium analysis, an ecosystem-level Yield-per-Recruit analysis.

increasing effort above its Ecopath baseline.

To accommodate a large number of groups, the y-scale can be represented as multiple of the biomasses in the underlying Ecopath files, with 8x the upper, and 1/8 the lower limit; further a linear scale for the biomass ratios can be activated by pressing the 'linear-scale' button.

Also, the total value and the total catch is shown on the plot (unless hidden using the 'Hide' button in Ecosim. This catch line often takes a roughly parabolic form, as appropriate given that it roughly corresponds to the catch levels predicted by surplus-production models.

9.12 Evaluation of equilibrium MSY reference points

Though most Ecosim harvest policy analyses are conducted by varying regulatory policies applied to fishing fleets, a command button on the Equilibrium tab in Ecosim can be used to carry out a series of long term (100+yr) simulations to estimate single species MSY and F_{msy} reference points and to evaluate ecosystem-scale performance if these reference points were simultaneously implemented. Three types of results are produced by the analysis:

- (1) An estimate of MSY and F_{msy} for each harvested group, obtained by running the Ecosim model to equilibrium for a range of F values while holding biomasses of all other groups constant (except other life history stanzas for the same species in split and multi-stanza cases). This essentially means treating the ecosystem that 'surrounds' each group as constant, then examining predicted compensatory responses by the group (and other stanzas representing the same species) caused by the foraging arena functional response and related foraging time adjustment parameters.
- (2) An estimate of the MSY that would be realized for each group if the single-species F_{msy} policy from (1) were applied simultaneously to all groups in the model. For each group, this estimate of MSY can be substantially different from the single-species MSY estimate from (1). Some groups may be more productive when the system is widely harvested (due to reduced competition and predation), while other groups may be less productive (due to harvesting of their food resources).
- (3) An estimate of the change in MSY from step (2), i.e. in MSY evaluated while considering species interactions, due to reducing the F for each group by 10% from the single-species F_{msy} value. This is a matrix of results; each row of the matrix shows how MSY for every other harvested group would be enhanced or reduced by reducing the harvest of any one group. This matrix identifies groups for which single-species (myopic) management would have the most impact on ability of the system to sustain harvests from other species.

Note that step (2) is not the same as producing an estimate of the change in MSY that would be expected if the F_{msy} from (1) were applied to just one group at a time, while holding F's for all other groups at Ecopath base values but allowing dynamic responses in all biomasses. That assessment typically produces a more optimistic estimate of MSY for each group than results from holding other groups constant as in (1), due to increases in food species abundances and decreases in predator abundances when any one group is harvested harder.

Three products are produced by the analysis. First, EwE writes a csv (comma delimited text) file for use in Excel. The file is placed in the same folder as the current database, and has a row for each harvested group and the following fields:

Group name;

Ecopath base F;

Single species F_{msy} estimate (holding other groups constant);

Single species MSY estimate (holding other groups constant);

Ecosystem-scale MSY estimate (MSY for the group if all other groups were harvested at F_{msy}).

Second, EwE produces a bar chart showing the single species MSY estimates and corresponding MSY estimates if all other groups were harvested at F_{msy} ; this chart allows quick identification of groups for which the single-species analysis would be overly optimistic or conservative if MSY harvest policies were applied to all other species at the same time. Third, EwE produces a bar-chart matrix, with each row of the chart representing 10% reduction in F

from F_{msy} for one group, and the bars across this row representing resultant change in equilibrium yield for each of the other harvested groups.

A particularly important result from the analysis is to help detect possible errors in Ecosim parameter settings. It is very common for default Ecosim “flow control” or vulnerability settings ($v = 0.3$) to result in F_{msy} estimates that are far too optimistic, especially for species/groups that are far below natural (unfished) biomass equilibrium in the Ecopath base state. The flow control column for such groups should be assigned high values (e.g. $v = 0.9$) to represent the prediction that the group could eat much more prey if allowed to recover in biomass, which also represents the prediction that there would not be much further improvement in compensatory response with further biomass decrease.

10. Spatial simulation: Ecospace

Real ecosystems are more complicated than the mass-balance fluxes of biomass in Ecopath, however large the number of functional groups we include in our models. Real ecosystems also have dynamics far more complex than represented in Ecosim. The issue to consider, when evaluating the realism of simulation software is, however, not how complex the software and the processes are therein. Rather, the question is which structure allows a representation of the basic features of an ecosystem, given a limited amount of inputs. On such criterion, it was obvious that the major deficiency of the Ecopath/Ecosim approach was its assumption of homogenous spatial behavior. This has been remedied through the development of Ecospace (Walters et al. 1999), a dynamic, spatial version of Ecopath, incorporating all key elements of Ecosim (incl. different vulnerabilities and split pools, see above).

Ecospace dynamically allocates biomass across a grid map (sketched with a mouse by the user, and typically defined by 20 x 20 cells), while accounting for:

- 1) symmetrical movements from a cell to its four adjacent cells, of rate m , modified by whether a cell is defined as ‘preferred habitat’ or not (running means over adjacent sets of five cells allows for smooth transitions between habitat types, which are also user defined);
- 2) user defined increased predation risk and reduced feeding rate in non-preferred habitat;
- 3) a level of fishing effort that is proportional, in each cell, to the overall profitability of fishing in that cell, and whose distribution can also be made sensitive to costs (e.g., of sailing to certain areas).

Given its recent origin, only few published applications of Ecospace have been published. However, those so far examined have a number of interesting implications, briefly reviewed below.

The first of these is that, as in the case of Ecosim, using Ecospace immediately after initial parameterization of an Ecopath model will often identify problems with that model. Particularly, predators assigned to a given habitat type must be able to encounter sufficient prey in that habitat. Indeed, this suggests that Ecopath models, though they do not explicitly consider space, always should contain implicitly spatial subsystems, with distinct food webs, corresponding to the habitat types to be defined in Ecospace. Moreover, definition of such subsystems leads to more robust simulations (less self-simplification) when the file is run under Ecosim. This, obviously reflects the fact that, in reality as well, spatial patterns do generate refuges from predation. It is those refuges that bring us to the last aspect of Ecospace to be discussed here.

Given its structure, Ecospace allows users to explore the potential role of Marine Protected Areas (MPAs) as a tool to mitigate, and perhaps reverse various ecosystem effects of fishing, notably the effects of ‘Fishing down marine food webs’. The results obtained so far (Walters et al. 1998, Walters 1999) suggest that, due to the effects of trophic cascades within MPA (as result of MPAs protecting predators, whose biomass will thus increase), and the net movements of predators toward food concentrations (i.e., out the MPA), the net effect of small MPAs may be to increase the catch of the fisheries that will invariably concentrate their operation near their perimeter. Only large MPAs, with short outer perimeter relative to their surface areas would be protected from this, as would MPAs in bays or gulfs, with limited adjacency to exploited areas.

Ecospace still needs much work in order to make it a useful policy exploration tool for many ecosystems. Case experience suggests that it particularly needs to include representation of oriented migration (seasonal, ontogenetic) as well as simple dispersal, a better way of specifying differences in trophic flows among habitat types than is

offered by aggregate Ecopath analysis, and that it needs linkage of habitat type designations to variable biotic factors (e.g. biomass of corals or benthic algae) as well as physical habitat features. These improvements are currently under development, but progress has been slow mainly due to ‘programming’ issues about how to make more detailed parameterizations easily accessible to Ecopath model users.

10.1 Ecospace scenarios

When working in Ecosim or Ecospace you work within a ‘scenario’. A given Ecopath model can have any number of Ecosim and Ecospace scenarios attached, they all inherit the basic parameters (such a number of groups, group names, diets and other parameters) from the parent Ecopath model. If you change a group name or delete a group in Ecopath the changes will be carried over to existing (and new) Ecosim and Ecospace scenarios. A scenario keeps track of all the information that is needed to store and later duplicate a simulation. Handling of Ecospace is carried out using the following commands from the Ecospace menu or from the icons on the second button bar:

- **Save scenario:** Save the current scenario under its current name
- **Save as:** Save the current scenario under a new (or the existing) name
- **Load scenario:** Load a new scenario. You will be prompted whether you want to save the current

The screenshot shows the 'Define habitat' dialog box in the EwE software. The table below represents the data shown in the dialog's table:

Habitat	Enter name of habitats	Fraction of total
0	All habitats (e.g., pelagic)	1.000
1	<10 m	0.140
2	11-50 m	0.310
3	51-100 m	0.068
4	101-200 m	0.019
5	201-1000 m	0.045
6	>1000 m	0.418
7	Reefs	0.000
8	Seamounts	0.000

On the right side of the dialog, there are several control panels:

- Habitat selection:** Radio buttons for 'Habitats' (selected) and 'Regions'.
- Habitat descriptions:** A text input field for 'Habitat descriptions:' and a numeric input field for 'Number of habitats:' with the value '8'. Below are buttons for 'Update # of habitats', 'Define protected areas', and 'Basemap from GIS'.
- Nutrient map:** A text input field for 'Nutrient map forcing file name (flabay):' with the value '\\flem\nutmap.nuo'.
- Movement response:** A numeric input field for 'Movement response of migratory species to fitness (0=none, 1=emig rate, 2=gradient)' with the value '0'.
- Inverse of emigration:** A numeric input field for 'Inverse of emigration response to fitness' with the value '100'.
- Spatial iteration info:** Two numeric input fields: 'SOR w:' with value '0.9' and 'move K:' with value '0.2', both followed by a '0'.

At the bottom of the dialog, there is a status bar with the text 'Press F1 for help (open a model first)' and a system tray showing 'CAPS NUM INS 11-Oct-04 23:29'.

Exhibit 63. Ecospace habitat definitions are not pre-defined but need to be entered. The habitat area shown as ‘fraction of total’ is calculated from the basemap.

	Name	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1	MPA1	+	+	+	+	+	+	+	+	+	+	+	+
2	Artificial reef area				+	+	+	+	+	+	+	+	+
3	MPA3	+	+	+	+	+	+				+	+	+

Exhibit 64. Definition of protected areas. By default protected areas are closed for fishing all year (indicated by “+” and yellow-colored cell background). Clicking a cell opens it to fishing in the given month. Additional protected areas can be entered using the control button at the top. The area can be renamed by entering a new name in the ‘Name’ column. Also define on the fishery tab if any fleets are allowed to operate in an MPA even when it is closed to fishing in general.

scenario before loading another.

- **Reset to defaults:** Use Ecospace default values for the current scenario (only available from menu).
- **Import basemap:** Import an existing basemap from another Ecopath model (only available from menu)

10.2 Define Ecospace habitats

‘Habitats’, in Ecospace, are sets of (water) cells sharing certain features affecting the movements, feeding rate, and survival of the Ecopath model components occurring therein. Any number of user defined habitats can be used in Ecospace along with the catch-all habitat no. 0, called ‘All habitats’.

Typically, the features defining habitats are distance from the coast (inshore, offshore...), or depth (shallow, intermediate, deep...) and/or bottom type (rocky, sandy, muddy...).

Habitats are thus as easy to define as it is to obtain rough bathymetric maps or maps indicating bottom types.

Ideally, the habitats defined in Ecospace should correspond to ‘sub-web’, i.e., to a set of primary producers, herbivorous and other consumers occurring only over that habitat. Such sub-webs, defined through the diet composition matrix of an Ecopath file may be linked, through higher trophic levels groups, with other sub-webs in the same system, as also occurs in nature. Herein, the higher trophic level groups, through their ability to feed in different habitats, integrate the different subsystem into a whole.

Assuming that such sub-webs are implicit in the Ecopath file underlying an Ecospace analysis, all that is needed is, thus to give names – preferably short and descriptive – to the habitat types in question. Up to eight habitat types can be distinguished, but less will usually suffice, given that data will usually not exist to allow linking the various components of an ecosystem to habitats that are not well differentiated.

Note organisms at the upper trophic levels, (i.e., nekton) due to their high mobility will tend to ‘prefer’ a wide range of habitats rather than a specific one. The habitat name ‘All’ should be used for organisms ranging across all habitat types.

Also note that definition of habitat in Ecospace usually includes the entire water column, from the surface to the bottom. Thus, while ‘rockfishes’ will tend to be limited to hard bottoms, and burrowing bivalves to soft bottoms, small coastal pelagics, which occur higher up in the water column, may ‘prefer’ hard and soft bottom habitats, as long as both are coastal.

To facilitate documentation of an Ecospace scenario, space is provided to add, besides the (short) name of each habitat, a longer definition, e.g., as taken from some published description. Longer descriptions can be entered through the ‘Remark’ field on the ‘change scenario’ tab.

10.3 Assign Ecospace habitats

Once habitats have been defined, (and sketched onto the basemap), the components of the underlying Ecopath file must be assigned to their ‘preferred’ habitat. ‘Preferred’ here means that the group in question will be adapted such that,

- its feeding rate and hence its growth rate as well are higher in that habitat than in others;
- its survival rate is higher in that habitat (because the predation rate is higher in non-preferred habitat);
- its movement rate is higher outside than within good habitat.

All three of these choices imply different mechanisms for defining what is good and bad habitat, and users can determine (through the ‘Movements’ tab) the relative strength of these mechanisms.

However, the first job is to assign groups to habitats, which is easy to do if the habitats have been defined in terms of parameters that are themselves easy to determine.

Thus, if the habits defined are ‘shallow’ and ‘deep’, assigning the groups to their preferred habitat simply consists of clicking ‘shallow’ for model components known to limit themselves to shallow waters, and conversely for ‘deep’.

Note, however, that organisms assigned e.g. to ‘deep’ waters will usually consume preys also assigned to ‘deep’ waters, and conversely for shallow water organisms. Only groups assigned to ‘All’ habitats can be expected to feed indiscriminately in all habitats.

In the special case of a ‘split pool’ of juvenile and adults, it will be appropriate, in most cases, to assign the juveniles to one or several inshore/shallow habitats, out of reach of the often ‘cannibalistic’ adults, assigned to habitats that are deeper, or further offshore.

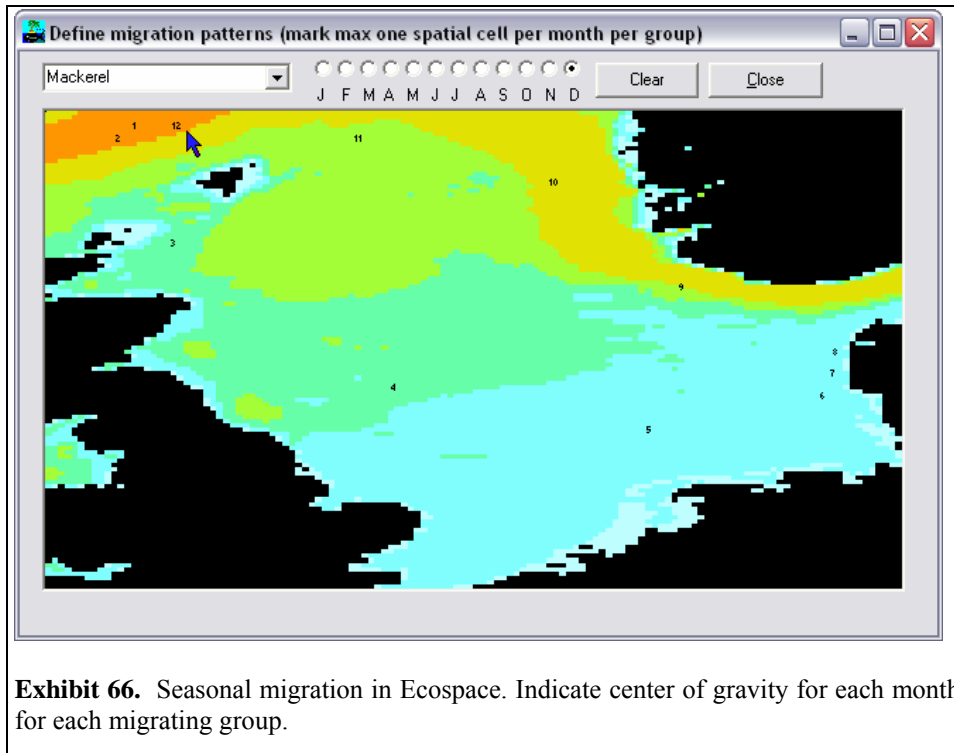
10.3.1 Representing seasonal migration in Ecospace

Larger organisms commonly have seasonal migration patterns that allow them to utilize favorable seasonal resource and environmental conditions over large spatial areas. Such movements can be represented in Ecospace in two ways. First is a simple “Lagrangian” approach that does not require explicit simulation of movement; the idea here is to simply think of the whole Ecospace map as moving in space so as to remain centered on the distribution of some dominant migratory specie(s). Second is a more complex “Eulerian” approach, which does involve explicitly modeling changes in instantaneous rates of biomass flow among the Ecospace spatial cells, in some way that approximates at least the changing center of distribution of the migratory species.

Group \Habitat #	All	shelf	coast	deep	Ecospace area	Ecopath area
1 Apex predators (tur)		+		+	0.954	1.000
2 Juv. apex		+	+		0.791	1.000
3 Mesopelagics		+		+	0.954	1.000
4 Epipelagics (macker)		+			0.745	1.000
5 Benthic fish				+	0.209	1.000
6 Benthopelagics				+	0.209	1.000
7 Zooplankt.large	+				1.000	1.000
8 Benthos		+		+	0.954	1.000
9 MicroZooplankt.	+				1.000	1.000
10 Phytoplankton	+				1.000	1.000
11 Detritus	+				1.000	1.000
12 Habitat area	1.000	0.745	0.046	0.209	-	-

Exhibit 65. Assign groups to Ecospace habitats. The ‘Ecospace area’ is calculated from the basemap, while the ‘Ecopath area’ is the habitat area fraction assigned to the individual group in the underlying Ecopath model. When Ecospace shows initial imbalance at the start of a simulation it may be because of inappropriate distribution of habitat areas, and a more careful allocation is often required to improve model behavior.

The Eulerian approach is implemented in Ecospace by allowing users to define a monthly sequence of “preferred” map cell positions (using the “Define migrations” button on the Ecospace Dispersal tab, see Exhibit 68), and to define how spread out the migrating fish are likely to be around these preferred cells by setting north-south and east-west “concentration parameters” on the Ecospace Dispersal tab. The Define migrations button causes a map of the Ecospace region to be displayed, with migratory species and months of the year listed, see Exhibit 68. Preferred position for each month (and the annual trajectory of preferred positions) is set by simply clicking on this map; each such mouse click also triggers the interface to increment the entry month by 1, making it very simple to “sketch” the annual migration trajectory.



Unfortunately, there is no way to make the Ecospace migration simulations very simple to set up. Generally the user must do considerable numerical experimentation to find reasonable migration parameter values and a stable numerical solution scheme; these cannot be computed in advance since they depend on a variety of details about the spatial map grid and species movement characteristics. Here are a few key points to keep in mind while experimenting (by repeated simulations) with the migration interface:

- (1) If the monthly preferred cell positions are far apart (>2 or 3 cells apart), the user will need to set the Ecospace simulation time step short enough (on order of $(1/12)/(\text{mean number of cells between preferred locations})$, e.g., $0.08333/3=0.028$ year when preferred cells are 3 rows-columns apart between months) to allow enough numerical integration time steps for animals to move between the preferred cells.
- (2) The concentration parameters are relative values that the user needs to set by trying alternatives (generally in the range 0.5 to 4.0) to see what values give general distribution patterns similar to those observed in the field. Low values (<1.0) lead to weak distortion of movement toward preferred cells and hence to more widely spread distributions, while high values (e.g. 3.0) give distributions strongly concentrated near the preferred cells.
- (3) Mean annual movement distances (Ecospace Dispersal Tab) have to be set large enough for migrating species to be able to “track” movements in preferred locations. As a general rule, set the base dispersal rate for migratory species to at least $100L$ km/yr., where L is mean body length in cm.
- (4) Setting high concentration parameter values (>2.0) and/or moving animals through a very complex map with many coastal blocking features can result in numerical instability in the Ecospace solution algorithm. The best way to correct this is to reduce the simulation time step; it may also be necessary to reduce the SOR w relaxation weight (Ecospace Define habitat tab) used in solving the linear equations involved in the numerical scheme for integrating the spatial rate equations (an alternating implicit method).
- (5) Setting high concentration parameter values can also result in “overfishing”: Ecospace allocates total fishing effort over the map proportional to the total number of cells initially used by each fishing fleet, so when the

model generates a concentrated distribution of some favored species, the total effort will concentrate accordingly and can sometimes generate very high fishing rates near the center of the migrating stock distribution. Remedies include reducing total effort (Ecospace Fishing tab, total effort multiplier) and distributing effort more widely (Fishing tab, reduce value of “effective power”).

(6) Concentrating a migratory predator can cause local depletion of food organisms and/or reduced predator feeding rates due to prey vulnerability limits. If these effects cause simulated total predator biomass to incorrectly decline over time (and if the user determines that the declines are not due to an artifactual overfishing effect), then it may be necessary to either increase total prey abundances (in Ecopath) or vulnerability of prey to the predator (Ecosim Flow control tab).

(7) Split group and multi-stanza population dynamics may behave strangely or incorrectly when one or more life history stages are migratory while other(s) are not. Ecospace does not keep track of the full population age/size distribution for each spatial cell (prohibitive memory and computing time requirement), and instead uses a running equilibrium approximation to the population composition. This approximation tends to “dampen” abundance fluctuations in the early life history stanzas that might be created by, for example, seasonal movement of the adults to spawning locations near preferred juvenile habitats.

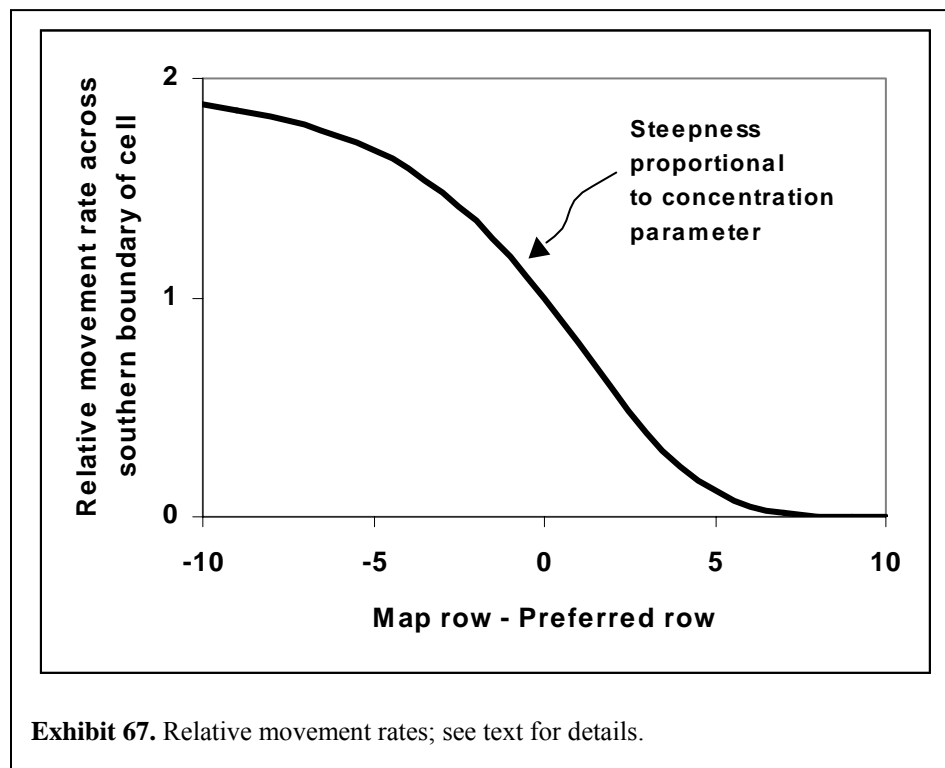


Exhibit 67. Relative movement rates; see text for details.

The mathematical method used in Ecospace to create migratory behavior is quite simple. Spatial movement is represented in general in Ecospace as a set of instantaneous exchange rates across the boundaries of adjacent spatial cells. For migratory species, these exchange rates are simply multiplied by relative factors at each simulation time step, where the factors depend on distance from the preferred cell for that time step as shown in the following diagram:

(The function is reversed for movement across northern cell boundary,

and similar function is used for east-west movements with map column-preferred column as the independent variable). The factor has no effect (multiplies movement rates by 1.0, so movement rates are similar in all directions) for cells near the preferred cell, and ‘shuts down’ movement away from the preferred cell for cells far from that preferred cell. Note that the base movement rates that are multiplied by the migration factors may not be the same in all directions to start with; these base rates can include advection effects and/or increased/oriented movement rates toward preferred habitat types. That is, migration effects can be combined with advection and orientation of movement toward preferred habitats; it was the desire to represent such combined effects that motivated the multiplicative factor formulation in the first place.

10.3.2 Fitness-driven dispersal behavior in Ecospace (by Bob Lessard)

The default assumption in Ecospace is that dispersal and migration rates for each biomass pool are stable over space and time, except for ‘hardwired’ seasonal migration patterns. This default setting ignores the possibility that movement rates (and possibly directions) are dependent on local ‘fitness’ conditions, as measured by food intake

rates and predation risk. For at least some species, at least dispersal (emigration) rates may well depend on local resource conditions and/or predation, with creatures having higher probabilities of leaving areas where fitness is lower. Such behaviors could have major implications for design of marine protected areas, since food resource densities (for predators) are likely to be lower in protected areas, and predation risks (for smaller species) are likely to be higher in protected areas. Thus for a variety of creatures, emigration rates from protected areas might be considerably higher than base rates measured under relatively low (pre-protection) conditions.

Ecospace allows you to explore two alternative hypotheses about fitness-driven dispersal rates:

- (1) total emigration rates are inversely proportional to fitness in each spatial cell, without these rates being spatially oriented or biased toward more favorable cells ('Type 1' fitness response)
- (2) emigration rates are proportional to the difference in fitness between each source cell and each cell around it, i.e. dispersal rates are higher across cell faces representing directions of higher fitness and are lower in directions toward cells or areas of lower fitness ('Type 2' fitness response).

The first of these hypotheses represents the idea that organisms may only be able to detect local "comfort" conditions, while the second represents the possibility that organisms can detect local spatial gradients in fitness. For both hypotheses, fitness for each cell i,j for each time step is represented by the per-capita growth minus mortality rate index $f = gq_{ij} - Z_{ij}$, where g is growth efficiency, q_{ij} is *per capita* food intake rate (Q/B) in cell ij , and Z_{ij} is total mortality rate in the cell. Note that q_{ij} can be a complex function of food resources in the cell, and Z_{ij} represents combined impact of all predators in the cell. Further, these fitness components may vary dramatically over both space and time.

To simulate fitness-driven dispersal in Ecospace, you must make three parameter settings:

- (1) For each species/group that is to show the behavior, click on the 'Migrating?' column for that species in the Ecospace Dispersal tab (species treated as migratory even if it does not have a particular seasonal migration pattern);
- (2) On the Ecospace Define Habitat tab, set the text box for movement type of migratory species to 1 or 2, representing the two alternative movement hypotheses defined above (the movement type hypothesis is applied to all migratory species in any one Ecospace run);
- (3) On the Ecospace Define Habitat tab, set the 'inverse of emigration response to fitness' text box to a scaling parameter for the severity of the movement response for low-fitness cells. High values of this parameter (e.g. 100) make the response very weak, while low values (e.g. 0.1) make the response very strong.

The main thing that can go wrong with these settings is to use too low a value of the emigration response scaling parameter. Low values like 0.1 commonly result in spatial instability in the predicted biomass patterns (organisms overreacting to local conditions so as to successively over- and under- use adjacent cells), and can result in numerical instability in the predictions of overall biomass change (typically indicated by growing total biomass over time).

Note that seasonal migration and fitness response hypotheses can be combined to give more realistic simulations of migratory species. That is, the migration interface button (Ecospace dispersal tab) can be used to set up a 'typical' or normal seasonal migration pattern, and this pattern will then be modified from year to year in response to changes in spatial distributions of prey resources and/or predation risk.

10.3.3 Ecospace movement rates

Dispersal rates

The organisms (i) in an Ecopath model have an aggregated biomass (B_i), and are not assumed to *move* within the area covered by that Ecopath model. In Ecospace, a fraction (B') of the biomass of each cell is always on the move, wherein

$$B' = m \cdot B_i$$

with m having the dimension of length / time (i.e., km / year) i.e., a velocity or 'speed'.

However, m is not a rate of *directed* migration, as occur seasonally in numerous fish populations. Rather, m should be regarded as dispersal and seen as the rate (km/year) the organisms of given ecosystem would disperse as a result of random movements.

Thus, Ecospace simulation are initiated by distributing all organisms evenly onto the basemap, at the density ($t \cdot km^{-2}$) defined by the underlying Ecopath model. Then all biomass pool start moving, as a function of their value of m , out of their cell and into adjacent cells, there consuming food, and being themselves consumed.

	Group	Base dispersal rate (km/year)	Rel. dispersal in bad habitat	Rel. vul.to pred. in bad habitat (prod for pp)	Rel. feed.rate in bad habitat	Advected?	Migrating?	North/south concentration	East/west concentration
1	Cod	300.0	5.0	2.0	0.50			0	0
2	Haddock	300.0	5.0	2.0	0.50			0	0
3	Herring	300.0	5.0	2.0	0.50			0	0
4	Mackerel	300.0	5.0	2.0	0.50		+	0	0
5	Norway pout	300.0	5.0	2.0	0.50			0	0
6	Plaice	300.0	5.0	2.0	0.50			0	0

Exhibit 68. Ecospace dispersal rates and habitat specific information. Migration patterns are also defined on this tab.

Given differential food consumption and survival rates in preferred vs. non-preferred habitat, this will soon generate richly patterned distributions, wherein each cell includes different biomass of each of the groups in the system.

As for the absolute value of m to be used in the simulation we use a default value of $300 \text{ km} \cdot \text{year}^{-1}$ for all groups apart from detritus groups to which discards are added, (and for which we use a default of $10 \text{ km} \cdot \text{year}^{-1}$)

Note that the final results of Ecopath simulations tend to be largely independent of the specific values of m used, and hence long debates on the best choice of these values may not be necessary – at least not until field estimate, based, e.g., on tagging studies have become available.

Note, finally that the biomass of a group within a given cell is usually not multiplied by the same value of m for each of the flows out of the cell (4 in the case of a cell not touching on land).

Rather, a distinct value of m' is used for each cell, resulting from the multiplication of a group's value of m with that cell's index of suitability S . This index is itself computed, for each cell as the mean of its 'preference values'. These preference values are automatically set at unity in non-preferred habitat, and a user-defined, higher value ($PV > 1$) can be entered for preferred habitat(s). Thus, if $S > 1$, the movement rate into preferred habitat (and out of non-preferred habitat) will be higher than into non-preferred habitat (and out of preferred habitat). Setting PV for preferred habitat equal to unity (1) makes this mechanism of habitat differentiation inoperative.

Relative dispersal in bad habitats

The dispersal rates are assumed to differ between preferred and non-preferred habitats, with higher values of m within non-preferred habitats than in preferred habitats. Such assumption is realistic as it implies that organisms in non-preferred habitats will strive to leave these, and attempt to return as rapidly as possible to their preferred habitats.

The default value for the multiplier of m is 2.0 and the upper limit 10.0.

Vulnerability to predation in bad habitats

The increased vulnerability to predation (or grazing) of various organisms outside their ‘preferred’ habitat can be changed using a multipliers. The default value of the multiplier is 2.0 for all groups, and it can be increased by up to a factor of 100, while entering a value of 1 will make this mechanism inoperative.

Conceptualizing this mechanism is straightforward: imagine as an extreme case how easy it would be for a pelagic carnivore to grab a typical coral reef fish, e.g. a butterfly fish, blown by a freak wave off its reef, into an open water area. A less extreme case would be a member of a very abundant population, pushed out of its preferred habitat by its competitors of the same species.

To avoid occurrence of groups outside of their preferred habitats you should set the vulnerability to a high value.

Relative feeding rates in bad habitats

Organisms outside their preferred habitat may be conceived as less likely to consume as much appropriate food as their congeners within preferred habitat, due to the unavailability of such food, or the danger associated with foraging.

To simulate this, Ecospace users can reduce the feeding rate of ecosystem components down to 0.01 times the Ecopath baseline (i.e., the Q/B value). The default is 0.5, and this mechanism can be made inoperative by setting the feeding rate multiplier equal to unity (1).

Advected?

Indicate here whether a group is advected or not, this may, e.g., be the case for plankton. See Section 10.7, Advection in Ecospace on page 138.

Migrating?

Indicate here whether a group is migrating or not. For migrating groups/life stages enter concentration parameters and define migration patterns (using the so named button). See Section 10.3.1, Representing seasonal migration in Ecospace on page 129.

10.3.4 Fishery in Ecospace

	Fleet \ Habitat use:	All	Shallow	Shelf	Deep	MPA	Effective power	Tot.Eff.multip.
1	Pelagic			+	+		1	1
2	Demersal	+					1	1

Prepare Ecosim | Effective fishing power: higher value means higher effort where the CPUE is higher, zero gives even c

Exhibit 69. Ecospace fishery settings. Use this to define where each fleet can operate. MPA is ‘marine protected area’, i.e., an area where some form for protection is in place; fleets may be allowed to operate in MPA’s. Additional protected areas can be defined using a form available from the Define habitat tab, see Exhibit 64 on page 128.

The ‘fishing’ tab is used to assign fleets, i.e., to define in which habitat(s) a fishing fleet may operate, and to identify whether a given fleet may operate within a restricted area.

For each fleet indicate where it may operate by clicking:

- All: if it can operate in all habitats (default setting), or;
- For each habitat click if may operate in the given habitat;

- MPA: click if the fleet is allowed to operate in the given protected areas.

Effective power: sets relative catchabilities by gear type, treating effort for each gear as starting at base value of 1.0 so that F for the gear ($F = qE = \text{Catch}/\text{biomass}$) is $1.0 \cdot q$ where q is relative catchability. This is to avoid measuring effort in some unnecessary unit. Effective power should be entered as a non-negative parameter, and has a default value of 1.

Total efficiency multiplier: a scaling factor for effort by fleet, it should be non-negative, and has a default value of 1.

10.3.5 Ecospace basemap

The basemap is used to mediate between an Ecopath file -- which assumes an homogenous distribution of the biomasses in an undefined space -- and a real ecosystem with geographic features (land vs. water, bathymetry, etc.) impacting on the distribution of the biomasses in that file.

- **The Ecospace basemap is defined**, at first, by entering the number of cells in rows and columns, and the cell length (in km). The cells are square units, but the maps not need be so; both square and rectangular maps can be accommodated, but rectangular maps should not be defined too 'thin', (i.e., their aspect ratio ($AR = \text{height}/\text{width}$) is recommended to remain in the range $5 \leq AR \leq 0.2$).

The number of homogenous cells in the basemap may range from 9 (for a square 3x3 map, used e.g. for verification or demonstration purposes) to 10 000, (e.g., for a square 100 x 100 map).

We recommend, unless otherwise required the intermediate 20 x 20 map provided as default, which represents a compromise between showing details and maintaining a high computing speed. When a desired number of cells is entered, the number of cells used in the basemap is computed as the number of square cells that is closest to the number entered, while remaining compatible with the aspect ratio of the map.

One defined in terms of its dimension, the basemap is used to sketch and show, by cell:

- **land vs. water areas:** The distinction between land and water areas is crucial to the definition of the basemap: this distinction determines the map's overall appearance (i.e., its resemblance to a geographic map) and, in case of detailed maps, the routes through which organisms move between adjacent cells.

Thus, a system including a number of narrow, crooked channels must be simplified, as movements on Ecospace map can only resemble those of rooks on chessboards, but not those of bishops.

Though not contributing to the results, the basemap cells defined as 'land' consume memory and computing time; thus, their number should be kept as small as possible, e.g. by orienting the basemap sideways where appropriate.

The basemap may include open borders, i.e., water areas not bounded by land. In such cases, the flow of organisms out of a border cell is compensated for by an equal flow of organisms into the cell, i.e., the system will not 'leak'.

- **Different habitat types:** These are defined on the 'Define habitats' tab.
- **Restricted or protected areas;** Restricted areas are here defined as set of (water) cells in which at least one fleet is restricted from fishing, and at least one other fleet may operate.

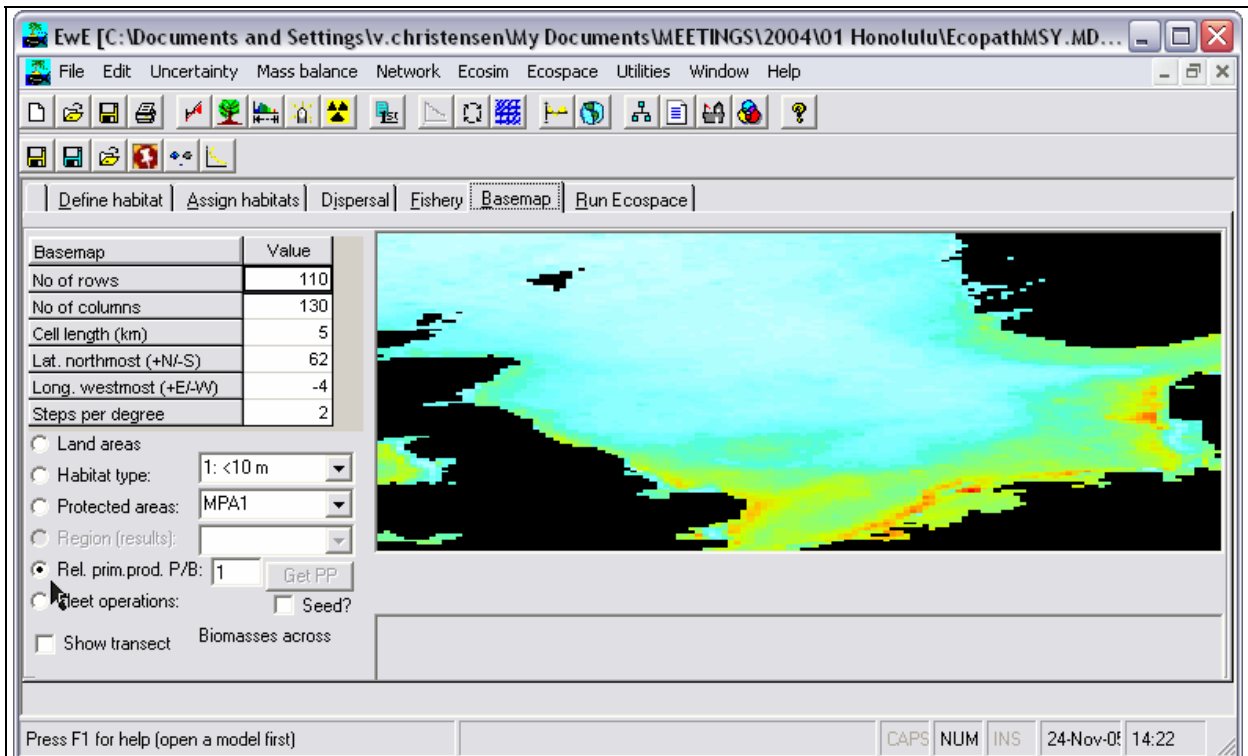


Exhibit 70. Ecospace basemap. Land areas, habitat types, MPA areas, relative primary production, and cost of fishing can be defined on the spatial grid. The ‘Set Advection field’ links to an advection model. This basemap is read via the Web from a linked server at UBC (available through ‘Define habitat’ map), and illustrates spatial primary productivity based on SeaWiFS data.

Protected areas are defined as set of cells in which no fleet is permitted to operate. (Thus, ‘cheating’, wherein one or several fleets illegally operate inside a protected area, can be accommodated by Ecospace).

Restricted or protected areas (R/PAs) may consist of one or several cells, adjacent or not, and may touch upon a coastline, or not.

Note that for a number of theoretical and practical reasons, marine protected areas (MPAs) and other forms of R/PAs are more effective when they have as few cells as possible that are adjacent to exploited cells. This can be achieved by making the R/PA as compact as possible (i.e., ‘round’ or square rather than elongated), and locating it adjacent to a coastline.

- **Distribution of primary producers P/B :** Primary production may vary in different areas of an ecosystem, e.g., due to terrigenous inflow of nutrients, or processes that lead to mixing or upwelling of water masses.

Mapping such areas is done by sketching a multiplier of the baseline P/B for primary producers. This multiplier, which may range from 0.01 to 100, can thus be used to depict anything from areas with very low primary production rates to areas with very high rates compared to the underlying Ecopath model. The values entered are relative and the total primary production is scaled so that it will be the same as in the base Ecopath model.

Warning: Ecospace is sensitive to this setting. Even if the range is 0.01 to 100 such extremes should be used with great care only.

- **and by fleet:** Pressing ‘fleet operations’ and choosing one of the fleets (defined in the underlying Ecopath file) opens a small text box, which allows:

1. **Identification of a port/landing place:** Ecospace allows only one port/landing place per fleet. Hence, if one's fleet use several ports/landing places, the underlying Ecopath file must be modified accordingly (by replacing the existing fleet by several fleets, of which each has its own port/landing place). Also note that, to avoid ambiguities, a port/landing place is defined by a (yellow) water cell, not by a land cell. Note: this feature not yet activated.
 2. **Mapping the cost of sailing:** Costs of sailing are multipliers of variable costs, sketched onto the map. These costs should reflect distance from the port/landing place, as modified by other factors (e.g., winds or currents).
- **Show transect:** Show a biomass transect, whose two ends (red buttons) can be moved. This is used to further facilitate interpretation of an Ecospace run. The small display below the distribution map shows the (log) biomass of the different groups along a transect defined by the position of the two red/orange buttons on the basemap.

As might be seen (once a simulation has been performed), the biomass drop when the transect line crosses cells defined as land. The transect line allows identification of trophic cascades (abundant predators, scarce prey, and vice versa) in an ecosystem context, notably when drawn across Restricted/Protected Areas, where top predator biomasses tend to be high.

Completing the basemap is achieved by clicking any of the buttons defined by the above bullets, then using the mouse to sketch the corresponding map information.

Details on 'Habitat' and the Fishery can be obtained by clicking the corresponding tabs.

10.4 Prediction of mixing rates

The instantaneous emigration rates from a given cell in Ecospace are assumed to vary based on the pool type, the groups preference for the habitat type represented by the cell, and a 'risk ratio' representing how the organisms in the cell respond to predation risk. Base dispersal rates are calculated based on this, but weighted based on a habitat gradient function increasing the probability of organisms moving towards favorable habitats. The mechanisms involved in this procedure are explained in more detail by Walters et al. (1999).

10.5 Predicting spatial fishing patterns

EwE works with multiple fishing fleets, with fishing mortality rates (F) initially distributed between fleets based on the distribution in the underlying Ecopath base model. In Ecospace the F 's are distributed using a simple 'gravity model' where the proportion of the total effort allocated to each cell is assumed proportional to the sum over groups of the product of the biomass, the catchability, and the profitability of fishing the target groups (Caddy, 1975; Hilborn and Walters, 1987). This profitability of fishing includes factors such as the cell-specific cost of fishing.

Assuming that there are N cells representing water areas, each fleet k can cause a total fishing mortality rate $N \cdot F_k$. For each step in the simulation this rate is distributed among cells, c , in proportion to the weights G_{kc} based on:

$$G_{kc} = O_{kc} \cdot U_{kc} \cdot \frac{\sum_i p_{ki} \cdot q_{ki} \cdot B_{ic}}{C_{kc}}$$

Eq. 65

where O_{kc} is 1 if cell c is open to fishing by fleet k , and 0 if not; U_{kc} is 1 if the user has allowed fleet k to work in the habitat type to which cell c belongs, and 0 if not; p_{ki} is the relative price fleet k receives for group i fish, q_{ki} is the catchability of group i by fleet k (equal to the F_{ki} in the Ecopath model); B_{ic} is the biomass of group i in cell c ; and C_{kc} is the cost for fleet k to operate in cell c . Based on the weights in Eq. 65 the total mortality rate is distributed over cells according to

$$F_{kc} = \frac{N \cdot F_k \cdot G_{kc}}{\sum_c G_{kc}}$$

Eq. 66

while each group in the cell is subject to the total fishing mortality

$$F_{ic} = \sum_k F_{kc} \cdot q_{ki}$$

Eq. 67

10.6 Numerical solutions

Ecospace is based on the same set of differential equations as used in Ecosim, and in essence performs a complete set of Ecosim calculations for each cell for each time step. This represents a formidable amount of computations, but fortunately it has been possible to take a number of shortcuts to speed the processing up to an acceptable rate. Briefly explained the background for this takes its starting point in Eq. 47 (on page 76), which expresses the rate of change for each biomass pool over time. If the rate constants were constant over time (they are not, but if!) the biomass would change as a linear dynamical system, and would move exponentially towards an equilibrium given by (omitting indices for cell and biomass pools)

$$B_e = \frac{1 + gC}{Z + E}$$

Eq. 68

while following the time trajectory

$$B_{t+\Delta t} = B_e + (B_t - B_e) \cdot e^{-(Z+E)\Delta t}$$

Eq. 69

Denoting the exponential weight term above W_t this can be re-expressed as,

$$B_{t+\Delta t} = W_t \cdot B_t + (1 - W_t) \cdot B_e$$

Eq. 70

Hence, if input and output rates were constant, the time solutions would behave as weighted averages of past values and equilibrium values with weights depending on the mortality and migration rates. Using expressions of the type in Eq. 70 the Ecospace computations can be greatly increased by using a variable time splitting where moving equilibria are calculated for groups with high turnover rates, (e.g., phytoplankton), while the integrations for groups with slower turnover rates, (e.g., fish and marine mammals) are based on a Runge-Kutta method. Comparisons indicate that this does not change the resulting time patterns for solutions in any noticeable way – hence, the ‘wrong’ assumption of time rate constancy introduced above is useful for speeding up the computations without noticeable detracting of the final results. The resulting computations are carried out orders of magnitude faster than it the time splitting was not included.

10.7 Advection in Ecospace

Advection processes are critical for productivity in most ocean areas. Currents deliver planktonic production to reef areas at much higher rates than would be predicted from simple turbulent mixing processes. Upwelling associated with movement of water away from coastlines delivers nutrients to surface waters, but the movement of nutrient rich water away from upwelling locations means that production and biomass may be highest well away from the actual upwelling locations. Convergence (down-welling) zones represent places where planktonic production from surrounding areas is concentrated, creating special opportunities for production of higher trophic levels.

Ecospace provides a user interface for sketching general current patterns or wind/geostrophic forcing patterns for surface currents. Based on these patterns Ecospace calculates equilibrium horizontal flow and upwelling/downwelling velocity fields that maintain continuity (water mass balance) and effects of Coriolis force. That is, the advection field is calculated by solving the linearized pressure field and velocity equations $df/dt = 0$, $dv_u/dt = 0$, $dv_v/dt = 0$ across the faces of each Ecospace grid (u, v) cell, where f is sea surface anomaly, the v 's are horizontal and velocity components (u, v directions) and the rate equations at each cell face satisfy (omitting grid size scaling factors for clarity):

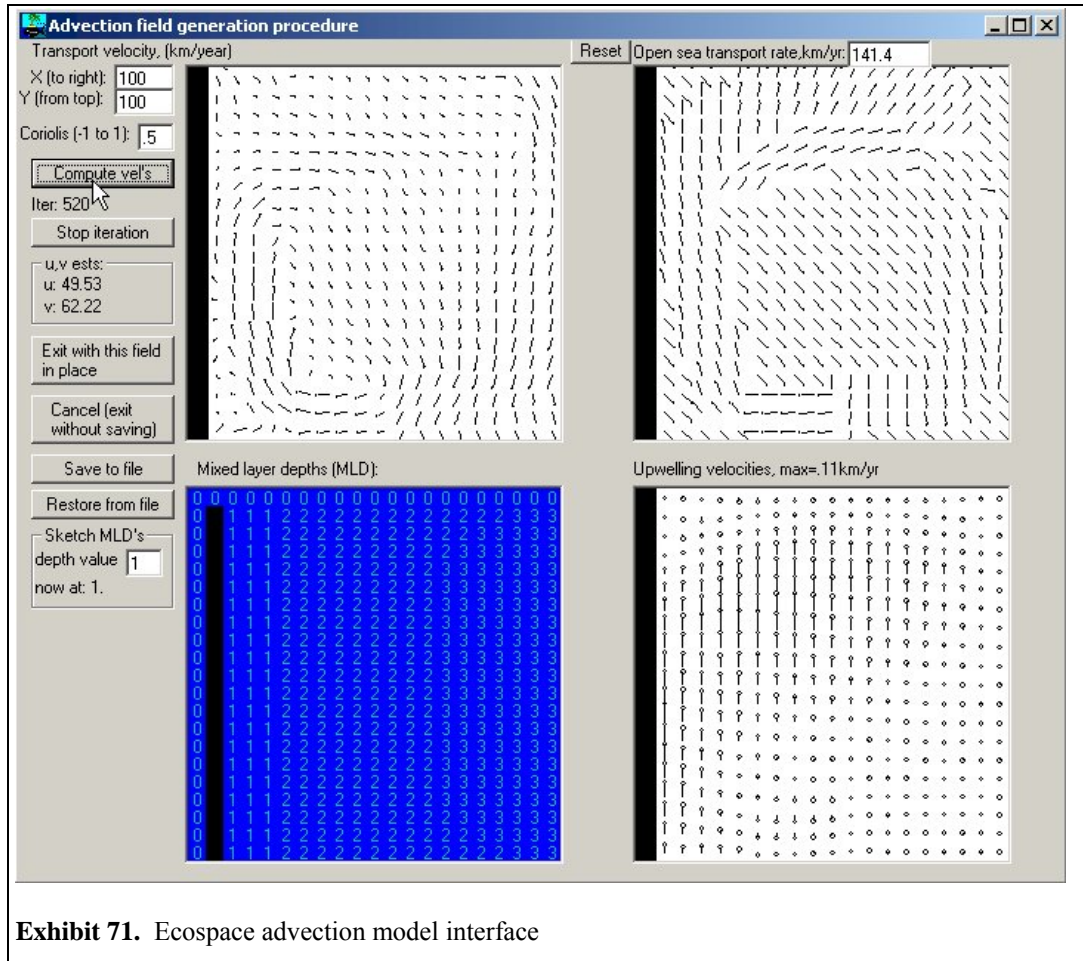


Exhibit 71. Ecospace advection model interface

$$\frac{dh}{dt} = \frac{v_{uh}}{u} + \frac{v_{vh}}{v} - D_h$$

Eq. 71

$$\frac{dv_u}{dt} = k \cdot W_u - k \cdot v_u - f \cdot v_v - \frac{g \cdot h}{u}$$

Eq. 72

$$\frac{dv_v}{dt} = k \cdot W_v - k \cdot v_v - f \cdot v_u - \frac{g \cdot h}{v}$$

Eq. 73

Here, the W 's represent the user sketched forcing or general circulation field, h sea surface anomaly, k represents bottom friction force, f the Coriolis force, D represents downwelling/upwelling rate, and g acceleration due to sea surface slope.

Solving these equations for equilibrium is not meant to be a replacement for more elaborate advection models; generally the W_u and W_v need to be provided either by such models or by direct analysis of surface current data, so the Ecospace solution scheme is only used to assure mass balance and correct for 'local' features caused by bottom topography and Coriolis forces. That is, absent shoreline, bottom, and sea surface anomaly (h) effects, the equilibrium velocities are just $v_u = W_u$, $v_v = W_v$ up to corrections for Coriolis force. We could just allow users to input the W fields and then calculate upwelling/downwelling rates needed to satisfy these, but solving the equations using general forcing sketches of W patterns allows us to internally correct for factors such as topographic steering of currents near shorelines, without demanding that the user enter W fields that precisely maintain mass balance (and/or correct upwelling/downwelling velocities) absent any correction scheme.

Once an advection pattern has been defined, the user can specify which biomass pools are subject to the advection velocities (v_u, v_v field) in addition to movement caused by swimming and/or turbulent mixing. This allows examination of whether some apparent 'migration' and concentration patterns of actively swimming organisms, (e.g., tuna aggregations at convergence zones) might in fact be due mainly to random swimming combined with advective drift.

Advection fields can be read from text files. The procedure for this is as follows:

Create a .txt file, (e.g., in Notepad) with the following structure:

Number of columns in Ecospace basemap ($nRow$) ; Number of columns in Ecospace basemap ($nCol$)

Number of Months

(For each of the months specify the following:

Month Number

(For this month specify for 0 to $nRow + 1$, and for 0 to $nCol+1$, unit: m/s)

Current X -velocity, Current Y -velocity

(Repeat this for all months)

Currents for the Central Pacific may be obtained in a suitable format from <http://www.oscar.noaa.gov/datadisplay/index.html>)

11. Capabilities and limitations

EwE has been developed largely through case studies, where users have challenged us to add various capabilities and as we have seen inadequacies through comparison to data; see as a good example the discussions in the proceedings from an FAO workshop on the application of EwE (Pauly 1998). Various capabilities have been added to EwE in response to these challenges, and there have inevitably been some uncertainty about what the approach and software presently can and cannot do, and about how it should be used in the design of sustainable fisheries policies. Such uncertainty may be expressed through too simplistic interpretations of what mass balance and biomass dynamics models are capable of representing, through to unwarranted optimism about how it should be used to replace or complement existing assessment tools. Here we review the capabilities and limitations through a series of 'frequently asked questions', followed by explanations of what we think EwE is actually capable of doing.

Note that many of the questions discussed below have their root in an assumption that EwE is somehow intended to supplant or replace single-species assessment methods. Our primary goal when developing EwE has been to develop a capability for asking policy questions that simply cannot be addressed with single-species assessment. Examples are questions about impacts of fishing on nontarget species, and the efficacy of policy interventions aimed at limiting unintended side effects of fishing. Also, as is shown through examples below, EwE can now incorporate time series data from single-species assessment as input and use these for parameter fitting. We indeed advocate an

iterative process where information is passed between single-species analysis and EwE to check and improve estimates in the process, addressing questions about the degree to which ecosystem events can and cannot be attributed to impact of fisheries, climate change, etc.

11.1 Does Ecopath assume steady state or equilibrium conditions?

Ecopath provides an ‘instantaneous’ estimate of biomasses, trophic flows, and instantaneous mortality rates, for some reference year or multi-year averaging window. Biomasses need not be at equilibrium for the reference year, provided the Ecopath user can provide an estimate of the rate of biomass ‘accumulation’ (or depletion) for each biomass for that reference year. In fact, in a number of cases, e.g., Christensen (1995b) it was necessary to recognize that biomasses were in fact changing over the period for which Ecopath reference data (B , P/B , Q/B , diet composition) were provided. In these cases, assuming equilibrium for the reference year led to overly optimistic estimates of sustainable fishing mortality rates.

11.2 Should Ecopath be used even if there is insufficient local information to construct models, or should more sampling go first?

It is a fairly common conception that since we do not know enough to make perfect models at the individual or species level there is no way we can have enough information at hand to embark on modeling at the ecosystem level. This may hold if we try to construct models bottom-up – we cannot account for all the actions and processes involving all the individuals of the world. This is, however, not what Ecopath models do. Instead they place piecemeal information in a framework that enables evaluation of the compatibility of the information at hand, gaining insights in the process. Adding to this is that there is much more information of living marine resources available than most will anticipate. The best demonstration of this can be obtained by searching the FishBase database on finfish (Froese and Pauly, 2000, www.fishbase.org) for Ecopath-relevant information using the semi-automated search routine available for this specific purpose at the website.

Another aspect is that ecosystem models can help direct research by pinpointing critical information and gaps in the present knowledge. As more information becomes available it is straightforwardly included in the model, improving estimates and reducing uncertainty.

11.3 Does EwE ignore inherent uncertainty in assembling complex and usually fragmentary trophic data?

Ecopath has a number of routines that encourage users to explore the effects of uncertainty in input information on the mass balance estimates. In particular, the ‘Ecoranger’ routine allows users to calculate probability distributions for the estimates when they specify probability distributions for the input data components. Similarly, Ecosim has a graphical interface that encourages policy ‘gaming’ and sensitivity testing.

Lack of historical data and difficulty in measuring some ecosystem components and processes will likely always plague efforts to understand trophic structure and interactions. This is not a problem with Ecopath, but rather with aquatic ecology in general. We need to respond to it not by complaining about the incompleteness of our data, but rather by using models like EwE to direct research attention toward components that are most uncertain and also make the most difference to policy predictions. We also need to use the models to search for robust policy options and management approaches that will allow us to cope with the uncertainty, rather than pretending that someday it will just go away.

When EwE is used for policy comparison, it is important to recognize that incorrect comparisons (EwE leading user to favor a wrong policy) are not due to uncertainty in general about the model parameters, but rather to errors in specific input data to which the particular policy comparison is sensitive. In other words, EwE can give correct answers for some policy comparisons but wildly incorrect ones for others, so it is meaningless to claim that it should not be used because of uncertainty in general. For example, EwE predictions of the impact of increasing fishing rates for a particular species are most sensitive to assumptions about vulnerability of prey to that species, since the vulnerability parameters largely determine the strength of the compensatory response by the species to increased mortality rate. But even if EwE predicts the strength of the compensatory response to fishing correctly, it may still fail to predict response of that same species to a policy aimed at increasing its productivity by reducing abundance

of one or more of its predators: EwE may have a good estimate of total mortality rate for the species, but a very poor estimate of how that mortality rate is distributed among (or generated by) predators included in the model.

11.4 Can Ecopath mass balance assessments provide information directly usable for policy analysis?

Instantaneous snapshots of biomass, flows, and rates of biomass change have sometimes been used to draw inferences about issues such as ecosystem health as measured by mean trophic level or other indices of fishing impact, (e.g., Christensen, 1995a; Pauly and Christensen, 1995; Pauly *et al.*, 1998a). But the snapshots cannot be used directly to assess effects of policy changes that would result in changes in rates, (e.g., reduction in fishing rates) since the cumulative effects of such changes cannot be anticipated from the system state at one point in time. In fact the Ecosim part of EwE was initially developed specifically to provide a method for predicting cumulative changes, while recognizing that all rate processes in an ecosystem may change over time, as biomasses change. For example, one might conclude from the Ecopath mortality rate estimates or mixed trophic impact analysis that reducing the abundance of some particularly important predator might result in lower mortality rates of its prey, and hence growth in abundance of these prey. This prediction may hold for a short time, but might be reversed entirely over longer time scales due to increases in abundance of other predators or on an intermediate time scale due to predator prey switching in response to the initial responses in prey density.

11.5 Can Ecopath provide a reliable way of estimating potential production by incorporating knowledge of ecosystem support capabilities and limits?

Ecologists have long sought simple ways of predicting productive potential of aquatic ecosystems from ‘bottom up’ arguments about efficiency of conversion of primary production into production of higher trophic levels, (e.g., Polovina and Marten, 1982). While Ecopath inputs can be organized so as to provide such predictions, we do not recommend using EwE for management this way. There are simply too many ways that simple efficiency predictions can go wrong, particularly in relation to ‘shunting’ of production into food web components that are not of direct interest or value in management, (e.g., ungrazeable algae, fish species that are not harvested). Ecopath can help provide broad bounds for potential abundances and production in an exploratory research mode, but these bounds are unlikely to be tight enough to be useful for management planning related to fishery development or recovery potential.

11.6 Can Ecopath predict biomasses of groups for which no information is available?

In most EwE applications today, we try very hard to avoid using the Ecopath biomass estimation capability for more biomass components than absolutely necessary. Estimation of biomass with Ecopath usually requires making explicit assumption about the ecotrophic efficiency, i.e., about the proportion of the total mortality rate of a group that we account for by the predation, migration, biomass accumulation and fishing rates included explicitly in the Ecopath data. There is rarely a sound empirical basis for using any particular value of EE, except perhaps for top predators in situations where total mortality rate ($Z=P/B$) is well estimated and EE represents a ‘known’ ratio of fishing rate (F) to total Z (and the rest of Z, e.g., the natural mortality (M) is known not to be due to other predators included in the model nor to other factors not considered).

Where biomasses really are unavailable or are known to be biased, e.g., if the only biomass estimates for pelagics are from swept-area analysis based on demersal trawling, it may still be better to use assumed EE’s than to stop short of constructing an ecosystem model pending, e.g., funding and development of capabilities to conduct acoustic surveys. In such cases one can assume reasonable EE values for groups where biomasses are missing – an example: small pelagics do not die of old age in an exploited ecosystems, most are either eaten or caught, hence EE is likely to be in the range 0.90 to 0.99. As confidence intervals can be assigned to all input parameters and can be estimated for the output parameters using the Ecoranger module of EwE (where a range for acceptable output parameters is also incorporated as part of the model evaluation process), the mass balance constraints of the model can be used to predict potential ranges for biomasses of the system in the system,

11.7 Should Ecopath mass balance modeling be used only in situations where data are inadequate to use detailed, more traditional methods like MSVPA?

Multispecies virtual population analysis (MSVPA) has been used to reconstruct age-size and time dependent estimates of trophic flows and mortality rate components, using the VPA assumption that historical abundances can be inferred by back-calculating how many organisms must have been present in order to account for measured and estimated removals from those organisms over time (Sparre, 1991; Magnússon, 1995). In a sense, Ecopath does this as well, but generally does not account for size-age dependency and temporal variation (biomasses are constrained to be large enough to account for assumed removals estimated from biomasses, consumption/biomasses, and diet composition of predators, just as in MSVPA).

But the really big difference between Ecopath and MSVPA is not in the detail of calculations; constructing an Ecopath model that details age, size and time components would be tedious but feasible. The more important difference is in the use of direct data on total mortality rate by Ecopath, in the form of the *P/B* ratio that Ecopath users must provide. Ecopath biomass and mortality estimates are ‘constrained’ to fit the total mortality rates entered as *P/B* data. In contrast, MSVPA (like single-species VPA) can produce cohort abundance patterns (die-off patterns over age-size and time) that do not agree in any way with apparent cohort decay patterns evident from direct examination of the size-age composition data. In effect, the MSVPA (and VPA) user must reject or ignore any direct evidence about total mortality rate *Z* that might be present in age-size composition data, and must treat discrepancies between apparent *Z* from the cohort reconstructions versus apparent *Z* from composition data as being due to size-age dependent changes in vulnerability to the composition sampling method. This can be unwise, just as it has been unwise to ignore information about *Z* in single-species VPA, (e.g., Newfoundland cod VPA's resulted in much lower estimates of *Z* than would be estimated from catch-curve analysis of the age composition data, and in this case it turned out that VPA tuning resulted in underestimates of fishing mortality rate, Walters and Maguire, 1996).

It is obviously comforting to us as biologists to be able to provide more detailed accounting of predation interactions, which are almost always size and age dependent. But in assessments of ecosystem-scale impacts of changes in trophic conditions, it is not automatically true that the best aggregate estimate is the sum of component estimates, any more than it is automatically true in single-species assessment that more detailed models and data always provide better assessments than simpler models. For statistical and logical reasons, the ‘more is better’ argument is no more valid in dynamic modeling than it is in multiple regression analysis, where we are familiar with how adding more independent variables often results in better fits but poorer predictions.

As noted in the following two points, Ecopath and Ecosim do not ‘ignore’ the fact that trophic interactions are strongly size-age and seasonally structured. Rather, we assume that initial (Ecopath base or reference period) structuring has been adequately captured in preparing average/total rate input data, and that changes in structural composition over time are not large enough to drastically and persistently alter interaction rates/parameters. This is very similar to the assumption in single-species biomass dynamics and delay-difference modeling that stock composition changes produce regular or predictable changes in overall (stock-scale) production parameters, not that there is no composition effect in the first place.

11.8 Do EwE models ignore seasonality in production, mortality, and diet composition?

In most applications, Ecopath calculates components of biomass change over a one-year accounting step. There is no explicit assumption about how mortality rates, consumption rates, and diet composition may have varied within this step, except that the Ecopath user is assumed to have calculated a correct, weighted average of the rates over whatever seasonality may have been present in the data. Such averages can be difficult to calculate in practice, and a program interface component has been developed to help users with this chore (Martell, 1999).

In Ecosim, model users can define seasonal ‘forcing shapes’ or functions that can be applied as seasonal multipliers to the modeled production and consumption rate functions. Generally, including seasonal variation in this way results in graphics displays that are hard to follow visually (strong seasonal oscillations in ecosystem ‘fast’ variables like phytoplankton concentration), but very little impact on predicted interannual (cumulative, long term) patterns of system change.

11.9 Do biomass dynamics models like Ecosim treat ecosystems as consisting of homogeneous biomass pools of identical organisms, hence ignoring, e.g., size-selectivity of predation?

The biomass rate equations in Ecosim (sums of consumption rates less predation and fishing rates) can be viewed as ‘sums of sums’, where each trophic flow rate for an overall biomass pool is the sum of rates that apply to biomass components within that pool. In this view, doing a single overall rate calculation for a pool amounts to assuming that the proportional contributions of the biomass components within the pool remain stable, i.e., the size-age-species composition of the pool remains stable over changes in predicted overall food consumption and predation rates. In fact, the assumption is even weaker: pool composition may indeed change over time provided that high and low rate components change so as to balance one another; or proportional contribution of major components is stable enough so that total rates per overall biomass are not strongly affected.

We know of at least one condition under which the compositional stability assumption may be violated – when ratios of juvenile to adult abundance can change greatly, (e.g., under changes in fishing mortality) for a species that has strong trophic ontogeny (very different habitat use and trophic interactions by juveniles). To deal with such situations, Ecosim allows model users to ‘split’ biomass pools representing single-species with strong trophic ontogeny or size-dependent vulnerability to harvest, into multiple-age stanza groups. For populations represented this way, the Ecosim biomass dynamics equations are replaced with an explicit age structured model for monthly age cohorts in each of the stanzas (animals are lumped into one adult age group after reaching 95% of the asymptotic maximum body weight). The cohorts in each stanza can have distinctive diet composition and predation risks. Food search rates and metabolic rates per individual are calculated so as to have the animals exhibit growth with a basic von Bertalanffy functional form, but with growth rates varying with food availability. Recruitment is calculated for each month from total egg production, and egg production per individual is assumed to increase linearly with body size above a size at maturity.

Thus, for ‘split pool’ species Ecosim replaces the biomass dynamics model with a much more detailed and realistic population model, (see ‘Life history handling’ on page 103). This allows Ecosim users to not only represent compositional effects, but also to examine the emergent stock-recruitment relationship caused by density-dependent changes in adult fecundity and juvenile growth and foraging time behavior.

11.10 Do ecosystem biomass models ignore behavioral mechanisms by treating species interactions as random encounters?

Historically, trophic interaction rates in biomass dynamics models have been predicted by treating predator-prey encounter patterns as analogous to ‘mass-action’ encounters between chemical species in chemical reaction vat processes, where reaction (encounter, ‘predation’) rates are proportional to the product of predator and prey densities. Such ‘Lotka-Volterra’ models generally predict much more violent dynamic changes, and considerably simpler ecosystem organization, than we see in field data.

Ecosim was constructed around the proposition that this mass-action principle is deeply incorrect for ecological interactions, and instead interactions take place largely in spatially and temporally restricted ‘foraging arenas’ where prey make themselves available to predation through activities such as foraging and dispersal. To represent this within-pool heterogeneity, we treat each biomass pool as consisting at any instant of two biomass components with respect to any predator, one sub-pool of individuals vulnerable to the predator and another sub-pool ‘safe’ from the predator. In this view, predation rate is limited jointly by search efficiency of the predator for vulnerable prey individuals, and exchange rate of prey between the invulnerable and vulnerable states. When Ecosim users set the vulnerability exchange rates to high values, the model moves toward ‘top down’ or mass-action control of predation rates. When users set the vulnerability rates to low values, the model moves toward ‘bottom up’ control where predation rates are limited by how fast prey move (or grow, or disperse) into the vulnerable state.

Obviously the two-state (vulnerable/invulnerable) representation of prey biomass composition is a first approximation to the much more complex distribution of vulnerabilities among prey individuals that is likely to be present in most field situations. But it goes a remarkable way toward explaining dynamic patterns (lack of predator-prey cycles, persistence of apparent competitors and high biodiversity) that we have been unable to explain with simpler Lotka-Volterra mass-action models.

11.11 Do Ecosim models account for changes in trophic interactions associated with changes in predator diet compositions and limits to predation such as satiation?

In nature, diet compositions and feeding rates can change due to five broad factors:

1. changes in ‘habitat factors’ such as water clarity, temperature, and escape cover for prey;
2. changes in prey abundance and activity, and hence encounter rates with predators;
3. changes in predator abundance, and hence interference/exploitation competition for localized available prey;
4. changes in predator search tactics (search images, microhabitat used for foraging);
5. handling time or satiation limitations to predator feeding rates.

Ecosim allows (or requires) representation of four of these factors, namely all but predator search tactic changes (4). Type (1) factors can be optionally introduced by including ‘time forcing’ functions representing temporal habitat change, and or ‘trophic mediation’ functions where other biomasses modify predation interaction rates for any predator-prey pair(s). Types (2), (3), and (5) are built into the calculations by default (though some effects can be disabled by particular parameter choices).

In Ecosim, changes in prey abundance (factor (2) above) lead to proportional changes in predator diet composition only when prey feeding times are deliberately held constant by ‘turning off’ Ecosim foraging time adjustment parameters. When prey foraging time is allowed to vary (default assumption), declines in prey density generally result in apparent sigmoid (type III) decreases in predator consumptions of that prey type: as the prey declines, it generally spends less time feeding (reduced intraspecific competition for its own prey) and hence reduced encounter rates with its predators. The user can exaggerate this sigmoid effect by turning on parameters that cause the prey to spend less time feeding when predation risk is high (i.e., direct response to perceived predation risk).

Predator satiation effects are represented in Ecosim by foraging time adjustments such that predators ‘try’ to maintain constant food consumption rates (unless foraging time adjustments are deliberately disabled), by spending more time feeding when feeding rates begin to decrease due to decreasing densities of one or more prey types. Likewise, handling time limits to feeding rate (lower attack rate on any one prey type as abundance of another increases, due to predator spending more time pursuing/handling individuals of the other type) are represented by a ‘multispecies disc equation’ (generalization of Holling’s type II functional response model).

Our philosophy in developing Ecosim predation rate predictions has been to look first at the fine-scale (space, time) behavioral ecology of prey and predators, and in particular at how they vary and ‘manage’ their time. Overall predation response patterns, such as Type II sigmoid effects of reduced prey density, then ‘emerge’ as effects of the time management representation rather than being ‘hardwired’ into the model by particular overall equations for predation rates and diet composition.

11.12 Are the population models embedded in Ecosim better than single-species models since they explain the ecosystem trophic basis for production?

In a number of case studies, Ecosim users have treated the model as though it were a single-species assessment tool, varying its parameters so as to fit time series data for a particular species, (e.g., yellowfin tuna in the Eastern Pacific, herring in southern British Columbia). In such cases, it generally turns out that the biomass dynamics or delay-difference ‘submodel’ for the target species behaves quite similarly when ‘embedded’ in Ecosim (with explicit accounting for production and mortality rate as function of food resources and predators) to the corresponding single-species assessment model where competition effects are represented as implicit functions of stock size, (e.g., stock recruitment model) and predation mortality rates are assumed constant.

So if one has an Ecosim model whose ‘production’ parameters have been estimated by fitting the model to single-species data, and a corresponding single-species model also fitted to the data, one should not be surprised that the two approaches usually give about the same answers to policy questions related to changing fishing mortality rate for the species, (e.g., fishing rates for MSY). Ecosim models may diverge from the single-species predictions at very low stock sizes (Ecosim may predict ‘delayed depensation’ effects due to changes in predation rates on

juveniles), but otherwise do not generally lead us to interpret the single-species data any differently with respect to single-species assessment issues, (e.g., MSY) than if we just used the single-species model.

Thus, it would be wrong when applying Ecosim for single-species harvest policy analysis to contend that Ecosim is 'better' than a single-species model, when both give the same answer. It may comfort us to know as biologists that the Ecosim representation has somehow explained production in terms of ecosystem relationships rather than implicit relationships on stock size, but making biologists 'feel better' should not be a criterion for judging the effectiveness of a policy tool. When fitting Ecosim to the data we encounter the same risks as in single-species assessment of incorrect biomass estimation, misinterpretation of trend data, (e.g., hyperstability of catch per effort data), and failure to account for persistent effects such as environmental regime changes or confounding of these effects with the effects of fishing.

11.13 Do Ecosim population models provide more accurate stock assessments than single-species models by accounting for changes in recruitment and natural mortality rates due to changes in predation rates?

As noted above, using Ecosim for single-species assessments usually results in similar fits to historical data as would be obtained with traditional surplus production or delay-difference models. In principle Ecosim should be able to improve a bit on models that assume stationary stock-recruitment relationships and constant natural mortality rates, at least for mid-trophic level species that may be subject to highly variable predation risk. But in practice we have so far not obtained substantial improvements in fit to data, which could be due to poor data or to stability in mortality rates of the sort predicted when Ecosim vulnerability parameters are set to mimic 'bottom up' control of predation rates.

In one case (the Strait of Georgia, British Columbia) where we have fit Ecosim to multiple time series data on major species (herring, salmon, hake, ling cod, seals) by estimating 'shared production anomalies' attributed in the fitting to changes in primary productivity, we were able to show that about half the total variance around single-species model fits to changes in relative abundance over time could be explained by ecosystem-scale effects. That is, we were able to 'improve' on the single-species fitting, but this improvement was due to assuming changes in ecosystem scale 'forcing' rather than to accounting for temporal variation in predation mortality rates associated with impacts of fishing on predators. In another case (French Frigate Shoals, Hawaii) we were again able to fit time series data (rock lobsters, monk seals) better by including effects of an ecosystem-scale regime shift (decreased primary production in the Central North Pacific after 1990), and were not able to explain deviations from single-species model fits through changes in trophic interactions alone.

These cases, along with experience that Ecosim generally does not behave much differently from single-species models when only fishing effects are considered, lead us to suspect that Ecosim (and perhaps other, more detailed trophic interaction assessments) will not lead to substantial improvements in stock size prediction just by accounting for predator-prey effects. However, there is a good chance that Ecosim will be very helpful in interpreting effects of large-scale, persistent regime changes that are likely to have caused ecosystem-scale changes in productivity. In such situations, Ecosim may be particularly helpful in finding some resolution for the so-called 'Thompson-Burkenroad' debates about the relative importance of fishing versus environmental changes in driving historical changes in abundance (see Skud, 1975 for a review).

Rather than treating Ecosim and single-species methods as if they were competitors, a useful assessment tactic may be to work back and forth between Ecosim and single-species assessment methods, using each to check and improve the other. For example, we have used ordinary VPA and stock synthesis results for Pacific herring as reference 'data' (summary of raw age composition, harvest, and spawn survey data) for fitting Ecosim models of the Georgia Strait. The Ecosim herring model predicts somewhat lower abundances than VPA during periods of low stock size, and somewhat higher abundances than VPA during high stock periods. Ecosim also estimates lower natural mortality rates (M) for herring during the low abundance periods. If Ecosim is correct in estimating that M has been (weakly) density-dependent, then VPA has probably overestimated abundance (used too high an M in the VPA backcalculation) during population lows, and is probably underestimating juvenile abundance now (due to using an M that is too low for the current high stock size).

11.14 Can one rely on the Ecosim search procedure time series fitting to produce better parameter estimates?

Ecosim users are cautioned that the search procedure in no way guarantees finding ‘better’ parameter estimates. Better fits to data can easily be obtained for the wrong reasons (some time series, particularly catch/effort data, can be misleading in the first place, as can historical estimates of changes in fishing mortality rates; many parameter combinations may equally well ‘explain’ patterns in the data). Nonlinear search procedures can become lost or ‘trapped’ at local parameter combinations where there are local minima in the SS function far from the combinations that would actually fit the data best. The best way to insure against the technical problems of searching a complex SS function is to use ‘multiple shooting’: start the search from a variety of initial parameter combinations, and see if it keeps coming back to the same final estimates. Look very closely at the time series data for possible violations of the assumption that the relative abundance, y , is a product of a scaling factor and the total biomass, due to progressive changes in the methods of y or nonlinearities caused by factors such as density-dependent catchability. If y is a biomass reconstruction from methods such as VPA that assume constant natural mortality rate M , spurious trends in y caused by the sort of changes in M that Ecosim predicts, particularly for younger animals, call for concern. Alternative combinations of Ecosim parameters may fit the data equally well but would imply quite different responses to policy changes such as increases in fishing rates.

Search procedures are most useful in diagnosing problems with both the model and data. That is, the greatest value of doing some formal estimation is while it seems not to be working, when it cannot find good fits to data. Poor fits can be informative about both the model and the data.

11.15 Does Ecosim ignore multispecies technical interactions (selectivity or lack of it by gear types) and dynamics created by bycatch discarding?

By separating groups into juveniles and adults, each with different biomasses and catches (and hence fishing mortalities), fundamental differences in selection can be accounted for. Moreover, Ecosim users can specify fishing mortality patterns over time either at the group level (fishing rate for each group over time) or the fleet level. Fleet level changes are specified as changes in relative fishing effort (relative to the Ecopath baseline model), and these changes impact fishing rates for the species caught by each gear in proportion to Ecopath base estimates for the species composition of the gear. That is, technical interactions (fishing rate effects on a variety of species caused by each gear type) are a basic part of the Ecopath data input and Ecosim simulations. However, Ecosim does not provide simple scenario development options for simulating tactics that might make each gear more or less selective in future.

Discarded bycatch can be treated as a biomass pool in Ecopath, i.e., as a diet component (and hence component of production) by species that consume discards (e.g. sharks, birds, shrimp, and crabs). Ecopath input data on bycatch and discard rates are passed to Ecosim, and Ecosim does time accounting for changes in discard rates and biomass in relation to simulated changes in fishing fleet sizes. In scenarios where some species are heavily dependent on bycatch, Ecosim will then track impacts of bycatch management on food availability and feeding rates of such species. For instance, Ecosim has produced some very interesting scenarios for shrimp fishery development and how shrimp often appear to become more productive under fishing, by including effects of both reducing abundance of predatory fishes (when they are killed as bycatch) and providing biomass from those fishes as food for the shrimp.

11.16 Does Ecosim ignore depensatory changes in fishing mortality rates due to range collapse at low stock sizes?

Ecosim users have two options for specifying fishing mortality rate patterns: (1) direct entry of fishing rate (F) values over time; or (2) entry of relative fishing effort values over time, with fishing rate calculated as $q(B) \cdot (\text{relative effort})$, where $q(B)$ is a biomass-dependent catchability coefficient. Under the second option, q is modeled as a hyperbolic function of B ($q = q_{max} / (1 + kB)$), so that q can be increased dramatically with decreases in stock size. The concept in this formulation is to recognize that catchability q can be expressed as a ratio $q = a / A$, where a is the area swept by one unit of effort and A is the area over which fish are distributed. Increases in q with decreasing stock biomass are usually assumed to be caused by decreases in stock area A occupied with decreases in B .

11.17 Does Ecosim ignore the risk of depensatory recruitment changes at low stock sizes?

Depensatory recruitment changes are apparently not common (Myers *et al.*, 1995; Liermann and Hilborn, 1997), but should not be ignored in risk assessments for situations where a depensatory recruitment decline would have large economic or social consequences. Depensatory effects are usually assumed to be due to Type II predator feeding effects, where predators would exert an increasing mortality rate on juvenile fishes if they tend eat a constant number of juveniles despite decreasing juvenile density. There are relatively few field situations where we would expect such type II predator feeding effects (like migrating pink salmon fry being eaten by resident trout in a small stream).

Ecosim has helped identify another possible depensation mechanism that may be more common, which we call the ‘delayed depensation’ or ‘cultivation-depensation’ effect (Walters and Kitchell, 2001). When a large, dominant species is fished down in Ecosim models, the model often predicts a substantial increase in smaller-sized predators that have been kept down in abundance by a combination of direct predation and competition effects with the large dominant species. These predators then cause an increase in predation mortality rate on (or compete for food with) juveniles of the large dominant. This causes a depensatory decrease in the recruitment rate per spawner for the large dominant, slowing or preventing population recovery even if the fishing effects are removed.

So far from ignoring depensatory recruitment effects, Ecosim warns us to be more careful about the risk of these effects. It warns us to be especially wary in the management of the most common, large, and dominant fish species that are the most valuable components of most fisheries.

12. Major Pitfalls in the Application of EwE

EwE can produce misleading predictions about even the direction of impacts of policy proposals. Erroneous predictions usually result from bad estimates or errors of omission for a few key parameters, rather than ‘diffuse’ effects of uncertainties in all the input information. We warn EwE users to be particularly careful about the following problems that we have seen in various case studies.

12.1 Incorrect assessments of predation impacts for prey that are rare in predator diets

It is easy to overlook a minor diet item in specifying diet composition for some predator. Unfortunately, while that prey type may not be important for the predator, it may represent a very large component of total mortality for the prey type. This is a particularly important problem in representation of mortality factors for juvenile fishes, which usually suffer high predation mortality rates but are often not major components of any particular predator’s diet and are notoriously difficult to measure in diet studies (fast digestion rates, highly erratic and usually seasonal occurrence in predator diets).

Another way that ‘minor’ diet items can come to assume considerable importance is through ‘cultivation-depensation’ effects (Walters and Kitchell, 2001). Suppose for example that some small predatory fish is kept at low densities by another, larger predator, but the number of predation events needed to exert this control is small compared to the total prey consumption by the larger predator. It would be easy to miss this linkage entirely in formulating the initial Ecopath model. But then suppose the larger predator is fished down, ‘releasing’ the smaller predator to increase greatly in abundance. The smaller predator may then cause substantial decrease in juvenile survival rates of the larger predator, creating a ‘delayed depensation’ effect on the larger predator’s recruitment. Possibly the larger predator was abundant in the first place at least partly because it was able to exert such control effects on predators/competitors of its own juveniles. Even if such ‘perverse’ trophic interactions are rare, they are certainly worth worrying about because they imply a risk that overfishing will result in delayed recovery or a persistent low equilibrium abundance for larger predators.

12.2 Trophic mediation effects (indirect trophic effects)

We use the term ‘mediation effect’ for situations where the predation interaction between two biomass pools is impacted positively or negatively by abundance of a third biomass type. For example, predation rates on juvenile fishes by large piscivores may be much lower in situations where benthic algae, corals, or macroinvertebrates provide cover for the juveniles. Pelagic birds like albatrosses that feed on small fishes may depend on large piscivores to drive these small fishes to the surface where they are accessible to the birds. Some large piscivores

may create enough predation risk for others to prevent those others from foraging on some prey types in some habitats.

When a mediation effect is in fact present but is not recognized in the Ecosim model development, it is not unlikely for the model to predict responses that are qualitatively incorrect. For example, fishing down tunas in a pelagic model is likely to result in predicted increases in abundance of forage fishes, and hence to predicted increases in abundance of pelagic birds. But in fact, reducing tuna abundance may have exactly the opposite effect, resulting in bird declines due to the baitfish spending less time at the surface when tuna are less abundant.

12.3 Underestimates of predation vulnerabilities

Predation impacts can be limited in Ecosim by assuming low values of the exchange parameters (v 's) between behaviorally invulnerable and vulnerable prey 'states'. We call these exchange parameters 'vulnerabilities', and they are estimated by assuming ratios of maximum to Ecopath base estimates of prey mortality rates for each predator-prey linkage. That is, if $M(o)_{ij}=C(o)_{ij}/B(o)_i$ is the base instantaneous natural mortality rate for prey type i caused by predator j base (Ecopath estimate) consumption rate $C(o)_{ij}$ on prey base biomass $B(o)_i$, we assume that the maximum possible rate for very high predator j abundance would be $v_{ij}B_i$ where $v_{ij}=KM(o)_{ij}$, $K>1$, represents the rate at which prey become vulnerable to predator j . By using a K near 1, i.e. v_{ij} only a little larger than $M(o)_{ij}$, Ecosim users can simulate the 'bottom up' control possibility that changes in predator abundances do not cause much change in prey mortality rates because these rates are limited by physiological or behavioral factors of the prey. The assumption that there are such limitations is supported by scattered observations where total mortality rates (Z) were poorly correlated with changes in predator abundances.

Another way of saying that vulnerabilities of prey to predators are very limited is to say that predators are already eating almost every prey that does become vulnerable. If this is indeed true, then there is likely intense exploitation competition among predators for the prey that do become vulnerable, i.e. the number of vulnerable prey seen by each predator is severely limited by the number of other predators competing for those prey. This has potentially large implications for the dynamics of the predator: reductions in predator abundance may be accompanied by large increases in the densities of vulnerable prey available to each remaining predator. In such cases, Ecosim will predict a strong compensatory effect on the predator of reduced predator abundance (strong increases in food consumption rate and growth, or large decreases in predator foraging time with attendant decreases in mortality risk faced by the predator).

So the net effect of assuming low prey vulnerabilities is also to assume that predators should exhibit strong compensatory responses to reduced abundance of conspecifics, which in simulations of increased fishing pressure means strong compensatory responses and hence lower risk of overfishing. An enthusiastic proponent of 'bottom up' control of trophic processes must therefore also be a strong proponent of the idea that it is hard to overfish. This is a very risky assumption.

12.4 Non-additivity in predation rates due to shared foraging arenas

The default assumption in Ecosim is to treat each predation rate linkage as occurring in a unique 'foraging arena' defined by the behaviors of the specific prey and predator. In this formulation, elimination of one predator will result in a decrease in total prey mortality rate equal (at least initially) to the Ecopath base estimate of that predator's component of the prey total mortality rate. This may be partly compensated by increases in mortality rate due to other predators if the prey increases in abundance and spends more time foraging in response to increased intraspecific competition, but in general this compensatory effect will not completely replace the initial mortality rate reduction.

But suppose this formulation is wrong, and in fact the mortality rate of the prey represents movement of the prey into behavioral or physiological states, (e.g., parasite loads) for which it is vulnerable to predators in general. In this case, removal of any one predator may simply result in the vulnerable prey individuals being taken just as fast, but by other predators. In this case, the total mortality rate of the prey will change much less than predicted by Ecosim.

For example, we recently used Ecosim to evaluate whether control of predatory sharks might help improve juvenile survival rates of monk seals off Hawaii. Sharks appear to be the proximate cause of many juvenile deaths, and it appears that juveniles are exposing themselves to much higher predation risk than normal due to decreases in prey abundance caused by a combination of lobster fishery and ocean productivity ('regime shift') effects. In this case,

Ecosim predicts that shark control will at least temporarily improve monk seal juvenile survival rates. But if the real problem is not sharks, but rather that juvenile seals are spending more time exposed to predators in general, the Ecosim prediction about efficacy of control may be grossly optimistic: other predators may just take up the 'slack' after shark removal.

12.5 Temporal variation in species-specific habitat factors

Attempting to fit Ecosim models to time series data has revealed some cases where an important species or biomass pool shows dramatic change that cannot be attributed to any known change in trophic relationships or harvesting. Then this dramatic but 'unpredictable' change appears to result in major trophic impact on the rest of the ecosystem. An example would be a planktivorous fish species that is important to piscivores in the system (so piscivores respond strongly to changes in its abundance), which shows high recruitment variation and occasional very strong year classes that support temporary piscivore increases. It is quite possible for such recruitment 'events' to be linked to very localized habitat factors that affect juvenile survival of the planktivore, so that each event results in a persistent cascade of abundance changes throughout the food web. Another example would be loss of specific spawning sites or habitat for one species, which causes it to decline despite favorable trophic conditions in terms of food supply and predation risk.

Ecosim can help us detect possible habitat problems, by revealing prediction 'anomalies' from biomass patterns expected under trophic and fishing effects alone. But there is also a risk of producing 'spurious' good fits to Ecosim, when Ecosim parameters are varied so as to explain as much of the biomass change as possible; that is, Ecosim may explain patterns as trophic/fishing effects that in fact have been due to habitat changes. This is a particular risk in situations where habitat change involves some fairly regular 'regime shifts' or cycles in habitat variables; Ecosim may well attribute cyclic biomass changes in such situations to predator-prey instabilities rather than environmental forcing.

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