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Ecopath with Ecosim version 6

User Guide

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Contents

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 modelling 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 behaviour. This has been remedied through the development of Ecospace (Note that in Walters et al., 1999 Eq. 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.

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1 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 EwE6. 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 modelling 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.

1.1 About Ecopath with Ecosim

EwE6 is an ecological software suite for personal computers that has been under development for more than a decade. The development is now centreed 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.

1.2 On modelling

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 behaviour 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 behaviour 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 behaviour 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 ‘modellers’ (who, traditionally being non-biologists, may have had scant knowledge of the intricate interactions between living organisms). However, ‘modelling’ does not necessarily imply ‘simulation modelling’. There are various ways of constructing quantitative models of ecosystems which avoid the intricacies of traditional simulation Modelling, 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 modeller 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 modeller 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 oneself 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 modelling 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 modelling thanks to the time dynamic model, Ecosim, and the spatial dynamic model, Ecospace, both fully integrated with Ecopath in the present software.

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2 Introductory material: Ecopath

This chapter contains details of the theory underpinning the functioning of Ecopath: Mortality for a prey is consumption for a predator; The energy balance of a box; On the need for input parameters; Defining the system; Dealing with open system problems; Production; Consumption; Other mortality; and Representation of multi-stanza life histories.

See Ecopath inputs and Ecopath outputs for links to instructions for using Ecosim.

2.1 Mortality for a prey is consumption for a predator

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 modelling). 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.

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,

$$P_i = Y_i + B_i . M2_i + E_i + BA_i + P_i(1 - EE_i) \quad \textbf{Eq. 2}$$

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 $M0_i = P_i \cdot (1\text{-}EE_i)$ 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. 2.2 can be re-expressed as

$$B_i \cdot (P/B)_i - \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - (P/B)_i \cdot B_i \cdot (1 - EE_i) - Y_i - E_i - BA_i = 0 \quad \textbf{Eq. 3}$$

$$B_i \cdot (P/B)_i \cdot EE_i - \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0 \quad \textbf{Eq. 4}$$

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. 2.3, for a system with *n* groups, *n* linear equations can be given, in explicit terms,

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

Eq. 5

This system of simultaneous linear equations can be re-expressed

$$a_{11}X_1 + a_{12}X_2 + \quad \ldots \quad a_{1m}X_m = Q_1$$
$$a_{21}X_1 + a_{22}X_2 + \quad \ldots \quad a_{2m}X_m = Q_2$$
$$\vdots$$
$$\vdots$$
$$a_{n11}X_1 + a_{n2}X_2 + \quad \ldots \quad a_{nm}X_m = Q_n$$ **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

$[A]_{nm} \,.\, [X]_m = [Q]_m$ ***Eq. 7***

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

$[X]_{nm} \,.\, [A^{-1}]_{n,m} = [Q]_m$ ***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 in Eq. 2.3, 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 *DCji* is the fraction of predator (*j*)'s diet contributed by prey (*i*). *Qj* is calculated as the product of *Bj*, the biomass of group (*j*) and *Qj/Bj*, 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 net growth efficiency, g_i, is estimated using

$$cg_i = (P_i/B_i)/(Q_i/B_i)$$ **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 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. 2.2.10.

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.

2.2 The energy balance of a box

A group (box) 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. See Defining the system for more about defining groups.

In a model, the energy input and output of all living groups must be balanced. The basic Ecopath equation includes only the production of a box (see Eq. 1). 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

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Consumption = production + respiration + 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).

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 (see 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.

2.3 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*. Bi is the biomass of group *i*; *Q/Bi* 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*.

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.

2.4 Defining the system

The ecosystems that can be modelled using Ecopath can be of nearly any kind: the modeller 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 considers 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).

2.5 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 Other production form 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:

> The '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. In the Diet composition form, 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.
>
> The '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 modelled 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 labelled '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 modelling 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 for further information.

2.6 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 labelled ‘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. Production over biomass is entered on the Basic input form. See Mortality coefficients and Predation mortality for description of Ecopath’s estimates of different mortality components in the system.

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 (Gayanilo et al., 1996).

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 Tc 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):

Fishing mortality = yield / biomass

where the yield is a rate, (e.g., $t/km^2/year$), the biomass lacks a time dimension, (i.e., is expressed as t/km^2), and thus the fishing mortality is an instantaneous rate, (e.g., per year).

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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:

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

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'.

2.7 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. Consumption over biomass is entered on the Basic input form.

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:

$$\log(Q/B) = 7.964 - 0.204 \log W_\infty - 1.965 \,.\, T' + 0.083 \,.\, A + 0.532 \,.\, h + 0.398 \,.\, d \quad \textbf{Eq. 17}$$

(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/Kelvin (Kelvin = °C + 273.15), A is the aspect ratio (see Figure 2.1), *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.

$\log(Q/B) = 8.056 + 0.300\log f - 0.201 \log W_\infty - 1.989 \,.\, T' + 0.081 \,.\, A + 0.522 \,.\, h + 0.393 \,.\, d$ **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) Eq. 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:

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

$$Q_{75} = S \Big/ \left[2 \log \left(N_{0.25-S} \Big/ N_{0.75-S} \right)\right]$$

Figure 2.1 Schematic representation of method to estimate the aspect ratio (*Ar = h2/s*) of the caudal fin of fish, given height (*h*) and surface area (*s*, in black).

2.8 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.) Th**Error! Hyperlink reference not valid.**is 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. *EE* is entered on the Basic input form.

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.

2.9 Representation of multi-stanza life histories in Ecopath, Ecosim and Ecospace

See Edit groups for instructions on defining multi-stanza groups in EwE6. See Edit multi-stanza groups for instructions on setting parameters for multi-stanza groups.

EwE users can create a set of biomass groups representing life history stages or stanzas for species that have complex trophic ontogeny. Mortality rates (*M0*, 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, *Q/B*, 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* x Z = 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.

Under the stable age distribution assumption, the relative number of age "*a*" animals is given by $l_a/\square l_a$ where the sum is over all ages, and l_a is the population growth rate-corrected survivorship,

$$l_a = e^{-\left(\sum Z_a - a\frac{BA}{B}\right)}$$

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 $e^{-a\frac{BA}{B}}$ 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, b, of animals in stanza s should be

$$b_s = \frac{\sum\limits_{a\ in\ s} l_a w_a}{\sum\limits_{all\ a} l_a w_a}$$

where $w_a = \left(1 - e^{-Ka}\right)^3$ is the von Bertalanffy (1938) prediction of relative body weight at age a.

Knowing the biomass, *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

$$B = \frac{B_{leading}}{b_{leadings}},$$

then setting $B_s = b_s B$ for the other stanzas. *Q/B* 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 *Q/B* 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).

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. Egg production is allowed to vary seasonally or over long-term through a user-defined forcing function (see Egg production). If an egg production curve is defined the egg production term is multiplied according to the user-defined function.

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:

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).

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).

Representation of stanzas that occur outside the modelled 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 modelled 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 modelled 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 modelled system (outside world treated as having constant trophic conditions). Most often, the stanzas that reside outside the modelled 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 modelled system, then the modelled 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.

3 Introductory material: Ecosim

Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model.

This chapter contains details of the theory underpinning the function of Ecosim: An overview of Ecosim; Ecosim basic; Vulnerabilities in Ecosim; Dealing with dynamic instability in Ecosim/Ecospace; Predicting consumption; Foraging time and predation risk; Time series fitting in Ecosim; Hints for fitting models to time series; Effect of P/B (Z) and vulnerability for time series fitting; Predator satiation and handling time effects; Modelling switching behaviour in Ecosim; Compensatory mechanisms; Using Ecosim to study compensation in recruitment relationships; Compensatory growth (overall P/B); Compensatory natural mortality; Linking mediation and time forcing functions to trophic interaction rates; Primary production; Nutrient cycling and nutrient limitation in Ecosim; Density-dependent changes in catchability; Modelling effort dynamics; Using Ecosim for Stock Reduction Analysis; Hatchery populations in Ecosim; and Parameter sensitivity.

See Ecosim inputs and Ecosim outputs for links to instructions for using Ecosim.

3.1 An overview of Ecosim

Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model. See Ecosim inputs and Ecosim outputs for links to instructions for using Ecosim.

The key computational aspects are in summary form:

- Use of mass-balance results (from Ecopath) for parameter estimation;
- Variable speed splitting enables efficient modelling of the dynamics of both ‘fast’ (phytoplankton) and ‘slow’ groups (whales);
- Effects of micro-scale behaviours 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;
    - 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 behaviour 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.

3.2 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 (see Eq. 1 in Mortality for a prey is consumption for a predator), and take the form

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

Eq. 50

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), $M0_i$ the non-predation ('other') natural mortality rate, F_i is fishing mortality rate, e_i is emigration rate, Ii 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 Bi'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.

Further reading: Walters et al. 1997; Walters et al. 2000

3.3 Vulnerabilities in Ecosim

One of the most important features of Ecosim is its ability to allow exploring the implications on system dynamics of different views of how the biomass of different groups in the ecosystem is controlled. The two extreme views are 'predator' control' (also called top-down control) and 'prey control' (or bottom-up). We model this using 'vulnerabilities,' which represent the degree to which 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 Figure 3.1). 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.

If we illustrate the relationship between predator biomass and *Q/B* (this is not an assumption in the actual Ecosim calculations) and 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 Figure 3.1). 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 Figure 3.2 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 keep biomass high. 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, 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 x 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. Such top-down control, also known as Lotka-Volterra dynamics, easily leads to rapid oscillations of prey and predator biomasses and/or unpredictable behaviour.

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 becomes available to predators only when it leaves the feature that protects it. Here being caught is a function of the prey's behaviour. 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 Figure 3.3). 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 Figure 3.3, 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.

The vulnerability parameters are among the most important parameters that users change to improve the agreement of the model's predictions with historical data (see Time series fitting in Ecosim, Hints for fitting models to time series reference data and Effect of P/B (Z) and vulnerability for time series fitting). See Vulnerabilities for help on setting vulnerabilities in Ecosim. See Fit to time series for help with Ecosim's parameter search interface.

Further reading: Walters and Juanes (1993), Walters et al. (1997), Walters and Korman 1999, and Walters and Martell (2004).

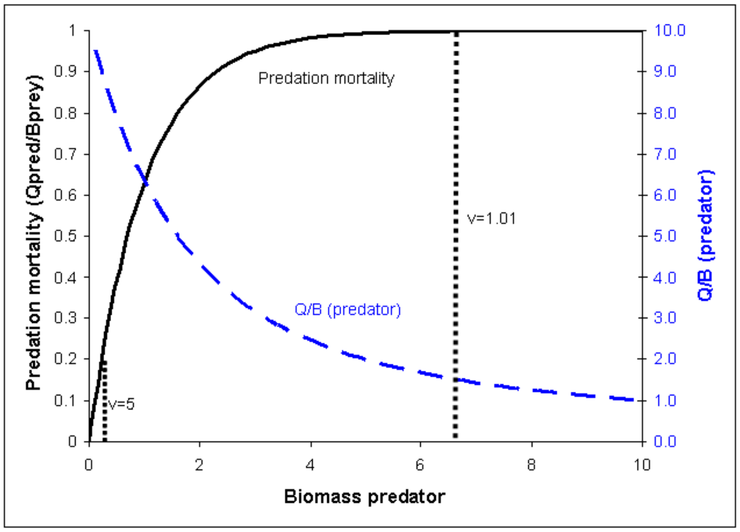

Figure 3.1 Relationship between biomass of a predator and the predation mortality it causes on a given prey, as well as the corresponding *Q/B* for the given predator and prey (assuming that the predator does not reduce prey biomass substantially). Vulnerability, *v*, is estimated as max. predation mortality/baseline predation mortality, (e.g., 5 at the leftmost stippled line). Baseline mortality is the mortality caused by the predator in the underlying Ecopath model.

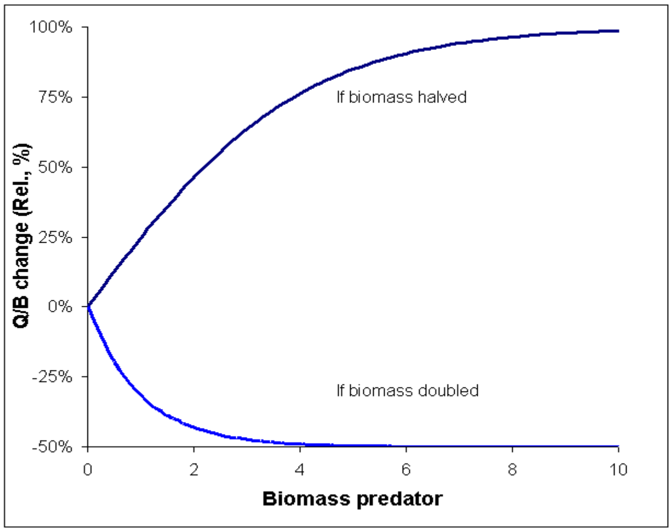

Figure 3.2 Relative increase in *Q/B* (%) as a function of predator biomass resulting from the predator biomass being halved or doubled. At high predator biomasses (i.e. near the carrying capacity for the given predator-prey interaction) a halving of predator biomass will result in nearly a doubling 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*.

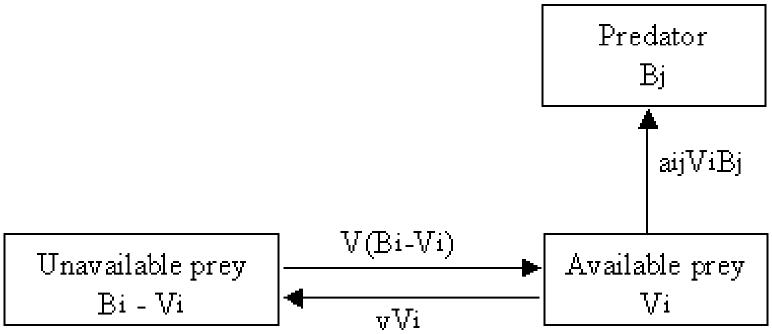

Figure 3.3 Simulation of flow between available (V_i) and unavailable (B_i - V_i) prey biomass in Ecosim. a_{ij} is the predator search rate for prey *i*, *v* is the exchange rate between the vulnerable and not-vulnerable state. Fast equilibrium between the two prey states implies $V_i = vB_i / (2v + aB_j)$. Based on Walters et al. (1997).

3.4 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 Vulnerabilities form, set values to 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 behaviours: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 behaviours (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 behaviours that create foraging arena patches, any physical or behavioural 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 = 100 in Vulnerabilities form) 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 form) for juvenile pools and reduce vulnerabilities of prey to juvenile fishes (Vulnerabilities form).

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 12/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/Ecospace 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.

3.5 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 Figure 3.3 in Vulnerabilities in Ecosim). 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,

$$C_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot P_j}{2v_{ij} + a_{ij} \cdot P_j} \quad \textbf{Eq. 51}$$

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:

$$C_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot P_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij} / D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot P_j \cdot S_{ij} \cdot T_j / D_j} \quad \textbf{Eq. 52}$$

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,

$$D_j = \frac{h_j \cdot T_j}{1 + \sum_k a_{kj} \cdot B_k \cdot T_k \cdot M_{kj}} \quad \textbf{Eq. 53}$$

where h_j is the predator handling time. The feeding time factors are discussed further in *Foraging time and predation risk* (see Eq. 65). A vulnerability setting of 1 will result in consumption being estimated using bottom-up conditions only through

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

3.6 Foraging time and predation risk

The food consumption prediction relationship in Eq. 52 (see Predicting consumption) 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'_{ij} for all predators j on i, is inversely related to T_{it}, i.e., $v'_{ij}t = v'_{ij} / T_{it}$. An alternative structure that gives similar results is to leave the a_{ij} constant, while varying the v_{ij} by setting $v_{ijt} = T_{jt} \cdot v_{ij}$ in the numerator of Eq. 52 in Predicting consumption) 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 $v'_{1j} = v_{ij}$. 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 behaviour as measured by v_{ji}. This is implemented in form of the relationship:

$$T_{i,t} = T_{i,t-1} \cdot \left(1 - a + \frac{a \cdot c_{i,opt}}{c_{i,t-1}}\right) \quad \textbf{Eq. 65}$$

where, a is a user-defined Feeding time adjustment rate [0, 1] on the Ecosim Group info form; $c_{i,opt}$ 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 (Maximum relative feeding time on the *Group info* form with default of two times the feeding rate in the Ecopath base model).

The relationship between foraging time, consumption and predator biomass is illustrated in Figure 3.4.

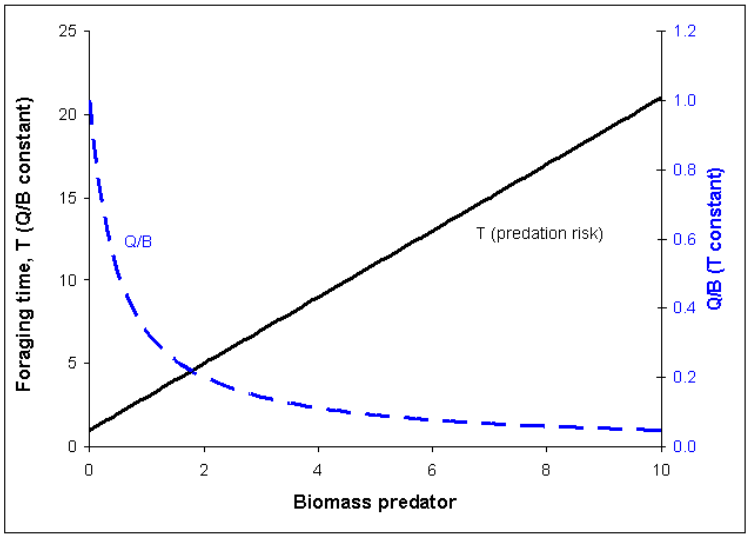

Figure 3.4 Relationship between relative foraging time (*T*), *Q/B* and predator biomass. If *Q/B* is held constant the foraging time (and hence predation risk) is a linear function of the predator biomass (solid line). If *T* is held constant the *Q/B* will decrease asymptotically with predator biomass (stippled line).

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

Ecosim can 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.

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 and applied (using the Time series form), a statistical measure of goodness of fit to these data is generated each time Ecosim is run (using the Run Ecosim form). 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 time series fitting uses 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 (see Fit to time series for help with implementing these analyses):

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).

3.8 Hints for 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. See also Time series fitting in Ecosim. See Time series for instructions for setting up time series data into your model.

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 series 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 behaviour.

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

> 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).
>
> 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.
>
> 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: (i) failure of the group to increase following reductions in mortality (due to preventing the group from increasing its total food intake); (ii) 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 form to determine whether vulnerability changes would cause changes in goodness of fit, and consider using the fitting interface to search for improved vulnerability estimates. See Effect of P/B (Z) and vulnerability for time series fitting for more information.
>
> 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 Ecosim form to see if the total mortality rate and its partitioning among factors are reasonable. See Effect of P/B (Z) and vulnerability for time series fitting for more information.
>
> 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 Fit to time series form 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'.

> 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 behaviour 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 modelled 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 for several reasons:

> 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;
>
> 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); and
>
> Potential value of the modelling 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).

$$l$$

Figure 3.5 Initial time series fit for the Benguela model. Estimated using default values in Ecosim.

$$w_c$$

Figure 3.6 Time series fit for Benguela model after estimating vulnerabilities (for 15 groups of consumers).

$$w_c = \sum_l w_l \cdot C_{c,l}$$

w_l **Figure 3.7** 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.

$C_{c,l}$

Figure 3.8 Time series fit for the Benguela model with primary production ‘anomaly’ estimated.

3.9 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 modelled in Ecosim. Mortality is considered a linear function of biomass (solid line in Figure 3.9), while the population increase will be a non-linear function of the biomass (dotted line in Figure 3.9). 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 modelled using a variable ‘vulnerability’ setting for top-down vs. bottom-up control.

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 Figure 3.10 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 C and D in Figure 3.10. 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 See Figure 3.10. 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." 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.

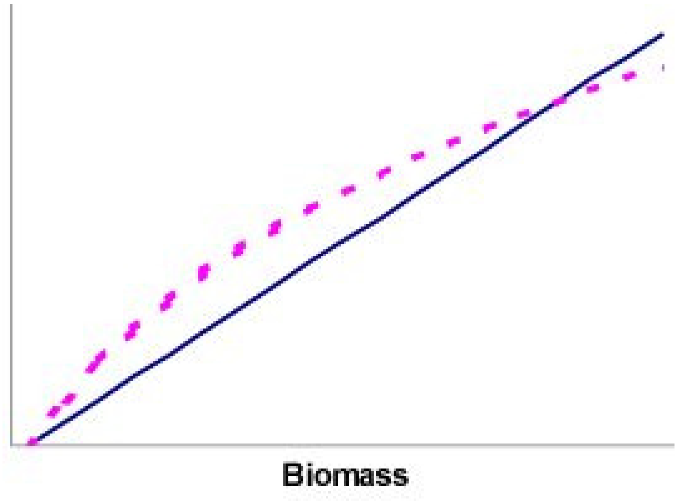

Figure 3.9 The solid line shows the predicted mortality calculated as Z ·B, and the dotted line the population growth estimated as a function of the consumption. The area between the lines can be considered 'surplus production'.

c'

Figure 3.10 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.

3.10 Predator satiation and handling time effects

Ecosim and Ecospace allow you to represent two factors that may limit prey consumption rates per predator (*Q/B*): i) foraging time adjustments related to predation risk and/or satiation; and ii) handling time effects. Parameters for both are specified via the Ecosim Group info form.

Satiation and/or choices to forage for short times in order to avoid higher predation risk are represented by setting non-zero values for the 'Feeding time adjustment rate' of a group: larger values of this rate represent more rapid adjustment of foraging time. Non-zero 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 form 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 form 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 / (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} = biomass of prey type i consumed per time per predator j, $Qb_{ij} = a_{ij} V_{ij} / (1 + hj\ Si\ a_{ij} V_{ij})$ where a_{ij} is the rate of effective search by predator j for type i prey, hj 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

$$dV_{ij}/dt = v(Bi-V_{ij}) - v'V_{ij} - a_{ij}PjV_{ij} / (1 + hj\ Sia_{ij}\ V_{ij})$$ 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 $P_{sj} = 1 / (1 + h_j\ S_i\ a_{ij}\ V_{ij})$ 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 Psj ratio (of search time to handling time, i.e. the denominator of the disc equation) for each predator type is given just by $P_{sj} = R_j / (R_j - 1)$, where R_j is the Group info form ratio of maximum to Ecopath base consumption rate per predator. P_{sj} is updated at each Ecosim/Ecospace time step by first calculating starting estimates of the V_{ij} using the P_{sj} from the previous (or initial) time step, then using these estimates in the sums $S_i\ a_{ij}\ V_{ij}$ that define P_{sj}.

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 Figure oscillatory behaviour, you need to consider two possibilities:

1. The oscillatory behaviour may be a numerical artifact of the procedure used to update P_{sj}; or
2. The model's 'correct' behaviour 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 Vulnerabilities form) 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 Psj 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.

3.11 Modelling switching behaviour 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 Feeding time adjustment is set >0 in the 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 behavioural choices by predators to spend more or less foraging time in the arenas where specific prey are concentrated. In this case, the behavioural 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

$$a_{ij}(t) = K_{ij} a_{ij} B_i(t)^{Pj} / \Sigma_i' a_{i'j} B_{i'}(t)^{Pj} \quad \textbf{Eq. 55}$$

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 (switching power parameter on the Group info form). In particular:

$P_j = 0$, no switching

$P_j << 1$, prey must become very rare before predator j stops searching for them

$P_j >> 1$, predator switches violently when any prey increases or decreases.

P_j is limited to the range [0,2]. While it 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 <<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 (Figure 3.11).

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Without switching

$$c^{*} \quad w_{l}^{\prime} N$$

With switching (power parameter = 2)

$$N = \frac{C_{tot}!}{C_{tot-prot}!\, C_{tot}\, C_{tot-prot}}$$

Figure 3.11 Effect of allowing switching for migratory striped bass (Chesapeake Bay model, Christensen et al., MS).

3.12 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:

- direct - changes caused over short time scales (order one year) by changes in behaviour of organisms, whether or not there is an ecosystem-scale change due to fishing; and
- 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. In the next three sections 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.

3.13 Using Ecosim to study compensation in recruitment relationships

The multi-stanza representation of juvenile and adult biomasses was originally included in Ecosim to allow representation of trophic ontogeny (big differences in diet between juveniles and adults). To implement this representation, we found that it was necessary to include population numbers and age structure, at least for juveniles, so as to prevent ‘impossible’ 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-structured 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 multi-stanza 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 Ecosim users create multi-stanza dynamics, they need to be careful in setting model parameters that define/create compensatory effects. This begins with the Ecopath input parameters; in order for the juvenile dynamics to Figure compensatory mortality changes, at least two conditions are needed or helpful:

the juvenile group(s) must have relatively high *P/B*, i.e. high total mortality rate (see Edit multi-stanza groups);

the juvenile group(s) must have either relatively high EE (so that most mortality is accounted for as predation effects within the model) or else the user must specify a high (near 1.0) value in the Ecosim Group info form entry for the juvenile group's 'Proportion of other mortality sensitive to changes in feeding time' column.

Compensatory effects can be increased (the recruitment relationship is flat over a wider range of adult stock sizes, with a steeper slope of recruitment curve near the origin) by:

1. Limiting the availability of prey to juveniles (forcing juveniles to use small 'foraging arenas' for feeding) by setting all elements of the Ecosim Vulnerabilities form column for the juveniles to a small value (1.5-5); or

2. Setting a higher value for the juvenile group's 'Feeding time adjustment rate' parameter on the Ecosim *Group info* form, which causes the effective time exposed to predation while feeding to drop directly with decreasing juvenile abundance (i.e., simulates the 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 you are fairly sure from field natural history observation that the juveniles do in fact restrict their distribution to safe habitats when at very low abundance.

It is especially important to test alternative values for the vulnerability of prey to juveniles (point i). If vulnerability is too high, the Ecosim emergent stock-recruitment relationship is likely to look almost like a straight line out of the origin, i.e. without compensatory effect. If vulnerability is too low, the relationship may develop a 'spurious' dome-shape.

Note that in Ecosim multi-stanza groups, the 'Adult' group is always the oldest stanza. The stock-recruitment relationship between this adult stage and each of the younger stages separately is calculated using the Stock recruitment (S/R plot) form.

A stock-recruitment exercise in Ecosim

Always check the stock-recruitment curve shape, and play with Group info and Stage parameters that may affect it, before proceeding to other policy analysis. The simplest way to check this shape while minimizing complicating and confounding effects of trophic interactions is to set up Ecosim for a fairly long time scenario (40+ yrs):

1. Go to the Run Ecosim form (Time dynamic (Ecosim) > Output > Run Ecosim), select *Groups* from the drop-down *Target* menu on and then the adult pool. Using the fishing rate sketch pad, set up a fishing rate time series pattern where fishing is first stopped for a decade or so then ramped up over the remaining years to a very high value relative to your baseline rate from Ecopath.

2. Open the *S/R plot* form, and select the same adult group (Time dynamic (Ecosim) > Output > S/R plot).

3. Then run a series of scenarios. If the stock 'crashes' completely under heavy fishing, reshape the fishing rate to stop a few years after the crash, to check for a 'multiple equilibrium' outcome: i.e., for some models, and especially for top predators, there may be 'delayed depensation' effect where the predator fails to recover after heavy fishing, due to increases in species that it eats that are in turn competitors/predators on its juveniles—these species can cause 'recruitment failure'.

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3.14 Compensatory growth

Compensatory growth rate responses are modelled by setting the ‘feeding time adjustment rate’ (Group info form) 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 or growth. The *Q/B* increase with decreasing pool biomass is increased by decreasing vulnerability of prey to the pool (Vulnerabilities form). 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*.

3.15 Compensatory natural mortality

Compensatory changes in natural mortality rate (*M*) can be simulated by combining two effects: nonzero ‘Feeding time adjustment rate’ (set on the Group info form), 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.

3.16 Linking mediation and time forcing functions to trophic interaction rates

The basic Ecosim prediction for “flow” rate of type-*i* prey biomass to type-*j* predators is of the functional form

$$\textit{flow (biomass/time)} = a_{ij} \cdot V_{ij} \cdot P_j$$

where aij is a “rate of effective search” parameter, V_{ij} is vulnerable prey biomass, and P_j is effective predator abundance (for simple models P_j is just predator biomass; for multi-stanza groups it is the sum over ages in that group of numbers at age times body weight to the 2/3 power, an index of per-predator search rate). If vulnerable prey were randomly distributed over the modelled spatial area, and *V, P* were expressed as abundances per unit area, then a_{ij} would be interpretable as a volume or area swept per unit predator abundance (per P_j) per unit time, corrected for the proportion of time actually spent searching for food (foraging time and handling time adjustments reduce a_{ij} from its theoretical maximum value for a predator that searched all the time for food).

To understand how effects of habitat changes as represented through time forcing functions, and mediation effects as expressed through mediation functions of abundances of other organisms, are likely to affect trophic flow rates, we need to be a bit more careful about the a_{ij} parameter. In particular, we need to recognize that for most trophic interactions, predators search for prey only over restricted spatial foraging arenas, and hence V_{ij} is distributed only over such areas rather than at random over the whole system. Suppose the (practically unmeasurable) restricted area where foraging by j on prey i takes place is A_{ij} per unit total model area. Suppose that while in this area, each unit of predator abundance (per P_j) searches an effective area a^*_{ij} for prey. On average, each such area searched should result in capture of V_{ij}/A_{ij} prey, since this ratio is prey density in the arena area. In other words, the flow rate could be modelled more precisely (if we could measure A_{ij}) as

$$\text{flow rate} = a^*_{ij}/A_{ij} \cdot V_{ij} \cdot P_j$$

i.e., the basic Ecosim equation’s aij can be interpreted as $a_{ij} = a^*_{ij}/A_{ij}$. Expressed this way, we see that time forcing and/or mediation effects can influence the flow rate in at least three quite distinct ways:

1. by altering the effective search rate a^*_{ij} of the predator, for example by using a turbidity time forcing function or a mediation function of algal biomass that reduces a^*_{ij} at high algal biomass;
2. by altering the area A_{ij} over which vulnerable prey and/or predators are distributed, for example by a mediation effect where macrophyte or seagrass biomass limits the foraging area usable by small predatory fish, so increases in those plant biomasses should be represented as causing increases in A_{ij} for all prey i of the small fish as predator j. Another example would be restriction of A_{ij} for feeding on small fishes by pelagic birds caused by large pelagic fishes, which drive small fishes nearer to the surface where they are more available to the birds.
3. by altering the vulnerability exchange rates v_{ij} that determine (along with a^*_{ij}/A_{ij}) V_{ij} from total prey biomass B_i (the basic equation for V from B is $V_{ij}= v_{ij}\cdot B_i/(v_{ij}+v'_{ij}+a^*_{ij}/A_{ij}P_j)$. For example, if small fish respond to increased large plant biomass by occupying a larger area, the mixing rate (*vij*) of planktonic food organisms into that larger area will increase as well.

Until recently, Ecosim only allowed users to apply a single time forcing function to each trophic flow rate (each *i,j*), and only as a multiplier (with base value 1.0) on the rate of effective search a_{ij} (Case 1 above). Likewise, users could only apply a single mediation function to each flow rate, as a multiplier on vij (Case 3 above). So, for example, users could model how increases in large plant biomass affect exchange rates of food organisms into areas adjacent to where small fish hide, but not how increases in A_{ij} imply less severe intraspecific competition (reduced effect of P_j on V_{ij}) and also reduced predation rates on *j* when it is spread over a larger area relative to its predators. Further, they could not represent such multiple impacts as reduced foraging efficiency (lower a^*_{ij}) associated with increased algal abundance, or reduction in area occupied by macrophytes due to shading by the algae.

We now allow users to apply up to 5 different multiplier (time forcing and/or mediation) functions to each trophic flow (*i,j*) rate prediction, and to specify whether each function multiplies a^*_{ij}, A_{ij}, and/or v_{ij}. Two simple forms are used to specify these multiplier options, and it is invoked simply by clicking on the *i,j* cell in the Ecosim Apply forcing function (consumer) or Apply mediation forms. Using these forms, users can choose the parameter which is multiplied by each forcing or mediation function, i.e. one of the following choices:

1. Multiply overall predator rate of effective search ($a_{i,j}$), for example to represent time-varying turbidity changes that affect predator search efficiency or mediation effects of algal biomass on search efficiency.
2. Multiply vulnerability exchange rate (v_{ij}), for example to represent increased movement rates of prey into vulnerable behavioural state at times when water mixing rates are higher;
3. Multiply area of foraging arenas (divide A_{ij} by multiplier), for example to represent increase in habitat area available for juvenile fish refuges;
4. Multiply area (divide A_{ij}) and also multiply v_{ij}, for example to represent increase in safe foraging habitat available to a predator that feeds on prey that become available in foraging arenas through passive drift/mixing processes such that increasing area used by predator results in higher proportion of total prey population being available in foraging areas at any moment.

Forms for setting up forcing and trophic mediation functions in Ecosim are found under the Ecosim input section of the *Navigator window* (*Time Dynamic (Ecosim)* > *Input* > *Forcing function; and Time Dynamic (Ecosim)* > *Input* > *Mediation*; see Forcing function and Mediation).

3.17 Primary production

For primary producers the production is estimated as a function of the producers' biomass, Bi, from a simple saturating relationship

$$f(B_i)=\frac{r_i\cdot B_i}{1+B_i\cdot h_i}$$ **Eq. 67**

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. If a Forcing function is applied to primary production (see Apply FF (primary producer)), it multiplies the r parameter in Eq. 67.

3.18 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 on the Ecosim parameters form, in which case N_T is calculated as N_T = ft N_{To} where N_{To} is the Ecopath base estimate of N_T (at the start of each simulation) and ft 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_To of total nutrient is entered by specifying the base free nutrient proportion $pf = Nf / N_To$ on entry to Ecosim (also on the Ecosim parameters form: *Time dynamic (Ecosim) >Input > Ecosim parameters*), from which the Ecosim initialization can calculate N_To as simply $N_{To} = \sum i\ \eta i\ Bi / (1-pf)$. 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 $P/B_j=P/B_{max,j}\ N_f/(K_j+N_f)$, where the parameters $P/B_{max,j}$ and K_j are calculated as part of the Ecosim initialization using input estimates by the user of the ratios $P/B_{max,j} / P/B_{Ecopath,j}$ (Ecosim Group Info form). The Michaelis constant K_j is set so that $P/B_j = P/B_{Ecopath,j}$ 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 P/B_j more variable with changes in N_T and N_f) by increasing the input $P/B_{max,j} / P/B_{Ecopath,j}$ ratio.

The default free nutrient proportion pf is set at unity, which causes N_f to be virtually constant over time (and hence P/B_j's to be virtually independent of nutrient concentration changes). Thus to "turn on" nutrient limitation effects, you must set a lower value for pf, (e.g., 0.3) on the Ecosim parameters form.

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 *Nf* 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 pf 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-P/B 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.

3.19 Density-dependent changes in catchability

In fisheries modelling 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 or Effort response power ganization 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 behaviours 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 Fo by using either the fishing rate 'sketch pad' interface (Ecosim Run Ecosim form) or time reference data files (see Time series). 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 form.

For example, setting a value of 5 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

$QRo = q_{\max} / q_o$

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 Bo 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 ft rather than absolute fishing rates Ft, 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=(historical catch)/(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*).

3.20 Modelling 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 by checking the box on the Ecosim parameters form. Input parameters must be set on the Fleet size dynamics form.

When the fleet/effort response option is invoked, using the checkbox on the Ecosim Run Ecosim form, 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*.

Fast time response model

Eg,t is the current amount of active, searching gear (scaled to 1.0 at the Ecopath base fishing mortality rates), and Kg,t is the fleet effort capacity (Eg,t<Kg,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 Bi) 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 thus:

$$PR_{g,t} = I_{g,t} - c_g$$

where c_g is the cost of a unit of fishing effort for gear g (cost and price factors are entered via the Definition of fleets and Market price forms). 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:

$$E_{g,t+1} = \frac{K_{g,t} I_{g,t}^{P}}{Ih_g^{P} + I_{g,t}^{P}}$$

Here, I_{hg} and p are fleet-specific response parameters. I_{hg} is the income level needed for half maximum effort to be deployed and p is 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 Figure 3.12.

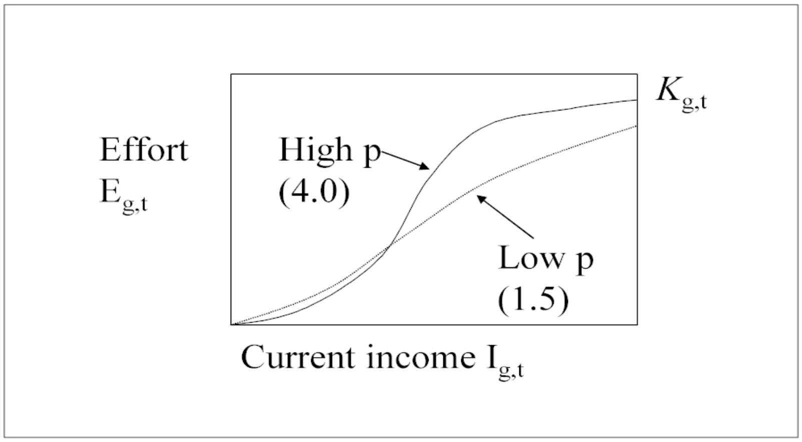

Figure 3.12 Effect of the 'heterogeneity' parameter, *p*, on effort/income function.

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Slow time reponse model

For each fleet, slow effort responses are modelled as changes in fleet capacity ($K_{g,t}$), which is a function of the capital depreciation rate ρ_g, the capital growth rate $r_{g,t}$ and profit $PR_{g,t}$. The capital growth rate is calculated via a growth factor gf_g,t, i.e.,

$$gf_{g,t+1} = \frac{K_{g,t}\left(r_{g,t} + \rho_g\right)}{PR_{g,t}}$$

where $K_{g,1}$, ρg and $r_{g,1}$ are set by the user. The annual capacity $K_{g,t}$ is then updated as

$$K_{g,t+1} = K_{g,t}\left(1 - \rho_g\right) + gf_{g,t}PR_{g,t+1}.$$

3.21 Using Ecosim for Stock Reduction Analysis

A very useful technique for using long term data in stock assessment is Kimura's "stock reduction analysis". In this technique, historical catches are treated as fixed, known quantities, and are subtracted from simulated stock size over time so as to aid in estimating how large (and/or productive) the stock must have been in order to have sustained those catches and to have been reduced by some estimated fraction from its historical level. In some assessment literature, treating catches as fixed knowns is also called "conditioning on catch". A drawback of treating catches as fixed values is that catches in fact arise from the interaction of fishing effort and abundance, and ignoring this dynamic interaction amounts to treating the catches as purely depensatory impacts on stock size (when simulated stock size declines, the fixed catches can cause progressively larger calculated fishing mortality rates F, leading to a depensatory spiral of rapid collapse in the simulated stock, which may or may not have been possible in the real system).

When creating historical reference csv files for model testing (see Import time series), all or part of a catch time series for any group(s) can be treated as a forcing input (with simulated F calculated each year as (input catch)/(simulated stock size)) by setting its data type to -6 (rather than the usual 6 for fitting catch data). Note that the catch time series for a group can be entered in two columns, with one column set to data type 6 and one to data type -6, where catches for years to be treated as forcing are placed in the -6 column and catches for years when catch is to be predicted from effort or assessment Fs placed in the 6 column. Most often, this splitting of catches into two columns should be used in cases where there are no independent assessments of F for some early years.

The Monte Carlo simulation interface in Ecosim can be used to search for ecopath biomasses needed to have sustained historical catches. We cannot search for such initial biomass values by simple nonlinear search methods, due to the biomass constraints implied by ecopath mass balance. The Monte carlo simulation interface can do a large number of simulations with randomly varying trial values of ecopath biomasses, and can retain trial values that result in improved model fit; such a search or fitting procedure is known as a "Matyas search".

3.22 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 Edit multi-stanza groups form for a population from the Ecopath menu, and enter a nonzero value for the hatchery forcing function number. Forcing functions can be sketched using Ecosim's Forcing function form or can be imported using Import time series on the Ecosim menu (set the data type to 2). Note that imported time series must be activated using the Time series form. After activating the imported time series, check the Forcing function form for the number allocated to your hatchery stocking time series. 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.

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 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 *P/B*) 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 modelled ecosystem).

3.23 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 Figure 3.3 in Vulnerabilities in Ecosim).

The vulnerability parameter is in general not subject to direct measurement. There are, however, other ways of estimating it, and Ecosim includes two 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. Through fitting to time series data (see Fitting to time series data and Hints for fitting models to time series data).

It is possible and indeed recommended to use all of these methods to obtain estimates for the vulnerability parameters.

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4 Introductory material: Ecospace

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).

For more details about Ecospace, see: An overview of Ecospace; Representing seasonal migration; Advection in Ecospace; Fitness-driven dispersal behaviour; Prediction of mixing rates; Predicting spatial fishing patterns; and Numerical solutions.

For instructions on using Ecospace see Ecospace inputs and Ecospace outputs.

4.1 An overview of 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 behaviour. This has been remedied through the development of Ecospace (Walters et al. 1999), a dynamic, spatial version of Ecopath, incorporating all the key elements of Ecosim.

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.

See Ecospace inputs for details on how to start using Ecospace.

4.2 Representing seasonal migration in Ecospace

Larger organisms commonly have seasonal migration patterns that allow them to utilize favourable 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 centreed on the distribution of some dominant migratory species. Second is a more complex "Eulerian" approach, which does involve explicitly modelling changes in instantaneous rates of biomass flow among the Ecospace spatial cells, in some way that approximates at least the changing centre of distribution of the migratory species.

The Eulerian approach is implemented in Ecospace by allowing users to define a monthly sequence of "preferred" map cell positions (using the Migration dialogue box accessible from the Ecospace Basemap form (Migration patterns are also defined on the *Basemap* form) 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 form.

The *Migration* dialogue box displays a map of the Ecospace region, with migratory species and months of the year listed. 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.

The mathematical method used in Ecospace to create migratory behaviour 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 Figure 4.3. The function is reversed for movement across a northern cell boundary. A 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 towards 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.

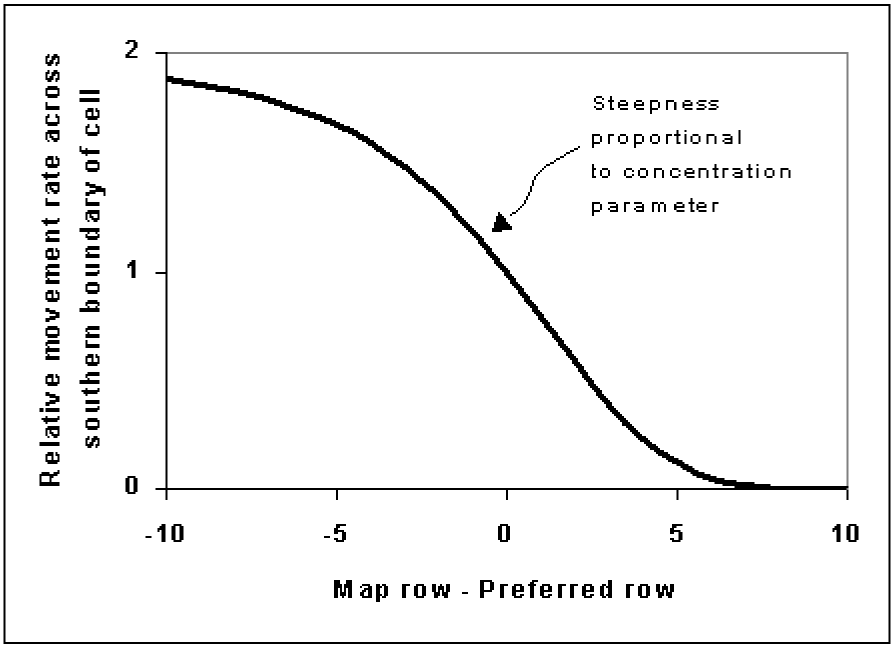

Figure 4.3 Relative movement rates; see text for details.

Tips for setting up migration in Ecospace

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)/(mean number of cells between preffered 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 form) 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 parameters form) 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 favoured species, the total effort will concentrate accordingly and can sometimes generate very high fishing rates near the centre of the

migrating stock distribution. Remedies include reducing total effort (Ecospace fishery form, total effort multiplier) and distributing effort more widely (Ecospace fishery form, reduce value of “effective power”).

6. Concentrating a migratory predator can cause local depletion of food organisms and/or reduced per-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 Vulnerabilities form).
7. 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.

4.3 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 (see Advection dialogue box, accessible from the Basemap form). Based on these patterns Ecospace calculates equilibrium horizontal flow and upwelling/down-welling 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 $df / dt = 0$, $dvu / dt = 0$, $dvv / dt = 0$ 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):

$$\frac{dh}{dt} = \frac{v_{uk}}{u} + \frac{v_{vk}}{v} - D_k \quad \textbf{Eq. 74}$$

$$\frac{dv_u}{dt} = k \cdot W_u - k \cdot v_u - f \cdot v_v - \frac{g \cdot h}{u} \quad \textbf{Eq. 75}$$

$$\frac{dv_v}{dt} = k \cdot W_v - k \cdot v_v - f \cdot v_u - \frac{g \cdot h}{v} \quad \textbf{Eq. 76}$$

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 $v_u = W_u$, $v_v = Wv$ 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:

1. 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

2. For each of the months specify the following:

    Month Number

3. For this month specify for 0 to *nRow* + 1, and for 0 to *nCol*+1, unit: m/s

    Current *X*-velocity, Current *Y*-velocity

4. 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)

4.4 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 favourable habitats. The mechanisms involved in this procedure are explained in more detail by Walters et al. (1999).

4.5 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:

$$G_{kc} = O_{kc} \cdot U_{kc} \cdot \frac{\sum_i p_{ki} \cdot q_{ki} \cdot B_{ic}}{C_{kc}} \quad \textbf{Eq. 68}$$

where Okc 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. 68 the total mortality rate is distributed over cells according to

$$F_{kc} = \frac{N \cdot F_k \cdot G_{kc}}{\sum_c G_{kc}} \quad \textbf{Eq. 69}$$

while each group in the cell is subject to the total fishing mortality

$$F_{ic} = \sum_k F_{kc} \cdot q_{ki} \quad \textbf{Eq. 70}$$

4.6 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. 50 (in Ecosim basic) 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)

$$B_e = \frac{1 + gC}{Z + E} \quad \textbf{Eq. 71}$$

while following the time trajectory

$$B_{t+\Delta t} = B_e + (B_t - B_e) \cdot e^{-(Z+e)\Delta t} \quad \textbf{Eq. 72}$$

Denoting the exponential weight term above Wt this can be re-expressed as,

$$B_{t+\Delta t} = W_t \cdot B_t + (1 - W_t) \cdot B_e \quad \textbf{Eq. 73}$$

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. 73 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 detraction of the final results. The resulting computations are carried out orders of magnitude faster than it the time splitting was not included.

4.8 Spatial optimization procedures

Duke University
Marine Geospatial Ecology Lab

LENFEST
OCEAN
PROGRAM

This section contains the methodology and scientific material for the *Spatial optimizations* tool in Ecospace. This routine is implemented using the *Spatial optimizations* form (*Spatial dynamic (Ecospace)* > *Tools* > *Spatial optimizations*). For instructions for implementing this routine, see Spatial optimizations.

We describe two approaches for spatial optimization of protected area placement, both based on maximizing an objective function that incorporates ecological, social, and economical criteria. Of these, a seed cell selection procedure works by evaluating potential cells for protection one by one, picking the one that maximizes the objective function, add seed cells, and continue to full protection. The other is a Monte Carlo approach, which uses a likelihood sampling procedure based on weighted importance layers of conservation interest (similar to Marxan's) to evaluate alternative protected area sizing and placement. The two approaches are alternative options in a common spatial optimization module, which uses the time- and spatial dynamic Ecospace model for the evaluations. The optimizations are implemented as components of the Ecopath with Ecosim approach and software. In a case study, we find that there can be protected area zoning that will increase economical and social factors, without causing ecological deterioration. We also find a tradeoff between including cells of special conservation interest and the economical and social interest, and while this does not need to be a general feature, it emphasizes the need to use modeling techniques to evaluate the tradeoff.

The most widely used approach for spatial planning with a conservation perspective is the Marxan approach and software, (http://www.uq.edu.au/marxan/) developed primarily by Hugh Possingham and colleagues at the Ecology Centre, University of Queensland. Marxan is a very flexible approach capable of incorporating large data sources and use categories, it is computationally efficient, and lends itself well to enabling stakeholder involvement in the site selection process.

We view the new importance layer sampling procedure as complimentary to the Marxan approach in that its strong side, through the underlying trophic modeling background is in evaluating ecological processes, including spatial connectivity; topics that are not well covered in Marxan analysis. In doing so, we, however, involve a rather complicated dynamic model, even if user-friendly, and this unavoidably has a cost. We therefore advocate that the two approaches, with their given advantages and limitations, be applied in conjunction – using two sources to throw light at a problem from different angles, beats one, any time. We have in order to facilitate such comparative studies developed a two-way bridge between Marxan and EwE, enabling exchange of spatial information and of optimization results between the two approaches. We describe only briefly aspects of this below, as we have applied the bridge elsewhere for a formal comparison (Ferdaña et al., MS).

Methodology

Objective function

We employ an objective function for the optimizations, which corresponds to the objective function used in the policy optimization module of EwE. This module, which has been applied to a number of case studies, (e.g., Christensen and Walters, 2004; Araújo et al., 2008; Arreguin-Sanchez et al., 2008) uses a non-linear search routine to find a combination of effort by fishing fleets that will maximize the objective function. The objective function in turn includes ecological, economical and social indicators, even legal constraints if pertinent, through considering profit, number of jobs, stock rebuilding, and two ecological measures. For the spatial optimizations we add a further indicator in form of a boundary weight factor (See Table 1)

The profit objective is calculated by summing revenue across all fleets, and subtracting the cost for operating. Cost is considered a linear function of effort with a fixed cost added. The following calculation is performed for each time (t t) step to estimate the revenue (R_t R_t),

$$R_t = \sum_f \sum_i [F_{fi} \cdot B_i \cdot V_{fi}] - \sum_f [E_f \cdot C_{v,f} - C_{p,f}]$$

$$R_t = \sum_f \sum_i [F_{fi} \cdot B_i \cdot V_{fi}] - \sum_f [E_f \cdot C_{v,f} - C_{p,f}] \qquad \text{Equation 1}$$

with F_{fi} F_{fi} being the fishing mortality for group (i i) caused by fleet (f f), B_i B_i is the biomass of (i i), and V_{fi} V_{fi} is the ex-vessel value per unit weight of (i i) caught by (f f). E_f E_f is the relative effort for (f f), the $C_{v,f}$ $C_{v,f}$ is variable cost per unit effort for (f f), and $C_{p,f}$ $C_{p,f}$ is the fixed cost for fleet (f f).

The calculations in Equation 1 are, as indicated, performed for each time step, with benefit summed over time. We, however, discount future values based on either a traditional discount rate, or an inter-generational discount rate (Sumaila and Walters, 2005), based on user preference.

As a social indicator, we use the number of jobs over time (J_t J_t) created in the ecosystem, and we estimate this for each time step (t t) from the landed value of the exploited group times the relative number of jobs per unit value ($N_{\downarrow}i)$ $N_{\downarrow}i)$, or

$$J_t = \sum_f F_{fi} \cdot B_i \cdot V_{fi} \cdot N_i$$

Similar to the profit objective, we discount the number of jobs over time.

We estimate the mandated rebuilding objective (M_t M_t) for each time step (t t) from

$$M_t = \sum_i {}^{B_{i'}}\!/_{B_{i\bullet}}$$

where $B_{i\bullet}$ $B_{i\bullet}$ is baseline Ecopath biomass for group (i i), and $B_{i'}$ $B_{i'}$ equals the group biomass B_i B_i if B_i B_i is lower than the mandated biomass, $B_{m,i}$ $B_{m,i}$ for the group, and $B_{m,i}$ $B_{m,i}$ if it is not.

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The mandated rebuilding objective can be used to set ‘minimum biological acceptable levels’ (or MBAL as commonly used). By setting high mandated biomasses ($B_{m,i}$ $B_{m,i}$) for a group it can also be used to capture ‘existence values,’ e.g., of marine mammals of interest for a whale watching industry. We do not discount the mandated rebuilding structure over time.

The ecosystem structure objective is meant to capture that mature (K-type) ecosystems tend to be dominated by long-lived species and individuals (Odum, 1969). We seek to capture this characteristic through the inverse production/biomass ratio, estimating for each time step (t t)

$$S_t = \sum_i B_i \cdot S_i$$

where S_t S_t is the overall ecosystem structure measure, and S_i S_i the ecosystem structure factor for (i i). We provide default values for S_i S_i in form of the inverse $\frac{P_i}{B_i}$ $\frac{P_i}{B_i}$ ratios (unit year), supplied as part of the basic parameterization of the Ecopath model. To avoid unduly influence by very short-lived species we have (arbitrarily) set S_i S_i to 0 for groups with an average lifespan of less than a year, (i.e. groups whose $\frac{P_i}{B_i}$ $\frac{P_i}{B_i}$ is less than 1 year-1).

The ecosystem structure objective is not discounted over time; having long-lived species in the future being deemed as important as having them now.

As a measure of biomass diversity, we used a modified version of Kempton’s Q75 index, originally was developed to describe species diversity (Kempton, 2002). We here used a biomass diversity indicator following Ainsworth and Pitcher (2006), albeit slightly modified. We estimate the biomass diversity index ($Q_1 75)$ $Q_1 75)$ from

$$Q_{75} = S \Big/ \left[2\, log\left(N_{0.25-S} \Big/ N_{0.75-S}\right)\right]$$

$$Q_{75} = S \Big/ \left[2\, log\left(N_{0.25-S} \Big/ N_{0.75-S}\right)\right]$$

here S S is the number of functional groups, and N_{i-S} N_{i-S} is the biomass of the ($i \cdot S$ $i \cdot S$)th most common group, using a weighted average of the two closest group if ($i \cdot S$ $i \cdot S$) is not an integer. The biomass diversity index describes the slope of a cumulative group abundance curve. As a sample with high diversity (evenness) will have a low slope, we reverse the index and express it relative to index value from the Ecopath base run (Q^{*}_{75} Q^{*}_{75})

$$Q'_{75} = 2 - Q_{75} \Big/ Q^{*}_{75}$$

$$Q'_{75} = 2 - Q_{75} \Big/ Q^{*}_{75}$$

We truncate the index in the extreme and unlikely case that Q_{75} Q_{75} would more than double from the base run. We only include higher trophic level groups (TL>3) in the calculation of the biomass diversity index – should this, for models with only few functional groups, lead to less than 10 groups being included in the calculations, we, however, base the calculations on all living groups. As for the other ecological indicators we do not discount future index values.

The final element in the objective function represents spatial connectivity, expressed through the boundary weight factor, L L

$$L = \sum_{b} \frac{I_b}{\sum_c A_c}$$

$$L = \sum_{b} \frac{I_b}{\sum_c A_c}$$

where the total protected area size (A_c A_c , km2) is summed over spatial cells (c c), and the boundary length is estimated by summing over all protected cell (b b) the side lengths (I_b I_b , km) that do not border another protected cell or land.

With the elements of the objective function being defined, we can now obtain the overall objective function measure (O O) from

$$O = w_R \cdot R + w_J \cdot J + w_M \cdot M + w_S \cdot S + w_Q \cdot Q'_{75} + w_L \cdot L$$

$$O = w_R \cdot R + w_J \cdot J + w_M \cdot M + w_S \cdot S + w_Q \cdot Q'_{75} + w_L \cdot L$$ Equation 2

Where each of the objective weighting factors, (w w), can assume any value, including zero, which is used for measures that are ignored in a given optimization. We use the objective function measure for both of the optimization methods described below.

Seed cell selection procedure

This optimization method is based on a previous study (Beattie 2001; Beattie et al. 2002), in which we use a very simple optimization scheme to evaluate tradeoff between proportion of area protected and the ecosystem-level objective function. We have modified the previous approach by securing a better program flow, and notably by changing the objective function from considering only profit from fishing and existence value of biomass groups to the more detailed function described above (Equation 2).

The procedure takes as its starting point the designation of one, more, or all spatial cells as ‘seed cells’, i.e. cells that are to be considered as potential protected cells in the next program iteration. The procedure will then run the Ecospace model repeatedly between two time steps, closing one of the seeds cells in each run, while storing the ecosystem objective function value. The seed cell that results in the highest objective function is then closed for fishing, and its four neighboring cells (above, below, and to either side) are then turned into seed cells, unless they are so already, or already are protected, or are land cells. This procedure will continue until all cells are protected.

The time over which the selection procedure is run is chosen dependent on the application. Typically, an ecosystem model is initially developed and tuned using time series data to cover a certain time period, e.g., from 1950 to 2005. Subsequently, the model is used in a scenario development mode to evaluate for instance protected area placement covering the period 2006-2020.

The major result from the seed cell selection procedure is an evaluation of the tradeoff between size of protected area, and each of the objectives in Equation 2. This can, for instance, be used to consider what proportion of the total area to close in subsequent, more detailed analysis based on importance layer sampling.

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Importance layer sampling procedure

An advantage of the seed cell modeling approach described above is that it allows a comprehensive overview of the tradeoff between proportion of area closed to fishing, and the ecological, social, and economical benefit and costs of the closures. This is done, based on the information already included in the EwE modeling approach, with no new information being needed. While this may be an advantage from one perspective, it does not allow use of other form for information, notably in form of spatial information, such as, for instance, critical fish habitat layers from GIS.

To address this shortcoming, we have developed an alternative optimization routine for the Ecospace model, which uses spatial layers of conservation interest ('importance layers') to set likelihoods for spatial cells being considered for protection. The optimizations are performed using a Monte Carlo approach where the importance layers are used for the initial cell selection in each MC realization. The Ecospace model is then run, the objective function (Equation 2) is evaluated, and the results, including which cells were protected, are stored for each run (see Figure 1).

The importance layers are defined as raster layers, with dimensions similar to the base map layers in the underlying Ecospace model, i.e. they are rectangular cells in a grid with a certain number of rows and columns. Each cell in a given layer has a certain 'importance' for conservation, expressed, e.g., as the probability of occurrence for an endangered species. For each importance layer (l l), we initially scale the importance layer values to sum to unity, and then calculate an overall cell weighting (w_c w_c) for each cell (c c) from

$$w_c = \sum_l w_l \cdot C_{c,l} \qquad \text{Equation 3}$$

where w_l w_l are the importance layer weightings, and $C_{c,l}$ $C_{c,l}$ the cell-specific, scaled importance layer values.

In order to evaluate how well the importance layers are represented in each optimization run, we estimate

$$w_l' = \left(\Sigma_{c'} w_l \cdot C_{c',l}\right) \Big/ \left(\Sigma_{c^*} w_l \cdot C_{c^*,l}\right) \qquad \text{Equation 4}$$

Where c' c' indicates cells selected in a given run, and c^* c^* the cell with the highest weightings for the given layer. The layer-specific indicator (w_l' w_l') can obtain values in the range between 0 and 1.

For each optimization search, one has to select the proportion of water cells to protect in the runs, as well as how many times to repeat the Monte Carlo runs. It is possible to set the search routine up to iterate over a range of protection levels, e.g., from 10% to 100% protected in steps of 10%.

Similar to the seed cell selection procedure, we typically develop and tune the model to an initial time period, and then use the sampling procedure to evaluate scenarios for protected areas for a subsequent time period.

We have developed a capability for Ecospace to read raster files with spatial information such as importance layers or other Ecospace base map layers. The reading is possible from comma separated text files (.csv), ESRI ASCII files (.asc), and ESRI shape files (.shp). The files need to have layers or columns with row and column numbers matching the Ecospace model. This capability is designed to allow straightforward exchange between the Ecospace modeling and Marxan analysis, with the constraint that it needs to be possible to represent the layers in raster form. The reading of the spatial files is described in more detail in Spatial optimization and Setting importance layers.

The spatial-dynamic modelling approach

The methodologies for spatial optimization described here rely on the Ecospace model, implemented within the Ecopath with Ecosim approach and software. The Ecospace model is described in a number of publications, notably by Walters et al. (1999; submitted). The Ecospace models builds on an underlying Ecopath trophic models, which can have any number of functional groups or age- and species-specific groups as appropriate for the questions to be addressed. The Ecospace runs picks up levels of fishing effort over time from an associated Ecosim runs, including mediation factors and most other factors that do not have a potentially important spatial dimension, which Ecosim cannot address.

Ecospace, in essence, employs the time-dynamic Ecosim model in each cell in a raster grid, while accounting for cell connectivity and fish movements explicitly. Fishing effort is distributed over space according to a gravity model, optimizing the gain obtained from fishing. Fish migration and advection can be modeled explicitly, and the base map can be populated from spatial layers.

The spatial model, Ecospace, can work with any number of protected cell types. For each of these, fishing may be banned for one or all fleets, and for all or part of the year. While Ecospace can handle multiple types of protected cells, it needs to be specified for the optimization routines, which type of protected cells they are to work with; we can only consider one type within a given optimization run.

Table 1. objective function employed for spatial optimization. Each objective is given a weighting factor, and the optimization seeks to optimize the summed, weighted objectives.

Objective	Description
Profit	Estimated by ‘fleet’, and summed over all such
Jobs	Estimated from value of fisheries, and relative number of jobs/value
Mandated rebuilding	A minimum acceptable level, by group
Ecosystem structure	Default values based on biomass/productivity ratios expressing average longevity, weighted by group
Biomass diversity	Biomass evenness among groups
Boundary weight	Estimated as total boundary length over the protected area size. Captures spatial connectivity

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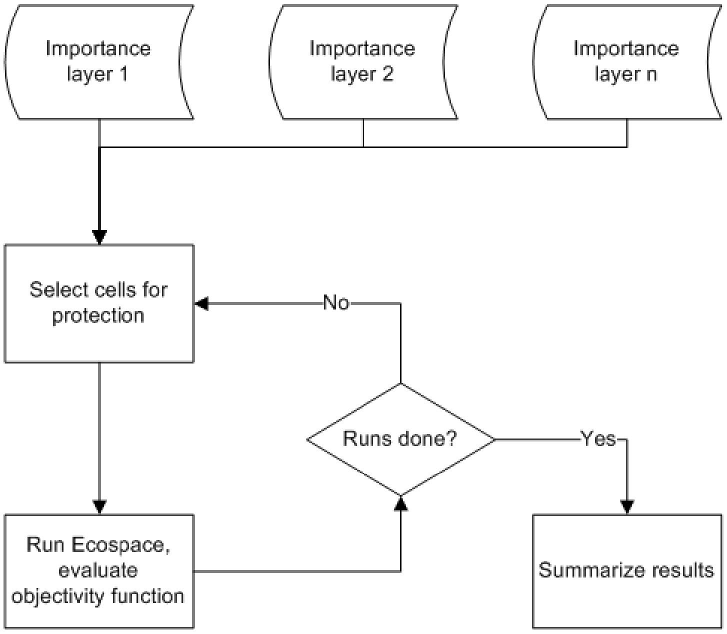

Figure 1. Logic of the importance layer sampling procedure. For each run a given percentage of all cells are protected based on weighted likelihood in importance layers. The evaluation of each run is done independently based on a defined objective function..

5 Ecopath with Ecosim 6: Getting started

This chapter contains information to help you get started using Ecopath with Ecosim 6 (How to obtain the Ecopath with Ecosim 6 software; Software support, copyright and liability; Installing and running Ecopath with Ecosim; Previous versions; Getting help; General features of the Graphic User Interface; File menu; View menu; Tools menu; Windows menu; and Help menu).

Please note that help for the Ecopath, Ecosim and Ecospace menus can be found at the beginning of Chapters 6, 8, and 10 of the EwE6 User Guide or by clicking on these links: Ecopath menu, Ecosim menu, Ecospace menu.

5.1 How to obtain the Ecopath with Ecosim 6 software

The setup programme for Ecopath with Ecosim 6 (EwE6) can be downloaded from www.ecopath.org. Simply download the set up file and follow the prompts. Alternatively (write, fax or email us (through the user support section of www.ecopath.org) and we will send you a CD with the setup 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.

5.2 Software support, copyright and liability

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 (through the user support section of www.ecopath.org) 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.

5.3 Installing and running Ecopath with Ecosim

Installation is done via a customized third-party setup program. Simply click on the link to the setup programme on the Ecopath website (www.ecopath.org) and choose *Run*. Some browsers will give a warning that the software is from an unknown publisher, click *Run* if you get this warning. Then follow the prompts to for installing the software.

If you wish to use the Network Analysis functions, make sure the *Network Analysis plug in* box is checked when prompted. Click *Install* then *Finish* to complete installation. An icon for running the software will be placed on your desktop. Otherwise, navigate to the directory in which the model was saved (default: C:\Program Files\Ecopath with Ecosim 6) and run the programme (EwE6.exe) from there.

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

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Currently EwE6 will only run on Windows 2000, Windows XP and Vista platforms. Other version of Windows have not be tested and we cannot ensure support. EwE6 will not run directly on systems running OS X (Mac) but will run on virtual Windows platforms on these computers.

If you have any other problems with installation, please contact us through the user support section of www.ecopath.org.

5.4 Previous versions

Any model built using a version of EwE5 later than version 1.67 can be converted to EwE6 format using the Ecopath database conversion wizard (see note below).

When you select the old database using *Open model* on the File menu you will be prompted by the wizard to choose a model to extract from the old database. Select the model and follow the prompts. EwE6 will extract the model to a new database and save it in the Ecopath with Ecosim 6 folder (where you saved EwE6 on installation - usually in Program files).

EwE6 no longer supports multiple models in the same database.

Note: To check the version of your EwE5 model, open the model's database with MS Access and open the table called "Database specifications". The version of your model is the last (i.e., highest) number listed in the *Version* field.

5.5 Getting help

Pressing *F1* at any time while running EwE6 will open the appropriate help file and give you context-sensitive help. You can also search the help files using the *Help menu*.

Should you have problems not easily solved using the help files or this guide we encourage you to contact us for support (through the user support section of www.ecopath.org).

5.6 General features of the Graphic User Interface

EwE6 has a markedly different look to any previous version of EwE, representing much improved navigability of the software. After opening an EwE model, you will see an interface similar to that shown in Figure 5.1, consisting of:

1. Menu bar
2. Shortcut buttons
3. Navigator window
4. Main screen
5. Tabs bar
6. Status tab
7. Remarks tab
8. Status bar

Note: click on *Basic input* on the *Navigator window* to see your Ecopath model groups.

All input and output forms are listed in a nested directory in the *Navigator window* (see section below), enabling users to move intuitively through the steps of building and using a model. A key feature of the Graphic User Interface (GUI) is the ability to select forms from the *Navigator window* and display them as tabulated windows on the *Tabs bar*. This allows you to switch easily among forms in current use.

Users can change the look of the GUI using a number of features available on the Tools menu. In addition, any of the windows in the GUI can be hidden or visible, docked (locked in place) or floating, or can be docked to new locations.

Floating windows are a particularly useful feature for users with multiple monitors as one form can be edited whilst referring to others.

A window can be switched from visible to hidden mode using the push pin icon (AutoHide) on its title bar. To switch from visible to hidden mode, click on the vertical AutoHide icon (📌) then move your mouse away from the window and click elsewhere on the screen. It will be hidden and a tab will appear that gives you access to the hidden window. To view the window temporarily click on the tab. To switch back to visible mode, click on the horizontal push pin icon (⊣) whilst viewing the window.

Any window that is in visible mode (📌) can be moved to a floating window or docked to a new location. To move a window, click on the title bar at the top of the window (or its tab if it is on the Tabs bar) and move the mouse whilst holding down the left mouse button. A transparent blue box and a set of window dropper icons will appear (e.g., ▣). To move to a floating window, drop the box anywhere on the screen except on the dropper icons. To move to a new docked location, position the mouse over the dropper icon where you would like to dock the window and release the mouse button. Use the centre docking icon (✚) to lock a window to the Tabs bar.

If you have checked “Save window layout” on the Tools menu, changes in layout will be preserved next time you open the model.

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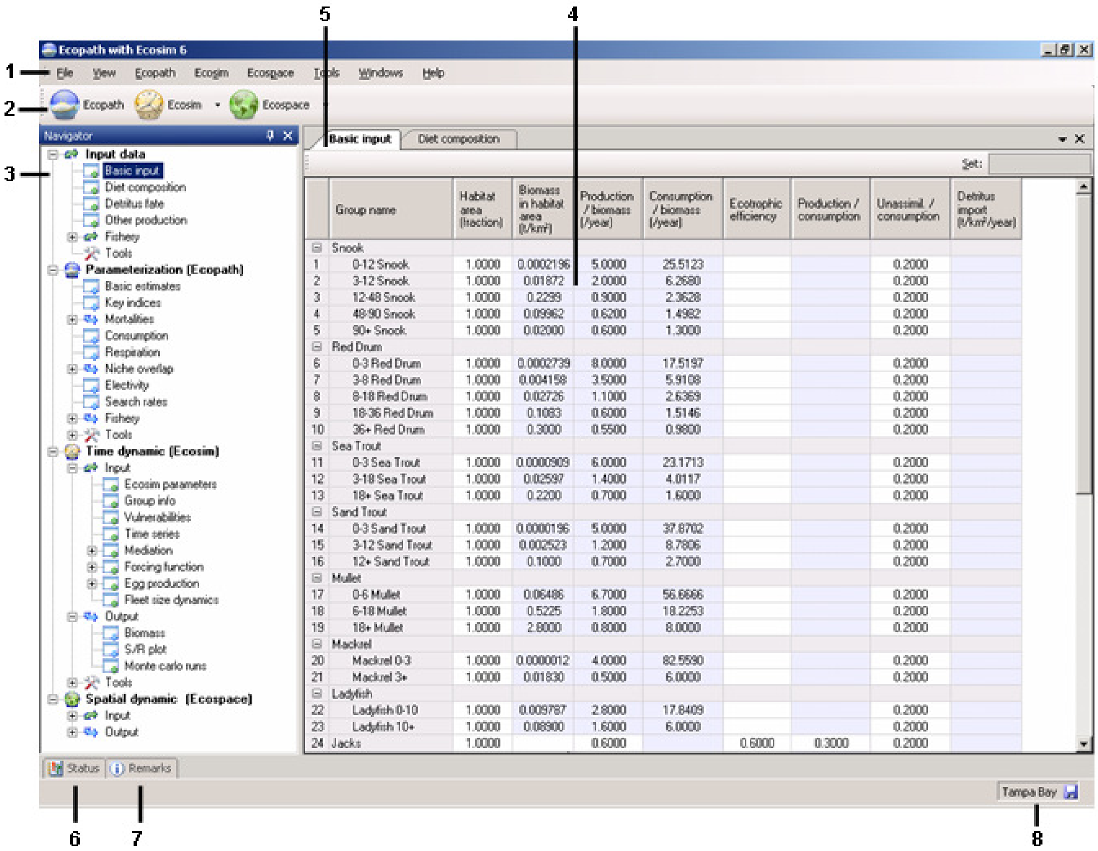

	Group name	Habitat area (fraction)	Biomass in habitat area (t/km²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic efficiency	Production / consumption	Unassimil. / consumption	Detritus import (t/km²/year)
⊟	Snook								
1	0-12 Snook	1.0000	0.0002196	5.0000	25.5123			0.2000	
2	3-12 Snook	1.0000	0.01872	2.0000	6.2680			0.2000	
3	12-48 Snook	1.0000	0.2239	0.9000	2.3628			0.2000	
4	48-90 Snook	1.0000	0.09962	0.6200	1.4982			0.2000	
5	90+ Snook	1.0000	0.02000	0.6000	1.3000			0.2000	
⊟	Red Drum								
6	0-3 Red Drum	1.0000	0.0002739	8.0000	17.5197			0.2000	
7	3-8 Red Drum	1.0000	0.004158	3.5000	5.9108			0.2000	
8	8-18 Red Drum	1.0000	0.02726	1.1000	2.6369			0.2000	
9	18-36 Red Drum	1.0000	0.1083	0.6000	1.5146			0.2000	
10	36+ Red Drum	1.0000	0.3000	0.5500	0.9800			0.2000	
⊟	Sea Trout								
11	0-3 Sea Trout	1.0000	0.0000909	6.0000	23.1713			0.2000	
12	3-18 Sea Trout	1.0000	0.02597	1.4000	4.0117			0.2000	
13	18+ Sea Trout	1.0000	0.2200	0.7000	1.6000			0.2000	
⊟	Sand Trout								
14	0-3 Sand Trout	1.0000	0.0000196	5.0000	37.8702			0.2000	
15	3-12 Sand Trout	1.0000	0.002523	1.2000	8.7806			0.2000	
16	12+ Sand Trout	1.0000	0.1000	0.7000	2.7000			0.2000	
⊟	Mullet								
17	0-6 Mullet	1.0000	0.06486	6.7000	56.6666			0.2000	
18	6-18 Mullet	1.0000	0.5225	1.8000	18.2253			0.2000	
19	18+ Mullet	1.0000	2.8000	0.8000	8.0000			0.2000	
⊟	Mackrel								
20	Mackrel 0-3	1.0000	0.0000012	4.0000	82.5590			0.2000	
21	Mackrel 3+	1.0000	0.01830	0.5000	6.0000			0.2000	
⊟	Ladyfish								
22	Ladyfish 0-10	1.0000	0.009787	2.8000	17.8409			0.2000	
23	Ladyfish 10+	1.0000	0.08900	1.6000	6.0000			0.2000	
24	Jacks	1.0000		0.6000		0.6000	0.3000	0.2000	

Figure 5.1 EwE6 user interface, showing the basic parameter input screen. Numbers refer to the features listed at the beginning of this section.

1. Menu bar

The *Menu bar* contains the File, View, Ecopath, Ecosim, Ecospace, Tools, Windows and Help menus, allowing users to open, close and save models, set preferences and access Help files.

Please note that help for the Ecopath, Ecosim and Ecospace menus can be found at the beginning of Chapters 6, 8, and 10 of the EwE6 User Guide or by clicking on these links: Ecopath menu, Ecosim menu, Ecospace menu.

2. Shortcut buttons

The Ecopath, Ecosim and Ecospace shortcut buttons provide quick access to existing Ecopath models and Ecosim and Ecospace scenarios.

3. Navigator window

The *Navigator window* is the main navigation tool in EwE6. Expanding menus provide access to all the features of Ecopath, Ecosim and Ecospace. Clicking on menu items (e.g., *Basic input* or *Diet composition*) displays these items in the *Main screen* where they can be viewed and edited.

To make navigation easier, the menu nodes in the *Navigator window* are colour coded. Green coded nodes indicate input forms (forms where you enter data). Blue coded nodes indicate output forms (forms where model results are displayed as tables or graphs). Menu nodes with a “+” icon can be expanded to reveal sub-nodes.

Close the *Navigator window* by unchecking the *Navigator* option on the *View menu* or by clicking the close button at the top of the bar. The *Navigator window* can be hidden using the AutoHide button (📌) on the title bar (see instructions above). Note that you must click elsewhere on the screen before the Navigator window will disappear.

4. Main screen

The *Main scree*n shows the forms where Ecopath, Ecosim and Ecospace model inputs are entered and edited. Model results are also displayed here. Note that nothing is displayed in the Main screen until a menu item is selected on the *Navigator window*. Once an item has been selected (e.g., *Basic input* table) it is added as a tab to the *Tabs bar* so that you can easily return to it after other items have been displayed.

General note about input forms. All input forms (coded with a green arrow in the *Navigator window*) have a *Set* box in the top right corner for entering values into multiple cells. For example, you may wish to enter the same value of a parameter for several groups at once. Highlight the cells for the groups you wish to have the same value and type it into the *Set* box. Note that you can only do this for one model variable at a time.

5. Tabs bar

The *Tabs bar* provides an easy means of switching between model forms. Tabs are added as they are selected on the *Navigator window*, enabling easy movement among forms currently in use. You can view forms simply by clicking on the tabs or by selecting them from the list under the down arrow on the right hand side of the toolbar. You can also select a form to display by checking it in the *Windows menu*.

The current form can be closed using the close button at the end of the Tab bar or by using the *Close* option on the *Windows menu*. You can close all open forms using the *Close All Tabs* option on the *Windows menu*.

Any form can be dragged and dropped to a floating window or docked to a new position by dragging it by the tab whilst holding down the left mouse button (see *General features of the Graphic User Interface* above).

6. Remarks tab

Many of the input tables allow you to enter comments and extra information about the data that have been entered.

To add a comment, select the desired cell and click on the *Remarks tab* to open the *Remarks panel*. Remarks can then be entered or edited here. Remarks can be viewed later by holding your mouse over commented cells (marked with a flag in the corner) or by selecting the commented cell and clicking on the remarks button. The *Remarks panel* can be switched to permanently visible mode by clicking on the horizontal push pin icon (📌) whilst the window is open.

7. Status tab/Status panel

EwE6 keeps a log of model actions in the *Status panel*, which opens when you pass your mouse over the *Status tab*. The *Status panel* can be switched to permanently visible mode by clicking on the horizontal push pin icon (📌) whilst the window is open.

Three types of message are displayed in the *Status panel**:

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> Information messages [ℹ]. Information messages provide feedback on regular events in EwE. Information events are confirmations of successful actions. Examples are opening the model; successful edits; and successful balancing (i.e., parameterization) of the model.
>
> Warning messages [⚠]. Warnings occur when EwE was not able to complete an action and requires the user to fix a problem, usually with the input data. For example, one of the most important of these is when parameterization fails (i..e., the model fails to balance). When this occurs, you will get the message "Your model is NOT balanced! Computed Ecotrophic Efficiencies (EE) invalid for one or more group(s)." Clicking on the "+" icon next to this message expands the message to show which groups are causing the problem.
>
> Critical messages [✖]. Critical messages are very rare and should not be encountered during normal use of the software. Users encountering critical messages should try closing and re-opening the program. If the problem persists, please contact us through the user support section of www.ecopath.org.
>
> *Note the icons will match those on your system so may appear slightly different.

You can clear one or all messages in the status panel by right clicking on the message or panel.

8. Status bar

The *Status bar* displays the name of the active model. If unsaved changes have been made to the model, a Save icon appears to remind you to save your model. The *Status bar* can be switched off by unchecking the *Status Bar* option on the *View menu*.

5.7 File menu

The *File menu* allows you to open, close and save your model.

Files are managed so that all data pertaining to a given Ecopath model (including its Ecosim and Ecospace scenarios, etc.) are saved in a Microsoft Access database (extension '.mdb').

Important note: EwE6 differs from previous versions in that there is only one model per database. See *Open model* section below for information about opening and saving models that were built using previous versions of EwE.

New model (Ctrl +N)

Use this option to create a new Ecopath model. You will be prompted to name your new model and save it in the location of your choice. Click OK, and the new model will be created. There will be one group initially, 'Detritus'. You should keep this group as your model must have at least one detritus group.

Note that you must create and balance an Ecopath model before you can use Ecosim or Ecospace.

See Ecopath inputs (Chapter 6 of the EwE6 user manual) for instructions on how to continue with creation of a new model.

Open model (Ctrl +O)

Choose *Open model* to open an existing Ecopath model. You will be prompted to locate and open your Ecopath database. Alternatively, use *Recent models* (see section below) to open models that have been used recently. Use the *Navigator window* to view and edit the components of the model once it is open.

Models built using EwE5 (versions 1.67 and later*), can be converted to EwE6 format using the Ecopath database conversion wizard. When you select the old database using *Open model* you will be prompted by the wizard to choose a model to extract from the old database. Select the model you wish to open and follow the prompts. EwE 6 will extract the model to a new database and save it in the same directory as the old EwE 5 database (or you can choose a new location). Any subsequent changes to the model will be saved to the new database.

*Note: To check the version of your EwE5 model, open the model's database with MS Access and open the table called "Database specifications". The version of your model is the last (i.e., highest) number listed in the *Version* field.

Close model

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

Save model (Ctrl +S)

Saves the model.

Save Model As…

Saves your model under a new name, i.e., creates a new copy, which you continue to work in.

Recent models

Recently-used models can also be opened from the list under the *Recent models* menu item.

Exit

Close EwE6. You will be prompted to save if the model has been edited since the last save operation.

5.8 View menu

The *View menu* allows you to choose which features of the user interface are displayed. Features that can be switched on or off are the *Start pane*, *Navigator window*, *Status panel*, *Remarks window* and *Status bar*.

5.9 Tools menu

Options…

The *Options...* menu item opens a dialogue box containing the following features that allow you to set your preferences for using the software.

General

Recent files

Set the number of recently-used files to display on the *File menu*. You can also clear the recently-used file list using the *Clear history* button.

Please note: All help topics are currently in draft format. Please send your comments to the email address given at www.ecopath.org (About >> Contact us).

Window layout

A feature of the EwE6 is the ability to customize the appearance (layout) of the Graphic User Interface (GUI) by dragging and docking any of the windows (see General features of the Graphic User Interface). Checking the Save windows layout box saves changes to the appearance of the GUI for the next time the model is opened. Unchecking the box means that the model will be re-opened with the default layout. You can also set where the layout file is saved by typing it directly or using the browse […] button. Note that a different layout file is saved for each model.

Message display

Select *Message* to set the way that critical messages, warning messages and information messages are displayed (i.e., as a pop-up message; in the *Status panel*; or as a pop-up message in the *Status panel*).

Colour

The *Colour* options allow you to set the colours for a large number of components of the GUI.

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·km2·year-1) can be run under Ecosim and Ecospace.

Selection of the time unit does not influence any of the calculations in Ecopath (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.

Default units for energy and time are wet weight (t/km^2) and year respectively.

Plug-ins

Displays which plug-ins are available with the current model.

Ecotracer

Opens the *Load Ecotracer scenario* dialogue box (after prompting to open an Ecosim scenario if one is not already open). See Ecotracer parameters, Ecotracer input and Ecotracer output for more information about using Ecotracer for contaminant tracing.

5.10 Windows menu

Use the *Windows menu* to choose which open tab is displayed on the *Main screen* (tabs are originally opened using the *Navigator window*). You can close individual tabs or all currently open tabs using the *Close* and *Close All* options.

5.11 Help menu

Use the Help menu to search or browse the Help files. Context-specific help can also be obtained by pressing F1 on your keyboard at any time.

Note that the information contained in these help files is identical to that in the EwE6 User Guide, which is provided when you download EwE6. It is also available from www.ecopath.org.

Please note: All help topics are currently in draft format. Please send your comments to the email address given at www.ecopath.org (About >> Contact us).

6 Using Ecopath. Part 1: Ecopath inputs

This chapter describes the steps taken to build, parameterize and balance an Ecopath model. The Introductory material (Chapter 2 of the User Guide) gave a scientific overview of the fundamental features of Ecopath and descriptions of the basic equations governing Ecopath, in particular, the system of linear equations that Ecopath solves under the assumption of mass balance. Other major assumptions are also discussed in the Introductory material and consideration is given to the types of data that are appropriate for use with Ecopath. Before proceeding with the instructions below for building an Ecopath model, you are strongly encouraged to read this material and thoroughly familiarise yourself with the relevant scientific literature, particularly the original Ecopath, Ecosim and Ecospace papers (Polovina 1984; Christensen and Pauly 1992; Walters et al. 1997; 1999; Christensen and Walters 2004).

The first task in building an Ecopath model is to define the model's functional groups and fishing fleets (see Edit groups, Edit multi-stanza groups and Edit fleets). Once the basic structure of the model is in place, you can enter parameters using the forms found under the Input data node in the Navigator window.

Once you have defined the model's functional groups and fishing fleets, you can enter the input parameters for functional groups and fisheries. Data is input into Ecopath using a number of entry forms accessible under the Input data node in the Navigator window. These forms include: Basic input, Diet composition, Detritus fate, Other production, Definition of fleets, Landings, Discards, Discard fate, Market price and Non-market price).

Before entering data, you are encouraged to read the introductory material on the mass balance approach to ecosystem modelling for information about how the input parameters are used in the model (see links in Introductory material Ecopath).

Generally, leaving an input blank on a data entry form implies it is unknown. For some required parameters defaults are supplied and skipping over these means accepting the default values. This is the case for biomass accumulation, detritus import, landings, discards, migrations and prices. You should be aware that opting for default values is as much a modelling decision as setting a new value, i.e., default values will not necessarily be appropriate for your ecosystem.

6.1 Getting started in Ecopath: The Ecopath menu

The *Ecopath menu* provides quick access to the forms you need to define the basic structure of your model. These are the *Edit groups*, *Edit multi-stanza groups* and *Edit fleets* forms. The EwE Network analysis plugin can also be accessed through the *Ecopath menu*.

Edit groups...

The first task in building an Ecopath model is to define the model's functional groups (called Groups or sometimes Boxes). Groups are species or collections of species that share similar population dynamics and ecological function. See Defining the system for more on how to define groups. Adding groups is done through the Edit groups form.

To open the *Edit groups* form, choose the *Edit groups...* option on the *Ecopath menu*.

Edit multi-stanza groups...

Multi-stanza groups are groups in which two or more life-stages are represented (e.g., juveniles and adults). Multi-stanza groups are defined using the *Edit groups* form but further parameters must be entered using the Edit multi-stanza groups form. To open this form, choose the *Edit multi-stanza groups...* option.

Edit fleets...

To add fishing fleets, delete, name and sort the fleets in your model, choose the *Edit fleets...* option. This will open the Edit fleets form.

EwE Network Analysis plugin

Ecopath enables you to perform a number of analyses based on the network analysis theory of Ulanowicz (1986). These forms are accessible by selecting EwE Network Analysis Plugin. Note that the *EwE Network Analysis plugin* can also be accessed from the *Navigator window* (*Parameterization (Ecopath) > Tools > EwE Network Analysis Plugin*).

Note: to be able to access the *EwE Network Analysis Plugin*, it must have been installed with EwE6. If you cannot access the *EwE Network Analysis Plugin*, you may need to re-install the software (see How to obtain the Ecopath with Ecosim 6 software). During the setup process, you will be prompted to check a box to install the *EwE Network Analysis Plugin*.

6.2 Edit groups

The first task in building an Ecopath model is to define the model's functional groups (called Groups or Boxes). Groups are species or collections of species that share similar population dynamics and ecological function. See Defining the system for more on how to define groups.

To add and edit functional groups to an Ecopath model, choose the *Edit groups...* option on the Ecopath menu on the *Menu bar*. This will open a form where you can add, delete, name and sort the functional groups in your model.

To close the *Edit groups* form and implement changes, click the *OK* button. To exit without implementing any changes, click the *Cancel* button.

After adding model groups on the *Edit groups* form, you can proceed to the *Input data* forms to enter parameters for your groups (i.e., Basic input, Diet composition, Detritus fate and Other production forms, accessible in the *Navigator window* under the *Input data* node).

Add/insert groups

Add groups using the *Insert* button. In a brand new model, groups will be inserted above the detritus group. In an existing model, select the row where you would like a new group inserted and click *Insert*. A new group will be added above the selected row. If no row is selected, new groups will be added above the first row. Note that when you add a new group, its status in the *Status* column will be given as "To create". Clicking the *OK* button closes the *Edit groups* form and implements the group insertion.

Group name

New groups are given the default name "New Group". Edit group names by clicking once in the appropriate *Group name* cell. The box will be highlighted and you can start typing. To edit an existing group name, click on the name and the name will be highlighted. You can then edit the name.

Important note: Group names should be unique. If you have multi-stanza groups in your model (see section below), each stanza should have a unique group name (e.g., Small juvenile cod; Large juvenile cod; Adult cod). The name of the multi-stanza group as a whole (e.g., Cod) is entered under *Multi-stanza group name*. See section on multi-stanza groups below for more detail on defining multi-stanza groups.

Define group type

You must define whether a functional group is a primary producer, consumer or detritus by checking the appropriate box.

- Primary producers (producers) obtain all of their energy from photosynthesis. By definition, their trophic level is 1.
- Consumers obtain their energy by consuming other organisms. They have trophic level > 1.
- Detritus groups are dead. Note that you must enter at least one detritus group and you can have as many detritus groups as you like. Note also that detritus groups must be placed after all living groups (i.e., they must have a higher group number than the last living group). You must also specify where the surplus detritus (left over after feeding by detritivores) will go using the Detritus fate form.

Sort groups

You can change the order of groups in the model using the *Up* and *Down* buttons. Clicking the OK button closes the *Edit groups* form and implements the new group numbers.

Delete groups

Groups can be deleted from the model using the *Delete* button. Models selected for deletion will be marked "To delete" in the *Status* column. Clicking the *OK* button closes the *Edit groups* form and implements the group deletion.

Note: if you change your mind about deleting the fleet before you close the form, click *Preserve* and the status will be returned to normal.

WARNING: Group deletion cannot be undone. When you click the *OK* button, you will receive a warning message for each group to be deleted. Click *Yes* to continue with group deletion or *No* if you do not wish to delete the group. The *Edit groups* form will close.

Defining multi-stanza groups

The *Edit groups* form allows you to create groups representing life history stages or stanzas for species that have complex trophic ontogeny (see introductory material on multi-stanza groups (Chapter 2 of the EwE6 User Guide) for more information on how these groups are modelled in Ecopath, Ecosim and Ecospace).

To define a multi-stanza group:

Add the stanzas as separate groups using the *Insert* button. Note that each stanza must have a unique group name (e.g., Juvenile cod; Adult cod).

Name the multi-stanza group as a whole (e.g., Cod) in the *Multi-stanza group name* column. Once you have created a multi-stanza group name, it is added to a pull-down menu in the *Multi-stanza group name* column.

Enter the start-age of each stanza in months in the *Stanza age (in months)* column. Note that your youngest stanza must have a start-age of zero months. If you do not have an age-zero stanza, Ecopath will set the youngest stanza's start age to zero (a message box will inform you of this).

IMPORTANT. After defining a multi-stanza group(s), you must set the values of additional parameters for the group(s). See Edit multi-stanza groups for details.

Colours

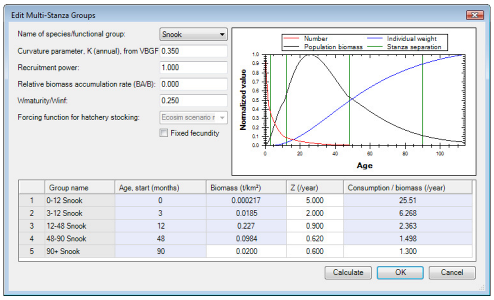
Click *Colour scale* to set a graded scale of colours for the model groups. Click *Colours alternating* for a set of alternating colours (light, dark and hue). You can change the colours for individual groups by clicking in the colour square. You can then select from a palette of colours.

6.3 Edit multi-stanza groups

Multi-stanza groups are defined using the Edit groups form, accessible from the *Ecopath menu* on the *Menu bar*. Multi-stanza groups represent life history stages or stanzas for species that have complex trophic ontogeny. Mortality rates (*M0*, predation, fishing) and diet composition are assumed to be similar for individuals within each stanza (e.g., larvae having high mortality and feeding on zooplankton, juveniles having lower mortality and feeding on benthic insects, adults having still lower mortality and feeding on fish). For Ecosim and Ecospace it is advised to split top predators into multi-stanza groups as this makes their dynamics more realistic, provides insights on stock-recruitment relationships, and allows consideration of stanza-specific habitat use. See the introductory material on multi-stanza groups and Using Ecosim to study compensation in recruitment relationships (Chapters 2 and 3 of the EwE6 User Guide) for more information on how these groups are modelled in Ecopath, Ecosim and Ecospace.

Once you have defined a multi-stanza group(s) you must go to the *Edit multi-stanza groups* form to set the parameters needed to calculate the biomass and numbers in each age category. To open the *Edit multi-stanza groups* form, choose the *Edit multi-stanza groups...* option on the *Ecopath menu*. Features of the *Edit multi-stanza groups* form are shown in Figure 6.1.

You must enter baseline estimates of total mortality rate *Z* (i.e., *P/B*) and diet composition for each stanza, and biomass and consumption (*Q/B*) for one "leading" stanza only (the oldest stanza). Biomass and consumption are then computed for the other stanzas, assuming a stable age distribution.



Name of species/functional group: Snook
Curvature parameter, K (annual), from VBGF 0.350
Recruitment power: 1.000
Relative biomass accumulation rate (BA/B): 0.000
Wmaturity/Winf: 0.250
Forcing function for hatchery stocking: Ecosim scenario r
☐ Fixed fecundity

	Group name	Age, start (months)	Biomass (t/km²)	Z (/year)	Consumption / biomass (/year)
1	0-12 Snook	0	0.000217	5.000	25.51
2	3-12 Snook	3	0.0185	2.000	6.268
3	12-48 Snook	12	0.227	0.900	2.363
4	48-90 Snook	48	0.0984	0.620	1.498
5	90+ Snook	90	0.0200	0.600	1.300

Figure 6.1. The Edit multi-stanza groups form

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Name of species/functional group

Use the pull-down menu to select the multi-stanza goup to edit.

Curvature parameter, K

Set the von Bertalanffy growth rate (von Bertalanffy 1938). Note that it is assumed that body growth for the species as a whole follows a von Bertalanffy growth curve with weight proportional to length-cubed.

Recruitment power

This parameter is used by Ecosim and sets the degree of density dependence in juvenile survival for juveniles outside the modelled area. Set a low value, (e.g., 0.1-0.5) for this 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).

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 modelled 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 modelled adult biomass due to recruitment of juveniles from some adult population 'egg source' outside the modelled area.

Relative biomass accumulation rate (BA/B)

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 $e^{-a\frac{BA}{B}}$ than the cohort born "*a*" years ago (see Multi-stanza groups). See Other production for notes about estimating the relative biomass accumulation rate.

Weight at maturity/W_infinity

Set the mean weight at maturity/w_∞. Note that it is assumed that body growth for the species as a whole follows a von Bertalanffy growth curve with weight proportional to length-cubed.

Forcing function number for hatchery stocking

Multi-stanza populations can be designated as hatchery populations (see Hatchery populations in Ecosim), and hatchery production can be varied over time in Ecosim using time forcing functions. To turn off natural reproduction select the hatchery forcing function from the pull-down menu in the *Forcing function number for hatchery stocking* box.

Note, you must already have a forcing time series loaded in Ecosim (see Time series and Forcing function). 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.

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.

Note also that if it is desired to simulate stocking of older fish (e.g., 18 months), the first stanza for the population should be set to have this duration, the mortality rate (*Z* or *P/B*) for the stanza should be set to .001, and the diet for the stanza should be set to 1.0 imported (i.e., do not have fish in the stanza feeding in the modelled ecosystem).

Fixed fecundity

Some types of organism (e.g., marine mammals or some sharks) may have a fixed number of young each year, regardless of adult body weight. Checking the *Fixed fecundity* check box sets the number of young.

Age, start (months)

The start age of each stanza is set on the *Edit groups* form. Note that the youngest stanza must have a start age of zero months.

Biomass

You must enter estimated absolute biomass (in appropriate units) for one “leading” stanza (i.e., the oldest stanza).

Z (Production/Biomass)

You must enter estimated total mortality rates for each stanza. A single-species age-structured model can be used to help estimate these parameters.

Consumption/Biomass

You must enter estimated consumption/biomass (*Q/B*) for one “leading” stanza (i.e., the oldest stanza).

A plot showing numbers at age, biomass age and weight at age is shown at the left of the form. This plot can be used to guide you in setting parameters for the group. To update the plot after changing parameters, click the *Calculate* button. To close the form and implement changes, click the *OK* button. To exit without implementing any changes, click the *Cance*l button.

6.4 Edit fleets

To define the fishing fleets in your model, choose the *Edit fleets*... option on the *Ecopath menu*. This will open a form where you can add, delete, name and sort the fleets in your model (see below). To close the *Edit fleets* form and implement changes, click the *OK* button. To exit without implementing any changes, click the *Cancel* button.

After adding fleets on the *Edit fleets* form, you can proceed to the *Input data* forms to enter parameters for your fleets (see Definition of fleets, Landings, Discards, Discard fate, Market price, Non-market price and Fleet size dynamics).

Add/insert fleets

Add fleets using the *Insert* button. In a brand new model, there is one default fleet ("Fleet1") and new fleets will be inserted above this fleet. In an existing model, select the row where you would like a new fleet inserted and click *Insert*. A new fleet will be added above the selected row. If no row is selected, new fleets will be added above the first row. Note that when you add a new fleet, its status in the *Status* column will be given as “To create”. Clicking the *OK* button closes the *Edit fleets* form and implements the group insertion.

Fleet name

New fleets are given the default name “New Fleet”. Edit fleet names by clicking once in the appropriate *Fleet name* cell. The box will be highlighted and you can start typing. To edit an existing fleet name, double click on the name and the name will be highlighted. You can then use your mouse to select the part of the name to be edited.

Sort fleets

You can change the order of fleets in the model using the *Up* and *Down* buttons. Clicking the *OK* button closes the *Edit fleets* form and implements the new fleet numbers.

Delete fleets

Fleets can be deleted from the model using the *Delete* button. Models selected for deletion will be marked “To delete” in the *Status* column. Clicking the *OK* button closes the *Edit fleets* form and implements the fleet deletion.

Note: if you change your mind about deleting the fleet before you close the form, click *Preserve* and the status will be returned to normal.

WARNING: Fleet deletion cannot be undone. When you click the OK button, you will receive a warning message for each fleet to be deleted. Click Yes to continue with fleet deletion or No if you do not wish to delete the fleet. The *Edit fleets* form will close.

6.5 Model description

Model

Use this form to store information on the model's author and contact details.

The form will also keep track the name of the model, date of any changes made to the model and the location of the database.

General options

Set the number of decimal digits shown in the model under *General options*. Relevant decimal digits are defined as digits that occur after the first non-zero decimal place. For example, if the number of relevant decimal digits is set to three, 0.3654 would be displayed as 0.365 and 0.0003654 would be displayed as 0.000365. Note that this is for display only and no rounding actually occurs in the running of the model. Double-clicking a number in a cell to edit it shows all the decimal places used in the calculations.

NOTE: For values calculated by the model (displayed in shaded cells, e.g., the Sum of the prey proportions in the *Diet composition*) the number you set in this box will be used to set number of decimal places.

6.6 Basic input

The *Basic input* form is accessed through the *Navigator window*. Click once with the left mouse key in the group name column to enter group information.

Habitat area

This is 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

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. 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.

Production/biomass

Enter the Production/Biomass (*P/B*) ratio for each group using consistent units, i.e., 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 includes fishery yield plus predation plus net migration plus biomass change plus other mortality; or

$$P/B = Z = F + M2 + NM + BA + M0.$$

For more details, see Production.

Consumption/biomass

Consumption/biomass (*Q/B*) ratios are entered using the same units as for *P/B*. Entry of consumption/biomass ratios is optional. For more details, see Consumption.

The *Q/B* input box will be blocked for primary producers. If your model unit is carbon, you can however, click the input box, and enter a *Q/B* value, which will be used to calculate respiration for the group.

Ecotrophic efficiency

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 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

Production/consumption expresses the ratio between production (*P*) and consumption (*Q*) and is a dimensionless parameter. *P/Q* corresponds to what was called the gross food conversion efficiency (*GE*) in early versions of the software.

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* values. The value of the ratio is checked, in Ecopath, and warnings are given if production exceeds consumption (as can occur in organisms with symbiotic algae, such as 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 *P/B* and/or *Q/B* is left blank. If *P/Q* is entered along with, e.g., *P/B*, then *Q/B* will be calculated as,

$Q/B = (P/B) / (P/Q)$.

Unassimilated consumption

An estimate of the fraction of the food that is not assimilated must be entered if the currency of your model is energy-related (see Units). 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 faeces) 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 - production / 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 dimensionless, 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.

6.7 Diet composition

In Ecopath predation links together the different groups in the model and diet composition must be entered for all groups. Unfortunately, quantitative information on diet composition is sparse. 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. Diet inputs should represent weight, volume or energy content of the preys, which are all equivalent (MacDonald and Green 1983).

The *Diet composition* form is accessed through the *Navigator window*. Enter diet composition, for all consumers, column by column (i.e., predators are represented by column and their prey by row). The diet compositions of each group should sum to 1. For guidance, the current sum of the fractions representing the food composition is summed at the second-last row (Sum). The last row (1 – Sum) shows the proportion of prey still to be entered. You can use the *Sum to one* button at the top of the *Diet composition* screen to raise a diet to unity. If diets do not sum to unity when you start basic estimation (i.e., try to balance the model) 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.

In Ecopath 'import' to a system is the consumption of preys that are not a part of the system as it is defined (for example for species that spend fractions of the year feeding outside the area of the model). Note that import is different from migration 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. See Dealing with open system problems for more information on how to treat groups that moves in and out of the modelled area.

A warning about zero order cycles, i.e., groups that feed on themselves ('cannibalism'): avoid situations where the fraction of the food of a group taken from that same group exceeds 0.1. This may occur when adults feed on their own juveniles. In such cases, it is advised to split the box into groups representing predator and prey stanzas, i.e., 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 groups with better-defined characteristics (because adults usually have P/B ratios lower than those of juveniles).

6.8 Detritus fate

The *Detritus fate* form is accessed through the *Navigator window*. 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. Surplus detritus can be directed to the same detritus group (equivalent to '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.

6.9 Other production

Other production refers to production represented in Ecopath by Migration and biomass accumulation. Migration is not the same as import – emigration and immigration are production factors, while import is food consumption. See Dealing with open system problems for more information on how to treat groups that moves in and out of the modelled area.

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.

The net migration is calculated as immigration less emigration. This means that net migration will be negativ**Error! Hyperlink reference not valid.**e 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. 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 entered, 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 underestimated.

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. Must be entered as a non-negative value. Unit is a flow, e.g., t / km² / year.

Emigration rate

Emigration can also be presented as the proportion of the population emigrating from the system in a year (unit is /year). The immigration rate can be entered by setting the emigration rate to a negative value.

Biomass accumulation

Ecopath is not necessarily 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 biomass accumulation (*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 detritus groups (Detritus fate). *BA* 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 modelled).

If *B, P/B, Q/B* and *EE* are 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.

Biomass accumulation rate

Biomass accumulation can also be represented as a rate (i.e., proportion of the total biomass; unit is /year).

6.10 Fishery

Forms for editing fishery parameters are found under the Fishery node in the Navigator window. See Definition of fleets, Landings, Discards, Discard fate, Market price, Non-market price and Fleet size dynamics.

6.11 Definition of fleets

You must first define your fleets using the Edit fleets form, accessible from the *Ecopath menu*. The *Definition of fleets* form can then be used to set the costs, profits and value for the fishing fleets in the model. Costs and values are used for calculations in Ecosim and Ecospace simulations.

Fixed cost

Fixed cost is the cost of operating a fleet unit, independent of effort, in the unit time defined in Ecopath (typically on annual basis). The definition of ‘fixed’ costs depends on the actual situation being modelled. To illustrate this consider some examples:

A new module of Ecospace, Ecoseed, allows for effort reduction to nil in connection with simulated increase in protected areas from 0 to 100% of total model 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 should 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.
- If the changes are major, the procedure outline for Ecoseed above should be adopted instead. Hence, consider the fixed costs to be effort-independent at the fleet level.

Effort related cost

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 *Effort related costs* for all variable costs (e.g., fuel, gear costs and crew wages);

Ecospace: use *Effort related costs* for variable costs that depend on effort, e.g., for gear costs (which mainly depend on how many hours the gears is used), but not for costs that depend on spatial effort allocation, e.g., sailing costs. See next section.

Sailing related cost

For Ecospace applications it is recommended to use two separate forms for variable costs: effort-related and spatially-related (i.e., sailing related). Do not enter sailing related costs if you are only using Ecosim, use Effort related costs for all variable costs.

If you are using Ecospace, use *Effort related costs* for variable costs that depend on effort, e.g., for gear costs. Enter costs that depend directly on spatial effort allocation, e.g., fuel costs and crew wages as *Sailing related costs*.

Profit

Profit is calculated as percentage of value, calculated from total value less all costs. It cannot be entered directly.

Total value

The total value is 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..

6.12 Landings

Landings and catches are not the same, as discarding is an integral part of most fishing operations. Ecopath calculates: Catch = landings + discards.

You should therefore enter only the landings here – while any discards should be entered on the discards form. 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 habitat area, or the area in which the fleet operates. For instance, if you 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 extractions over the time period considered in the model, (e.g., a year), for each of the groups modelled. 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 modelled, 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 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').

6.13 Discards

Discarding is a normal practice in most fisheries. If you do not enter any information, you are assuming that discarding does not take place. If discarding does take place this is worse than guessing! Therefore, it is better to use information from similar fisheries in other areas or perhaps based on interviews with fishers in your area.

Discarding may affect trophic and population dynamics. For example, in 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. Note that you must tell Ecopath where to send discards using the Discard fate form.

6.14 Discard fate

Ecopath needs to be told what to do with the discards you enter as part of the catches. Discards 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 directed to a given detritus group (or exported).

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.

6.15 Off-vessel 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 among groups.

The off-vessel prices are fleet-specific on the entry forms, as quality and hence price varies more between fleets than within fleets. See also Non-market price.

6.16 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. See also Off-vessel price.

7 Using Ecopath. Part 2: Parameterization and outputs

Once you have entered the input parameters for your model you can parameterize (balance) the model (see Notes on parameterizing an Ecopath model and Balancing a model in this chapter). This chapter also contains the information on Ecopath's outputs (Basic estimates; Key indices; Mortalities; Mortality coefficients; Predation mortality; Consumption; Respiration; Niche overlap; Electivity; Search rates; Fishery; Flow diagram; and the EwE Network Analysis plugin)

7.1 Notes on parameterizing an Ecopath model

Below are some important considerations for parameterizing (i.e., balancing) your Ecopath model so that mass balance is achieved. Make sure you are also familiar with the introductory material on Ecopath parameterization (Mortality for a prey is consumption for a predator, The energy balance of a box and On the need for input parameters).

For more detailed notes on balancing your model we recommend you also read Balancing a model.

Ecopath parameterization

Once you have entered sufficient input parameters you can proceed to estimate the parameters of Ecopath by selecting *Basic estimates* under the *Parameterization node* in the *Navigator window*. The missing parameters will be estimated so that mass balance is achieved. The estimation is performed using a number of algorithms and a routine for matrix inversion described in the topic Mortality for a prey is consumption for a predator.

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., biomass · (consumption / biomass);

Production excludes primary production, i.e., is defined by biomass · (production / biomass) · (1 - PP),

where PP is the proportion of total production that can be attributed to primary production (thus (1 - PP) = 0 in plants, 1 in heterotrophic consumers, and intermediate in 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.

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.

Note: Warnings are displayed in the *Status panel*.

The sections below may help you evaluate the results of a run.

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 modelling: for most groups, the *EE* should be close to one, the exceptions being top predators and primary producers.

If, in a first run, any of the *EE* values are larger than 1, something is wrong: it is not possible for 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 in the Remarks window, to record en route what you do and why.

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.

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.

7.2 Balancing a model

Once you have entered sufficient input parameters you can proceed to estimate the parameters of Ecopath by selecting Basic estimates under the *Parameterization node* in the *Navigator window*. The missing parameters will be estimated so that mass balance is achieved.

Important note: If Ecopath has NOT been balanced already since opening or making changes to the input parameters, selecting any of the forms under the *Parameterization node* in the *Navigator window* will cause Ecopath to attempt to balance the model. Note also that you will not be able to balance your model if the sum of the Diet composition for each predator does not sum to 1. Return to the *Diet composition* form and fix the problem if this is the case.

Below are some important notes to help you during model parameterization (balancing). Before commencing balancing, we recommend you first read Notes on parameterizing an Ecopath model and are familiar with the introductory material on Ecopath parameterization (Mortality for a prey is consumption for a predator, The energy balance of a box and On the need for input parameters).

Problems in parameter estimation will be shown in the *Status panel*. Two types of message may be displayed in the *Status panel* while you are balancing your model:

> Information messages [ℹ]. Information messages provide feedback on regular events in EwE. Information events are confirmations of things that went well. Examples are opening the model; successful edits; and successful balancing (i.e., parameterization) of the model.
>
> Warning messages [⚠]. Warnings occur when EwE was not able to complete an action and requires the user to fix a problem, usually with the input data. For example, one of the most important of these is when parameterization fails (i..e., the model failed to balance). When this occurs, you will get the message “Your model is NOT balanced! Computed Ecotrophic Efficiencies (*EE*) invalid for one or more group(s).” Clicking on the “+” icon next to this message expands the message to show which groups are causing the problem.

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;
- 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 form, 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* us 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*) 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;

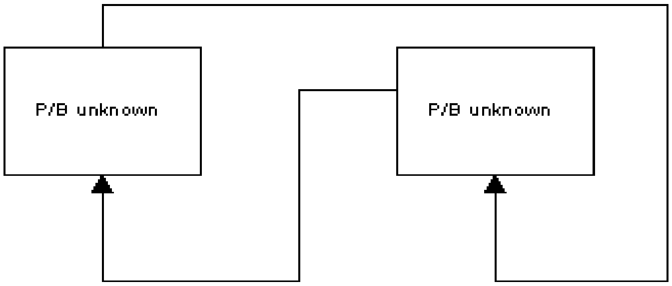
- Examine the respiration/biomass (R/B) ratios for each group. Generally this ratio reflects activity level. For fish it should as a rule be in the range 1-10 year-1, for copepods perhaps around 50-100. Please consult physiology handbooks for more information. If the ratio seems high it may be necessary to change the (assumed) proportion of the food that is not assimilated on the basic input form;
- Examine the Electivity form. Do the preferences seem reasonable?
- Examine the Predation mortalities under the*Mortalities* node in the *Navigator window*. 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, re-evaluate your model's diet compositions. The information on the mortality forms is very important!
- 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 a larger flow to the detritus. The latter may be necessary to balance the model if there is only little system surplus production.

See below for notes about some common causes of problems during balancing.

Problem 1: 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.



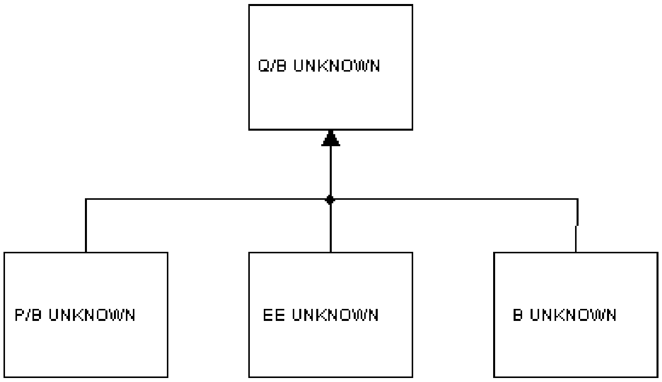
Problem 2: Cannibalism (0-order cycles)

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.

Problem 3: 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.



7.3 Basic estimates

Once you have entered sufficient input parameters you can proceed to estimate the parameters of Ecopath by selecting Basic estimates under the Parameterization node in the Navigator window. The missing parameters will be estimated so that mass balance is achieved. Both input (black font) and calculated (blue font) parameters are displayed on the Basic estimates form.

Before attempting to balance your model, we recommend you read Notes on parameterizing an Ecopath model and Balancing a model.

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. These can be found in the current (*Basic estimates*) form as well as on the Key indices, Mortalities, Consumption, Respiration, Niche overlap, Electivity, Search rates and Fishery forms.

Notes on most of the parameters below have already been provided in the notes on Basic parameters, but we repeat them here as a reminder.

Trophic level

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 (1975). A routine assigns definitional trophic levels (TL) of 1 to producers and detritus and a trophic level of 1 + [the weighted average of the preys' trophic level] to consumers.

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.

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.

Please note: All help topics are currently in draft format. Please send your comments to the email address given at www.ecopath.org (About >> Contact us).

Biomass in habitat area

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. 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.

Biomass

This is the Biomass in habitat area x Habitat area.

Production/biomass

Enter the Production/Biomass (*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 includes fishery yield plus predation plus net migration plus biomass change plus other mortality; or

$$P/B = Z = F + M2 + NM + BA + M0.$$

For more details, see Production.

Consumption/biomass

Consumption/biomass (*Q/B*) ratios are entered using the same units as for *P/B*. Entry of consumption/biomass ratios is optional. For more details, see Consumption.

The *Q/B* input box will be blocked (blue colour) for primary producers. If your model unit is carbon, you can however, click the blue input box, and enter a Q/B value, which will be used to calculate respiration for the group.

Ecotrophic efficiency

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 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.

7.4 Key indices

Biomass accumulation

Ecopath is not necessarily 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 biomass accumulation (*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 detritus groups (see Detritus fate). *BA* 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 modelled).

Biomass accumulation rate

Biomass accumulation can also be represented as a rate (i.e., proportion of the total biomass; unit is /year).

Net migration

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. 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 entered, 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 underestimated.

See Other production and Dealing with open system problems for important notes about migration in Ecopath.

Flow to 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·km-2·year-1, should be positive for all groups.

Problem 4: Estimation of *Q/B* for detritivores

It is not possible to estimate the *Q/B* 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).

Net efficiency

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

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

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

Net efficiency = Production / (production + 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*.

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

$$OI_i = \sum_{j=1}^{n} (TL_j - (TL_i - 1))^2 \cdot DC_{ij} \qquad \textbf{Eq. 22}$$

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.

7.5 Mortalities

The *Mortalities* node in the *Navigator window* contains two forms that summarise the sources of mortality in the model.

The Mortality coefficients form breaks down mortality for each group in the model into its component parts (*P/B, F*, predation mortality, biomass accumulation, net migration and *EE*).

The Predation mortality form further breaks down the predation mortality for each prey group by showing the predation mortality rate caused by each of its predators.

These two forms are arguably the most important reference for the user during the model-balancing process, as they can be used to indicate which mortality components are most likely to be causing problems.

See Notes on parameterizing an Ecopath model and Balancing a model for more advice about balancing your model.

7.6 Mortality coefficients

The *Mortality coefficients form* (Figure 7.1) is one of the most important forms on the *Parameterization menu* and it is, as a rule, the first one that should be checked when balancing a model.

This form gives the Ecopath-predicted values of each type of mortality for each group in the model (see below). During balancing, the *Mortality coefficients form* will guide you in identifying where problems are (e.g., if it's fishing or predation mortality that is too high). If predation mortality is too high, then you can use the Predation mortality form to identify which predators are causing the problem.

Components of mortality in Ecopath

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

$$N_t = N_0 \cdot e^{-Zt} \quad \textbf{Eq. 25}$$

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):

$$Z_i = (production / biomass)_i = P/B_i \quad \textbf{Eq. 26}$$

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.,

$Z_i = P/B_i =$ Fishing mortality + Predation mortality + Biomass accumulation + Net migration + Other mortality

or

$$P/B_i = F_i + M2_i + BA_i + E_i + M0 \quad \textbf{Eq. 27}$$

In some models, (e.g., the Multispecies Virtual Population Analysis model of the North Sea, Sparre, 1991), the 'other mortality' component is split between $M1_i$, i.e., predation by predators not included in the model, and $M0_i$, 'other mortality', caused by diseases, senescence, etc. In Ecopath, $M1$ is not included, as all predation mortality should be described explicitly. Further, $M0_i$ is not entered directly, but is computed from the ecotrophic efficiency, EE_i, Thus:

F_i is the Fishing mortality coefficient;

$M2_i$ is the Predation mortality coefficient;

BA_i is the Biomass accumulation coefficient;

E_i is the Net migration coefficient (immigration less emigration).

$M0_i$ is the Other mortality coefficient.

Ecopath-predicted values for these coefficients are given on the *Mortality coefficients* form. The mortality coefficients are estimated from the following equations:

$Z_i = P/B_i$

$$M2_i = (\sum B_i \cdot Q/B_i \cdot DC_{ji}) / B_i$$

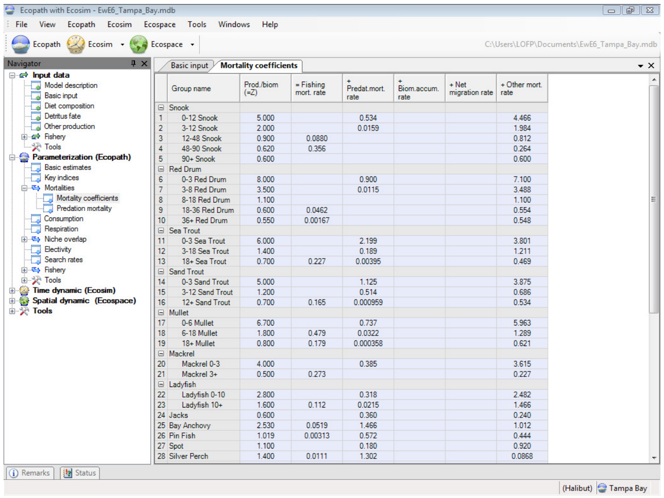
$$F_i = Y_i/B_i$$

$$M0_i = (1\text{-}EE_i) \cdot P/B_i$$

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 (M_0), 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.

See also introductory material on Production, Consumption, Dealing with open system problems and Other mortality.



	Group name	Prod./biom (=Z)	= Fishing mort. rate	+ Predat.mort. rate	+ Biom.accum. rate	+ Net migration rate	+ Other mort. rate
⊟	Snook						
1	0-12 Snook	5.000		0.534			4.466
2	3-12 Snook	2.000		0.0159			1.984
3	12-48 Snook	0.900	0.0880				0.812
4	48-90 Snook	0.620	0.356				0.264
5	90+ Snook	0.600					0.600
⊟	Red Drum						
6	0-3 Red Drum	8.000		0.900			7.100
7	3-8 Red Drum	3.500		0.0115			3.488
8	8-18 Red Drum	1.100					1.100
9	18-36 Red Drum	0.600	0.0462				0.554
10	36+ Red Drum	0.550	0.00167				0.548
⊟	Sea Trout						
11	0-3 Sea Trout	6.000		2.199			3.801
12	3-18 Sea Trout	1.400		0.189			1.211
13	18+ Sea Trout	0.700	0.227	0.00395			0.469
⊟	Sand Trout						
14	0-3 Sand Trout	5.000		1.125			3.875
15	3-12 Sand Trout	1.200		0.514			0.686
16	12+ Sand Trout	0.700	0.165	0.000959			0.534
⊟	Mullet						
17	0-6 Mullet	6.700		0.737			5.963
18	6-18 Mullet	1.800	0.479	0.0322			1.289
19	18+ Mullet	0.800	0.179	0.000358			0.621
⊟	Mackrel						
20	Mackrel 0-3	4.000		0.385			3.615
21	Mackrel 3+	0.500	0.273				0.227
⊟	Ladyfish						
22	Ladyfish 0-10	2.800		0.318			2.482
23	Ladyfish 10+	1.600	0.112	0.0215			1.466
24	Jacks	0.600		0.360			0.240
25	Bay Anchovy	2.530	0.0519	1.466			1.012
26	Pin Fish	1.019	0.00313	0.572			0.444
27	Spot	1.100		0.180			0.920
28	Silver Perch	1.400	0.0111	1.302			0.0868

Figure 7.1 Mortality rates. *Z* is total mortality; *F* is fishing mortality; *M0* other mortality; and *M2* predation mortality. $Z = P/B = F + E + M0 + M2$.

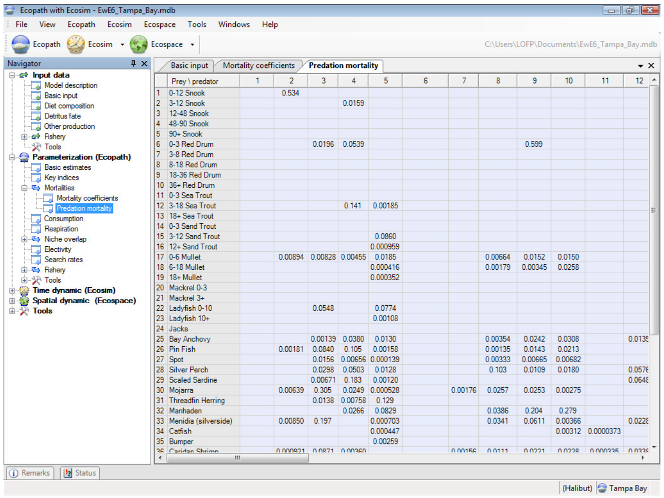
7.7 Predation mortality

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.

The *Predation mortality* form (Figure 7.2) is very important and should be checked frequently when balancing a model.

To begin with, the Mortality coefficients form will guide you to particular mortality coefficients that are causing problems with balancing. If predation mortality is too high then the *Predation mortality* form will help you identify which predators are causing the problem for a particular prey group.

To help you identify possible problem predators, cells with unusually high predation mortalities will be shown with a different-coloured background instead of the usual blue background. Note that this is intended as a guide only to show which predators are contributing most to a prey species' mortality. You should use the literature, expert opinion and your understanding of the ecosystem to decide which predation mortalities should be changed and by how much.



	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12
1	0-12 Snook		0.534										
2	3-12 Snook				0.0159								
3	12-48 Snook												
4	48-90 Snook												
5	90+ Snook												
6	0-3 Red Drum			0.0196	0.0539					0.599			
7	3-8 Red Drum												
8	8-18 Red Drum												
9	18-36 Red Drum												
10	36+ Red Drum												
11	0-3 Sea Trout												
12	3-18 Sea Trout				0.141	0.00185							
13	18+ Sea Trout												
14	0-3 Sand Trout												
15	3-12 Sand Trout					0.0860							
16	12+ Sand Trout					0.000959							
17	0-6 Mullet		0.00894	0.00828	0.00455	0.0185			0.00664	0.0152	0.0150		
18	6-18 Mullet					0.000416			0.00179	0.00345	0.0258		
19	18+ Mullet					0.000352							
20	Mackrel 0-3												
21	Mackrel 3+												
22	Ladyfish 0-10			0.0548		0.0774							
23	Ladyfish 10+					0.00108							
24	Jacks												
25	Bay Anchovy			0.00139	0.0380	0.0130			0.00354	0.0242	0.0308		0.0135
26	Pin Fish		0.00181	0.0840	0.105	0.00158			0.00135	0.0143	0.0213		
27	Spot			0.0156	0.00656	0.000139			0.00333	0.00665	0.00682		
28	Silver Perch			0.0298	0.0503	0.0128			0.103	0.0109	0.0180		0.0576
29	Scaled Sardine			0.00671	0.183	0.00120							0.0648
30	Mojarra		0.00639	0.305	0.0249	0.000528		0.00176	0.0257	0.0253	0.00275		
31	Threadfin Herring			0.0138	0.00758	0.129							
32	Manhaden				0.0266	0.0829			0.0386	0.204	0.279		
33	Menidia (silverside)		0.00850	0.197		0.000703			0.0341	0.0611	0.00366		0.0228
34	Catfish					0.000447					0.00312	0.0000373	
35	Bumper					0.00259							
36	Caridan Shrimp		0.000921	0.0871	0.00360			0.00156	0.0111	0.0221	0.0228	0.000335	0.0335

Figure 7.2 Predation mortality form showing the quantitatively important predators and prey for all groups. 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.

7.8 Consumption (Ecopath parameterization)

Ecopath's estimates of consumption (food intake) can be obtained by selecting Consumption under the Parameterization node in the Navigator window.

The consumption 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/km^2/ year. The consumption table also displays all flows to the detritus group(s).

7.9 Respiration

Ecopath's estimates of respiration can be obtained by selecting *Consumption* under the *Parameterization node* in the *Navigator window*. The *Respiration* form displays the predicted values for respiration and assimilation of food by all groups.

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 coloured 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,

$$Resp_i = (1 - GS_i) \cdot Q_i - (1 - TM_i) \cdot P_i \quad \textbf{Eq. 23}$$

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/km^2/year. If the currency is a nutrient, (e.g., nitrogen or phosphorus), respiration is zero: nutrients are not respired, but egested and recycled within systems.

Assimilation

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

$$B_i \cdot Q/B_i \cdot (1 - GS_i) \quad \textbf{Eq. 24}$$

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/km^2/year.

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.

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.

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 /year.

7.10 Niche overlap

Ecopath-predicted values for *Prey overlap* and *Predator* overlap are displayed in separate forms under the *Niche overlap* node in the *Navigator window*.

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

$$O_{jk} = \sum_{i=1}^{n} (p_{ji} \cdot p_{ki}) / \sqrt{(\sum_{i=1}^{n} p_{ji}^2 p_{ki}^2)} \qquad \textbf{Eq. 29}$$

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 Eq. 29 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 behaviour is caused by the geometric mean implied in the denominator of Eq. 29, and can be circumvented by the use of an arithmetic mean. For this Eq. 29 is changed to

$$O_{jk} = \sum_{i=1}^{n} (p_{ji} \cdot p_{ki}) / (\sum_{i=1}^{n} (p_{ji}^2 + p_{ki}^2)/2) \qquad \textbf{Eq. 30}$$

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 Eq. 30 can be interpreted as the fraction prey *i* contributes to the diets of *j* and *k*, respectively.

Please note: All help topics are currently in draft format. Please send your comments to the email address given at www.ecopath.org (About >> Contact us).

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 'predator' composition, estimated from

$$X_{ml} = Q_i P_{lm} / \sum_{l=1}^{n} (Q_l \cdot P_{lm}) \quad \textbf{Eq. 31}$$

and

$$X_{nl} = Q_i P_{ln} / \sum_{l=1}^{n} (Q_l \cdot P_{ln}) \quad \textbf{Eq. 32}$$

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

$$P_{mn} = \sum_{i=1}^{n} (X_{ml} \cdot X_{nl}) / (\sum_{l=1}^{n} (x_{ml}^2 + x_{nl}^2) / 2 \quad \textbf{Eq. 33}$$

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 Eq. 30.

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.

7.11 Electivity

The electivity (selection index) describe a predator's preference for prey. It scales from -1 to 1; where -1 indicates total avoidance of a prey; 0 indicates that a prey is taken in proportion to its abundance in the ecosystem; and 1 indicates total preference for a prey. The electivity values are highlighted using a colour scale for the background, scaling from –1 (white) to 1 (red) using shades of red for intermediate values. The electivity index displayed is the standardized forage ration of Chesson (1983), see below.

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

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

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

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

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

$$S_i = \frac{(r_i / P_i)}{\sum_{n=1}^{n} r_n / P_n}$$

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

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

7.12 Search rates

One surprising feature of the system of linear equations underlying the Ecopath approach is that it can be used to estimate the Lotka-Volterra mass-action term *a*, which has the dimension of a volume searched per unit time by a given predator *j* seeking a certain prey *i*. If we start from the first Ecopath Master Eq.:

$$B_i \cdot (P/B)_i \cdot EE_i - \sum_j B_j \cdot (Q/B)_j \cdot DC_{ji} - C_i - E_i - BA_i = 0$$

where *B* is biomass, *P* production rate, *EE* the ecotrophic efficiency, *C* the catch rate, *BA* the biomass accumulation rate, *E* the net migration rate, *Q* the consumption rate, DC_{ji} the proportion *i* contributes to the diet of *j* (each of the consumers). Separating the biomass accumulation rate, *BA*, and re-expressing as a differential equation:

$$BA_i = \frac{dB}{dt} = B_i \cdot (P/B)_i \cdot EE_i - \sum_j B_j \cdot (Q/B)_j \cdot DC_{ji} - C_i - E_i - BA_i$$

$$\ldots = B_i \cdot (P/B)_i \cdot EE_i - C_i - E_i - \sum_j Q_{ij}$$

where Q_{ji} expresses the consumption rate for consumer j of prey i. We can then solve for $a_{ji} = Q_{ji}/(B_j \cdot B_i)$, which defines the Lotka-Volterra mass-action term a the quotient of the amount of *i* consumed by *j*, divided by the product of their biomasses.

This mass-action term is used as ‘fixed support’ for the ‘lever’ which, in Ecosim, regulates the consumption of predators, given the changing biomasses of their preys, and their own changing biomasses.

The values of *a* depend obviously on the units used, and the biomass units used in Ecopath render difficult a direct interpretation of the numbers in the ‘Search rate’ table. However, they can easily be converted into values of *a* applying to single organisms, given that the ratio of the individual prey and predator weights are divided into the values of *a* for each pair of prey and predator.

7.13 Fishery (Ecopath parameterization)

The *Fishery* node under *Parameterization node* in the *Navigator window* summarizes total catch (*Quantity*) and *Value* of each fished group by fleet. Only groups for which landings and/or discards have been entered are shown.

Quantity

The *Quantity form* shows total catch for fished groups by fleet, where

$$\text{Catch} = \text{Landings} + \text{Discards}$$

where Landings and Discards are entered as Ecopath inputs under the Fishery node under *Input data* in the *Navigator window*. The form also displays the Trophic level of each fleet and of the fishery in total.

Value

The *Value form* shows the calculated value for fished groups (i) by fleet (g), where

$$\text{Value}_{i,g} = \text{Market price}_{i,g} \,.\, \text{Landings}_{i,g}$$

where Market price and Landings are entered as Ecopath inputs under the Fishery node under Input data in the Navigator window.

The Non-market value of each resource is also shown in a separate column on the Value form (if any Non-market prices have been defined under the Fishery node under Input data in the Navigator window), where

$$\text{Non-market value}_{i,g} = \text{Non-market Price}_{i,g} \,.\, \text{Biomass}_{i,g}$$

7.14 Ecopath tools

Tools currently available in Ecopath are the Flow diagram and the EwE network analysis plugin.

7.15 Flow diagram

One of the characteristics of network ecosystem models is that all flows and biomasses can be shown in a single graph.

The traditional method of representing trophic flow in 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:

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

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

You might consider (i) and (ii) when constructing flow charts using the flow diagram in this version of Ecopath. The size of each (round) box is 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.

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.

EwE6 automatically builds a trophic flow diagram. **Right click on the *Flow diagram* form and select *Settings*** to set the colour of the nodes, colours, width and types of lines, the shape of the nodes (square or circular) and whether the nodes are to be scaled or not.

Hover your mouse over a node to see its connections. Trophic levels are shown in the background.

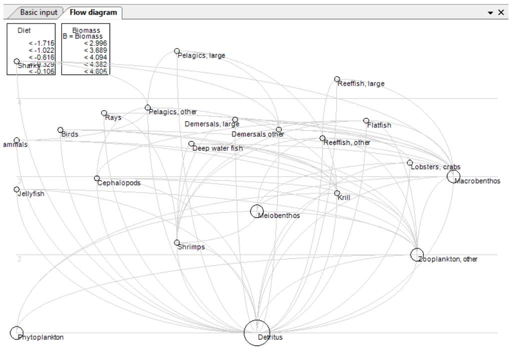


Figure 7.3 Ecopath flow diagram

7.16 EwE network analysis plugin

The Ecopath software links concepts developed by theoretical ecologists, especially the network analysis theory of Ulanowicz (1986), with those used by biologists involved with fisheries, aquaculture and farming systems research. The *Network analysis* component of Ecopath is included as a plugin under the *Tools* node under *Parameterization* in the *Navigator window*. It can also be accessed from the *Ecopath menu*.

The output forms included in the plug in include: Trophic level decomposition, Flows and biomasses, Primary production required, Mixed trophic impact, Ascendancy, Flow from detritus, Cycles and pathways, Network analysis indices in Ecosim. The notes on these sections give only brief accounts of the concepts from theoretical ecology included in Ecopath. For complete descriptions, we refer to the literature cited in the respective sections.

Note that because the network analysis feature is a plugin, the above components are accessed via a separate menu that is displayed when you select the *Network analysis* node (see Figure 7.4). You can re-size the *Navigator window* and the Network analysis menu by dragging the side of their respective windows. You can also hide the *Navigator window* using the AutoHide button (📌) in the top corner of the window.

Note: to be able to access the *EwE Network Analysis Plugin*, it must have been installed with EwE6. If you cannot access the *EwE Network Analysis Plugin*, you may need to re-instal the software (see How to obtain the Ecopath with Ecosim 6.0 software). During the setup process, you will be prompted to check a box to install the *EwE Network Analysis Plugin*.

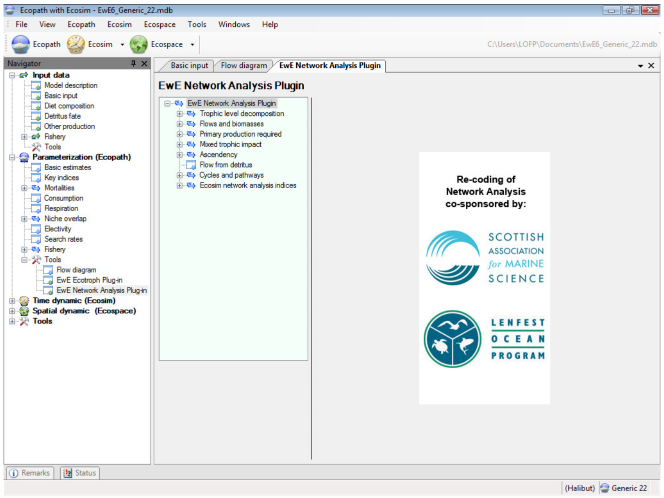


Figure 7.4 EwE Network Analysis Plugin menu.

7.17 Trophic level decomposition

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 results of this analysis are presented in the *Relative flows* table under the *Trophic level decomposition* node (these are proportions adding up to 1). These proportions are converted to absolute amounts, presented in the *Absolute flows* table (t/km^2/year or grams of carbon/m^2/year), thus enabling the flows to be aggregated by trophic level and summarized in different ways. See Flows and biomasses and Summary of flow data for descriptions of these summaries.

Flows from detritus to the different model groups are calculated when you select the Flow from detritus menu item.

7.18 Summary of flow data

Transfer efficiency

Based on the trophic aggregation tables (see Flows and biomasses), 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.

Flow pyramid

The transfer efficiencies (see above) can be used for constructing a figure presenting the trophic flows in the form of a pyramid that can be produced by selecting the Flow pyramid menu item on the *EwE Network Analysis Plugin* menu (*Trophic level decomposition* > *Summary of flow data* > *Flow pyramid*). 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.

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 by trophic level and Biomass pyramid

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.

Catch by trophic level and Catch pyramid

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

7.19 Flows and biomasses

The absolute flows calculated in the Trophic level decomposition and Flow from detritus analyses can be aggregated to produce useful summaries by trophic level. Results are presented in three tables, where the import (on Trophic Level I only), consumption by predators, export, flow to the detritus, respiration, and throughput are given by trophic level. The throughput is the sum of the flows in the other columns.

From primary producers

The first table presents flows originating from the primary producers.

From detritus

The second table summarizes the flows originating from the detritus.

From all combined

The third table presents the summed flow for the system as a whole.

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7.20 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 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, corresponding to the catch of Y is:

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

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’s

$$PPR_C = \sum_{Paths} [\, Y \cdot \prod_{Pred,prey} \frac{Q_{Pred}}{P_{Pred}} \cdot DC'_{Pred,prey} \,] \qquad \textbf{Eq. 44}$$

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 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).

7.21 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 x n matrix, where the i,jth element representing the interaction between the impacting group i and the impacted group j is

$$\mathrm{MTI}_{i,j} = \mathrm{DC}_{i,j} - \mathrm{FC}_{j,i} \quad \textbf{Eq. 45}$$

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.,

$$MTI_{i,i} = 1 + MTI_{i,i} \quad \textbf{Eq. 46}$$

The matrix is inversed using a standard matrix inversion routine.

The mixed trophic impact graph can be opened using the *Graph of mixed trophic impacts* form. The number of group included in the mixed trophic impact graph can be limited using the *Show/hide groups on mixed trophic impacts plot* form.

Figure 7.5 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 Figure 7.5 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.

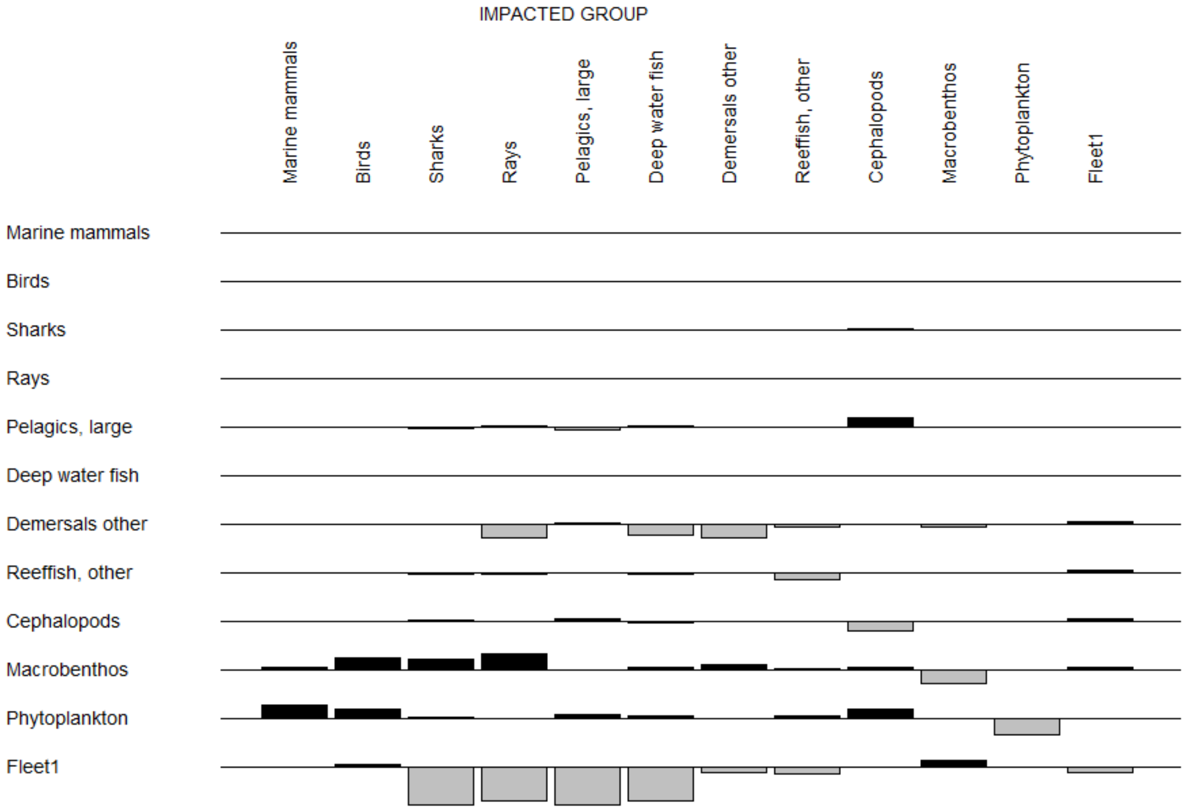

Figure 7.5 Mixed trophic impacts showing the combined direct and indirect trophic impacts that an infinitesimal increase of any of the groups on the left is predicted to have on the groups in the columns.

7.22 Ascendancy

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 knows 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’,

$$I = \sum_{i=1,j=1}^{n} f_{ij} Q_i \log\left(f_{ij} \Big/ \sum_{k=1}^{n} f_{kj} Q_k\right) \qquad \textbf{Eq. 37}$$

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,

$$f_{ij} = T_{ij} \Big/ \sum_{k=1}^{n} T_{kj}$$ **Eq. 38**

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

$$Q_i = \sum_{k=1}^{n} T_{ki} \Big/ \sum_{l=1,m=1}^{n} T_{lm}$$ **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 'ascendency'. The ascendency is symmetrical and will have the same value whether calculated from input or output.

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

$$C = H \cdot T$$ **Eq. 42**

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

$$H \sum_{i=1}^{n} Q_i \log Q_i$$ **Eq. 43**

The difference between the capacity and the ascendency is called 'system overhead'. The overheads provide limits on how much the ascendency can increase and reflect the system's 'strength in reserve' from which it can draw to meet unexpected perturbations (Ulanowicz, 1986). As an example, the part of the ascendency that is due to imports, A_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 ascendency, 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., t/km^2/year) and bits. Here the 'bit' 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 ascendency / 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).

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Ecopath calculates ascendency, overheads and capacity for the whole system (Total form) and by group (By group form).

7.23 Flow from detritus

The Trophic level decomposition analysis calculated the the fractions of the flow from each trophic level through each model group. The *Flow from detritus* analysis is equivalent, but calculates the flow from detritus through each group and converts it to absolute flows (t/km^2/.year). The results are summarized in the *Trophic aggregation analyses* (see Flows and biomasses).

7.24 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.).

Each routine below has two forms: *Pathway* and *Summary of pathways*. The summary routine counts the number of all pathways leading from the prey to the selected consumer. The mean path length will be calculated and displayed on the form. This mean path length is calculated as the total number of trophic links divided by the number of pathways.

Note: For each of the subheadings below, to activate the *Pathway* and *Summary of pathways* routines, you must first select the appropriate *Pathway* menu item and select the groups to be used in the analysis.

Consumer <- TL1

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 (under the *Summary of pathways* menu item). The latter is calculated as the total number of trophic links divided by the number of pathways.

Consumer <- prey <- TL1

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 pull-down list of all consumers in the system will be displayed after the heading “Pathways leading to:”. Select the consumer of interest from this list then choose a specific prey from the right-hand pull-down list. 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. A summary presents the total number of pathways and the mean length of the pathways (under the *Summary of pathways* menu item).

Top predator <- prey

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 (under the *Summary of pathways* menu item).

Cycles (living)

The routine identifies all cycles in the system excluding detritus 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.

Cycles (all)

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.

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 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.

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

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

As diversity of flows and recycling is expected to increase with maturity, so is the path length. The effects of changes in the ecosystem on the network analysis indices (such as total systems throughput, Finn and predatory cycling indices, ascendency, overhead and their breakdown into various components) can then be plotted over time and compared for various scenarios of Ecosim (see Network analysis indices in Ecosim).

7.25 Ecosim network analysis indices

Some network analysis indices have been extended into Ecosim.

To obtain these indices and their changes over time from Ecosim, the “Indices” checkbox should be checked on the Ecosim Run Ecosim form. 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 you click on the *Without primary production node*, Ecosim will calculate time series of the FIB index, Kempton’s Q, Total catch and Mean Trophic level of catch. A graph will appear in the *Main screen*.

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 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.

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When you click on the *With primary production node*, Ecosim will calculate time series of the FIB index, Kempton's Q, Total catch and Mean Trophic level of catch, Primary production required for the catch and Detritus required for the catch.

8 Using Ecosim. Part 1: Ecosim inputs

Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model. This chapter describes the steps taken to set up Ecosim scenarios (The Ecosim menu; Ecosim parameters; Group info; Vulnerabilities); read in Time series data; set up Mediation, Forcing and Egg production functions; and set parameters for Fishing effort dynamics.

Before proceeding with Ecosim, we recommend you read the introductory material on Ecosim (see links in Introductory material Ecosim), also found in Chapter 3 of the User Guide). You should also be familiar with the published literature on Ecosim, particularly Walters et al. 1997; Walters et al. 2000; Christensen and Walters 2004).

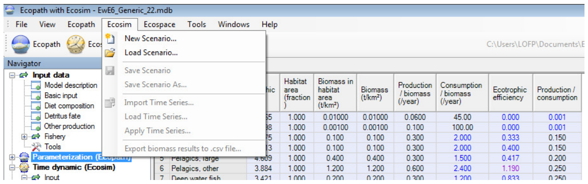
8.1 Getting started in Ecosim: The Ecosim menu

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 as 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.

Important note: Before using Ecosim you must have a balanced Ecopath model. Once you have finished balancing your Ecopath model you can begin using Ecosim. Note that once you start using Ecosim, especially when you start fitting to time series data, you will most likely encounter unexpected problems that require you to iteratively make adjustments to your Ecopath model (for example, groups becoming extinct because predation or fishing pressure is too high). Iterating between Ecopath and Ecosim in this way can be time-consuming but is very informative. Indeed, running Ecosim is an important test of the viability of a newly-balanced model and can raise interesting research questions.

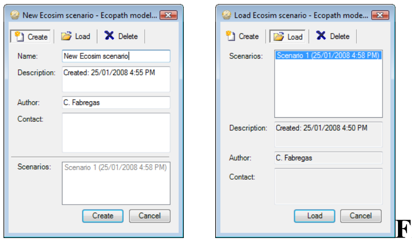
New scenario...

When you are ready to start using Ecosim, you must first create a new Ecosim scenario. You can do this by selecting *New Scenario...* on the Ecosim menu (Figure 8.1). This will open the *New Ecosim scenario* dialogue box (Figure 8.2a) where you can name your new scenario and add a description. Alternatively, you can click once on the *Ecosim shortcut button* [ ], which will open the *Load Ecosim scenario* dialogue box (Figure 8.2 b). Select the *Create* option to change it into the *New Ecosim scenario* dialogue box.



		Habitat area (fraction)	Biomass in habitat area (t/km²)	Biomass (t/km²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic efficiency	Production / consumption
		1.000	0.01000	0.01000	0.0600	45.00	0.000	0.001
		1.000	0.00100	0.00100	0.100	100.00	0.000	0.001
		1.000	0.100	0.100	0.300	2.000	0.333	0.150
		1.000	0.100	0.100	0.300	2.000	0.400	0.150
5	Pelagics, large	1.000	0.400	0.400	0.300	1.500	0.417	0.200
6	Pelagics, other	1.000	1.200	1.200	0.600	2.400	1.190	0.250
7	Deep water fish	1.000	0.200	0.200	0.300	1.200	0.833	0.250

Figure 8.1 The *Ecosim menu*. The *Ecosim shortcut button* can also be seen immediately to the left of the open menu.



Name: New Ecosim scenario
Description: Created: 25/01/2008 4:55 PM
Author: C. Fabregas
Contact:
Scenarios: Scenario 1 (25/01/2008 4:58 PM)

Scenarios: Scenario 1 (25/01/2008 4:58 PM)
Description: Created: 25/01/2008 4:50 PM
Author: C. Fabregas
Contact:

Figure 8.2 a) The *New Ecosim scenario* dialogue box. b) The *Load Ecosim scenario* dialogue box.

Load scenario...

The procedure for opening an existing Ecosim scenario is similar to that for creating a new scenario. Open the *Load Ecosim scenario* dialogue box by selecting Load scenario from the *Ecosim menu*. Existing scenarios will be listed in the *Scenarios* window (Figure 8.2b). Select the scenario you wish to load and click the *Load* button at the bottom of the dialogue box.

Alternatively, you can open a scenario directly using the *Ecosim shortcut button* []. Click on the down arrow on the right of the bottom to open a list of available scenarios and click on the name of the desired scenario. Note that the model must be closed and re-opened before new scenarios are added to menu under the *Ecosim shortcut button*. New scenarios can always be accessed from the *Load Ecosim scenario* dialogue box, regardless of when they were created.

To delete an Ecosim scenario select the scenario you wish to delete in the *Scenarios* window and click the *Delete* button at the top of the dialogue box. The *Load* button at the bottom of the box will then change to a *Delete* button, which must be clicked. You will be given the option to proceed or cancel. Clicking *Yes* implements deletion. Clicking *No* cancels deletion and you can then exit the dialogue box by clicking the *Cancel* button.

WARNING: Scenario deletion cannot be undone.

Save Scenario

You can save a scenario at any time by selecting *Save scenario* on the Ecosim menu.

Save Scenario As...

The Ecosim menu also has a *Save As...* option, allowing you to save your scenario under a new name. This is an important feature that allows you to preserve properties of an Ecosim scenario that you are happy with (e.g., Vulnerabilities, Group info), while exploring the impact of other factors in different scenarios. It is also a useful way to create a backup of a successful scenario before trying out new parameter values.

Import time series

There are two main types of data that you can read in to Ecosim: historical comparison data and time forcing data. Use *Import time series* to open a dialogue box that enables you to import a data file containing these types of data. For further instructions on using this dialogue box, see Import time series.

Important note: Imported time series are loaded into your database but not into your scenario. Use *Load time series* and *Apply time series* on this menu or in the Time series form to load and apply time series into your scenario.

For important introductory information about fitting Ecosim models to time series data, see Time series fitting in Ecosim and Hints for fitting models to time series reference data.

Load time series...

You can import multiple time series into your database but, if you wish, only use a subset of them. Select *Load time series...* to load the current time series into your model. This option is also available on the Time series form.

Apply time series...

All imported and loaded time series must be applied before they are available to Ecosim. To apply all loaded time series to your model, click *Apply time series...*. For more information on applying time series, see Time series. Use the *Time series* form to selectively apply individual time series to your model.

Export biomass results to .csv file

Exports the raw biomass results of the last Ecosim run to a csv file. See the Run Ecosim form for more details about these results.

8.2 Ecosim parameters

Enter and store key information on the current Ecosim simulation using the *Ecosim parameters* form (*Time dynamic (Ecosim) >Input > Ecosim parameters*).

Scenario

The top panel of the Ecosim parameters form provides fillable boxes where you can add a scenario **Description** and fill in **Author** and **Contact** details. You can also change the **Name** of the scenario.

Initialization

Duration of simulation (years)

Default is 50 years.

Base proportion of free nutrients

The *Base proportion of free nutrients* parameter sets the base proportion of free nutrients in the algorithm used to represent nutrient cycling. You should read the section on Nutrient cycling and nutrient limitation in Ecosim before attempting to simulate nutrient forcing.

The default free nutrient proportion is set at unity, which causes the free nutrient concentration to be virtually constant over time. Thus to “turn on” nutrient limitation effects, you must set a lower value for the base proportion of free nutrients parameter, (e.g., 0.3). You can also assign a forcing function to drive nutrient cycling (see below).

Nutrient loading forcing function number

Changes in nutrient loading can be simulated by assigning a time forcing function number to the annual total nutrient concentration on the Ecosim parameters form (the forcing time series can be read from a csv file, see Import time series, or typed directly using the Time series form). In this case, total nutrient concentration 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 $N_{T}o$) supplied by the user the same as any other time forcing function.

Before attempting to simulate nutrient forcing, you should read the section on Nutrient cycling and nutrient limitation in Ecosim.

Fleet/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 (Run Ecosim);

(2) by entering annual patterns via reference csv files along with historical ecological response data (see Time series); or

(3) by treating dynamics of fleet sizes and resulting fishing effort as unregulated and subject to fisher investment and operating decisions.

To invoke the fleet/effort dynamics model (Option (3) above), check the *fleet/effort dynamics* box on the *Ecosim parameters* form. When this box is checked, Ecosim erases all previously entered time patterns for fishing efforts and fishing rates, and replaces these with simulated values generated as each simulation proceeds. See Modelling effort dynamics for detailed description of the effort dynamics model. Set the input parameters for this model, using the Fleet size dynamics form.

Contaminant tracing

When the *Contaminant tracing* box is checked, Ecosim 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. Set the parameters for contaminant tracing using the Ecotrace input form. This form also contains description of how contaminant tracing is handled in Ecosim.

8.3 Group info

The *Group info* form (*Time dynamic (Ecosim)* > *Input* > *Group info*) enables entry of the Ecosim parameters listed below. You must already have an Ecosim scenario loaded (see Ecosim menu) before you can us this form. Each scenario can have its own set of Group info parameters.

Maximum relative 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.

Maximum 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. For more information see Foraging time and predation risk.

Feeding time adjustment rate (Range: [0,1])

This factor determines how fast organisms adjust feeding times so as to stabilize consumption rate per biomass (see Foraging time and predation risk). 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 this parameter to zero also results in simulation of compensatory growth rate responses (see Compensatory growth). 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. See Compensatory recruitment for recommendations for using this parameter to create the effects of compensation in recruitment in models with multi-stanza groups. See Compensatory natural mortality for recommendations for using this parameter to create the effects of compensation in natural mortality.

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.

Fraction of other mortality sensitive to changes in feeding time [0-1]

This is the proportion of the unexplained natural mortality rate (M0, 1-EE x total mortality rate) that is assumed to be sensitive to changes in feeding time. Setting it to 0.0 causes M0 to remain constant. Setting it to a higher value causes that proportion of M0 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. See Compensatory recruitment for recommendations for using this parameter to create the effects of compensation in recruitment in models with multi-stanza groups.

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 behaviour’. 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 introductory material on Density-dependent changes in catchability, also in Chapter 3 of the User Guide.

QBmax/QBo (handling time) [>1]

See introductory material on Predator satiation and handling time effects, also in Chapter 3 of the User Guide.

Switching power parameter [0-2]

Default 0 is no switching. See introductory material on Modelling switching behaviour, also in Chapter 3 of the User Guide.

8.4 Vulnerabilities (flow control: foraging arena parameter)

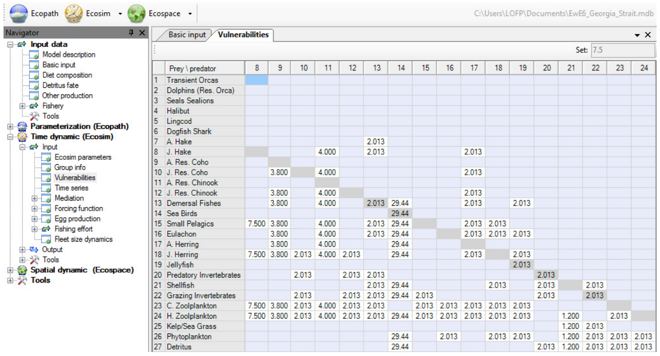
One of the most important features of Ecosim is its ability to allow exploring the implications on system dynamics of different views of how the biomass of different groups in the ecosystem is controlled. The two extreme views are 'predator' control' (also called top-down control) and 'prey control' (or bottom-up). We model this using 'vulnerabilities', which represent the degree to which a large increase in predator biomass will cause in predation mortality for a given prey (see Vulnerabilities in Ecosim for details).

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. 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. The vulnerability parameters are among the most important parameters that can be changed to improve the agreement of the model's predictions with historical data (see Time series fitting in Ecosim, Hints for fitting models to time series reference data and Effect of P/B (Z) and vulnerability for time series fitting). See also Fit to time series.

Vulnerabilities are entered on (or transferred from the time series fitting routine to) the *Vulnerabilities* form (*Time dynamic (Ecosim) > Input > Vulnerabilities*; see Figure 8.3). You must already have an Ecosim scenario loaded (see Ecosim menu) before you can set vulnerabilities. You must set the vulnerabilities for each new scenario, as all new scenarios have a default setting of 2.0. Note that the default value of 2.0 is arbitrarily assigned. Choosing to keep the default values is as much a decision as setting them to a new value. See Vulnerabilities in Ecosim for further scientific guidance on setting vulnerabilites.

Vulnerabilities can be set for the entire system (using the *Set* box in the upper right corner of the form). In general, because the vulnerability settings concern foraging behaviour, the same vulnerability is set for all of the prey of a certain predator (i.e., vulnerabilities are set column-wise). Individual values can be entered to characterize, e.g., the interactions of one (or several) predator/prey pair(s) under special conditions. We caution against setting different vulnerability parameters for every predator-prey interaction. While doing so may provide a better statistical fit to the time series data, it is unlikely that there is enough information in the data to distinguish among different parameter-combinations: i.e., the model will be overparameterized.

To transfer a set of vulnerabilities to a new scenario, use the *Save scenario as* option on the Ecosim menu to save an existing scenario and its associated vulnerabilities under a new name. Alternatively, use different scenarios to test for sensitivity to different sets of vulnerability values.



	Prey \ predator	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Transient Orcas																	
2	Dolphins (Res. Orca)																	
3	Seals Sealions																	
4	Halibut																	
5	Lingcod																	
6	Dogfish Shark																	
7	A. Hake						2.013											
8	J. Hake				4.000		2.013				2.013							
9	A. Res. Coho																	
10	J. Res. Coho		3.800		4.000						2.013							
11	A. Res. Chinook																	
12	J. Res. Chinook		3.800		4.000						2.013							
13	Demersal Fishes		3.800		4.000		2.013	29.44			2.013		2.013					
14	Sea Birds							29.44										
15	Small Pelagics	7.500	3.800		4.000		2.013	29.44			2.013	2.013						
16	Eulachon		3.800		4.000		2.013	29.44			2.013	2.013	2.013					
17	A. Herring		3.800		4.000			29.44										
18	J. Herring	7.500	3.800	2.013	4.000	2.013		29.44			2.013		2.013					
19	Jellyfish												2.013					
20	Predatory Invertebrates			2.013		2.013	2.013							2.013				
21	Shellfish						2.013	29.44				2.013		2.013		2.013		
22	Grazing Invertebrates			2.013		2.013	2.013	29.44	2.013					2.013		2.013		
23	C. Zoolplankton	7.500	3.800	2.013	4.000	2.013	2.013		2.013	2.013	2.013	2.013	2.013					
24	H. Zoolplankton	7.500	3.800	2.013	4.000	2.013	2.013	29.44	2.013	2.013	2.013	2.013	2.013		1.200		2.013	
25	Kelp/Sea Grass														1.200	2.013		
26	Phytoplankton							29.44		2.013		2.013	2.013		1.200	2.013	2.013	2.013
27	Detritus							29.44						2.013	1.200	2.013	2.013	2.013

Figure 8.3 Ecosim vulnerability settings reflecting how far a consumer is from its carrying capacity with regards to a prey.

8.5 Time series

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 (see introductory material on Time series fitting in Ecosim, Hints for fitting models to time series reference data as well as the help section on Ecosim's Time series fit search interface, which searches for Vulnerabilities that can help improve the model's fit).

There are two main types of data that you can read in to Ecosim: historical comparison data and time forcing data. Historical comparison data enable comparison between historical observations and the model's predictions. Time forcing data are used to force certain variables in the model (i.e., 'drive' the model). Fishing effort (by gear or by pool) and fishing mortality can be forced in Ecosim.

The *Time series* form (*Time dynamic (Ecosim)* > *Input* > *Time series*) provides an interface where users can read in, view and activate time series for use in Ecosim.

Reading time series into Ecosim

There are two ways to read time series data into Ecosim: (i) time series can be imported from a csv file or your computer's clipboard (see *Import…* below); or (ii) time series can be typed or pasted in directly using the *Time series* form (see *Values…* below).

When you open the *Time series* form for the first time, there will be no time series displayed in the lower panel (Figure 8.4). To get started, use either the *Import…, Load...* or *Add…* buttons on the lower panel of the form.

Important note: After importing or loading time series, they must be activated using *Weight...* (see below).

Import…

Opens the *Import time series* dialogue box. This allows you to import multiple time series simultaneously from a csv (comma separated values) format file and is the most commonly-used means of reading time series data into Ecosim. See Import time series for instructions on using this form. Note that this form can also be accessed from the main Ecosim menu.

After importing time series, they must be weighted using *Weight...* (see below).

Load...

Opens the *Load time series* dialogue box, where you can load previously imported time series using the check-boxes provided (Figure 8.5). After loading time series, they must be weighted using the *Weight* button at the top of the *Weight time series* dialogue box (see *Weight...*below).

Add…

Opens the *Add time series* dialogue box for adding time series manually (Figure 8.6). To add a time series using the *Add time series* dialogue box:

1.Type or select the number of years for the time series.

2.Click the *Set* button.

3.Select the data type from the drop-down menu in the *Type* window. Available data types are Absolute biomass, Average weight (for multi-stanza groups only), Catches, Fishing mortality*, Fleet/gear effort*, Force biomass*, Force catches*, Relative biomass or Total mortality.

*Indicates forcing time series;

4.Select the Ecopath group to which the time series applies from the drop-down *Group* menu.

5.Assign the data series a relative weight using the *Weight* window. This represents 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 or unreliable data; higher weights imply low variance or reliable data).

6.Type the *y*-values of the time series in the right hand column. Annual time-steps are automatically displayed in the left hand column.

7.Click OK. The time series will be displayed in the main panel of the form and also as a thumbnail in the lower panel.

After adding a time series, it must be activated using *Weight...* (see below).

Duplicate

Copies the currently-selected time series.

Remove...

Removes the currently-selected time series.

Weight...

Assign the data series a relative weight using the *Weight* window. This represents 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 or unreliable data; higher weights imply low variance or reliable data).

To weight time series:

1. Click *Weight...* in the bottom panel of the *Time series* form to open the *Weight time series* dialogue box (Figure 8.6) and alter the weights for individual time series.

2. Click the *Apply* button on the dialogue box.

Note that this dialogue box offers the option to enable or disable time series for use in Ecosim. Clearing the enabled flag on a time series has the same effect as setting the series' weight to 0. However, the enabled flag allows a user to exclude a time series from use in Ecosim without having to alter the relative weight value.

Thumbnails of enabled time series with a positive weight will be shown with a check mark (Figure 8.7).

There are two additional buttons at the top of the *Time series* form. First select a time series from the thumbnails in the bottom panel, then:

Values

Displays information and values for the currently-selected time series.

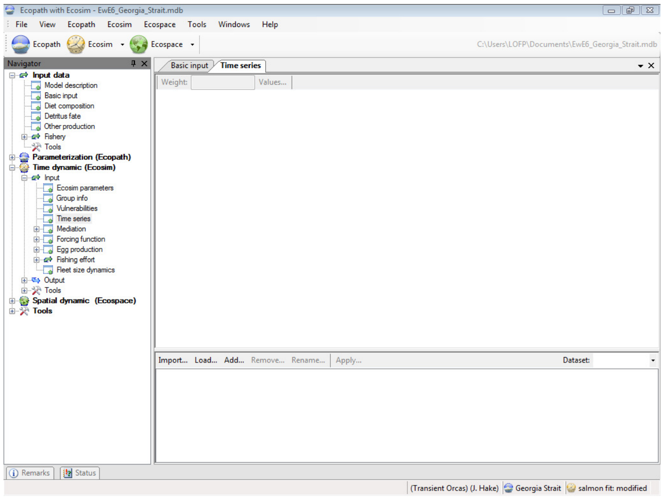
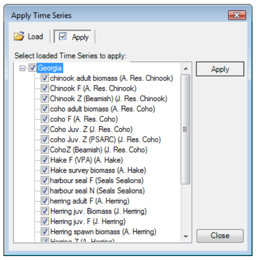


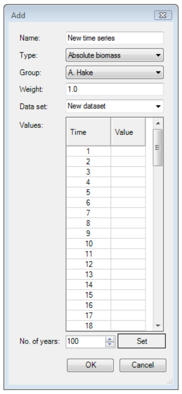
Figure 8.4 When you open the *Time series* form for the first time, there will be no time series displayed in the lower panel



☑ Georgia
- ☑ chinook adult biomass (A. Res. Chinook)
- ☑ Chinook F (A. Res. Chinook)
- ☑ Chinook Z (Beamish) (J. Res. Chinook)
- ☑ coho adult biomass (A. Res. Coho)
- ☑ coho F (A. Res. Coho)
- ☑ Coho Juv. Z (J. Res. Coho)
- ☑ coho Juv. Z (PSARC) (J. Res. Coho)
- ☑ CohoZ (Beamish) (J. Res. Coho)
- ☑ Hake F (VPA) (A. Hake)
- ☑ Hake survey biomass (A. Hake)
- ☑ harbour seal F (Seals Sealions)
- ☑ harbour seal N (Seals Sealions)
- ☑ herring adult F (A. Herring)
- ☑ Herring juv. Biomass (J. Herring)
- ☑ Herring juv. F (J. Herring)
- ☑ Herring spawn biomass (A. Herring)

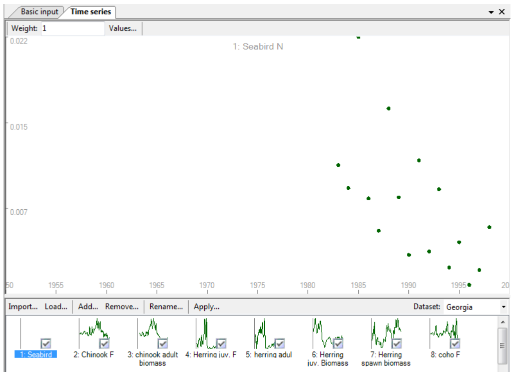
Figure 8.5 The *Apply time series* dialogue box showing the apply function. Click on the *Load* button to select time series to load from the database.

Please note: All help topics are currently in draft format. Please send your comments to the email address given at www.ecopath.org (About >> Contact us).



Name: New time series
Type: Absolute biomass
Group: A. Hake
Weight: 1.0
Data set: New dataset
No. of years: 100

Figure 8.6 The *Add time series* dialogue box.



Weight: 1
Dataset: Georgia

Figure 8.7 Thumbnails of enabled time series will be shown with a check mark

8.6 Import time series

There are two main types of data that you can read in to Ecosim: historical comparison data and time forcing data. Historical comparison data enable comparison between historical observations and the model's predictions. Time forcing data are used to actually force certain variables (fishing effort, fishing mortality) in the model (i.e., 'drive' the model). You can load both types of data with the same data file, using the codes for different data types listed below (forcing data types are indicated in parentheses).

The time series data file

For historical comparison data, 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., 1976) is to be the simulation start year. Forcing time series must have an entry for every year of the simulation. 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).

The spreadsheet must be identical in format as shown in Figure 8.8 (i.e., cells 1-3 in the first column must read "Name", "Pool code" and "Type" respectively and the years of the simulation must be listed below these in the first column). For each data series (column) you must enter the Ecopath group or fleet number (Pool code) and specify the data type (see list of data types below). You can use the first row (Name) to describe the group and the data. This information will be displayed on output graphs.

Optionally, a row labelled “Weight” can be inserted between the name and pool code rows, in which users can specify time series weights. If this row is omitted, time series will be imported with a default weight of 1.

Overview of data types:

-1 Force biomass (forcing)

0 Relative biomass

1 Absolute biomass

2 Time forcing data (forcing) *

3 Effort data by gear type (forcing)

4 Fishing mortality, (F) by pool (forcing)

5 Total mortality, (Z) by pool

-5 Forced total mortality (Z) (forcing)

6 Catches

-6 Forced catches (forcing) †

7 Average weight (stanzas only)

* Using data type 2, you can force nutrient concentrations (see Ecosim parameters and links therein); parameters that affect trophic interactions through abiotic factors (see Forcing function and Apply FF (consumer)) or primary production (see Apply FF (primary producer)).

† Forcing catches enables Use of Ecosim for Stock Reduction Analysis.

How to import a time series data file

Important note. After importing a time series file, you must weight the time series using the Time series form.

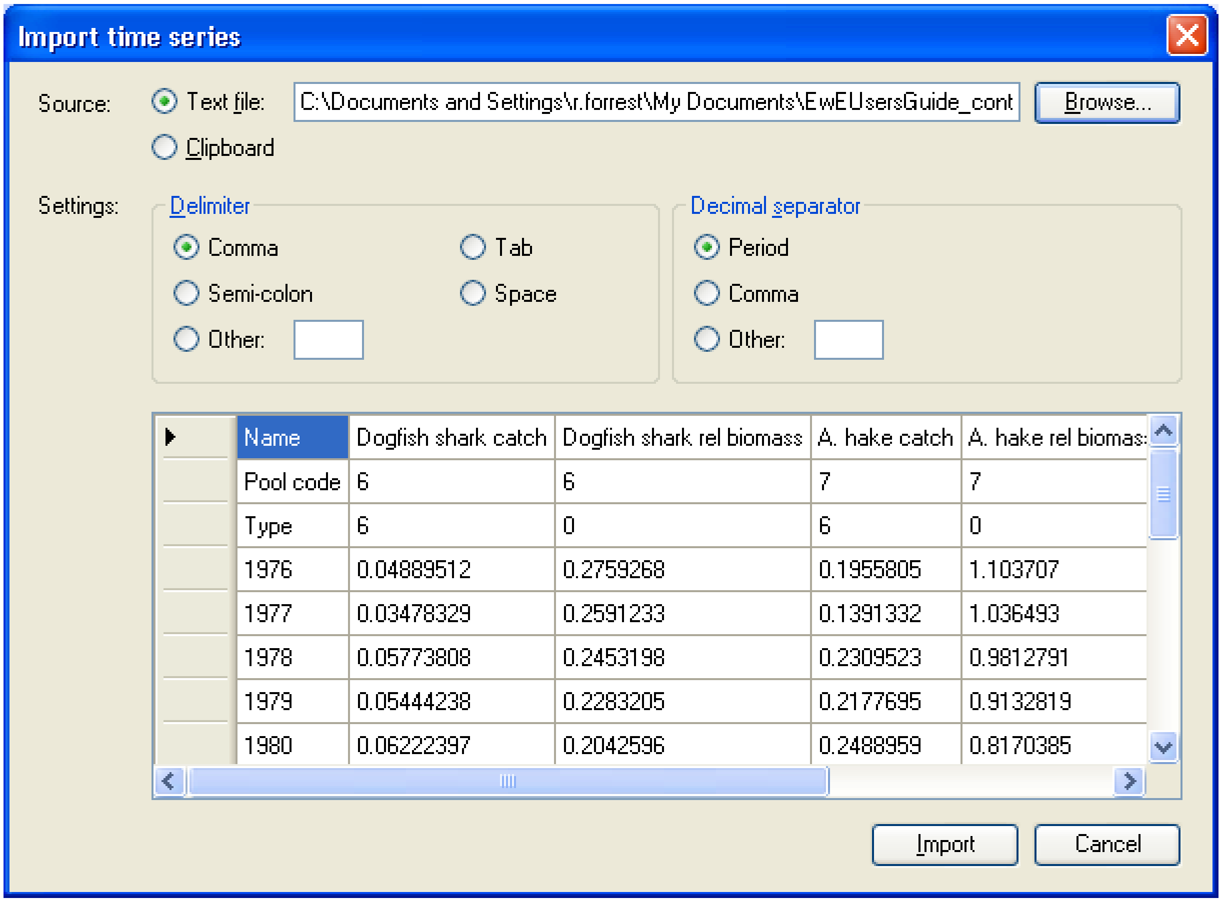
Note that you must already have an Ecosim scenario loaded before you can import a time series data file (see Ecosim menu for instructions for creating and loading Ecosim scenarios).

The Import time series dialogue box (Figure 8.8) allows you to load time series data stored in CSV (comma separated values) or similar text format. It can be accessed:

(i) from the *Ecosim menu*; or

(ii) from the *Time series* form (Import…).

To read in a data file, click *Browse* to locate your file or select it from the clipboard. You must then set the delimiter used to separate the values in the csv or text file and the separator used as a decimal point. Your data will be displayed in the bottom window of the form (see Figure 8.8). If everything looks as you expected it, click the *Import* button. If the data is not displaying as expected, first double-check that the *Delimiter* and *Decimal separator* settings are correct before checking that your file is in the correct format.



Source: ● Text file: C:\Documents and Settings\r.forrest\My Documents\EwEUsersGuide_cont

○ Clipboard

Settings:

Delimiter

● Comma ○ Tab
○ Semi-colon ○ Space
○ Other:

Decimal separator

● Period
○ Comma
○ Other:

Name	Dogfish shark catch	Dogfish shark rel biomass	A. hake catch	A. hake rel biomas
Pool code	6	6	7	7
Type	6	0	6	0
1976	0.04889512	0.2759268	0.1955805	1.103707
1977	0.03478329	0.2591233	0.1391332	1.036493
1978	0.05773808	0.2453198	0.2309523	0.9812791
1979	0.05444238	0.2283205	0.2177695	0.9132819
1980	0.06222397	0.2042596	0.2488959	0.8170385

Figure 8.8. The Import time series dialogue box.

8.7 Mediation

You can define a series of 'trophic mediation functions' that are used to modify vulnerabilities of selected prey types i to their predators j using Ecosim's Mediation form (see Using the trophic mediation form below for instructions, although you should read this brief introduction first).

It is not uncommon for some third type of organism (i.e., mediating organism) to affect the feeding rate of one type of organism j on another i. At least two types of effects are possible:

<u>Facilitation</u>: 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 for marine mammals and birds in the Eastern Pacific Ocean, at least in areas where heavy fishing has reduced abundances of tunas and billfishes.

<u>Protection</u>: 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.

Each trophic mediation function is defined in the following steps (described in more detail in sections below):

1. Sketch a functional form for the mediation effect (i.e. the mediation affect as a function of the biomass of the mediating organism);
2. Define the *x* variable (i.e. independent variable) for each function by specifying relative weightings for the effects of different mediating organisms. Weightings can be specified for one or more Ecopath groups, so that *x* becomes a weighted sum of mediating organism biomasses (i.e., more than one group can have the same trophic mediation effect but to different degrees); and
3. Applying the 'trophic mediation function' to specific predator-prey interactions (using the Apply mediation form).

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* a weighted sum of third organism biomasses is to:

1. Allow differential protective 'quality' for alternative organisms that provide cover for prey; and
2. Recognize that several different groups 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.

Internally, the Ecosim routines use the trophic mediation functions to modify prey vulnerabilities $v_{i,j}$ 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 $v_{i,j} = v_{i,j}\ base \cdot y/yo$, where *y* is the current value of the mediation function, which depends on the current *x* of that function, and *yo* is the value of the function when $x =$ Ecopath base weighted sum of mediating biomasses.

Using the trophic mediation form

To implement trophic mediation in Ecosim, open the *Mediation* form (*Time dynamic (Ecosim)* > *Input* > *Mediation*; see Figure 8.9). Note you must have an Ecosim scenario loaded before you can use the *Mediation* form. There are three steps to the process:

Step 1. Define trophic mediation shapes;

Step 2. Define and edit relative weight of impacting groups; and

Step 3. Apply trophic mediation shapes to predator-prey interactions.

Step 1. Define trophic mediation shapes

When you open the Mediation form for the first time, you will see several 'blank' mediation shapes (Figure 8.9). To define a mediation shape, first select one of these blank shapes. You can then define trophic mediation shapes in one of two ways:

Please note: All help topics are currently in draft format. Please send your comments to the email address given at www.ecopath.org (About >> Contact us).

> 1. Shapes can be drawn freehand using the blue sketch pad. You will see your sketched shape transferred to the thumbnail in the bottom pane;
>
> 2. Alternatively, you can use standard mathematical shapes. Click *Change shape …* at the top of the form to open the *Change shape* dialogue box (Figure 8.10). Select a shape type (e.g., linear, sigmoid, exponential) from the menu in the window. You can tailor the shape to your specific requirements by setting the *Y Zero*, *Y End, Y Base* and *Steepness* parameters (where appropriate) in the cells provided.

Save as image …

Clicking the *Save as image …* button at the top of the form opens a dialogue box prompting you to save the current trophic mediation shape to a bitmap file (.bmp). Use this dialogue box to name the file and browse for a location to save it.

Values ...

Displays the values of the current mediation shape.

Change shape ...

See point 2 above.

Reset

Resets the current trophic mediation shape to the value of 1.0.

Options ...

Opens the *Graph display options* dialogue box. Set the way the mediation shape is displayed in the main window of the *Mediation* form.

There are four additional menu items on the bottom pane that allow you add, copy, delete and rename mediation shapes.

Add…

Adds an extra blank mediation shape.

Duplicate

Copies the currently-selected mediation shape.

Remove ...

Removes the currently-selected mediation shape. A warning that shape-deletion cannot be undone will appear. Click *Yes* to remove the shape.

Rename

Rename the currently-selected mediation shape by selecting *Rename*. You will then be able to type in a new name for the shape.

Step 2. Define and edit relative weight of impacting groups

The *Edit relative weight* (*Edit…*) button is found in the middle of the *Mediation* form just above the *Mediating groups* graph (see Figure 8.9). As discussed above, the relative weightings are used to assign a weighted sum of third-party group biomasses to the *x*-axis of each trophic mediation function. This allows several different groups to have the same trophic mediation effect but to different degrees. Note that third-party groups can be functional groups of organisms (Ecopath groups) or fishing fleets.

Assign relative weightings in the following steps:

1. First, you must select a mediation shape from the set of mediation shapes at the bottom of the *Mediation* form. Once you have selected the desired mediation shape, click the *Edit…* button to open the *Define biomass percentage* form to assign relative weightings by group to that particular mediation shape (Figure 8.11).

2. On the *Define biomass percentage* form, select third-party groups/fleets from the menu on the left and move them to the *Assigned groups and fleets* table using the green arrow.

3. For each third-party group, assign a relative weighting using the *Relative weight* box at the top of the form. For example, if you believe three of your model groups (Group 3, Group 4 and Group 5) act as third-party groups by facilitating a particular predator-prey interaction (represented by Mediation Shape 1), and you enter 2 for Group 3, 1 for Group 4, and 0.5 for Group 5, the biomasses on the *x*-axis of Mediation Shape 1 will be weighted as 2B3 + B4 + 0.5B5.

4. When you have finished assigning relative weightings, click *OK*.

Relative weights for each group will now be displayed as a bar graph on the lower panel of the *Mediation* form, with Ecopath Groups on the X-axis and Relative weight on the Y-axis (Figure 8.12).

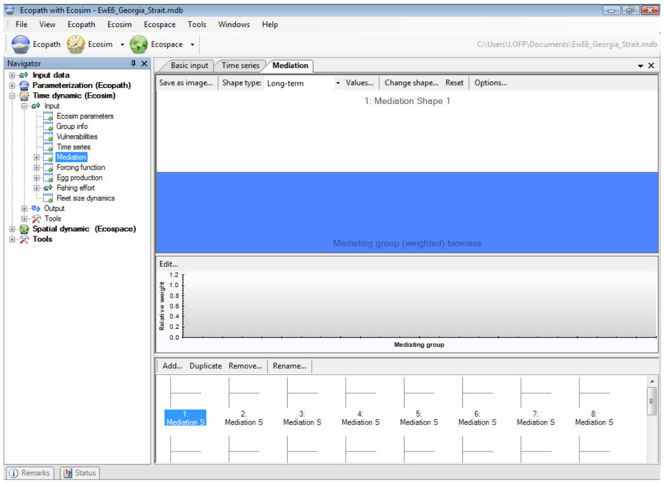
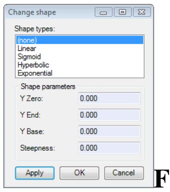
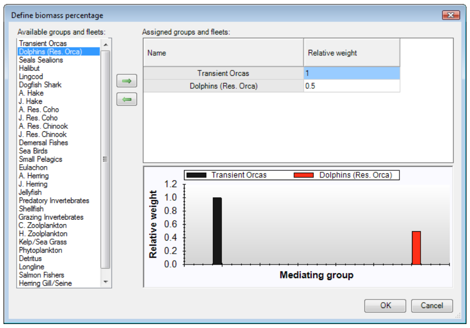


Figure 8.9 The *Mediation* form showing the mediation shape panel (top), the mediating groups panel (centre) and the thumbnails panel (bottom). In this form, mediation functions have not yet been defined.



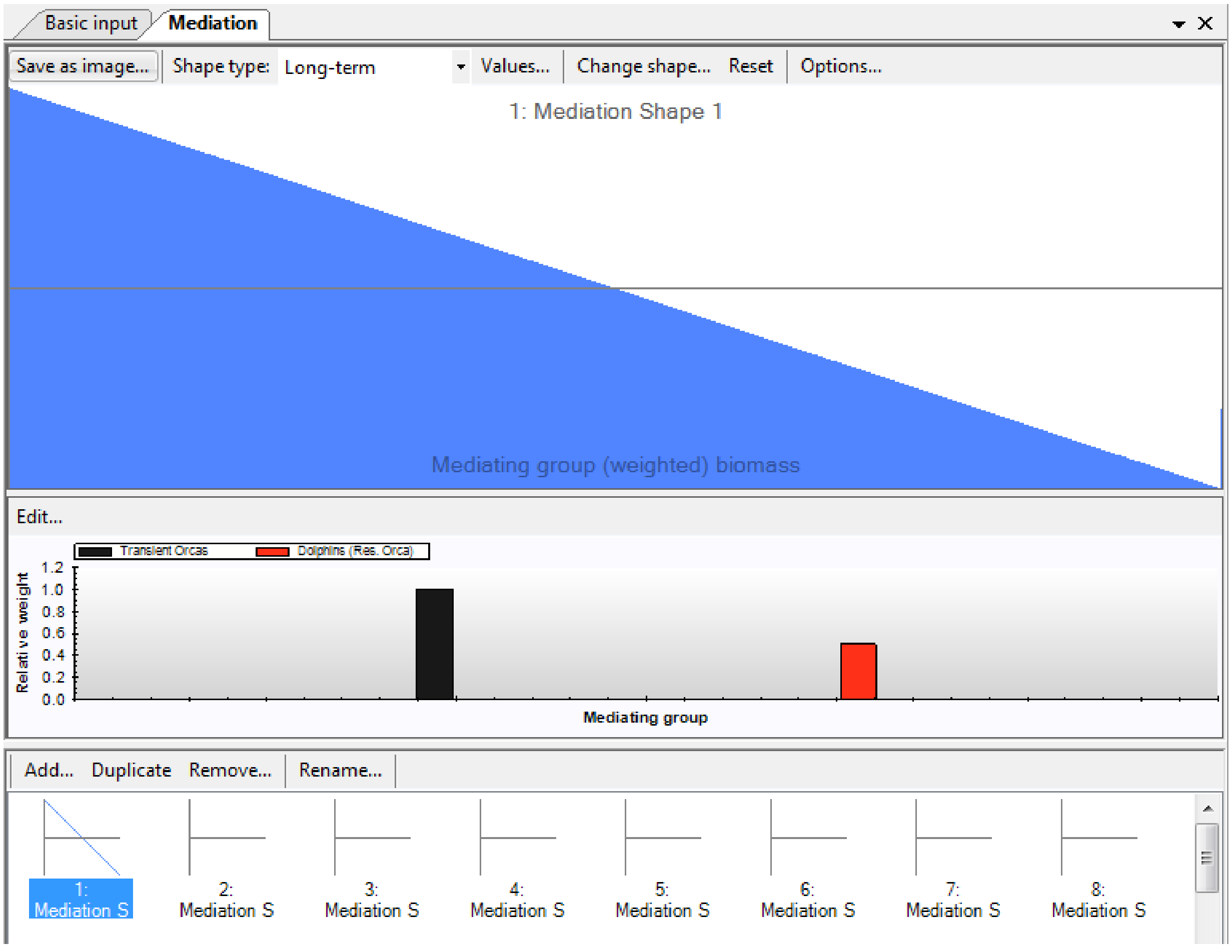
Y Zero: 0.000
Y End: 0.000
Y Base: 0.000
Steepness: 0.000

Figure 8.10 The *Change shape* dialogue box.



Name	Relative weight
Transient Orcas	1
Dolphins (Res. Orca)	0.5

Figure 8.11 The *Define biomass percentage* dialogue box.



Shape type: Long-term

Figure 8.12 The *Mediation* form after one mediation function has been defined. In this example, Transient orcas and Dolphins are treated as a mediating, third party group with a negative impact on the affected predator-prey relationship (which is defined in the *Apply mediation* form). Transient orcas here have twice the mediating effect of Dolphins.

Step 3. Apply mediation shapes

After you have defined the mediation shapes you must continue to the Apply mediation form to define the predator-prey relationships that each of the mediation functions impact.

8.8 Apply mediation

The *Apply mediation* form (*Time dynamic (Ecosim)* > *Input* > *Mediation* > *Apply Mediation*) is used to apply the trophic mediation functions you defined using the Mediation form.

Before using the *Apply mediation* form, you must first define at least one trophic mediation function following the instructions for using the Mediation form. It is recommended you first read the introductory material on Linking mediation and time forcing functions to trophic interaction rates to understand how trophic mediation functions are applied in Ecosim.

Selecting *Apply mediation* opens a form that consists of a grid representing predator (j) / prey (i) interactions (Figure 8.13). Predators are represented in columns with prey in rows. Predator/prey interactions, as defined in the Diet composition are indicated by white cells.

1. To apply a trophic mediation function, click once in the i,j cell representing the predator/prey interaction to which you wish to apply the function. This will open the *Apply forcing and mediation functions* dialogue box (Figure 8.14). The affected prey and predator group will be displayed at the top of the form.

Next, select the parameter to which the mediation multiplier is to be applied using the radio buttons at the bottom of the dialogue box. There are four possible options:

a. Multiply overall predator rate of effective search ($a_{i,j}$), for example to represent time-varying turbidity changes that affect predator search efficiency or mediation effects of algal biomass on search efficiency.
b. Multiply vulnerability exchange rate ($v_{i,j}$), for example to represent increased movement rates of prey into vulnerable behavioural state at times when water mixing rates are higher;
c. Multiply area of foraging arenas (divide $a_{i,j}$ by multiplier), for example to represent increase in habitat area available for juvenile fish refuges;
d. Multiply area (divide $a_{i,j}$) and also multiply $v_{i,j}$, for example to represent increase in safe foraging habitat available to a predator that feeds on prey that become available in foraging arenas through passive drift/mixing processes such that increasing area used by predator results in higher proportion of total prey population being available in foraging areas at any moment.

The selected modifier will be shown in the *Applied shape function*s window (Figure 8.14).

2. Next, select the desired mediation shape from the_Available shape functions_window at the left of the dialogue box by clicking the green arrow. This will move the shape function into the Applied shape functions window. You can remove a shape from this window by clicking the remove button immediately below the green arrow. Note that a common form is used to apply Mediation and Seasonal/Forcing functions. Do not select a seasonal or forcing function.

3. Finally, click *OK*. You should see the number of the mediation function (preceded by 'M') you selected in the predator/prey cell.

Note that you can apply up to five seasonal, forcing and/or mediation functions to each predator-prey interaction.

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Clear all

You can clear all applied seasonal, forcing and/or mediation functions from the predator-prey grid by selecting *Clear all* from the top of the *Apply mediation* form.

To apply a mediation function to the interactions between a particular predator and all of its prey species, click on the number of the predator at the top of the form. When the *Apply forcing and mediation functions* dialogue box opens you will see a message at the top of the box reflecting that all the prey are affected.

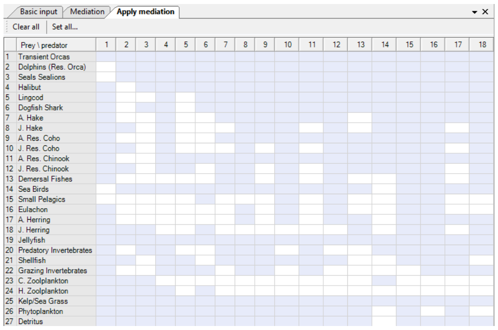
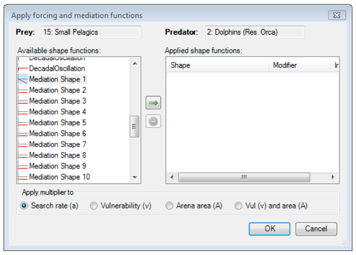


Figure 8.13 The *Apply mediation* form.



Prey: 15: Small Pelagics

Predator: 2: Dolphins (Res. Orca)

Apply multiplier to

● Search rate (a) ○ Vulnerability (v) ○ Arena area (A) ○ Vul (v) and area (A)

Figure 8.14 The *Apply forcing and mediation functions* dialogue box. Select only Mediation shapes.

8.9 Forcing function

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. Ecosim does, however, contain a routine to allow a '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 (see Linking mediation and time forcing functions to trophic interaction rates). You can also use a forcing function to force primary production directly (see Primary production in Ecosim. Forcing functions in Ecosim are of two types:

- Seasonal (i.e. cycles within a year that repeat annually); and
- Long-term (monthly).

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 period of years equal to the duration of the simulation (calculated with monthly time steps). If your time series has annual time steps, Ecosim will use the same value for each month in the year. Such shapes may be used to represent e.g., decadal regime shifts, such as occur in the North Pacific.

Defining Seasonal/Long-term forcing shapes

Important note: after you have defined forcing shape(s) as described below, you must continue to one of the *Apply forcing function* forms (Apply FF (consumer) or Apply FF (primary producer)) to set the groups affected by the forcing function.

There are a number of ways to define forcing shapes in Ecosim. First, forcing functions can be read in as time series from a csv file using the Import time series on the Time series form or the Ecosim menu. Set the 'data type' to 2 in the csv file. Note the series must be activated using the *Apply time series* dialogue box, accessible from the *Ecosim menu* or the *Time series* form.

Alternatively, you can define a forcing function using the *Forcing function* form (*Time dynamic (Ecosim)* > *Input* > *Forcing function*). Note you must have an Ecosim scenario loaded before you can open this form.

When you open the *Forcing function* form for the first time, you will see four 'blank' forcing shapes (three seasonal shapes and one annual forcing shape), each with constant default value of 1.0. If there is currently a data file activated containing one or more time series of data type 2, these will also be displayed.

To define a forcing shape using the *Forcing function* form, first select one of the 'blank' shapes in the lower pane. Be sure to select a 'Seasonal shape' for monthly data or a 'Forcing shape' for long-term data. You can then define forcing shapes in one of two ways:

1. Shapes can be drawn freehand using the red sketch pad. If you have selected a Seasonal shape, the *x*-axis will appear as the months January to December and your sketch will be drawn in monthly blocks (Figure 8.15a). If you have selected an annual Forcing shape, the *x*-axis will be shown as Years 1-100. The sketch will be smooth (Figure 8.15b). You will see your sketched shape transferred to the selected shape in the bottom pane;

2. Alternatively, you can use standard mathematical shapes. Click *Change shape…* at the top of the form to open the *Change shape* dialogue box. Select a shape type (e.g., linear, sigmoid, exponential) from the menu in the window. You can tailor the shape to your specific requirements by setting the *Y Zero*, *Y End, Y Base* and *Steepness* parameters (where appropriate) in the cells provided.

Save as image …

Clicking the *Save as image …* button at the top of the form opens a dialogue box prompting you to save the current trophic mediation shape to a bitmap file (.bmp). Use this dialogue box to name the file and browse for a location to save it.

Shape type

Select whether the selected shape is a seasonal or long-term forcing shape.

Values ...

Displays the values of the current forcing shape.

Change shape ...

See point 2 above.

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Reset

Resets the current forcing or seasonal shape to the default constant value of 1.0.

Options ...

Opens the *Graph display options* dialogue box. Set the way the forcing shape is displayed in the main window of the *Forcing function* form.

There are four additional menu items on the bottom pane of the *Forcing function* form that allow you add, copy, rename and delete forcing or seasonal shapes.

Add…

Adds an extra blank long-term forcing shape. If necessary, use *Shape type* to change the long-term forcing shape to a seasonal shape.

Duplicate

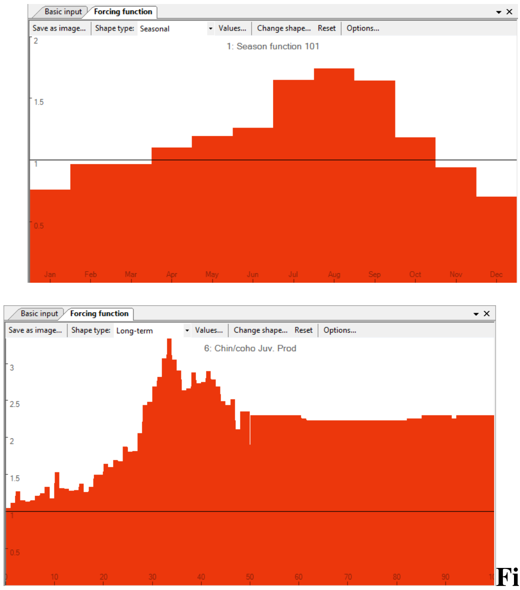
Copies the currently-selected shape.

Remove...

Removes the currently-selected shape. A warning that shape-deletion cannot be undone will appear. Click *Yes* to remove the shape.

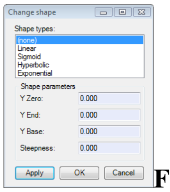
Rename...

Rename the currently-selected shape by selecting *Rename*. You will then be able to type in a new name for the shape.


Shape type: Seasonal

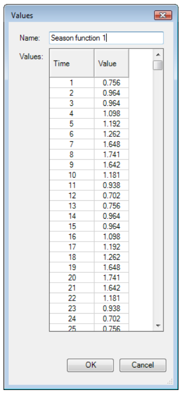
Shape type: Long-term

Figure 8.15 Examples of a) a seasonal forcing function and b) a long-term (annual) forcing function.



Y Zero: 0.000
Y End: 0.000
Y Base: 0.000
Steepness: 0.000

Figure 8.16 The *Change shape* dialogue box.



Name: Season function 1

Values:

Time	Value
1	0.756
2	0.964
3	0.964
4	1.098
5	1.192
6	1.262
7	1.648
8	1.741
9	1.642
10	1.181
11	0.938
12	0.702
13	0.756
14	0.964
15	0.964
16	1.098
17	1.192
18	1.262
19	1.648
20	1.741
21	1.642
22	1.181
23	0.938
24	0.702
25	0.756

Figure 8.17 The *Values* dialogue box.

8.10 Apply forcing function (consumer)

Forcing functions represent physical or other environmental parameters that may influence trophic interactions. These forcing functions can be used to modify the Q/B ratio of the consumer groups in the model (see Linking mediation and time forcing functions to trophic interaction rates), or to directly influence primary production (see Primary production in Ecosim).

To apply a forcing function to trophic flows (i.e., predator-prey interactions), use the *Apply FF (consumer)* form (*Time dynamic (Ecosim)* > *Input* > *Apply FF (consumer)*). To apply a forcing function to primary productivity directly, use the Apply FF (primary producer) form. Before using either *Apply FF* form, you must first define at least one seasonal or long-term forcing function following the instructions for using the Forcing function form.

The *Apply FF (consumer)* form consists of a grid representing predator (*j*) / prey (*i*) interactions (Figure 8.18). Predators are represented in columns with prey in rows. Predator/prey interactions, as defined in the Diet composition are indicated by white cells.

To apply a long-term forcing or seasonal function, select the *i,j* cell representing the predator/prey interaction to which you wish to apply the function. This will open the *Apply forcing and mediation functions* dialogue box (Figure 8.19). The affected prey and predator group will be displayed at the top of the form.

Next, select the parameter to which the forcing multiplier (represented by the forcing function) is to be applied using the radio buttons at the bottom of the dialogue box. There are four possible options:

a. Multiply overall predator rate of effective search ($a_{i,j}$), for example to represent time-varying turbidity changes that affect predator search efficiency or mediation effects of algal biomass on search efficiency.
b. Multiply vulnerability exchange rate ($v_{i,j}$), for example to represent increased movement rates of prey into vulnerable behavioural state at times when water mixing rates are higher;

c. Multiply area of foraging arenas (divide $a_{i,j}$ by multiplier), for example to represent increase in habitat area available for juvenile fish refuges;
d. Multiply area (divide $a_{i,j}$) and also multiply $v_{i,j,}$ for example to represent increase in safe foraging habitat available to a predator that feeds on prey that become available in foraging arenas through passive drift/mixing processes such that increasing area used by predator results in higher proportion of total prey population being available in foraging areas at any moment.

The selected modifier will be shown in the window *Applied shape functions* window (Figure 8.19).

Next, select the desired forcing or seasonal shape from the *Available shape functions* window at the left of the dialogue box by clicking the green arrow. This will move the shape function into the Applied shape functions window. You can remove a shape from this window by clicking the remove button immediately below the green arrow. Note that a common form is used to apply Mediation and Seasonal/Forcing functions. Do not select a mediation function.

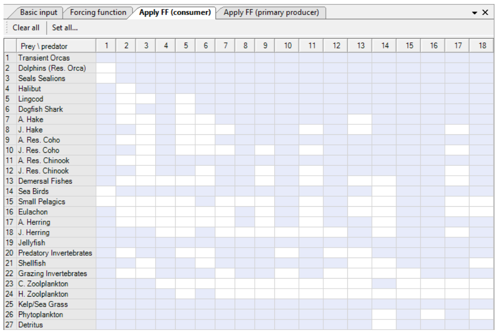
Finally, click *OK*. You should see the number of the forcing or seasonal function you selected in the predator/prey cell (preceded by 'F').

Note that you can apply up to five seasonal, long-term forcing and/or mediation functions to each predator-prey interaction.

Clear all

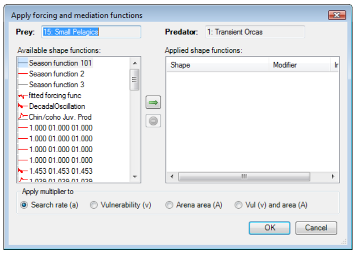
You can clear all applied seasonal, forcing and/or mediation functions from the predator-prey grid by selecting *Clear all* from the top of the form.

To apply a forcing function to the interactions between a particular predator and all of its prey species, click on the number of the predator at the top of the form. When the *Apply forcing and mediation functions* dialogue box opens you will see a message at the top of the box reflecting that all the prey are affected.



1 Transient Orcas
2 Dolphins (Res. Orca)
3 Seals Sealions
4 Halibut
5 Lingcod
6 Dogfish Shark
7 A. Hake
8 J. Hake
9 A. Res. Coho
10 J. Res. Coho
11 A. Res. Chinook
12 J. Res. Chinook
13 Demersal Fishes
14 Sea Birds
15 Small Pelagics
16 Eulachon
17 A. Herring
18 J. Herring
19 Jellyfish
20 Predatory Invertebrates
21 Shellfish
22 Grazing Invertebrates
23 C. Zoolplankton
24 H. Zoolplankton
25 Kelp/Sea Grass
26 Phytoplankton
27 Detritus

Figure 8.18 The *Apply FF (consumer)* form



Prey: 15: Small Pelagics
Predator: 1: Transient Orcas

Season function 101
Season function 2
Season function 3
fitted forcing func
DecadalOscillation
Chin/coho Juv. Prod
1.000 01.000 01.000
1.000 01.000 01.000
1.000 01.000 01.000
1.000 01.000 01.000
1.453 01.453 01.453

● Search rate (a) ○ Vulnerability (v) ○ Arena area (A) ○ Vul (v) and area (A)

Figure 8.19 The *Apply forcing and mediation functions* dialogue box. Select only Forcing shapes.

8.11 Apply forcing function (primary producer)

Forcing functions represent physical or other environmental parameters that may influence trophic interactions. These forcing functions can be used to directly influence primary production (see Primary production in Ecosim), or to modify the Q/B ratio of the consumer groups in the model (see Linking mediation and time forcing functions to trophic interaction rates).

To apply a forcing function to primary productivity directly, use the Apply FF (primary producer) form (*Time dynamic (Ecosim)* > *Input* > *Apply FF (primary producer)*). To apply a forcing function to trophic flows (i.e., predator-prey interactions), use the Apply FF (consumer) form. Before using either Apply FF form, you must first define at least one seasonal or long-term forcing function following the instructions for using the Forcing function form.

The *Apply FF (primary producer)* form consists of a grid representing only primary producers. Active cells are coloured white.

To apply a long-term forcing or seasonal function, select the cell representing the primary producer of interest. This will open the *Apply forcing and mediation functions* dialogue. The primary producer group will be displayed in both predator and prey boxes at the top of the form. In this case the multiplier can only be applied to the primary production rate (selected automatically at the bottom of the dialogue box).

Next, select the desired forcing or seasonal shape from the *Available shape functions* window at the left of the dialogue box by clicking the green arrow. This will move the shape function into the *Applied shape functions* window. You can remove a shape from this window by clicking the remove button immediately below the green arrow. Note that a common form is used to apply Mediation and Seasonal/Forcing functions. Do not select a mediation function.

Finally, click *OK*. You should see the number of the forcing or seasonal function you selected in the predator/prey cell (preceded by 'F').

Clear all

You can clear all applied seasonal, forcing and/or mediation functions from the grid by selecting *Clear* all from the top of the *Apply FF (primary producer)* form.

Set all …

Opens the *Apply forcing and mediation functions* dialogue box. The selected forcing function will be applied to all primary producer groups.

8.12 Egg production

Ecosim allows linking a seasonally and long-term oscillating forcing function with the function through which the adults of multi-stanza groups are made to generate eggs/larvae, i.e., the earliest form of the youngest stanza (see Representation of multi-stanza life histories in Ecopath, Ecosim and Ecospace). 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.

Defining egg production shapes

To link a multi-stanza group with a seasonally oscillating or long-term forcing function, go to the Egg production form (*Time dynamic (Ecosim)* > *Input* > *Egg production*). Note you must have an Ecosim scenario loaded before you can open the *Egg production* form. You must also have multi-stanza groups defined in your Ecopath model to be able to use this form.

Important note: after you have defined the egg production shape(s) as described below you must continue to the Apply egg production form to define the multi-stanza group(s) affected by the egg production function(s).

When you open the *Egg production* form for the first time, there will be no egg production shapes.

To define an egg production shape, click *Add...*. Use the *Shape type* menu at the top of the form to set whether the function is long-term (occurs over a number of years) or seasonal (repeating over a 12 month period). The *x*-axis of the yellow sketch pad will change accordingly.

You can then define egg production shapes in one of two ways:

> 1. Shapes can be drawn freehand using the yellow sketch pad. If you have selected a Seasonal shape, the *x*-axis will appear as the months January to December and your sketch will be drawn in monthly blocks (Figure 8.20a). If you have selected a long-term shape, the *x*-axis will be shown as the annual time steps of the model. The sketch will be smooth (Figure 8.20b). You will see your sketched shape transferred to the selected shape in the bottom pane;
>
> 2. Alternatively, you can use standard mathematical shapes. Click *Change shape …* at the top of the form to open the *Change shape* dialogue box. Select a shape type (e.g., linear, sigmoid, exponential) from the menu in the window. You can tailor the shape to your specific requirements by setting the *Y Zero*, *Y End, Y Base* and *Steepness* parameters (where appropriate) in the cells provided.

Save as image …

Clicking the *Save as image …* button at the top of the form opens a dialogue box prompting you to save the current trophic mediation shape to a bitmap file (.bmp). Use this dialogue box to name the file and browse for a location to save it.

Shape type

Select whether the selected shape is a seasonal or long-term egg production shape.

Values ...

Displays the values of the current egg production shape.

Change shape ...

See point 2 above.

Reset

Resets the current egg production or seasonal shape to the default constant value of 1.0.

Options ...

Opens the *Graph display options* dialogue box. Set the way the egg production shape is displayed in the main window of the *Egg production function* form.

There are four additional menu items on the bottom pane of the *Egg production function* form that allow you add, copy, rename and delete egg production or seasonal shapes.

Add…

Adds an extra blank long-term egg production shape. If necessary, use *Shape type* to change the long-term egg production shape to a seasonal shape.

Duplicate

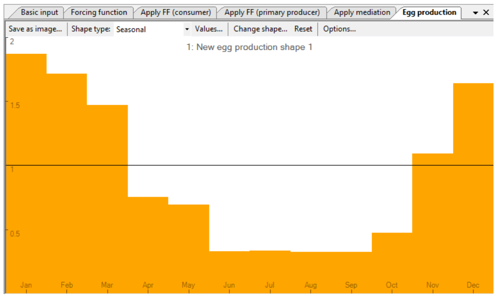
Copies the currently-selected shape.

Remove...

Removes the currently-selected shape. A warning that shape-deletion cannot be undone will appear. Click *Yes* to remove the shape.

Rename...

Rename the currently-selected shape by selecting *Rename*. You will then be able to type in a new name for the shape.



Shape type: Seasonal

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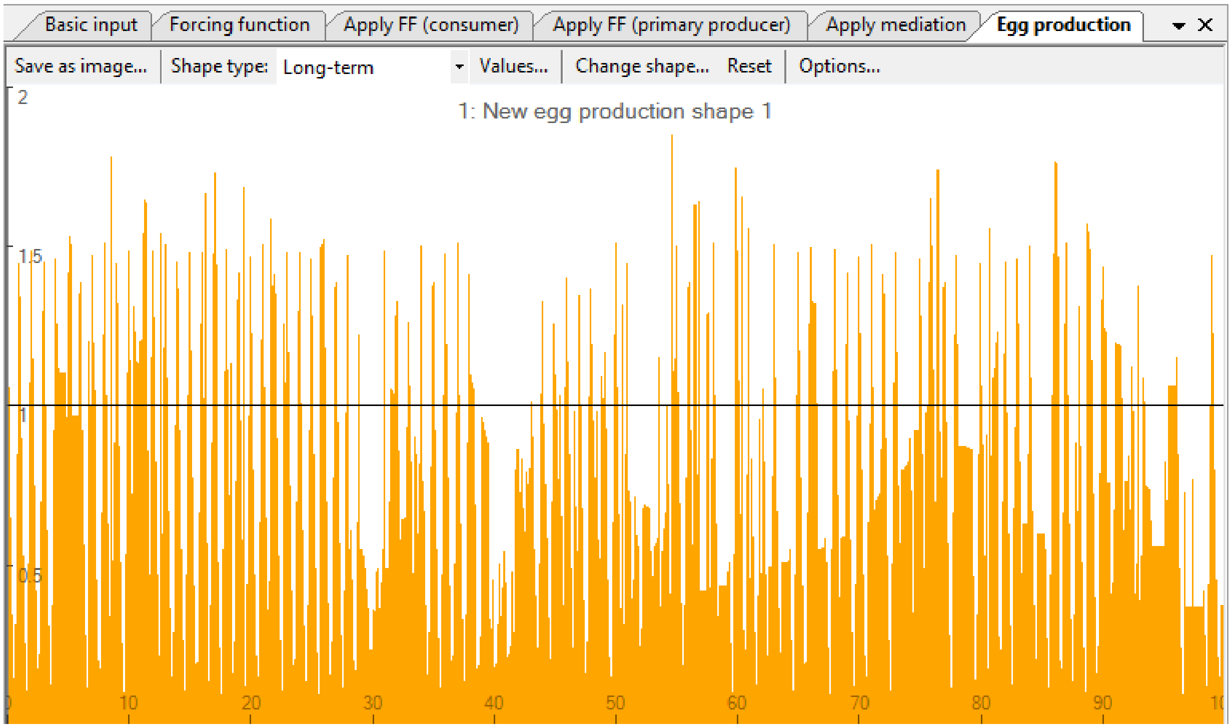
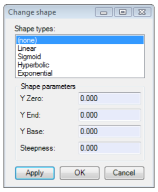


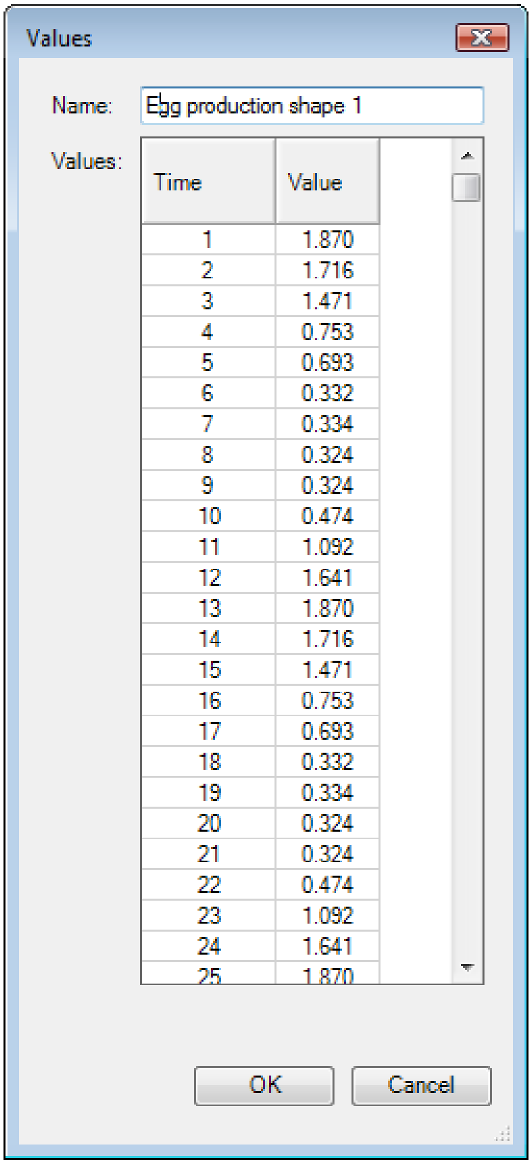
Shape type: Long-term

Fig 8.20 Examples of a) a seasonal egg production function and b) a long-term (annual) egg production function. Note that in the long-term series, egg production is still resolved on a monthly basis.



Y Zero: 0.000
Y End: 0.000
Y Base: 0.000
Steepness: 0.000

Figure 8.21 The *Change shape* dialogue box.



Name: Egg production shape 1

Values:

Time	Value
1	1.870
2	1.716
3	1.471
4	0.753
5	0.693
6	0.332
7	0.334
8	0.324
9	0.324
10	0.474
11	1.092
12	1.641
13	1.870
14	1.716
15	1.471
16	0.753
17	0.693
18	0.332
19	0.334
20	0.324
21	0.324
22	0.474
23	1.092
24	1.641
25	1.870

Figure 8.22 The *Values* dialogue box.

8.13 Apply egg production

The *Apply egg production* form (Figure 8.23) is used to apply the forcing functions you defined using the *Egg production* form.

Egg production forcing can only be applied to multi-stanza model groups, whose population dynamics are represented using an age-structured model that explicitly includes a function for fecundity, based on average weight of the adults. 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. See also the introductory material on Representation of multi-stanza life histories in Ecopath, Ecosim and Ecospace.

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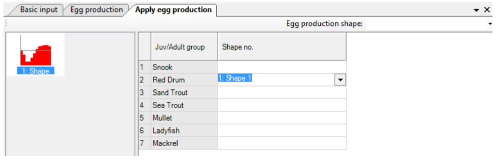
Before using the *Apply egg production* form, you must first define at least one egg production function following the instructions for using the Egg production form. The egg production forcing function must then be applied in Ecosim, using this form.

Available egg production shapes are shown in the left-hand panel on the Egg production form. To apply egg forcing to a group, simply select the number of the desired egg production shape from the drop-down menu in the cell next to the name of the appropriate multi-stanza group.



Egg production shape:

	Juv/Adult group	Shape no.
1	Snook	
2	Red Drum	1: Shape 1
3	Sand Trout	
4	Sea Trout	
5	Mullet	
6	Ladyfish	
7	Mackrel	

Figure 8.23 The *Apply egg production* form.

8.14 Fleet size dynamics

Ecosim users can choose to treat dynamics of fleet sizes and resulting fishing effort as unregulated and subject to fisher investment and operating decisions. The models are described in detail in the introductory material (Modelling effort dynamics) and are also described briefly here.

Users wishing to use the fleet/effort dynamics model should check the “fleet/effort response” box on the Ecosim parameters form. When this box is checked, Ecosim erases all previously entered time patterns for fishing efforts and fishing rates (e.g., from the sketch pad or from the time series data file), and replaces these with simulated values generated as each simulation proceeds.

In this model, there are two time scales of fisher response: (1) a short time response of fishing effort to potential income from fishing, and (2) a longer time investment/depreciation model for capital capacity. You need to set two parameters for the short time response model (‘Effort response power’ and ‘Initial effort/capital capacity’) and two for the longer time model (‘Capital depreciation rate’and ‘Initial capital growth rate’).

1. Fast time response model

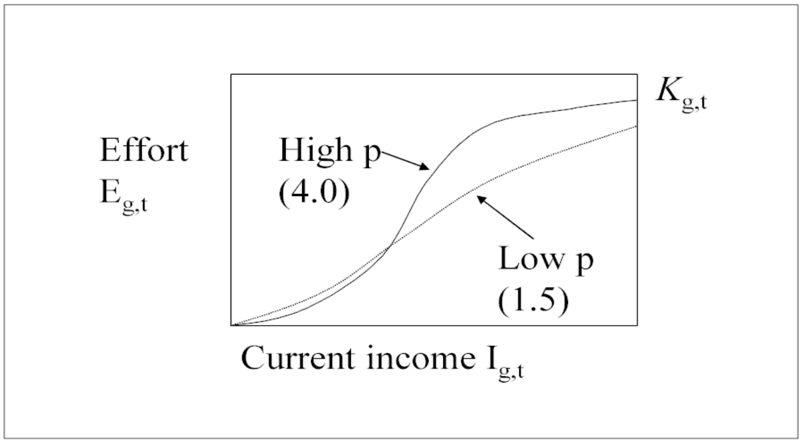
For each time step, the “fast” effort response for the next (monthly) time step is predicted by a sigmoid function of income per effort and current fleet capacity. For each gear, g, at each monthly timestep, t, Effort, $E_{g,t}$ is the current amount of active, searching gear, i.e.,

$$E_{g,t+1} = \frac{K_{g,t} I_{g,t}^{p}}{Ih_{g}^{p} + I_{g,t}^{p}}$$

where p and Ih_g are fleet-specific response parameters, $K_{g,t}$ is fleet capacity and $I_{g,t}$ is income. Fleet capacity $K_{g,t}$ is initialised using ‘Initial effort/capital capacity’ (see below) and is updated using the slow time response model (see next section).

Effort response power

Use ‘Effort response power’ to set the parameter p, which represents a “heterogeneity” parameter for fishers: high p values imply all fishers “see” income (I) opportunity similarly, while low p values imply fishers “turn on” their effort over a wide range of mean incomes (see figure).



Initial effort / capital capacity

This parameter is the ratio of initial fishing effort to fleet capacity (i.e., the proportion of maximum effort deployed in the first time step). It is used to set the initial fleet capacity $K_{g,1}$ as well as the income level needed for half the maximum effort to be deployed (Ih_g).

Calculating $K_{g,1}$: For each fleet, initial fleet capacity *K1* is calculated as the inverse of 'Initial effort/capital capacity' (initial effort is scaled to be 1 at Ecopath base condition), i.e., if 'Initial effort/capital capacity' is set at 0.5, then the fleet capacity will be set to 2 because half of the maximum effort is deployed. $K_{g,t}$ is updated at each time step using the slow time response model.

Calculating Ih_g: 'Initial effort/capital capacity' is also used to calculate Ih_g. When the ratio is set at the 0.5 default value, Ih_g is set to the initial income (summed over pools of Ecopath base catches x prices for each fleet).

2. Slow time response model

For each fleet, slow effort responses are modelled as changes in fleet capacity ($K_{g,t}$), which is a function of the 'Capital depreciation rate', the 'Capital growth rate' and Profit (calculated dynamically in Ecosim). See Modelling effort dynamics for full description of the model.

Capital depreciation rate

Set the rate of capital depreciation here. Capital depreciation rates for fishing fleets are typically in the range 0.04 to 0.10 (equipment lasts 10-25 yrs), although will vary on a fleet by fleet basis.

Initial capital growth rate

Set the initial rate of annual capital growth here. A value of zero would represent a fleet with no growth (e.g., at bionomic equilibrium). For rapidly growing fleets, set the value at 0.5 or higher. If you have data on the maximum effort deployed for a number of years before and after the Ecopath base year, you can estimate this parameter empirically.

9 Using Ecosim. Part 2: Ecosim outputs

Once you have set up your Ecosim scenario(s) using the Ecosim input forms, you can test your model's predictions using Ecosim. This chapter describes the forms used to run Ecosim (Run Ecosim, Ecosim plots, Ecosim results and Stock-Recruitment plotC:\Ecopath\Ecopath6\Documentation\Content\EWE_UsersGuide\Monte Carlo runs.htm - _Monte_Carlo_runs), as well as important Ecosim tools: Monte Carlo runs, Fishing policy search and Fit to time series.

An Ecosim exercise to help you test your model is also included.

Before using Ecosim, we recommend you read the introductory material on Ecosim (see links in Introductory material Ecosim, also found in Chapter 3 of the User Guide). You should also be familiar with the published literature on Ecosim, particularly Walters et al. 1997 and Walters et al. 2004).

9.1An Ecosim exercise

Below is a cursory check of Ecosim's behaviour, which it is advised that you check out.

After loading an Ecosim scenario:

- Go straight to the Run Ecosim form. Click '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 Ecosim parameters: set the Duration of simulation to 30-50 years. Make a small disturbance for the combined fishery using the sketch pad on the Biomass form. If everything is okay in the settings it should come back to the initial value eventually. Are all groups reacting at the speed you expect them to?
- Next, go to the Group info form
- Next take out feeding time dynamics, set to zero.
- Set the unexplained predation to 0 throughout.
- Next, go to Vulnerabilities (the most important tab in Ecosim). Set to 100 (top down control).
- Reset F's.
- Run: seems okay?
- Create a small disturbance.
- Run and you will get chaotic behaviour, violent oscillations and groups dropping out completely. Typical Lotka-Volterra behaviour
- Put in flow control setting of 2 throughout. [Interpretation: curves go through 0, the Ecopath value and two times the base (*Zmax/Zbase*)] Run: it will generally run OK.
- Try to increase vulnerability settings to 4, then 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 and set the run duration 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 there are more top predators. This will help you get more reliable vulnerability settings. You need to have reasonable vulnerability settings before you can proceed.
- Turn the feeding time factor back on. This will change the feeding time, 1 can cause numerical instability. If this happens it will create violent oscillations and more groups may drop out. Try, e.g., 0.2 will change feeding behaviour with some 20% per month. If groups are still dropping out the

foraging behaviour is slowing things down, so the the feeding time factor is not big 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 a group is willing to give up feeding if predation risk is high. Zero means the group is ignoring predation risk but feeds 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? Trying to maintain the mass interaction model by adding behaviour to equation.
- Next, look at multi-stanza groups. Increase fishing heavily for 5-10 years, and then shut the fishery down. The juvenile groups should be hit hard.
- Open the Stock-Recruitment plot: There will often be erratic behaviour for short to medium- lived groups, and Beverton-Holt (BH) 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 phytoplankton (using Apply FF (primary producer)), and look at how it propagates up through the food web.
- Use *Overlay* on the *Run Ecosim* form for an easy (sensitivity) check of how parameter values impact the results.

9.2 Run Ecosim

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 (see below for help with this approach).

2. Formal optimization methods can be used to search for fishing policies that would maximize a particular policy goal or ‘objective function’ for management (see Using Ecosim for policy exploration for help with this approach).

The first approach has been widely applied for exploring ecosystem effects of changes in fishing effort and is implemented using the Biomass form, the main form for running Ecosim (Time dynamic (Ecosim) > Output > Biomass).

Before running Ecosim, you should be familiar with the introductory material (see links in Introductory material Ecosim, also found in Chapter 3 of the User Guide).

Running Ecosim

The *Run Ecosim* form (Figure 9.1) consists of a lower panel, where users can sketch or set fishing rates by fleet/gear or Ecopath group and an upper panel where output biomasses are displayed.

Run

Click the *Run* button at the bottom right of the form to generate time series of biomasses. The magnitude of changes for each group will depend on many factors, chiefly the fishing regime and the vulnerability settings.

Note that fishing regimes should generally change gradually from one fishing mortality level to the next, not abruptly. Also, the baseline (Ecopath) fishing mortality should be left unchanged for a year or so.

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After running Ecosim, use Ecosim plot and Ecosim results to see detailed results in graphic and tabular form.

Features of the lower (Fishing rate) panel

Target

Use this drop down list to select which fleets or groups you want to change fishing rate for. Note: if an Ecopath group is selected, then relative Fs sketched on the sketch pad will be applied across all fleets.

Set to 0

Set fishing for the fleet/group selected to zero.

Set to value ...

For entry of a fishing intensity value to be applied to the fleet/group selected (or enter a list of comma separated values to set Fs for all fleets).

Reset All

Reset all fishing rates (all groups all fleets) to their Ecopath base values.

Fishing rate sketch pad

The sketch pad is used to display time series of relative fishing rates when the fishing mortality is applied to an individual group. When the fishing mortality is applied to a ‘fleet’ the *y*-scale of the sketch pad consists of effort multipliers. In either case (individual group or fleet), the default uniform series (representing the Ecopath base values) can be replaced by a time-varying shape, representing temporal changes in the pattern of fishing, by sketching with the mouse (left button held down). The *y*-axis will automatically re-scale as you drag your mouse up or down on the sketchpad. 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 shift + the left 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.

Features of the upper (Ecosim biomass output) panel

Show groups...

Opens a form for hiding/displaying groups on the biomass graph.

Autoscale

Use the Autoscale button to tell Ecosim to automatically set the scale of the *y*-axis.

Scale Y axis to

Manually set the *y*-axis upper value using the *Scale Y axis to* box.

Graph options

You can choose whether to display the current annual output in the main screen or whether to overlay results, in which case results are can be viewed under the *Layers* tab.

Sum of squared deviations (SS)

This is an Ecosim output. When an Ecosim model is loaded, you can load time series 'reference' data on relative and absolute biomasses of various groups over a particular historical period, along with estimates of changes in fishing impacts over that period. After time series data have been loaded and applied (see Time series), 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).

See Time series fitting in Ecosim for more details about the sum of squared deviations measure.

Main display panel

Displays Ecosim's predicted time series of biomass for groups selected using the Show groups form. Biomasses are shown relative to their baseline Ecopath values. If time series have been loaded and applied, they will be displayed as coloured dots on the graph, while Ecosim's predicted outputs will be displayed as coloured lines (Figure 9.1).

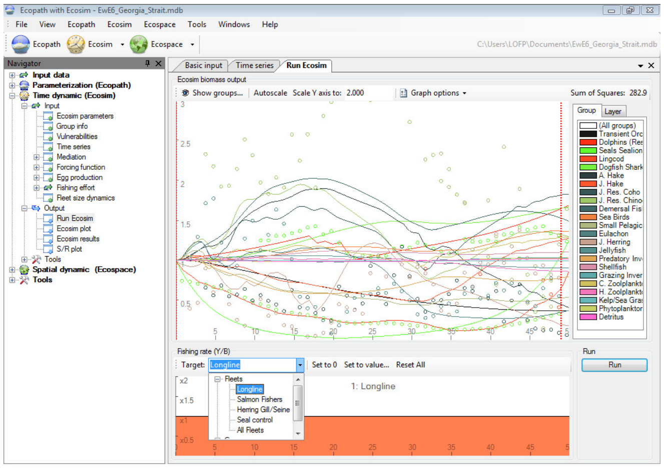
Vertical red lines indicate when to start averaging results for before/after comparisons (displayed using the Ecosim results form). Use a left mouse-click to drag the lines to their desired positions.

Group tab

To the right of the upper panel, under the *Group* tab, a smaller panel displays the groups' names, in the same colours as used for the biomass lines. Clicking on the name of any group in this panel (and releasing the mouse button) results in all other groups being greyed out so that the group of interest can be clearly seen. Click on *All groups* at the top of the list to return all groups to their original colours.

Layer tab

Behind the *Group* tab is the *Layer* tab. If the user has selected *Overlay* under *Graph options*, outputs of different runs will be displayed on different layers.



Scale Y axis to: 2.000

Sum of Squares: 282.9

Target: Longline

Figure 9.1 The *Run Ecosim* form showing predicted (coloured lines) and observed (coloured dots) biomass trajectories. The red fishing mortality sketch pad can be seen in the bottom panel. The longline fleet has been selected from the drop-down *Target* menu.

9.3 Ecosim plot

Selecting *Ecosim plot* after running Ecosim (see *Run Ecosim*) opens a form displaying a series of plots of the results of the Ecosim simulations. Select the group to be displayed by clicking on its name in the *Groups* window on the right of the form. Plots will be displayed showing time series of predicted biomass, consumption/biomass, predation mortality, total mortality, feeding time, percentage of prey, yield and production/consumption (see Figure 9.3).

If you have loaded and applied time series of historical data using the Time series form, dots will appear on the Biomass plot showing the observed biomass time series, while dots on the Yield plot will show observed catches ($t \cdot km^{-2} \cdot year^{-1}$). Ecosim's predicted biomasses and catches are shown as lines.

Time series

Displays values of currently-loaded time series for the selected group.

Save data …

Saves eight csv-files, one for each of the displayed plots, storing the data for all groups.

Show all fits

Opens the *Show all fits* form, which displays all fits to time series in a form suitable for printing (Figure 9.4). Customize the plot and outputs using the following settings on the form:

> Use *Display options* and *Show/hide plots* to select which plots to display (by data type and by group, respectively).
>
> Use *General options* (left-hand side of the form) to set font, number of plots per row, dot size, line size and margins.

Use *Save as image...* to save the plots as a bitmap (.bmp) file.

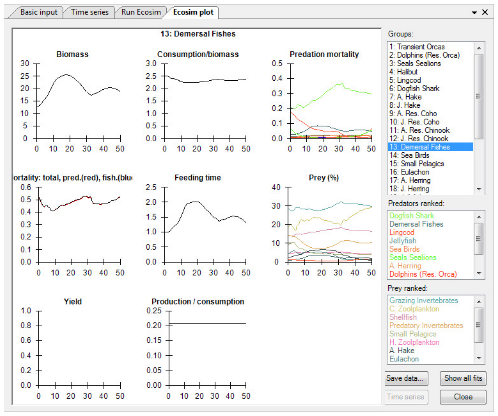
Export the data to three csv files showing results for biomasses, catches and mortality using *Save data to .csv...*

Change Y scale allows you to set the maximum Y-value for each individual plot.

Print the plots directly using *Print…* and *Print preview…*

Close

Closes the *Ecosim plot* form.

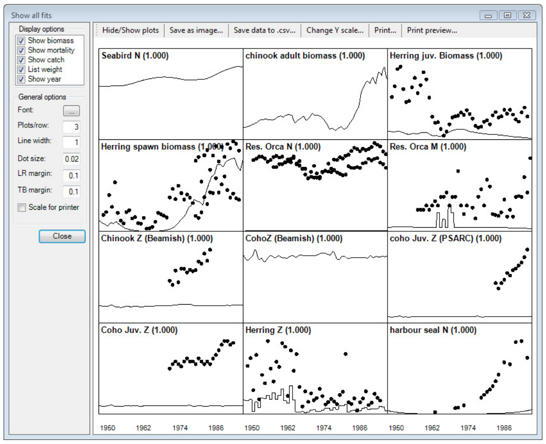


Groups:
1: Transient Orcas
2: Dolphins (Res. Orca)
3: Seals Sealions
4: Halibut
5: Lingcod
6: Dogfish Shark
7: A. Hake
8: J. Hake
9: A. Res. Coho
10: J. Res. Coho
11: A. Res. Chinook
12: J. Res. Chinook
13: Demersal Fishes
14: Sea Birds
15: Small Pelagics
16: Eulachon
17: A. Herring
18: J. Herring

Predators ranked:
Dogfish Shark
Demersal Fishes
Lingcod
Jellyfish
Sea Birds
Seals Sealions
A. Herring
Dolphins (Res. Orca)

Prey ranked:
Grazing Invertebrates
C. Zoolplankton
Shellfish
Predatory Invertebrates
Small Pelagics
H. Zoolplankton
A. Hake
Eulachon

Figure 9.3 The *Ecosim plot* form showing predictions for the Demersal fishes group.



Display options
☑ Show biomass
☑ Show mortality
☑ Show catch
☑ List weight
☑ Show year

General options
Font:
Plots/row: 3
Line width: 1
Dot size: 0.02
LR margin: 0.1
TB margin: 0.1
☐ Scale for printer

Figure 9.4 The *Show all fits* form showing initial fits for select groups (prior to any fitting). See Time series fitting and Hints for fitting models to time series reference data for more on fitting models to data.

9.4 Ecosim results

Selecting *Ecosim results* after running Ecosim (see Run Ecosim) shows a summary of results for the run, with start and end dates set using the vertical red lines in the main panel of the *Run Ecosim* form. If you wish to compare results from the beginning and end of the run, place the vertical red lines accordingly (this is the default setting).

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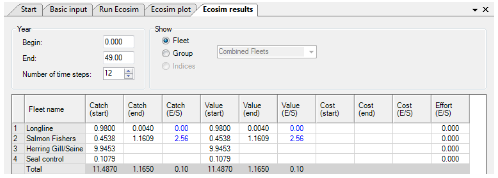
You can choose to see results by *Fleet* or by individual *Group*. Results by *Group* can be viewed by individual gears or by combined gears (selected using the drop-down menu).

Raw biomass results can be exported, using *Export biomass results to .csv file...* on the Ecosim menu or by clicking the *Save data* button on the Ecosim plot form.



Begin: 0.000

End: 49.00

Number of time steps: 12

● Fleet

○ Group

○ Indices

	Fleet 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	Longline	0.9800	0.0040	0.00	0.9800	0.0040	0.00				0.000
2	Salmon Fishers	0.4538	1.1609	2.56	0.4538	1.1609	2.56				0.000
3	Herring Gill/Seine	9.9453			9.9453						0.000
4	Seal control	0.1079			0.1079						0.000
	Total	11.4870	1.1650	0.10	11.4870	1.1650	0.10				

Figure 9.2 The *Ecosim results* form.

9.5 Stock recruitment (S/R) plot (multi-stanza groups only)

The *S/R plot* form displays the emerging stock-recruitment plot for the multi-stanza groups in your model, enabling users to test for the effects of compensatory recruitment in the model. 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 (the stock-recruit relationship). There is a way to create such an effect in Ecosim:

On the Group info form, set a non-zero feeding time adjustment for the juvenile group, with high EE, or high proportion of the 'other' mortality (the mortality not accounted for) being sensitive to changes in predator feeding time.

This represents density-dependent changes in juvenile mortality rate associated with changes in feeding time and predation risk. It is usually also important that the vulnerabilities of prey to the juvenile group (Vulnerabilities form) also be relatively low.

See Using Ecosim to study compensation in recruitment relationships for a more detailed description of density dependent recruitment in Ecosim. There you will find details of an Ecosim exercise you should do to check the stock recruitment curve of each multi-stanza group in your model. Always check the stock-recruitment curve shape, and play with Group info parameters that may affect it before proceeding to other policy analysis.

Running the stock-recruitment analysis

The S/R plot form utilizes the fishing mortality and biomass patterns from the Run Ecosim form. Therefore you should first run the Ecosim simulation on the *Run Ecosim* form before running the stock-recruitment analysis.

Ecosim calculates the stock-recruitment relationship between the oldest stanza in the group (i.e., the adult group) and each of its juvenile groups (i.e., separate plots are generated for the relationship between the adult stock size and each of the juvenile groups you have specified). To run the stock-recruitment analysis, select the juvenile group you wish to view from the menu at the left-hand side of the form (Figure 9.5) and click the *Run* button at the bottom right of the form.

Note that all stock-recruitment relationships are calculated simultaneously, so once you have run the analysis you can use the menu to look through all relationships.

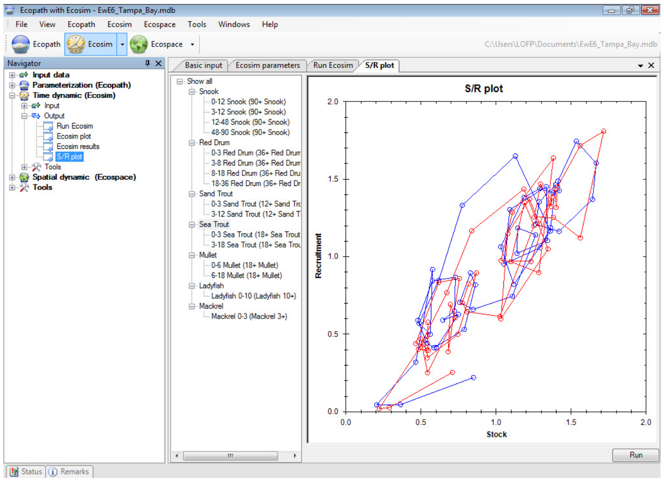


Figure 9.5 The *S/R plot* form showing predicted stock-recruitment between adult Sea Trout and its two juvenile stanzas (shown in different colours).

9.6 Ecosim tools

Tools currently available in Ecosim are Monte Carlo runs, Fishing policy search and Fit to time series.

9.7 Monte Carlo runs

Ecosim allows users to use a Monte Carlo approach to search for Ecopath parameter-combinations that improve the fit of the model to time series data (i.e., reduce the weighted sum of squared deviations, SS; see Time series fitting in Ecosim). The Monte Carlo approach can also be used to test for sensitivity of Ecosim's outputs to Ecopath input parameters.

To use the Monte Carlo interface, open the *Monte Carlo runs* form (*Time dynamic (Ecosim)* > *Output* > *Tools* >*Monte Carlo runs*; Figure 9.6).

Monte Carlo inputs

Number of simulation trials

Set the number of trials. Each trial represents an Ecosim run with a randomly-selected set of Ecopath parameters (B, P/B, EE, BA) for each group. Parameters are drawn from a uniform distribution centred on the base Ecopath value with coefficient of variation (c.v.) set by the user.

Show biomass trajectories on Ecosim plot

Displays Ecosim results on the *Biomass plot* tab in the lower panel of the form.

Apply time series

Opens a dialogue box where you can apply time series that have been loaded into Ecosim (i.e., you do not have to return to the Time series form to apply time series). You can also remove time series from the analysis using this dialogue box. See Time series for more information about loading time series in Ecosim.

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B, P/B, EE, BA

The Ecopath parameters tabs in the lower panel show the mean, lower limit and upper limit of the distribution used to draw random values for B, P/B, EE and BA for each group in the model. The mean of the distribution is set as the base Ecopath value of the parameter. Users can set the coefficient of variation (c.v.) which is then used to calculate the upper and lower limits of the distribution (upper limit = mean + 2*c.v.*mean; lower limit = mean - 2*c.v.*mean). For parameters you do not wish to change, set the c.v. to zero.

Note that the parameter combinations resulting from the random draw must result in a balanced Ecopath model (i.e., before running each trial, Ecosim keeps drawing new sets of parameters until a balanced Ecopath model is achieved). This means that the range of the parameter values actually used may be smaller than that set by the user. Users should check the range of the input parameters that were actually used in the trials in the output .csv file(see below).

Monte Carlo outputs

Trial

Tracks the current trial number.

Ecopath runs

Tracks the number of parameter-combinations tried until a balanced Ecopath model is achieved. Note that the maximum number of tries is 2000. If a trial reaches 2000 Ecopath runs then a balanced model could not be achieved with any parameter combinations and the simulation trial is run with an unbalanced model. This may indicate that the cv's have been set too large, reducing the likelihood of finding parameter values that combine to produce a balanced model.

SS measures

At the top right-hand side of the form, the original (i.e., before the simulation) weighted sum of squared deviations (SS) is shown. Current SS shows the value of SS achieved for the current trial. Best SS shows the lowest SS achieved for any of the runs.

Data from best fitting trial

After all trials have been completed, the parameter-values that resulted in the lowest SS are shown on the second-last tab in the lower panel of the form. When the trials are complete, the software automatically displays this tab.

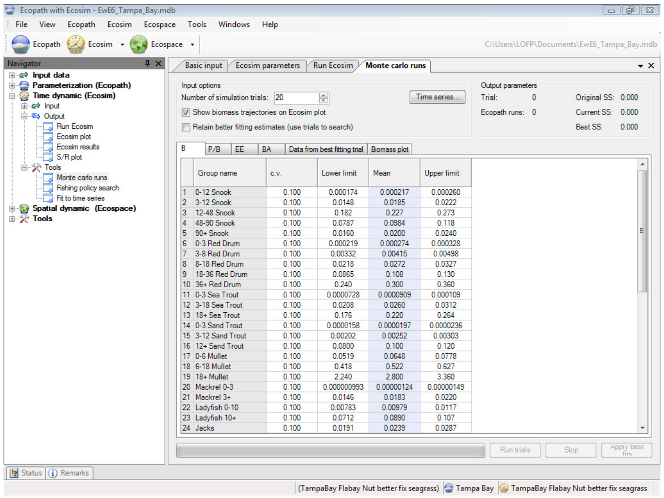
Biomass plot

If the *Show biomass trajectories* on Ecosim plot box is checked, biomass trajectories are displayed for each trial on the *Biomass plot* tab (Figure 9.7). This tab is automatically displayed when you click *Run trials*.

You can choose to overlay trajectories for each trial, switch from monthly to annual output and scale the results using check boxes. *Show/hide groups*, highlighting of trajectories for a single group and viewing of layers is also enabled, with the same functionality as for the Run Ecosim form.

The *Apply best fits* button applies the parameter-values that resulted in the lowest SS (shown on the *Data from best fitting trial* tab) to your Ecopath model (i.e., overwrites the original values).

Warning: it is a good idea to save a backup of your model using *Save as* on the File menu before you overwrite your original parameters using *Apply best fits*!



Input options

Number of simulation trials: 20

☑ Show biomass trajectories on Ecosim plot

☐ Retain better fitting estimates (use trials to search)

Output parameters

Trial: 0

Ecopath runs: 0

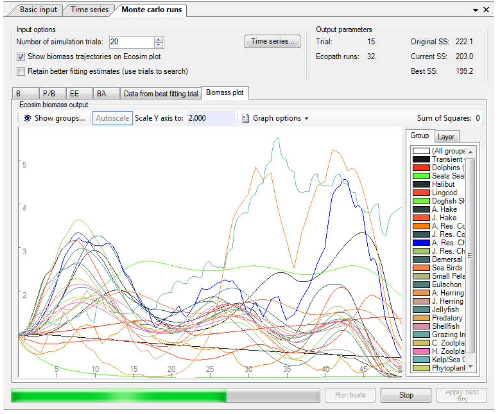
Original SS: 0.000

Current SS: 0.000

Best SS: 0.000

	Group name	c.v.	Lower limit	Mean	Upper limit
1	0-12 Snook	0.100	0.000174	0.000217	0.000260
2	3-12 Snook	0.100	0.0148	0.0185	0.0222
3	12-48 Snook	0.100	0.182	0.227	0.273
4	48-90 Snook	0.100	0.0787	0.0984	0.118
5	90+ Snook	0.100	0.0160	0.0200	0.0240
6	0-3 Red Drum	0.100	0.000219	0.000274	0.000328
7	3-8 Red Drum	0.100	0.00332	0.00415	0.00498
8	8-18 Red Drum	0.100	0.0218	0.0272	0.0327
9	18-36 Red Drum	0.100	0.0865	0.108	0.130
10	36+ Red Drum	0.100	0.240	0.300	0.360
11	0-3 Sea Trout	0.100	0.0000728	0.0000909	0.000109
12	3-18 Sea Trout	0.100	0.0208	0.0260	0.0312
13	18+ Sea Trout	0.100	0.176	0.220	0.264
14	0-3 Sand Trout	0.100	0.0000158	0.0000197	0.0000236
15	3-12 Sand Trout	0.100	0.00202	0.00252	0.00303
16	12+ Sand Trout	0.100	0.0800	0.100	0.120
17	0-6 Mullet	0.100	0.0519	0.0648	0.0778
18	6-18 Mullet	0.100	0.418	0.522	0.627
19	18+ Mullet	0.100	2.240	2.800	3.360
20	Mackrel 0-3	0.100	0.000000993	0.00000124	0.00000149
21	Mackrel 3+	0.100	0.0146	0.0183	0.0220
22	Ladyfish 0-10	0.100	0.00783	0.00979	0.0117
23	Ladyfish 10+	0.100	0.0712	0.0890	0.107
24	Jacks	0.100	0.0191	0.0239	0.0287

Figure 9.6 The *Monte Carlo runs* form.



Input options

Number of simulation trials: 20

☑ Show biomass trajectories on Ecosim plot

☐ Retain better fitting estimates (use trials to search)

Output parameters

Trial: 15

Ecopath runs: 32

Original SS: 222.1

Current SS: 203.0

Best SS: 199.2

Scale Y axis to: 2.000

Sum of Squares: 0

Figure 9.7 If the *Show biomass trajectories on Ecosim plot* box is checked, biomass trajectories are displayed for each trial on the *Biomass plot* tab.

9.8 Fishing policy search - background

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 modelling 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.

Ecosim 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.

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 has been implemented in Ecosim since its first version, and has been widely applied for exploring ecosystem effects of changes in fishing effort (see Ecosim basic and the help topic for the Run Ecosim form). 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.

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 favour 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.

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.

See Implementing policy optimization in Ecosim for help with implementing these two approaches in Ecosim.

Policy objectives

Ecosim allows users to implement ‘open loop’ policy exploration simulations that acknowledges that policy may be defined as an approach towards reaching a broadly defined goal. 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 third objective, 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 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 (using Ecosim's Group info form), 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.

Optimization procedure

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 colour-coded 'year/fleet block' defines one parameter to be varied by the procedure (e.g. setting four colour 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 labelled 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.

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 favour 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 favouring 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 Implementing policy optimization in Ecosim

The *Fishing policy optimization search* is implemented using the Fishing policy search form (*Time dynamic (Ecosim)* > *Tools* > *Fishing policy search*) (Figure 9.8). Alternatively, the form can be opened from the Ecosim menu.

Two different approaches can be taken to identification of optimum levels of fishing efforts for multiple fleets that may each harvest multiple species from an ecosystem, the 'Sole owner' approach and the more complex 'Multiple fishing rights' approach (see Christensen and Walters 2004). Implementation of the policy search in Ecosim using each of these two approaches is detailed below.

1. The 'sole owner' or societal approach

The aim of the '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.

Several steps are involved:

Step 1. Select *Maximize system objectives* from the ***Optimization approach*** drop down menu on the top left panel of the form.

Step 2. Set the **Discount rate** and **Generational discount rate**.The discount rate is the annual rate (entered in %) applied to discount the present value of future catches relative to present base value. See Ainsworth and Sumaila 2005 for description of intergenerational discounting.

Step 3. Define 'fleet/year parameter blocks' for the search procedure. In the top right panel of the form, click on a fishing rate colour code from the colour bar then, on the fleet/year box below, hold down the left mouse button and sketch the colour onto a block of cells representing a set of years for a fleet, where each colour-coded 'year/fleet block' defines one parameter (i.e., fishing rate) to be varied by the DFP search procedure (i.e., the procedure will iteratively try to improve the objective function by varying the relative fishing rates in each of the colour-coded year/fleet blocks).

Then select a second colour code and sketch the year/fleet block for this colour. Continue until all year/fleet blocks have been specified (you can increase the number of blocks using the box at the end of the colour bar). 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). You can also use the *Set gear* button to automatically set a different colour block for each gear (i.e., apply a single effort level over time for each fleet).

If you want to set more than one colour block for each fleet, you can set the number of years per colour block using the **Years/block** box, where the default number of years per block is the number of years in the series. If you reduce the number of years per block, this is taken into account when you use ***Set gear***. Use the **Start** and **End** year boxes to set the years over which the search procedure operates. Note that the colours are used only to differentiate the fleet/year blocks from each other and have no intrinsic value.

Step 4. Define objective function weights for **Net economic value** (total landed value of catch minus total operating cost to take this landed value); **Social value (employment)**, i.e., 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 two ecological objectives: 1. **Mandated rebuilding** of one group (value of the objective function is measured by departures of biomasses over time from target biomass levels specified by entering ratios of target to Ecopath base biomasses) and ; 2. **Ecosystem structure**, which favours biomasses of large, long-lived organisms. See Policy objectives in Fishing policy search and Christensen and Walters 2004b for more details about these objectives. Note that you may initially need play with different values for the objective function weight for each factor to find ranges that produce contrast in the final value of the objective function.

Note that there are two possible economic optimization criteria. The first is to imagine 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 totalled 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 ***Prevent costs > earnings*** 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.

Step 5. If you are placing weight on Employment, Mandated rebuilding or Ecosystem structure you may also need to set extra parameters for these in the two tables in the bottom panel of the form.

Jobs/catch value

Use this table to set the number of jobs relative to the catch value. The default is 1 for each fleet, implying that if the catch doubled, the number of jobs would also double.

Mandated rel. biomass

Use this column to set a threshold biomass (relative to the biomass in Ecopath) for the species or group of interest. The search routine will search for the fleet effort structure that will most effectively ensure this objective.

Structure rel. weight

When Ecosystem structure is included in the objective function, the search routine favours larger biomasses of long-lived organisms, indicated by B/P (i.e., P/B-1). These values are listed in the *Structure rel. weight* column and can be changed if users wish to place more or less weight on some groups than indicated by their B/P or if the user wishes to optimize for something other than B/P under the ecological objective.

Max. fishing mortality

For some groups, a threshold fishing mortality that should not be exceeded may be legislated. Use Max. fishing mortality instead of Mandated rel. biomass (with a weight placed on Mandated rebuilding in the Value component table) to explore, for example, the effects of using non-selective gears that catch species with low threshold fishing mortalities as bycatch.

Step 6. Set the maximum number of evaluations using the ***Max # eval*** drop-down list. The default is 2000. Quite often the maximum of the objective function will be found before the maximum number of iterations is reached. If the results have not converged on a solution by the end of the iterations, try the search again with a greater number of iterations.

Step 7. Invoke the search procedure by clicking the *Search* button at the bottom of the form. Results will be pasted to the Iteration results (table) tab in the bottom left hand panel of the form. Each row shows the results from one evaluation, showing the value of each objective then the fleet effort values for each colour block that resulted in the objective values. If the routine converges on a maximum value for the objective function, the last row will represent the optimum fleet effort values.

Step 8. Test for local maxima and sensitivity to objective weights. 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 (***Initialize using*** drop-down menu), and check final answers by forcing additional iterations using the 'start at current F's' option. 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.

Maximise portfolio utility

Note that instead of setting relative weights to different objectives as described above, users may wish to us an alternative objective function that invokes risk-averse utility measures that favour a balanced 'investment portfolio' of fishing activities. This function makes use of the B/P values set under *Structure rel. weight*. To find out more about this function, see Maximize portfolio utility. If you wish to proceed, check the ***Maximise portfolio utility*** check box.

2. Multiple fishing rights

A fundamental problem with the 'sole owner' 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.

The '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 modelling 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 described above 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).

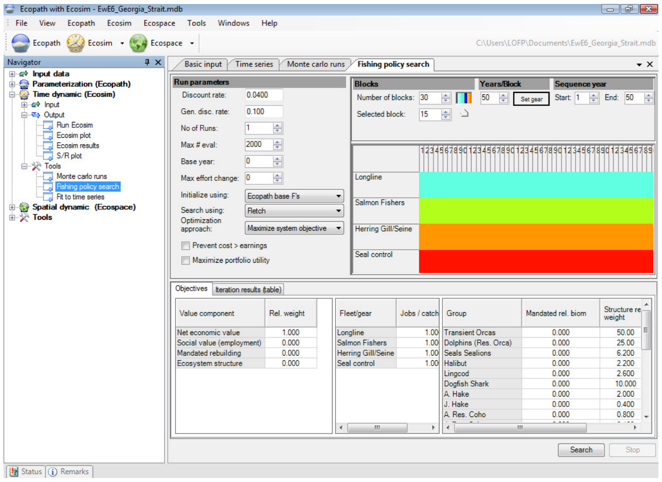
Besides explicitly recognizing rights to existence for various fishing fleets or methods, this iterative approach typically produces fleet size solutions that (1) preserve diversity of economic activities and options; (2) avoid loss of biological diversity through deliberate or inadvertent ‘fishing down 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.

Implementing an iterative approach for multiple fishing rights optimization

Implementation of the iterative approach described above for multiple fishing rights optimization is very simple:

1. First reset 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).
2. Open the *Fishing policy search* form and select *Maximize by fleet* values from the ***Optimization approach*** drop down menu on the top left panel of the form.
3. Click the ***Set gear*** button to apply a single effort level over time for each fleet,
4. Click the ***Search*** button at the bottom of the form. 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).



Run parameters

Discount rate: 0.0400
Gen. disc. rate: 0.100
No of Runs: 1
Max # eval: 2000
Base year: 0
Max effort change: 0
Initialize using: Ecopath base F's
Search using: Fletch
Optimization approach: Maximize system objective
☐ Prevent cost > earnings
☐ Maximize portfolio utility

Blocks

Number of blocks: 30
Selected block: 15

Years/Block

50 Set gear

Sequence year

Start: 1 End: 50

Value component	Rel. weight
Net economic value	1.000
Social value (employment)	0.000
Mandated rebuilding	0.000
Ecosystem structure	0.000

Fleet/gear	Jobs / catch
Longline	1.00
Salmon Fishers	1.00
Herring Gill/Seine	1.00
Seal control	1.00

Group	Mandated rel. biom	Structure re weight
Transient Orcas	0.000	50.00
Dolphins (Res. Orca)	0.000	25.00
Seals Sealions	0.000	6.200
Halibut	0.000	2.200
Lingcod	0.000	2.600
Dogfish Shark	0.000	10.000
A. Hake	0.000	2.000
J. Hake	0.000	0.400
A. Res. Coho	0.000	0.800

Figure 9.8 The *Fishing policy search* form.

9.10 Maximize portfolio utility

Maximizing risk-averse log utility for economic and existence values

One option in the search procedure for optimum fishing patterns is to search for relative fleet sizes that would maximize a utility function of the form w1log(NPV)+w2Slog(B)-w3V, where the wi are utility weights chosen by the user and the utility components NPV, Slog(B), and V are defined as:

1. NPV is net present economic value of harvests, calculated as discounted sum over all fleets and times of catches times prices minus costs of fishing, ie the discounted total profit from fishing the ecosystem.
2. Slog(B) is an existence value index for all components of the ecosystem over time. It is calculated as the discounted sum over times and biomass pools of user-entered Structure weights times logs of biomasses, scaled to per-time and per-pool by dividing the sum by the number of simulation years and number of living biomass pools.
3. V is a variance measure for the prediction of log(NPV)+Slog(B). It is assumed to be proportional to how severely the ecosystem is disturbed away from the Ecopath base state, where disturbance is measured at each time in the simulation by the multidimensional distance of the ecosystem biomass state from the Ecopath base state. This term is negative, implying that increased uncertainty about the predictions for more severe disturbances causes a decrease in the mean of log(NPV); this term represents both aversion to management portfolio choices that have high variance in predicted returns, and the observation that the mean of the log of a random variable (NPV*PB) is approximately equal to the log of the mean of that variable minus ½ the variance of the variable. Large w3 can be used to represent both high uncertainty about predictions that involve large deviations of biomass from the Ecopath base state, and strong risk aversion to policy choices that have high uncertainty.

This utility function combines several basic concepts of utility.

> First, the log scaling of value components represents the notion of "diminishing returns", that adding some amount to any value measure is less important when the value measure is already large than when the value measure is small.
>
> Second, the log scaling also represents the notion of "balance", that no value component should be ignored entirely (unless it is assigned a zero wi); the overall utility measure approaches minus infinity if either net economic performance (NPV) or if any biomass component of the ecosystem (any biomass Bi in Slog(B)) approaches zero.
>
> Third, it represents the notion that our predictions about the future of both economic performance and biodiversity (biomasses) become progressively more uncertain for policies that policies that result in more extreme departures from the Ecopath base state about which we presume to have at least some knowledge.

In the terminology of portfolio selection theory in economics, fishing policies result in a portfolio of value components with "expected total returns on investment" equal to NPV+SB. But policies that have higher expected total returns are most often also ones that would push the ecosystem into more extreme states, and hence represent portfolio choices with higher variance in total returns. For example, maximizing the deterministic prediction of NPV in Ecosim often involves a "farming policy", in which fishing is deployed so as to severely simplify the ecosystem to maximize production of one or a few species that appear at present to be the most valuable (price, potential total catch). This may even involve deploying some fleets just to remove predators and competitors for the most valued species, just like deploying pesticides and herbicides to remove "pests" in agricultural systems. But simplifying an ecosystem in such ways can make the behaviour of the system deeply unpredictable, by creating opportunities for ecological response (population growth) by a variety of species that are rare in the "normal" ecosystem and hence are not well researched or understood in terms of their potential impacts on valued species should they become abundant. Simplifying an ecosystem is hence much like investing in high-risk, high-return stock market options; such investments may make you rich, but they may also bankrupt you. Most people are risk-averse as investors, and seek to "spread risk" by investing in "balanced portfolios" with lower expected returns on investment but much lower probabilities of severe loss.

The prediction variance measure V is not meant to represent all components of variation or uncertainty about future biomasses and fishery values. V goes to zero for policies that hold or maintain the ecosystem at the Ecopath base state Bo for every biomass, for all simulation times. It is obviously not correct to suggest that we would expect no variance in future biomasses (and hence in the harvest components of NPV as well) if such a policy were implemented. Imagine running a very large number of simulations of future biomass changes under such a policy, while varying all possible uncertain quantities such as the Ecopath base biomasses and biomass accumulation rates, productivities, Ecosim vulnerability parameters, environmental forcing inputs representing oceanographic productivity regimes, future demand and price patterns, and changing vulnerabilities to fishing due to biophysical and technological factors.

Even for the baseline policy where Ecosim predicts stable ("flat line trajectory") expected or mean biomasses over time, these simulations would likely reveal high variances and complex covariance patterns for most biomasses over time, i.e. we would see wide probability distributions of possible future biomass states for the ecosystem. We should not be arrogant enough to suggest that we can describe all the uncertainties well enough to accurately calculate the variances of such distributions. But note that much of that variance in predictions of future biomasses (and hence variance in the value components) would be due to sources of uncertainty and variability that are the same no matter what the policy choice, i.e. would cause about the same amount of variance in predictions for any future harvest policy that we might simulate. When comparing policy choices using an optimization objective function, there is no point in including extra constant terms that do not change with the policy variables (e.g. a base variance Vo in predictions that does not change with fishing rate policy and just represents uncertainty about any prediction that Ecosim might make). Hence the V distance measure is meant to represent only extra variance or uncertainty in predictions for policy scenarios that would likely drive biomasses far from the Ecopath mean state.

Note that Ecosim does not deliberately advocate or promote any particular risk-averse portfolio approach to public investment in ecosystem harvest and existence values. Rather, it provides the logarithmic utility function option so that users who do have highly risk-averse attitudes about ecosystem values can identify policy options that would better meet their objectives. Users should always construct a series of policy scenarios with varying utility weights w1, w2, and w3 on the log utility components, to see how placing different emphases on these components would alter the predicted best policy choice.

9.11 Fit to time series

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 and applied (see Time series), 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 *Fit to time series* search interface (*Time dynamic (Ecosim)* > *Outputs* > *Tools* > *Fit to time series*; Figure 9.9) allows users to do four types of analysis with the SS measure:

1. Determine sensitivity of SS to the critical Ecosim vulnerability parameters (Vulnerabilities form), 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). See Option (1) below;

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). See Option (2) and/or (3) below;
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, the user must have linked a time forcing function to primary production using the Apply forcing function to primary production form and setting the i,i element of the forcing table for i = primary producers to the number of the forcing function). See Option (2) and/or (3) below;
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 Option (4) below.

1. Option (1)

Option 1 is invoked by clicking one of the two **Sensitivities of SS to V** button at the bottom of the screen. You can choose whether to determine sensitivity of SS to vulnerabilities associated with individual predator-prey interactions (i.e., by predator-prey cell) or to vulnerability settings for all of a predator's foraging arena (i.e., by predator column).

Progress in this assessment is shown by placing an X in the vulnerability layout grid (on the right of the form) as the sensitivity to each vulnerability is computed. When all tests are completed, relative sensitivities are shown on a colour 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 colours 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.

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 row, which biologically makes less sense.

2/3. Options (2) and/or (3)

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 for one or both of Vulnerability search and Anomaly search:

Vulnerability search

Checking the ***Vulnerability search*** box and setting its variance > 0 causes the 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.

Anomaly search

Check the ***Anomaly search box*** and click on the ***Anomaly search tab*** on the right of the form. You must also select an applied time series forcing shape from the thumbnails at the bottom of the form (see Apply forcing function for primary production). You must also set the ***First year*** and ***Last year*** for the search, the ***PP Variance*** (> 0) and the ***Spline points*** for smoothing.

> The variance values are then 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, progress of the SS minimization procedure is shown in the ***Iterations*** panel (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). For most runs, the algorithm incrementing 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 function* form (for PP time series) and/or the *Vulnerabilities* form (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.

See Option 4 for important notes about obtaining spurious fits.

4. Option (4)

Time series random effects

Option 4 is necessary because, when you use the search interface to estimate time series values of a forcing function, 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).

The Null hypothesis distribution SSred/SSo button allows you to estimate a probability distribution for the F statistic SSreduced/SSbase 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".

Use the *Time series weight* box to set relative weights. This represents 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 or unreliable data; higher weights imply low variance or reliable data). This grid will/will not overwrite weights that were set on the *Time series* form.

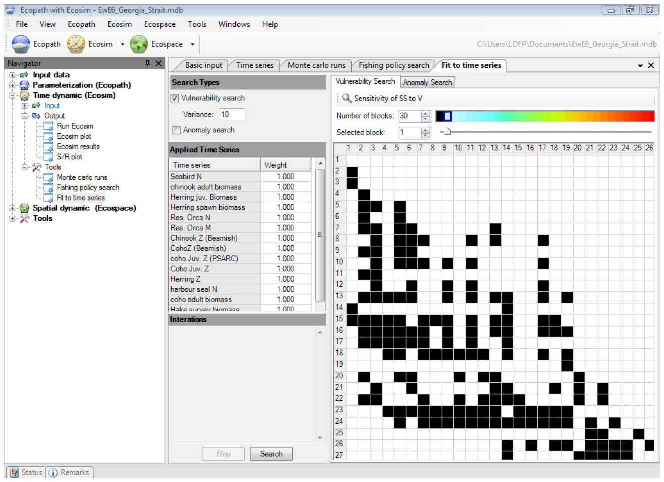
For users familiar with nonlinear estimation procedures used in single-species stock assessment, e.g., for fitting production models to time series CPUE data, searches on the vulnerability parameters should look quite familiar. In essence, the Ecosim search procedure for vulnerabilities is just an 'observation 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 primary production ‘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 and/or vulnerability settings in flow control interface) and check whether 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.



Search Types

☑ Vulnerability search

Variance: 10

☐ Anomaly search

Number of blocks: 30

Selected block: 1

Applied Time Series

Time series	Weight
Seabird N	1.000
chinook adult biomass	1.000
Herring juv. Biomass	1.000
Herring spawn biomass	1.000
Res. Orca N	1.000
Res. Orca M	1.000
Chinook Z (Beamish)	1.000
CohoZ (Beamish)	1.000
coho Juv. Z (PSARC)	1.000
Coho Juv. Z	1.000
Herring Z	1.000
harbour seal N	1.000
coho adult biomass	1.000
Hake survey biomass	1.000

Figure 9.9 The *Fit to time series* form.

10 Using Ecospace. Part 1: Ecospace inputs

Ecospace (Walters et al. 1999) is a dynamic, spatial version of Ecopath, incorporating all the key elements of Ecosim. This chapter describes the steps taken to set up Ecospace scenarios (the Ecospace menu, Ecospace parameters, Define Ecospace habitats, Basemap, Assign habitats, Dispersal, Ecospace fishery).

Important note: Before using Ecospace you must have a balanced Ecopath model. It is also recommended you have fit the model to time series data by adjusting the Vulnerability settings (see Time series, Time series fitting in Ecosim, Hints for fitting Ecosim models to time series data and Fit to time series).

See links in Introductory material Ecospace (Chapter 4 in the Ecopath Users Guide) for more detailed introduction of Ecospace.

10.1 Getting started in Ecospace: The Ecospace menu

Ecospace (Walters et al. 1999) is a dynamic, spatial version of Ecopath, incorporating all the key elements of Ecosim. 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).

See Introductory material Ecospace for links to more detailed introduction of Ecospace.

When working in Ecospace you work within a 'scenario'. A given Ecopath model can have any number of Ecospace scenarios attached. Ecospace scenarios inherit their basic parameters (such as 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) Ecospace scenarios.

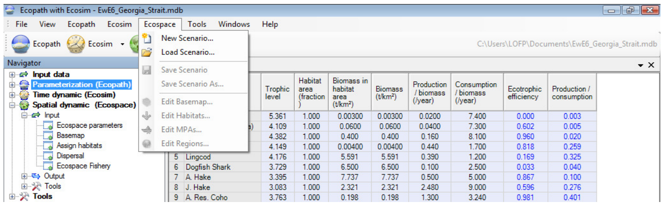
Important note: Before using Ecospace you must have a balanced Ecopath model. It is also recommended you have fit the model to time series data (see C:\Ecopath\Ecopath6\Documentation\Content\EWE_UsersGuide\Time series.htm - _Time_seriesTime series fitting in Ecosim, Hints for fitting Ecosim models to time series data and Fit to time series).

New scenario

When you are ready to start using Ecospace, you must first create a new Ecospace scenario. Note that you must have an Ecosim scenario loaded before you can create an Ecospace scenario. You will be prompted to do this or you can use the *Ecosim menu*. Subsequent Ecospace simulations will use the parameter values from the loaded Ecosim scenario.

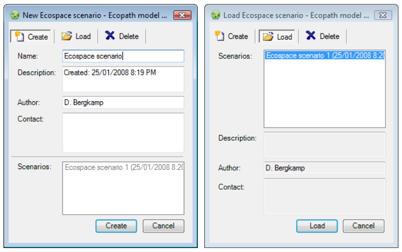
Please note: All help topics are currently in draft format. Please send your comments to the email address given at www.ecopath.org (About >> Contact us).

After loading an Ecosim scenario, select *New Scenario...* on the Ecospace menu (Figure 10.1). Alternatively, you can click once on the Ecospace shortcut button [ ], which will open the *Load Ecospace scenario* dialogue box (Figure 10.2a). Select the *Create* option. This will open the *New Ecospace scenario* dialogue box (Figure 10.2b). Use this box to name your new scenario, add a description, author and contact details.



		Trophic level	Habitat area (fraction)	Biomass in habitat area (t/km²)	Biomass (t/km²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic efficiency	Production / consumption
		5.361	1.000	0.00300	0.00300	0.0200	7.400	0.000	0.003
		4.109	1.000	0.0600	0.0600	0.0400	7.300	0.602	0.005
		4.382	1.000	0.400	0.400	0.160	8.100	0.960	0.020
		4.149	1.000	0.00400	0.00400	0.440	1.700	0.818	0.259
5	Lingcod	4.176	1.000	5.591	5.591	0.390	1.200	0.169	0.325
6	Dogfish Shark	3.729	1.000	6.500	6.500	0.100	2.500	0.033	0.040
7	A. Hake	3.395	1.000	7.737	7.737	0.500	5.000	0.867	0.100
8	J. Hake	3.083	1.000	2.321	2.321	2.480	9.000	0.596	0.276
9	A. Res. Coho	3.763	1.000	0.198	0.198	1.300	3.240	0.981	0.401

Figure 10.1 The *Ecospace menu*.



Name: Ecospace scenario
Description: Created: 25/01/2008 8:19 PM
Author: D. Bergkamp
Contact:
Scenarios: Ecospace scenario 1 (25/01/2008 8:2

Scenarios: Ecospace scenario 1 (25/01/2008 8:2
Description:
Author: D. Bergkamp
Contact:

Figure 10.2 a) The *New Ecospace scenario* dialogue box. b) The *Load Ecospace scenario* dialogue box.

Load scenario

The procedure for opening an existing Ecospace scenario is similar to that for creating a new scenario. You must have an Ecosim scenario loaded before you can open an Ecospace scenario. You will be prompted to do this or you can use the *Ecosim menu*. After loading the Ecosim scenario, open the Load Ecospace scenario dialogue box by selecting *Load scenario* from the Ecospace menu. Existing Ecospace scenarios will be listed in the *Scenarios* window (Figure 10.2b). Select the scenario you wish to load and click the *Load* button at the bottom of the dialogue box.

Alternatively, you can open a scenario directly using the Ecospace shortcut button [ ]. Click on the down arrow on the right of the bottom to open a list of available scenarios and click on the name of the desired scenario. Note that the model must be closed and re-opened before new scenarios are added to menu under the Ecopath shortcut button. New scenarios can always be accessed from the *Load Ecospace scenario* dialogue box, regardless of when they were created.

To delete an Ecospace scenario, select the scenario you wish to delete in the *Scenarios* window and click the *Delete* button at the top of the dialogue box. The *Load* button at the bottom of the box will then change to a *Delete* button, which must be clicked. You will be given the option to proceed or cancel. Clicking *Yes* implements deletion. Clicking *No* cancels deletion and you can then exit the dialogue box by clicking the *Cancel* button.

WARNING: Scenario deletion cannot be undone.

Save Scenario

You can save a scenario at any time by selecting *Save* scenario on the *Ecospace menu*.

Save Scenario As...

Save As allows you to save your scenario under a new name. This is an important feature that allows you to preserve properties of an Ecospace scenario that you are happy with, while exploring the impact of other factors in different scenarios. It is also a useful way to create a backup of a successful scenario before trying out new parameter values.

Edit basemap...

Opens the *Edit basemap* dialogue box, used for setting the dimensions and location of the Ecospace Basemap. See Define Ecospace habitats for help with this dialogue box.

Edit habitats…

Opens the Edit habitats dialogue box, used for setting up the Ecospace basemap. See Define Ecospace habitats for help with this dialogue box.

Edit MPAs…

Opens the Edit MPAs dialogue box, used for setting up the Ecospace basemap. See Define Ecospace habitats for help with this dialogue box.

Edit regions…

Opens the Edit regions dialogue box, used for setting up the Ecospace basemap. See Define Ecospace habitats for help with this dialogue box.

10.2 Ecospace parameters

Use the *Ecospace parameters* form to set non-spatial parameters for the Ecospace scenario. See Define Ecospace habitats for details on setting up the spatial map.

Initialization

Users are given two options for initialising biomasses in Ecospace cells.

Ecopath base biomasses

Assigns the Ecopath mean biomass for each pool to every spatial cell that has suitable habitat for that type of organism and lower biomass to every non-suitable cell. In this case the Ecosim estimates of predation parameters (vulnerabilities, predator search rates) are left unchanged. However, this option generally results in underestimates of biomass density in favourable habitats, especially for biomass types that actually have high biomass on just a few spatial sites or cells.

Habitat-adjusted biomasses

Distributes the entire Ecopath mean biomass for each pool into just those cells that are suitable for the organism, i.e., concentrates the overall mean biomass into those map cells where the biomass is actually found. For example, a creature with overall Ecopath mean biomass of 10 t/km² would be assigned a biomass of 100 t/km² in suitable cells, if just 10% of the cells are assigned a habitat type suitable for it. In this second option, predation vulnerabilities, predator search rates, and primary producer P/B vs B parameters are adjusted to reflect the new, localized 'mean' biomasses expected in habitat types where animals actually are abundant.

See Assign habitats for further details on setting suitable habitats.

Model

Model type

EwE6 represents a major overhaul of the functioning of Ecospace and there are now three approaches to running Ecospace simulations. Documentation on the three approaches listed below will shortly be available.

EwE6 multi-stanza model

IBM (individual-based model)

EwE5 approach

Threading

Threading allows a program to split itself into multiple simultaneously running tasks. By default, Ecospace sets the number of threads to the number of processors available on your computer.

The greater the number of threads, the more of your computer's processing power will be used (hence faster calculations). If you have limited processing power or wish to work on other applications while running Ecospace, set the number of threads lower (hence slower calculations).

Run time

Set the **Total run time** and the **Number of time steps** per year (i.e., set this to 12 for monthly time steps). You should always check the effect of changing this parameter. If your model is unstable if is advisable to try to lower the number of time steps to see if this will change the behaviour.

Max no. of iterations

Ecospace uses an iterative method to solve the systems of differential equation it uses for prediction of flow of biomass among cells. In simple terms, the maximum number of iterations is the maximum number of iterations the algorithm is allowed to try until it finds a satisfactory (i.e., non-changing) solution to the system of equations. If the algorithm reaches the maximum number of iterations and the solution has not converged, the final value will be used anyway. The default for this parameter is 40. Setting the value higher may, in some cases, result in better convergence of solutions but will make the model run slower in these cases. In many cases, convergence will be achieved before the maximum number of iterations is reached.

See Walters and Martell (2004; Box 11.2) for more details about solving systems of differential equations that include spatial mixing effects.

Tolerance

Tolerance sets how close the iterative solutions to the system of equations have to be before the algorithm is determined to have converged (and the solution accepted). Default is 0.01.

See Walters and Martell (2004; Box 11.2) for more details about solving systems of differential equations that include spatial mixing effects.

Successive over-relaxation

By solving for whole rows or columns at the same time, successive over-relaxation (SOR) can be used to improve the efficiency of the algorithm (Press et al. 1996). The default setting is 0.9.

Predict effort

Ecospace can be used to predict distribution of fishing effort over space for each of the fleets. Fishing effort is assigned to spatial cells through a 'gravity model', wherein effort is proportional to the net benefits gained from exploiting a given cell.

In the simple case that all exploited group have the same economic value (default = 1 monetary unit per tonne), and that all cells require the same sailing cost (default), fishing effort will be assigned to the (water) cells of the base map in proportion to their fishable biomass. Thus, for example, fishing effort will tend to concentrate at the edges of protected areas – one reason, incidentally, why these edges should be as short as possible.

Use exact calculations for migratory species

Documentation will shortly be available for this feature.

Summary

At the end of the Ecospace run (see Run Ecospace), you can view a summary of results, using the *Results* button.

Start time sets the start year for the summary.

End time sets the end year for the summary.

Start time and *End time* are equivalent to the red lines used to set the start and end time for the Summary of Results in Ecosim (see Ecosim results).

Summary length (timesteps) sets the timesteps over which the results are averaged in the start and end year, i.e., when Ecospace reaches the Start time it will average results over the next number of set timesteps. Similarly, when it reaches the End time it will average over the next same number of timesteps.

Therefore, for example, if you set the number to 12, Ecospace will show the average results for the whole first and last year.

10.3 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.

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 to give short descriptive names to the habitat types in question, using the *Edit habitats* dialogue box (see below).

Habitats can be set as marine protected areas (MPAs) for all or part of the year, using the *Edit MPAs* dialogue box (see below). Users can also define regions, using the *Edit Regions* dialogue box (see below).

Edit basemap

Before creating an Ecospace basemap (see Basemap) you must set the dimensions of the map, using the *Edit basemap* dialogue box. The *Edit basemap* dialogue box is accessible from the Ecospace *Basemap* form (click on the symbol) or directly from the Ecospace menu.

Set the dimensions of the map using *Number of rows* and *Number of cols*. Set the length of each (square) cell using *Cell length*. You can set the physical location of the map using *Top-left latitude* and *Top-left longitude*.

The cells are square units, but the maps not need be so, both square and rectangular maps can be accommodated. Rectangular maps should not be defined too 'thin', (i.e., their aspect ratio (AR = height/width) is recommended to remain in the range 5 £ AR £ 0.2).

The number of cells in the basemap may range from 4 (for a square 2x2 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.

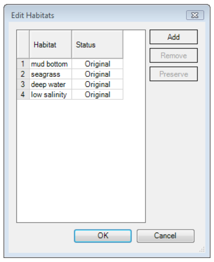
Though not contributing to the results, the basemap cells defined as 'land' consume memory and computing time. Thus, their number should be kept as small as possible, e.g. by orienting the basemap sideways where appropriate.

Edit habitats

Habitats are defined using *Edit habitats* dialogue box (Figure 10.3), accessible from the Ecospace Basemap form (click on the symbol) or directly from the Ecospace menu.

Any number of user defined habitats can be used in Ecospace. Add habitats using the *Add* button then type names for the habitats in the *Habitat* cell. Habitats can be deleted using the *Remove* button.

Assign the habitats to the base map using the *Basemap* form.



	Habitat	Status
1	mud bottom	Original
2	seagrass	Original
3	deep water	Original
4	low salinity	Original

Figure 10.3 The *Edit habitats* dialogue box.

Edit MPAs

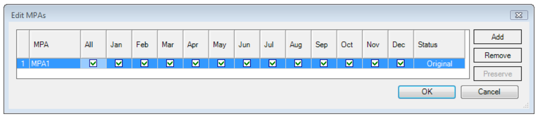
Users can overlay habitats with designated marine protected areas (MPAs).

MPAs are defined using *Edit MPAs* dialogue box (Figure 10.4), accesible from the Ecospace Basemap form (click on the symbol) or directly from the Ecospace menu.

Add MPAs using the *Add* button. MPAs will automatically be named MPA1, MPA2 etc. They can be renamed by typing directly in the MPA cell. MPAs can be deleted using the *Remove* button.

You can simulate seasonal MPAs by setting the months of the year that the MPA is operational in the check boxes provided. Use the Ecospace fishery form to assign which fleets can and cannot fish in the MPA.

Assign the MPAs to the base map using the *Basemap* form.



	MPA	All	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Status
1	MPA1	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	☑	Original

Figure 10.4 The *Edit MPAs* dialogue box. In this model there is only one MPA and it is operational for all months of the year.

Edit regions

Users can also overlay habitats with statistical ‘regions’ (i.e., groups of cells). Regions represent areas of management interest and may or may not have biological significance. Organisms cannot be assigned to regions, only habitats.

Regions are defined using *Edit regions* dialogue box (Figure 10.5), accessible from the Ecospace Basemap form (click on the symbol) or directly from the Ecospace menu.

Add regions using the *Add* button. Regions will automatically be named Region 1, Region 2 etc. They can be renamed by typing directly in the Regions cell. Regions can be deleted using the *Remove* button.

Assign the regions to the base map using the *Basemap* form.

To set each habitat as a region, click the Habitat = regions button on the Edit regions dialogue box. In this case, the regions will automatically be updated on the basemap to be the same as the habitats. Note, you must assign habitats on the basemap before setting each habitat as a region. To set each cell as a region, click the Make each cell a region button. Again, regions will automatically be updated on the basemap.

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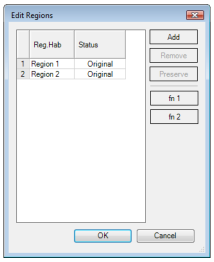

	Reg.Hab	Status
1	Region 1	Original
2	Region 2	Original

Figure 10.5 The *Edit regions* dialogue box.

10.4 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.

Before sketching your basemap you must first set the dimensions of the map using the *Edit basemap* dialogue box (see below). You must also set the number of habitats and any marine protected areas and regions (see *Edit habitats...*, *Edit MPAs...* and *Edit regions...* below).

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.

See *Considerations for building the basemap* below for a short list of issues to consider when building the basemap.

1. Basemap setup

Edit basemap

Opens the *Edit basemap* dialogue box, used for setting the dimensions and location of the Ecospace basemap. See Define Ecospace habitats for help with this dialogue box.

Edit 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. The names and number of habitats are set using the *Edit habitats* dialogue box, available by clicking on the icon at the top right of the *Basemap* form. The dialogue box can also be opened from the *Ecospace menu*. See Define Ecospace habitats for help with this dialogue box.

Edit MPAs

Users can overlay habitats with marine protected areas (MPAs), which are areas closed to fishing for all or part of the year. The names and number of MPAs are set using the *Edit MPAs* dialogue box, available by clicking on the icon at the top right of the *Basemap* form. The dialogue box can also be opened from the *Ecospace menu*. See Define Ecospace habitats for help with this dialogue box.

Edit regions

Users can also overlay habitats with statistical 'regions' (i.e., groups of cells). Regions represent areas of management interest and may or may not have biological significance. Organisms cannot be assigned to regions, only habitats. The names and number of regions are set using the *Edit regions* dialogue box, available by clicking on the icon at the top right of the *Basemap* form. The dialogue box can also be opened from the *Ecospace menu*. See Define Ecospace habitats for help with this dialogue box.

2. Sketching the basemap

Once you have defined the dimensions of the basemap and the number of habitats, MPAs and regions to include, you are ready to begin sketching the map.

Using the *Basemap* form is intuitive. Simply click on the name of the layer you wish to activate and begin sketching with the mouse (holding down the left button). You can change the size of the pen using the *Size* scale under the **Pen** heading.

Layers

The *Basemap* form uses the concept of overlaid layers, commonly found in graphics software. One type of habitat/MPA/Region etc is shown on each layer.

Layers are grouped under the headings: Land; Habitats; MPAs; Regions and Numerical layers. Expand each heading by clicking on the plus icon. There will be one land layer. The number of habitat layers will depend on the number of habitats set using the *Edit habitats* dialogue box (and so on for the number of MPAs and Regions). You can add new habitats etc. while the *Basemap* form is open.

In addition to defining water cells as habitats, MPAs and regions, users can assign numerical values to each cell. Currently this can only be done for primary production relative to the Ecopath base level. This is shown as Relative PP under the Numerical layers heading.

Edit the appearance of each layer using the *Edit layers* dialogue box, accessible by clicking on the coloured box next to the layer name. There you can set the colours, patterns and transparency of the cells as well as see summary statistics for the layer (see Edit layers for details).

Show or hide layers by clicking on the eye symbol (👁) next to the layer name.

Land

It is recommended that you begin by sketching the land cells.

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. Note that movements on the Ecospace map can only resemble those of rooks on chessboards, but not those of bishops (i.e., sideways not diagonal movement). Thus, a system including, e.g., a number of narrow, crooked channels must be simplified.

Though not contributing to the results, the basemap cells defined as 'land' consume memory and computing time. Their number should therefore be kept as small as possible, e.g., by orienting the basemap sideways where appropriate.

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Habitats

Every water cell in the basemap needs to be assigned as a habitat.

Typically, the features defining habitats are distance from the coast (inshore, offshore…), or depth (shallow, intermediate, deep…) and/or bottom type (rocky, sandy, muddy…).

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.Assign habitat preferences of the models's groups using the Assign habitats form.

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’.

MPAs

MPAs are overlaid on top of habitats. MPAs can occupy as many or few cells as desired and can span different habitats.

Note, however that the size and position of individual MPA cells correspond directly with that of individual habitat cells (i.e., an MPA cell cannot be in half of one habitat cell and half of another).

Assign which fleets can and cannot fish in MPAs using Ecospace fishery form.

Regions

Regions also overlay habitats. Regions represent areas of management interest and may or may not have biological significance. Organisms cannot be assigned to regions, only habitats.

Numerical layers

Primary production

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 in one of two ways.

1. 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.

To sketch in the multipliers, first select the *Relative PP* layer. Each cell will display 1 (i.e., every cell starts with the same amount of primary production as in the Ecopath base model). Next, set the new value of the multiplier in the *Value* box at the bottom right of the form. Finally, while holding down the left mouse button, sketch over the cells to be changed to the new value (see Figure 10.6b). Repeat the process as many times as needed.

2. Reading in the data from an external source (e.g., Sea WiFS). This is done using the Edit layers dialogue box, accessible by clicking on the # symbol under **Numerical layers** on the *Layers* menu.

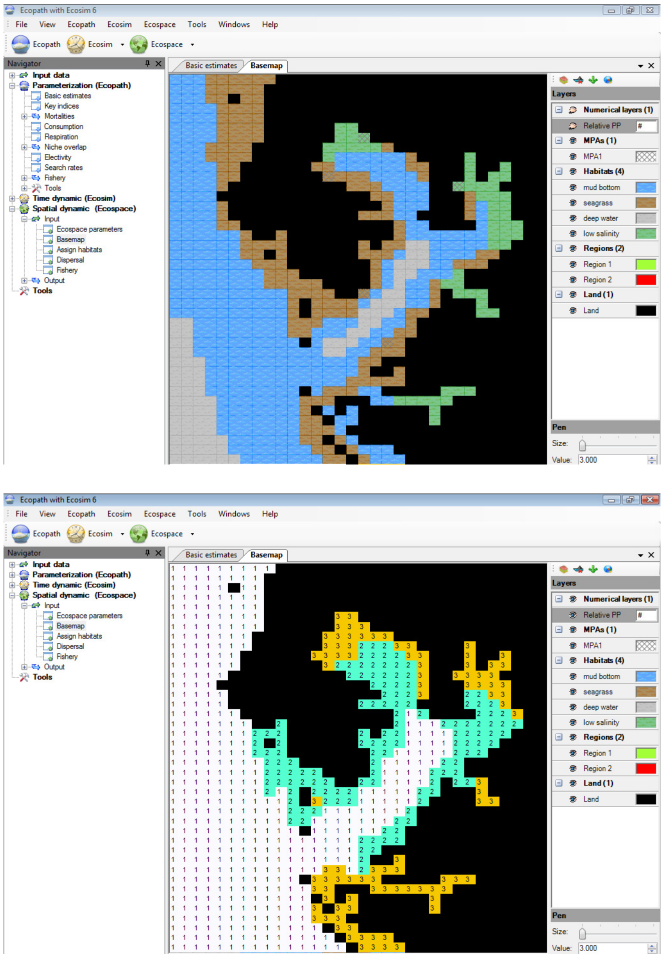


Figure 10.6 Ecospace basemap showing a) habitat layers and b) a numerical (relative PP) layer

3. Considerations for building the basemap

- The cells are square units, but the maps not need be so, both square and rectangular maps can be accommodated. Rectangular maps should not be defined too ‘thin’, (i.e., their aspect ratio (AR = height/width) is recommended to remain in the range 5 £ AR £ 0.2).
- The number of cells in the basemap may range from 4 (for a square 2x2 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.
- Protected areas are defined as set of cells in which no fleet is permitted to operate(although ‘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.

•

10.5 Assign habitats

Once habitats have been defined (see Define Ecospace habitats), (and sketched onto the Basemap), the components of the underlying Ecopath model 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. Users can determine (through the Dispersal form) 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.

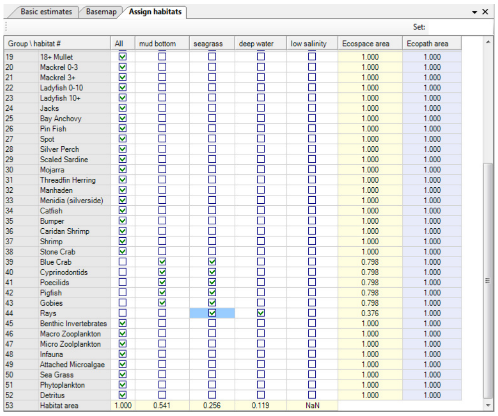
Note organisms at the upper trophic levels, due to their high mobility will tend to ‘prefer’ a wide range of habitats rather than a specific one.

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.

Thus, if the habits defined are ‘shallow’ and ‘deep’, assigning the groups to their preferred habitat simply consists of clicking ‘shallow’ for model groups 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 multi-stanza groups, 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.



Set:

Group \ habitat #		All	mud bottom	seagrass	deep water	low salinity	Ecospace area	Ecopath area
19	18+ Mullet	☑	☐	☐	☐	☐	1.000	1.000
20	Mackrel 0-3	☑	☐	☐	☐	☐	1.000	1.000
21	Mackrel 3+	☑	☐	☐	☐	☐	1.000	1.000
22	Ladyfish 0-10	☑	☐	☐	☐	☐	1.000	1.000
23	Ladyfish 10+	☑	☐	☐	☐	☐	1.000	1.000
24	Jacks	☑	☐	☐	☐	☐	1.000	1.000
25	Bay Anchovy	☑	☐	☐	☐	☐	1.000	1.000
26	Pin Fish	☑	☐	☐	☐	☐	1.000	1.000
27	Spot	☑	☐	☐	☐	☐	1.000	1.000
28	Silver Perch	☑	☐	☐	☐	☐	1.000	1.000
29	Scaled Sardine	☑	☐	☐	☐	☐	1.000	1.000
30	Mojarra	☑	☐	☐	☐	☐	1.000	1.000
31	Threadfin Herring	☑	☐	☐	☐	☐	1.000	1.000
32	Manhaden	☑	☐	☐	☐	☐	1.000	1.000
33	Menidia (silverside)	☑	☐	☐	☐	☐	1.000	1.000
34	Catfish	☑	☐	☐	☐	☐	1.000	1.000
35	Bumper	☑	☐	☐	☐	☐	1.000	1.000
36	Caridan Shrimp	☑	☐	☐	☐	☐	1.000	1.000
37	Shrimp	☑	☐	☐	☐	☐	1.000	1.000
38	Stone Crab	☑	☐	☐	☐	☐	1.000	1.000
39	Blue Crab	☐	☑	☑	☐	☐	0.798	1.000
40	Cyprinodontids	☐	☑	☑	☐	☐	0.798	1.000
41	Poecilids	☐	☑	☑	☐	☐	0.798	1.000
42	Pigfish	☐	☑	☑	☐	☐	0.798	1.000
43	Gobies	☐	☑	☑	☐	☐	0.798	1.000
44	Rays	☐	☐	☑	☑	☐	0.376	1.000
45	Benthic Invertebrates	☑	☐	☐	☐	☐	1.000	1.000
46	Macro Zooplankton	☑	☐	☐	☐	☐	1.000	1.000
47	Micro Zoolplankton	☑	☐	☐	☐	☐	1.000	1.000
48	Infauna	☑	☐	☐	☐	☐	1.000	1.000
49	Attached Microalgae	☑	☐	☐	☐	☐	1.000	1.000
50	Sea Grass	☑	☐	☐	☐	☐	1.000	1.000
51	Phytoplankton	☑	☐	☐	☐	☐	1.000	1.000
52	Detritus	☑	☐	☐	☐	☐	1.000	1.000
53	Habitat area	1.000	0.541	0.256	0.119	NaN		

Figure 10.7 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 my be because of inappropriate distribution of habitat areas, and a more careful allocation if often required to improve model behaviour.

10.6 Dispersal

Introduction

The organisms (i) in an Ecopath model have an aggregated biomass (Bi), and are not assumed to move within the area covered by that Ecopath model. In Ecospace, a fraction (B'i) of the biomass of each cell is always on the move, wherein

$B' = m \cdot Bi$

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 · 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.

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.

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).

Base dispersal rate

This is the absolute value of *m* to be used in the simulation. The default value is 300 km/year for all groups apart from detritus groups to which discards are added (and for which we use a default of 10 km/year).

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.

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 Advection for more details on implementing advection in Ecospace.

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 C:\Ecopath\Ecopath6\Documentation\Content\EWE_UsersGuide\Representing seasonal migration.htm - _Representing_seasonal_migrationMigration for more details on implementation of seasonal migration in Ecospace.

North/south and East/west concentration

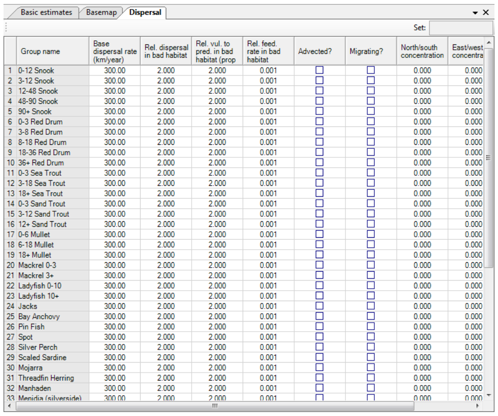
Larger organisms commonly have seasonal migration patterns that allow them to utilize favourable seasonal resource and environmental conditions over large spatial areas. Such movements can be represented in Ecospace in two ways. First is a simple "Lagrangian" approach that does not require explicit simulation of movement; the idea here is to simply think of the whole Ecospace map as moving in space so as to remain centred on the distribution of some dominant migratory specie(s). Second is a more complex "Eulerian" approach, which does involve explicitly modelling changes in instantaneous rates of biomass flow among the Ecospace spatial cells, in some way that approximates at least the changing centre of distribution of the migratory species.

The Eulerian approach is implemented in Ecospace by allowing users to define a monthly sequence of "preferred" map cell positions 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".

For more detail see Representing seasonal migration in Ecospace.

Barrier avoidance weight

To prevent migrating fish getting stuck in complex habitat, Ecospace contains an algorithm to help fish move around obstacles. The Barrier avoidance weight is the weight placed on the path finding algorithm. Default is 0 (it does nothing). If fish are getting stuck, gradually increase the value up to 1. Increasing this weight tends to concentrate the fish more tightly. The EW/NS concentrations can be lowered if this is a problem.



	Group name	Base dispersal rate (km/year)	Rel. dispersal in bad habitat	Rel. vul. to pred. in bad habitat (prop	Rel. feed. rate in bad habitat	Advected?	Migrating?	North/south concentration	East/west concentra
1	0-12 Snook	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
2	3-12 Snook	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
3	12-48 Snook	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
4	48-90 Snook	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
5	90+ Snook	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
6	0-3 Red Drum	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
7	3-8 Red Drum	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
8	8-18 Red Drum	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
9	18-36 Red Drum	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
10	36+ Red Drum	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
11	0-3 Sea Trout	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
12	3-18 Sea Trout	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
13	18+ Sea Trout	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
14	0-3 Sand Trout	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
15	3-12 Sand Trout	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
16	12+ Sand Trout	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
17	0-6 Mullet	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
18	6-18 Mullet	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
19	18+ Mullet	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
20	Mackrel 0-3	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
21	Mackrel 3+	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
22	Ladyfish 0-10	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
23	Ladyfish 10+	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
24	Jacks	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
25	Bay Anchovy	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
26	Pin Fish	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
27	Spot	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
28	Silver Perch	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
29	Scaled Sardine	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
30	Mojarra	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
31	Threadfin Herring	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
32	Manhaden	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000
33	Menidia (silverside)	300.00	2.000	2.000	0.001	☐	☐	0.000	0.000

Figure 10.8 Ecospace dispersal rates and habitat specific information. Migration patterns are also defined on this form.

10.7 Ecospace fishery

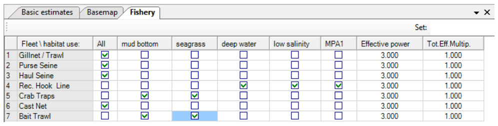
The *Ecospace fishery* form (Figure 10.9) is used to assign fleets, i.e., to define in which habitat(s) a fishing fleet may operate, and to identify whether a given fleet may operate within a restricted area.

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 ($F = qE = \text{Catch/biomass}$) 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.



	Fleet \ habitat use:	All	mud bottom	seagrass	deep water	low salinity	MPA1	Effective power	Tot.Eff.Multip.
1	Gillnet / Trawl	☑	☐	☐	☐	☐	☐	3.000	1.000
2	Purse Seine	☑	☐	☐	☐	☐	☐	3.000	1.000
3	Haul Seine	☑	☐	☐	☐	☐	☐	3.000	1.000
4	Rec. Hook Line	☐	☐	☐	☑	☑	☑	3.000	1.000
5	Crab Traps	☐	☑	☑	☐	☐	☐	3.000	1.000
6	Cast Net	☑	☐	☐	☐	☐	☐	3.000	1.000
7	Bait Trawl	☐	☑	☑	☐	☐	☐	3.000	1.000

Figure 10.9 The Ecospace fishery form.

10.8 Edit layers

The *Edit layers* dialogue box contains summary information about each layer and allows you to customize the appearance of layers on the Ecospace basemap. It also contains the facility to import spatial primary production data from external sources.

Each layer on the basemap has its own *Edit layers* dialogue box, which is opened by clicking once on the coloured box next to the layer's name in the Basemap form.

The left hand side of the dialogue box displays the cells of the basemap represented by the layer. The *Properties* window contains summary information. The *Representation* windows allows customization of the layer's cells.

Properties

For non-numerical layers (i.e., Land, Habitats, MPAs and Regions), the properties window shows a summary of the properties of the layer (i.e., *Name*, *Type* and *Size*). Use the *Remarks* window to enter any extra information about the layer.

Representation

Pattern tab

Use the *Pattern tab* to change the pattern/colour/image used for MPAs and Regions.

MPAs: MPAs are differentiated using different patterns. You can select from a range of different patterns (click in the large pattern square to see list of patterns). You can set the colour of both the cell foreground and background.

Regions: Regions are differentiated using blocks of solid colour. Change the colour of the cells by adjusting the Red, Green and Blue levels.

For MPAs and Regions, use *Alpha* to adjust transparency of the colour. Note that, because they overlay Habitats, MPAs and Regions are always partially transparent regardless of the Alpha setting.

Image tab

Habitats: Use the Image tab to select an image file to use for Habitat cells. Select from the list shown or import your own image file using the *Import* button. You will be prompted to browse for a file.

NOTE: the maximum allowed dimension for an image file is 100 x 100 pixels.

11 Using Ecospace. Part 2: Ecospace outputs

Once you have set up your Ecospace scenario(s) using the Ecospace input forms, you can test your model's predictions using Ecospace. This chapter describes the form used to run Ecospace (Run Ecospace).

Before using Ecospace, we recommend you read the introductory material on Ecospace (see links in Introductory material Ecospace, also found in Chapter 4 of the User Guide). You should also be familiar with the published literature on Ecospace, particularly Walters et al. 1999).

11.1 Run Ecospace

The business of Ecospace is predicting distributions. Its main outputs are distribution maps, one for each ecosystem component. Here, positive deviations (biomass increases) from the Ecopath baseline levels are shown in red, and negative deviation (decrease) in blue (see colour scale on right of panel representing map.

Ecospace runs thus imply the display of a succession of maps, one per iteration and group. Usually, the features of these maps will be gradually converging toward some stable equilibrium distribution. Alternatively these maps may regularly 'flip' between two states, suggesting some sort of dynamic equilibrium.

Which of these alternative occurs can be seen more clearly from the time plot (the small panel to the mid left of the Ecospace run window), which traces the progress of the run.

Relative biomass

Show relative biomasses on the plots.

Fishing effort

Show distribution of fishing effort over space for each of the fleets. In Ecospace, fishing effort is assigned to spatial cells through a 'gravity model', wherein effort is proportional to the net benefits gained from exploiting a given cell.

In the simple case that all exploited group have the same economic value (default = 1 monetary unit per tonne), and that all cells require the same sailing cost (default), fishing effort will be assigned to the (water) cells of the base map in proportion to their fishable biomass.

Thus, for example, fishing effort will tend to concentrate at the edges of protected areas – one reason, incidentally, why these edges should be as short as possible.

Show all

Show plots for all groups

Show non-hidden

Show plots for groups which are not-hidden on the Show/hide dialogue box.

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Show only group below

Show plot for only the group that is selected in the drop-down list box below. You can change which group to display by selecting another group.

Time plot

Plot showing biomass over time relative to biomass in Ecopath base run for each group. The scale is logarithmic spanning from 0.1 over 1 (same biomass as in Ecopath) to 10.

The time plot panel shows the (log) biomass of each group over time, from the start of the simulation, to its end. Usually, this will consist of a phase of rapid change, followed by a convergence of all groups toward their equilibrium states (flat lines). In other case, the lines representing the biomasses will oscillate more or less regularly (the preys usually displaying troughs when their predators show peaks, and vice versa), which will diagnose the dynamic equilibrium mentioned above.

Finally, one or several of the lines representing the biomass of various groups may decrease or increase continuously, indicating that this (or these) group(s) cannot be accommodated in the system. Thus, a group may decrease because it cannot find sufficient food in its assigned habitats, or encounters too many predators when feeding, non-withstanding it being mass-balanced in the underlying Ecopath file.

Alternatively, a group may increase due its ability to outgrow predatory control in its assigned habitats, or in another habitat, a feature sometimes due to an excessively high value of P/B, or to a diet composition that is too broad.

Enlarge plot

Enlarge the time plot and show it in the main window. You can use the mouse pointer to see the group names linked to the lines.

Run

Start the run. Will change to ‘Stop’ once pressed, and to ‘Run’ again at the end of the run

Pause

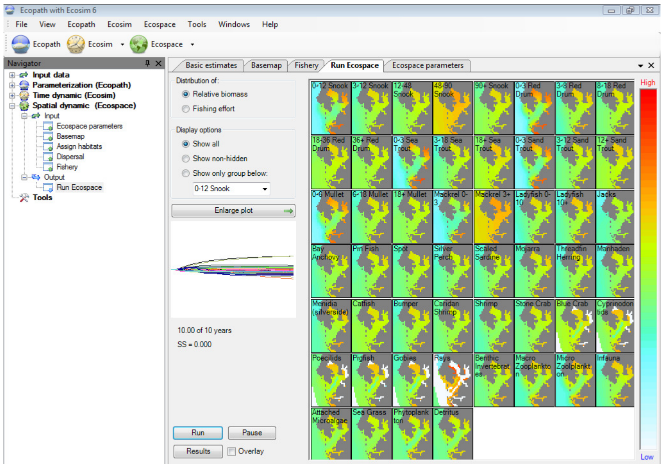
Pause the run, e.g., to set up a protected area on the basemap.

Results

Will display a summary of the results for the Start and End times set on the Ecospace parameters form. Results are averaged in the start and end year, i.e., when Ecospace reaches the Start time it will average results over the next number of timesteps (set in *Summary timesteps* on the *Ecospace parameters* form). Similarly, when it reaches the End time it will average over the next same number of timesteps.

Overlay

Check to overlay the time plots on the time plot. Use this to check for initialization errors, i.e. this feature is mainly used to ensure that successive runs give the same results.



Distribution of:
● Relative biomass
○ Fishing effort

Display options
● Show all
○ Show non-hidden
○ Show only group below:
0-12 Snook

10.00 of 10 years
SS = 0.000

☐ Overlay

Figure 11.1 The *Run Ecospace* form.

11.2 Ecospace results

Results from Ecospace simulations are shown on the Ecospace results form (*Spatial dynamic (Ecospace)* > *Output* > *Ecospace results*). Users can choose to show results by **Gear** (i.e., fishing fleet), by **Group** or by **Region**.

Gear results are shown in terms of **Catch**, **Value** and **Cost** at the beginning and end of the simulation period.

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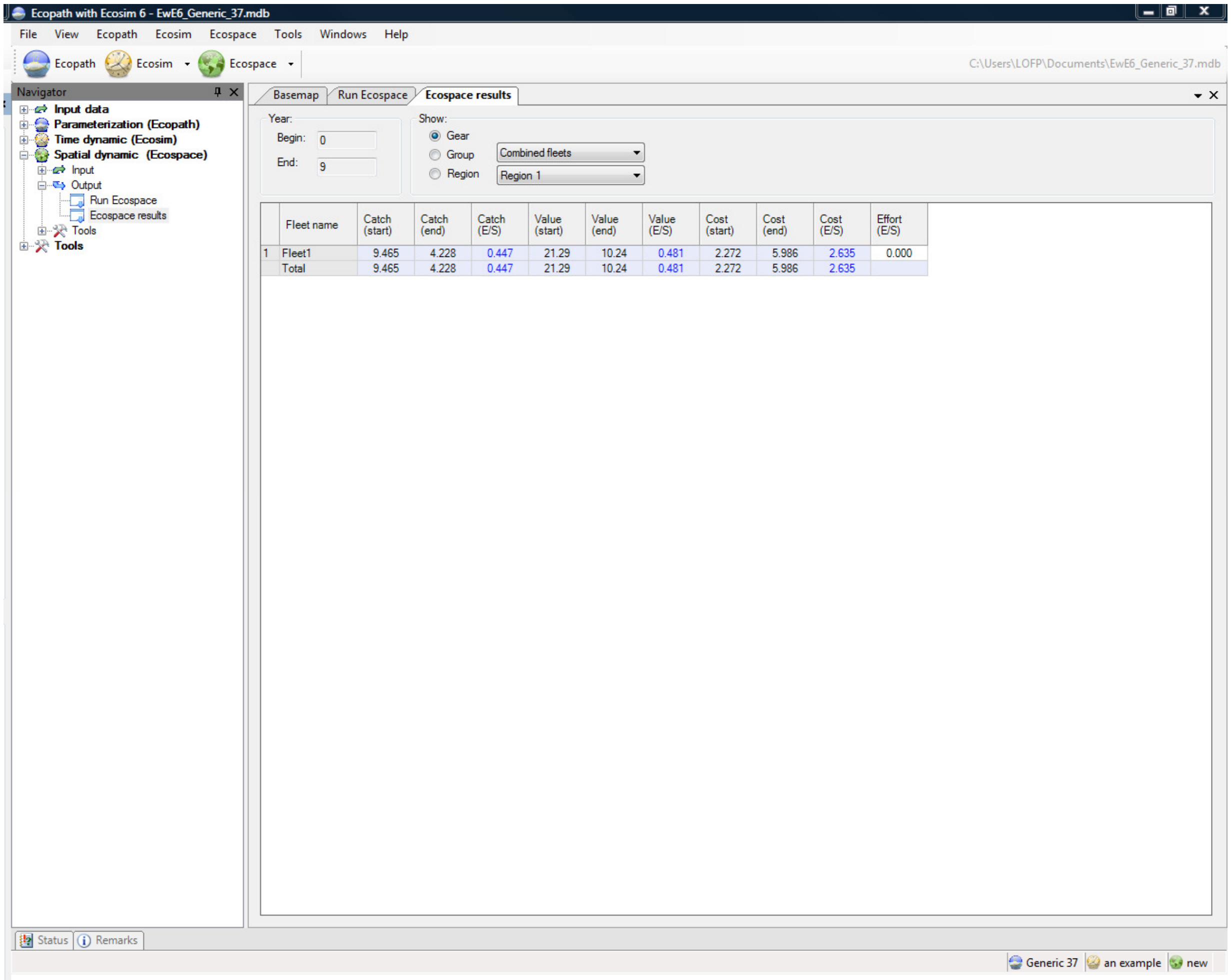
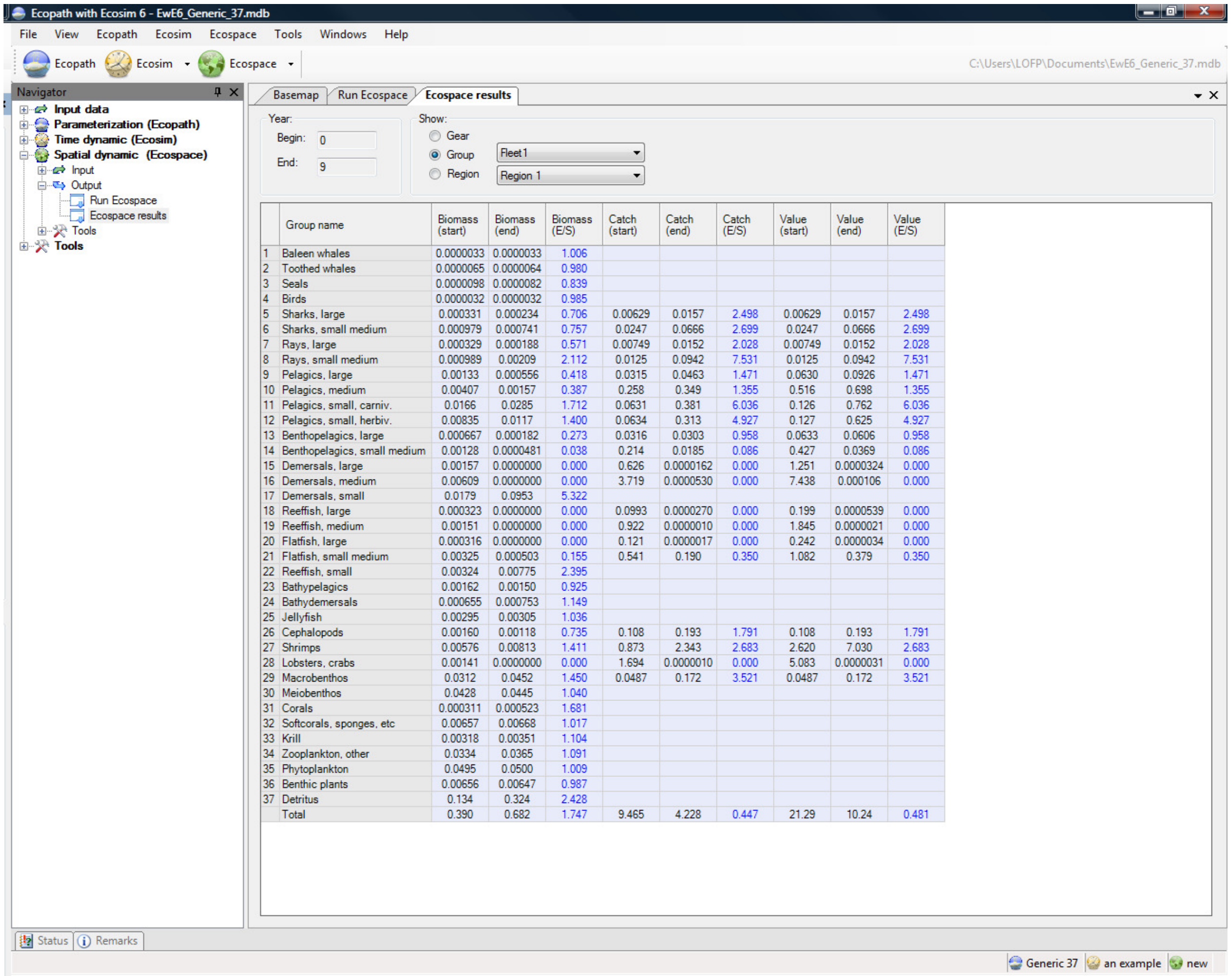


Year:
Begin: 0
End: 9

Show:
● Gear
○ Group
○ Region
Combined fleets
Region 1

	Fleet 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	Fleet1	9.465	4.228	0.447	21.29	10.24	0.481	2.272	5.986	2.635	0.000
	Total	9.465	4.228	0.447	21.29	10.24	0.481	2.272	5.986	2.635	

Group results are shown in terms of Biomass, Catch and Value at the beginning and end of the simulation period. Users can elect to see Catch and Value results from all fleets combined or from individual fleets, using the pull-down menu on the form.



Year:
Begin: 0
End: 9

Show:
○ Gear
● Group Fleet1
○ Region Region 1

	Group name	Biomass (start)	Biomass (end)	Biomass (E/S)	Catch (start)	Catch (end)	Catch (E/S)	Value (start)	Value (end)	Value (E/S)
1	Baleen whales	0.0000033	0.0000033	1.006						
2	Toothed whales	0.0000065	0.0000064	0.980						
3	Seals	0.0000098	0.0000082	0.839						
4	Birds	0.0000032	0.0000032	0.985						
5	Sharks, large	0.000331	0.000234	0.706	0.00629	0.0157	2.498	0.00629	0.0157	2.498
6	Sharks, small medium	0.000979	0.000741	0.757	0.0247	0.0666	2.699	0.0247	0.0666	2.699
7	Rays, large	0.000329	0.000188	0.571	0.00749	0.0152	2.028	0.00749	0.0152	2.028
8	Rays, small medium	0.000989	0.00209	2.112	0.0125	0.0942	7.531	0.0125	0.0942	7.531
9	Pelagics, large	0.00133	0.000556	0.418	0.0315	0.0463	1.471	0.0630	0.0926	1.471
10	Pelagics, medium	0.00407	0.00157	0.387	0.258	0.349	1.355	0.516	0.698	1.355
11	Pelagics, small, carniv.	0.0166	0.0285	1.712	0.0631	0.381	6.036	0.126	0.762	6.036
12	Pelagics, small, herbiv.	0.00835	0.0117	1.400	0.0634	0.313	4.927	0.127	0.625	4.927
13	Benthopelagics, large	0.000667	0.000182	0.273	0.0316	0.0303	0.958	0.0633	0.0606	0.958
14	Benthopelagics, small medium	0.00128	0.0000481	0.038	0.214	0.0185	0.086	0.427	0.0369	0.086
15	Demersals, large	0.00157	0.0000000	0.000	0.626	0.0000162	0.000	1.251	0.0000324	0.000
16	Demersals, medium	0.00609	0.0000000	0.000	3.719	0.0000530	0.000	7.438	0.000106	0.000
17	Demersals, small	0.0179	0.0953	5.322						
18	Reeffish, large	0.000323	0.0000000	0.000	0.0993	0.0000270	0.000	0.199	0.0000539	0.000
19	Reeffish, medium	0.00151	0.0000000	0.000	0.922	0.0000010	0.000	1.845	0.0000021	0.000
20	Flatfish, large	0.000316	0.0000000	0.000	0.121	0.0000017	0.000	0.242	0.0000034	0.000
21	Flatfish, small medium	0.00325	0.000503	0.155	0.541	0.190	0.350	1.082	0.379	0.350
22	Reeffish, small	0.00324	0.00775	2.395						
23	Bathypelagics	0.00162	0.00150	0.925						
24	Bathydemersals	0.000655	0.000753	1.149						
25	Jellyfish	0.00295	0.00305	1.036						
26	Cephalopods	0.00160	0.00118	0.735	0.108	0.193	1.791	0.108	0.193	1.791
27	Shrimps	0.00576	0.00813	1.411	0.873	2.343	2.683	2.620	7.030	2.683
28	Lobsters, crabs	0.00141	0.0000000	0.000	1.694	0.0000010	0.000	5.083	0.0000031	0.000
29	Macrobenthos	0.0312	0.0452	1.450	0.0487	0.172	3.521	0.0487	0.172	3.521
30	Meiobenthos	0.0428	0.0445	1.040						
31	Corals	0.000311	0.000523	1.681						
32	Softcorals, sponges, etc	0.00657	0.00668	1.017						
33	Krill	0.00318	0.00351	1.104						
34	Zooplankton, other	0.0334	0.0365	1.091						
35	Phytoplankton	0.0495	0.0500	1.009						
36	Benthic plants	0.00656	0.00647	0.987						
37	Detritus	0.134	0.324	2.428						
	Total	0.390	0.682	1.747	9.465	4.228	0.447	21.29	10.24	0.481

Region results are shown in terms of Biomass and Catch. Users can select the region to display from the pull-down menu on the form,

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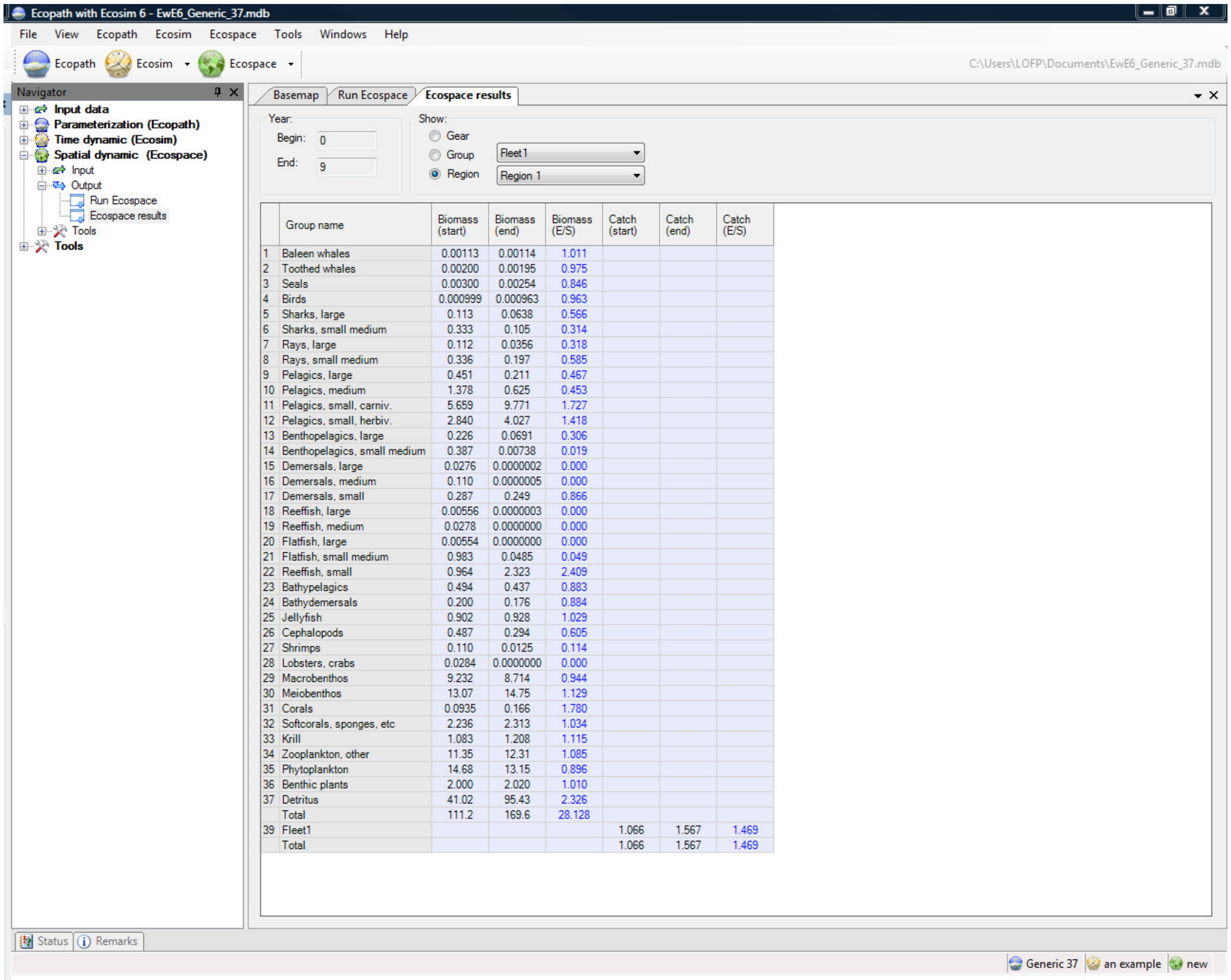


Year:
Begin: 0
End: 9

Show:
○ Gear
○ Group
● Region

Fleet1
Region 1

	Group name	Biomass (start)	Biomass (end)	Biomass (E/S)	Catch (start)	Catch (end)	Catch (E/S)
1	Baleen whales	0.00113	0.00114	1.011			
2	Toothed whales	0.00200	0.00195	0.975			
3	Seals	0.00300	0.00254	0.846			
4	Birds	0.000999	0.000963	0.963			
5	Sharks, large	0.113	0.0638	0.566			
6	Sharks, small medium	0.333	0.105	0.314			
7	Rays, large	0.112	0.0356	0.318			
8	Rays, small medium	0.336	0.197	0.585			
9	Pelagics, large	0.451	0.211	0.467			
10	Pelagics, medium	1.378	0.625	0.453			
11	Pelagics, small, carniv.	5.659	9.771	1.727			
12	Pelagics, small, herbiv.	2.840	4.027	1.418			
13	Benthopelagics, large	0.226	0.0691	0.306			
14	Benthopelagics, small medium	0.387	0.00738	0.019			
15	Demersals, large	0.0276	0.0000002	0.000			
16	Demersals, medium	0.110	0.0000005	0.000			
17	Demersals, small	0.287	0.249	0.866			
18	Reeffish, large	0.00556	0.0000003	0.000			
19	Reeffish, medium	0.0278	0.0000000	0.000			
20	Flatfish, large	0.00554	0.0000000	0.000			
21	Flatfish, small medium	0.983	0.0485	0.049			
22	Reeffish, small	0.964	2.323	2.409			
23	Bathypelagics	0.494	0.437	0.883			
24	Bathydemersals	0.200	0.176	0.884			
25	Jellyfish	0.902	0.928	1.029			
26	Cephalopods	0.487	0.294	0.605			
27	Shrimps	0.110	0.0125	0.114			
28	Lobsters, crabs	0.0284	0.0000000	0.000			
29	Macrobenthos	9.232	8.714	0.944			
30	Meiobenthos	13.07	14.75	1.129			
31	Corals	0.0935	0.166	1.780			
32	Softcorals, sponges, etc	2.236	2.313	1.034			
33	Krill	1.083	1.208	1.115			
34	Zooplankton, other	11.35	12.31	1.085			
35	Phytoplankton	14.68	13.15	0.896			
36	Benthic plants	2.000	2.020	1.010			
37	Detritus	41.02	95.43	2.326			
	Total	111.2	169.6	28.128			
39	Fleet1				1.066	1.567	1.469
	Total				1.066	1.567	1.469

11.3 Ecospace tools

Tools currently available in Ecospace are Spatial optimizations.

11.4 Spatial optimizations

Duke University
Marine Geospatial Ecology Lab

LENFEST
OCEAN
PROGRAM

EwE6 now allows you to use Ecospace to search for optimum placement of marine protected areas (MPAs) that would maximize a user-defined objective function. This routine is implemented using the *Spatial optimizations* form (*Spatial dynamic (Ecospace)* > *Tools* > *Spatial optimizations*).

NOTE: Before using this routine you must have already defined an Ecosim scenario (see Ecosim menu) and an Ecospace scenario (see Ecospace menu). Load the scenarios from the Ecosim and Ecospace menus or from the Ecosim [ ] and Ecospace [ ] shortcut buttons.

Introduction

While Ecospace has been applied quite extensively in a gaming- and scenario-development mode, we have only seen very limited effort applied to spatial optimization and zoning. A first attempt in this direction is represented, though, by the 'Ecoseed' approach, developed for Ecospace some years ago as part of a thesis project (Beattie 2001; Beattie et al. 2002), but never fully implemented and released as part of the software. We have developed this approach to incorporate a new objectivity function, bringing it to a level where it is part of the released EwE6. Further, we describe a new spatial optimization module, which uses the same objectivity function as the updated seed cell, but where the spatial cell selection process is influenced by spatial reference layers, typically of conservation interest.

Two alternative approaches to running the routine have been developed: (i) 'Seed cell', based on the original approach of Beattie (2001) and Beattie et al. (2002); and (ii) 'Importance layer', a variation on the approach, which allows the user to incorporate other forms of spatial information in the selection of seed cells.

Seed cell selection procedure ('Seed cell' method)

This optimization method (user selects 'Seed cell' method) is based on a previous study (Beattie 2001; Beattie et al. 2002), in which we use a very simple optimization scheme to evaluate the trade-off between proportion of area protected and the value of the objective function. We have modified the previous approach by securing a better program flow, and by changing the objective function from considering only profit from fishing and existence value of biomass groups to a more detailed objective function described in Equation 2 of Spatial optimization procedures.

The procedure takes as its starting point the designation of one, more, or all spatial cells as 'seed cells', i.e. cells that are to be considered as potential protected cells in the next program iteration. The procedure will then run the Ecospace model repeatedly between two time steps, closing one of the seeds cells in each run, while storing the ecosystem objective function value. The seed cell that results in the highest objective function value is then closed for fishing, and its four neighbouring cells (above, below, left, right) are then turned into seed cells, unless they are so already, or already are protected, or are land cells. This procedure will continue until all cells are protected. Finally, the routine will return the set of cells to be protected that would maximize the objective function.

The time over which the selection procedure is run is dependent on the application. Typically, an ecosystem model is initially developed and tuned using time series data to cover a certain time period, e.g., from 1950 to 2005. Subsequently, the model is used in a scenario development mode to evaluate, for instance, protected area placement covering the period 2006-2020.

The major result from the seed cell selection procedure is an evaluation of the trade-off between size of protected area, and each of the objectives in the objective function. This can, for instance, be used to consider what proportion of the total area to close in subsequent, more detailed analysis based on importance layer sampling (see next section).

Importance layer sampling procedure ('Importance layer' method)

An advantage of the seed cell modelling approach described above is that it allows a comprehensive overview of the trade-off between proportion of area closed to fishing, and the ecological, social, and economical benefit and costs of the closures. This is done, based on the information already included in the EwE modelling approach, with no new information being needed. While this may be an advantage from one perspective, it does not allow use of other form for information, notably in form of spatial information, e.g., critical fish habitat layers from GIS.

To address this shortcoming, we have developed a new optimization routine for the Ecospace model (user selects 'Importance layer' method), which uses spatial layers of conservation interest ('importance layers') to set likelihoods for spatial cells being considered for protection. The optimizations are performed using a Monte Carlo approach where the importance layers are used for the initial cell selection in each MC realization. The Ecospace model is then run, the objective function (Equation 2 in Spatial optimization procedures) is evaluated, and the results, including which cells were protected, are stored for each run (see Figure 11.2).

NOTE: importance layers are not used to evaluate the objective function. The information in the importance layers is used only to influence initial cell selection.

The importance layers are defined as raster layers, with dimensions similar to the base map layers in the underlying Ecospace model, i.e. they are rectangular cells in a grid with a certain number of rows and columns. Each cell in a given layer has a certain 'importance' for conservation, expressed, e.g., as the probability of occurrence for an endangered species. For each importance layer (l), we initially scale the importance layer values to sum to unity, and then calculate an overall cell weighting (w_c) for each cell (C) from

$$w_c = \sum_l w_l C_{c,l}$$

where w_l are the importance layer weightings, and the $C_{c,l}$ cell-specific, scaled importance layer values.

Similar to the seed cell selection procedure, we typically develop and tune the model to an initial time period, and then use the sampling procedure to evaluate scenarios for protected areas for a subsequent time period.

We have developed a capability for Ecospace to read raster files with spatial information such as importance layers or other Ecospace base map layers. The reading is possible from comma separated text files (.csv), ESRI ASCII files (.asc), and ESRI shape files (.shp). The files need to have layers or columns with row and column numbers matching the Ecospace model (see below for details).

Further information can be found in Spatial optimization procedures and it is strongly recommended you read this section before proceeding with the *Spatial optimizations* routine.

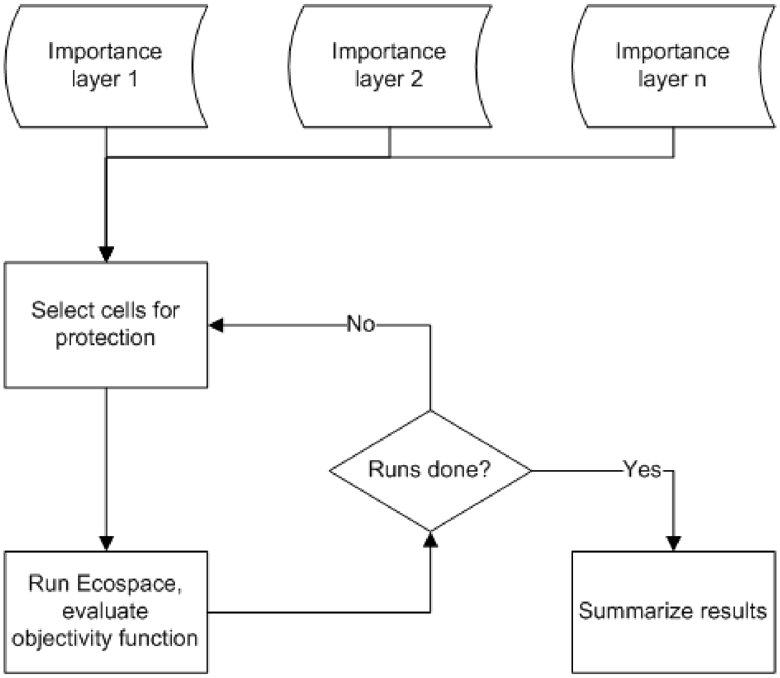
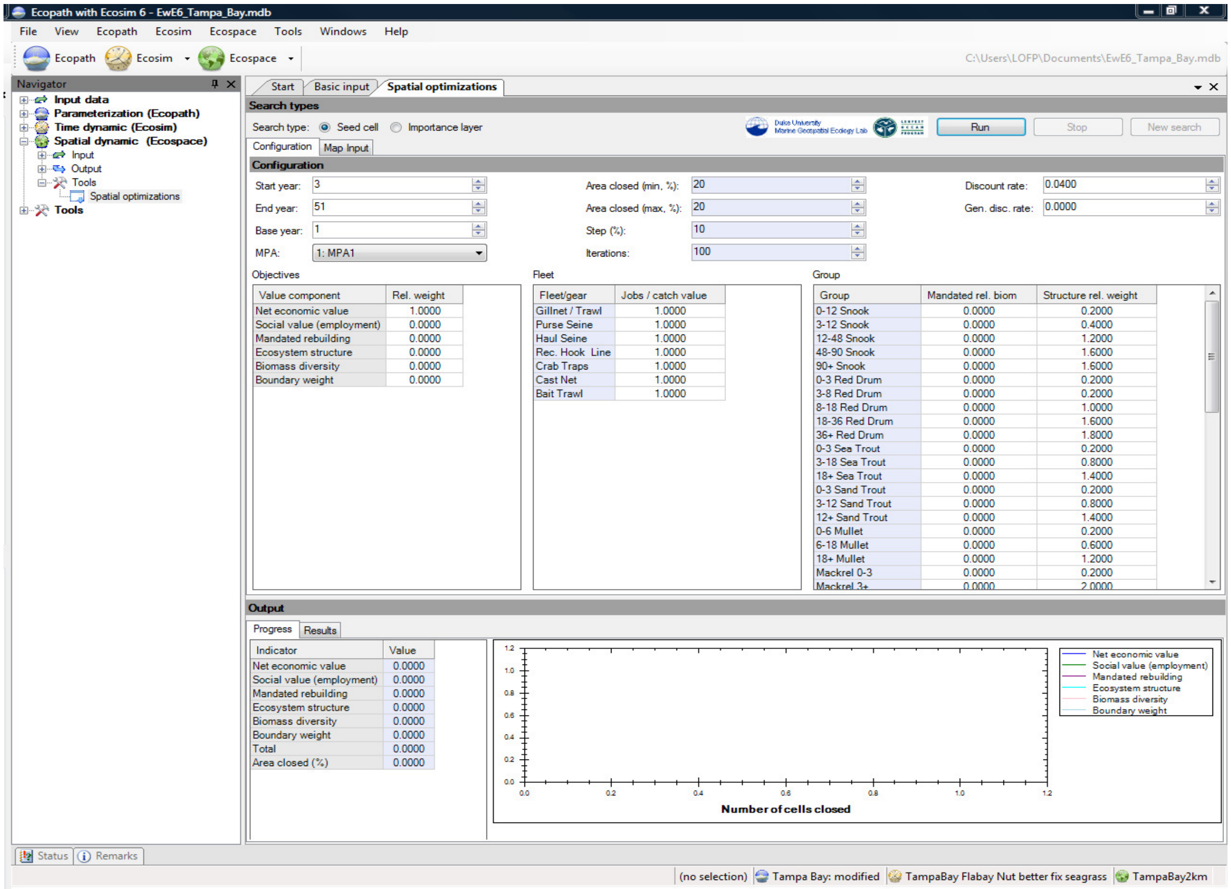


Figure 11.2 Logic of the importance layer sampling procedure. For each run a given percentage of all cells are protected based on weighted likelihood in importance layers. The evaluation of each run is done independently based on a defined objective function (see **Objectives** below).

Implementing *Spatial optimizations* in Ecospace

The *Spatial optimizations* form is divided into two sections. Inputs are entered in the top half of the form in the **Configuration** and **Map Input** tabs. Results are displayed on the bottom half of the form on the **Progress** and **Results** tabs.



Search type: ● Seed cell ○ Importance layer

Start year: 3
End year: 51
Base year: 1
MPA: 1: MPA1
Area closed (min, %): 20
Area closed (max, %): 20
Step (%): 10
Iterations: 100
Discount rate: 0.0400
Gen. disc. rate: 0.0000

Objectives

Value component	Rel. weight
Net economic value	1.0000
Social value (employment)	0.0000
Mandated rebuilding	0.0000
Ecosystem structure	0.0000
Biomass diversity	0.0000
Boundary weight	0.0000

Fleet

Fleet/gear	Jobs / catch value
Gillnet / Trawl	1.0000
Purse Seine	1.0000
Haul Seine	1.0000
Rec. Hook Line	1.0000
Crab Traps	1.0000
Cast Net	1.0000
Bait Trawl	1.0000

Group

Group	Mandated rel. biom	Structure rel. weight
0-12 Snook	0.0000	0.2000
3-12 Snook	0.0000	0.4000
12-48 Snook	0.0000	1.2000
48-90 Snook	0.0000	1.6000
90+ Snook	0.0000	1.6000
0-3 Red Drum	0.0000	0.2000
3-8 Red Drum	0.0000	0.2000
8-18 Red Drum	0.0000	1.0000
18-36 Red Drum	0.0000	1.6000
36+ Red Drum	0.0000	1.8000
0-3 Sea Trout	0.0000	0.2000
3-18 Sea Trout	0.0000	0.8000
18+ Sea Trout	0.0000	1.4000
0-3 Sand Trout	0.0000	0.2000
3-12 Sand Trout	0.0000	0.8000
12+ Sand Trout	0.0000	1.4000
0-6 Mullet	0.0000	0.2000
6-18 Mullet	0.0000	0.6000
18+ Mullet	0.0000	1.2000
Mackrel 0-3	0.0000	0.2000
Mackrel 3+	0.0000	2.0000

Indicator	Value
Net economic value	0.0000
Social value (employment)	0.0000
Mandated rebuilding	0.0000
Ecosystem structure	0.0000
Biomass diversity	0.0000
Boundary weight	0.0000
Total	0.0000
Area closed (%)	0.0000

Figure 11.3 The *Spatial optimizations* form, **Configuration** tab.

Configuration tab

Users can choose between two methods of implementing the spatial optimisation routine: **Seed cell** or **Importance layer** (see _Ref493389844above). Before proceeding with the optimization routine, users should first select one of these two options in the **Search** box on the **Parameters** panel of the form (Figure 11.3). Selection of one of these methods will determine the inputs required.

In both cases, users must set the **Start year** and **End year** for the optimization search. If **Start year** is set to 1, the routine will start running Ecospace and evaluating the objective function from the first year of simulations. However, in many cases, users will wish to run Ecospace for a period of time, possibly to obtain some degree of equilibrium under fishing, before optimization begins. In this case, set **Start year** to the first year that the objective function is to be evaluated, e.g., if **Start year** is set to five, Ecospace will run for four years and then start the search routine in year five. Set **End year** to the year in which the search routine is to stop. The appropriatelength of time over which to run the optimization routine will depend on the time horizon of the particular management question and the life span of the species affected by the MPA.

In both cases, users can also select an **MPA** previously defined on the Ecospace Basemap (see also Define Ecospace habitats). The cells bordering the MPA will then also be used as seed cells and the selected MPA may be modified during the search. Any other MPAs will be unaffected by the search.

Additionally, if **Importance layer** is selected, the user defines the minimum and maximum area (**Min area %** and **Max area %**, with step size **Step %**) to be set aside as MPA. The percentage area can be set to a fixed value by setting **Min area %** and **Max area %** to the same value. Users also set the number of **Iterations** that will be implemented in the Monte Carlo search routine (see above).

The search routine is initialized using the **Run** button. It can be stopped using the **Stop** button.

NOTE: If you initialize a search then stop the search, you cannot restart it or change input parameter values. You must use the **New Search** button to start a new search.

Objectives

The objective function used in the routine is analogous to that used in Ecosim's Policy optimization routine. It is strongly recommended you read Spatial optimization procedures for detailed description of the objective function.

Use the **Objectives** table (Figure 11.3) to define objective function weights for **Net economic value** (total landed value of catch minus total operating cost); **Social value (employment)**, i.e., 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 two ecological objectives: 1. **Mandated rebuilding** of one group (value of the objective function is measured by departures of biomasses over time from target biomass levels specified by entering ratios of target to Ecopath base biomasses); and 2. **Ecosystem structure**, which favours biomasses of large, long-lived organisms. See **Policy objectives** in Fishing policy search and Christensen and Walters (2004b) for more details about these objectives.

Use **Boundary** weight to adjust the weight given to size of the protected area in the objective funtion. This is estimated as total boundary length over the protected area size and captures spatial connectivity of protected areas.

Note that you may initially need play with different values for the objective function weight for each factor to find ranges that produce contrast in the final value of the objective function.

You may also need to set extra parameters for these using the two tabs on the **Configuration** panel. Use the **Fleet** table to set the number of jobs relative to the catch value. The default is 1 for each fleet, implying that if the catch doubled, the number of jobs would also double. For economic objectives, you may wish to adjust the **Discount rate** and **Generational discount rate**. The discount rate is the annual rate (entered in %) applied to discount the present value of future catches relative to present base value. See Ainsworth and Sumaila (2005) for description of intergenerational discounting.

The **Group** table has two columns:

Mandated rel. biomass

Use this column to set a threshold biomass (relative to the biomass in Ecopath) for the species or group of interest.

Structure rel. weight

When Ecosystem structure is included in the objective function, the search routine favours larger biomasses of long-lived organisms, indicated by B/P (i.e., P/B^{-1}). These values are listed in the *Structure rel. weight* column and can be changed if users wish to place more or less weight on some groups than indicated by their B/P or if the user wishes to optimize for something other than B/P under the ecological objective.

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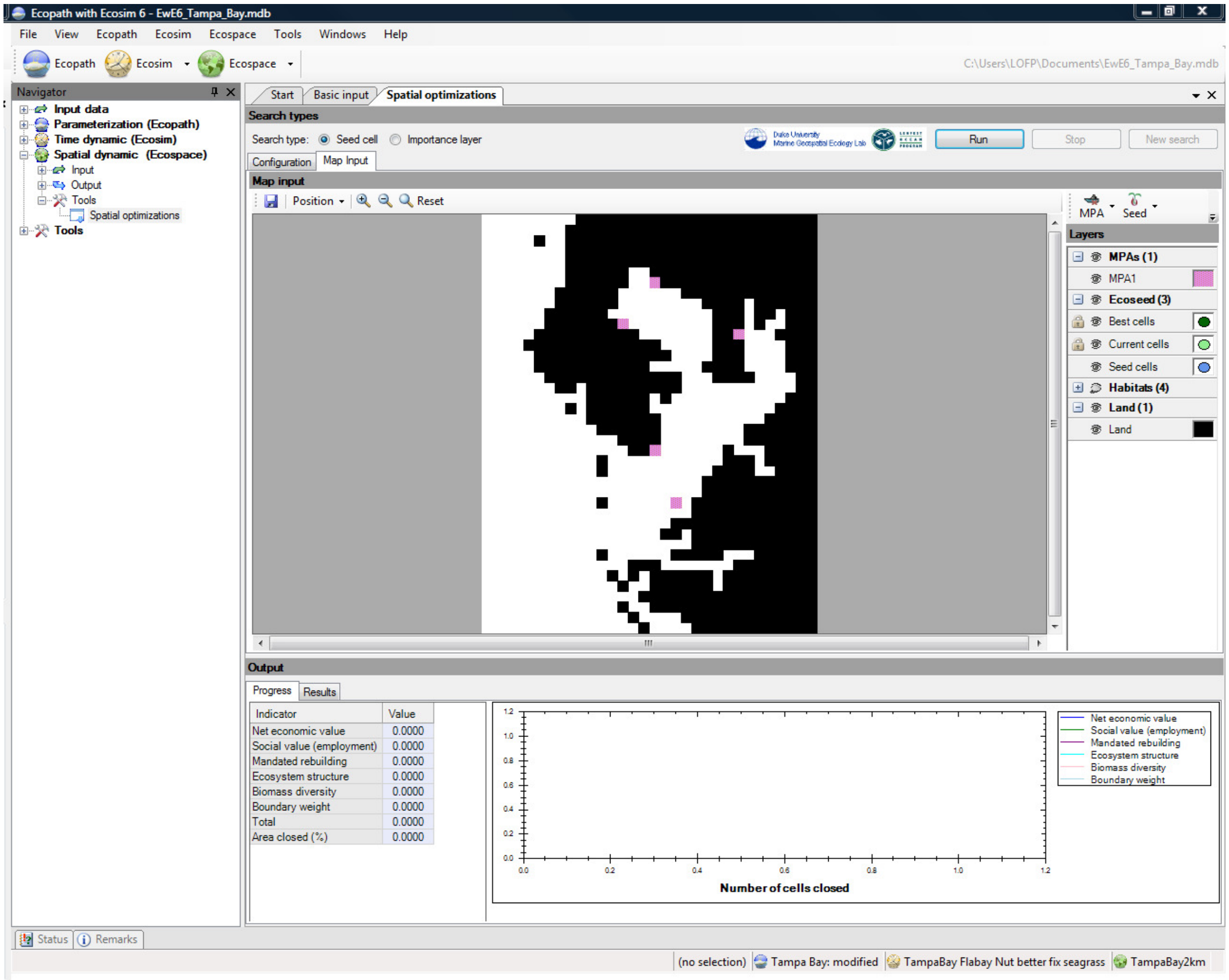
Map Input tab

The **Map Input** tab displays the Ecospace basemap associated with the Ecospace scenario that has been loaded. It displays progress of the search and the final results of the analysis.



Search type: ● Seed cell ○ Importance layer

Indicator	Value
Net economic value	0.0000
Social value (employment)	0.0000
Mandated rebuilding	0.0000
Ecosystem structure	0.0000
Biomass diversity	0.0000
Boundary weight	0.0000
Total	0.0000
Area closed (%)	0.0000

Figure 11.4 The Spatial optimizations form, **Map Input** tab.

Layers

The **Layers** panel is also found on the **Map Input** tab. Available options will change, depending on whether the **Seed cell** or **Importance layer** search is selected. Note that the Layers panel has a root directory format, which can be collapsed or expanded using the plus and minus icons. Use the eye symbols to show [👁] or hide [👁] layers on the **Map**.

Seed cell

When **Seed cell** has been selected on the **Configuration** tab, use the **Layers** panel (see image below) to set seed cells.

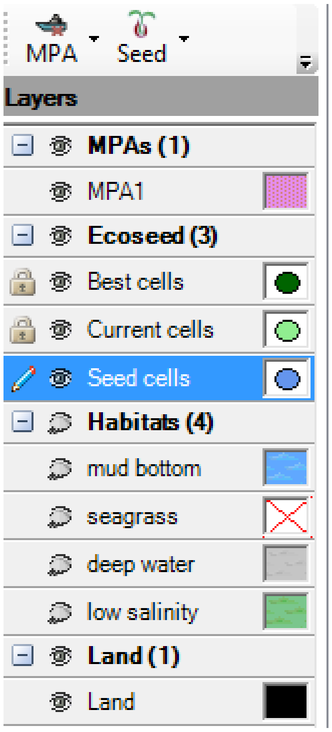
You cannot set **Best cells** or **Current cells**, as these are output results, but you can edit their appearance (i.e., colour) by clicking once on the symbol (coloured circles in the image below). This will open a dialogue box (the **Edit layer** dialogue box, see image below) where the colour of the symbol can be set.

You can also change the appearance of **Seed cells** in this way. Once you have set the appearance of seed cells, click **OK** to close the dialogue box.

Click to the left of the **Seed cells** eye symbol to pick up the pen tool [✏]. You can now click on the **Map** to select cell(s) to be used as seed cells. These will be indicated by a coloured circle (blue in this example). Note that you can use the **Seed** button at the top of the panel (see image below) to **Clear all** seed cells or **Set all** cells as seed cells.

Note also that if you now click on the **Seed cells** symbol (blue circle in the image below) the **Edit layer** dialogue box will now display the location of the seed cell(s) in the **Description and Appearance** tab. The **Data** tab of the **Edit layer** dialogue box displays the map as a spreadsheet of numbered cells corresponding to the cells on the map. Seed cells are indicated by 1 and all other cells are indicated by 0. Note that 1s and 0s relate only to the layer currently being edited. These data can be exported to a csv file using the **Export ...** button on the **Data** tab.

Habitats, **MPAs** and **Land** can also be modified using the Layers panel. Again, use the eye icon [👁] to show or hide layers. Use the pen tool [✏] to modify location of these layers on the **Map**. Note that you can use the **MPA** button at the top of the panel (see image below) to **Clear all** MPAs or **Set all** cells as MPAs.



The **Layers** panel on the **Map Input** tab (**Seed cell** configuration).

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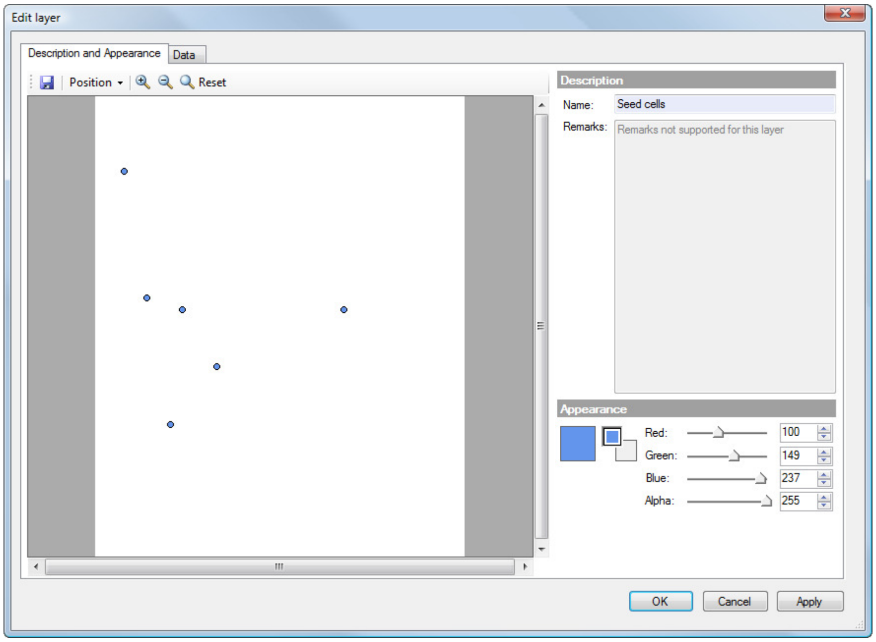


Name: Seed cells

Remarks: Remarks not supported for this layer

Red: 100

Green: 149

Blue: 237

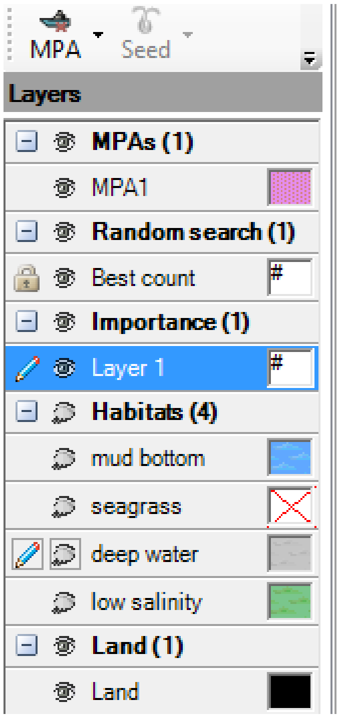
Alpha: 255

The **Edit layer** dialogue box.

Importance layer

When **Importance layer** has been selected on the **Configuration** tab, the **Layers** panel (see image below) is used to set **Importance layers** (users do not set seed cells). Note that importance layers are not used in calculation of the objective function, but rather are used to give greater importance to certain cells during random selection of seed cells. There are a number of ways to read in data for setting or importing importance layers. See Setting importance layers for full details on importing data importance layers. See Spatial optimization procedures for more on Importance layers.

After you have imported the importance layers, they will be displayed in the **Layers** panel.

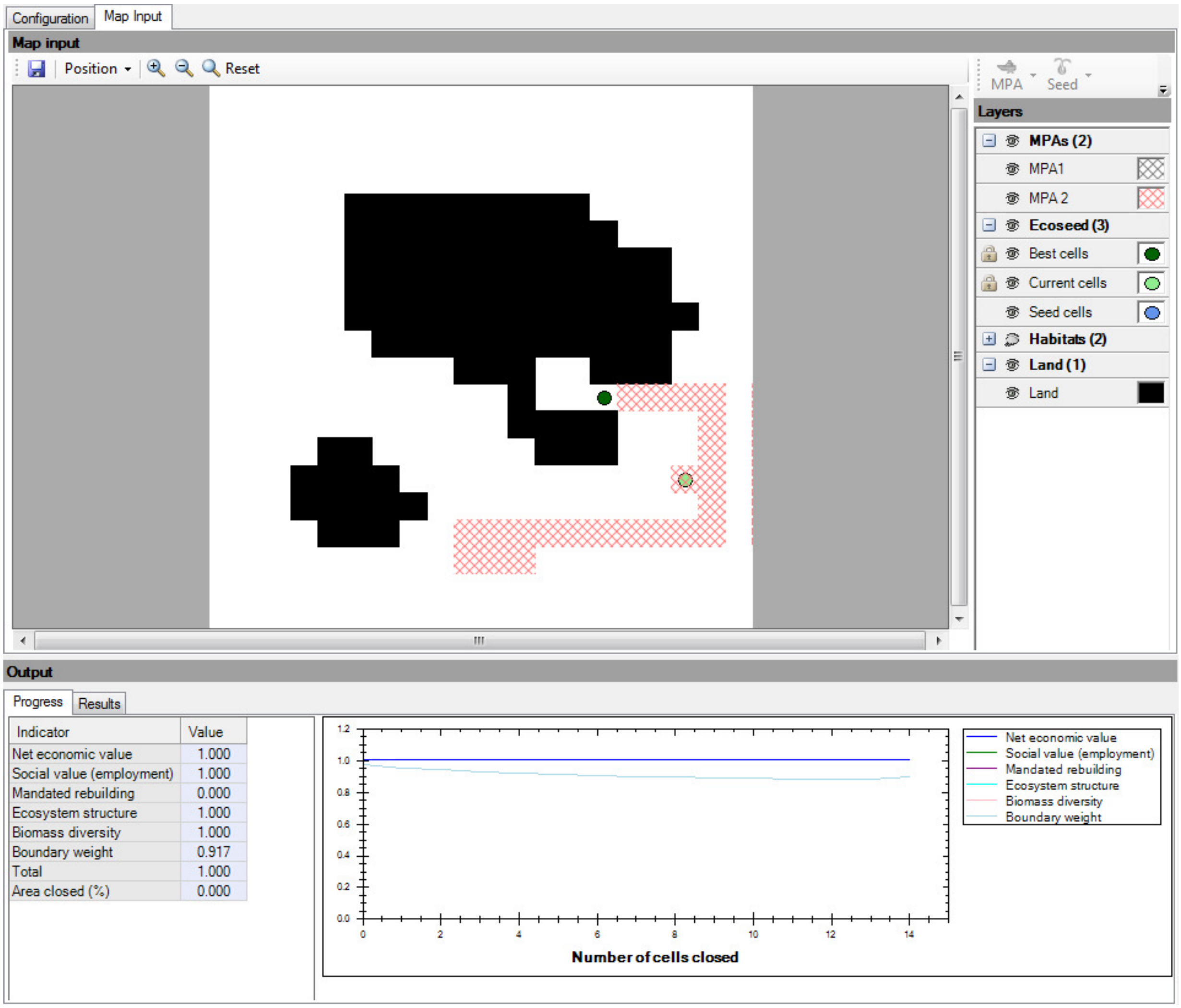


The **Layers** panel on the **Map Input** tab (**Importance layer** configuration).

Output

Progress tab

As the search algorithm proceeds, progress is displayed on the **Progress** tab of the **Output** window (image below). On the left of the Progress tab, relative values of the components of the objective function are displayed. On the right, relative values of the components of the objective function are shown as a function of number of cells closed.



Indicator	Value
Net economic value	1.000
Social value (employment)	1.000
Mandated rebuilding	0.000
Ecosystem structure	1.000
Biomass diversity	1.000
Boundary weight	0.917
Total	1.000
Area closed (%)	0.000

Results tab

When the algorithm has finished, results are shown on the **Results** tab. Results are displayed graphically, as on the progress tab, as relative values of the components of the objective function, and are displayed as a function of the number of cells closed. Results are also shown in tabular form at the right of the **Results** panel and as MPAs on the **Map Input** panel.

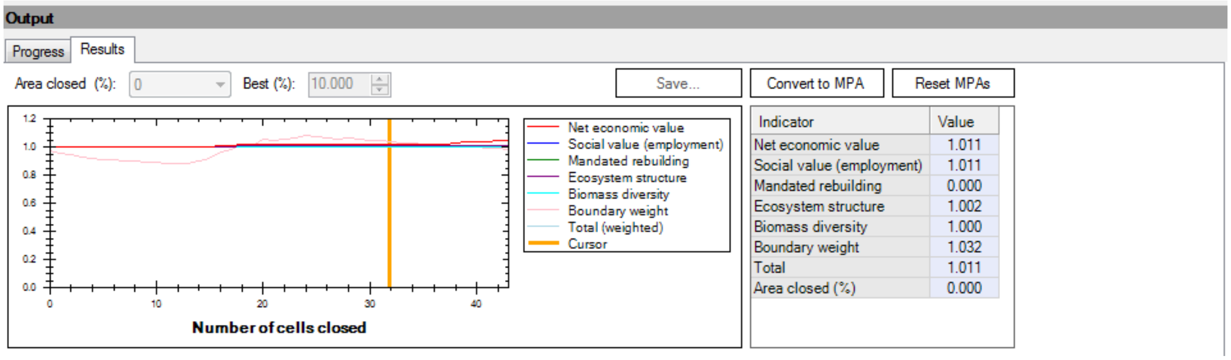
Results can be filtered in three ways.

1. You can mouse over the final results graph to display results at that location on the graph (vertical orange line below). Results at this location are displayed in tabular form on the right of the panel.

2. You can also use the **Area closed (%)** window, above the graph, to select results to display.

3.You can also use the **Best (%)** window on the **Results** tab to filter which results are displayed on the map (e.g., if 10% is selected, only results that produced the top 10% of objective function values will be displayed).

Final filtered results can be saved to csv file using the **Save...** button. The final filtered results can be converted to MPAs on the base map using the **Convert to MPA** button. This will result in MPAs being placed on the Basemap for the current Ecospace scenario. Original MPAs can be reset using the **Reset MPAs** button.



Area closed (%): 0

Best (%): 10.000

Indicator	Value
Net economic value	1.011
Social value (employment)	1.011
Mandated rebuilding	0.000
Ecosystem structure	1.002
Biomass diversity	1.000
Boundary weight	1.032
Total	1.011
Area closed (%)	0.000

11.5 Setting importance layers

Duke University
Marine Geospatial Ecology Lab

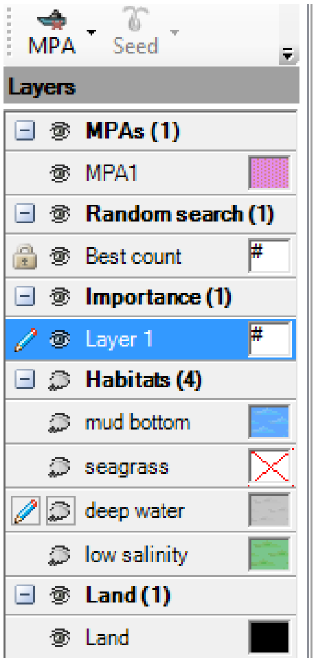
LENFEST
OCEAN
PROGRAM

When **Importance layer** has been selected on the Spatial optimizations form, the **Layers** panel on the **Map Input** tab is used to set **Importance layers**. Importance layers are used to give greater importance to certain cells during random selection of seed cells during the **Spatial optimization** procedure.

NOTE: Importances in importance layers have no effect on calculation of the objective function (see Spatial optimizations procedures). There are a number of ways to read in data for setting importance layers, listed here.

Reading in importance layers

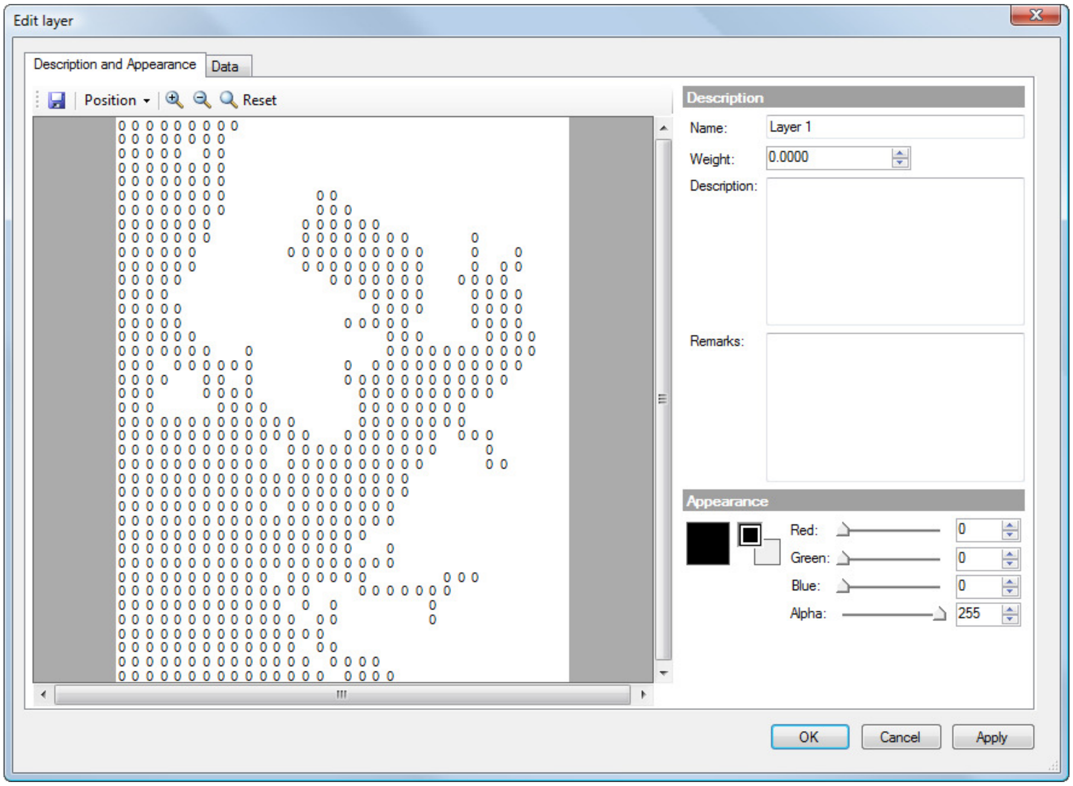
1. To read in importance layers, make sure you have first, loaded an Ecosim and Ecospace scenario, and opened the Spatial optimizations form. After setting input parameters and selecting **Search type: Importance layer** on the **Configuration** tab, go to the **Map Input** tab.



The **Layers** panel on the **Map Input** tab of the *Spatial optimizations* form (**Importance layer** configuration).

2. In the **Layers** panel, double click on the layer for which you want to import data (highlighted in the image above). This will open the **Edit layer** dialogue box. You can use this dialogue box to edit the description and appearance (i.e., display colour) of the importance layer.

IMPORTANT NOTE: You must also assign the layer a **Weight** on the **Description and Appearance** tab (see image below). Importances are normalised within each importance layer. Therefore the **Weight** assigns relative importance of layers relative to one another.



Name: Layer 1

Weight: 0.0000

Red: 0

Green: 0

Blue: 0

Alpha: 255

The **Edit layer** dialogue box (**Description and Appearance** tab), before data entry.

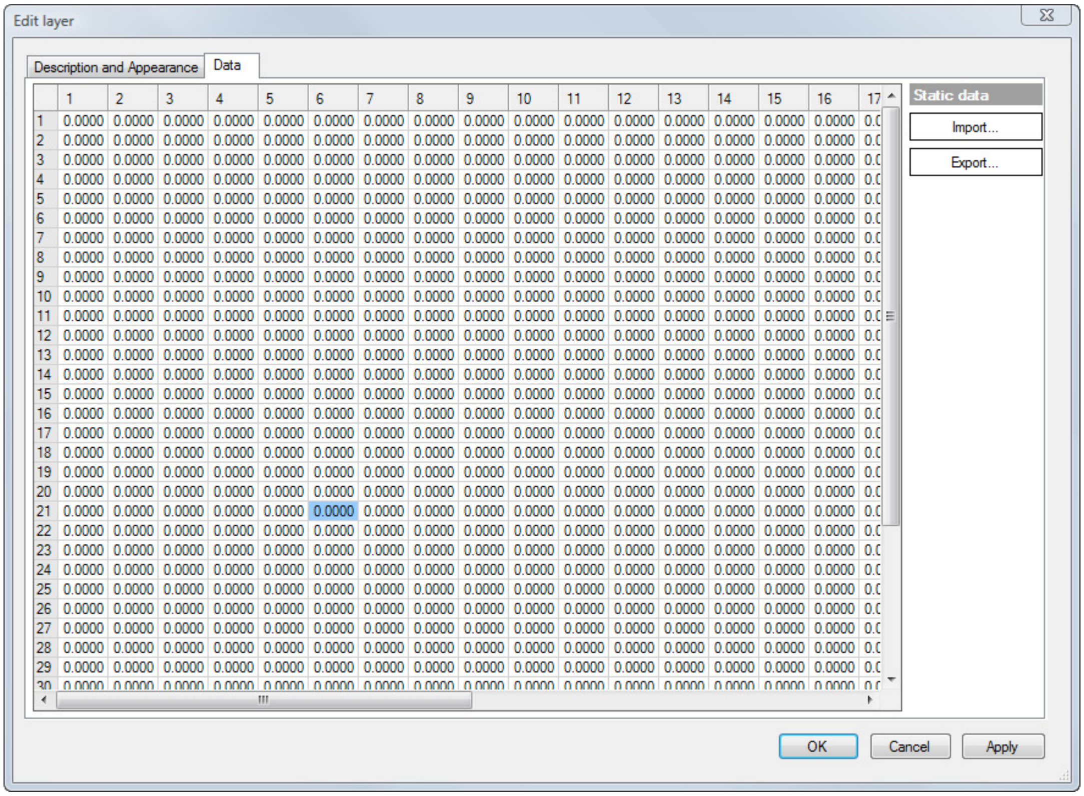
3. Next, click on the **Data** tab (image below). The tab contains a spreadsheet with exactly the same row and column configuration as the Ecospace Base map. Numbers entered into the cells on the **Data** tab represent relative importance weights for each cell within the layer. Note that the routine will normalise all values on the sheet, so only relative values are required (i.e., units are unimportant).

NOTE: There are two methods to enter data into the **Data** tab.

In the first method, copy and paste cells directly from a spreadsheet into the cells on the **Data** tab. Note that the data must be in exactly the same configuration as the cells in the base map. Assign greater importance to the cells of conservation interest (e.g., marine mammal breeding habitat; fish nursery areas; known habitat of rare species). Assign zero importance to cells of no conservation interest and land cells. After entering data this way, close the dialogue box and return to the Spatial optimizations form.

In the second method, Ecospace can read in raster files with spatial information such as importance layers or other Ecospace base map layers. It is possible to read from comma separated text files (.csv), ESRI ASCII files (.asc), and ESRI shape files (.shp).

To use this method, first click on the **Import ...** button on the **Data** tab. This will open the **Import layer data** dialogue box. Proceed to Step 4 below.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
2	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
3	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
4	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
5	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
6	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
7	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
8	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
9	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
10	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
11	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
12	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
13	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
14	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
15	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
16	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
17	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
18	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
19	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
20	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
21	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
22	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
23	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
24	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
25	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
26	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
27	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
28	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0
29	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0

The **Edit layer** dialogue box (**Data** tab), before data entry.

4. Click on the **Open** icon [] on the **Import layer data** dialogue box (image below) and navigate to the location of the data file.

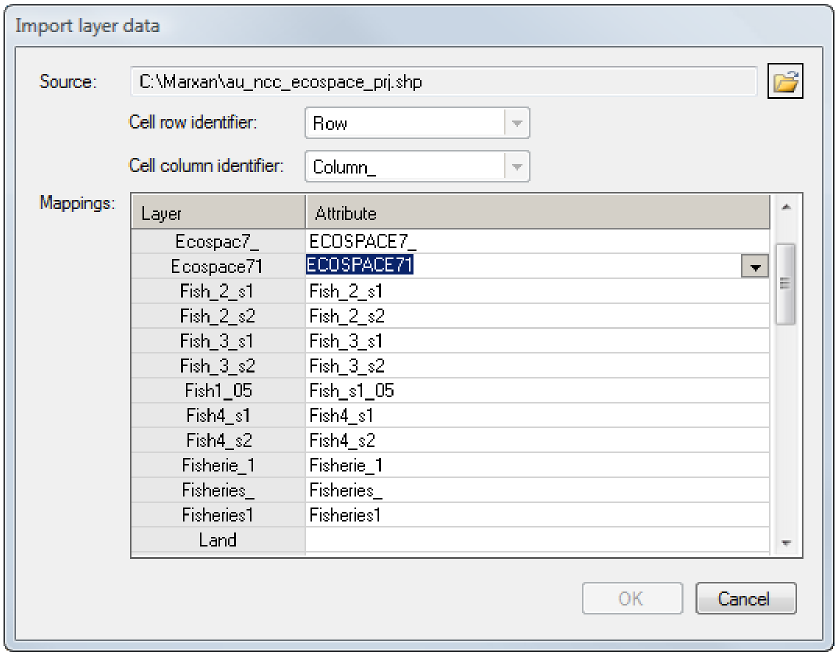
NOTE: at the bottom right of the **Open** dialogue box, there is a pull-down menu labelled **Comma separated text file** (see bottom image below). Use this pull-down menu to select the type of file (.csv, .asc, .shp) you will be importing. Click **Open** to open the file you wish to import.

<u>IMPORTANT: To correctly import shape files, files must have row and column attributes identified and must have the same dimensions as the base map</u>.

Use **Cell row identifier** and **Cell column identifier** to select the attributes of the rows and columns in the shape file. Note that shape files may have several layers (e.g., see image below). These will be displayed in the **Mappings** panel of the dialogue box.

Select **OK** to close the **Import layer data** dialogue box. Select **OK** again to close the **Edit layer** dialogue box. Imported layer(s) will now be visible on the **Layer** panel of the **Map Input** tab.

Click [here](#) to return to the *Spatial optimizations* documentation.



Source: C:\Marxan\au_ncc_ecospace_prj.shp

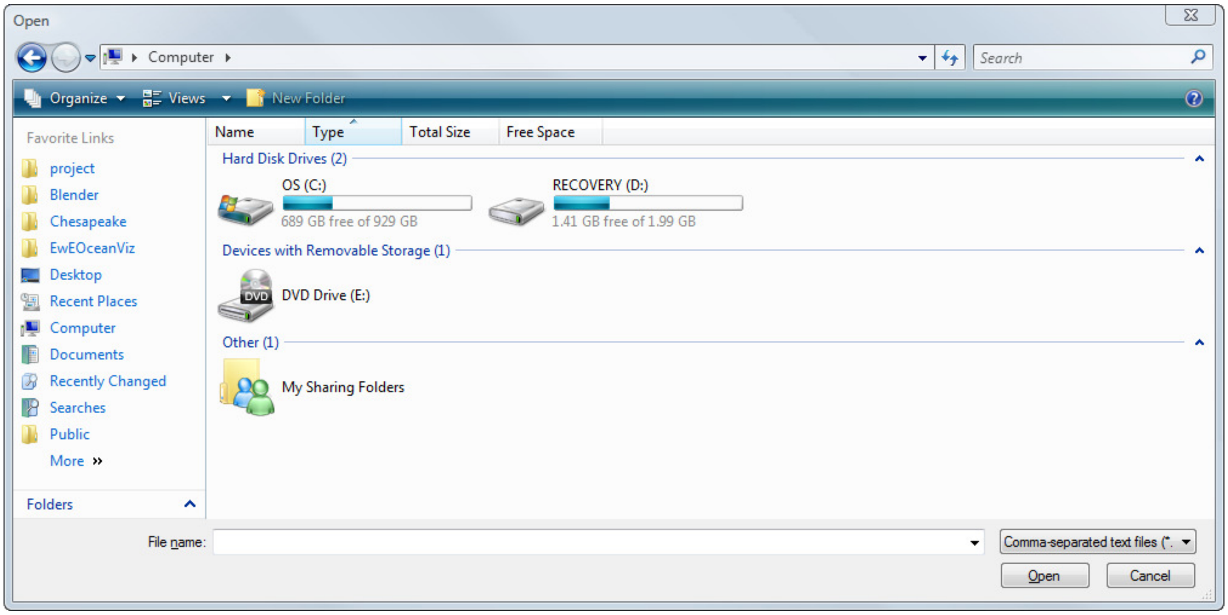
Cell row identifier: Row

Cell column identifier: Column_

Mappings:

Layer	Attribute
Ecospac7_	ECOSPACE7_
Ecospace71	ECOSPACE71
Fish_2_s1	Fish_2_s1
Fish_2_s2	Fish_2_s2
Fish_3_s1	Fish_3_s1
Fish_3_s2	Fish_3_s2
Fish1_05	Fish_s1_05
Fish4_s1	Fish4_s1
Fish4_s2	Fish4_s2
Fisherie_1	Fisherie_1
Fisheries_	Fisheries_
Fisheries1	Fisheries1
Land	

The **Import layer data** dialogue box.



File name:

Comma-separated text files (*.

The **Open** dialogue box. Note the **Comma separated text file** pull-down menu at the bottom right.

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12 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.

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.

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 modelling 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.

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 favour 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.

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.

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.

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,

Should Ecopath mass balance modelling 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 modelling 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 modelling 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.

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 modelled 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.

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 Figure 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 multi-stanza species Ecosim replaces the biomass dynamics model with a much more detailed and realistic population model, (see Representation of multi stanza life histories). 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 behaviour.

Do ecosystem biomass models ignore behavioural 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.

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) behavioural 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.

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.

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).

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.

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.

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 $q(B)\cdot$(relative effort), where $q(B)$ is a biomass-dependent catchability coefficient. Under the second option, q is modelled as a hyperbolic function of B ($q = qmax / (1 + kB)$), 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.

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.

13 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.

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.

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.

Underestimates of predation vulnerabilities

Predation impacts can be limited in Ecosim by assuming low values of the exchange parameters (v's) between behaviourally 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 vijBi 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. vij 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 behavioural 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 Figure 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.

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 behaviours 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 behavioural 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.

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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 favourable 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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