Ecopath with Ecosim: methods, capabilities and limitations[☆]

Villy Christensen[*], Carl J. Walters

Fisheries Centre, University of British Columbia, 2204 Main Mall, Vancouver, BC, Canada V6T 1Z4

Abstract

The Ecopath with Ecosim (EwE) modeling approach combines software for ecosystem trophic mass balance analysis (Ecopath), with a dynamic modeling capability (Ecosim) for exploring past and future impacts of fishing and environmental disturbances as well as for exploring optimal fishing policies. Ecosim models can be replicated over a spatial map grid (Ecospace) to allow exploration of policies such as marine protected areas, while accounting for spatial dispersal/advection effects.

The Ecopath approach and software has been under development for two decades, with Ecosim emerging in 1995, and Ecospace in 1998, leading to an integrated and widely applied package. We present an overview of the computational aspects of the Ecopath, Ecosim and Ecospace modules as they are implemented in the most recent software version. The paper summarizes the capabilities of the modeling system with respect to evaluating how fisheries and the environment impact ecosystems. We conclude by a warning about pitfalls in the use of the software for policy exploration.
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1. Introduction

The modeling approach 'Ecopath with Ecosim' (EwE, http://www.ecopath.org) is being widely used as a tool for analysis of exploited aquatic ecosystems, having reached 2400 registered users in 120 countries, and leading to in excess of 150 publications. EwE combines software for ecosystem trophic mass balance (biomass and flow) analysis (Ecopath) with a dynamic modeling capability (Ecosim) for exploring past and future impacts of fishing and environmental disturbances. It has an elaborate user interface that eases a variety of data management chores and calculations that are a cumbersome but necessary part of

any endeavor to systematically examine an ecosystem, its resources, and their interactions and exploitation.

Recent versions of the software have brought Ecosim much closer to traditional single-species stock assessment, by allowing age-structured representation of particular, important populations and by allowing users to 'fit' the model to data. Ecosim models can be replicated over a spatial map grid (Ecospace) to allow exploration of policies such as marine protected areas, while accounting for spatial dispersal/advection effects and migration.

The Ecopath approach was initiated by Polovina (1984) in the early 1980s, and has been under continuous development since 1990 (Christensen and Pauly, 1992), with Ecosim emerging in 1995 (Walters et al., 1997, 2000), and Ecospace in 1998 (Walters et al., 1999), leading to an integrated software package, 'Ecopath with Ecosim'. We give an overview of the computational aspects and capabilities of the Ecopath, Ecosim and Ecospace modules as they are

implemented in the most recent software version (EwE Version 5), along with some reflections of potential pitfalls related to application of the software.

2. Mass-balance modeling: Ecopath

The core routine of Ecopath is derived from the Ecopath program of Polovina (1984), and since modified to make superfluous its original assumption of steady state. Ecopath instead bases the parameterization on an assumption of mass balance over a given time period (usually 1 year, but see discussion below about seasonal modeling). In its present implementation Ecopath parameterizes models based on two master equations, one to describe the production term (Eq. (1)), and one for the energy balance for each group (Eq. (7)). A summary of symbols used for variables is presented in Table 2.

2.1. Prey mortality is predator consumption

The total production rate P_i for each group i can be split in components:

$$P_i = Y_i + M2_i \times B_i + E_i + \mathrm{BA}_i + M0_i \times B_i \qquad (1)$$

where Y_i is the total fishery catch rate of i, $M2_i$ is the instantaneous predation rate for group i, E_i the net migration rate (emigration − immigration), BA_i is the biomass accumulation rate for i, while $M0_i$ is the 'other mortality' rate for i. P_i is calculated as the product of B_i, the biomass of i and $(P/B)_i$, the production/biomass ratio for i. The $(P/B)_i$ 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 rate including all mortality not elsewhere included, and is internally computed from

$$M0_i = \frac{P_i \times (1 - \mathrm{EE}_i)}{B_i} \qquad (2)$$

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 as described, see Eq. (6).

The predation term, $M2$, in Eq. (1) serves to link predators and prey as

$$M2_i = \sum_{j=1}^{n} \frac{Q_j \times \mathrm{DC}_{ji}}{B_i} \qquad (3)$$

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

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

For parameterization Ecopath sets up a system with (at least in principle) as many linear equations as there are groups in a system, and it solves the set for *one* of the following parameters for each group, biomass, production/biomass ratio, consumption/biomass ratio, or ecotrophic efficiency. The other three parameters along with 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:

1. The gross food conversion efficiency, g_i, is estimated using

$$g_i = \frac{(P/B)_i}{(Q/B)_i} \qquad (4)$$

while $(P/B)_i$ and $(Q/B)_i$ are attempted solved by inverting the same equation.

2. The P/B ratio is then estimated (if possible) from

$$\frac{P_i}{B_i} = \frac{Y_i + E_i + \mathrm{BA}_i + \sum_j Q_j \times \mathrm{DC}_{ji}}{B_i \times \mathrm{EE}_i} \qquad (5)$$

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.

3. The EE is sought estimated from

$$EE_i = \frac{Y_i + E_i + BA_i + B_i \times M2_i}{P_i} \quad (6)$$

where the predation mortality $M2$ is estimated from Eq. (3).

4. 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 the EwE Help System, Appendix 4, Algorithm 3 (available at http://www.ecopath.org and distributed with EwE).

5. 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 the EwE Help System, Appendix 4, Algorithm 4.

6. 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.

7. 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 for which the 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 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. As a consequence, the estimated ecotrophic efficiency can be considered an expression of model uncertainty rather than an ecologically meaningful term.

In some, but very rare, cases it may not be possible to estimate the 'missing' parameters using the methods referred to above, for instance if a feeding cycle (e.g. A eats B eats C eats A), is included where the biomasses of all groups in the cycle are unknown. In such cases a routine will break the cycle by removing the link where the difference between the trophic level of the consumer and the prey has the lowest value, typically this will be where a low trophic-level consumer eats high trophic-level prey (which are actually lower trophic-level juveniles). An iterative routine will then estimate all 'missing' biomasses.

The mass balance constraint implemented in the two master equations of Ecopath (see Eqs. (1) and (7)) 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 the outcome will be.

2.2. The energy balance of a group

After the 'missing' parameters have been estimated so as to ensure mass balance between groups energy balance is ensured within each group using the following equation:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (7)$$

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 focused on measuring growth, where we focus on estimating losses, and that the Ecopath formulation does not explicitly include gonadal growth. The Ecopath equation treats this as included in the predation term (where nearly all gonadal products end up in any case). This may be a shortcoming, but it is one that can be remedied, and actually is in Ecosim as described below.

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. If a nutrient-based currency is used in Ecopath the respiration term is excluded from the above equation (as nutrients are not respired), and the unassimilated food term is estimated as the difference between consumption and production.

2.3. Addressing uncertainty

A resampling routine, Ecoranger, has been included in EwE to accept input probability distributions for the biomasses, consumption and production rates, ecotrophic efficiencies, catch rates, and diet compositions. Using a Monte Carlo approach a set of random input variables is drawn from user-selected frequency distributions and the resulting model is evaluated based on user-defined criteria, and physiological and mass balance constraints. The results include probability distributions for the estimated parameters along with distributions of parameters in the accepted model realizations.

The Ecoranger routine can provide probability distributions for transformation of the input variables. The derived probability distributions are likely to be narrower than the original distributions indicating that we have gained information in the process of checking for mass balance constraints, and eliminating parameter combinations that violate thermodynamic constraints. The information that is gained comes from evaluation of structural relationships as implemented in the Ecopath model, contrary to standard Bayesian approaches, which rely on data sampling. Combining such structural information from Ecopath with prior probabilities (the original probability distributions) corresponds to combining data with priors to derive the posterior distributions in the Bayesian sense. A procedure implementing such an approach using a 'sampling–importance–resampling' scheme

(McAllister et al., 1994) is included in the Ecoranger module of EwE making it straightforward to derive what may be called 'Bayes marginal posterior distributions' (Walters, 1996).

2.3.1. Categorizing data sources

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

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

The pedigree index values in Table 1 are also used to calculate an overall pedigree index for a given model.

Table 1
Options included in EwE for definition of 'pedigree' for consumer production/biomass and consumption/biomass ratios in Ecopath

Option	Index	CI (%)
Estimated by Ecopath (other model)	0.0	±80
Guesstimate	0.1	±70
From other model	0.2	±60
Empirical relationship	0.5	±50
Similar group/species, similar system	0.6	±40
Similar group/species, same system	0.7	±30
Same group/species, similar system	0.8	±20
Same group/species, same system	1.0	±10

Similar option tables are implemented for biomasses, catches, and diets. For each group in an ecosystem one of these options is used to define the pedigree of the input parameter. The index value is used for calculation of a pedigree index. The confidence intervals (CI) are used to describe parameter uncertainty in the balanced ecosystem model using the Ecoranger, auto mass balance, and Ecosim modules. Index values and confidence intervals are defaults that can be changed by users.

Table 2
List of symbols used

Symbol	Description	Unit
B	Biomass	$t\,km^{-2}$
BA_i	Biomass accumulation rate	$t\,km^{-2}$ per year
c	Per biomass food intake, same as Q/B	Per year
DC_{ji}	Fraction of predator j's diet contributed by prey i	
E	The net migration rate (emigration $-$ immigration), or $e_i \times B_i - I_i$	$t\,km^{-2}$ per year
e	Emigration rate per unit biomass	$t\,km^{-2}$ per year
EE	Ecotrophic efficiency	
F	Instantaneous fishing mortality rate	Per year
g	Gross food conversion efficiency, estimated as the P/Q ratio	
I	Immigration rate	$t\,km^{-2}$ per year
i	Index used for prey groups (all consumer groups can be prey as well as predators)	
j	Index used for predator groups	
K	von Bertalanffy curvature parameter	Per year
$M0$	Instantaneous 'other mortality' rate	Per year
$M2$	Instantaneous predation rate	Per year
n	Number of living groups in the model	
P	Total production rate	$t\,km^{-2}$ per year
P/B	Production/biomass ratio	Per year
Q	Total consumption rate, calculated as the product of B and Q/B	$t\,km^{-2}$ per year
Q/B	Consumption/biomass ratio	Per year
SS	Summed squared residuals	
v_{ij}	Vulnerabilities (rescaled to range $[1, \omega]$)	
Y	Total fishery catch rate	$t\,km^{-2}$ per year
Z	Total mortality rate, equivalent to the production/biomass ratio	Per year

Omits symbols that are used in only one section. Many symbols will have an index (or indices) referring to a group.

The index values for input data scale from 0 for data that is not rooted in local data up to a value of 1 for data that are fully rooted in local data. Based on the individual index value an overall 'pedigree index', τ, is calculated as the average of the individual pedigree value based on

$$\tau = \sum_{i=1}^{n} \frac{\tau_{i,p}}{n} \tag{8}$$

where $\tau_{i,p}$ is the pedigree index value for group i and input parameter p for each of the n living groups in the ecosystem; p can represent either B, P/B, Q/B, Y or the diet composition, DC. To scale based on the number of living groups in the system, an overall measure of fit, t^* is calculated (using an equation based on how the t-value for a regression is calculated) as

$$t^* = \tau \times \frac{\sqrt{n-2}}{\sqrt{1-\tau^2}} \tag{9}$$

This measure of fit is seen to describe how well rooted a given model is in local data. It addresses an often-aired concern of to which degree 'models feed on models', i.e. whether models are based on data from other models, which again are based on data from other models, etc. Work is presently in progress to describe the pedigree indices for all published Ecopath models where we have access to the model descriptions (in excess of 140 cases; Lyne Morisette, Fisheries Centre, UBC, personal communication).

2.4. Automated mass-balance

Getting hold of and entering input parameters for an Ecopath model is only the start of the modeling process, ensuring mass-balance is the next major step. Previously this had to be done by manually adjusting biomasses, mortality rates, diets, etc., searching for data inconsistencies and gradually obtaining a balanced model. An iterative method for obtaining mass-balance has, however, been added to EwE, offering a well defined, reproducible, approach, while also allowing exploration of alternative solutions based on parameter confidence intervals. Background,

implementation and computational aspects of the auto-mass balance routine are described by Kavanagh et al. (2004).

The auto-balancing routine uses the pedigree routine described above to obtain confidence intervals, which in turn constrains how far the routine can perturb parameters from their original values as part of the balancing. While seeking to obtain a balanced model (i.e. $EE_i \leq 1$ for all groups i) with minimal changes to input parameters, especially for well-known parameters (with narrow confidence intervals), which are allowed less adjustment than parameters with wide confidence intervals.

At each iteration step, the model is perturbed by adjusting the biomass and diet components affecting groups with $EE > 1$. Model perturbation may be performed in three different ways:

(1) Random lookup of parameters within confidence interval (no memory of current state) similar to the Ecoranger approach discussed above, except for changing only parameters affecting unbalanced groups;
(2) Random steps in the neighborhood of the current state;
(3) Gradient descent method using the first derivative of EE with respect to the parameter to be perturbed.

The approach allows for user-defined specification of the cost function as well as of the decision logic, which includes a simulated annealing method. Also, a Monte Carlo approach allows for quantification of sensitivity to starting conditions and perturbations.

2.5. Particle size distributions

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

The time spent in each of a user-defined number of weight class is calculated starting at time 0, using

$$t = \frac{\ln[1 - (W_t/W_\infty)^{-b}]}{-K} + t_0 \qquad (10)$$

where W_t is the lower limit of the weight interval, W_∞ is the asymptotic weight, b the exponent in the length-weight relationship, K the curvature parameter of the von Bertalanffy Growth Function (VBGF), and t_0 is the usually negative 'age' at which the weight is estimated to be zero in the VBGF. Once the time spent to reach each weight class limit is calculated, the time spent in each weight class is calculated by subtraction.

The survival is calculated as

$$N_t = N_{t-\Delta t} \times e^{-Z \times \Delta t} = N_{t-dt} \times e^{-Z \times \Delta t} \qquad (11)$$

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

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

$$B_t = N_t \times W_t \times \Delta t \qquad (12)$$

where B_t is the biomass contribution, Δt is the time the groups spends to grow through the given weight class (t), and the rest as explained above. B_t is scaled over all weight classes so as to sum up to the total biomass of the group. The system PSD is calculated, finally, by summing up over all groups within each weight class.

2.6. Ecosystem 'health'

The health status of a patient can often be captured with a single parameter, the temperature. Many have tried to find an index with similar ability to describe the health of an ecosystem to avoid the insurmountable task associated with bottom-up approach summing up the health of all ecosystem components, but a clear candidate has not appeared. The effort has led to development and description of a variety of system indicators, typically though with a given researcher exploring only one or a few of the potential indicators and on one or a few systems only.

We have sought to include a selection of ecosystem indicators in EwE using the criteria that the indicators can be estimated based on information included or potentially includable in EwE, typically based on quantified descriptions of food webs. In doing so we have facilitated straightforward calculation of the indices, opening for a comparison of their properties through application to a variety of the models described using Ecopath.

One area of research where we have used this approach relates to ecosystem maturity, a perceived

descriptor of ecosystem 'health'. Odum (1969, 1971) described how ecosystems in a non-deterministic way develop over time. We can assume an undisturbed ecosystem to be mature *sensu* Odum. Implications of this include that in a more mature system all niches should tend to be filled; that a larger part of the energy flows should be through detritus-based food webs; that primary production should be more efficiently utilized; that the total system biomass/energy throughput ratio should be higher, etc.

When ecosystems are disturbed, notably by fishing, we expect their maturity to decrease. This was indicated by the findings of Christensen (1995a), who used a series of indicators to rank a large number of ecosystem representations after maturity, and concluded that the ranking obtained was in agreement with the expected state of maturity. The study included several ecosystems for which the maturity state could be compared before and after a disturbance, and the findings were in all cases in agreement with disturbances leading to a reduction in maturity. Christensen and Pauly (1998) modeled the recent and the unfished state for two marine ecosystems, and for both systems concluded that the indices of ecosystem maturity for the fished and unfished states in all cases were in agreements with Odum's theory.

While these studies cannot be seen as providing definitive answers, they do indicate that it is feasible to use a composite of ecosystem indices to describe the state of a given system and how it may have changed over time. We intend to explore this further, and to include a number of additional measures of ecosystem 'health' in EwE.

The selection of ecosystem indicators referred to above is included in EwE as part of a series of network analyses. In overview form (see references below and the EwE Help system for more detailed descriptions) the following routines are among those included:

- *Cycling index*: fraction of an ecosystem's throughput that is recycled (Finn, 1976).
- *Predatory cycling index*: corresponds to the cycling index but computed with cycles involving detritus groups excluded.
- *Cycles and pathways*: a routine presents the numerous cycles and pathways that are defined by the food web representing an ecosystem based on an approach suggested by Ulanowicz (1986).

- *Connectance index*: defined for a given food web as the ratio of the number of actual links to the number of possible links. Feeding on detritus (by detritivores) is included in the count, but the opposite links (i.e. detritus 'feeding' on other groups) are disregarded.
- *System omnivory index*: defined as the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake. The logarithms are used as weighting factors because it can be expected that the intake rates are approximately log normally distributed. The system omnivory index is a measure of how the feeding interactions are distributed between trophic levels. An omnivory index is also calculated for each consumer group, and it here is a measure of the variance of the trophic level estimate for the group.
- *Trophic level decomposition*: aggregates the system into discrete trophic levels *sensu* Lindeman based on an approach suggested by Ulanowicz (1995). The routine reverses the routine for calculation of fractional trophic levels.
- *Trophic transfer efficiencies*: calculated for a given trophic level as the ratio between the sum of the exports plus the flow that is transferred from one trophic level to the next, and the throughput on the trophic level. The transfer efficiencies are used for construction of trophic pyramids, and others.
- *Primary production required (PPR)*: to estimate the PPR (Christensen and Pauly, 1993) to sustain the catches and the consumption by the trophic groups in an ecosystem the following procedure is used. All cycles are removed from the diet compositions, and all pathways in the flow network are identified using the method suggested by Ulanowicz (1995). For each pathway 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.
- *Mixed trophic impact (MTI)*: Leontief (1951) developed a method for input–output analysis to assess the direct and indirect interactions in the economy of the USA, using what has since been called the 'Leontief matrix'. A modified input–output analysis based on the procedure described by Ulanowicz and Puccia (1990) is implemented in EwE. The MTI

describes how any group (including fishing fleets) impacts all other groups in an ecosystem trophically. It includes both direct and indirect impact, i.e. both predatory and competitive interactions.

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

$$\text{MTI}_{ji} = \text{DC}_{ji} - \text{FC}_{ij} \tag{13}$$

where DC_{ji} is the diet composition term expressing how much i contributes to the diet of j, and FC_{ij} 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 each fishing fleet a 'diet composition' 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 matrix is inversed using a standard matrix inversion routine.

- *Ascendency*: EwE includes a number of indices related to the ascendency measure described in detail by Ulanowicz (1986). Ascendency is seen as a measure of ecosystem growth and development.

3. Time-dynamic simulation: Ecosim

The basics of Ecosim are described in detail by Walters et al. (1997, 2000), and will only be given a cursory treatment here, omitting details that have been previously published, focusing instead in describing more recent additions to the modeling approach. In overview, Ecosim consists of biomass dynamics expressed through a series of coupled differential equations. The equations are derived from the Ecopath master Eq. (1), and take the form

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i$$
$$- (M0_i + F_i + e_i) \times B_i \tag{14}$$

where $\mathrm{d}B_i/\mathrm{d}t$ represents the growth rate during the time interval $\mathrm{d}t$ of group i in terms of its biomass, B_i, g_i is the net growth efficiency, Eq. (4), $M0_i$ the non-predation ('other') natural mortality rate esti-
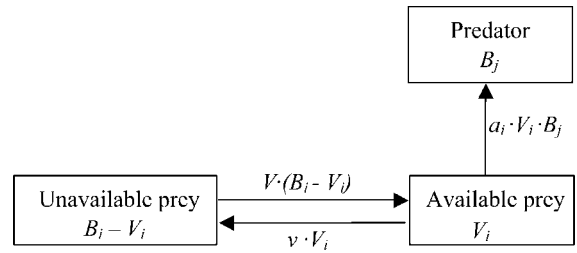

Fig. 1. Simulation of flow between available (V_i) and unavailable ($B_i - V_i$) prey biomass in Ecosim. a_i is the predator search rate for prey i, v is the exchange rate between the vulnerable and un-vulnerable state. Fast equilibrium between the two prey states implies $V_i = vB_i/(2v + aB_j)$. Based on Walters et al. (1997).

mated from the ecotrophic efficiency, F_i is fishing mortality rate, e_i is emigration rate, I_i is immigration rate (assumed constant over time, and hence independent of events in the ecosystem modeled), and $e_i \times B_i - I_i$ is the net migration rate of Eq. (1). The two summations estimates consumption rates, the first expressing the total consumption by group i, and the second the predation by all predators on the same group i. The consumption rates, Q_{ji}, are calculated based on the 'foraging arena' concept, where B_i's are divided into vulnerable and invulnerable components (Walters et al., 1997, Fig. 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 an Adams–Basforth integration routine (default) or a Runge–Kutta fourth-order routine.

Detritus flows are for each detritus group and for each time step estimated from the amount of detritus imported, transferred from other detritus groups, and produced by ecosystem groups (from unassimilated food plus contribution from dead organisms) less the amount of detritus eaten by living groups, transferred to other detritus groups and the export of detritus.

3.1. Predicting consumption

Ecosim bases the crucial assumption for prediction of consumption rates on a simple Lotka–Volterra or 'mass-action' assumption, modified to consider 'foraging arena' properties. Following this, prey can be in 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 (Fig. 1). In the original Ecosim formulations (Walters et al., 1997, 2000) the consumption rate for a given predator feeding on a prey was thus predicted from the effective search rate for predator–prey specific interactions, base vulnerabilities expressing the rate with which prey move between being vulnerable and not vulnerable, prey biomass, predator abundance (numbers for split pool groups as discussed later, and biomasses for other groups).

The model as implemented implies that 'top-down versus bottom-up' control is in fact a continuum, where low v's implies bottom-up and high v's top-down control. The input vulnerability rates (v_{ij}) in EwE are scaled to range from 0 to 1, with 0.3 serving as default for mixed control, and 0 implying bottom-up, 1 implying top-down control. The actual vulnerabilities (v_{ij}) used in the computations are rescaled from the entered v_{ij}'s as: $v_{ij} = \exp[2 \times (\exp(v_{ij}) - 1)]$.

As a consequence of user requests for adding new facilities the equation for describing consumption has gradually grown to the following, more elaborate expression:

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times B_j \times T_i \times T_j \times S_{ij} \times M_{ij}/D_j}{v_{ij} + v_{ij} \times T_i \times M_{ij} + a_{ij} \times M_{ij} \times B_j \times S_{ij} \times T_j/D_j} \quad (15)$$

where a_{ij} is the rate of effective search for i by j, T_i represents prey relative feeding time, T_j the predator relative feeding time, S_{ij} the user-defined seasonal or long term forcing effects, M_{ij} the mediation forcing effects, and D_j represents effects of handling time as a limit to consumption rate:

$$D_j = \frac{h_j \times T_j}{1 + \sum_k a_{kj} \times B_k \times T_k \times M_{kj}} \quad (16)$$

where h_j is the predator handling time. The feeding time factors, allocation of food for growth and recruitment, fecundity constraints, etc. are discussed by Walters et al. (1997, 2000). The consumption Eq. (15) above includes terms to describe forcing functions and mediation effects. These are described in more detail below.

3.1.1. Forcing functions

The impact of physical or other environmental factors on ecosystem groupings may be modeled using forcing functions are of two types:

- seasonal, which may be applied to biomass production or to egg production (for groups with ontogenetic representation) occurring within a year and repeated in all years of the run; and
- longer term, which may be applied to modify the Q/B ratio of the consumer groups, to represent, for instance, decadal regime shifts, and to force contaminant contributions (see Section 3.4) below.

3.1.2. Mediation

It is not uncommon for some third type of organism to affect the feeding rate of one type of organism on another. At least two types of effects are possible:

- *Facilitation*: The third organism type behaves in some way that makes prey more available to a predator when the third organism is more abundant. For example, pelagic piscivores like tuna may drive smaller fishes to the surface making them more accessible for birds. This is a concern for modeling marine mammals and bird dynamics, especially in areas where fishing has reduced abundances of tunas and billfishes.
- *Protection*: The third organism provides protection for a prey type when the third organism is more abundant. For example, juvenile fishes may use corals, macrophytes, and/or sponges for protection from predators, and fishing may directly impact these 'cover' types, making the juvenile fishes accessible for predation.

3.2. Life history handling

Ecosim offers to ways to handle life history dynamics, through splitting groups in adult and juvenile components, and through a recently added facility for modeling of multiple life stages.

3.2.1. Adult–juvenile split

To better represent ontogenetic shifts in Ecosim groups can be split in juvenile and adult components, Ecosim applies a Deriso–Schnute delay-difference model (Deriso, 1980; Schnute, 1987) to keep track of the number that recruits from juvenile to adult stages,

and the number at age/size in the adult groups. The implementation and computational aspects of this are described by Walters et al. (2000).

The delay-difference representation of population age and size structure permits explicit representation of changes in growth, mortality, and recruitment processes with changing feeding conditions. It also makes it straightforward to include: (1) changes in how food intake is allocated between growth and reproduction as food conditions varies; (2) changes in vulnerability to predation associated with changes in feeding behavior as prey densities vary; and (3) recruitment constraints related to juvenile size and fecundity. These aspects will be described further below.

3.2.2. Multiple stanza representations

EwE users can create a set of biomass groups representing life history stages or stanzas for species that have complex trophic ontogeny. Mortality rates and diet composition are assumed to be similar for individuals within each stanza. The procedure requires baseline estimates of total mortality rate, Z and diet composition for each stanza, but biomass, Q/B, and biomass accumulation, 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. 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 the length-cubed;
(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 $l_a / \sum l_a$, where the sum is over all ages, and l_a is the population growth rate-corrected survivorship:

$$l_a = \mathrm{e}^{-\sum_a Z_a - a \times \mathrm{BA}/B} \tag{17}$$

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. Further, the relative

biomass of animals in stanza s should be

$$b_s = \frac{\sum_{a=a_{s,\min}}^{a_{s,\max}} l_a \times w_a}{\sum_{a=1}^{a_{\max}} l_a \times w_a} \tag{18}$$

where $w_a = [1 - \exp(-K \times a)]^3$ is the von Bertalanffy prediction of relative body weight at age a, s, min and s, max are the youngest and oldest age for animals in stanza s, and $a_{\max}$ is the oldest age included overall. Knowing the biomass for one leading stanza, and the b_s for each stanza s, the biomasses for the other stanzas can be calculated by first calculating population biomass $B = B_{\text{leading } s}/b_{\text{leading } s}$, then setting $B_s = b_s \times B$ for the other stanzas. Q/B estimates for non-leading stanzas are calculated with a similar approach. This assumes that the 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 '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 done in monthly age steps, so as to allow finer resolution than 1 year in the stanza biomass and mortality structure (e.g. larval and juvenile stanzas that last only one or a few months).

The stanza age–size distribution information (l_a, w_a) is used to initialize a fully age–size 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 for in an 'accumulator' age group). The body growth $w_{a,t}$ calculations are parameterized so as to follow von Bertalanffy growth curves, with growth rates dependent on body size and (size- and time-varying) food consumption rates. Fecundity is assumed proportional to body weight above a weight at maturity, and size-numbers-dependent monthly egg production is used to predict changes in recruitment rates of age 0 fish. Compensatory juvenile mortality is represented through changes in Z for juvenile stanzas associated with changes in foraging time and predator abundances, as in split-group calculations.

In Ecospace (see below), it is not practical to dynamically update the full multi-stanza age structures for every spatial cell due to 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). 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, even though the 'dynamic' calculation in Ecospace is really just a stepwise movement toward predicted spatial equilibrium values for all variables.

3.3. Nutrient recycling and limitation

Ecosim uses a simple strategy to represent nutrient cycling and potential nutrient limitation of primary production rates. It is assumed that the system at any instant in time has a total nutrient concentration, NT, 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:

$$NT = \sum_i \eta_i \times B_i + N_f \tag{19}$$

where η_i is (fixed) nutrient content per unit of pool i biomass, and N_f is free nutrient concentration. Then assuming that NT varies as

$$\frac{dNT}{dt} = I - v \times NT \tag{20}$$

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, NT is approximated in Ecosim by the (possibly moving) equilibrium value $NT = I/v$. Changes in nutrient loading can be simulated by assigning a time forcing function number to NT, in which case NT is calculated as $NT = f_t \times NT_0$, where NT_0

is the Ecopath base estimate of NT, and f_t is a time multiplier ($f_t = 1$ implies Ecopath base value of NT). 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 NT_0 of total nutrient is entered by specifying the base free nutrient proportion $p_f = N_f/NT_0$ on entry to Ecosim, from which we can calculate NT_0 as simply

$$NT_0 = \frac{\sum_i \eta_i \times B_i}{1 - p_f} \tag{21}$$

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

$$\left(\frac{P}{B}\right)_j = \frac{(P/B)_{\max, j} \times N_f}{K_j + N_f} \tag{22}$$

3.4. Predicting movement and accumulation of tracers in food webs

Ecosim flow rates along with auxiliary information about factors such as isotope decay rate and physical exchange rates can be used to predict changes in concentrations of chemicals (e.g. organic contaminants and isotope tracers) that passively follow the biomass flows. The dynamic equations for such passive flow differ from biomass flow rate equations, and are generally linear dynamical equations with time-varying rate coefficients that depend on the biomass flow rates.

A routine, Ecotracer, has been implemented to model such movement and accumulation of contaminants and tracers in food webs allowing simulation of one tracer or contaminant type while the biomass dynamics equations in Ecosim are being solved in parallel. Tracer molecules are assumed to be either in the 'environment' (typically the water), or in the biota at any moment. Molecules are assumed to flow between pools at instantaneous rates equal to the probabilities of being 'sampled' as part of the biomass flow. The routine also allows for direct flows from the environment into pools, representing direct uptake or absorption of the tracer material, and for differential decomposition/decay/export rates by pool and from the environmental pool. Schematically, the flow of tracer molecules through any biomass pool
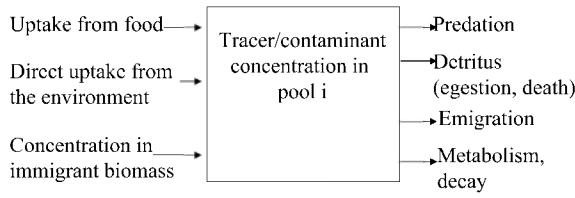
Fig. 2. Representation of the flow of tracer molecules through a biomass pool.

is represented by the components shown below (see also Fig. 2).

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

(1) *Uptake from food*: $C_j \times GC_i \times Q_{ji}/B_j$, where C_j: concentration in food j; GC_i: proportion of food assimilated by type i organisms; Q_{ji}: biomass flow rate from j to i, B_j: biomass of food j;

(2) *Direct uptake from environment*: $u_i \times B_i \times C_0$, where u_i: parameter representing uptake per biomass per unit time and per unit environmental concentration; B_i: biomass in pool i; C_0: environmental concentration;

(3) *Concentration in immigrating organisms*: $c_i \times I_i$, where c_i: a parameter giving tracer per unit biomass in immigrating biomass; I_i: biomass of pool i immigrants per time;

(4) *Predation*: $C_i \times Q_{ij}/B_i$;

(5) *Detritus*: $C_i \times M0_i + (1 - GC_i) \times \sum_j C_j \times Q_{ji}/B_j$, where $M0_i$: non-predation mortality rate of type i (per year);

(6) *Emigration*: $e_i \times C_i$, where e_i: emigration rate (per year);

(7) *Metabolism*: $d_i \times C_i$, where d_i is the summed metabolism and decay rate for the material while in pool i.

3.5. Fleet and effort dynamics

Ecosim users can specify temporal changes in fishing fleet sizes and fishing effort in three ways: (1) by sketching temporal patterns of effort in the model run interface; (2) by entering annual patterns via reference 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).

When the fleet/effort response option is invoked, Ecosim replaces all previously entered time patterns for fishing efforts and fishing rates with simulated values generated as each simulation proceeds. The fleet/effort dynamics simulation model uses 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/deprecation 'population dynamics' for capital capacity to fish (fleet size, vessel characteristics). These response scales are represented by two 'state variables' for each gear type g: $E_{g,t}$ is the current amount of active, searching gear (scaled to 1.0 at the Ecopath base fishing mortality rates), and $K_{g,t}$ is the fleet effort capacity ($E_{g,t} < K_{g,t}$). At each time step, a mean income per effort index $I_{g,t}$ is calculated as $I_{g,t} = \sum_i q_{g,i} \times B_i \times P_{g,i}$, where i is the ecological species or biomass group, $q_{g,i}$ is the catchability coefficient (possibly dependent on B_i) for species i by gear g, and $P_{g,i}$ is the market price obtained per biomass of i by gear g fishers. Also, mean fleet profit rates $PR_{g,t}$ for fishing are calculated, equal to $(I_{g,t} - c_g) \times E_{g,t}$, where c_g is the cost of a unit of fishing effort for gear g. 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:

$$E_{g,t+1} = \frac{K_{g,t} \times I_{g,t}^p}{I_{hg}^p + I_{g,t}^p} \qquad (23)$$

Here, I_{hg} and p are fleet-specific response parameters, where the income level needed for half of the maximum effort is I_{hg} and p represents a 'heterogeneity' parameter for fishers: high p values imply all fishers 'see' income opportunity similarly, while low p values imply fishers initiate their effort over a wide range of mean incomes, as shown in Fig. 3.

3.6. 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 a variety of specific hypotheses about compensatory
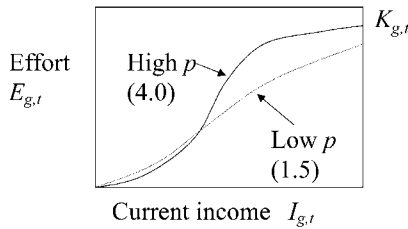
Fig. 3. Effort response relationship describing the statistical behavior of a fleet of fishers that have heterogeneous fishing abilities and perceptions of the current income level needed to attract their participation. The slope of the plot represents the amount of additional fishing effort expected for each increment in mean income; it is steepest at the mean income level where the majority of fishers see the possibility of just breaking even by going out.

mechanisms, and these mechanisms broadly fall in two categories:

- *direct*—changes caused over short time scales (of the order of 1 year) by changes in behavior 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. Here we describe how to generate alternative models or hypotheses about direct compensatory responses; these hypotheses fall in three obvious categories: recruitment, growth, and natural mortality.

3.6.1. Compensatory recruitment (models with split pools/multiple stanza only)

Compensatory recruitment effects are usually expressed as a flat or dome-shaped relationship between numbers of juveniles recruiting to the adult pool versus parental abundance (stock-recruit relation). There are two main ways to create such effects in Ecosim:

(a) non-zero feeding time adjustment for the juvenile pool combined with fixed time in juvenile stage and high EE, or high proportion of the 'other' mortality (the mortality not accounted for) being sensitive to changes in predator feeding time;
(b) zero feeding time adjustment combined with variable time in juvenile stage.

Mechanism (a) represents density-dependent changes in juvenile mortality rate associated with changes in feeding time and predation risk, while (b) represents density-dependent changes in juvenile growth rate and hence total time spent exposed to high predation rates over the juvenile life stage. Other, generally weaker compensatory responses can also be caused by changes in adult energy allocation to reproduction. For mechanisms (a) and (b), it is usually also important that the vulnerabilities of prey to the juvenile group also be relatively low.

3.6.2. Compensatory growth

Compensatory growth rate responses are modeled by setting the feeding time adjustment rate to zero, so that simulated Q/B is allowed to vary with a group's biomass (non-zero 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 (for groups where ontogenetic changes are modeled) or growth. The Q/B increase with decreasing pool biomass is enhanced by lowering vulnerability of prey to the pool. 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.

3.6.3. Compensatory natural mortality

Compensatory changes in natural mortality rate (M) can be simulated by combining two effects: non-zero feeding time adjustment, and either high EE from Ecopath or high proportion of 'other' mortality being sensitive to changes in predator feeding time. 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.

3.6.4. Compensation in recruitment

The 'split pool' representation of juvenile and adult biomasses was originally included in Ecosim to allow representation of trophic ontogeny (differential diets for juveniles and adults). To implement this representation it was necessary to include population numbers and age structure, at least for juveniles, so as to prevent

'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 structure dynamics, we in effect created a requirement for model users to think carefully about the dynamics of compensatory processes that have traditionally been studied in terms of the 'stock-recruitment' concept and relationships. To credibly describe the dynamics of split-pool populations, Ecosim parameters for split pools usually need to be set so as to produce an 'emergent' stock-recruitment relationship that is at least qualitatively similar to the many, many relationships for which we now have empirical data (see data summary in http://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).

Ecosim can generate direct (as opposed to just predator–prey) compensatory changes in juvenile recruitment via at least three alternative mechanisms or hypotheses:

1. simple density-dependence in juvenile production rate by adults, due to changes in adult feeding rates and fecundity (not a likely mechanism);
2. changes in duration of the juvenile stage and hence in total time exposed to relatively high predation risk;
3. changes in juvenile foraging time (and hence exposure to predation risk) with changes in juvenile feeding rates.

For all of these mechanisms, compensatory effects are increased (recruitment relationship flat over a wider range of adult stock size, steeper slope of recruitment curve near the origin) by

1. limiting availability of prey to juveniles by forcing juveniles to use small 'foraging arenas' for feeding;
2. make effective time exposed to predation while feeding drop directly with decreasing juvenile abundance (simulates possibility that when juveniles are less abundant, remaining ones may be able to forage 'safely' only in refuge sites without exposing themselves to predation risk). This option should be used only if field natural history observation indicates that the juveniles do in fact restrict their distribution to safe habitats when at very low abundance.

3.7. Parameter sensitivity

Ecosim does not include complete formal sensitivity analyses to test the effect of all input parameters. There are, however, a number of routines that can be used to examine various aspects of the model sensitivity, and we expect that additional routines will be added.

Ecosim runs can be repeated as Monte Carlo simulations with initial Ecopath biomass estimates chosen from normal distributions centered on the initial input estimates (with confidence intervals that can be based on the model pedigree, as discussed above). Each Monte Carlo simulation trial begins by selecting at least one random biomass combination and re-balancing the Ecopath model; the random selection is repeated until a balanced model is found—a process is similar to the Ecoranger method for analysis of uncertainty for Ecopath parameters described above. Then the resulting balanced Ecopath model is used to initialize an Ecosim run.

The results can be shown as simple 'bands of uncertainty' giving indications for how sensitive Ecosim results are to input parameter quality. Strong divergence in biomass time patterns among simulation trials under this option is usually associated with changes in fishing mortality rate estimates.

If time series data have been included in the analysis (see below) it is possible to retain the best fitting estimates, i.e. the parameters which minimize the sums of squared residuals (SS) between model and observations. This approach (technically known as a 'Matyas search' technique) is useful in parameter estimation and optimization problems where the parameters being varied can result in non-feasible solutions (constraint violations) but where the feasible parameter values are not readily predicted from constraint equations. Non-feasible solutions commonly arise when Ecopath biomasses are changed so as to violate mass balance (e.g. to values that would imply $EE > 1.0$). In fact, we cannot use other nonlinear estimation procedures to search for better initial (Ecopath) biomass estimates as

we do for some Ecosim parameters, since these procedures generally rely upon there being smooth change in the SS criterion with changes in the parameters. Such procedures use the gradient in SS to decide steps in the parameter estimates, and good steps cannot be efficiently estimated when any step can unpredictably result in violation of mass balance constraints.

While there has been no comprehensive study published of Ecosim parameter sensitivity, our preliminary experience indicates that simulations are very sensitive to the 'behavioral exchange rate', or 'vulnerability'. This parameter expresses the exchange rate between the prey being in vulnerable and non-vulnerable states (Fig. 1). It is generated by a multitude of processes, e.g. physical mixing, movement of organisms between resting/hiding and active feeding states, dispersal (vulnerability to predators while moving), growth into and out of vulnerable size range, and behavioral reactions to growth in body parasite loads.

The vulnerability parameter is not subject to direct measurement. There are, however, other ways of estimating it:

1. Sensitivity analysis (see the section below);
2. Fitting to time series data (see the section below);
3. Two model comparisons, 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;
4. Estimate biomass depletion relative to the Ecopath base biomasses ($B_{unfished}/B_0$);
5. Estimate maximum fishing mortality relate to natural mortality (F_{max}/M).

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

Ecosim simulations are very sensitive to variations in primary productivity, see, e.g. Martell et al. (2002), therefore a variety of tools have been added for comparing simulations with series data as described in more detail below.

3.8. Fitting Ecosim to time series data

Based on time series 'reference' biomass data, and on total mortality of various pools over a particular historical period, along with estimates of changes in fishing impacts over that period Ecosim estimates a statistical measure of goodness-of-fit to these data 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 (y) by the maximum likelihood estimate of the relative abundance scaling factor (q) in the equation $y = q \times B$, where B is the absolute abundance. The reference data series can be assigned a relative weight expressing how variable or reliable that type of data is compared to the other reference time series. Based on the time series three types of analyses with the SS measure are available:

1. determine sensitivity of SS to the critical Ecosim vulnerability parameters by changing each one slightly then re-running the model to see how much SS is changed;
2. search for vulnerability estimates that give better 'fits' of Ecosim to the time series data;
3. search for time series values of forcing functions, e.g. annual relative primary productivity that may represent historical productivity 'regime shifts' impacting biomasses throughout the ecosystem.

The searches include a SS minimization procedure based on a Marquardt nonlinear search algorithm with trust region modification of the Marquardt steps (see, e.g. More, 1977). For users familiar with the nonlinear estimation procedures used in single-species stock assessment, e.g. for fitting production models to time series CPUE data, the procedure implemented in Ecosim should be quite familiar. In essence, the Ecosim search procedure for vulnerabilities is 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 productivity 'anomalies' corresponds to searching also for 'nuisance parameter' estimates of what is usually called the 'process errors' in single-species assessment (Hilborn and Walters, 1992).

3.9. In search of an optimum fishing policy

Fisheries management aims to regulate fishing mortality rates over time so as to achieve defined

sustainability objectives, and modeling serves a role for providing insight about how high these mortality rates should be, and how they should be varied over time. The impacts of alternative exploitation patterns can be explored using two different approaches in Ecosim, either by sketching fishing mortalities over time and evaluate the results, or by a formal optimization routine to evaluate the fishing effort over time that would maximize particular performance measures or 'objective functions' for management.

The objective function is defined (by the user) as a combination of net economic value, employment, mandated rebuilding of target species, and ecological 'stability' criteria, see Walters et al. (2002) for details.

Ecosim uses the Davidson–Fletcher–Powell (DFP; Fletcher, 1987) nonlinear optimization procedure to iteratively improve an objective function by changing relative fishing rates, where each year/fleet block defines one parameter to be varied by the procedure. 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.

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. 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 directional guidance for where the system can/should be heading. 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).

3.9.1. 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

$$w_1 \times \log(\text{NPV}) + w_2 \times S \times \log(B) - w_3 \times V \quad (24)$$

where the w_i's are utility weights, and the utility components NPV, $S \times \log(B)$, and V are defined as follows:

(1) NPV is net present economic value of harvests, calculated as discounted sum of catches over all fleets and time multiplied with prices minus costs of fishing, i.e. the discounted total profit from fishing the ecosystem;

(2) $S \times \log(B)$ 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-group 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 $\log(\text{NPV}) + S \times \log(B)$. 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 subtracted, implying that increased uncertainty about the predictions for more severe disturbances causes a decrease in the mean of $\log(\text{NPV})$. The 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 1/2 the variance of the variable. Large w_3-values 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

it is 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 w_i); the overall utility measure approaches minus infinity if either net economic performance (NPV) or if any biomass component of the ecosystem (any biomass B_i in $S \times \log(B)$) 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 result in more extreme departures from the Ecopath base state.

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 $NPV + S \times B$. 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.

3.10. Closed-loop simulations

In order to model not only ecological dynamics over time, but also the dynamics of the stock assessment and regulatory process, a 'closed-loop' simulation routine has been added to Ecosim (see Walters et al., 2002, for more details). This routine includes 'submodels' for the dynamics of assessment (data gathering, random and systematic errors in biomass and fishing rate estimates), and for the implementation of assessment results through limitation of annual fishing efforts. The closed-loop policy simulation model, allows specification of:

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

Closed-loop policy simulations could obviously include a wide range of complications related to the details of annual stock assessment procedures, survey designs, and methods for direct F estimation. We as-

sume that users will use other assessment modeling tools to examine these details, and so need only enter overall performance information (coefficients of variation in estimates) into the ecosystem-scale analysis.

4. Spatial simulation: Ecospace

Ecospace is a dynamic, spatial version of Ecopath, incorporating all key elements of Ecosim and is described in detail by Walters et al. (1999). It works by dynamically allocating biomass across a user-defined grid map while accounting for:

1. symmetrical movements from a cell to its four adjacent cells modified by whether a cell is defined as 'preferred habitat' or not;
2. user-defined increased predation risk and reduced feeding rate in non-preferred habitat; and
3. a level of fishing effort that is proportional, in each cell, to the overall profitability of fishing in that cell, and whose distribution is sensitive to spatial fishing costs.

4.1. Prediction of mixing rates

The instantaneous emigration rates from a given cell in Ecospace are assumed to vary based on the pool type, the groups preference for the habitat type represented by the cell, and a 'risk ratio' representing how the organisms in the cell respond to predation risk. Base dispersal rates are calculated based on this, but weighted based on a habitat gradient function increasing the probability of organisms moving towards favorable habitats. The mechanisms involved in this procedure are explained in more detail by Walters et al. (1999).

4.2. Predicting spatial fishing patterns

EwE works with multiple fishing fleets, with fishing mortality rates (F) initially distributed between fleets based on the distribution of catch rates 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.

4.3. 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 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. (14), 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. 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 such expressions 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 if the time splitting was not included.

4.4. Advection in Ecospace

Advection processes are critical for productivity in most ocean areas. Currents deliver planktonic production to reef areas at much higher rates than would be predicted from simple turbulent mixing processes. Upwelling associated with movement of water away from coastlines delivers nutrients to surface waters, but the movement of nutrient rich water away from upwelling locations means that production and biomass may be highest well away from the actual upwelling locations. Convergence (down-welling) zones represent places where planktonic production from surrounding areas is concentrated, creating special opportunities for production of higher trophic levels.

Ecospace provides a user interface for sketching general current patterns or wind/geostrophic forcing patterns for surface currents. Based on these patterns Ecospace calculates equilibrium horizontal flow and upwelling/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 $df/dt = 0$, $dv_u/dt = 0$, $dv_v/dt = 0$ across the faces of each Ecospace grid (u, v) cell, where f is sea surface anomaly, the v's are horizontal and velocity components (u, v directions) and the rate equations at each cell face satisfy (omitting grid size scaling factors for clarity):

$$\frac{dh}{dt} = \frac{v_{uh}}{u} + \frac{v_{vh}}{v} - D_h \qquad (25)$$

$$\frac{dv_u}{dt} = k \times W_u - k \times v_u - f \times v_v - \frac{g \times h}{u} \qquad (26)$$

$$\frac{dv_v}{dt} = k \times W_v - k \times v_v - f \times v_u - \frac{g \times h}{v} \qquad (27)$$

Here, the W's represent the user sketched forcing or general circulation field, h the sea surface anomaly, k the bottom friction force, f the Coriolis force, D represents downwelling/upwelling rate, and g acceleration due to sea surface slope.

Solving these equations for equilibrium is not meant to be a replacement for more elaborate advection models; generally the W_u and W_v need to be provided either by such models or by direct analysis of surface current data, so the Ecospace solution scheme is only used to assure mass balance and correct for 'local' features caused by bottom topography and Coriolis forces. That is, absent shoreline, bottom, and sea surface anomaly (h) effects, the equilibrium velocities are just $v_u = W_u$, $v_v = W_v$ up to corrections for Coriolis force. Solving the equations using general forcing sketches of W patterns allows internal correction for factors such as topographic steering of currents near shorelines, without requiring entered W fields that precisely maintain mass balance (and/or correct upwelling/downwelling velocities) absent any correction scheme.

Once an advection pattern has been defined, a 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.

4.5. Seasonal migration

Larger organisms commonly have seasonal migration patterns that allow them to utilize favorable seasonal resource and environmental conditions over large spatial areas. Such movements can be represented in Ecospace through a 'Eulerian' approach involving explicitly modeling changes in instantaneous rates of biomass flow among the Ecospace spatial cells, in some way that approximates at least the changing center of distribution of the migratory species. The approach is implemented by defining a monthly sequence of 'preferred' map cell positions, and how spread out the migrating fish are likely to be around these preferred cells by specifying north–south and east–west 'concentration parameters'.

The mathematical method used in Ecospace to create migratory behavior is quite simple. Spatial movement is represented in general in Ecospace as a set of instantaneous exchange rates across the boundaries

of adjacent spatial cells. For migratory species, these exchange rates are 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 Fig. 4. The factor has no effect for cells near the preferred cell, and 'shuts down' movement away from the preferred cell for cells far from that preferred cell. 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.

5. 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 two recent FAO/UBC workshops on the application of EwE (Pauly and Weingartner, 1998; Pitcher and Cochrane, 2002). Various capabilities have been added to EwE in response to these challenges, and there has 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. This is clearly not the case; ecosystem-based methods rely on information from traditional assessment, and have their force when it comes to addressing strategic management questions, not tactical management questions to which single-species assessment is much better suited. Our
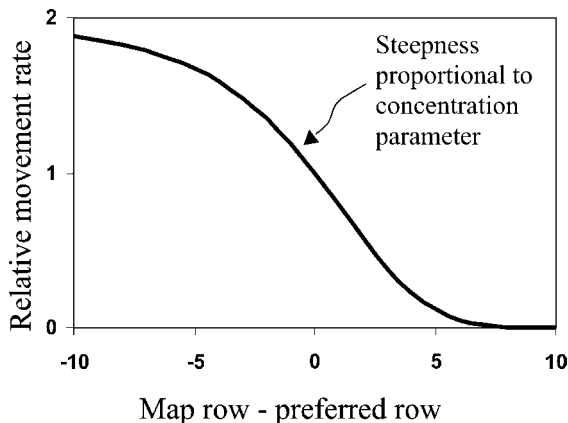

Fig. 4. Representation of the relative movement rate across the southern boundary of a cell as a function of gradient steepness in the seasonal migration module of Ecospace. The function is reversed for movement across the northern cell boundary, and a similar function is used for east–west movements with map column-preferred column as the independent variable.

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 non-target species, and the efficacy of policy interventions aimed at limiting unintended side effects of fishing. Also, as is shown through examples below, EwE can 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.

5.1. Does Ecopath assume steady state or equilibrium conditions?

Ecopath provides an 'instantaneous' estimate of biomasses, trophic flows, and instantaneous mortality rates, for some reference year or multi-year averaging window. Biomasses need not be at equilibrium for the reference year, provided the Ecopath user can provide an estimate of the rate of biomass 'accumulation' (or depletion) for each biomass for that reference year. In fact, in a number of cases, e.g. in a model of the North Sea in 1981 (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.

5.2. Should Ecopath be used even if there is insufficient local information to construct models, or should more sampling go first?

It is a fairly common conception that since we do not know enough to make perfect models at the individual or species level there is no way we can have enough information at hand to embark on modeling at the ecosystem level. This may hold if we try to construct models bottom-up—we cannot account for all the actions and processes involving all the individuals of the world. This is, however, not what Ecopath models do, instead they place piecemeal information in a framework that enables evaluation of the compatibility of the information at hand, gaining insights in the process. Adding to this is that there is much more information of living marine resources available than most will anticipate. A good demonstration of this can be obtained by searching the Fish-Base database on finfish (Froese and Pauly, 2000, http://www.fishbase.org) for Ecopath-relevant information using the semi-automated search routine available for the 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 (see 'Addressing uncertainty' above).

5.3. Does EwE ignore inherent uncertainty in assembling complex and usually fragmentary trophic data?

Ecopath has a number of routines that encourage users to explore the effects of uncertainty in input information on the mass balance estimates. In particular, the 'Ecoranger' routine allows users to calculate probability distributions for the estimates when they specify probability distributions for the input data components. Similarly, Ecosim has a graphical interface that encourages policy 'gaming' and sensitivity testing.

Lack of historical data and difficulty in measuring some ecosystem components and processes will likely always plague efforts to understand trophic structure and interactions. This is not a problem with Ecopath, but rather with aquatic ecology in general (Ludwig et al., 1993). We need to respond to it not by complaining about the incompleteness of our data, but rather by using models like EwE to direct research attention toward components that are most uncertain and also make the most difference to policy predictions. We also need to use the models to search for robust policy options and management approaches that will allow us to cope with the uncertainty, rather than pretending that someday it will just go away.

When EwE is used for policy comparison, it is important to recognize that incorrect comparisons (EwE leading user to favor a wrong policy) are not due to uncertainty in general about the model parameters, but rather to errors to which the particular policy compar-

ison 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.

5.4. Can Ecopath mass balance assessments provide information directly usable for policy analysis?

Instantaneous snapshots of biomass, flows, and rates of biomass change have sometimes been used to draw inferences about issues such as ecosystem 'health' as measured by mean trophic level or other indices of fishing impact (e.g. Christensen, 1995a; Pauly and Christensen, 1995; Pauly et al., 1998). 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 (see above) 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.

5.5. Can Ecopath provide a reliable way of estimating potential production by incorporating knowledge of ecosystem support capabilities and limits?

Ecologists have long sought simple ways of predicting productive potential of aquatic ecosystems from 'bottom-up' arguments about efficiency of conversion of primary production into production of higher trophic levels (e.g. Polovina and Marten, 1982). While Ecopath inputs can be organized so as to provide such predictions, we do not recommend using EwE for management this way. There are simply too many ways that simple efficiency predictions can go wrong, particularly in relation to 'shunting' of production into food web components that are not of direct interest or value in management (e.g. ungrazeable algae, inedible zooplankton, etc.) 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.

5.6. Can Ecopath predict biomasses of groups for which no information is available?

We try 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 estimates 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 0.90–0.99. 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 in the system.

5.7. Should Ecopath mass balance modeling be used only in situations where data are inadequate to use more detailed and realistic 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 (e.g. Sparre, 1991; Magnusson, 1995). In a sense, Ecopath does this as well, but generally does not account for age–size 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 is 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 age–size 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 age–size-dependent changes in vulnerability to the composition sampling method. As an example, 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, see, e.g. Walters and Maguire (1996).

It is obviously comforting to us as biologists to be able to provide more detailed accounting of predation interactions, which are almost always size and age-dependent. But in assessments of ecosystem-scale impacts of changes in trophic conditions, it is not automatically true that the best aggregate estimate is the sum of component estimates, any more than it is automatically true in single-species assessment that more detailed models and data always provide better assessments than simpler models. For statistical and logical reasons, the 'more is better' argument is no more valid in dynamic modeling than it is in multiple regression analysis, where we are familiar with how adding more independent variables is often an invitation to 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 age–size and seasonally structured. Rather, we assume that initial (Ecopath base or reference period) structuring has been adequately captured in preparing average/total rate input data, and that changes in structural composition over time are not large enough to drastically and persistently alter interaction rates/parameters. This is very similar to the assumption in single-species biomass dynamics and delay-difference modeling that stock composition changes produce regular or predictable changes in overall (stock-scale) production parameters, not that there is no composition effect in the first place.

5.8. Do EwE models ignore seasonality in production, mortality, and diet composition?

In most applications, Ecopath calculates components of biomass change over a 1-year accounting

step. There is no explicit assumption about how mortality rates, consumption rates, and diet composition may have varied within this step, except that the Ecopath user is assumed to have calculated a correct, weighted average of the rates over whatever seasonality may have been present in the data. Such averages can be difficult to calculate in practice, and a program interface component has been developed to help users with this chore (Martell, 1999).

In Ecosim, model users can define seasonal 'forcing shapes' or functions that can be applied as seasonal multipliers to the modeled production and consumption rate functions. Generally, including seasonal variation in this way results in graphics displays that are hard to follow visually (strong seasonal oscillations in ecosystem 'fast' variables like phytoplankton concentration), but very little impact on predicted inter annual (cumulative, long term) patterns of system change.

5.9. Do biomass dynamics models like Ecosim treat ecosystems as consisting of homogeneous biomass pools of identical organisms, hence ignoring, e.g. size-selectivity of predation?

The biomass rate equations in Ecosim (sums of consumption rates less predation and fishing rates) can be viewed as 'sums of sums', where each trophic flow rate for an overall biomass pool is the sum of rates that apply to biomass components within that pool. In this view, doing a single overall rate calculation for a pool amounts to assuming that the proportional contributions of the biomass components within the pool remain stable, i.e. the age–size–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, into 'juvenile' and 'adult' pools (or if desired in to multiple stanza). If so, the Ecosim biomass dynamics equations are replaced with an explicit age structured model for monthly age cohorts in the juvenile pool, and a delay-difference model for the adult pool. That is, for 'split pool' species Ecosim replaces the biomass dynamics model with a much more detailed and realistic population model (see Section 3.2 above). This allows Ecosim users to not only represent compositional effects, but also to examine the emergent stock-recruitment relationship caused by density-dependent changes in adult fecundity and juvenile growth and foraging time behavior.

5.10. Do ecosystem biomass models ignore behavioral mechanisms by treating species interactions as random encounters?

Historically, trophic interaction rates in biomass dynamics models have been predicted by treating predator–prey encounter patterns as analogous to 'mass-action' encounters between chemical species in chemical reaction vat processes, where reaction (encounter, 'predation') rates are proportional to the product of predator and prey densities. Such 'Lotka–Volterra' models generally predict much more violent dynamic changes, and considerably simpler ecosystem organization, than we see in field data.

Ecosim was constructed around the proposition that this mass-action principle is deeply incorrect for ecological interactions, and instead interactions take place largely in spatially and temporally restricted 'foraging arenas' where prey make themselves available to predation through activities such as foraging and dispersal. To represent this within-pool heterogeneity, we treat each biomass pool as consisting at any instant of two biomass components with respect to any predator, one sub-pool of individuals vulnerable to the predator and another sub-pool 'safe' from the predator. In this view, predation rate is limited jointly by search efficiency of the predator for vulnerable prey individuals, and exchange rate of prey between the invulnerable and vulnerable states. When Ecosim users set the

vulnerability exchange rates to high values, the model moves toward 'top-down' or mass-action control of predation rates. When users set the vulnerability rates to low values, the model moves toward 'bottom-up' control where predation rates are limited by how fast prey move (or grow, or disperse) into the vulnerable state.

Obviously the two-state (vulnerable/invulnerable) representation of prey biomass composition is a first approximation to the much more complex distribution of vulnerabilities among prey individuals that is likely to be present in most field situations. But it goes a remarkable way toward explaining dynamic patterns (lack of predator–prey cycles, persistence of apparent competitors and high biodiversity) that we have been unable to explain with simpler Lotka–Volterra mass-action models.

5.11. Do Ecosim models account for changes in trophic interactions associated with changes in predator diet compositions and limits to predation such as satiation?

In nature, diet compositions and feeding rates can change due to five broad factors:

(1) changes in 'habitat factors' such as water clarity, temperature, and escape cover for prey;
(2) changes in prey abundance and activity, and hence encounter rates with predators;
(3) changes in predator abundance, and hence interference/exploitation competition for localized available prey;
(4) changes in predator search tactics (search images, microhabitat used for foraging);
(5) handling time or satiation limitations to predator feeding rates.

Ecosim allows (or requires) representation of four of these factors, namely all but predator search tactic changes (4). Type (1) factors can be optionally introduced by including 'time forcing' functions representing temporal habitat change, and or 'trophic mediation' functions where other biomasses modify predation interaction rates for any predator–prey pair(s). Types (2), (3), and (5) are built into the calculations by default (though some effects can be switched off through 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 (3)) 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 switched off), 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).

Ecosim, for regions of parameter space with fairly slow dynamics, offers a reasonable approximation of most types of studied functional response forms. It is possible, as in all functional responses that the shape of the curves as evidenced in Ecosim departs substantially from the actual mechanisms which give rise to those shapes in nature. Further, good fits to one type of data (e.g. biomass) may hide poor fits to other types (e.g. capture inappropriate changes in feeding rate).

Our philosophy in developing Ecosim predation rate predictions has been to look first at the fine-scale (space, time) behavioral ecology of prey and predators, and in particular at how they vary and 'manage' their time. Overall predation response patterns, such as Type II sigmoid effects of reduced prey density, then 'emerge' as effects of the time management representation rather than being 'hardwired' into the model by particular overall equations for predation rates and diet composition.

5.12. Are the population models embedded in Ecosim better than single-species models since they explain the ecosystem trophic basis for production?

In a number of case studies, Ecosim users have treated the model as though it were a single-species assessment tool, varying its parameters so as to fit time series data for a particular species (e.g. Cox et al., 2002). 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 en-vironmental regime changes or confounding of these effects with the effects of fishing.

5.13. Do Ecosim population models provide more accurate stock assessments than single-species models by accounting for changes in recruitment and natural mortality rates due to changes in predation rates?

As noted above, using Ecosim for single-species assessments usually results in similar fits to historical data as would be obtained with traditional surplus production or delay-difference models. In principle Ecosim should be able to improve a bit on models that assume stationary stock-recruitment relationships and constant natural mortality rates, at least for mid-trophic level species that may be subject to highly variable predation risk. But in practice we have so far not obtained substantial improvements in fit to data, which could be due to poor data or to stability in mortality rates of the sort predicted when Ecosim vulnerability parameters are set to mimic 'bottom-up' control of predation rates.

In one case 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 (Martell et al., 2002). 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 (Polovina, 2002).

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 accounting for

predator–prey effects by itself may not lead to substantial improvements in stock size prediction. 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 (Skud, 1975).

Rather than pretending that Ecosim and single-species methods are 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 back calculation) 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).

5.14. Can one rely on the Ecosim search procedure time series fitting to produce better parameter estimates?

Ecosim users are cautioned that the search procedure in no way guarantees finding 'better' Ecosim parameter estimates. Better fits to data can easily be obtained for the wrong reasons, e.g. 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 by 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.

5.15. Does Ecosim ignore multispecies technical interactions (selectivity or lack of it by gear types) and dynamics created by bycatch discarding?

By separating groups into juveniles and adults, each with different biomasses and catches (and hence fishing mortalities), fundamental differences in selection can be accounted for. Moreover, Ecosim users can specify fishing mortality patterns over time either at the group level (fishing rate for each group over time) or the fleet level. Fleet level changes are specified as changes in relative fishing effort (relative to the Ecopath baseline model), and these changes impact fishing rates for the species caught by each gear in proportion to Ecopath base estimates for the species composition of the gear. That is, technical interactions (fishing rate effects on a variety of species caused by each gear type) are a basic part of the Ecopath data input and Ecosim simulations. However, Ecosim does not provide simple scenario development options for simulating tactics that dynamically might make each gear more or less selective.

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). 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.

5.16. Does Ecosim ignore depensatory changes in fishing mortality rates due to range collapse at low stock sizes?

Ecosim users have two options for specifying fishing mortality rate patterns: (1) direct entry of fishing rate (F) values over time; or (2) entry of relative fishing effort values over time, with fishing rate calculated as $q(B) \times$ (relative effort), where $q(B)$ is a biomass-dependent catchability coefficient. Under the second option, q is modeled as a hyperbolic function of B ($q = q_{max}/(1 + kB)$), so that q can be increased dramatically with decreases in stock size. The concept in this formulation is to recognize that catchability q can be expressed as a ratio $q = a/A$, where a is the area swept by one unit of effort and A is the area over which fish are distributed. Increases in q with decreasing stock biomass are usually assumed to be caused by decreases in stock area A occupied with decreases in B.

5.17. Does Ecosim ignore the risk of depensatory recruitment changes at low stock sizes?

Depensatory recruitment changes are apparently not common (Myers et al., 1995; Liermann and Hilborn, 1997), but should not be ignored in risk assessments for situations where a depensatory recruitment decline would have large economic or social consequences.

Depensatory effects are usually assumed to be due to Type II predator feeding effects, where predators would exert an increasing mortality rate on juvenile fishes if they tend eat a constant number of juveniles despite decreasing juvenile density. There are relatively few field situations where we would expect such Type II predator feeding effects (like migrating pink salmon fry being eaten by resident trout in a small stream).

Ecosim has helped identify another possible depensation mechanism that may be more common, which we call the 'delayed depensation' or 'cultivation-depensation' effect (Walters and Kitchell, 2001). When a large, dominant species is fished down, Ecosim 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, previously dominant group. 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. Thus, 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.

6. 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.

6.1. Incorrect assessments of predation impacts for prey that are rare in predator diets

It is easy to overlook a minor diet item in specifying diet composition for some predator. Unfortunately,

while that prey type may not be important for the predator, it may represent a very large component of total mortality for the prey type. This is a particularly important problem in representation of mortality factors for juvenile fishes, which usually suffer high predation mortality rates but are often not major components of any particular predator's diet and are notoriously difficult to measure in diet studies (fast digestion rates, highly erratic and usually seasonal occurrence in predator diets).

Another way that 'minor' diet items can come to assume considerable importance is through 'cultivation-depensation' effects (Walters and Kitchell, 2001) as discussed above. 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.

6.2. Trophic mediation effects (indirect trophic effects)

We use the term 'mediation effect' for situations where the predation interaction between two biomass pools is impacted positively or negatively by abundance of a third biomass type. For example, predation rates on juvenile fishes by large piscivores may be much lower in situations where benthic algae, corals, or macroinvertebrates provide cover for the juveniles. Pelagic birds like albatrosses that feed on small fishes may depend on large piscivores to drive these small fishes to the surface where they are accessible to the birds. Some large piscivores may create enough predation risk for others to prevent those others from foraging on some prey types in some habitats.

When a mediation effect is in fact present but is not recognized in the Ecosim model development, it is not unlikely for the model to predict responses that are qualitatively incorrect. For example, fishing down tunas in a model of a pelagic ecosystem 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.

6.3. Underestimates of predation vulnerabilities

Predation impacts can be limited in Ecosim by assuming low values of the exchange parameters (v's) between behaviorally invulnerable and vulnerable prey 'states'. We call these exchange parameters 'vulnerabilities', and they are estimated by assuming ratios of maximum to Ecopath base estimates of prey mortality rates for each predator–prey linkage. That is, if $M(o)_{ij} = Q(o)_{ij}/B(o)_i$ is the base instantaneous natural mortality rate for prey type i caused by predator j base (Ecopath estimate) consumption rate $Q(o)_{ij}$ on prey base biomass $B(o)_i$, we assume that the maximum possible rate for very high predator j abundance would be $v_{ij} \times B_i$, where $v_{ij} = K \times M(o)_{ij}$, $K > 1$, represents the rate at which prey become vulnerable to predator j. By using a K near 1, i.e. v_{ij} only a little larger than $M(o)_{ij}$, Ecosim users can simulate the 'bottom-up' control possibility that changes in predator abundances do not cause much change in prey mortality rates because these rates are limited by physiological or behavioral factors of the prey. The assumption that there are such limitations is supported by scattered observations where total mortality rates (Z) were poorly correlated with changes in predator abundances.

Another way expressing that vulnerabilities of prey to predators are very limited is to say that predators are already eating almost every prey that does become vulnerable. If this is indeed true, then there is likely intense exploitation competition among predators for the prey that do become vulnerable, i.e. the number of vulnerable prey seen by each predator is

severely limited by the number of other predators competing for those prey. This has potentially large implications for the dynamics of the predator: reductions in predator abundance may be accompanied by large increases in the densities of vulnerable prey available to each remaining predator. In such cases, Ecosim will predict a strong compensatory effect on the predator of reduced predator abundance (strong increases in food consumption rate and growth, or large decreases in predator foraging time with attendant decreases in mortality risk faced by the predator).

So the net effect of assuming low prey vulnerabilities is also to assume that predators should exhibit strong compensatory responses to reduced abundance of conspecifics, which in simulations of increased fishing pressure means strong compensatory responses and hence lower risk of overfishing. An enthusiastic proponent of 'bottom-up' control of trophic processes must therefore also be a strong proponent of the idea that it is hard to overfish. This is a very risky assumption.

6.4. Non-additivity in predation rates due to shared foraging arenas

The default assumption in Ecosim is to treat each predation rate linkage as occurring in a unique 'foraging arena' defined by the behaviors of the specific prey and predator. In this formulation, elimination of one predator will result in a decrease in total prey mortality rate equal (at least initially) to the Ecopath base estimate of that predator's component of the prey total mortality rate. This may be partly compensated by increases in mortality rate due to other predators if the prey increases in abundance and spends more time foraging in response to increased intraspecific competition, but in general this compensatory effect will not completely replace the initial mortality rate reduction.

But suppose this formulation is wrong, and in fact the mortality rate of the prey represents movement of the prey into behavioral or physiological states (e.g. parasite loads) for which it is vulnerable to predators in general. In this case, removal of any one predator may simply result in the vulnerable prey individuals being taken just as fast, but by other predators. In this case, the total mortality rate of the prey will change much less than predicted by Ecosim.

6.5. Temporal variation in species-specific habitat factors

Attempting to fit Ecosim models to time series data has revealed some cases where an important species or biomass pool shows dramatic change that cannot be attributed to any known change in trophic relationships or harvesting. Then this dramatic but 'unpredictable' change appears to result in major trophic impact on the rest of the ecosystem. An example would be a planktivorous fish species, which shows high recruitment variation and occasional very strong year classes. If this species is important to piscivores in the system, the piscivores may respond strongly to changes in the planktivores abundance. 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 that causes it to decline despite favorable trophic conditions in terms of food supply and predation risk.

Ecosim can help us detect possible habitat problems, by revealing prediction 'anomalies' from biomass patterns expected under trophic and fishing effects alone. But there is also a risk of producing 'spurious' good fits to Ecosim, when Ecosim parameters are varied so as to explain as much of the biomass change as possible; that is, Ecosim may explain patterns as trophic/fishing effects that in fact have been due to habitat changes. This is a particular risk in situations where habitat change involves some fairly regular 'regime shifts' or cycles in habitat variables. Ecosim may well attribute cyclic biomass changes in such situations to predator–prey instabilities rather than environmental forcing.

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