

Representing Density Dependent Consequences of Life History Strategies in Aquatic Ecosystems: EcoSim II

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ABSTRACT

EcoSim II uses results from the Ecopath procedure for trophic mass-balance analysis to define biomass dynamics models for predicting temporal change in exploited ecosystems. Key populations can be represented in further detail by using delay-difference models to account for both biomass and numbers dynamics. A major problem revealed by linking the population and biomass dynamics models is in representation of population responses to changes in food supply; simple proportional growth and reproductive responses lead to unrealistic predictions of changes in mean body size with changes in fishing mortality. EcoSim II allows users to specify life history mechanisms to avoid such unrealistic predictions: animals may translate changes in feeding rate into changes in reproductive rather than

growth rates, or they may translate changes in food availability into changes in foraging time that in turn affects predation risk. These options, along with model relationships for limits on prey availability caused by predation avoidance tactics, tend to cause strong compensatory responses in modeled populations. It is likely that such compensatory responses are responsible for our inability to find obvious correlations between interacting trophic components in fisheries time-series data. But EcoSim II does not just predict strong compensatory responses: it also suggests that large piscivores may be vulnerable to delayed recruitment collapses caused by increases in prey species that are in turn competitors/predators of juvenile piscivores.

Key words: trophic interactions; cascades; risk-sensitive foraging; ecosystem management.

INTRODUCTION

Population models used for fisheries assessment usually treat growth, recruitment, and natural mortality as fixed rates or functions of stock size. We have long recognized that this is a dangerous practice in view of how fish populations are embedded in, and at least to some degree must be influenced by, aquatic ecosystems that are constantly changing. Attempts to link population processes to ecosystem change have involved mainly two types of models:

(a) multispecies virtual population analyses (MSVPA) that performs detailed reconstruction of mortality rates caused by trophic interactions (Pope 1991; Sparre 1991); and (b) much simpler biomass dynamics models that include trophic linkages (Pope 1979; Larkin and Gazey 1982). Also, models that seek to explain recruitment variation in terms of “environmental factors” (for example, Cury and Roy 1989) may be considered an empirical way to summarize the consequences of ecosystem linkages that have particularly large effects on larval/juvenile fishes.

MSVPA and biomass dynamics approaches have been plagued by difficulties in obtaining enough data to make reasonable estimates of trophic interac-

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tion parameters. Recently, we have been able to make some progress toward simplifying the parameter estimation problem by using Ecopath trophic mass-balance assessments (Polovina 1984; Christensen and Pauly 1992a) to provide most of the parameters needed to drive a biomass dynamics model called EcoSim (Walters and others 1997). Ecopath provides a structured way to incorporate bioenergetics, biomass, production rate, mortality rate, and feeding habits data into a static mass-balance “snapshot” of trophic flows. It has been very widely used to describe aquatic ecosystems around the world (see for example, contributions in Christensen and Pauly 1993). The original EcoSim turned such snapshots into biomass dynamics models and additionally allowed a crude representation of population processes for a subset of species that have complex trophic ontogeny. Biomass pools could be split into juvenile and adult stages with different trophic parameters and with delay-differential accounting for changes in numbers as well as biomass. The split pool representation allowed EcoSim users to make predictions about a variety of worrisome issues in ecosystem management, such as the impact of reducing by-catch of juvenile fish in trawl fisheries and the food web impacts of “bottom-up” changes in primary production and harvesting from lower trophic levels (for example, Bundy 1997). However, we were not comfortable with the delay-differential representation of population processes as formulated in the original version of EcoSim; this representation does not account for a variety of physiological and behavioral changes that are likely to accompany changes over time in predation risk and foraging opportunity. We were concerned that such life history responses can profoundly affect trophic linkages, mainly by reducing the impact of these linkages on recruitment and mortality rates.

This article describes the structure and some initial findings from EcoSim II, which deliberately aims to account for effects of life history responses on trophic linkages by embedding relatively realistic population dynamics models in simpler biomass dynamics representations. EcoSim II continues to use Ecopath assessment as a means to provide initial biomass and trophic interaction parameters but replaces the delay-differential model for split biomass pools with a much more realistic age-size-structured model for at least the juvenile life stages in key species that show strong trophic ontogeny. Age structure effects in the adult dynamics of these species are represented using a delay-difference population model (Deriso 1980; Schnute 1987). The age-size structure representation permits explicit analysis of how growth, mortality, and recruitment

processes may change with changes in trophic conditions, in particular how the “stock-recruitment” models of single-species assessment may arise through trophic interactions and be modified by such interactions. Furthermore, the model allows us to more realistically represent (a) changes in allocation of food intake between growth and reproduction as food availability varies; (b) changes in vulnerability to predation associated with changes in feeding behavior as prey densities vary (effects of risk-sensitive foraging behavior); and (c) constraints on recruitment associated with juvenile size and fecundity.

In the following sections, we first review the EcoSim representation of trophic interactions and the delay-difference structure used in EcoSim II to avoid overly simplistic predictions based on biomass changes alone. Then we describe how EcoSim II represents alternative hypotheses about effects of changing trophic status on reproductive effort and vulnerability to predation and show how these hypotheses affect predictions about the impact of changes in fishing rate on recruitment and growth rates, within an ecosystem context. Finally, we discuss applications for EcoSim II and offer warnings about ways the model can fail.

BACKGROUND: TROPHIC REPRESENTATION IN ECOSIM

Ecopath provides a structured method for estimating biomasses B_i over a set of ecosystem “pools” $i = 1, \dots, n$, and trophic flows C_{ij} (biomass per time) between prey pools i and predator pools j . That is, Ecopath provides a way to organize baseline (or average historical) observations on abundances and trophic flows (feeding rates, diet compositions, and growth efficiencies) into an initial, static picture of ecosystem state. In the EcoSim models, we turn these static flows into dynamic, time-varying predictions by assuming that the flows are determined by the prey and predator biomasses by using a particular representation derived by thinking about the patchy spatial organization of most trophic interactions in aquatic systems:

$$C_{ij} = v_{ij}a_{ij}B_iB_j / (v_{ij} + v'_{ij} + a_{ij}B_j) \quad (1)$$

where a_{ij} is a rate of effective search for prey type i by predator j ; and v_{ij} , v'_{ij} are prey vulnerability parameters with default setting $v_{ij} = v'_{ij}$.

This relationship (Walters and others 1997) assumes that prey can be in two “behavioral states” (or spatial patch “positions”) with respect to vulnerability to predator j , with animals moving from an invulnerable state at rate v_{ij} into a vulnerable state,

and returning to the invulnerable state at rate v'_{ij} . The ratio $v_{ij}/(v_{ij}+v'_{ij} + a_{ij}B_j)$ represents the equilibrium proportion of B_i that will be vulnerable at any moment, assuming very rapid equilibration of prey numbers between the two states relative to the time scales for biomass change. We use this structure to represent the very general observation that prey and predators do not move around at random (which would lead to the Lotka-Volterra model $C_{ij} = a_{ij}B_iB_j$). Prey animals generally have a range of spatial behavior tactics for limiting vulnerability to predation, ranging from hiding in shallow areas or under rocks to forming schools and migrating into very deep water (Werner and Hall 1988; Walters and Juanes 1993). Such behavior generates complex and patchy spatial structures of interactions and can lead to very strong competitive interactions between predators, even when total prey biomass is very large [the $a_{ij}B_j$ term in the denominator of Eq. (1) represents local depletion effect of predators on the biomass density of available prey]. Note that Eq. (1) does not include effects of predator satiation on feeding rates per biomass (no denominator term for B_i as would be used to represent type II predator functional response). This is a very deliberate choice on our part, based on two arguments: (a) satiation, as measured by full stomachs, is rare in nature (Ricker 1975, p. 224); and (b) for most animals, increasing a_{ij} (for example, by spending more time feeding) enough to cause large handling time effects does generally not make evolutionary sense—considering that it will expose them to additional risk of predation (Jones 1982). In short, we think there are bigger issues to worry about in modeling feeding behavior and feeding rates than the relatively trivial matter of handling times and satiation. The traditional concern about functional response shapes in species interaction modeling is caused by the importance of handling time effects in laboratory experiments, not field conditions.

EcoSim uses a very simple procedure to estimate the parameters of Eq. (1). We ask the user to hypothesize maximum consumption rates C_{ij}^{\max} relative to the Ecopath base rates, if predator numbers were very high. This ratio provides an estimate of v_{ij} (from $C_{ij}^{\max}=v_{ij}B_i$). Then substituting this estimate of v_{ij} (and $v'_{ij}=v_{ij}$) into Eq. (1), along with the Ecopath base C_{ij} and B_i , B_j , allows us to solve for a_{ij} . The Lotka-Volterra analog of this solution would be $a_{ij} = C_{ij}/(B_iB_j)$. Obviously the choice of C_{ij}^{\max}/C_{ij} has a profound effect on EcoSim predictions over time; high values of the ratio imply strong trophic linkages and effects (and strong top-down, competitive, trophic cascade effects), whereas low values imply “donor-controlled” (bottom-up) decoupling of the predation interactions.

DELAY-DIFFERENCE MODEL WITH TROPHIC LINKAGES

In the simplest EcoSim versions, we use Eq. (1) along with estimates of nonpredation mortality (and primary production) to set up biomass dynamics models of the form

$$dB_i/dt = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_i \quad (2)$$

where g_i = net growth efficiency, I_i = biomass immigration rate, M_i = nonpredation mortality/metabolic rate, F_i = fishing mortality rate, e_i = emigration rate, and where the C_{ij} are predicted from Eq. (1). Splitting pools into juveniles and adults can be used in Ecopath to represent steady state differences in diets, mortality, migration, and fishing rates between juvenile and older animals, but the biomass dynamics in Eq. (2) can give unrealistic predictions for nonequilibrium situations. For example, it can predict persistence of juveniles B_i if feeding opportunities are good, even when their adult group has been eradicated by high fishing mortality. We overcame this problem in the first version of EcoSim by linking juvenile and adult pools through flow of numbers of individuals as well as biomass, by using a delay-differential equation system for each split pool pair (see Walters and others 1997 for details). However, the delay-differential equation system was computationally inefficient and required a complex numerical scheme to capture the delay structure adequately for simulations involving rapid biomass change over time.

EcoSim II replaces the delay-differential equation structure with a delay difference model for each split pool case. Denoting the pool index for adults as A , and for juveniles as J , the basic model structure is

$$B_{A,t+1} = e^{-Z_{A,t}}[\alpha_{A,t}(C_{A,t})N_{A,t} + \rho_A B_{A,t}] + I_A + w_{J,k,t}N_{J,k,t} \quad (3A)$$

$$N_{A,t+1} = N_{A,t}e^{-Z_{A,t}} + N_{J,k,t} \quad (3B)$$

$$N_{J,l,t+1} = R(B_{A,t}, N_{A,t}, C_{A,t}) \quad (3C)$$

$$N_{J,a,t+1} = e^{-Z_{J,t}}N_{J,a-1,t} \quad a = 1, \dots, k \quad (3D)$$

$$w_{J,a,t+1} = w_{J,a-1,t} + g' C_{J,t}/N_{J,t} \quad (3E)$$

where t = time (in months to increase flexibility to represent seasonality, short lives); $Z_{A,t}$ = total mortality rate of adult pool $M_{A,0} + e_{A,0} + F_{A,t} + \sum C_{A,j}/B_{A,t}$; $Z_{J,t}$ = total mortality rate of juvenile pool $M_{J,0} + e_{J,0} + F_{J,t} + \sum C_{J,j}/B_{J,t}$; $N_{J,a,t}$ = number at time t of juveniles with age a (in months); $R(B_{A,t}, N_{A,t}, C_{A,t})$ = predicts

the number of juveniles with age 0, produced in month t , as a function of adult numbers, biomass, and food consumption $C_{A,t}$; k = age (months) at graduation to the adult pool; $w_{J,a,t}$ = body weight at time t of juveniles of age a ; $C_{J,t}$ = total food consumption by juveniles J in month t ; $N_{J,t}$ = total number of juveniles at start of month t (summed over ages a); g' = juvenile growth efficiency; $\alpha_{A,t}$ ($C_{A,t}$) = intercept of plot of $w_{A,t+1}$ vs. $w_{A,t}$ (for $w_A > w_k$), or Ford-Brody growth model, assumed to depend on adult food consumption $C_{A,t}$ in month t ; and ρ = slope of Ford-Brody plot, representing metabolism.

Eqs. (3A) and (3B) are the well-known Deriso-Schnute equations for biomass and numbers dynamics in age-structured populations (Deriso 1980; Schnute 1987; see derivation in Hilborn and Walters 1992), and Eqs. (3C) to (3E) represent additional accounting needed to move juveniles from birth to the age k at recruitment to the adult pool. Base estimates of ρ can be obtained from the von Bertalanffy growth parameter K , as $\rho = e^{-K/12}$ (the factor 12 here converts from usual K in years to a monthly value). The juvenile growth rate $g'C_{J,t}/N_{J,t}$ is assumed linear with age a , and hence represents only an average over all juveniles (that is, the model does not represent the acceleration with age that would normally be expected). Basic model predictions are not affected by this simplification, and it will be important only if we choose in the future to disaggregate juvenile mortality and growth processes to capture some of the rapid changes that can occur in $Z_{J,t}$ with juvenile age and size.

The delay-difference structure in Eq. (3) is similar to the delay-differential biomass production model derived by Horbowy (1996) as a way to simplify the Andersen and Ursin (1977) multispecies age-structured model, though we make quite different functional assumptions about impacts of changing prey availability on food consumption and growth (Horbowy assumes constant total ration $C_{A,t}$ and growth, and so deals only with changes in diet composition with changes in availability of alternate prey).

Ecosystem linkages occur at four places in Eq. (3): (a) the mortality rates $Z_{A,t}$ and $Z_{J,t}$; (b) the adult growth rate intercept $\alpha_{A,t}$; (c) the juvenile recruitment function R ; and (d) the juvenile growth rate $g'C_{J,t}/N_{J,t}$ (assumed proportional to food consumption per juvenile). The simplest reasonable assumption for α would be $\alpha_{A,t} = gC_{A,t}/N_{A,t}$, that is, that the growth intercept (which represents per capita food consumption rate) is just proportional to per capita food consumption, as suggested in Walters and Post (1993). The simplest reasonable assumption for recruitment would be $R(B_{A,t}, N_{A,t}, C_{A,t}) = fC_{A,t}$, where

f is the number of juveniles produced per unit food consumption (another simple option for R would be $fB_{A,t}$, where f is juveniles per adult biomass). Note that these simple assumptions imply density dependent feedbacks on recruitment only through effects of density on growth and food consumption rates (unless $Z_{J,t}$ includes a cannibalism component $C_{J,A}$, which may occur, but should be avoided in Ecopath analyses). Density-dependent effects on food consumption rates can occur in turn through both depletion effects on available prey for constant total prey biomass [via denominator term in Eq. (1)], and through longer term impacts on total prey biomasses B_i .

To initialize the variables in Eq. (3) for time simulations, we begin with the same equilibrium assumption as used to parameterize the Ecopath model. Setting the biomasses $B_{A,t}$ and $B_{J,t}$, consumptions $C_{A,t}$ and $C_{J,t}$, and mortality rates $Z_{A,t}$ and $Z_{J,t}$ to baseline values from Ecopath turns Eq. (3) to a set of static equations including a base recruitment rate R_0 and the numbers at age $N_{A,0}$ and $N_{J,a,0}$. We solve these equations for the required N values, by using as few additional assumptions as possible. The net intake efficiencies g and g' are provided from Ecopath, whereas we must supply the following additional information: energy allocation to reproduction (see below) and $w_{J,k,0}$ and ρ from growth data (for example, from the FishBase CD-ROM, which includes over 5000 sets of growth parameters, see Froese and Pauly 1997).

One touchy point about the initialization is that the adult biomass $B_{A,0}$ together with $w_{J,k,0}$ define equilibrium recruitment R_0 , which in turn along with $Z_{J,0}$ determines the initial juvenile numbers and weights by age. But the juvenile biomass computed as $\sum N_{J,a,0}w_{J,a,0}$ from R_0 generally will not be the same as the Ecopath $B_{J,0}$. We treat this as a scale problem: in setting $w_{J,k,0}$ for the adult pool, we recompute juvenile sizes so as to satisfy the Ecopath $B_{J,0}$, and then apply a computational body weight scale shift from the internal juvenile weight units to the user-specified $w_{J,k,0}$ as juveniles are moved into the adult pool. This scale shift does not affect the trophic flow or population dynamics calculations; it simply means that the units of measurement of adult body size do not necessarily need to agree with the units of measurement of juvenile sizes.

A compensatory mechanism that is not obviously represented in Eq. (3) is density-dependent juvenile growth (which is represented) coupled with juvenile size-dependent vulnerability to predation. EcoSim II offers two options for dealing with this mechanism: (a) the user may specify that juveniles recruit to the adult pool at a constant, arbitrary body

weight, w^* , so only those juvenile age classes $N_{j,a,t}$ that have reached body weight $w_{j,a,t} \geq w^*$ are included in the recruit term of Eqs. (3A) and (3B); or (b) juveniles can be forced to recruit at age k , with weight at recruitment $w_{j,k,t}$ varying with trophic conditions. The second of these options does not account for the cumulative effect of spending a longer period exposed to high Z_j when growth is slower. It would be possible to model this size mortality interaction more precisely in the general EcoSim setting by replacing B_i in Eq. (1), for links where the prey type i is juveniles J , with a vulnerable prey biomass $V_{j,j}$ that represents a weighted sum over juvenile ages a of $v_{j,j,a,t} N_{j,a,t} w_{j,a,t}$, where vulnerability weights $v_{j,j,a,t}$ for each predator type j would be computed with a function that is inversely related to body size $w_{j,a,t}$. This formulation, however, would require entering far more information about each predation link than is now provided through Ecopath analysis. Still, we will try to make it available in future versions of EcoSim if we can solve some technical problems with setting up the v functions so as to insure compatibility with Ecopath estimates of overall juvenile mortality rates.

Whereas the formulation above begins with an equilibrium mass-balance analysis, the resulting dynamic model does not necessarily produce stable population sizes over time. For instance, in a study currently underway on trophic interactions in the central North Pacific, Chris Boggs and Xi Hse (National Marine Fisheries Service, Honolulu) have found that EcoSim II predicts a 2–3-year biomass cycle for mahi-mahi (*Coryphaena hippurus*) over a wide range of model parameter estimates. Catch statistics suggest that this cycle actually occurs in the field. Mahi-mahi grow extremely rapidly (Uchiyama and Burch 1986), and when represented as foraging virtually all the time in the model, the simulated population exhibits density-dependent changes in juvenile growth rate that translate into variable time delays to recruitment into the adult biomass pool; high juvenile mortality rates combine with this variation in time to maturity to produce variable, cyclic recruitment. This EcoSim hypothesis for the natural abundance cycle can be tested by measuring growth rates and ages at maturity for a sequence of cohorts; we predict that the cyclic strong cohorts will be found to have had relatively rapid juvenile growth.

A computational point needs to be made concerning the linkage between Eqs. (2) and (3). Eq. (3) is based on fairly crude, discrete time steps (monthly by default). But most Ecopath models include biomass pools like phytoplankton and microzooplankton that have much more rapid turnover rates than

once per month. This creates a computational “stiffness” problem: we need to either integrate the fast variable dynamics in Eq. (2) over a much shorter time step than one month, or else assume that fast variables stay near moving equilibrium values that change from month to month with changing impacts on these variables by pools that change more slowly (see, for example, Walters and others 1987). We have chosen the second option in EcoSim II: we compute moving equilibria from month to month for all biomass pools k whose turnover time (as measured by total mortality/consumption rates Z_k) is less than 2 months. Computational checks of this option against the original EcoSim model, which usually does numerical integrations at time steps of 1 day or less, indicate that the moving equilibrium assumption for fast variables generally gives results virtually identical to full integration. Numerical stability of the speed splitting algorithm is maintained even when we include quite violent seasonal changes in primary production and feeding rates (EcoSim II includes a user interface for “shaping” both seasonal and long-term changes in primary production and feeding parameters, mainly so we can examine hypotheses about the trophic consequences of long term “regime shifts” sensu Bakun (1996).

COMPENSATORY GROWTH AND MORTALITY HYPOTHESES

Though the delay-difference structure of Eq. (3) appears superficially reasonable as a way of linking population dynamics and trophic effects, it (and the original delay-differential formulation) usually makes one key prediction that most fisheries scientists would consider pathologically incorrect if we assume recruitment and growth rates simply proportional to food consumption. Figure 1 shows predicted changes in equilibrium biomasses and in equilibrium average body weight for a general “apex predator” (for example, tuna), with increasing fishing mortality rate on the apex predator. These calculations are for a simple pelagic ecosystem structure that has been widely used to demonstrate the construction of Ecopath models (OCEANSCS model of Christensen and Pauly 1992b; details in Pauly and Christensen 1993). For such a scenario, our expectation from simple population dynamics theory and experience would be to see juvenile abundances remain relatively high over a range of low to moderate fishing rates, and to see average adult body size decline steadily with increasing F . Though the juvenile abundance (at least as measured by biomass) prediction accords with expecta-

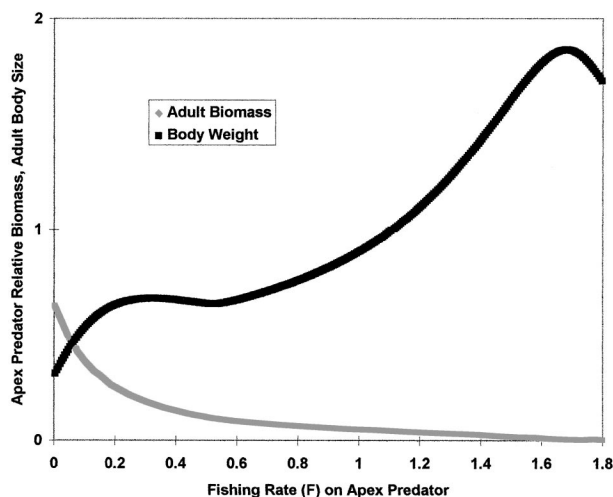


Figure 1. Changes in equilibrium biomass, catch, and mean adult body size for an apex predator (for example, tuna) predicted by an EcoSim run based on an Ecopath file representing the oceanic part of the South China Sea (OCEANSCS; Christensen and Pauly 1992b). Note that average adult body size is predicted to decrease with decreasing fishing rate (and increased adult abundance), due to intraspecific competition for food. Most fisheries assessment models would predict the opposite response, due to accumulation of more large animals in the stock under reduced fishing mortality.

tion, adult body weight does exactly the opposite. Generally, our first version of EcoSim II predicted increasing adult body size with increasing fishing mortality rate; predicted growth rates (via effects of food consumption on α) increased more rapidly than numbers decline, so average size increased even though average age decreases greatly. This effect can be alleviated somewhat by assuming high prey vulnerabilities [high v_{ij} in Eq. (2)], but nonetheless it appeared that EcoSim II with proportional recruitment and growth predicts much larger changes in growth rates with density than we would expect from experience.

This model “failure” raised what we consider to be a very fundamental question about population ecology. Almost certainly the opportunity for increased feeding rates and growth has accompanied the decline of many fish populations under increasing fishing mortality. Why have we often not seen such strong compensatory increases in growth rate predicted by models like EcoSim? There are at least two likely answers to this question, and we have included both (as options for hypothesis generation and policy testing) in the EcoSim II structure:

1. reproduction versus growth allocation hypothesis: faced with opportunities to increase food intake, animals may allocate progressively more

of the increased intake to production of juveniles (more precisely, selection may have favored physiologies that allocate surplus to reproduction rather than growth); and/or

2. predation risk avoidance hypothesis: faced with increased feeding opportunity, animals may elect to maintain stable food consumption, and to spend less time foraging, decreasing time at risk to predation.

The following subsections describe how we have represented these hypotheses in EcoSim II.

By including these hypotheses in the EcoSim II formulation, we do not mean to imply that there is no evidence for strong density-dependent changes in growth rate, in both freshwater and marine ecosystems. For example, many fish species in the Laurentian Great Lakes have shown growth rate changes of up to 50% with the violent changes in abundance that accompanied lamprey invasion and control, fishery development, and salmonid stocking (Kitchell 1991; Eby and others forthcoming). Changes in stocking rate commonly cause substantial growth changes in salmonid fisheries (Walters and Post 1993). Stunting patterns in many freshwater and coastal lagoon fishes are well documented (Alm 1959; Carlander 1977; Longhurst and Pauly 1987) and are easy to link with metabolic considerations (Pauly 1984).

There has been more controversy about the importance or generality of density-dependent growth responses in marine systems (Bakun 1996; Ross 1997), though there are some striking examples of patterns like those EcoSim II would predict. Growth changes in Pacific salmon have been closely related to changes in total abundance (Bigler and others 1996). Decreases in Pacific halibut (*Hippoglossus stenolepis*) growth, especially in the Gulf of Alaska, accompanied stock increases but did not respond when the stock decreased later (IPHC 1997). The decline, off Peru, of anchoveta (*Engraulis ringens*), and the simultaneous increase of sardine (*Sardinops sagax*), from the 1950s to the 1980s, was accompanied by a strong increase of size at age in the former and a decline in the latter species (Palomares and others 1987; Muck 1989). Growth responses followed stock depletion of the sandbar shark (*Carcharhinus plumbeus*) (Sminkey and Musick 1995). Increases in growth made Atlantic herring (*Clupea harengus*) more vulnerable to fishing as exploitation rates increased (Anthony and Fogarty 1985). Several Georges Bank fishes have shown growth increases with stock size reductions (Ross and Almeida 1986; Ross and Nelson 1992).

Food Allocation between Growth and Reproduction

We can think of the net (of assimilation and SDA losses) food intake $gC_{A,t}$ by an adult pool as being divided through physiological allocation processes into two components: food used for growth, $F_g = P_g gC_{A,t}$ and food used for reproduction $F_r = gC_{A,t} - F_g$. Here P_g is the proportion of net intake allocated to growth. Assume for the moment that $C_{A,t}$ is allowed to vary with feeding opportunities as predicted from Eq. (1). So that the growth curve α remains constant at some value α_o , where $\alpha = F_g/N_{A,t}$ (the per capita allocation of food to growth), the allocation proportion P_g must vary as

$$P_g^{\text{constant growth}} = \alpha_o / (gC_{A,t}/N_{A,t}), \quad (4)$$

subject to $P_g^{\text{constant growth}} \leq 1.0$

The opposite extreme from this assumption is that a constant proportion P_o of the net food intake goes into growth, which implies that both α and fecundity will be proportional to food intake (the assumption that leads to “incorrect” behavior in Figure 1). It also may be that natural selection has favored a wide range of actual energy allocation strategies (Koch and Wieser 1983; Keenleyside 1991; Stearns 1992).

In EcoSim II, we allow the user to move between these two extreme hypotheses ($\alpha = \alpha_o$ versus α proportional to C/N) by specifying a “life history weighting factor” W_g :

$$P_g^{\text{realized}} = W_g P_g^{\text{constant growth}} + (1 - W_g) P_o \quad (5)$$

That is, at every model time step we calculate the net food intake per animal $gC_{A,t}/N_{A,t}$, and use this to calculate $P_g^{\text{constant growth}}$. The P_g^{realized} for that time step is then given by Eq. (5). The user can freely vary W_g to generate a range of physiological allocation scenarios. Setting $W_g = 1$ results in constant growth (except at low food availability) and substantial changes with density in the allocation of food intake to reproduction (more juveniles in the R function rather than more somatic growth). $W_g = 1$ completely eliminates the pathological problem with mean body weight in Figure 1 and generates strong compensatory responses in juvenile abundance as adult abundance decreases. In fact, it generally predicts compensatory responses that are probably too optimistic for fisheries management, unless used in conjunction with the other behavioral and reproductive changes discussed in following sections.

This formulation requires the EcoSim II model user to specify a baseline estimate of P_o , or α_o . We cannot compute α_o from Eq. (4) by using the

Ecopath input estimates of g and $C_{A,t}$ and $N_{A,t}$. Ecopath inputs and outputs do not include estimates of numbers in general. Thus, we use P_o to obtain an initial $N_{A,0}$ estimate in the first place [by setting $B_{A,t+1} = B_{A,t}$ in Eq. (3A), substituting $P_o g C_{A,0}/N_{A,0}$ for $\alpha_{A,0}$, and solving the resulting equation for an initial equilibrium R_o , this then along with $Z_{A,0}$ and $w_{J,k,0}$ implies a starting $N_{A,0}$]. We see no obvious way to predict P_o from life history characteristics such as $Z_{A,0}/Z_{J,0}$. On the other hand, we generally associate low values of P_o with species that have low adult and high juvenile mortality rates. Parameter estimation can possibly be facilitated through identification of empirical patterns in the (P_o, W_g) relationship across taxa of aquatic organisms. For the present, we have elected to “scale out” P_o effects as much as possible in EcoSim II calculations, by using recruitment relationships that predict departure of R from R_o as a function of relative changes in food intake and adult biomass from the values implied by P_o (see below).

Foraging Time and Predation Risk

Foraging can be a risky activity, especially for smaller juvenile organisms (Jones 1982; Abrams 1993; Werner and Anholt 1993; McNamara and Houston 1994). The relationship predicting food consumption [Eq. (1)] contains two parameters that directly reflect time spent feeding, and the predation risk that feeding may entail: a_{ij} and v'_{ij} . We need to specify how changes in $c_{i,t}$ will influence at least relative time spent foraging to model possible linked changes in these parameters with changes in food availability as measured by per biomass food intake rate $c_{i,t} = C_{i,t}/B_{i,t}$ ($i =$ juvenile index J or adult index A —note that $C_{i,t}$ here refers to the total food intake rate by pool i at time t , not consumption of i by pool t).

Let us denote the relative time spent foraging as $F_{i,t}$, measured such that the rate of effective search during any model time step can be predicted as $a_{jit} = F_{it} a_{ji}$ for each prey type j that i eats. Furthermore, we assume that time spent vulnerable to predation, as measured by v'_{ij} for all predators j on i , is inversely related to F_{it} , that is, $v'_{ijt} = v'_{ij}/F_{it}$. An alternative structure that gives similar results is to leave the a_{ij} constant, while varying the v_{ij} by setting $v_{ijt} = F_{it} v_{ij}$ in the numerator of Eq. (1) and $v_{ijt} = F_{it} v_{ij}$ in the denominator. For convenience in estimating the a_{ij} and v'_{ij} parameters, we scale F_{it} so that $F_{i0} = 1$, and $v'_{ijt} = v_{ij}$. When we use these scaling conventions, the key issue then becomes how to functionally relate F_{it} to food intake rate c_{it} so as to represent the hypothesis that animals with lots of food available will simply spend less time foraging, rather than increase food intake rates.

Unfortunately, there is no simple functional form for F_{it} that will result in near constant feeding rates, but changing time at risk to predation, in situations where rate of effective search a_{ji} along with prey behavior (as measured by v_{ji}) jointly limit feeding rate. We are forced to use an iterative adjustment procedure :

$$F_{i,t+1} = F_{it}[(1 - w_i) + w_i(c_{io}/C_{it})], \quad F_{i,t+1} < F_i^{\max} \quad (6)$$

where F_i^{\max} = maximum relative increase in time spent foraging when intake c_{it} is low; c_{io} = base food intake per biomass at Ecopath starting equilibrium; and w_i = adjustment rate weighting factor (1 = fast, 0 = none).

Setting F_i^{\max} to a very high value (for example, 100) amounts to assuming that animals "normally" (under conditions for which Ecopath consumptions were estimated) spend only a very small proportion of their time feeding. Think of the iteration procedure this way: if you are getting half of what you "want" as predicted by the Ecopath base rate c_{io} , so that $c_{io}/c_{it} = 2$, then you spend twice as much time foraging. Setting low values for F_i^{\max} implies the belief or assumption that animals already are spending most of their time foraging and have little flexibility to change rates of effective search (or return rates v_{ij} from predation-vulnerable behavioral states).

Whereas Eq. (6) makes sense as a way of representing the mechanisms like hunger (as measured by c_{it}/c_{io}) that might drive animals to spend more time foraging when food intakes drop below normal, it is not clear that it is so sensible to assume such a direct linkage between foraging time and predation risk as is assumed with $v'_{jit} = v'_{ij}/F_{it}$ as suggested above. In particular, there may be some predators k who, in fact, specialize on attacking animals that move rapidly into behavioral states (such as schooling or seeking shelters in coral reefs) so as to reduce vulnerability to other predators. An example is provided by piscivorous reef predators whose vision is adapted for hunting under twilight when the diurnal and nocturnal fish shift between shelter and feeding grounds (Hobson 1972; Hobson and others 1981). In that case, increasing v'_{jit} to reduce predation risk by predator j should be linked to increase in vulnerability to predator k . Presumably, the basic risk due to such k -type predators is not that high, or that risk would have driven selection against using the avoidance behavior in the first place. The ubiquity of strong predator avoidance behaviors argues that there are dominant types of predation risk. We do not know how to deal with this problem further. The EcoSim interface

allows setting of v_{ij} values for individual predator types j , so as to capture basic differences in prey exposure patterns and exposure rates (see Walters and others 1997). But we cannot at this point offer a comprehensive interface that defines predation risk more broadly by behavior type rather than exposure to particular predators. There are simply too many kinds of behaviors that can alter predation risk in the first place, and these are linked in complex ways to the behaviors associated with foraging.

Including high F_i^{\max} values in an EcoSim II scenario can lead to strong compensatory predation effects on the prey of species i and hence to effects such as multiple equilibria in community structure. Increasing F with decreasing feeding rate is essentially the same as including a type II functional response in feeding rate representation. Whereas our derivation is conceptually different from accounting for effects of handling time, the overall consequence is the same in terms of feeding rates that do not drop off proportionally with decreasing prey density.

Setting large F_i^{\max} values for juveniles of split pools causes density-dependent mortality (exposure to predation increasing with decreasing feeding rate) that is similar to the effect expected from combining density dependent growth with size dependent mortality as in the mahi-mahi example mentioned above. In this example, we suspect that the juveniles must forage nearly all the time to achieve their high growth rates, and so F_i^{\max} for mahi-mahi must be near 1.0. Indeed, we cannot reproduce the observed population cycles with values much larger than 1.0. Thus, EcoSim II may correctly predict density dependent effects of reduced food availability to juveniles even if it fails to display the growth effect of such reductions. However, this may not be a serious flaw considering that size-selective mortality will tend to cause increased average body size in the first place, leaving survivors with growth patterns similar to what EcoSim II will predict. Thus, we can view the behavioral exposure mechanism as a way to partially mimic the apparent growth increase due to selective removal of smaller individuals that ordinarily would be modeled with much more complex individual-based calculations.

FECUNDITY CONSTRAINTS

For split biomass pools, we can estimate a baseline recruitment rate R_0 to each adult pool by assuming equilibrium in Eq. (3) as noted above. These animals recruit to the simulated population at age k months, and we can backcalculate baseline recruit-

ment R^*_o at age 0 months from $R^*_o = R_o \exp(Z_{J,0}k)$. A basic problem is then to predict how R^* will vary over time with changes in adult abundance, feeding rate, and/or body size, that is, to define a reasonable recruitment function $R(B_{A,t}, N_{A,t}, C_{A,t})$. For EcoSim II, we have elected to assume that R^* is limited by recent feeding rate rather than accumulated food intake as reflected in body size. We use the following function to represent this limitation:

$$R(B_{A,t}, N_{A,t}, C_{A,t}) = R^*_o (N_{A,t}/N_{A,0}) \times [(1 - P_g^{\text{realized}})C_{A,t}/((1 - P_0)C_{A,0})]^r \quad (7)$$

This relationship scales R relative to R^*_o by the ratio of adult abundance at time t to initial ($N_{A,t}/N_{A,0}$), and by the ratio of per biomass food consumption allocated to reproduction $(1 - P_g^{\text{realized}})C_{A,t}$ to the baseline food allocated. The power parameter r can be used to generate nonlinear effects of the food consumption rate on recruitment per adult individual. As an example, setting $r \ll 1$ implies that adults maintain near constant per capita production of recruits except when food consumption rates are very low.

We have explored other recruitment relationships, for example substituting adult body weight $w_{A,t} = B_{A,t}/N_{A,t}$ for per capita consumption rate $C_{A,t}$ in Eq. (7) or substituting an index of cumulative consumption allocated to reproduction over several time steps for the single step index $C_{A,t}$. These alternatives appear to have little effect on the basic time predictions, except to alter transient patterns somewhat under simulation regimes where fishing mortality rates change very rapidly over time. We also have explored the possibility of applying the r power parameter to the ($N_{A,t}/N_{A,0}$) ratio as well as food allocated to reproduction, so as to force less dependence of R on both adult abundance and feeding rate. This amounts to assuming density dependence in survival rate at some undefined early life history stage before recruitment to the juvenile stage, and we consider this a very dangerous assumption to make.

POTENTIAL APPLICATIONS FOR ECOSIM II

EcoSim I has been fairly widely distributed, and there is a growing demand for EcoSim II. Judging from interests expressed by and applications already underway by initial users of these programs, we see at least four types of applications where the model may prove useful: (a) test of hypotheses from theoretical ecology about ecosystem functions; (b) policy screening for proposed ecosystem manage-

ment strategies; (c) consistency checking for hypotheses about impact of long-term regime shifts; and (d) evaluation of possible trophic causes for nonstationarity in single-species recruitment relationships. Vasconcellos and others (1999), based on the original version of EcoSim, provide an example for the first type of application.

As a policy screening tool, EcoSim II should be able to provide at least two useful outputs. First, it should be able to show whether minor adjustments (aimed at giving the appearance of integrated ecosystem management without in fact involving major policy change) are likely to have measurable effects. Second, it should be able to help detect whether there is a significant risk that proposed changes will "backfire," either by causing unintended trophic side effects or by failing to account for transient effects of moving from the current ecosystem state to a more desirable one. For example, there is a strong public demand for protection of marine mammals. However, allowing a rapid increase in mammal populations while their fish prey populations are depressed from fishing easily leads to conflicts, as is presently the case off Newfoundland, where seals now have a significant impact on the much reduced cod stock. Likewise it might be worthwhile to reduce by-catches of juveniles of valuable fish species in shrimp trawl fisheries. However, the by-catch reduction measures may result in substantial increases in abundance of fish species that are not valued along with substantial reductions in net juvenile survival rate of the shrimp due to having more of these predators around (Pauly 1982).

Many plausible verbal explanations exist for the major abundance changes in some marine ecosystems that have accompanied changes in fishing and climate regimes. For example, NAS (1996) describes an interesting hypothesis about how changes in whale populations in the Bering Sea may have permitted increases in pollock (*Theragra chalcogramma*) populations just as the pollock fishery was developing, which in turn may have led to a chain of impacts that eventually resulted in reduced productivity of other marine mammal and sea bird populations. There is a real need to complement such "word models" with the "mechanized deductions" that models can do, so as to track all interactions at once, and hence avoid "hidden assumptions" and logical inconsistencies that are all too easy to overlook in verbal explanation. Such consistency checks obviously do not prove anything about what is really going on in the field but should help in formulation of more precise hypotheses for field evaluation and testing.

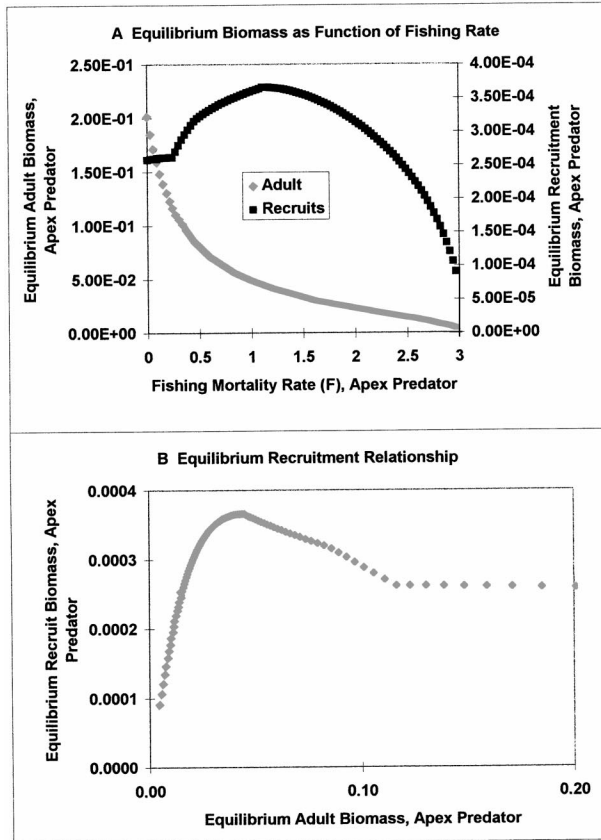


Figure 2. Equilibrium relationships predicted by EcoSim II, from an Ecopath file representing the oceanic part of the South China Sea (OCEANSCS; Christensen and Pauly 1992b). (A) Equilibrium spawning biomass and recruitment as a function of fishing mortality rate on apex predators. (B) Recruitment as a function of spawning biomass. Dome-shaped recruitment relationships as in B are commonly predicted by EcoSim II, with declining recruitment biomass at high stock sizes due to a mixture of cannibalism and competitive effects.

For split biomass pools that are modeled by delay-difference relationships, EcoSim II “generates” a stock-recruitment relationship as an emergent consequence of trophic interactions and life history responses to trophic opportunity and risk. Indeed, when we run EcoSim II with slowly varying fishing mortality, leading to a set of near equilibrium stock sizes and recruitment rates over time, we see stock-recruitment patterns that look generally like the traditional Beverton-Holt and Ricker relationships (Figure 2). Changes in trophic interactions can even lead to dome-shaped equilibrium relationships that are caused not by cannibalism, but by changes in competitive conditions for juveniles when adult abundance is high. But EcoSim II warns that we may see gross nonstationarity (Walters 1987) in recruitment patterns sampled from communities

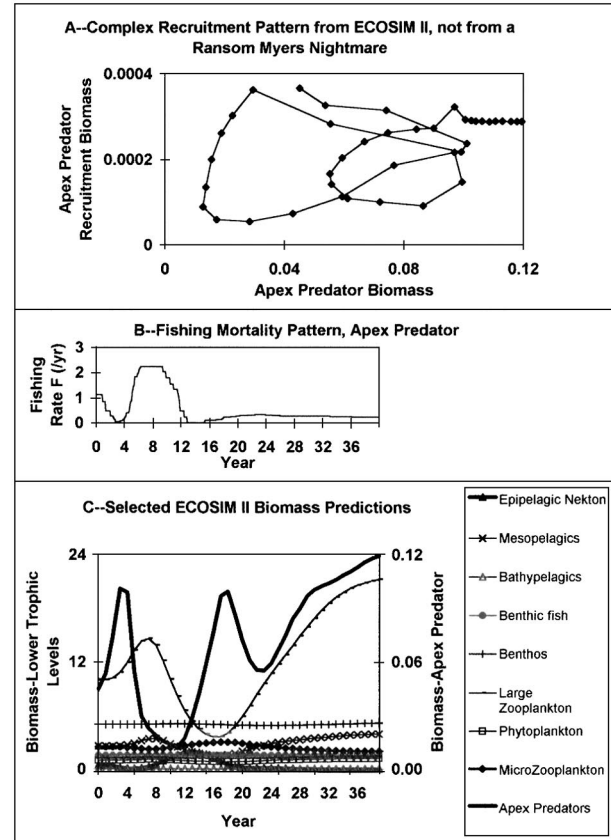


Figure 3. Transient relationship between adult spawning biomass and biomass of recruits (A) predicted by EcoSim II, based on an Ecopath file representing the oceanic part of the South China Sea (OCEANSCS; Christensen and Pauly 1992b). Test fishing mortality pattern (B) and simulated biomass responses (C) for main model biomass pools shown for comparison to the recruitment pattern in B and C.

subject to rapid changes in fishing regimes over time (Figure 3). The severity of this nonstationarity appears to depend mainly on what we assume about the behavioral vulnerability parameters v_{ij} ; when these vulnerabilities are assumed low (so that biomass pools are weakly coupled by predation interactions), nearly stationary relationships of Beverton-Holt form appear to be the most likely EcoSim II prediction. High vulnerabilities, and hence larger changes over time in other pools besides the one(s) modeled explicitly by delay-difference relationships, appear more likely to result in dome-shaped recruitment relationships as well as worse nonstationarity. Hence, EcoSim II may help us define more precise hypotheses to explain the nonstationarity that has been observed in many recruitment relationships.

One startling and very worrisome prediction that has appeared for several case systems is the possibil-

ity of recruitment failures by dominant, large piscivores when overfished. In *Ecosim II*, dominant piscivores are generally species that “cultivate” the ecosystem by cropping down smaller fishes that are in turn potential predators/competitors with juveniles of the dominant species. When the piscivore is severely depleted, these smaller fish can increase dramatically in abundance (if not limited by other predation/competition interactions in the model), causing severe decrease in juvenile survival for the piscivore. Such “delayed depensation” effects obviously can result in multiple population equilibria, or at least severely hamper efforts at population rebuilding.

THE MESOSCALE GAP AND OTHER POSSIBLE PITFALLS

EcoSim II focuses on processes and interactions at two very different space–time scales. Eqs. (1), (5), and (6) are essentially concerned with the description of foraging and prey avoidance processes on very small spatial scales and over time scales of hours and days. Eqs. (2) to (4) and (7) aim to predict the integrated effects of trophic processes over much larger areas and time scales on the order of years to decades, and have helped us see how microscale behavioral effects may have profound long-term impacts on the dynamic responses of aquatic ecosystems to harvesting impacts. But there is a profound gap in *EcoSim II*, and this gap involves mesoscale spatial and temporal processes (seasonal time scales, spatial scales over which the life histories of many animals are spread) that have been very difficult for ecologists to study. We do not, for an obvious example, explicitly model the spatial and seasonal dynamics associated with “match–mismatch” hypotheses about recruitment variation (Cushing 1981), as demonstrated dramatically in a recent study of striped bass recruitment (McGovern and Olney 1996), or for that matter any of the other mechanisms that have been proposed to explain short-term variation in recruitment rates. We do not model the mesoscale trophic ontogeny that accompanies changes in juvenile body size and habitat occupancy patterns, except in terms of a two-stage shift between juvenile and adult biomass categories. We do not represent the seasonal variation in key physical factors like temperature and currents that substantially influence immigration, emigration, metabolic, and predator–prey encounter rates. There is, however, a seasonal and long term “shaper” interface in *EcoSim II* that potentially can be used to test the effects of mesoscale temporal variation in factors such as primary production and feeding

rates, but it cannot deal at all with variation that arises from mesoscale spatial processes that affect such things as overlap patterns between prey and predators.

On the positive side, it is not entirely clear that we must understand all the mesoscale complexity to design wise policies for long-term ecosystem management. Mesoscale effects, such as strong interannual variation in recruitment rates, are certainly important for management, especially in settings where fishery managers are required to set annual quotas and other harvest regulations that can result in compensatory fishing effects should stock sizes be less than expected. But aside from such management effects, it is not obvious that erratic interannual variation in recruitment to many fish species has any major, persistent consequences for ecosystem structure and overall trophic interactions. Certainly, a strong year-class of *X* may provide extra food for species *Y* for several years, so the variation in *X* will reverberate through the ecosystem to at least some degree. But most of the microscale processes that we have described in *EcoSim II* should tend to dampen such effects and lead to the appearance of weak coupling among species. However, the lack of short-term response and obvious year-to-year coupling of variations is not evidence at all for ignoring long-term trophic support structure and biodiversity in food web interactions. To design sustainable ecosystem management policies, we surely will have to account very carefully for the unfolding of trophic effects on longer time scales as emphasized in *EcoSim II* time integrations.

There is possibly a more fundamental weakness in *EcoSim II*, and other existing models for trophic interaction effects, than inadequate representation of mesoscale effects. Existing models assume additivity in mortality components, such that the total mortality rate *Z* is simply the sum of all predator, fishing, and other natural loss rates. The additivity assumption would be wrong if there is a limited subset of animals that have relatively high risk of loss to all/any mortality agents, so that *Z* represents the loss of this subset and component loss agents trade off against each other without affecting *Z*. *EcoSim II* represents a step toward the limited subset assumption, through the notion that only limited numbers of animals may become behaviorally vulnerable to predation per unit time. But if it is more broadly applicable, then we may be wasting our time to do assessments of trophic linkages in the first place, except in situations where we are concerned about the impact of competitive interactions implied by having a strictly limited subset of prey available per time.

Another potentially dangerous weakness in EcoSim II is use of equilibrium assumptions to simplify parameter estimation (mass balance assumed in Ecopath, and equilibrium biomass numbers in setting up delay-difference parameters and initial population structure). This is the same simplification often used in fitting surplus production and delay-difference population models to single-species time-series data under "observation error" assumptions (set initial biomass B_0 equal to carrying capacity K , so as to omit one of these parameters from the estimation scheme; see Hilborn and Walters 1992; Polacheck and others 1993). Unless the initial Ecopath assessment accounts for biomass trends underway at the reference time point for which consumption and fishing rates are provided, it will force EcoSim II state and parameter estimates to imply that the initial state and flow structure are sustainable. Thus, we encourage Ecopath users to estimate the "biomass accumulation" term included in versions 3.0 and later of Ecopath (Christensen and Pauly 1995), which allows accounting for at least some of the lack of equilibrium in modeled systems and thus leads to more realistic EcoSim parameterizations.

CONCLUSIONS

The mesoscale gap and the question of additivity, along with uncertainty about the best choices for process assumptions in the microscale relationships, imply that EcoSim II predictions must be treated strictly as hypotheses. But exactly the same uncertainties apply to all models that have attempted to describe and predict effects of trophic interactions; the basic uncertainties about behavioral responses and capabilities have not been resolved by detailed modeling based on MSVPA techniques or individual-based models and cannot be resolved by appeal to general "principles" about ecosystem organization. Furthermore, it is absurd to assume that the best model is one in which all the parameter settings are such that species are effectively decoupled from one another (very low v_{ij} , high W_g , high F_{it}), such that only single-species compensatory responses need be considered in management design. Indeed, this is precisely what we are doing now in single-species assessment and policy making. We do not have the functional and quantitative information to design very credible ecosystem management models, but we are not ever going to get that information if we insist on describing every detail before proceeding to make and test predictive models, or if we insist at the other extreme that there are no ecosystem effects worth worrying about.

Intersystem comparisons may be useful to address at least some of these issues. For such comparisons, suitably standardized and structured information about ecosystem function and exploitation are required from as many systems as possible. The combined use of Ecopath and EcoSim offers an avenue for this, especially as they are integrated in the new release of "Ecopath 4 with EcoSim," freely available for download from the web sites (www.ecopath.org, www.fisheries.com). Many applications using Ecopath have been published worldwide over the last decade, and these in turn have facilitated global syntheses of the state and structure of aquatic ecosystems (for example, Pauly and Christensen 1995; Christensen 1996). Many more are forthcoming, notably through a recently started activity, funded by the European Commission. This 4-year project will involve 31 institutions through the Atlantic and Eastern Pacific in a series of courses and workshops at which Ecopath and EcoSim will be used to construct and compare models of a variety of marine ecosystems and to help identify suitable ecosystem management regimes.

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