Wikiprint Book

Title: 12 Capabilities and limitations

Subject: Ecopath Developer Site - EwEugCapabilitiesAndLimitations

Version: 4

Date: 2024-03-29 07:13:26

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EwE has been developed largely through case studies, where users have challenged us to add various capabilities and as we have seen inadequacies through comparison to data; see as a good example the discussions in the proceedings from an FAO workshop on the application of EwE (Pauly 1998). Various capabilities have been added to EwE in response to these challenges, and there have inevitably been some uncertainty about what the approach and software presently can and cannot do, and about how it should be used in the design of sustainable fisheries policies. Such uncertainty may be expressed through too simplistic interpretations of what mass balance and biomass dynamics models are capable of representing, through to unwarranted optimism about how it should be used to replace or complement existing assessment tools. Here we review the capabilities and limitations through a series of 'frequently asked questions', followed by explanations of what we think EwE is actually capable of doing.

Note that many of the questions discussed below have their root in an assumption that EwE is somehow intended to supplant or replace single-species assessment methods. Our primary goal when developing EwE has been to develop a capability for asking policy questions that simply cannot be addressed with single-species assessment. Examples are questions about impacts of fishing on nontarget species, and the efficacy of policy interventions aimed at limiting unintended side effects of fishing. Also, as is shown through examples below, EwE can now incorporate time series data from single-species assessment as input and use these for parameter fitting. We indeed advocate an iterative process where information is passed between single-species analysis and EwE to check and improve estimates in the process, addressing questions about the degree to which ecosystem events can and cannot be attributed to impact of fisheries, climate change, etc.

Does Ecopath assume steady state or equilibrium conditions?

Ecopath provides an 'instantaneous' estimate of biomasses, trophic flows, and instantaneous mortality rates, for some reference year or multi-year averaging window. Biomasses need not be at equilibrium for the reference year, provided the Ecopath user can provide an estimate of the rate of biomass 'accumulation' (or depletion) for each biomass for that reference year. In fact, in a number of cases, e.g., Christensen (1995b) it was necessary to recognize that biomasses were in fact changing over the period for which Ecopath reference data (B, P/B, Q/B, diet composition) were provided. In these cases, assuming equilibrium for the reference year led to overly optimistic estimates of sustainable fishing mortality rates.

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

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

Another aspect is that ecosystem models can help direct research by pinpointing critical information and gaps in the present knowledge. As more information becomes available it is straightforwardly included in the model, improving estimates and reducing uncertainty.

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

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

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

When EwE is used for policy comparison, it is important to recognize that incorrect comparisons (EwE leading user to favour a wrong policy) are not due to uncertainty in general about the model parameters, but rather to errors in specific input data to which the particular policy comparison is sensitive. In other words, EwE can give correct answers for some policy comparisons but wildly incorrect ones for others, so it is meaningless to claim that it should not be used because of uncertainty in general. For example, EwE predictions of the impact of increasing fishing rates for a particular species are most sensitive to assumptions about vulnerability of prey to that species, since the vulnerability parameters largely determine the strength of the compensatory response by the species to increased mortality rate. But even if EwE predicts the strength of the compensatory response to fishing correctly, it may still fail to predict response of that same species to a policy aimed at increasing its productivity by reducing abundance of one or more of its predators: EwE may have a good estimate of total mortality rate for the species, but a very poor estimate of how that mortality rate is distributed among (or generated by) predators included in the model.

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

Instantaneous snapshots of biomass, flows, and rates of biomass change have sometimes been used to draw inferences about issues such as ecosystem health as measured by mean trophic level or other indices of fishing impact, (e.g., Christensen, 1995a; Pauly and Christensen, 1995; Pauly et al., 1998a). But the snapshots cannot be used directly to assess effects of policy changes that would result in changes in rates, (e.g., reduction in fishing rates) since the cumulative effects of such changes cannot be anticipated from the system state at one point in time. In fact the Ecosim part of EwE was initially developed specifically to provide a method for predicting cumulative changes, while recognizing that all rate processes in an ecosystem may change over time, as biomasses change. For example, one might conclude from the Ecopath mortality rate estimates or mixed trophic impact analysis that reducing the abundance of some particularly important predator might result in lower mortality rates of its prey, and hence growth in abundance of these prey. This prediction may hold for a short time, but might be reversed entirely over longer time scales due to increases in abundance of other predators or on an intermediate time scale due to predator prey switching in response to the initial responses in prey density.

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

Ecologists have long sought simple ways of predicting productive potential of aquatic ecosystems from 'bottom up' arguments about efficiency of conversion of primary production into production of higher trophic levels, (e.g., Polovina and Marten, 1982). While Ecopath inputs can be organized so as to provide such predictions, we do not recommend using EwE for management this way. There are simply too many ways that simple efficiency predictions can go wrong, particularly in relation to 'shunting' of production into food web components that are not of direct interest or value in management, (e.g., ungrazeable algae, fish species that are not harvested). Ecopath can help provide broad bounds for potential abundances and production in an exploratory research mode, but these bounds are unlikely to be tight enough to be useful for management planning related to fishery development or recovery potential.

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

In most EwE applications today, we try very hard to avoid using the Ecopath biomass estimation capability for more biomass components than absolutely necessary. Estimation of biomass with Ecopath usually requires making explicit assumption about the ecotrophic efficiency, i.e., about the proportion of the total mortality rate of a group that we account for by the predation, migration, biomass accumulation and fishing rates included explicitly in the Ecopath data. There is rarely a sound empirical basis for using any particular value of EE, except perhaps for top predators in situations where total mortality rate (Z=P/B) is well estimated and EE represents a 'known' ratio of fishing rate (F) to total Z (and the rest of Z, e.g., the natural mortality (M) is known not to be due to other predators included in the model nor to other factors not considered).

Where biomasses really are unavailable or are known to be biased, e.g., if the only biomass estimates for pelagics are from swept-area analysis based on demersal trawling, it may still be better to use assumed EE's than to stop short of constructing an ecosystem model pending, e.g., funding and development of capabilities to conduct acoustic surveys. In such cases one can assume reasonable EE values for groups where biomasses are missing - an example: small pelagics do not die of old age in an exploited ecosystems, most are either eaten or caught, hence EE is likely to be in the range 0.90 to 0.99. As confidence intervals can be assigned to all input parameters and can be estimated for the output parameters using the Ecoranger module of EwE (where a range for acceptable output parameters is also incorporated as part of the model evaluation process), the mass balance constraints of the model can be used to predict potential ranges for biomasses of the system in the system,

Should Ecopath mass balance modelling be used only in situations where data are inadequate to use detailed, more traditional methods like MSVPA?

Multispecies virtual population analysis (MSVPA) has been used to reconstruct age-size and time dependent estimates of trophic flows and mortality rate components, using the VPA assumption that historical abundances can be inferred by back-calculating how many organisms must have been present in order to account for measured and estimated removals from those organisms over time (Sparre, 1991; Magnússon, 1995). In a sense, Ecopath does this as well, but generally does not account for size-age dependency and temporal variation (biomasses are constrained to be large enough to account for assumed removals estimated from biomasses, consumption/biomasses, and diet composition of predators, just as in MSVPA).

But the really big difference between Ecopath and MSVPA is not in the detail of calculations; constructing an Ecopath model that details age, size and time components would be tedious but feasible. The more important difference is in the use of direct data on total mortality rate by Ecopath, in the form of the P/B ratio that Ecopath users must provide. Ecopath biomass and mortality estimates are 'constrained' to fit the total mortality rates entered as P/B data. In contrast, MSVPA (like single-species VPA) can produce cohort abundance patterns (die-off patterns over age-size and time) that do not agree in any way with apparent cohort decay patterns evident from direct examination of the size-age composition data. In effect, the MSVPA (and VPA) user must reject or ignore any direct evidence about total mortality rate Z that might be present in age-size composition data, and must treat discrepancies between apparent Z from the cohort reconstructions versus apparent Z from composition data as being due to size-age dependent changes in vulnerability to the composition sampling method. This can be unwise, just as it has been unwise to ignore information about Z in single-species VPA, (e.g., Newfoundland cod VPA's resulted in much lower estimates of Z than would be estimated from catch-curve analysis of the age composition data, and in this case it turned out that VPA tuning resulted in underestimates of fishing mortality rate,Walters and Maguire, 1996).

It is obviously comforting to us as biologists to be able to provide more detailed accounting of predation interactions, which are almost always size and age dependent. But in assessments of ecosystem-scale impacts of changes in trophic conditions, it is not automatically true that the best aggregate estimate is the sum of component estimates, any more than it is automatically true in single-species assessment that more detailed models and data always provide better assessments than simpler models. For statistical and logical reasons, the 'more is better' argument is no more valid in dynamic modelling than it is in multiple regression analysis, where we are familiar with how adding more independent variables often results in better fits but

poorer predictions.

As noted in the following two points, Ecopath and Ecosim do not 'ignore' the fact that trophic interactions are strongly size-age and seasonally structured. Rather, we assume that initial (Ecopath base or reference period) structuring has been adequately captured in preparing average/total rate input data, and that changes in structural composition over time are not large enough to drastically and persistently alter interaction rates/parameters. This is very similar to the assumption in single-species biomass dynamics and delay-difference modelling that stock composition changes produce regular or predictable changes in overall (stock-scale) production parameters, not that there is no composition effect in the first place.

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

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

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

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

The biomass rate equations in Ecosim (sums of consumption rates less predation and fishing rates) can be viewed as 'sums of sums', where each trophic flow rate for an overall biomass pool is the sum of rates that apply to biomass components within that pool. In this view, doing a single overall rate calculation for a pool amounts to assuming that the proportional contributions of the biomass components within the pool remain stable, i.e., the size-age-species composition of the pool remains stable over changes in predicted overall food consumption and predation rates. In fact, the assumption is even weaker: pool composition may indeed change over time provided that high and low rate components change so as to balance one another; or proportional contribution of major components is stable enough so that total rates per overall biomass are not strongly affected.

We know of at least one condition under which the compositional stability assumption may be violated - when ratios of juvenile to adult abundance can change greatly, (e.g., under changes in fishing mortality) for a species that has strong trophic ontogeny (very different habitat use and trophic interactions by juveniles). To deal with such situations, Ecosim allows model users to 'split' biomass pools representing single-species with strong trophic ontogeny or size-dependent vulnerability to harvest, into multiple-age stanza groups. For populations represented this way, the Ecosim biomass dynamics equations are replaced with an explicit age structured model for monthly age cohorts in each of the stanzas (animals are lumped into one adult age group after reaching 95% of the asymptotic maximum body weight). The cohorts in each stanza can have distinctive diet composition and predation risks. Food search rates and metabolic rates per individual are calculated so as to have the animals Figure growth with a basic von Bertalanffy functional form, but with growth rates varying with food availability. Recruitment is calculated for each month from total egg production, and egg production per individual is assumed to increase linearly with body size above a size at maturity.

Thus, for multi-stanza species Ecosim replaces the biomass dynamics model with a much more detailed and realistic population model, (see Representation of multi stanza life histories?). This allows Ecosim users to not only represent compositional effects, but also to examine the emergent stock-recruitment relationship caused by density-dependent changes in adult fecundity and juvenile growth and foraging time behaviour.

Do ecosystem biomass models ignore behavioural mechanisms by treating species interactions as random encounters?

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

Ecosim was constructed around the proposition that this mass-action principle is deeply incorrect for ecological interactions, and instead interactions take place largely in spatially and temporally restricted 'foraging arenas' where prey make themselves available to predation through activities such as foraging and dispersal. To represent this within-pool heterogeneity, we treat each biomass pool as consisting at any instant of two biomass components with respect to any predator, one sub-pool of individuals vulnerable to the predator and another sub-pool 'safe' from the predator. In this view, predation rate is limited jointly by search efficiency of the predator for vulnerable prey individuals, and exchange rate of prey between the invulnerable and vulnerable states. When Ecosim users set the vulnerability exchange rates to high values, the model moves toward 'top down' or mass-action control of predation rates. When users set the vulnerability rates to low values, the model moves toward 'bottom up' control where predation rates are limited by how fast prey move (or grow, or disperse) into the vulnerable state.

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

simpler Lotka-Volterra mass-action models.

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

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

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

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

In Ecosim, changes in prey abundance (factor (2) above) lead to proportional changes in predator diet composition only when prey feeding times are deliberately held constant by 'turning off' Ecosim foraging time adjustment parameters. When prey foraging time is allowed to vary (default assumption), declines in prey density generally result in apparent sigmoid (type III) decreases in predator consumptions of that prey type: as the prey declines, it generally spends less time feeding (reduced intraspecific competition for its own prey) and hence reduced encounter rates with its predators. The user can exaggerate this sigmoid effect by turning on parameters that cause the prey to spend less time feeding when predation risk is high (i.e., direct response to perceived predation risk).

Predator satiation effects are represented in Ecosim by foraging time adjustments such that predators 'try' to maintain constant food consumption rates (unless foraging time adjustments are deliberately disabled), by spending more time feeding when feeding rates begin to decrease due to decreasing densities of one or more prey types. Likewise, handling time limits to feeding rate (lower attack rate on any one prey type as abundance of another increases, due to predator spending more time pursuing/handling individuals of the other type) are represented by a 'multispecies disc equation' (generalization of Holling's type II functional response model).

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

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

In a number of case studies, Ecosim users have treated the model as though it were a single-species assessment tool, varying its parameters so as to fit time series data for a particular species, (e.g., yellowfin tuna in the Eastern Pacific, herring in southern British Columbia). In such cases, it generally turns out that the biomass dynamics or delay-difference 'submodel' for the target species behaves quite similarly when 'embedded' in Ecosim (with explicit accounting for production and mortality rate as function of food resources and predators) to the corresponding single-species assessment model where competition effects are represented as implicit functions of stock size, (e.g., stock recruitment model) and predation mortality rates are assumed constant.

So if one has an Ecosim model whose 'production' parameters have been estimated by fitting the model to single-species data, and a corresponding single-species model also fitted to the data, one should not be surprised that the two approaches usually give about the same answers to policy questions related to changing fishing mortality rate for the species, (e.g., fishing rates for MSY). Ecosim models may diverge from the single-species predictions at very low stock sizes (Ecosim may predict 'delayed depensation' effects due to changes in predation rates on juveniles), but otherwise do not generally lead us to interpret the single-species data any differently with respect to single-species assessment issues, (e.g., MSY) than if we just used the single-species model.

Thus, it would be wrong when applying Ecosim for single-species harvest policy analysis to contend that Ecosim is 'better' than a single-species model, when both give the same answer. It may comfort us to know as biologists that the Ecosim representation has somehow explained production in terms of ecosystem relationships rather than implicit relationships on stock size, but making biologists 'feel better' should not be a criterion for judging the effectiveness of a policy tool. When fitting Ecosim to the data we encounter the same risks as in single-species assessment of incorrect biomass estimation, misinterpretation of trend data, (e.g., hyperstability of catch per effort data), and failure to account for persistent effects such as environmental regime changes or confounding of these effects with the effects of fishing.

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

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

In one case (the Strait of Georgia, British Columbia) where we have fit Ecosim to multiple time series data on major species (herring, salmon, hake, ling cod, seals) by estimating 'shared production anomalies' attributed in the fitting to changes in primary productivity, we were able to show that about half the total variance around single-species model fits to changes in relative abundance over time could be explained by ecosystem-scale effects. That is, we were able to 'improve' on the single-species fitting, but this improvement was due to assuming changes in ecosystem scale 'forcing' rather than to accounting for temporal variation in predation mortality rates associated with impacts of fishing on predators. In another case (French Frigate Shoals, Hawaii) we were again able to fit time series data (rock lobsters, monk seals) better by including effects of an ecosystem-scale regime shift (decreased primary production in the Central North Pacific after 1990), and were not able to explain deviations from single-species model fits through changes in trophic interactions alone.

These cases, along with experience that Ecosim generally does not behave much differently from single-species models when only fishing effects are considered, lead us to suspect that Ecosim (and perhaps other, more detailed trophic interaction assessments) will not lead to substantial improvements in stock size prediction just by accounting for predator-prey effects. However, there is a good chance that Ecosim will be very helpful in interpreting effects of large-scale, persistent regime changes that are likely to have caused ecosystem-scale changes in productivity. In such situations, Ecosim may be particularly helpful in finding some resolution for the so-called 'Thompson-Burkenroad' debates about the relative importance of fishing versus environmental changes in driving historical changes in abundance (see Skud, 1975 for a review) .

Rather than treating Ecosim and single-species methods as if they were competitors, a useful assessment tactic may be to work back and forth between Ecosim and single-species assessment methods, using each to check and improve the other. For example, we have used ordinary VPA and stock synthesis results for Pacific herring as reference 'data' (summary of raw age composition, harvest, and spawn survey data) for fitting Ecosim models of the Georgia Strait. The Ecosim herring model predicts somewhat lower abundances than VPA during periods of low stock size, and somewhat higher abundances than VPA during high stock periods. Ecosim also estimates lower natural mortality rates (M) for herring during the low abundance periods. If Ecosim is correct in estimating that M has been (weakly) density-dependent, then VPA has probably overestimated abundance (used too high an M in the VPA backcalculation) during population lows, and is probably underestimating juvenile abundance now (due to using an M that is too low for the current high stock size).

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

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

Search procedures are most useful in diagnosing problems with both the model and data. That is, the greatest value of doing some formal estimation is while it seems not to be working, when it cannot find good fits to data. Poor fits can be informative about both the model and the data.

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

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

Discarded bycatch can be treated as a biomass pool in Ecopath, i.e., as a diet component (and hence component of production) by species that consume discards (e.g. sharks, birds, shrimp, and crabs). Ecopath input data on bycatch and discard rates are passed to Ecosim, and Ecosim does time accounting for changes in discard rates and biomass in relation to simulated changes in fishing fleet sizes. In scenarios where some species are heavily dependent on bycatch, Ecosim will then track impacts of bycatch management on food availability and feeding rates of such species. For instance, Ecosim has produced some very interesting scenarios for shrimp fishery development and how shrimp often appear to become more productive under

fishing, by including effects of both reducing abundance of predatory fishes (when they are killed as bycatch) and providing biomass from those fishes as food for the shrimp.

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

Ecosim users have two options for specifying fishing mortality rate patterns: (1) direct entry of fishing rate (F) values over time; or (2) entry of relative fishing effort values over time, with fishing rate calculated as q(B)·(relative effort), where q(B) is a biomass-dependent catchability coefficient. Under the second option, q is modelled as a hyperbolic function of B ($q = q_{max} / (1 + kB)$), 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.

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

Depensatory recruitment changes are apparently not common (Myers et al., 1995; Liermann and Hilborn, 1997), but should not be ignored in risk assessments for situations where a depensatory recruitment decline would have large economic or social consequences. Depensatory effects are usually assumed to be due to Type II predator feeding effects, where predators would exert an increasing mortality rate on juvenile fishes if they tend eat a constant number of juveniles despite decreasing juvenile density. There are relatively few field situations where we would expect such type II predator feeding effects (like migrating pink salmon fry being eaten by resident trout in a small stream).

Ecosim has helped identify another possible depensation mechanism that may be more common, which we call the 'delayed depensation' or 'cultivation-depensation' effect (Walters and Kitchell, 2001). When a large, dominant species is fished down in Ecosim models, the model often predicts a substantial increase in smaller-sized predators that have been kept down in abundance by a combination of direct predation and competition effects with the large dominant species. These predators then cause an increase in predation mortality rate on (or compete for food with) juveniles of the large dominant. This causes a depensatory decrease in the recruitment rate per spawner for the large dominant, slowing or preventing population recovery even if the fishing effects are removed.

So far from ignoring depensatory recruitment effects, Ecosim warns us to be more careful about the risk of these effects. It warns us to be especially wary in the management of the most common, large, and dominant fish species that are the most valuable components of most fisheries.