Walters, C. V. Christensen and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* 7(2): 139-172.

Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments

CARL WALTERS[1*], VILLY CHRISTENSEN[2] and DANIEL PAULY[1,2]

[1]*Fisheries Centre, The University of British Columbia, 2204 Main Hall, Vancouver, BC, Canada V6T 1Z4*
[2]*International Center for Living Aquatic Resources Management, MC PO Box 2631, 0718 Makati City, Philippines*

Contents

*Author to whom correspondence should be addressed. *E-mail: Walters@fisheries.com*

Abstract

The linear equations that describe trophic fluxes in mass-balance, equilibrium assessments of ecosystems (such as in the ECOPATH approach) can be re-expressed as differential equations defining trophic interactions as dynamic relationships varying with biomasses and harvest regimes. Time patterns of biomass predicted by these differential equations, and equilibrium system responses under different exploitation regimes, are found by setting the differential equations equal to zero and solving for biomasses at different levels of fishing mortality. Incorporation of our approach as the ECOSIM routine into the well-documented ECOPATH software will enable a wide range of potential users to conduct fisheries policy analyses that explicitly account for ecosystem trophic interactions, without requiring the users to engage in complex modelling or information gathering much beyond that required for ECOPATH. While the ECOSIM predictions can be expected to fail under fishing regimes very different from those leading to the ECOPATH input data, ECOSIM will at least indicate likely directions of biomass change in various trophic groups under incremental experimental policies aimed at improving overall ecosystem management. That is, ECOSIM can be a valuable tool for design of ecosystem-scale adaptive management experiments.

Introduction

There is an emerging consensus among fisheries scientists and managers of aquatic resources, that traditional single-species approaches in fisheries management ought to be replaced by 'ecosystem management' – that is, with approaches that explicitly account for ecological interactions, especially those of a trophic nature, as well as for other uses of ecosystem resources than for fisheries. There is more to this trend than the obvious concern that we cannot simply batter away at the parts of an ecosystem as though these parts were isolated. Taking an ecosystem view also invites the use of other instruments of management in addition to harvest regulation, such as enhancement of basic productivity, stock enhancement, and provision of physical structure to moderate trophic interactions by providing refugia for prey in predator–prey interactions, or marine protected areas.

There is, on the other hand, less of a consensus concerning the tools (conceptual and analytical) that should be used to formalize and study trophic interactions among the elements of fisheries resources systems. Three approaches have gained some ground, but none has received general acceptance. First, there is the detailed approach represented by multispecies virtual population analysis (MSVPA, Sparre, 1991), inspired by the multispecies age-structured population models of Andersen and Ursin (1977). MSVPA utilizes extensive time series of catch-at-age data to produce natural mortality rates and population estimates for the exploited part of ecosystems. Further it makes prognosis of the impact of changes in fishing intensity, mesh sizes, etc. MSVPA has been applied to only a few systems, but considerable experience has been gained on its properties. However, its data intensiveness will preclude its application to many systems, at least in its original form (but see Christensen, 1996). A second potentially useful class of models are less data-driven, simpler differential equation models for biomass dynamics, which have a long, if chequered tradition (Larkin and Gazey, 1982). Such biomass dynamics models can be viewed as ecosystem-scale extensions of single-species surplus production models. A third approach has been bioenergetics modelling to assess at least impacts of changing predation regimes, mainly in freshwater ecosystems (Stewart *et al*., 1981; Kitchell *et al*., 1994, 1996).

The major problems with the simulation models, as far as practical application to fisheries resource systems, have been that: (1) they require a high degree of expertise on the part of the modeller; (2) they are difficult to parameterize by piecemeal analysis of component trophic interactions (trophic models with 'reasonable' parameter estimates have a nasty way of self-simplifying, losing trophic groups due to competitive and predation interactions), and this parameterization often involves concepts from theoretical ecology not familiar to fisheries practitioners; (3) time series data usually lack adequate contrast in effort and abundance regimes to permit clear discrimination (accurate estimation) of parameters representing intraspecific versus interspecific effects; and (4) the lack of transparency resulting from (1)–(3), combined with the occasional output of doubtful results, has tended to prevent ecosystem simulation models from being routinely used by fisheries scientists.

A simpler approach for analysis of trophic interactions in fisheries resource systems is the ECOPATH system of Polovina (1984), further developed by Christensen and Pauly (1992a,b, 1995), and widely applied to aquatic ecosystems (fisheries resource systems, aquaculture ponds and natural systems; see contributions in Christensen and Pauly, 1993), and recently also to farming systems (Dalsgaard *et al*., 1995). Like bioenergetics modelling, ECOPATH has been appreciated by a wide variety of authors as an approach for summarizing available knowledge on a given ecosystem, to derive various system properties and to compare these with the properties of other ecosystems. Also, systematic application of ECOPATH has enabled a number of generalizations about the structure and functioning of ecosystems, and thus to revisit earlier inferences based on smaller data sets (Pauly and Christensen, 1993, 1995; Christensen, 1995b,c; Pauly, 1996). However, ECOPATH provides only a static picture of ecosystem trophic structure (it answers the question: what must trophic flows be to support the current ecosystem trophic structure and be consistent with observed growth and mortality patterns?). This precludes the use of its results for answering 'what if' questions about policy or ecosystem changes that would cause shifts in the balance of trophic interactions.

Here we present an approach for using the results of ECOPATH assessments to construct dynamic ecosystem models, as systems of coupled differential equations that can be used for dynamic simulation and analysis of changing equilibria. We show how this approach, which we call the ECOSIM module of ECOPATH, can be used for study of fishery response dynamics in any ecosystem for which there are sufficient data to construct a simple mass-balance model. We begin with a basic biomass dynamics formulation in the following section, and present some general results from this approach. One of these results is an inadequacy in representation of fishes that show strong trophic ontogeny, feeding widely across the food web as they grow. We show in a later section how this inadequacy can be corrected by using a more complex delay-differential equation structure that represents numbers/body size dynamics as well as biomass dynamics.

From ECOPATH to differential equations

Here we first review the mass-balance relationships used in ECOPATH assessment, then show how relatively simple biomass dynamics models can be derived from the

ECOPATH results. We point out that these models are likely to give unrealistic results unless they include effects of prey behaviour/spatial distribution on availability of prey to predators. We suggest an approach to model dynamics of availability in a way that allows users of ECOSIM to generate a range of predictions representing alternative hypotheses about 'top-down' versus 'bottom-up' control of trophic interactions. Symbols used in the following presentation are summarized in Appendix 1.

THE ECOPATH MASTER EQUATION

Trophic mass-balance models in ECOPATH are defined by the master equation:

Production of (i) utilized $=$ catch of (i) $+$ consumption of (i) by its predators (1)

where (i) is any functional group within the ecosystem in question, over any period (e.g. a year or a decade), at the end of which the system had the same biomass state as at the beginning.

Equation 1 can be broken up into its components:

$$B_i{\cdot}(P/B)_i{\cdot}EE_i = Y_i + \sum_{j=1}^{n} B_j{\cdot}(Q/B)_j{\cdot}DC_{ji} \tag{2}$$

where: B_i is the biomass of (i) during the period in question, with the system having $i = 1, \ldots, n$ functional groups; $(P/B)_i$ is the production/biomass ratio of (i) equal to total mortality rate (Z_i) under the assumption of equilibrium (Allen, 1971); EE_i is the ecotrophic efficiency, i.e. the fraction of the production ($P_i = B_i{\cdot}(P/B)_i$) that is consumed within the system or harvested; Y_i is the yield of (i), i.e. its catch in weight, with $Y_i = F_i{\cdot}B_i$, where F is the fishing mortality; B_j is the biomass of the consumers or predators; $(Q/B)_j$ is food consumption per unit of biomass for consumer j, and DC_{ji} is the fraction of i in the diet of j ($DC_{ji} = 0$ when j does not eat i). Note that $Q_{ij} = B_j(Q/B)_j DC_{ji}$ is the total consumption of pool (i) by pool j per time.

The parametrization and solving of Equation 2, which leads to trophic flow analyses such as in Fig. 1, was discussed in Christensen and Pauly (1992a,b), and numerous contributions in Christensen and Pauly (1993), and need not concern us here, except to mention that it is very straightforward as it allows combining original data with information previously published on the various groups included in a system. A recently developed Monte Carlo routine ('EcoRanger') has been added to the Windows version of ECOPATH, enabling consideration, in a Bayesian context, of uncertainty in the input data (Christensen and Pauly, 1995).

FROM MASS BALANCE TO A DYNAMIC MODEL

Here we concentrate on how the system of linear equation in (2) can be re-expressed as a system of differential equations. At equilibrium we have

$$0 = B_i{\cdot}(P/B)_i - F_i{\cdot}B_i - M_{\mathrm{o}}B_i - \sum_{j=1}^{n} Q_{ij} \tag{3}$$

where Q_{ij} is the amount of (i) consumed by (j), and M_{o} is the mortality rate not accounted for by consumption within the system. Except for primary producers, ECOPATH computes $B_i{\cdot}(P/B)_i$ to be equal to a growth efficiency g_i times the food

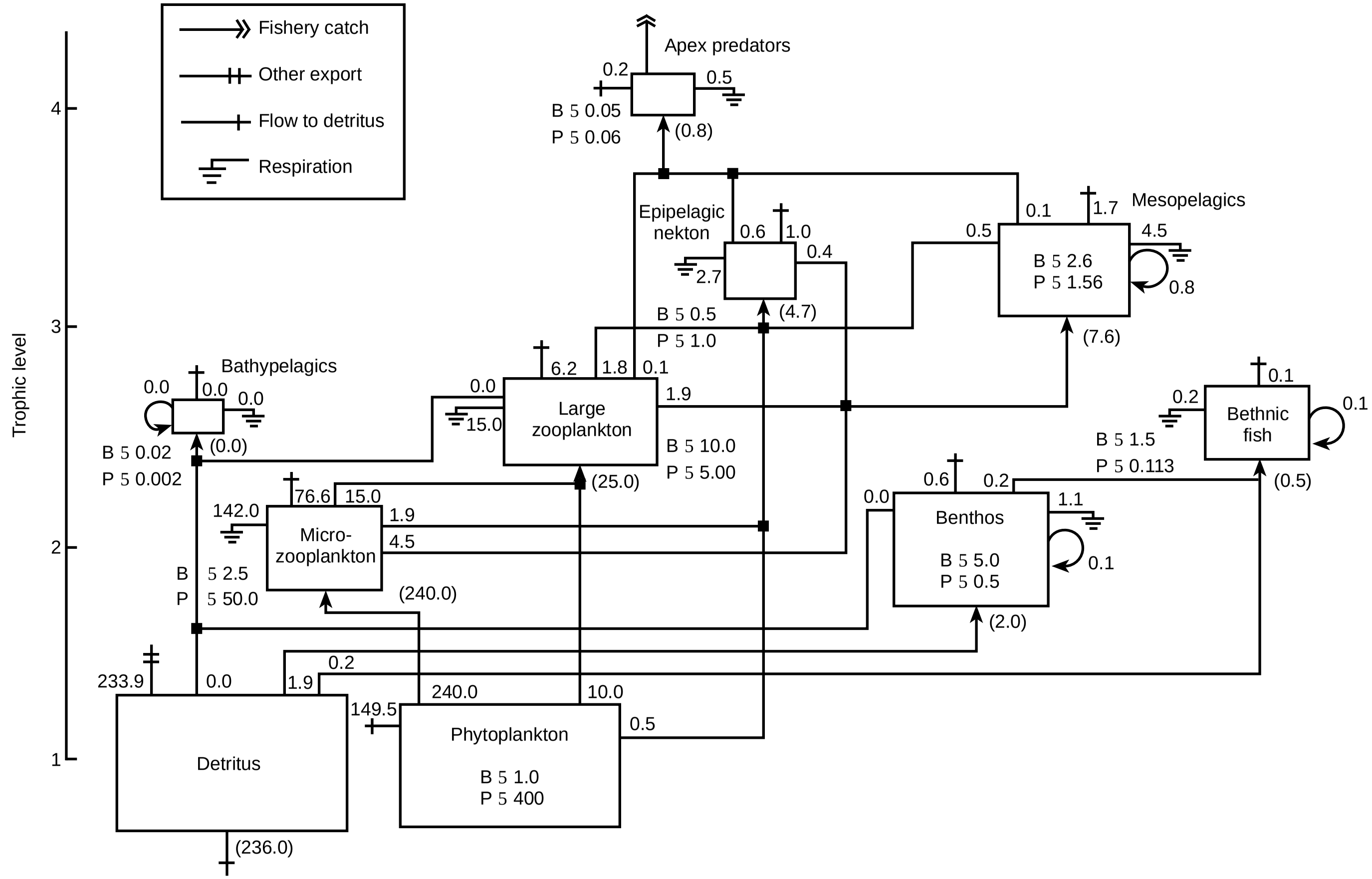

Fig. 1. Flow diagram of the central South China Sea pelagic ecosystem in the 1980s, as constructed using ECOPATH and documented in Pauly and Christensen (1993). The size of the boxes is roughly proportional of the logarithm of the biomasses (B; t km^{-2}), while the arrows document the fate of production (P; t km^{-2} year^{-1}).

consumed by group (i), i.e. trophic flows Q_{ij} into consumer pools (i) are computed so as to satisfy $B_i \cdot P/B_i = g_i \sum_j Q_{ji}$.

To construct a dynamic model from Equation 3, we must (1) replace the left side of Equation 3 with rate of biomass change $\mathrm{d}B_i/\mathrm{d}t$; (2) for primary producers, provide a functional relationship to predict changes in $(P/B)_i$ with biomass B_i, with this functional relationship representing competition for light, nutrients, and space; and (3) replace the static Q_{ij} pool-to-pool consumption estimates with functional relationships predicting how the consumptions will change with changes in the biomasses B_i and B_j.

Generalizing Equation 3 for both equilibrium and non-equilibrium situations, we have

$$dB_i/dt = f(B) - M_o B_i - F_i B_i - \sum_{j=1}^{n} c_{ij}(B_i, B_j) \tag{4}$$

where $f(B)$ is a function of B_i if (i) is a primary producer, or $f(B) = g_i \sum_{j=1}^{n} c_{ji} \cdot (B_i, B_j)$ if (i) is a consumer, and $c_{ij}(B_i, B_j)$ is the function used to predict Q_{ij} from B_i and B_j. If we can provide reasonable predictions of the $f(B)$ and $c_{ij}(B_i, B_j)$ functions, the system of Equation 4 can be integrated with F_i varying in time, to provide dynamic biomass predictions of each (i) as affected directly by fishing and predation on (i) and changes in food available to (i), and indirectly by fishing or predation on other pools with which (i) interacts.

Primary production

For primary producers, we propose the simple saturating production relationship

$$f(B_i) = r_i B_i/(1 + B_i h_i) \tag{5}$$

where r_i is the maximum P/B that (i) can exhibit when B_i is low, and r_i/h_i is the maximum net primary production rate for pool (i) when biomass (i) is not limiting to production (B_i high). Assuming the ECOPATH user can provide an estimate of the ratio of maximum to initial or base P/B (ratio of r_i to $(P/B)_i$ entered for ECOPATH estimation), r_i can then be computed from this ratio, and h_i from the ECOPATH base estimates of primary production rate $B_i \cdot (P/B)_i$ and biomass B_i as $h_i = [(r_i/(P/B)_i) - 1]/B_i$. Setting r_i very large (ratio very large) in this formulation has the effect of making primary production rates in the system remain constant at ECOPATH estimates independent of primary producer biomasses. It is obviously wise to include at least some limitation on primary production rates in the model, to represent competition among plants for light, nutrients and space. When in doubt about how to quantify this limitation, the conservative choice would be to make production rates very sensitive to biomass and to assume maximum rates r_i/h_i not much higher than the initial ECOPATH rate estimate.

Predicting consumption

Various functional relationships have been proposed in the ecosystem and fisheries modelling literature for predicting consumption flows $c_{ij}(B_i, B_j)$, to represent predator–prey encounter patterns and physiological-behavioural phenomena such as satiation of predators. In fisheries contexts, predation interactions have usually been represented or predicted from the simple Lotka–Volterra or 'mass action' assumption:

$$c_{ij}(B_i, B_j) = a_{ij}B_iB_j \tag{6}$$

where a_{ij} represents the instantaneous mortality rate on prey i caused by one unit of predator j biomass (contribution to Z_i by presence of a unit of consumer j biomass; e.g. Andersen and Ursin, 1977). This 'catchability' interpretation of a_{ij} corresponds in the ecological literature to interpreting a_{ij} as the 'rate of effective search' (Holling, 1959) of the consumer, measured per unit consumer biomass. Equation 6 is convenient from an ECOPATH perspective, because every a_{ij} can be estimated directly from the corresponding ECOPATH flow estimate: $a_{ij} = Q_{ij}/(B_i \cdot B_j)$.

A potential weakness of Equation 6 is that it does not represent satiation by predators; however, usually we do not view this as a serious issue (but see discussion below), because field observation of stomach contents in aquatic ecosystems suggests that most consumers are rarely able to achieve satiation (or are unwilling to take the predation risks necessary to achieve full stomachs most of the time).

Probably the most serious weakness in the simple mass-action predictor (Equation 6) is that predator–prey encounter patterns in nature are seldom random in space, and are most often associated with behavioural or physical mechanisms that limit the rates at which prey become available to encounters with predators. For example, consider the flow from phytoplankton in the water column to benthic filter feeders; here only a small fraction of B_i is available to the consumer, that fraction being limited by physical mixing and sinking processes that bring phytoplankton near the bottom. For other examples: zooplankton often show strong vertical migration patterns that limit their availability to planktivorous fish; planktivorous fish often spend much of their time in behavioural (schooling) or spatial (shallow water, holes) refuges that limit their encounter rates with (or the time they are exposed to) piscivores. In view of how ubiquitous these spatial and behavioural limiting mechanisms are, Equation 6 may well grossly overestimate the potential for increasing flow to consumer pools when consumer biomasses increase (e.g. in model scenarios where fishing rates on the consumers are decreased to test whether the ecosystem could support higher abundances to meet some fishery management objectives). We have chosen in ECOSIM to represent such limitations by viewing each prey pool B_i as having an available component to each consumer j, V_{ij}, at any moment in time (Fig. 2). This biomass V_{ij} may exchange fairly rapidly with the unavailable biomass according to the exchange equation:

$$\mathrm{d}V_{ij}/\mathrm{d}t = v_{ij}(B_i - V_{ij}) - v_{ij}V_{ij} - a_{ij}V_{ij}B_j. \tag{7}$$

That is, V_{ij} gains biomass from the currently unavailable pool $(B_i - V_{ij})$ at rate v_{ij}, biomass returns to the unavailable state at rate $v_{ij}V_{ij}$, and biomass is removed from V_{ij} by the consumer at a mass-action encounter rate $a_{ij}V_{ij}B_j$. Assuming the exchange process between V and B operates on short time scales relative to changes in B_i and B_j, V_{ij} should stay near the equilibrium implied by setting $\mathrm{d}V/\mathrm{d}t = 0$ in the above exchange equation:

$$V_{ij} = v_{ij}B_i/(2v_{ij} + a_{ij}B_j). \tag{8}$$

At this equilibrium varies with B_i and B_j, the consumption flow from i to j is then predicted to vary as

$$c_{ij}(B_i, B_j) = a_{ij}v_{ij}B_iB_j/(2v_{ij} + a_{ij}B_j). \tag{9}$$

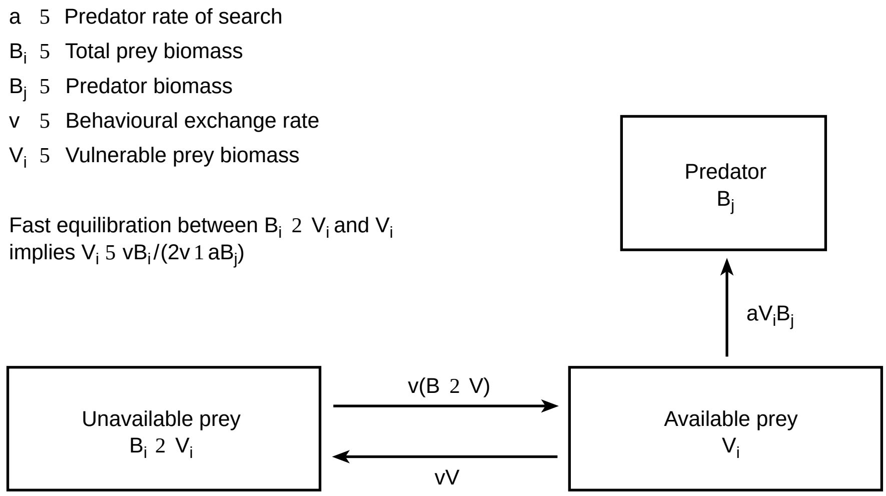

Fig. 2. ECOSIM approach to simulation of biomass flow between unavailable biomass of prey ($B_i - V_i$), available biomass of prey (V_i), and flow to predator j with biomass B_j.

For low consumer biomasses, this functional relationship reduces to mass-action flow, $c = a9B_iB_j$, where $a9$ is half of the a_{ij} value predicted without considering limitation of prey availability. But for high consumer biomass $B_j(a_{ij}B_j \gg 2v_{ij})$, c approaches a maximum 'donor controlled' flow rate $c = v_{ij}B_i$. Thus v_{ij} represents the maximum instantaneous mortality rate that consumer j could ever exert on food resource (i). In ECOSIM, parameter estimates for v_{ij} and a_{ij} in Equation 9 are obtained by having the user specify an estimate of the ratio of the maximum to the ECOPATH base estimate of the instantaneous mortality rate. Given this ratio, say x_{ij}, the vulnerability exchange rate is calculated as $v_{ij} = x_{ij}Q_{ij}/B_i$ and substituting this estimate into Equation 9 along with ECOPATH Q_{ij}, B_i, B_j estimates gives $a_{ij} = 2Q_{ij}v_{ij}/(v_{ij}B_iB_j - Q_{ij}B_j)$. Note here that the estimate a_{ij} approaches infinity and becomes negative for ratios approaching 1 or less (i.e. for ratios implying that not even the initial estimated flow Q_{ij} could be sustained). In addition, Equation 9 can be made to approach the simpler mass-action prediction of Equation 6 by setting the ratio of maximum to estimated Q_{ij} very large.

ECOSIM offers two other functional forms for predicting consumption flows. The first is a simple donor-control option:

$$c_{ij}(B_i, B_j) = v_{ij}B_i \tag{10}$$

which ignores consumer abundance entirely in computing the flow (v_{ij} estimated from ECOPATH estimates as $v_{ij} = Q_{ij}/B_i$); this option is useful for representing the 'flow' of biomass between pools representing different life stages of a species or functional group, where i is the pool of younger individuals.

The second is a 'joint limitation' relationship intended to approximate flow changes in situations where there is a limit on total flow when either prey biomass or predator biomass or both increase to high levels:

$$c_{ij}(B_i, B_j) = a_{ij}m_{ij}B_iB_j/(m_{ij} + a_{ij}B_iB_j). \tag{11}$$

This relationship predicts mass-action flow for low B_i and/or B_j, but flow reaching a maximum m_{ij} when either B_i or B_j becomes very large (m_{ij} estimated by having the user specify the ratio of m_{ij} to ECOPATH estimate of Q_{ij}).

Beyond the primary production and consumption relationships defined by Equations 2–4, ECOPATH and ECOSIM account for one other basic type of trophic process, namely the production and consumption of detritus. ECOSIM adds at least one additional dynamic equation, for detritus biomass. Input rates to this biomass include the $M_0 B_i$ 'other mortality' rates not accounted for by consumption within the system, plus the non-assimilated fraction of each consumption flow (default set to $0.2 \cdot c_{ij}$ for each flow from j to i; Winberg, 1956), plus 'import' (user defined) of detritus from surrounding ecosystems. Losses to the detritus pool (which may include a number of specified detritus groups) are c_{ij} flows for $i =$ detritus by detritivores (modelled as any other consumption flows, by Equation 4), plus an export rate $e_{\text{detritus}} B_{\text{detritus}}$ where the instantaneous export rate e_{detritus} is the value needed to balance detritus biomass gains and losses when all explicit inputs and outputs are accounted for at ECOPATH equilibrium.

Note that Equations 9 and 11 allow us to represent a strategic range of alternative hypotheses about 'top-down' versus 'bottom-up' control of trophic structure and abundance (Hunter and Price, 1992; Matson and Hunter, 1992). Setting low values for the vulnerability ratios v_{ij} leads to 'bottom-up' control of flow rates from prey to predators, such that increases in prey productivity will lead to prey biomass increases and then to increased availability to predators. Setting high values for v_{ij} leads to 'top-down' control and 'trophic cascade' effects (Carpenter and Kitchell, 1993); increases in top predator abundance can lead to depressed abundance of smaller forage fishes, and this in turn to increases in abundance of invertebrates upon which these forage fishes depend.

Numerical implementation of ECOSIM

Equations 2–4 represent a very modest step towards predicting how ecosystem flows might change as biomasses depart from base levels that result in Q_{ij} patterns estimated by ECOPATH. We emphasize that these equations are not likely to apply globally over wide ranges of biomasses. Examples of how they could easily fail for large changes in B_i and B_j include: (1) limitations on consumer $(Q/B)_j$ ratios at high prey densities due to satiation; (2) explicit switching in foraging strategies by predators when some prey pool B_i becomes scarce, to increase encounter rates with other prey types; and (3) changes in prey behaviour or prey pool species/size composition so as to reduce v_{ij} when predation risk (as measured by B_j) increases.

ECOSIM implements two types of numerical assessments using Equations 3–4. First, the user may specify an arbitrary temporal pattern of changes in fishing mortality rates F_i, using a graphical user interface for 'sketching' the temporal pattern with the computer mouse. The dynamical equations are then integrated to give predicted biomass patterns over time, using a fourth-order Runge–Kutta numerical integration scheme that has been tested for numerical stability and accuracy with inputs from a large number of ECOPATH files, including all those listed in Appendix 4 of Christensen and Pauly (1993).

ECOSIM can calculate predicted changes in equilibrium biomasses over a range of values for F for a particular functional group or for a gear type that generates Fs over several groups. For small increments in F, this procedure predicts marginal or directions of change in all biomasses due to increasing F on any one group. For wider ranges of F, the basic ECOSIM output is a graphical display of the relationship between equilibrium biomasses, catch and F (an ecosystem version of plotting equilibrium biomass and catch versus effort or F for surplus production models). The equilibrium procedure uses a Newton method to search for the zeros of the equation system defined by Equations 3–4. It is not guaranteed to be numerically stable, and in fact often fails to find the equilibria when the v_{ij} are large, and the model hence approaches Equation 6 form. In such cases, approximate equilibrium solutions and/or cyclic patterns can be found by integrating the equations over time while slowly changing Fs.

A preliminary stand-alone version incorporating these numerical procedures and graphic routines for interpretation of results is available for testing purposes; the preliminary ECOSIM module is available through the University of British Columbia Fisheries Centre home page (http://fisheries.com). Further work is in progress to integrate the ECOSIM module as a routine of the Windows version of the ECOPATH software (contact the second author: v.christensen@cgnet.com, or see the ICLARM home page http://www.cgiar.org/iclarm).

General ECOSIM predictions

A large number of ECOPATH trophic flow applications have been published (over 60 data files from around the world are available now for general use and analysis), and we have run test ECOSIM simulations with 40 of these cases. We have examined questions such as the following.

- Are transient predictions (of response over time to experimental harvest disturbances) from ECOSIM very different from the predictions obtained from single-species analysis, when indirect effects propagating through the trophic structure are included in assessment?
- Do ECOSIM time simulations predict maintenance of the trophic complexity measured in ECOPATH, or are many simulated pools lost to competitive/predator–prey interactions that are incorrectly modelled due to oversimplification of the interactions and mechanisms that permit coexistence in real systems?
- How do ECOSIM predictions of *MSY* and F_{max} compare with predictions from traditional single-species analysis, for fish at various trophic levels?
- How sensitive are the ECOSIM predictions to particular assumptions about v_{ij} or m_{ij} in the flow functional responses?

PREDICTIONS OF TRANSIENT RESPONSES TO HARVEST RATE CHANGES

ECOPATH has been used primarily for basic biomass estimation and for analysis of ecosystem ‘support services’ leading to fish production. From a ‘bottom-up’ trophic perspective, ECOPATH has been useful in assessing ecological limits to fish production, and in identifying key trophic linkages that are necessary for sustained production. Figure 3 illustrates just how different a set of issues and questions can arise when we examine system dynamics with ECOSIM. The figure shows sample results for a dynamic simulation based on Equation 9 for the Gulf of Mexico ecosystem (Browder, 1993) with

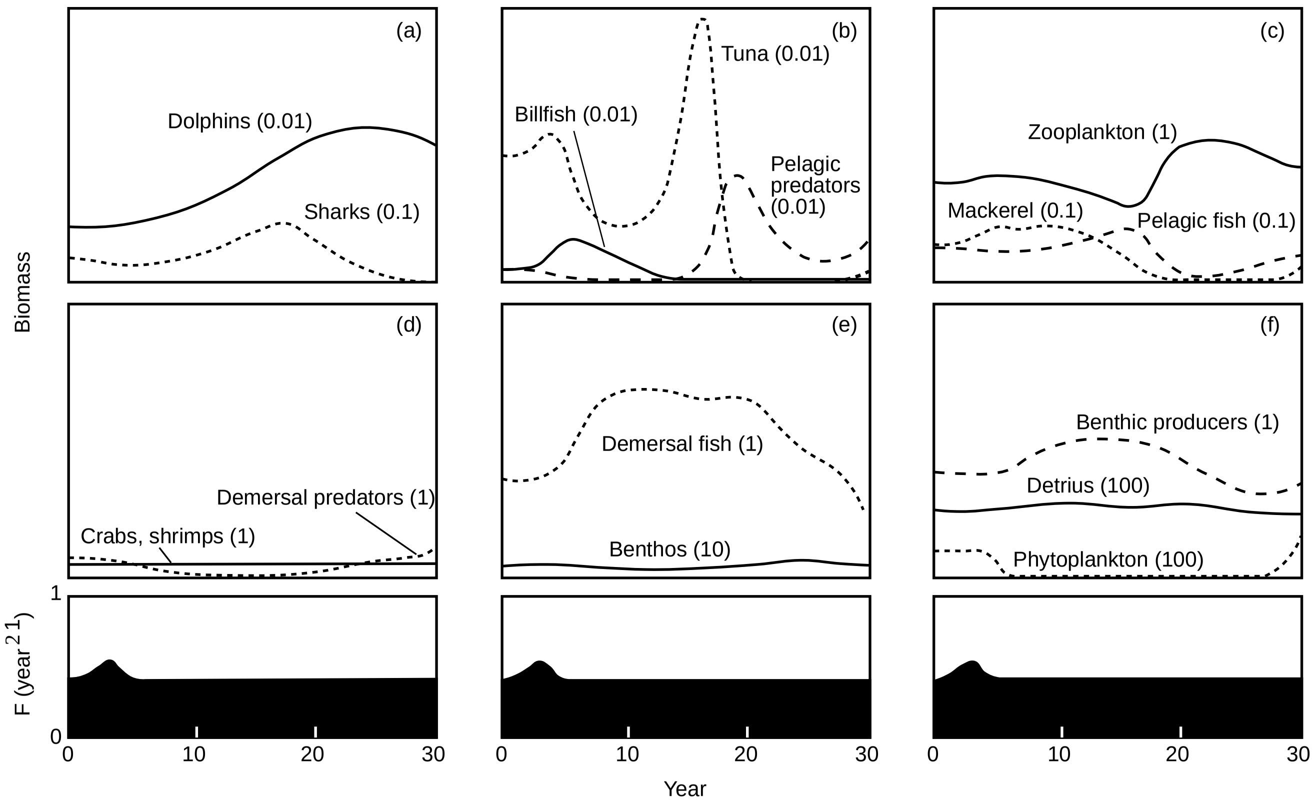

Fig. 3. A 30 year run of a Gulf of Mexico ecosystem model, assuming a temporary increase in fishing mortality for sharks; simulation based on ECOPATH model of Browder (1993). Simulations assume high availability of prey to predators, i.e. strong ‘top-down’ control in the ecosystem. (Biomasses for all groups are expressed on the same relative scale; use multipliers (in parentheses) for comparisons among groups.)

the v_{ij} set large (high ratios, 40:1, of potential to initial flows for all biomass flow pathways).

Here we simulated the effects of a transient increase in the fishery for sharks, followed by a conservation closure. For simpler ECOPATH models (fewer than a dozen biomass pools), and/or with low values for the v_{ij} to limit vulnerability of lower trophic levels to predation, ECOSIM generally predicts that such disturbances would be followed by a return to the original ECOPATH equilibrium on roughly the same time scales as would be predicted by single-species surplus production analysis. But in some cases, and for many tests we have done with models containing many functional groups while assuming high v_{ij} values, we see a very striking and disturbing pattern in the long-term dynamic predictions: instead of returning promptly to the original equilibrium, the system undergoes continuing long-term change as interactions propagate through the food web. These changes may involve violent biomass explosions and collapses starting as much as 30 years after the initial system perturbation. Hence, complex trophic interaction and flow structures appear to create system response lags and potential instabilities on time scales that would not readily be predicted from single-species analysis.

We do not have enough phenomenological experience with long-term dynamics in fisheries ecosystems to say whether very disturbing predictions of long response lags and violent community changes are credible or not. There have certainly been some large and unexpected changes in marine ecosystems during this century, but these have been largely attributed to 'bottom-up' changes in ecosystem support processes such as upwelling and ocean circulation, for instance for the Peru upwelling ecosystem (see contributions in Pauly *et al.*, 1989). In other cases it is an open discussion if such major ecosystem changes are due to environmental or trophic, fishery-induced impacts, e.g. for the North Sea 'gadoid outburst' (Cushing, 1980). Perhaps ECOSIM and other trophic interaction models will open new directions in the search for explanation of such changes.

The only obvious conditions we have seen in the ECOSIM tests that lead to such complex time dynamics are: (1) high v_{ij}, m_{ij} values, i.e. strong 'top-down' predation effects and predator–prey linkages; and (2) 'long' food chains (three or more trophic levels above primary producers). Most marine ecosystems would satisfy property (2), while we do not have enough experimental evidence of changes in predation regimes to say whether condition (1) is common under natural conditions. However, we may argue on evolutionary grounds, and on grounds of ecosystem development that, through continuing colonization and extinction, strong trophic linkages may have given way over eons to linkages with low v_{ij} values, allowing relatively large biomass of 'preys' to build up even in the presence of large predator populations (Pauly and Christensen, 1996).

It might be that violent changes as shown in Fig. 3 are associated with unrealistically large predicted changes in consumption per biomass (Q/B) ratios for consumers, e.g. the 'outbreak' shown after year 20 in Fig. 2 could be because the model incorrectly predicts that too much food is available to the expanding group, and too rapid a response to this food through the assumption that consumption (and production) are proportional to prey biomass, B_i, as well as to predator biomass, B_j. Indeed, high values of potential Q/B would, under natural conditions, represent a 'vacuum' where food is available to support something. Under such conditions, our general experience in ecology is that nature will use the opportunity, and move towards a state that might well include creatures not originally included in the ECOPATH and ECOSIM models. We cannot of course predict what shape such invasions might take.

As a warning sign in ECOSIM of a simulated condition where the predictions might be breaking down due to unrealistic Q/B values, the user interface offers an option to plot predicted Q/B ratios over time. In the example shown in Fig. 2, the predicted Q/B ratios generally did not differ by more than a factor of 2 from the ECOPATH base estimates, and there was no clear Q/B 'signal' to indicate the onset of major changes.

Figure 4 shows how the predictions in Fig. 3 are altered when lower ratios of maximum to initial flow are assumed (smaller v_{ij}), and when lower ratios are combined with the 'joint limitation' assumption of Equation 11. We conclude from results like these that if trophic flows are assumed to be limited by prey vulnerability and/or predator limitation mechanisms, resulting predictions of short-term transient response will be quite sensitive to the particular form of model used to represent the flow limitation. In particular, assuming bottom-up control of flows is likely to lead to overly optimistic predictions of recovery and stabilization patterns. Natural ecosystems most likely have a mixture of low-v_{ij} and high-v_{ij} 'linkages', i.e. weak and strong predation linkages; we have not yet explored the consequences for ECOSIM predictions of assuming various mixtures or distributions of linkage strength, nor have we attempted to quantify the trade-off relationship that likely exists between v_{ij} and other parameters like a_{ij} (presumably increasing rates of search for prey as measured by a_{ij} necessarily results in greater vulnerability to predators as measured by v_{ij}).

In a systematic examination of time dynamics for 40 ECOPATH models, we found that competitive or predator–prey exclusion of one or more functional groups after an arbitrary fishing disturbance (indicating the initial ECOPATH equilibrium to be dynamically unstable) occurred in roughly half the cases (Fig. 5) when v_{ij}, m_{ij} were set at high values (to allow 40 3 or more of initial flow rates at maximum). For all of these cases, restriction of flow rates (to lower ratios of maximum to initial rates for all groups simultaneously) led to persistence of all groups, and in only a few worst-case situations was it necessary to restrict the ratio of maximum to initial flow to as low as 4.0.

Surprisingly, there was no strong relationship between number of ECOPATH groups and tendency for the models to self-simplify. The worst case was in fact a very simply model of Lake Victoria, which had separate functional groups for cichlids, but which did not represent the resource partitioning (as separate groups) that apparently allows competitive coexistence of numerous cichlid species (Fryer and Iles, 1972). In this worst case, a low vulnerability ratio (maximum to initial flow of 4) did result in simulated coexistence, essentially by forcing a partitioning and limitation in the flow from the shared food pool at rates low enough to prevent any one cichlid type from driving food density low enough to exclude the other types.

The two largest ECOPATH models for which relatively accurate diet composition data were used (North Sea model of Christensen, 1995a, and Virgin Islands coral reef model of Opitz, 1993) did not exhibit self-simplification even for very high v_{ij} values. This suggests the very interesting possibility that strong interactions do occur even in complex situations, but lead to a sorting process (colonization/extinction/coevolution) such that what finally persists long enough to be studied as an 'equilibrium' in the field is a very peculiar or particular set of interaction parameter values. Perhaps we can only

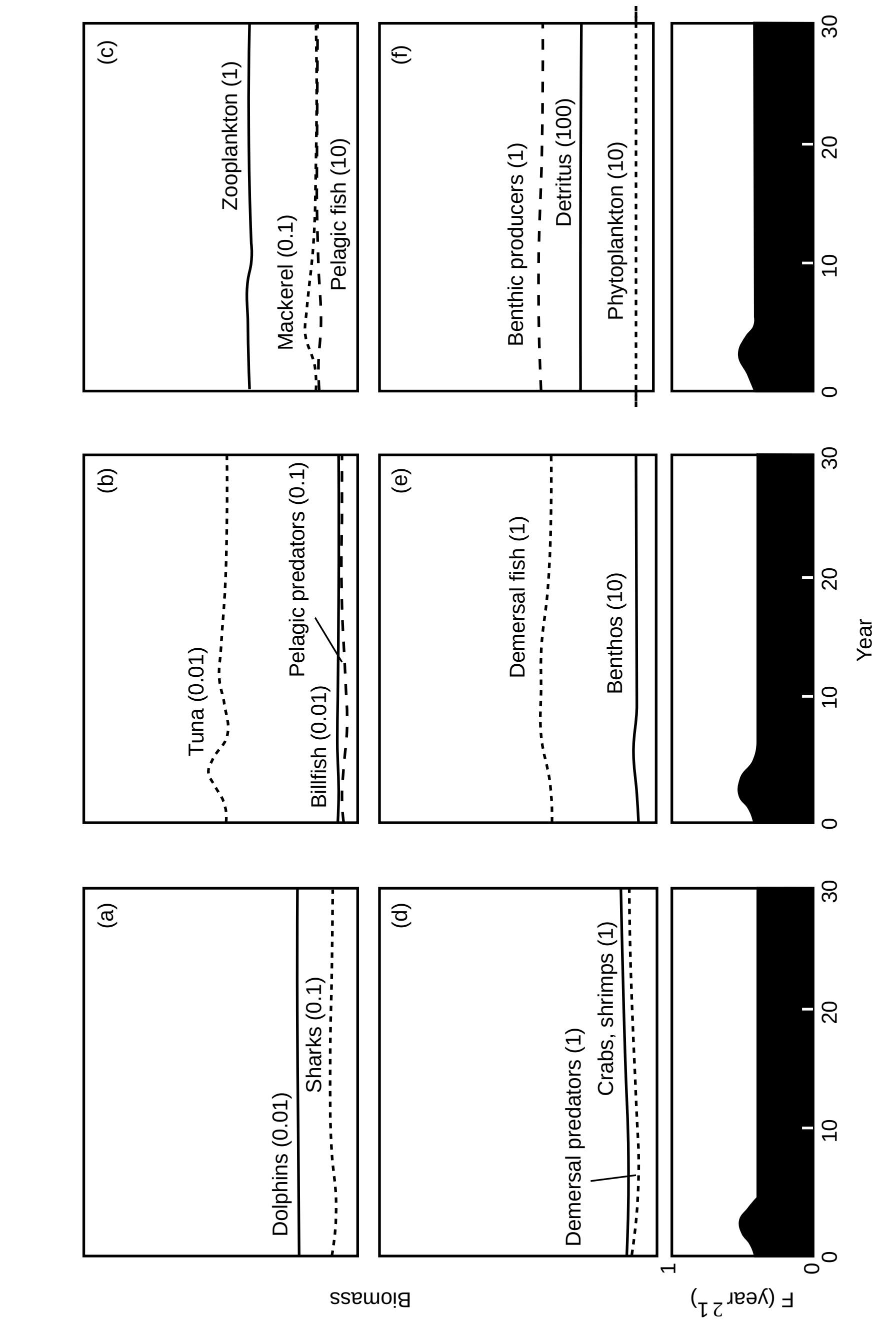

Fig. 4. Effects on the Gulf of Mexico model predictions in Fig. 3 of assuming strong limitation of availability of prey to their predators (strong 'bottom-up' control) using low values of v in Equation 9, i.e. vulnerabilities set to generate maximum predation mortality rates equal to 3 times the initial ECOPATH equilibrium estimates. (Biomasses for all groups are expressed on the same relative scale; use multipliers (in parentheses) for comparisons among groups.)

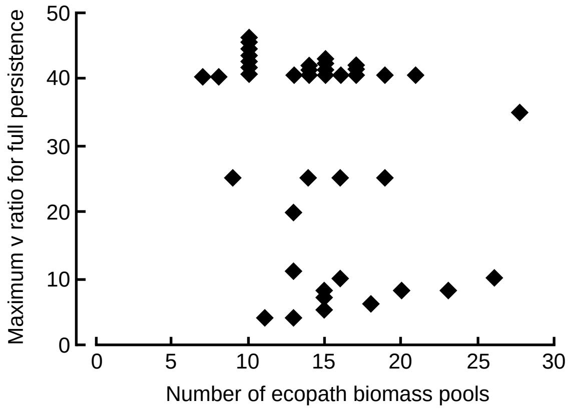

Fig. 5. Maximum vulnerability ratios (ratios of maximum to initial prey consumption) that result in stability and persistence of all pools for 40 ECOPATH models. Each point represents an ECOPATH model with number of biomass pools shown on the *x*-axis; *y*-axis value of maximum tolerable vulnerability found by running repeated time simulations with small state perturbation at the start of each simulation, and progressively increasing v_{ij} (Equation 9) values for all trophic flows. (See Christensen, 1995a, Pauly and Christensen, 1993, and Appendix 4 in Christensen and Pauly, 1993, for details on the models and files used here.)

see these particular values in systems where these interaction parameters have been accurately measured.

While ECOSIM predictions for moderate to high v_{ij} values can generally be interpreted as involving some sort of trophic cascade effect (reduction in top predators allowing some increase in smaller predators and this in turn reducing abundance of at least some invertebrate food groups), for many ECOPATH models of complex tropical food webs we do not see the simple alternation of effects across trophic levels proposed by authors like Carpenter and Kitchell (1993). Sometimes we see 'complex weblike' interaction patterns as suggested by authors like Strong (1992) and Stein *et al.* (1995), and sometimes we see abrupt shifts to alternative 'stable states' (Holling, 1973) that usually involve loss of at least some parts of the initial food web structure.

PREDICTION OF EQUILIBRIUM REGIMES

Simulations such as Figs 3–4 are not straightforward to interpret, and understanding the effects of harvest rate perturbations can sometimes be done more credibly by simply plotting predicted changes in equilibrium biomasses with changes in fishing rates. To some degree, such predictions at least avoid the issue of whether ECOSIM is correct in predicting long-term instabilities as in Fig. 3.

In general we have found that predicted patterns of biomass and equilibrium harvest response to changes in fishing rate F for single biomass pools look very much like the predictions from single-species production theory, provided relatively low values of v_{ij}, m_{ij} are assumed in the calculation. That is, biomass decreases monotonically with increasing F, and catch is a dome-shaped function of F with only one maximum (see Fig. 6a for an example).

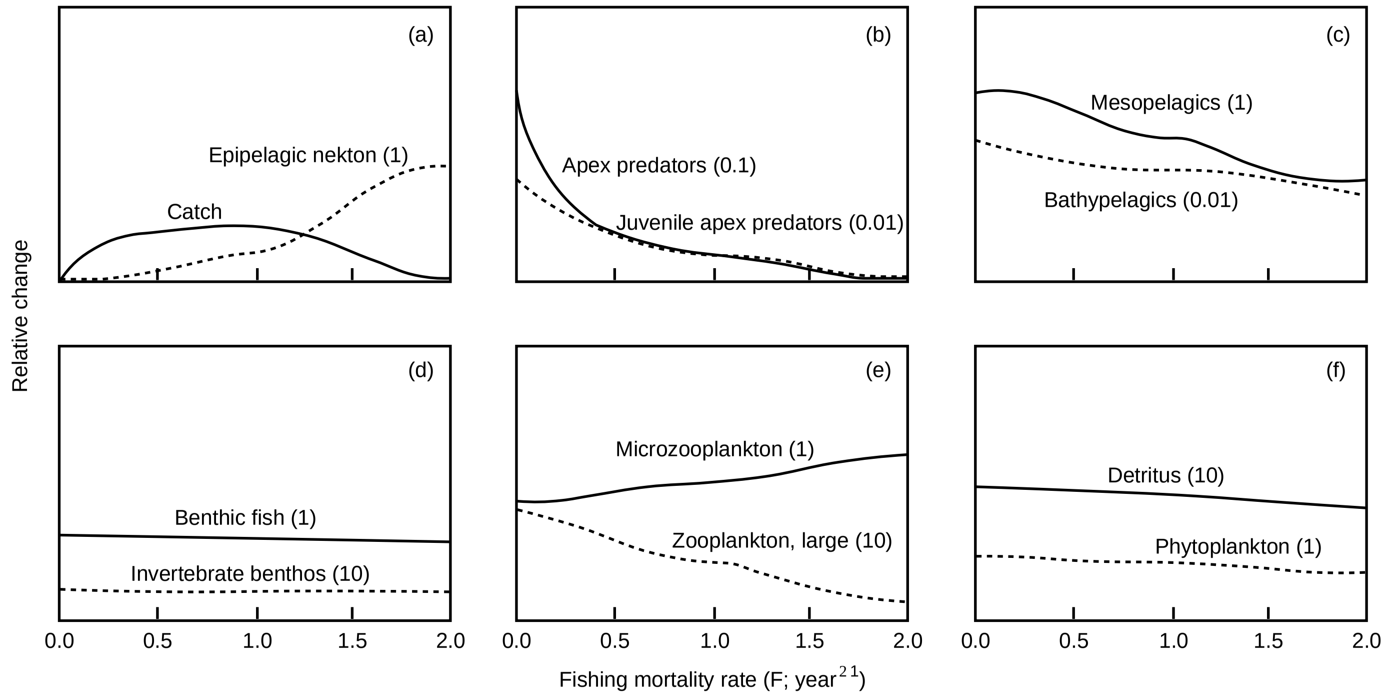

Fig. 6. Predicted equilibrium relationship between fishing mortality on large pelagic piscivores, catch (arbitrary weight units), and pool biomasses for the OCEANSCS model used to test ECOPATH (see Fig. 1), but with the apex predator pool ($\approx$ tunas) split into mainly zooplanktivorous juvenile and mainly piscivorous adult components, with subsequent adjustment of the P/Bs and Q/Bs. In this case, the ecosystem-level prediction of catch versus F for 'tunas' looks much like classic predictions based on single population production theory. (Biomasses for all groups are expressed on the same relative scale; use multipliers (in parentheses) for comparisons among groups.)

Assuming pure donor control usually results in unrealistic, asymptotic increase in catch with increasing *F*. The *F* value generating *MSY* is, as would be expected, generally lower for top predators (piscivores) than for smaller species like planktivores. Typical F_{msy} for top predators are on order 0.3–0.6 year^{-1}, a bit higher than indicated by many recent single-species analyses but not very unrealistic. Typical F_{msy} for planktivores (e.g. pelagic clupeoids) are on order 0.4–0.8 year^{-1}, again generally higher than suggested by recent fisheries experience (Patterson, 1992).

A difference for planktivores from single-species modelling is that ECOSIM often predicts no biomass decrease at all as planktivore *F* is increased from low to moderate levels. The model predicts instead that this decrease in net planktivore productivity should be transmitted up the food chain into decreases in top predator biomass (which in turn reduces the predation mortality rates for planktivores, and allows them to sustain higher fishing mortalities than would be predicted from single-species theory). For higher levels of *F*, ECOSIM predicts a sharp drop in biomass and catch, when predator levels become low.

For larger ECOPATH models (15+ pools) and high v_{ij}, m_{ij} values, the ECOSIM predictions of equilibrium response to fishing mortality become much more complex. As an example, Fig. 7 shows predicted changes in equilibrium biomasses of all functional groups, and catch of engraulids (anchovies), in San Miguel Bay, Philippines (A. Bundy, UBC, PhD in prep.), when only the fishing mortality on the engraulids is changed. This is compared to a case where fishing mortality by all gears in the bay is varied simultaneously. In both cases, whether or not the change in fishing patterns is complex, the equilibrium biomass relationship to *F* for engraulids is not a simple monotonic decrease. The predicted single-species yield relationship has a single peak, but the group is not predicted to persist at all (it is outcompeted by other planktivores, and hit heavily by large predators) under conditions where all fishing mortalities in the ecosystem are reduced. Zooplanktonic leiognathids, a similar trophic group in this model, are also predicted to be very rare in the absence of fishing, and further to even have a yield relationship with two peaks (two *F*s that give high catch; not shown in Fig. 7).

We have seen quite a number of complex relationships like these, and we have been unable to generalize about expected patterns of response. Under high v_{ij}, m_{ij} assumptions, there are strong feedbacks both up and down the food web as fishing mortalities are changed, and the net impact of changes in predation and competition regimes on each biomass pool appears to be quite unpredictable (except for large piscivores, which profit mightily in most models from reduction in fishing mortality).

As in time-transient cases, we simply cannot say at this time whether predictions of violent changes in equilibrium biomass patterns under changing fishing regimes are unrealistic. Some of the common predicted changes, such as large increases in biomass and production of prawns in tropical cases, accord in a general way with fisheries development experience (Gulland and Garcia, 1984). But very often ECOSIM predicts substantial simplification of ecosystems, through dominance by large predators, when fishing is substantially reduced. It is certainly not a matter of common wisdom in fisheries that reducing fishing might actually lead to reduced diversity at lower trophic levels. The development of marine refuges around the world promises to offer excellent opportunities to test this prediction and to gain experience needed to set more realistic values for parameters that limit the strength of top-down trophic effects (v_{ij}, m_{ij}).

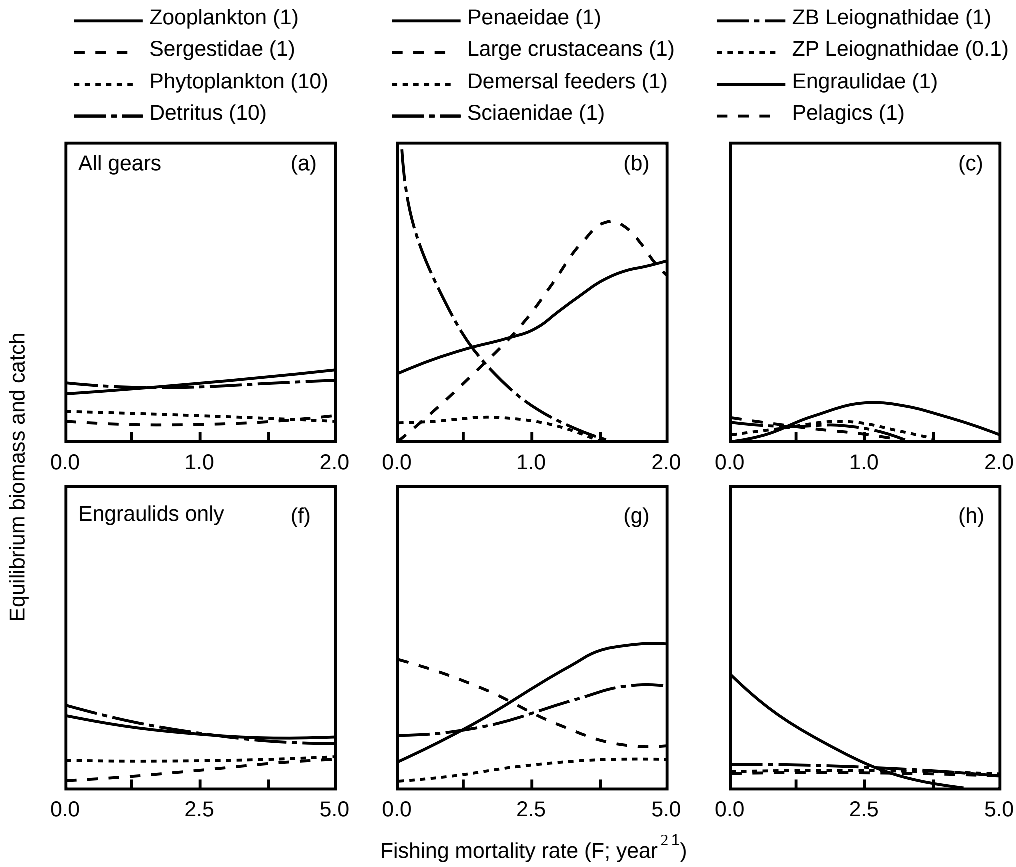

Fig. 7. Predicted equilibrium relationship between fishing mortality (by all gears in upper panels, and by gears targeting engraulids in lower panels), biomass by group, and engraulid catch (arbitrary weight units) in San Miguel Bay, Philippines. (Biomasses are expressed on the same relative scale; use multipliers (in parentheses) for comparisons among groups.) Note that the engraulids are predicted to have a low biomass in the natural system, i.e. when F for all gears is low (panel c). Such complex response predictions are not unusual in ECOSIM representations of smaller fishes in tropical trophic webs.

TOP-PREDATOR TAKE-OVERS

Novice ECOPATH users are encouraged to work with and develop a simple pelagic food web model, for which estimation results are distributed with the program (OCEANSCS data file). This model represents flows from primary production through plankton to planktivorous fish to a tuna-like piscivore. When this model is run in ECOSIM with high v_{ij} or m_{ij} values (maximum flows 3 3 or more the initial ECOPATH Q_{ij}s), and when equilibrium analysis is used to predict the effect of reducing F on the piscivore, a pathological prediction occurs.

The piscivore builds up dramatically in abundance, as might be expected if it were being fished hard in the ECOPATH base situation. But as it builds up, its main food

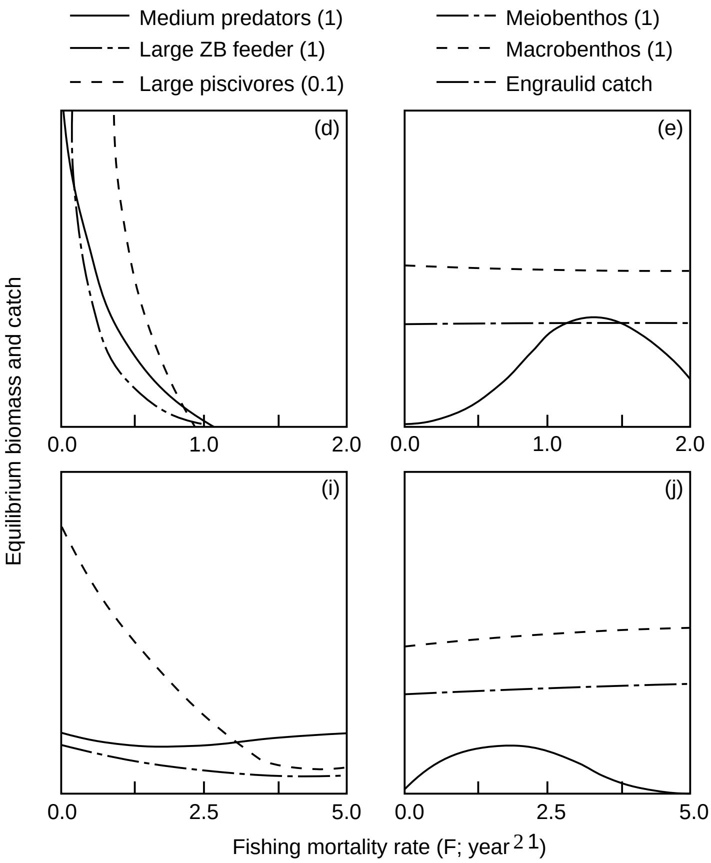

Fig. 7. continued.

source, planktivorous fish, is driven towards extinction, and may even reach this state in the absence of fishing. This prediction is clearly wrong, and arises from not accounting directly in ECOSIM for the ontogeny of feeding patterns in the piscivore. In the ECOPATH analysis, the piscivore is correctly portrayed as obtaining part of its diet from zooplankton. Small individuals among the piscivore may feed at lower trophic levels than the adults. But if the piscivore is represented as a single group in ECOSIM, this group is computed to be both a predator on, and a competitor with, the planktivore group. So ECOSIM allows the piscivore to build up, eat up its competition, and persist at high biomass by feeding only on zooplankton at unfished equilibrium.

The obvious solution to this problem is to divide ECOPATH pools representing species with broad ontogenetic changes in diet into a series of life stage pools with biomass moving directly between pools using a donor-controlled flow calculation. However, it is not obvious how to correctly set parameter values for such flows; if the values are not set correctly, life stage pools may 'take off' on their own, reaching higher biomasses than would actually be possible, and end up acting as competitors rather than parts of a single population. Ultimately, the only safe answer is to model the internal size/numbers structure of pools properly, using concepts and methods extended from single-species analysis; this extention of the biomass dynamics model is presented in the next section.

Delay-differential representation of trophic ontogeny

A TWO-POOL APPROACH

A simple solution to the problem of dealing with trophic ontogeny, especially for top predators, would be to divide each group into two (sub-)groups representing the juvenile planktivore/benthivore stage, and the adult stage. But we cannot apply purely biomass-related consumption/mortality rules, following Equation 4 above, to the dynamics of each of such groups with an added linkage representing maturation flow from juvenile to adult. With no constraint on the two groups besides biomass flow due to 'graduation' from the juvenile to the adult group, the groups would generally show unrealistic biomass dynamics.

BEVERTON–HOLT FACTORS

ECOSIM deals with this problem by allowing users to specify a two-pool delay-differential model structure that simultaneously accounts for numbers of fish in the groups as well as their biomasses. Numbers are included in the model because they 'constrain', and are better predictors of, food consumption rates (predicted Q). In essence, we require that the 'adult' pools for top predators receive numbers of recruits as well as biomass from 'juvenile' pools, and that the juvenile pools in turn receive numbers of recruits from the adult pools.

In two-pool cases, we allow the user to replace flow functions like $Q_{ij} = a_{ij}B_iB_j$ with $Q_{ij} = a_{ij}B_iN_j$ or $Q_{ij} = B_iA_j$ where N_j is number of predators in pool j and A_j is the 'total age' (Equation 7 below) of these predators. This predator number or total age proportionality rather than predator biomass proportionality is easily justified.

Assume that predator food consumption per individual of age a, $(\mathrm{d}Q/\mathrm{d}t)_a$, varies with age approximately as suggested by Pauly (1986) and Temming (1994a,b):

$$(\mathrm{d}Q/\mathrm{d}t)_a = Æ[1 - \exp(-\mathrm{K}a)]^2 \tag{12}$$

where $Æ$ is maximum body weight and K is the von Bertalanffy growth parameter. Then total consumption rate Q integrated over age will vary as

$$Q = \int_a N_a(\mathrm{d}Q/\mathrm{d}t)_a\,\mathrm{d}a = Æ\left\{\int_a N_a - 2\int_a N_a\,\mathrm{e}^{-\mathrm{K}a} + \int_a N_a\,\mathrm{e}^{-2\mathrm{K}a}\right\}. \tag{13}$$

We can write Equation 13 more compactly by calling each of the three integrals on the right side of (13) a 'Beverton–Holt factor' $N^{(m)}$, defined simply by

$$N^{(m)} = \int_a N_a \, \mathrm{e}^{-m\mathrm{K}a} \quad \text{for } m = 0, 1, 2 \tag{14}$$

so that $Q = Æ\{N^{(0)} - 2N^{(1)} + N^{(2)}\}$. Note here that $N^{(0)}$ is simply the number of animals in the pool. If individuals recruit continuously to N at rate R_t per time (this rate need not be constant), if these individuals are subject to total mortality rate Z, and if they leave the pool after time T (to die or enter another pool as, say, adults), then the Beverton–Holt factors can be found by solving the simple differential equations

$$\mathrm{d}N^{(m)}/\mathrm{d}t = R_t - R_{t-T}\,\mathrm{e}^{-(Z+m\mathrm{K})T} - (Z + m\mathrm{K})N^{(m)}, \quad m = 0, 1, 2. \tag{15}$$

This very remarkable result was first found by Cooke (1983). If Equations 15 are accompanied by a fourth biomass equation of the general form $\mathrm{d}B/\mathrm{d}t = w_k R_t - w_0 R_{t-T} + gQ - (Z + 3\mathrm{K})B$, the resulting system of four equations will exactly mimic the behaviour of the Beverton–Holt dynamic pool model with continuous recruitment and knife-edge entry to the pool at size w_0 (and exit from the pool at size w_k). This is a delay-differential equation (continuous time) analogue of the delay-difference equations for B and N derived by Deriso (1980) and Schnute (1987) using a simpler growth model. In other words, by solving Equations 15 for each group along with the biomass equation, we can in principle make ECOSIM behave exactly like a set of Beverton–Holt dynamic pool models, with trophic linkages included through ECOSIM predictions of Q and Z. For this we should have $Æ$ Equation 13 include prey density effects ($Æ = a_{ij}B_i$ or $a_{ij}V_{ij}$), and Z be the sum of mortalities due to all consumers/fisheries. This then would require solving four differential equations rather than two for each ECOSIM functional group.

SIMPLIFICATION BY TREATING POPULATION AGE AS A PREDICTOR OF FEEDING RATE

Equation 15 leads to an unnecessary explosion in the number of differential equations to be solved when ECOSIM is faced with many juvenile–adult paired pools. We avoid unnecessary complication by noting, following Pauly (1986), that Equation 12 implies that food consumption rate varies almost linearly with age over the range of ages which contributes most to the consumption within groups. Hence, if consumption per predator is proportional to age for constant food density B_i, the rate of effective search a_{ija} for age a predators is about proportional to age also. Adopting this simplification and integrating consumption rates over numbers of fish by age then gives

$$Q_{ij} = \int_a N_a(\mathrm{d}c/\mathrm{d}t)_a \, \mathrm{d}a = \int_a N_a \mathrm{s}aB_i = \mathrm{s}B_i N\bar{\mathrm{a}} \tag{16}$$

where N denotes total numbers over all ages and rate of effective search a_{ija} is set to $a_{ija} = \mathrm{s}a$ with s being the slope of the feeding rate–age relationship. So Q will act as $a_{ij}{\cdot}B{\cdot}N$ with $a_{ij} = \mathrm{s}{\cdot}\overline{a}$ (mean age). For juveniles, mean age should not vary greatly unless there are violent changes in mortality rate. For adults where we may wish to examine policies that could cause mean age to vary greatly, we replace N with total adult age:

$$A = \int_a aN_a \, \mathrm{d}a \text{ and } Q_{ij} = a_{ij}B_i A_j. \tag{17}$$

We can write a simple differential equation for the time behaviour of A just as we can for the Beverton–Holt factors in Equation 15. Using that method, the delay differential equation model for any juvenile–adult pair of ECOPATH groups in ECOSIM is then given by five differential equations, here shown for a single species with subscript J denoting the juvenile (planktivore/benthivore) stage and A the adult stage:

$$\mathrm{d}B_\mathrm{J}/\mathrm{d}t = gQ_\mathrm{J} - Z_\mathrm{J}B_\mathrm{J} + Rw_0 - w_\mathrm{k}R_{t-T}\exp\{-Z_\mathrm{J}T\} \tag{18}$$

$$\mathrm{d}N_\mathrm{J}/\mathrm{d}t = R_t - R_{t-T}\exp\{-Z_\mathrm{J}T\} - Z_\mathrm{J}N_\mathrm{J} \tag{19}$$

$$\mathrm{d}B_\mathrm{A}/\mathrm{d}t = w_\mathrm{k}R_{t-T}\exp\{-Z_\mathrm{J}T\} - R_t w_0 + gQ_\mathrm{A} - Z_\mathrm{A}B_\mathrm{A} \tag{20}$$

$$\mathrm{d}N_\mathrm{A}/\mathrm{d}t = R_{t-T}\exp\{-Z_\mathrm{J}T\} - Z_\mathrm{A}N_\mathrm{A} \tag{21}$$

$$\mathrm{d}A/\mathrm{d}t = TR_{t-T}\exp\{-Z_\mathrm{J}T\} + N_\mathrm{A} - Z_\mathrm{A}A \tag{22}$$

Here the biomass rate equations for B_A and B_J are as described in previous sections. Zs represent all loss components, and each Q_{ij} prey consumption component of Q is predicted using N_j or A_j rather than B_j in Equations 6, 9 and 10. Added terms involving recruitment R represent biomass flows from adults to juveniles (Rw_0 with w_0 being an initial juvenile body weight) and graduation from juvenile to adult groupings ($w_k R_{t-T}\exp\{-Z_\mathrm{J}T\}$ terms, with w_k being body weight at graduation, and T being the age at which body weight w_k is reached and graduation takes place). The numbers dynamics equations are just recruitment rates less mortality rates. Here R represents the number of new recruits to juvenile numbers N_J per unit of time, and in ECOSIM we assume $R = b{\cdot}B_\mathrm{A}$, i.e. no density dependence in production of early juveniles (b represents juveniles produced per unit adult biomass per time; assumption here is that fecundity per unit adult biomass stays constant, which does not preclude density dependence in juvenile survival and/or indirect density dependence through effects on adult biomass).

For precise prediction in scenarios where varies Z_J varies greatly over time, we should in principle replace Z_J in the $\exp\{-Z_\mathrm{J}T\}$ of Equations 18–22 with the time integral of Z_J over time from $t - T$ to t. However, our experience with test ECOPATH models and a variety of time-varying policies is that this integral generally changes slowly relative to T, because the predators that generate Z_J generally have slower dynamic responses than the smaller juveniles that they eat. This means that the current value of Z_J at any moment in a time simulation is a good 'predictor' or index of the Z_J integral over recent time (back to lag T), and the integral need not be stored during simulations.

PARAMETER ESTIMATION

Equations 18–22 appear to pose a formidable parameter estimation problem. But in practice this estimation can be simplified greatly if we assume to begin with that $Rw_0 = w_k R_{t-T}\exp\{-Z_\mathrm{J}T\}$ at the initial ECOPATH equilibrium, i.e. at initial equilibrium the reproductive 'investment' Rw_0 by adults just balances gain to adult biomass from the investment. Under this assumption, the ECOPATH user can proceed with estimation of Bs, Qs, and Zs without having to deal explicitly with the graduation flow between juvenile and adult groups. We find this reasonable as calculations for typical growth/survival rates and w_k values indicate this flow will generally be small compared with other flows, in any case.

The user need only specify w_k and W_∞, which we use to calculate R by the following steps:

1. substituting Z_A into the Beverton–Holt equation for mean adult body weight (Beverton and Holt, 1957; e.g. equation (6) in Hoenig *et al*., 1987);
2. using this mean body weight to calculate adult numbers ($N_A = B_A/\text{mean weight}$);
3. computing adult recruitment rate needed to balance $Z_A(R_{t-T}\exp\{-Z_J T\} = Z_A N_A$ at initial ECOPATH equilibrium, so initial $R = Z_A N_A/\exp\{-Z_J T\}$); and
4. calculating initial juvenile numbers at ECOPATH equilibrium as $N_J = R(1 - \exp\{-Z_J T\})/Z_J$.

In this procedure, we take w_0 to be whatever 'effective entry weight' is needed to make Rw_0 equal to the biomass graduation rate $w_k R_{t-T}\exp\{-Z_J T\}$.

Density-dependence in juvenile mortality rates can be represented in the delay-differential structure by having the time spent in the juvenile stage be variable around an initial value given by

$$T_k = 1/\mathrm{K}\cdot\ln[1 - (w_k/\mathrm{W}_\infty)^{1/3}] \tag{23}$$

which is the age, k, at which fish reach weight w_k given von Bertalanffy parameters K and W_∞. In particular, one simple option is to assume

$$T = (T_k Q_0/N_0)N_J/Q_J, \tag{24}$$

i.e. juvenile time needed to reach size w_k proportional to feeding rate. This option gives $T = T_k$ when the food consumption rate per juvenile is at its base or ECOPATH initial value (Q_0/N_0). Time T then increases whenever either N_J increases above N_0 without Q_j increasing, or vice versa. Equation 24 gives density- and food-dependent juvenile mortality, and thus provides an ecosystem-linked recruitment model. It is based on the Werner and Hall (1988) and Walters and Juanes (1993) models, which propose that juveniles must spend more time foraging (and hence exposed to predation with total mortality rate Z_J) as juvenile density increases (see also Jones, 1982).

The parameter estimation procedure outlined above is not necessarily consistent with the Equation 23 estimate of T_k. An alternative and more robust estimation procedure is to begin by asking the ECOPATH user to provide estimates of w_k and T_k, along with the Bs and Qs. Assuming roughly linear growth in weight for juveniles results in the relation

$$w_k = w_0 + gQ_J/N_J T_\mathrm{k}, \tag{25}$$

i.e. growth rate for weight is growth efficiency, g, times consumption per individual Q_J/N_J. Given the ECOPATH values for Q_J, N_J and Z_J, we first compute w_0 as above (assume $w_0 = w_k\exp(-Z_J T_0)$), then solve Equation 25 for N_J. Taking this N_J to be an ECOPATH equilibrium, it must satisfy $N_J = R[1 - \exp(-Z_J T_0)]/Z_J$, which we can solve for R. Then finally we solve for N_A from the initial equilibrium relation $N_A = R\exp(-Z_J T_0)/Z_A$, where Z_A is given by ECOPATH. This alternative estimation procedure guarantees that simulated juveniles will reach weight w_k after time T_0 while feeding at rates estimated from ECOPATH rather than the rates implicit in the growth Equation 23 estimate of T_k. However, there is a hidden price to be paid by following this procedure: it may produce an initial adult body size B_A/N_A that is not consistent with available data on W_∞ and Z_A, i.e. the estimates may not agree with mean size estimated from the Beverton–Holt formula. In such cases a diagnostic will be output by the ECOSIM to assist user in reexamination of data and methods used to estimate Q_J, Q_A, c

and B_A, as these parameters may be inconsistent with the growth pattern implicit in ECOSIM.

EXAMPLE OF TROPHIC ONTOGENY EFFECTS: SHOULD CANNIBALISM CAUSE DOME-SHAPED RECRUITMENT PATTERNS IN LAKE VICTORIA NILE PERCH?

The Nile perch, *Lates niloticus*, introduction to Lake Victoria, Central Africa, led to massive changes in the lake's endemic fish fauna. There has been little hope for the persistence of the unique natural cichlid community. However, Kitchell *et al*. (1996) argue that high fishing rates on the Nile perch may allow at least some components of the cichlid fauna to persist and hopefully recover. In a caveat to their predictions based on bioenergetics modelling and constant recruitment rates to the Nile perch population, Kitchell *et al*. (1996) warn that because the Nile perch is highly cannibalistic, reductions in adult stock could well allow substantial increases in juvenile abundance (dome-shaped recruitment relationship). Juvenile increases could in turn lead to complex, unstable dynamic patterns or at least cancellation of the effect of reducing adult density.

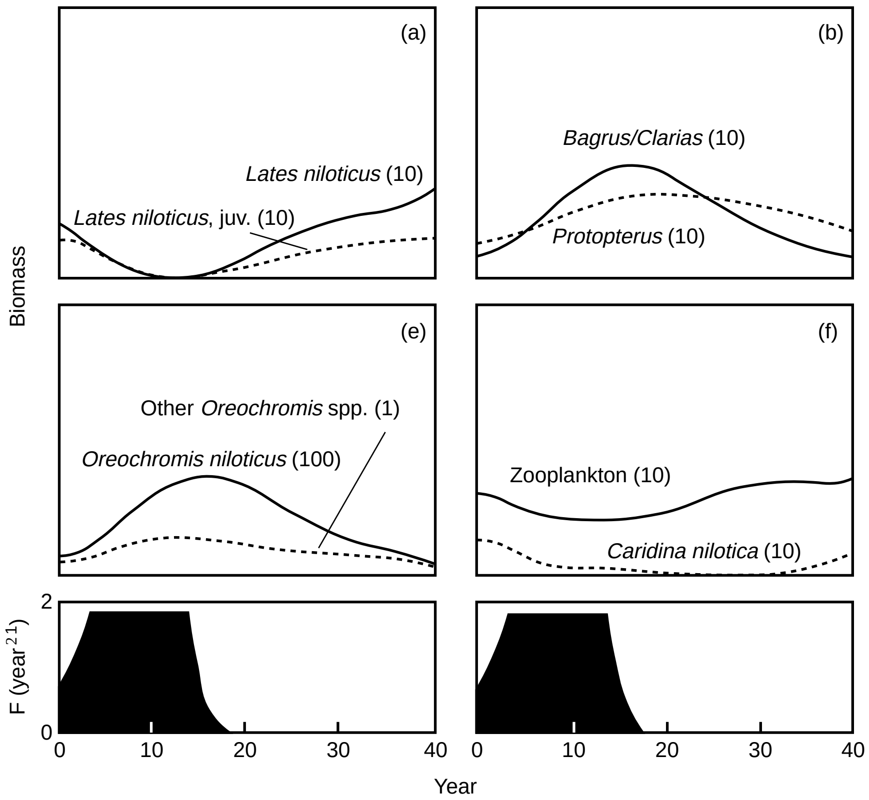

Fig. 8. Predicted effects of fishing down the adult Nile perch, *Lates niloticus*, in Lake Victoria, Africa, then allowing the population to rebuild in a repeat of its introduction. Note how *Caridina* and *Rastrineobola* stabilize at lower levels, then actually decrease for some time following reduction in fishing, before they increase later in the simulation. (Biomasses for all groups are expressed on the same relative scale; use multipliers (in parentheses) for comparisons among groups.)

We used an ECOSIM model based on ECOPATH models for the Kenyan sector of the lake (Moreau, 1995) to examine Kitchell *et al.*'s concern about cannibalism. The Nile perch pool was split into juvenile and adult components with *N-B-A* dynamics as in Equations 18–22. Our basic prediction (Figure 8) is essentially the same as that of Kitchell *et al*. We do not predict large increases in juvenile abundance if the adult Nile perch stock is fished more heavily, nor do we predict that recruitment would increase or decrease greatly if adult density were allowed to increase. That is, we predict a recruitment relationship of the Beverton–Holt form. This prediction nicely illustrates the substantial difference between ecosystem and single population dynamic theory. Single population theory, accounting only for changes in cannibalism rate, would predict a dome-shaped recruitment curve. With ECOSIM, we predict instead that increases in adult density would lead instead to increased density of foods available to juveniles (especially the freshwater shrimp *Caridina*), which would allow juveniles to grow faster and hence reduce time exposed to the cannibalism risk. This is a trophic cascade effect: increasing adult density is predicted to lead to decreases in density of

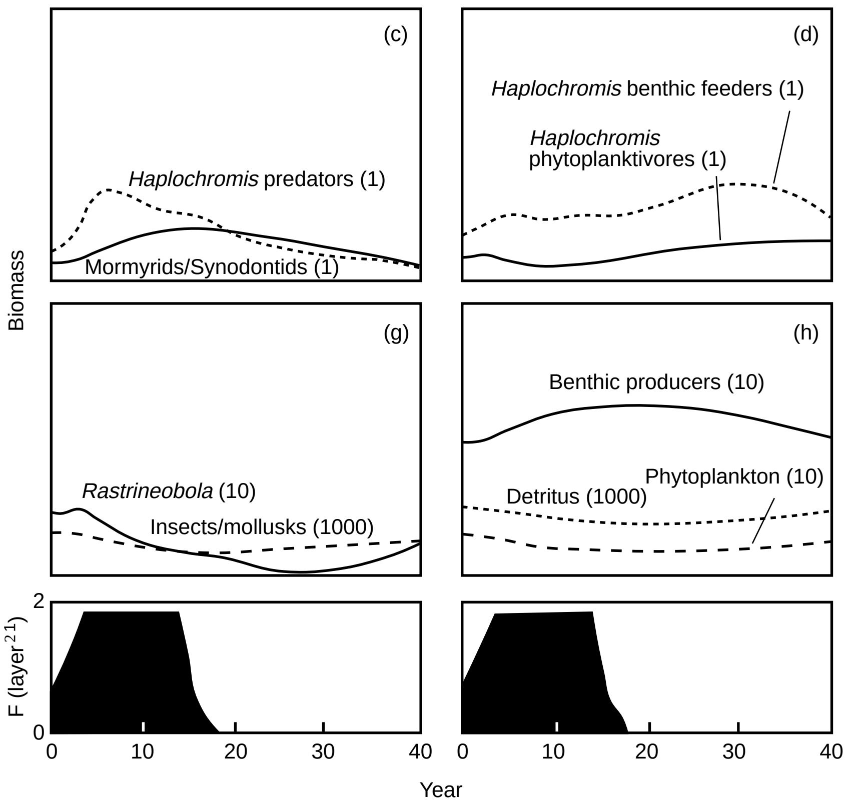

Fig. 8. continued.

cichlids and other competitors/predators of the juveniles, and this in turn to improved feeding conditions for the juveniles (and reduced predation risk from the cichlid community). Perhaps this is why in general we do not see strikingly dome-shaped recruitment relationships in large piscivorous fish: they eat the babies, but they also eat the competition.

When we reduce adult Nile perch densities to very low levels in the ECOSIM model, which allows the simulated cichlid community to recover as predicted by Kitchell *et al*., we predict that *Caridina* densities should fall from the 1985 level of around 5.9 t km^{-2} to around 2.9 t km^{-2}. An ECOPATH analysis for the 1971 situation, when the Nile perch stock was still very low, estimated *Caridina* density at 2.6 t km^{-2}. Thus ECOSIM is successful at predicting not only the direction of the trophic cascade effect on *Caridina* abundance, but also the magnitude of this response (note that the ECOSIM model used only data from the 1985 ECOPATH analysis, not from both 1971 and 1985 analyses). ECOSIM also correctly predicts the massive increase in the cyprinid *Rastrineobola argentea* that followed the Nile perch introduction (Ogutu-Ohwayo, 1990, 1993).

Discussion

We initiated the development of ECOSIM with a view to providing a very simple biomass dynamics models. As we began to test this approach, we found it useful to include two complications that have not previously been incorporated into multispecies biomass models: (1) the notion of vulnerable prey pools (V_{ij}) which can act to limit top-down predation effects; and (2) the use of delay-differential equations to model population properties besides biomass (N, A). We believe that each of these extensions will be deserving of future modelling and empirical research on its own. In particular, there is an exciting possibility of developing Beverton–Holt dynamic pool models that are fully coupled to ecosystem context through variable growth and natural mortality rates. However, it is by no means clear that this coupling is best or necessarily done just by embedding the dynamic pool model in a larger whole ecosystem model with many uncertain parameters and feedback relationships. The Lake Victoria example suggests strongly that much is to be learned from looking at least two trophic levels away from predatory species of direct management interest, i.e. we should not treat 'lower trophic levels' as constant just because we do not have fisheries data on them. But perhaps we can gain such perspectives without developing detailed ecosystem models.

WHAT GOES WRONG: SOME LIMITS TO ECOSIM PREDICTIONS

In scanning ECOPATH data sets, we have seen at least four types of predictions that appear to us to be dangerously incorrect or potentially misleading:

1. overestimation of potential productivity for low-fecundity species;
2. overly optimistic assessments of F_{max} for intermediate trophic levels;
3. indeterminate outcomes in complex food webs; and
4. misleading parameter estimates due to the equilibrium assumption of ECOPATH.

All of these problems relate to the warning above about the risk of using ECOSIM to extrapolate to circumstances far from the equilibrium for which ECOPATH data are available. We will discuss these problems further in this section, both as a warning to ECOSIM users and to help stimulate further research on how to correct them by future improvements in the approach.

Productivity for low-fecundity species

When we run ECOSIM on an ECOPATH system that includes marine mammals (porpoises, seals, whales, etc.) or sharks, we generally find that ECOSIM predicts $F_{\max}$ for these species on order 0.2 year^{-1}. This prediction is clearly too high, at least for non-age-selective harvesting, for animals with such low fecundity.

The ECOSIM approach can deal only in biomass or nutrient-related currency, and therefore cannot represent the fact that marine mammals (and possibly some low-fecundity elasmobranchs) simply have no way to translate increasing foraging opportunities under reduced population density into more than modest responses in fecundity and survivorship. These animals may well feed at the higher rates predicted by ECOSIM when food is abundant, but under such conditions they would also exhibit apparent reduction in growth efficiency simply because they do not have the physiological machinery to turn the increased food intake into biomass production.

We propose for future ECOSIM versions to deal with this problem by allowing users to (1) specify parameters to reduce the efficiency of converting food into biomass under unusually favourable trophic conditions, and (2) use the biomass-numbers dynamics (*N-B-A* Equations 18–22) even for pools that are not split into juvenile/adult pairs, and allow users to limit the numbers recruitment rate (set b in $R = \mathrm{b}B$ or $R = \mathrm{b}N$ relationship). Note that this argument does not apply in reverse; under conditions of declining food availability (under increasing population size or with competition for prey from a developing fishery), ECOSIM should be able to provide reasonable predictions of the risk of decline due to inadequate food resources for low-fecundity species; that is, we should find reasonable ways to model the dependence of birth rates b on per capita feeding rates Q/N.

Over-optimistic assessments for intermediate predators

As noted above, ECOSIM often appears to overestimate $F_{\max}$ and potential production for selective fisheries targeted on planktivores such as clupeoids in upwelling ecosystems. This is because ECOSIM predicts, as in other predator–prey models, that declining productivity available to predators will translate first into decreases in predator abundance. That is, ECOSIM predicts that increasing F will result in decreasing M due to the system not supporting as many piscivorous creatures.

The fundamental problem here is not in assuming that predatory creatures will respond: in all likelihood, they will respond to some degree to decreasing food supply. Rather, the problem is in assuming that M consists of a series of additive components, such that decrease in one component will in fact result in a lower overall value of M. We have little field evidence to support this contention, and it appears that M may in fact be quite stable, a conserved quantity (Pauly, 1980), and at least partly independent of the abundance of natural risk factors, with the predators acting as 'agents' rather than as cause of mortality (Jones, 1982).

The topic is obviously a matter for further careful analysis and experimental study. It is straightforward to build '*M*-conservation' into the ECOSIM equations to force the mortality rate to remain stable, and to limit predation rate components of M by setting low v_{ij} values. Still, it remains an entirely open question whether such a 'conservative' approach leading to relatively low estimates of sustainable Fs is in fact the wisest.

Indeterminate outcomes in complex food webs

For tropical food webs represented by ECOPATH models with many components, we sometimes cannot generate any clear qualitative prediction of response to changing fishing regimes. Small changes in the vulnerability parameters (v_{ij}) in such cases can cause predictions to change violently (e.g. change the predicted direction of response for some pools), and small changes in fishing rate inputs can sometimes lead to qualitative changes in community structure (usually loss of some food web components due to changes in predation/competition patterns). Indeed, the rich variety of abundance patterns seen in such systems on intermediate spatial scales (e.g. over the parts of a coral reef or on adjacent reef platforms) may mean that such systems actually do have alternative 'stable' states within areas small enough to have the strong trophic interactions assumed in ECOSIM.

There is a real risk that users of ECOSIM for such systems will be discouraged by the complexity of the simulated patterns, and will then refuse to work at testing the predictions and developing improved models. As we develop more experience with such models, perhaps we will be able to devise a 'taxonomy' of response patterns to guide users in selecting parameters and interpreting the results.

Misleading parameter estimates from assuming equilibrium in ECOPATH

This last weakness is perhaps the most worrisome. The assumption of mass balance in ECOPATH results in greatly simplified parameter estimation, but only at the cost of making an equilibrium assumption that is unrealistic in many situations. If for example we simulate Lake Victoria forward in time with parameter values from an ECOPATH model for 1971 (Moreau, 1995), we do not even predict the violent increase in Nile perch that actually occurred: in effect, the 1971 ECOPATH assessment was implicitly treating Nile perch as already being at a steady state. Problems like this can be corrected during ECOPATH model development by using the routine of the Windows version which allows for entry of biomass changes for those pools that are known to be changing rapidly in a consistent direction at the time for which biomass and flow data are entered. But it is not easy to put this principle into practice, especially in situations where there is only limited time series information from which to infer rates of change or where there are biomass pools that could be changing rapidly but have not been abundant enough to monitor closely as of the time when the ECOPATH model is developed.

ECOSIM AS A TOOL FOR ADAPTIVE POLICY DESIGN

Particularly in cases where ECOSIM makes a set of diametrically opposed predictions depending on its parameter settings, it can act as a tool to define a precise set of alternative hypotheses about the effects of such management changes as increasing fishing pressure and establishing marine protected areas. Indeed, one of our motives for developing it in the first place was to give crude predictions about how long it should take for various pools to exhibit measurable responses to changes such as cessation of fishing in marine refuges, so as to allow better monitoring design for evaluation of such policies.

There is a real risk that scientists engaged in multispecies modelling will come to believe that we need only gather more precise and detailed trophic interaction data to eventually produce accurate prediction models. That approach would ignore some really fundamental uncertainties about the additivity of mortality effects, behavioural limitations on trophic flows, and importance of indirect effects like how corals and macroalgae can moderate trophic interactions by providing cover for juvenile fish (Sainsbury, 1988, 1991). In simplest form, these uncertainties are now expressed through debates about ‘top-down’ versus ‘bottom-up’ control of trophic processes. We cannot in principle resolve such debates just by modelling interactions in more detail, because such debates involve assertions about how interactions would change under circumstances not seen in routine data gathering programmes. Thus we have learned a great deal from relatively simple trophic and fishery manipulation experiments like the trophic cascade studies of Carpenter and Kitchell (1993) and Kitchell *et al*. (1994) or the trawl experiment of Sainsbury (1988, 1991).

It might be argued that experimental manipulations of trophic structure are not practical on the relatively large spatial scales of marine ecosystems. This may indeed be true of the largest pelagic ecosystems, but we can do informative experiments (indeed, managers will do them in any case) at most scales. Experiments can certainly be used to examine interactions in marine benthic communities, for example Chilean shellfisheries (Castilla, 1994) and tropical trawl fisheries (Sainsbury, 1991). Experiments have been suggested or are under way that can test the influence of salmonid stocking densities on coastal pelagic ecosystems of the North Pacific (Perry, 1995). Manipulative experiments have been suggested to understand trophic interaction effects in the relatively large Bering Sea ecosystem (Collie, 1991). The main assistance that models like ECOSIM can provide in such settings is in identification of possible magnitudes of effects (needed for power analysis of alternative design proposals) and in helping to focus monitoring effort on variables most likely to show large change.

ECOSIM IN THE SPECTRUM OF MULTISPECIES MODELLING APPROACHES

Multispecies models vary from very simple extensions of Lotka–Volterra equations to complex simulations of age–size structured interactions. ECOSIM has advantages over the simplest multispecies surplus production models through its structured parameter estimation from ECOPATH, representation of limitation in trophic flows, and representation of trophic ontogeny via numbers/biomass delay-difference equations. It has a potential advantage over several existing large models based on MSVPA assessment, in that it examines interaction effects at all trophic levels, rather than treating lower trophic levels as ‘other food’ without dynamics or with only very simple dynamics (Sparre, 1991). We could not capture multi-trophic-level ‘cascade effects’ like those discussed above for Lake Victoria without this breadth of representation. Pope (1991) notes that a critical area for multispecies model development is in representation of early life history and recruitment dynamics; he notes that some simpler approach than simulations based on MSVPA may be needed to understand early life history interactions. ECOSIM, with its representation of trophic components important to small juvenile fish, is one possible approach to this simplification; basic features of trophic ontogeny are represented (e.g. differences in diets of and predation regimes suffered by juveniles compared with older animals), but without a massive demand for data on all the creatures that may interact with juvenile fishes.

There are at least three major disadvantages of ECOSIM compared with more detailed simulation models. First, it does not represent phenomena of switching and satiation in predators, i.e. it makes basically the same assumption about search-limited attack rates as suggested by Shepherd (1988) for use in MSVPA assessments where there are only limited feeding rate data. Second, it does not represent the smooth and complex changes in size-dependent predation rates that appear to characterize trophic ontogeny in large piscivores. Such patterns could be particularly important for situations far from trophic equilibrium and for policies aimed at size structure (e.g. changes in mesh size of nets), when size structures change rapidly such that total interaction rates cannot be predicted from average rates over the heterogeneous individuals making up each ECOSIM biomass/numbers pool. Third, it depends strongly on the mass balance or equilibrium assumption of ECOPATH to simplify parameter estimation, as noted above.

To deal effectively with both ecological interactions and policy initiatives such as marine refuges, fisheries stock assessment may have to move much more to use of explicit spatial models. The computational and data requirements of such models are daunting even for single-species assessment. Spatial biomass/surplus production models based on simple differential equations with advection/diffusion terms are unlikely to properly capture the size–age structuring of most spatial movement processes (e.g. movement of animals offshore during trophic ontogeny). ECOSIM models can capture at least the bare essentials of such size-structured spatial processes, without impossibly large computational requirements for situations where a fairly large number of spatial grid cells need to be simulated to compare policy options related to questions like how large to make refuges for juvenile fish. A useful strategy in such situations may be to use spatially replicated ECOSIM models for initial policy 'screening', then develop more detailed space–size structured models for more precise analysis of options identified during the screening process. Too often in fisheries assessment we have tried to leap directly into very detailed models without stopping to ask whether the extra effort was really needed; this has created a real risk of getting so bogged down in modelling details and data gathering that no useful analysis can be produced in a timely fashion for use in fisheries policy design and ecosystem management.

Acknowledgements

The ECOPATH project at ICLARM is funded by the Danish International Development Assistance. We are especially grateful to Alida Bundy for many helpful comments and participation in the model development and testing. This is ICLARM Contribution No. 1276.

Appendix 1: List of symbols used in model development

A	denotes adult stage
A_j	'total age' of predators. See Equation 17
$a9$	one half of the a_{ij} predicted, not considering prey limitations
a	age
$\overline{a}$	mean age
a_{ij}	instantaneous mortality rate on i caused by one unit of j, 'catchability' or 'rate of effective search'; in ECOPATH estimated from $a_{ij} = Q_{ij}/(B_i \cdot B_j)$

a_{ijt}	a_{ij} at time t
Æ	a parameter relating food quality and density to a power of body weight
B	biomass
B_A	biomass of adults
B_i	biomass of prey in group i ('food density')
B_J	biomass of juveniles
B_j	biomass of predators in group j
b	juveniles produced/unit adult biomass/time
c	food consumption rate per unit biomass, predicted in ECOSIM
$c_{ij}(B_i, B_j)$	functions used to predict Q_{ij} from B_i and B_j
DC_{ji}	diet composition giving the proportion that i contributes to the diet of j
e_{detritus}	instantaneous export rate of detritus
EE	ecotrophic efficiency = proportion of production utilized in the system
F	instantaneous fishing mortality rate
F_{msy}	fishing mortality giving maximum sustainable yield
$f(B)$	functions of B
g	gross food conversion efficiency = P/Q
h_i	r_i/maximum net primary production
i	used for any functional group but usually for the prey
J	denotes juvenile stage
j	index for predators or consumers
K	constant in VBGF
k	time at recruitment to the adult stage
M_0	other (non-predation) mortality
m_{ij}	maximum flow between i and j
N	total number in population (over all ages)
N_A	number of adults
N_a	number at age a
N_J	number of juveniles
N_j	number of predators in group j
$N^{(m)}$	'Beverton–Holt factor' (Equation 14)
N_0	number at time 0
P	production term = $B \cdot (P/B)$
P/B	production/biomass ratio (= Z under equilibrium conditions)
Q	total consumption rate
Q_A	consumption rate for adults
Q_{ij}	consumption rate of prey i for consumer j
Q_J	consumption rate for juveniles
Q_0	consumption at time 0
Q/B	food consumption per unit of biomass in ECOPATH
R	recruitment to juvenile population = bB_A
R_t	recruitment to adult population/unit time
R_{t-T}	same as R, lagged
r_i	the maximum P/B that i can exhibit
t	time, units defined in ECOPATH estimation set-up
T	age at which transition to the next pool occurs
T_k	age at weight k

T_0	age (= 0) at recruitment to juvenile group
V_{ij}	biomass of prey i available to j
v_{ij}	maximum instantaneous mortality rate that j can exert on i
VBGF	von Bertalanffy growth function
w_0	weight at recruitment to the juvenile stage (at time 0)
w_k	weight at recruitment to the adult stage
W_∞	asymptotic weight in the VBGF
Y	F/B; yield, harvest, or catch in weight
Z	instantaneous rate of mortality (= P/B ratio under equilibrium)
Z_A	mortality rate of adults
Z_J	mortality rate of juveniles

References

Allen, K.R. (1971) Relation between production and biomass. *J. Fish. Res. Bd Can.* **28,** 1573–1581.

Andersen, K.P. and Ursin, E. (1977) A multispecies extension of the Beverton and Holt theory of fishing with accounts of phosphorus circulation and primary production. *Meddr. Danm. Fisk.-og Havunders, N.S.,* **7,** 319–435.

Beverton, R.J.H. and Holt, S.J. (1957) On the dynamics of exploited fish populations. *U.K. Minist. Agric. Fish. Fish. Invest.* (Ser. II) **19,** 533 pp.

Browder, J.A. (1993) A pilot model of the Gulf of Mexico continental shelf. In Christensen, V. and Pauly, D., eds. *Trophic Models of Aquatic Ecosystems (ICLARM Conf. Proc.* **26**). Manila: ICLARM, pp. 279–284.

Carpenter, S.R. and Kitchell, J.F. (eds) (1993) *The Trophic Cascade in Lakes*. New York: Cambridge University Press. 385 pp.

Castilla, J.C. (1994) The Chilean small-scale shellfisheries and the institutionalization of new management practices. *Ecology Int. Bull.* **21,** 47–63.

Christensen, V. (1995a) A model of trophic interactions in the North Sea in 1981, the year of the stomach. *Dana* **11**(1), 1–28.

Christensen, V. (1995b) A multispecies virtual population analysis incorporating information of size and age. *ICES C.M.* 1995/D:8; 14 pp.

Christensen, V. (1995c) Ecosystem maturity – towards quantification. *Ecol. Modelling* **77,** 3–32.

Christensen, V. (1996) Virtual population reality. *Rev. Fish Biol. Fish.* **6,** 243–247.

Christensen, V. and Pauly, D. (1992a) ECOPATH II – a software for balancing steady-stage models and calculating network characteristics. *Ecol. Modelling* **61,** 169–185.

Christensen, V. and Pauly, D. (1992b) *A Guide to the ECOPATH II Program* (version 2.1). (*ICLARM Software* 6). Manila: ICLARM. 72 pp.

Christensen, V. and Pauly, D. (eds) (1993) *Trophic Models of Aquatic Ecosystems* (*ICLARM Conf. Proc.* **26**). Manila: ICLARM. 390 pp.

Christensen, V. and Pauly, D. (1995) Fish production, catches and the carrying capacity of the world oceans. *NAGA, the ICLARM Q.* **18**(3), 34–40.

Collie, J.S. (1991) Adaptive strategies for management of fisheries resources in large marine ecosystems. In Sherman, K., Alexander, L.M. and Gold, B.D., eds *Food Chains, Yields, Models, and Management of Large Marine Ecosystems*. Boulder, Co: Westview Press, pp. 225–242.

Cooke, J.G. (1983) The assessment of exploited marine populations from catch data. DPhil thesis, Univ. York, UK. 437 pp.

Cushing, D.H. (1980) The decline of the herring stocks and the gadoid outburst. *J. Cons. Int. Explor. Mer* **39,** 70–81.

Dalsgaard, J.P.T., Lightfoot, C. and Christensen, V. (1995) Towards quantification of ecological sustainability in farming systems analysis. *Ecol. Eng.* **4,** 181–189.

Deriso, R.B. (1980) Harvesting strategies and parameter estimation for an age-structured model. *Can. J. Fish. Aquat. Sci.* **37,** 268–282.

Fryer, G. and Iles, T.D. (1972) *The Cichlid Fishes of the Great Lakes of Africa: Their Biology and Evolution*. Edinburgh: Oliver and Boyd. 641 pp.

Gulland, J.A. and Garcia, S. (1984) Observed patterns in multispecies fisheries. In May, R.M., ed. *Exploitation of Marine Communities* (*Dahlem Konferenzen, Life Sciences Research Report* **32**). Berlin: Springer-Verlag, pp. 155–190.

Hoenig, J.M., Csirke, J., Sanders, M.J., Abella, A., Andreoli, M.G., Levi, D., Ragonese, S., Al-Shoushani, M. and El-Musa, M.M. (1987) Data acquisition for length-based assessments: report of Working Group I. p. 343–352. In Pauly, D. and Morgan, G.R., eds. *Length-Based Methods in Fisheries Research* (*ICLARM Conf. Proc*. **13**). Manila: ICLARM, pp. 343–352.

Holling, C.S. (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol.* **91**, 203–320.

Holling, C.S. (1973) Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* **4,** 1–23.

Hunter, M.D. and Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73,** 724–732.

Jones, R. (1982) Ecosystems, food chains and fish yields. In Pauly, D. and Murphy, G.I., eds. *Theory and Management of Tropical Fisheries* (*ICLARM Conf. Proc.* **9**). Manila: ICLARM, pp. 195–240.

Kitchell, J.F., Eby, E.A., He, X., Schindler, D.E. and Wright, R.M. (1994) Predator–prey dynamics in an ecosystem context. *J. Fish Biol.* **45**, 209–226.

Kitchell, J.F., Schindler, D.E., Ogatu-Ohwayo, R. and Reinthal, P.M. (1996) The Nile perch in Lake Victoria: interactions between predation and fisheries. *Ecol. Appl.* (in press).

Larkin, P.A. and Gazey, W. (1982) Applications of ecological simulation models to management of tropical multispecies fisheries. In Pauly, D. and Murphy, G.I., eds. *Theory and Management of Tropical Fisheries* (*ICLARM Conf. Proc.* **9**). Manila: ICLARM, pp. 123–140.

Matson, P.A. and Hunter, M.D. (1992) The relative contributions of top-down and bottom-up forces in population and community ecology. *Ecology* **73,** 723.

Moreau, J. (1995) Analysis of species changes in Lake Victoria using ECOPATH, a multispecies trophic model. In Pitcher, T.J. and Hart, P.J.B., eds. *The Impact of Species Changes in African Lakes* (Fish and Fisheries Series **18**). London, UK: Chapman & Hall, pp. 137–161.

Ogutu-Ohwayo, R. (1990) The decline of the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Env. Biol. Fishes* **27,** 81–96.

Ogutu-Ohwayo, R. (1993) The effects of predation by the Nile perch, *Lates niloticus* L., on the fishes of Lake Nabugabo, with suggestions for conservation of endangered endemic cichlids. *Conserv. Biol.* **7,** 701–711.

Opitz, S. (1993) A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem. In Christensen, V. and Pauly, D., eds. *Trophic Models of Aquatic Ecosystems* (*ICLARM Conf. Proc.* **26**). pp. 259–267.

Patterson, K. (1992) Fisheries for small pelagic species: an empirical approach to management targets. *Rev. Fish Biol. Fisheries* **2,** 321–338.

Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer* **39,** 175–192.

Pauly, D. (1986) A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. *Fish. Bull. U.S.* **84,** 829–842.

Pauly, D. (1996) One hundred million tonnes of fish and fisheries research. *Fish. Res.* **25,** 25–38.

Pauly, D. and Christensen, V. (1993) Stratified models of large marine ecosystems: a general approach, and an application to the South China Sea. In Sherman, K., Alexander, L.M. and Gold, B.D., eds. *Stress, Mitigation and Sustainability of Large Marine Ecosystems*. Washington, DC: AAAS Press, pp. 148–174.

Pauly, D. and Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature* **374,** 255–257.

Pauly, D. and Christensen, V. (1996) Rehabilitating fished ecosystems: insights from the past. *NAGA*, *ICLARM Q.* **19**(3), 13–14.

Pauly, D., Muck, P., Mendo, J. and Tsukayama, I. (eds) (1989) *Peruvian Upwelling Ecosystem: Dynamics and Interactions* (*ICLARM Conf. Proc.* **18**). Manila: ICLARM. 438 pp.

Perry, E.A. (1995) Salmon stock restoration and enhancement strategies and experiences in British Columbia. *Am. Fish. Soc. Symp.* **15,** 152–160.

Polovina, J.J. (1984) Model of a coral reef ecosystem I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* **3,** 1–11.

Pope, J.G. (1991) The ICES Multispecies Assessment Working Group: evolution, insights, and future problems. *ICES Mar. Sci. Symp.* **193,** 22–33.

Sainsbury, K.J. (1988) The ecological basis of multispecies fisheries, and management of a demersal fishery in tropical Australia. In Gulland, J., ed. *Fish Population Dynamics*, 2nd edn. London: Wiley, pp. 350–381.

Sainsbury, K.J. (1991) Application of an experimental approach to management of a tropical multispecies fishery with highly uncertain dynamics. *ICES Mar. Sci. Symp.* **193,** 301–320.

Schnute, J. (1987) A general fishery model for a size-structured fish population. *Can. J. Fish. Aquat. Sci.* **44,** 924–940.

Shepherd, J.G. (1988) An exploratory method for the assessment of multispecies fisheries. *J. Cons. Int. Explor. Mer* **44,** 189–199.

Sparre, P. (1991) Introduction to multispecies virtual population analysis. *ICES Mar. Sci. Symp.* **193,** 12–21.

Stein, R.A., DeVries, D.R. and Dettmers, J.M. (1995) Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Can. J. Fish. Aquat. Sci.* **52,** 2518–2526.

Stewart, D.J., Kitchell, J.F. and Crowder, L.B. (1981) Forage fishes and their salmonid predators in Lake Michigan. *Trans. Am. Fish. Soc.* **110,** 751–763.

Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology* **73,** 747–754.

Temming, A. (1994a) Food conversion efficiency and the von Bertalanffy growth function I: a modification of Pauly's model. *NAGA, ICLARM Q.* **17**(1), 38–39.

Temming, A. (1994b) Food conversion efficiency and the von Bertalanffy growth function, Part II and conclusion: Extension of the new model to the generalized von Bertalanffy growth function. *NAGA, ICLARM Q.* **17**(4), 41–45.

Walters, C. and Juanes, F. (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can. J. Fish. Aquat. Sci.* **50,** 2058–2070.

Werner, E.E. and Hall, D.J. (1988) Ontogenetic habitat shifts in bluegill: the foraging rate–predation risk trade-off. *Ecology* **69,** 1352–1366.

Winberg, G.G. (1956) *Rate of Metabolism and Food Requirements of Fishes* (Transl. Fisheries Res. Bd Canada **253**). 202 pp. + tables.

Accepted 2 December 1996