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A CRITICAL LOOK AT THE POTENTIAL OF ECOPATH WITH ECOSIM TO ASSIST IN PRACTICAL FISHERIES MANAGEMENT

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Ecosystem-orientated thinking is increasingly incorporated into fishery management. Given the complexity of ecosystem processes, there is a need to evaluate the tools used to steer this thinking critically. ECOPATH with ECOSIM (EwE), an aggregate system-modelling package, is currently the most widely employed approach to assess the ecosystem effects of fishing. The basic equations and assumptions, strengths and weaknesses, and the potential of this approach to contribute to practical fisheries management advice are reviewed. Strengths include the structured parameterization framework, the inclusion of a well-balanced level of conceptual realism, a novel representation of predator-prey interaction terms, and the inclusion of a Bayes-like approach (ECORANGER) to take account of the uncertainty associated with values for model inputs. Weaknesses in model structure include the constraining nature of the mass-balance assumption (of ECOPATH) for initiating projections, the questionable handling of life history responses such as compensatory changes in the natural mortality rates of marine mammals, overcompensatory stock-recruit relationships that result from default parameter settings, possible problems in extrapolating from the microscale to the macroscale, as well as some (not too far-reaching) mathematical inconsistencies in the underlying equations. There is a paucity of systematic and stepwise investigations into model behaviour and properties, and users are cautioned against non-critical use of the default settings. An important limitation related to the predominant use of EwE as a "black-box" modelling tool is that some users fail to consider a range of alternative interaction representations. As with all multispecies approaches, the major limitation in applying the EwE approach lies in the quality and quantity of available data. Current EwE applications generally do not adequately address uncertainty in data inputs and model structure. Prudent EwE applications that utilize good data and are based upon rigorous statistical analyses can complement the quantitative predictions of traditional single-species models. They could be particularly useful in some contexts if output in the form of probability distributions encompassing a range of likely ecosystem responses were to be coupled with attempts to extend Operational Management Procedure (OMP) approaches to fisheries management beyond the single-species level. In particular, such applications could serve as the operating models of the underlying dynamics that are used for computer simulation testing of OMPs.

Key words: assessment, ECOPATH, ECOSIM, EwE, fisheries, foraging arena, functional response, management, multispecies, review

Worldwide concerns relating to overexploited fish stocks are complicated by the demonstrated inadequacies of single-species models to address some of these concerns (e.g. to what extent will exploitation of forage fish impact predators of those fish, themselves perhaps subject to fishing). However, have multispecies modelling approaches matured sufficiently to provide information that can usefully be incorporated into *practical* fishery management advice? The focus here is on biological interactions, in contrast to operational or technical interactions, such as bycatch issues and problems related to animals becoming entangled in fishing gear. To contribute to practical advice, a multispecies modelling approach should provide at least qualitative, and ideally defensible quantitative guidance as to the modifications in annual catch levels deemed necessary because of the predicted effects that fishing on a target species will have on other components of the ecosystem. Figure 1 provides a simple framework summarizing a range of multispecies models constructed to inform the management of commercially important stocks. In most cases, movement to ecosystem management will involve unprecedented, untested policy changes so that modelling is unavoidable and the choice is only about which one(s) to use (C. J. Walters, University of British Columbia, pers. comm.).

A key prerequisite for multispecies management advice involves taking explicit account of the major sources of uncertainty and their consequences. Multispecies modelling approaches differ greatly in this regard in addition to differences in their representations of the three fundamental processes structuring ecological systems, namely predation, competition and environmental disturbance (Hollowed *et al.* 2000). In general, as models are made more complex (Fig. 1) to take better account of biological realism, there is an inevitable increase in scientific uncertainty, as a result both of a lack of knowledge of functional relationships and of imprecision in estimates of the associated parameter values. Single-species model analyses used

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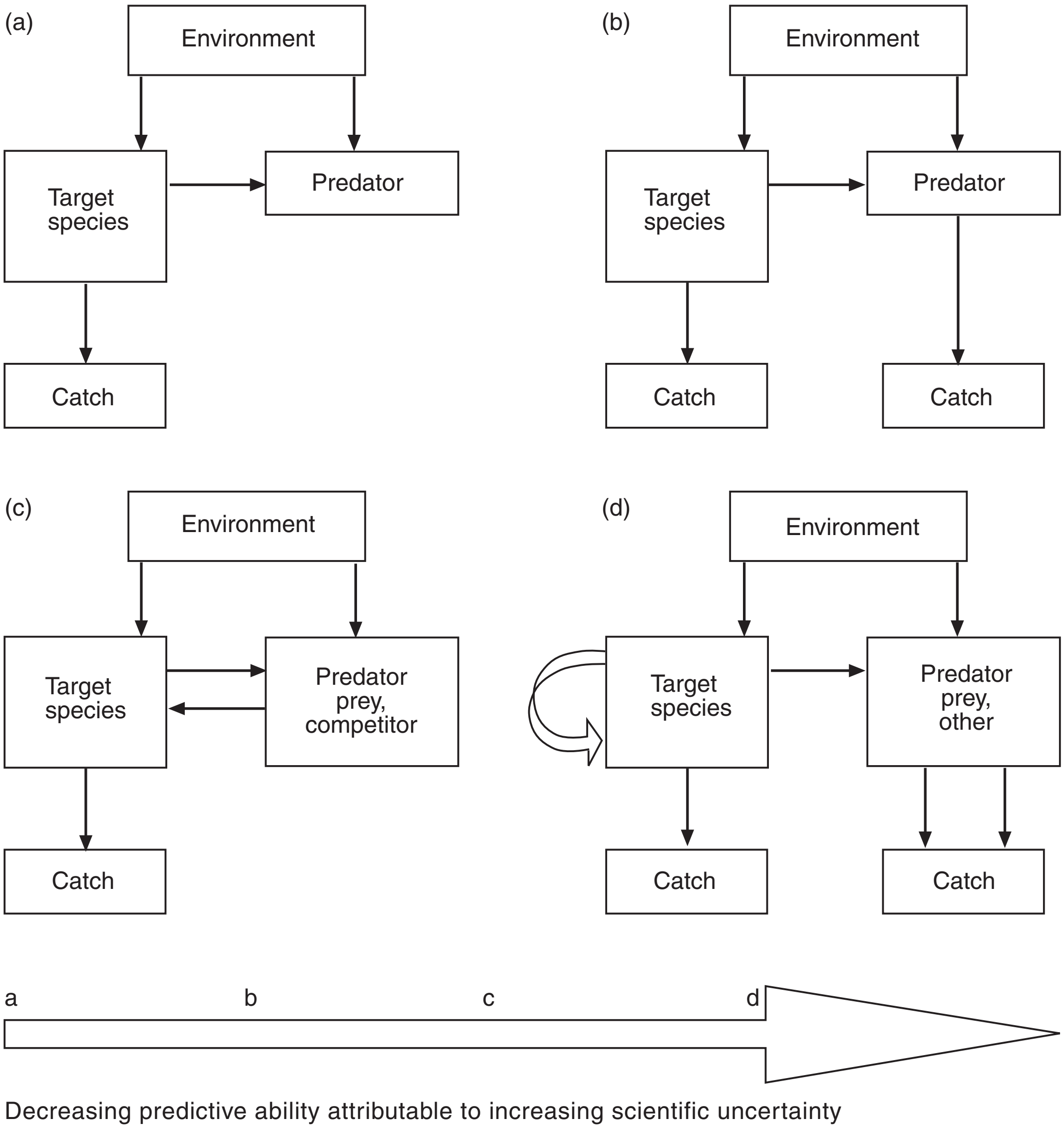

Fig. 1: Schematic of an increasing hierarchy of multispecies model complexity to account for biological (as distinct from technical) interactions that pertain to commercially important species. Basic multispecies models (a) may be used to explore how to harvest a target population appropriately, while simultaneously accounting for the needs of a predator dependent on that population as prey. If both predator and prey are subject to exploitation (b), it is necessary simultaneously to model both predator and prey populations as functions of physical variability, catch levels and the strength and nature of the functional relationship between the two populations. If an intermediate trophic level species is targeted (in a "wasp-waist" system in particular), it may be necessary to account for the functional relationships between the targeted species and its key predators, competitors and prey items (c). In this case, appropriate catch levels are likely to be affected by variability in both upper and lower trophic levels. The most complex multispecies models (d) strive to suggest modifications in the catch level of a species based on the direct and indirect predation and competition effects associated with the simultaneous removal of other foodweb components. In addition, it may be necessary to consider negative feedback loops such as cannibalism (d). The major disadvantage of increasing model complexity to take better account of biological realism is the associated increase in scientific uncertainty, as a result both of lack of knowledge of functional relationships and of imprecision in estimates of the associated parameter values

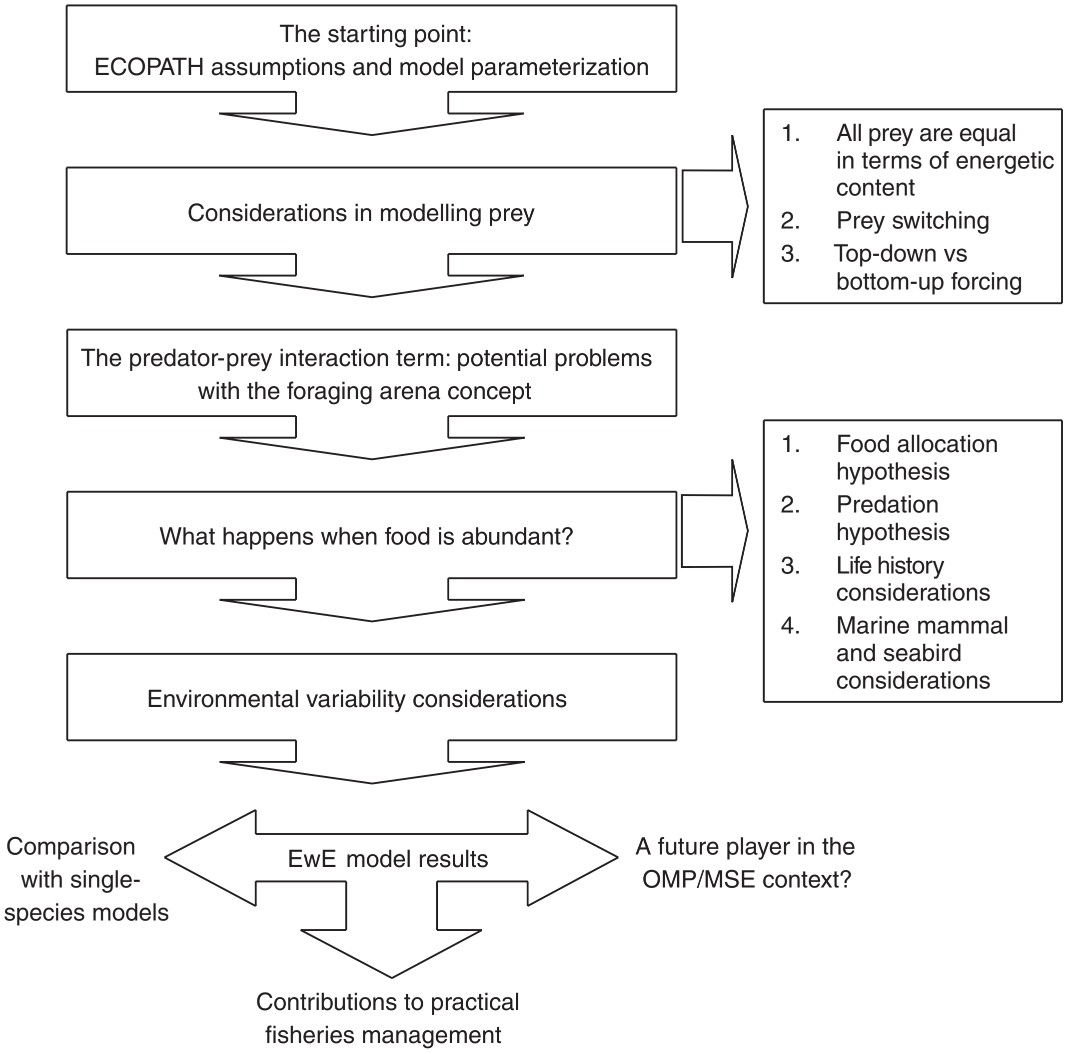

Fig. 2: Summary of the structure of this article's walk through EwE, showing selected detours for more detailed discussion

to advise on catch limits generally concentrate heavily on checking sensitivities and the implications of estimation imprecision. In contrast, these considerations are frequently virtually ignored in evaluations of the more complex multispecies models.

The ECOPATH (Polovina 1984, Christensen and Pauly 1992), ECOSIM (Walters *et al.* 1997) and ECOSPACE (Walters *et al.* 2000a) suite is currently dominating attempts worldwide to provide information on how ecosystems are likely to respond to changes in fishery management practices. The model structure is described in various formats by the model developers (e.g. Walters *et al.* 1997, Christensen and Walters 2000, Pauly *et al.* 2000). The development and ongoing evolution of ECOPATH with ECOSIM (EwE) is undoubtedly a major driving force behind the pursuit of an ecosystem approach to fisheries management. First appearances by ECOPATH and then ECOSIM were roundly criticized by practising stock assessment scientists. However, the current authors consider that the approach and model structure have now matured to the point where they merit serious attention in assessment circles, and that, when properly used, EwE can complement (though not replace) traditional stock assessment methods and assist in policy decisions through an increased understanding of ecosystem structure and functioning.

This document is an attempt to assess independently some potential successes and failures of applying EwE in a management context. This analysis is presented in the form of a walk through EwE (see Fig. 2), with various detours to highlight selected aspects of model structure and use. This review examines aspects of the actual EwE model structure as well as the way in which the model has been used, acknowledging that poor or misuse of EwE and misunderstandings of its limitations should not be interpreted as a criticism of the model structure itself. Comments in the text are not separated under "structure" and "use" headings in the interests of presentational flow, but a summary is given under each heading in the final discussion section.

While recognizing that many of the problems raised could apply also to other multispecies modelling approaches (e.g. Hollowed *et al.* 2000, Fulton *et al.* 2003), detailed discussion is precluded by space limitations, so the focus is restricted to EwE as conventionally applied to marine ecosystems. Further discussion of other multispecies methods such as multispecies virtual population analysis MSVPA/MSFOR (Pope 1991, Sparre 1991, Magnússon 1995, Vinther 2001), BORMICON (Stefansson and Palsson 1998) and GADGET (Globally Applicable Area-Disaggregated Generic Ecosystem Evaluation Tool; e.g. http://www.hafro.is/dst2/report2/) is presented in Plagányi (2004), so detailed comparisons of the various multispecies approaches are not given here. Moreover, Butterworth and Plagányi (2004) provide more general discussion regarding how ecosystem/multispecies modelling might best be developed to contribute to the management of South African fisheries. Further, Plagányi and Butterworth (in press) compare these different modelling approaches with respect to their appropriateness as tools to assess competitive interactions between marine mammals and fisheries.

This review is based in the main on model formulations and results given in the available literature. However, ECOSIM is constantly being improved, patched and extended, so some of the criticisms made may no longer apply to the most recent version/s of ECOSIM. Given the difficulties in defining what exactly constitutes "ECOSIM" (because the package is constantly evolving), together with typical delays before work is published, the focus here is on EwE studies published before the end of 2002, and on software versions up to EwE 4.0, as described in the software manual by Christensen *et al.* (2000). "ECOSIM" may have changed since then, but then this might also bring the results of published studies based on earlier versions of ECOSIM into question.

BACKGROUND TO MODEL EQUATIONS

Full details of the EwE modelling approach, as well as the associated software, can be obtained from www.ecopath.org. Briefly, the fundamental ECOPATH mass balance equation is based on that originally proposed by Polovina (1984). This balance for each functional group *i* in an ecosystem (excluding detritus) is described by

$$B_i \times (P/B)_i \times EE_i = Y_i + \sum_j B_j \times (Q/B)_j \times DC_{ji} + BA_i \, , \tag{1}$$

where

B_i and B_j	are the biomasses of *i* and the consumers (*j*) of *i*, respectively;
$(P/B)i$	is the production/biomass ratio for *i*;
EE_i	is the fraction of production of *i* that is consumed within, or caught from the system (the balance being assumed to contribute to detritus);
Y_i	is the fisheries catch ($Y = FB$; F is the proportion fished);
$(Q/B)_j$	is the food consumption per unit biomass of *j*[1];
DC_{ji}	is the fractional contribution by mass of *i* to the diet of *j*; and
BA_i	is a biomass accumulation term that describes a change in biomass over the time period studied and/or net immigration (Christensen 1995).

The ECOSIM models convert the above "steady-state"[2] trophic flows into dynamic, time-dependent predictions. For prey *i* and predator *j*, Walters and Kitchell (2001) model the dynamics of the vulnerable (V_{ij}) and non-vulnerable ($N_i – V_{ij}$) components of the prey abundance (by number) of *i* as

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[1] Note that throughout the discussions in this paper, the term *per capita* is used equivalently to the term *per unit biomass* because the EwE notation includes references to both numbers and biomass of species groups

[2] Strictly in applications where some *BA* term is non-zero, the ECOPATH approach does not reflect "steady-state"/"equilibrium". However, in the interests of parsimony of expression in what follows, this terminology is retained (in quotes for this reason) as the spirit of the approach, even with this adjustment, is to represent balances in a "steady" (possibly steadily changing) situation, in contrast to modelling the dynamics fully

$$\frac{d\left(N_i - V_{ij}\right)}{dt} = -v_{ij}\left(N_i - V_{ij}\right) + v'_{ij} V_{ij} \tag{2}$$

$$\frac{dV_{ij}}{dt} = +v_{ij}\left(N_i - V_{ij}\right) - v'_{ij} V_{ij} - a_{ij} V_{ij} N_j \quad , \tag{3}$$

where the total consumption rate Q_{ij} of prey i by predator j is $a_{ij}V_{ij}N_j$, and N_j represents the number of predator group j.

Under the assumption that the dynamics of V_{ij} are much faster than those of N_i, $^{dV_{ij}}/_{dt}$ is set to zero, yielding

$$V_{ij} = v_{ij} N_i / \left(v_{ij} + v'_{ij} + a_{ij} N_j\right) \quad , \tag{4}$$

and hence (taking biomass to be proportional to numbers) the standard ECOSIM interaction term form describing trophic flows Q_{ij} between prey group i and predator group j:

$$Q_{ij} = a_{ij}\, v_{ij}\, B_i\, B_j / \left(v_{ij} + v'_{ij} + a_{ij}\, B_j\right) \quad , \tag{5}$$

where a_{ij} is the rate of effective search for prey i by predator j, and v_{ij}, v'_{ij} are prey vulnerability parameters, with $v_{ij} = v'_{ij}$ as the default setting (Walters *et al.* 2000b).

As in the classic Lotka–Volterra formulation ($Q_{ij} = a_{ij}B_iB_j$), flows are determined by both prey and predator biomasses, but Equation (5) incorporates an important modification in that it encompasses a framework for limiting the vulnerability of a prey species to a predator, thereby including the concept of prey refugia and also tending to dampen the unrealistically large population fluctuations usually predicted by the Lotka–Volterra formulation. Note that the vulnerability v^*_{ij} as input to ECOSIM is a rescaling of the vulnerability parameter v_{ij} above, so this is expressed relative to the rate at which an individual predator of species j consumes species i; specifically this is such that the recommended ECOSIM input default $v^*_{ij} = 0.3$ corresponds to (K. Y. Aydin, US National Marine Fisheries Service, pers. comm.):

$$R_{ij} = {}^{2v_{ij}}\!\Big/_{a_{ij}B_j} = 1 \tag{6}$$

or

$$a_{ij}B_j = 2v_{ij} \quad . \tag{7}$$

Some more technical points regarding the derivation of the form of the ECOSIM functional response are given in the Appendix. In particular, when using the default vulnerability settings, the above equations are shown to be inconsistent with the notion of only a small proportion of prey being vulnerable at any time. The reader is referred to the Appendix for discussion of the implications of some mathematical inconsistencies underlying the ECOSIM interaction term, which fortunately are not far-reaching (C. Walters, pers. comm.).

The early ECOSIM versions (e.g. ECOSIM II) modelled consumers as follows (Walters *et al.* 2000b):

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - \left(M_i + F_i + e_i\right) B_i \, , \tag{8}$$

where

g_i represents net growth efficiency per unit of consumption by i;
I_i is the biomass immigration rate for i;
M_i is the mortality rate on i not accounted for by predation within the system;
F_i is the fishing mortality on i; and
e_i is the emigration rate of i.

To overcome the limitations of a biomass dynamics framework, where relevant, juvenile and adult pools in ECOSIM II are linked using a delay-differential equation system that keeps track of flows in terms of numbers as well as biomass. The dynamics are based on the Deriso–Schnute equations and are described in more detail in Walters *et al.* (2000b). More recently, the latest version of EwE includes a facility to model fully age-structured population dynamics with multiple life history stanzas and recommends the use of this approach in favour of the adult/juvenile splitting implemented earlier (see www.ecopath.org). Note that, although ECOSIM focuses on feeding interactions, it also includes a facility in the form of a (seasonal or longer term) forcing function routine to represent the mediation of physical or other environmental parameters influencing these trophic interactions (Christensen *et al.* 2000).

In many respects, EwE achieves a good balance in model structure between simplicity and the level of complexity that often accompanies other ecosystem model representations. Although users have tended to include a large number of components in their EwE models, EwE can also be used in more of a Minimum Realistic Model (MRM) sense (V. Christensen, University of British Columbia, pers. comm.; Butterworth and Plagányi 2004).

A CLOSER LOOK AT EwE

In the sections below, some weaknesses in model structure and potential pitfalls in the application of EwE as a tool to address management issues in situations such as those summarized in Figure 1 are reviewed.

Points to be borne in mind in interpreting output from the EwE software packages are also discussed.

"Equilibrium"/"steady-state" assumption

The "steady-state" requirement of ECOPATH models implies that the model outputs apply only to the period for which the inputs are deemed valid (Christensen and Pauly 1992). Specification of the period for which these models are expected to have predictive power is therefore critical. For example, the choice of a decade for a slowly changing ecosystem such as a coral reef (e.g. Arias-Gonzalez *et al.* 1997) seems appropriate. However, the choice of a decade as a suitable time scale for models of upwelling systems (e.g. Jarre-Teichmann 1998, Shannon and Jarre-Teichmann 1999) seems open to question because of the fundamental role of variability in mediating important interactions on smaller spatial and temporal scales. There is the added danger that the construction of such models over different (arbitrary) time intervals (e.g. for the 1980s to compare with the 1990s) may lead to the conclusion that a sudden regime shift has occurred. However, given short-lived small pelagic species have highly variable annual recruitment, averages over 10-year periods of random variability can differ appreciably even though there is in fact no underlying change in the system.

It is possible to include trends (e.g. in the biomass of groups) in the ECOPATH analysis that is used to initiate projections, but the critical concern remains: the parameter values themselves are constrained by "steady-state" assumptions. Hollowed *et al.* (2000) point out that such models fail in adequately determining the impacts of fishing on marine ecosystems precisely because the multispecies interactions of most interest are exactly those that could cause marked departures from the current situation (and hence likely also from values of key associated parameters).

As an example, Christensen (1998) concludes that ECOSIM shows promise for developing management options for multispecies fisheries through, for example, simulations to predict the exploited state of the ecosystem based upon knowledge of the pre-exploitation state. Although ECOSIM users are generally cautioned against studying the impact of drastic changes in fishing pressure, Christensen (1998) does explore the degree to which the heavily fished state of the Gulf of Thailand in 1980 could be reproduced based on a model of the pre-exploitation state of the ecosystem in 1963. Because many predicted biomass changes were in reasonable agreement with the changes observed, Christensen (1998) suggests that his results indicate that the imposed constraints that keep parameters at their pre-exploitation "equilibrium" values do not seriously compromise ECOSIM's predictive ability. However, an alternative conclusion could be that it provides an example of how readily it is possible to obtain a reasonable fit to a set of data without correctly specifying the underlying causal mechanisms. Indeed, whereas the estimated changes in the biomass of some groups were in reasonably good agreement with changes estimated from trawl surveys, at the other extreme ECOSIM's predicted 1980/1963 biomass change of crabs and lobsters (admittedly only a minor part of the system) was >1 000-fold compared with an only threefold change observed. Nonlinearities in species interactions and in the response of individual species to fishing pressure are likely to play an increasingly important role the greater the departure from initial assumed "equilibrium" conditions. Managers must always take care when inferences drawn from models have involved substantial extrapolation, as in this case.

The use by some authors of the same *P/B* ratio per species group for two ECOPATH models of the same ecosystem for different time periods is questionable practice. Even some of the most erudite ECOSIM applications can be criticized on this point. For example, Trites *et al.* (1999) assume the same constant *P/B* ratio (0.5 year^{-1}) for adult pollock *Theragra chalcogramma* when trying to explain the large changes between the 1950s (prior to large-scale commercial fisheries) and the 1980s (characterized by an increase of groundfish such as pollock) in the eastern Bering Sea ecosystem, despite a 500% increase in adult pollock biomass over this period.

Potentially one of the most useful applications of ECOSIM – to assist in resolving the debate concerning the extent to which major changes in ecosystem structure between two periods can be explained by the relative roles of fishing, predation and the environment (e.g. Bundy 2001, Trites *et al.* 1999) – is similarly handicapped by the "equilibrium" assumption. A valuable suggestion put forward by Bundy (2001) is to assemble a second ECOPATH model for the later period, to be used in conjunction with direct biological parameter estimates for that period to assess the extent of change in the values assumed for the model of the first period.

Parameterization

In traditional ecosystem models, modellers often confess to some level of *ad hoc* adjustment or "tuning" in an effort to find a feasible solution. An attraction of the ECOPATH approach is that, for each species/species group, one of the quantities *B*, *P/B*, *Q/B* or *EE* is obtained by solving the linear equations and hence, given the other values needed, a unique mass-balance solution is always obtained. However, the robustness of the model output to variability and uncertainty in these input values generally needs to be better explored.

The Bayes-like approach incorporated in the ECORANGER routine allows explicit consideration of uncertainty in input values (Pauly *et al.* 2000) and is an important step forward for the EwE approach. Analyses based on ECOPATH models that do not fully explore the consequences of uncertainty in the inputs are potentially misleading, especially when current knowledge of all the components in an ecosystem is such that, for example, actual biomass estimates for some species may vary by as much as a factor of 10 (in contrast to the ECORANGER default of 10%). Moreover, the multiplicative effects of uncertainty in all input values (for diet proportions, as well as abundance and *P/B* ratios) also need to be considered. Unfortunately, to date few ECOPATH applications appear to have attempted to represent and consider uncertainty about parameter values adequately.

A further issue with the use of the ECORANGER approach is that Monte Carlo integration over a strongly peaked function is computationally inefficient. This difficulty arises because the very large number of constraints imposed by the ECOPATH relations, such as that all *EE* parameters in the mass-balance equations must be <1, means that the feasible region is a very small proportion of the total parameter space. ECORANGER does incorporate a Sampling-Importance-Resampling (SIR) scheme (McAllister *et al.* 1994) to improve computational efficiency. This approach depends on a user-defined input function that measures the extent to which alternative solutions best satisfy some criterion (Christensen *et al.* 2000), and which presumably serves as the "importance" function for the SIR process. The difficulty is that, unless most of the mass of that function falls within the feasible region (i.e. is consistent with the ECOPATH-related constraints, which anyway would be difficult to know before conducting the analysis), little increase in computational efficiency would be expected. This situation might be improved by the use of the Monte Carlo Markov Chain (Gilks *et al.* 1996) approach to such integration, which could readily incorporate the ECOPATH constraints directly in the function effectively integrated (e.g. Sobahle *et al.* 2004).

The possible double use of information is also a concern here, because of the data-intensive requirements of ecosystem approaches. Caution must be exercised to ensure the independence of parameter values input and the data used for fitting purposes. A further potential abuse of these models lies in the practice of parameter value "swapping", whereby the choice of unknown parameter values is justified on the basis of values obtained by other researchers – often for different temporal and spatial scales. Careful thought needs to be given to the source of values for parameters. A common fault in EwE applications lies in the use of diet composition data from a different time period without adjusting to account for the differences in the relative abundances of prey species between the two time periods. This is because, even if there is no prey-switching, the use of non-representative dietary data will compromise both the ECOPATH mass-balance results and projections using ECOSIM.

Improvements in this regard may be achievable through the use of techniques to smooth spatial and temporal variability in food composition and predator abundance, such as the geostatistical approach of kriging (Bulgakova *et al.* 2001). A good example of the importance of separating prey size preference from prey availability is given in Floeter and Temming (2003; for North Sea cod *Gadus morhua*). In fairness, the criticism that multispecies outputs will be uncertain until there is an improved understanding of how predators respond to changes in *per capita* food availability (Butterworth and Punt 2003a) applies to all multispecies approaches. In response, it could be argued that this is particularly problematic in ecosystem models with their many components, in contrast with, say, "minimal realistic models", as considered in the analysis of fishery interactions between Cape fur seals *Arctocephalus pusillus pusillus* and Cape hake *Merluccius capensis* and *M. paradoxus*, documented by Punt and Butterworth (1995). On the other hand, the incorporation of greater ecosystem detail permits at least a first attempt at investigating less well-understood effects. Fulton *et al.* (2003) provide some guidelines, such as advocating the use of functional groups (chosen on the basis of similar body size and shared predators and prey), to achieve an appropriate degree of trophic aggregation within an ecosystem model.

One of the most important steps necessary to enhance the utility of the EwE approach in management contexts is an extension towards more soundly based statistical estimation methods. The application by Savenkoff *et al.* (2001) of inverse models to minimize the imbalances between inputs and outputs in an ECOPATH model constitutes a move in the right direction. Rather than the *ad hoc* adjustments generally made to achieve mass balance, Savenkoff *et al.* (2001) propose obtaining an optimal (balanced) solution by estimating trophic flows using a specific least-squares criterion. The criterion used attempts to minimize the sum of the flows through the foodweb, with the mass balance thus being closed by residuals (inputs – outputs) rather than ecotrophic efficiencies, as in ECOPATH. A particular advantage of that approach is its ability to refine estimates of diet composition in a manner that weights the evidence from different sources in a statistically defensible manner (Savenkoff *et al.* 2001).

Large ecosystem models based on poor data obviously have no place in the management arena. However, a viable solution is not necessarily found in the call for more holistic studies and future data collections (e.g. Toral-Granda *et al.* 1999). A timely suggestion by Mace (2001) concerns evaluating what is attainable in an ecosystem management context relative to the costs and benefits associated with obtaining the necessary information.

Differences in energetic content of prey

There is no energetic content parameter included in the rightmost term of Equation (1), so alternative prey types are treated as energetically equivalent in EwE.

Contrary to this assumption, Winship and Trites (2003) recently drew attention to the need to consider not only the quantity, but also the distribution and quality, of food available to predators. They estimate that in South-East Alaska, seasonal changes in the energy density of the diet of Steller sea lions *Eumetopias jubataus* resulted in animals requiring approximately 45–60% more food per day in early spring than in late summer. Regional differences in the energy density of the diet similarly accounted for substantial (up to 24%, based on summer diets) differences in food requirements among the South-East and Western Alaska populations of Steller sea lions (Winship and Trites 2003). The same considerations likely apply in the case of some fish species.

Prey-switching and the stability of prey suitabilities for predators[3]

Prey-switching occurs when the suitability of a prey for a predator exhibits a sudden change as a function of prey abundance, such as when a predator switches to another prey species when its original preferred species drops below a certain level of abundance. Mechanisms responsible for switching include predators developing a search image for a certain prey type, an increase in capture success with increasing abundance and the occupation of different sub-habitats by different prey types (Murdoch *et al.* 1975). The extent of prey-switching is still open to debate, with some authors finding no evidence of it (e.g. Bell *et al.* 1999 – bluefish *Pomatomus saltatrix*) and others arguing that it had taken place (e.g. Murdoch *et al.* 1975 – fish, Estes *et al.* 1998 – marine mammals, Mayfield *et al.* 2000 – rock lobster *Jasus lalandii*).

As noted by Walters *et al.* (1997), a potential problem with the use of ECOSIM to model situations far from the initial trophic "equilibrium" is that it cannot replicate the phenomenon of prey-switching by predators. This can be problematic in modelling highly dynamic ecosystems such as upwelling systems, where species have adapted to their variable environment by evolving extremely flexible feeding behaviour, with both feeding behaviour and rate of food consumption determined by the size and density of available prey (e.g. James and Findlay 1989). Walters *et al.* (1997) furnish further examples and discussion of situations in which the ECOSIM equations are likely to fail. The impacts of various multispecies harvesting strategies on community structure and fishery yields will most likely be incorrectly predicted (in a qualitative sense) for situations far from the initial "equilibrium", *inter alia* because it is under such scenarios that prey-switching is more likely to manifest itself.

Both EwE and MSVPA models assume constant suitabilities (also referenced in the literature as the constant predator preference assumption). Some support for using near-constant suitabilities derives from the extensive analyses of North Sea field collection data for MSVPA. Rice *et al.* (1991) deduced that suitabilities were quite stable over time when the effects of changing abundance and age structure are taken into account, such that multispecies models parameterized with good field data have the potential to be useful in management. Subsequently, however, Rindorf *et al.* (1998) concluded that cod and whiting *Merlangius merlangus* exhibit positive switching, i.e. they keep eating a given food item to a greater extent than suggested by the constant suitability model when the food item becomes relatively scarce. Their findings highlight the need for caution in assuming constant suitabilities (as in both EwE and MSVPA models), particularly when extrapolating to situations far from the initial model state.

Adlerstein and Welleman (2000) note a potential bias in predation-mortality estimates because predator stomach contents can vary appreciably within a 24-h period. They stress the need for time stratification in stomach sampling to improve the quality of the data used to implement multispecies models. McQueen and Griffiths (2004) propose careful analyses to obtain accurate dietary description for snoek *Thyrsites atun*, a top predator of the southern Benguela.

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[3] "Suitability" is used here in its technical sense. This reflects how desirable prey of one type are to a predator relative to other prey types: specifically, it expresses the relative frequency of selection of a prey type if all prey types were equally abundant. In contrast, the term "preference" is used here in a purely colloquial sense

FORAGING ARENA MODEL CONSIDERATIONS

Direction of flows: bottom-up vs top-down control

ECOSIM users are able to set vulnerability parameters to control the extent to which the model moves towards top-down and away from bottom-up control. The two-state (vulnerable/invulnerable) representation of prey biomass (see Equations 2–5) is a first approximation to modelling the complex spatial and temporal overlaps between predators and prey (Christensen and Walters 2000), and represents a substantial improvement on predation rate formulations employed by most other multispecies models. The major disadvantage relates to the difficulties of choosing appropriate values for prey vulnerability parameters because of the obvious problems in trying to quantify these processes. This is one of the biggest potential limitations to modelling ecosystem interactions with any confidence because, as emphasized by Shannon *et al.* (2000), ECOSIM predictions can be highly sensitive to the choice of vulnerability settings.

Utility in a management context therefore warrants careful explorations of model sensitivity to a range of energy flow assumptions, as has been done, for example, by Bundy (2001) in her study of Newfoundland-Labrador ecosystems. Another example of the way in which uncertainties as regards vulnerability settings have not necessarily impeded attempts to provide guidance for fisheries managers is provided by Arreguín-Sánchez (2000). By conducting ECOSIM simulations over a range of vulnerability and fishing mortality scenarios, he was able to investigate the importance of the interdependence between two important fishery resources, octopus *Octopus maya* and red grouper *Epinephelus morio* (which preys on the former), in relation to the impact of fishing on octopus biomass. Daskalov (2002) used an EwE approach to assess the relative roles of overfishing (top-down forcing) and eutrophication (bottom-up forcing) in mediating changes in the Black Sea ecosystem though a trophic cascade mechanism. These examples show that ECOSIM studies can play an important role in investigating the impacts of changes in fishing mortality in the context of the relative roles of changes in top-down and bottom-up forcing.

Functional response formulation and the problem of using default values

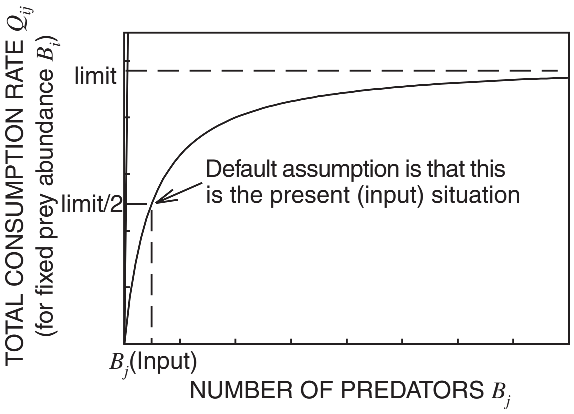

Fig. 3: A depiction of the ECOSIM "foraging arena" representation and the implications of default vulnerability settings for model computations of the total consumption Q_{ij} of species i by an abundance B_j of predators of species j. The curve shown corresponds to the default setting of the vulnerability parameter $v^* = 0.3$ (see text for details)

Given the difficulties associated with an appropriate choice of vulnerability values, there is a strong temptation for users to revert to using the default values and/or to assume the same value for all species. The default vulnerability value implies that the current abundance corresponds to the "half-saturation" point on the consumption curve, as shown in Figure 3. Specifying such a default for all predators seems questionable, because differences in their prior exploitation histories mean that the current abundances of different predators would correspond to different proportions of their pre-exploitation levels, and likely also to different points on their consumption curves. The use of the same vulnerability value for all species is therefore problematic because, *inter alia*, it assumes that the species are all currently at the same point of the curve shown in Figure 3, irrespective of their prior exploitation histories. Moreover, *a priori* assumptions of vulnerability settings can strongly influence model outcomes.

Consider, for example, the fundamental ECOSIM relationship between total consumption Q_{ij} of prey pool i by marine mammal predator j, and the abundance of predators B_j as shown in Figure 3. Marine mammals have generally been heavily harvested in the past and therefore have been reduced to levels that are low compared with their pre-exploitation levels. As is evident from Figure 3, if a scenario is run in which numbers of marine mammals (as predators) that were low reach numbers that are "high" (towards the right hand side of the plot), and these numbers are subsequently halved and maintained at that level (e.g. via culling), the total consumption Q_{ij} hardly drops under

ECOSIM's default vulnerability values. This is because the *per capita* consumption (Q_{ij}/B_j) nearly doubles. Therefore, ECOSIM cannot yield exact-replacement results when predicting the extent to which consumption by another "predator" (e.g. a fishing fleet, which acts identically in terms of prey selection) can increase sustainably in response to a marine mammal cull. Expressed another way, this is to argue that default parameter value selections for the model effectively hard-wire to such an extent that they effectively swamp other signals pertinent to predicting the effects of a marine mammal population reduction. Confidence in the ECOSIM predictions would in this case hinge on the extent to which the ECOSIM interaction representations (with their associated vulnerability parameter settings) are considered realistic and reliable.

The argument above serves also as a partial explanation of the simulation results of Aydin and Friday (2001), who implemented a simple three-compartment model (zooplankton – fish – marine mammals) in ECOSIM to investigate the effects of removing a top predator from the ecosystem. They found that reducing the abundance of marine mammals in the system by harvesting them (given default vulnerability settings) hardly changed the Maximum Sustainable Yield (*MSY)* for commercial fish. Cooke (2002) reinforces these concerns with ECOSIM defaults by demonstrating through the use of a simple model that whether or not a reduction in whale numbers results in higher fishery yields than would otherwise, (other things being equal), be obtained, depends critically on the assumed vulnerability of fish prey of the whales. It is only under scenarios that assume a relatively high vulnerability of fish to whales that fishery yields are predicted to be sensitive to the abundance of whales.

Unlike in the Lotka–Volterra representation of a predator-prey interaction, the foraging arena model in ECOSIM does not treat predators and prey symmetrically. If the number of *predators* is raised or lowered (while keeping prey numbers fixed), in view of the fact that ECOSIM has a "predator interference" functional response (Equation 5), the individual predators then eat less or more respectively, because this formulation assumes implicitly that the predators are competing with one another for limited prey. Therefore, as shown above, the immediate effect of this (if predator numbers are towards the right on the curve in Figure 3) is that the total consumption of prey stays about the same. On the other hand, consumption (both total and *per capita*) is a linear function of prey abundance in ECOSIM (see Implication 3 in the Appendix), so if *prey* abundance is halved (e.g. through fishing), total consumption of prey by the predators is decreased proportionately. Therefore, if fishing reduces the abundance of a commercial fish species by half, the result would be a halving of the total consumption of that species by marine mammals and hence the ultimate effects of this fishing on marine mammals may be appreciable.

ECOSIM incorporates a "seek evolutionary stable strategy" routine that can be used to either set *all* vulnerability parameters to the same "evolutionary stable" value or permit estimation of vulnerability values (that make sense in evolutionary terms) for each functional group (Christensen *et al.* 2000). The EwE manual (Christensen *et al.* 2000) notes that the routine that sets a single vulnerability value for all groups usually produces scaled values in the range 0.3–0.5, and that this corresponds to the range that produces reasonable[4] ecosystem behaviour when performing simulations. Although several ECOSIM studies include analyses making alternative assumptions, such as that vulnerabilities are proportional to trophic level (e.g. Bundy 2002, Mackinson 2002), published studies typically set a blanket value for all groups. A useful insight is to be found in the work of Fulton and Smith (2002), who conclude that their model of the Port Philip Bay ecosystem often performs best (in the sense of providing better fits to historical time-series data) when prey vulnerabilities for higher trophic levels or heavily depleted groups are high, whereas values for lower trophic levels are in the range 0.4–0.5.

The assertion by Walters and Kitchell (2001), based on unpublished data, to motivate the foraging arena model that "predators with full stomachs are not a common field observation" (and hence are usually hungry and seeking food) is one that remains open to debate. Digestion time constraints likely put a cap on the consumption rates of both marine mammals (Rosen and Trites 2000) and fish (Punt and Butterworth 1995, Jeschke *et al.* 2002, Rindorf 2002, Gill 2003). Moreover, in a study of the effect of stomach fullness on food intake of whiting (in the wild) in the North Sea (Rindorf 2002), the presence of food in the stomach had an appreciable dampening effect on search activity. Although whiting intensify their search for food as their stomach empties, they do not continue searching until the stomach is completely filled (Rindorf 2002). Further evidence suggesting that not all species act like an "ECOSIM predator" is provided by Punt and Leslie (1995), who computed estimates of daily ration for Cape hake. A key feature of that study was the conclusion that hake inter-meal frequency de-

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[4] "Reasonable " ecosystem behaviour is described in the EwE manual as "species unlikely to drop out due to predation or competition, predator-prey cycles rare or absent, recruitment relationships with realistic compensatory responses"

creased rapidly with hake size, so that the largest hake were feeding about only once every 10 days. Without this low feeding rate, the population model of Punt and Butterworth (1995) resulted in a "perpetual-fishing-machine" – large hake became so effective at eating small ones, that the harder one fished and removed larger hake, the more smaller hake escaped such predation and became available to make for even larger sustainable fishery catches!

The foraging arena model is fundamentally different from approaches such as MSVPA and associated predictive models such as MSFOR, which assume that a predator is always able to consume its desired daily ration of food. In contrast, in the ECOSIM formulation, a predator competes with others of the same species for a limited proportion of the prey population that is "vulnerable" for consumption by that predator species alone. As a consequence, Butterworth and Plagányi (2004) categorize MSVPA and ECOSIM approaches as "efficient predator models" and "hungry predator models" respectively.

The choice between such feeding interactions in a model can lead to large differences in the model's predictions. For example, both Mackinson *et al.* (2003) and Koen-Alonso and Yodzis (subm.) explore the consequences of alternative feeding interactions and demonstrate greatly different predicted model outcomes depending on the type of functional response formulation being implemented. Koen-Alonso and Yodzis (subm.) fitted a trophodynamic model, constructed using a bioenergetic-allometric approach, with five different functional response formulations. The models that provided the best fits to the data shared Type III (predator-independent) functional responses, whereas the ECOSIM functional response[5] performed the worst, in terms of its Akaike Information Criterion score corrected for sample size (AIC_c; Burnham and Anderson 2002). The ECOSIM functional response could be viewed as a Type 0[6] single-species functional response (because the predation rate on a prey species is unaffected by changes in the abundance of alternative prey; Koen-Alonso and Yodzis subm.). They underscore the need to scrutinize the nonlinear mathematical structures of multispecies models (such as the functional response) with the same level of rigour as accorded to parameter estimates by traditional single-species fishery modellers. Mackinson *et al.* (2003) have made a start in this regard by evaluating the effects of particular combinations of ECOSIM settings that can be used to produce alternative "emergent" forms of functional responses, specifically Types I and II behaviours. This is discussed further in the following sections.

Dealing with an increasing food supply: a critical look at the food allocation and predation hypotheses

The maturation of an ECOSIM model into a predictive modelling tool warrants *inter alia* a more thorough analysis of some of its ecological assumptions. This point is illustrated by focusing on attempts by Walters *et al.* (2000b) to rectify one of the more serious conflicts between field observations and model predictions in their first version of ECOSIM II: the model-predicted increase in average adult body weight of an apex predator (for example, tuna) with an increase in fishing rate. Considering the reduced abundance of most apex predators (and many tuna stocks in particular) over the past few decades at least, it is highly implausible that they are currently food-limited and hence that a further increase in predator/tuna fishing rates would lead to an increase in feeding rates and somatic growth. This unlikely prediction from the first version of ECOSIM II arises because reproductive and somatic growth rates are formulated as proportional to *per capita* food consumption. This formulation is presumably also responsible for "interesting" results such as those of Arreguín-Sánchez (2000), who found a predicted increase in the frequency of oscillations in abundance with increasing trophic level.

Walters *et al.* (2000b) introduce two options to counter strong compensatory increases in somatic growth rate predicted by the first version of the ECOSIM II model. With increasing food supply, animals may either:

(i) allocate surplus to reproduction rather than growth ("food allocation hypothesis"); or
(ii) spend less time foraging so as to decrease time at risk to predation (so that the density-dependent response to population reduction would be in the

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[5] The "ECOSIM functional response" as referenced here corresponds to the formulation as given in Equation 5. This is the form used by the majority of ECOSIM users so that it has come to be taken as synonymous with ECOSIM. However, as demonstrated by Mackinson *et al.* (2003), by choosing certain parameter values in the EwE model package (e.g. feeding time adjustment rate) in more complex versions of the foraging arena model (see, e.g. Equation A17 in the Appendix), one can get a different "emergent" functional response type

[6] A Type 0 functional response is one in which predation rate increases linearly with prey density so that there is no saturation term. A Type II response is linear at first but then plateaus when the consumer is satiated (Holling 1959). In a Type II functional response, the predation rate increases at a decreasing rate with prey density until it becomes constant at satiation, whereas in a Type III (sigmoid) functional response, predation rate accelerates at first and then decelerates towards satiation (Holling 1959)

form of a drop in natural mortality – "predation hypothesis").

THE FOOD ALLOCATION HYPOTHESIS AND ITS IMPLICATIONS FOR STOCK-RECRUITMENT RELATIONSHIPS

Users of later versions of ECOSIM II specify a "life history weighting factor" W_g, which essentially determines the proportion of net intake (the $\sum_j Q_{ji}$ term in Equation 8) allocated to somatic growth compared with reproduction, as follows (Walters *et al.* 2000b):

$$P_g^{\text{realized}} = W_g\, P_g^{\text{constant growth}} + \left(1 - W_g\right) P_0 \quad , \quad (9)$$

where P_0 is the proportion at the initial equilibrium ($t = 0$), and $P_g^{\text{constant growth}}$ is the proportion that will maintain somatic growth at the same level as initially (i.e. the amount allocated to growth remains the same, but the proportion changes because of changes in the net intake rate). As the weighting factor W_g changes from 0 to 1, model behaviour shifts from one of these extremes to the other. Recruitment levels at each timestep in the model are then determined by a combination of the current status of the adult stock relative to that at time $t = 0$ ($N_{A,t}/N_{A,0}$), and the ratio of food consumption per unit biomass allocated to reproduction $(1 - P_g^{\text{realized}})Q_{A,t}$ to baseline ($t = 0$) food allocated $(1 - P_0)c_{A,0}$. The recruitment function R is thus scaled relative to baseline recruitment R_0^* as follows (Walters *et al.* 2000b):

$$R\left(B_{A,t}, N_{A,t}, Q_{A,t}\right) = R_0^*\left(N_{A,t}/N_{A,0}\right) \times \left[\frac{\left(1 - P_g^{\text{realized}}\right) Q_{A,t}}{\left(1 - P_0\right) c_{A,0}}\right]^r \quad , \quad (10)$$

where

$Q_{A,t}$ is the adult food consumption (per unit biomass) at time t (that varies with feeding opportunities as given by Equation 5 above – see Appendix Equation A17 for a revised form of Equation 5); and

$c_{A,0}$ is the baseline adult food consumption (per unit biomass) at time $t = 0$[7].

The formulation above includes an option for generating non-linear effects of the food environment on *per capita* recruitment rates (by setting the power parameter $r \ll 1$). For simplicity, the discussion below assumes the default value of $r = 1$.

The assertion that when food availability increases, adults may increase the proportion of net intake allocated to reproduction at the expense of the proportion (though not the amount) allocated to growth is unlikely to hold unless adults are currently food-limited. Given the general trend of fishing down foodwebs (Pauly *et al.* 1998), it seems unlikely that many commercial fish stocks are currently food-limited. Most studies citing density-dependent changes in growth rates in marine systems (e.g. Anthony and Fogarty 1985, Ross and Nelson 1992, Bigler *et al.* 1996) are consistent with the notion that density-dependent effects on somatic growth rate should be most pronounced when stock density is high, and reduced or absent under low stock densities (Ross and Almeida 1986). In contrast, Equation (10, with default value $r = 1$) depicts the *per capita* rate of reproduction as linearly proportional to *per capita* food consumption for all levels of stock density. The scaling of Equation (10) as relative to conditions at the ECOPATH starting "equilibrium" ($t = 0$) rather than relative to a measure of "true" base food consumption (from metabolic considerations for example) and/or pre-exploitation population levels therefore merits further consideration.

Equation (10), with $r = 1$, can be rewritten in a simpler form, familiar to stock assessment scientists, which shows the relationship between recruits per spawner (R/S_N, where $S_{N,t} = N_{A,t}$ in the EwE notation) and *per capita* food consumption:

$$\left(R/S_N\right)_t = c_1\left[c_2 \frac{Q_{A,t}}{c_{A,0}}\right]^1 \quad , \quad (11)$$

where

c_1 is a constant ($\mathrm{R}_0^*/\mathrm{N}_{A,0}$) that describes the "baseline" number of Age 0 recruits per adult at time $t = 0$ (the ECOPATH starting "equilibrium"); and

c_2 is another constant $[(1 - P_g^{\text{realized}})/(1 - P_0)]$ that effectively scales the linear relationship between R/S and food consumption.

ECOSIM converts from numbers (of adults) to adult biomass $B_{A,t}$ using the relation

$$B_{A,t} = \alpha_{A,t}(\mathrm{C}_{A,t})\,\mathrm{N}_{A,t} \quad , \quad (12)$$

where $\alpha_{A,t}(\mathrm{C}_{A,t})$ is the Ford-Brody growth model intercept, assumed to depend on (total) adult food consumption $C_{A,t}$ at time t (Christensen *et al.* 2000).

Rearranging Equation (5) to represent *per capita* food consumption and substituting Equations (5), with default setting $v_{ij} = v'_{ij}$, and (12) into Equation (11) yields

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[7] Note that this paper has retained the conventional EwE notation, but here, as in many other published descriptions of EwE, this notation is somewhat confusing: thus, for example, Q represents *total* food consumption in Equation (5), but here represents consumption *per unit biomass*. Note also that $c_{A,0} = Q_{A,0}$

$$(R/S)_t = \frac{\alpha_{A,t}\left(C_{A,t}\right) * {}^{c1\,c2}\!\big/_{2\,c_{A,0}}\, a_{ij} B_{i,t}}{1 + {}^{a_{ij}}\!\big/_{2\,v_{ij}}\, S_t} \qquad (13)$$

where S_t is the adult (spawning stock) biomass (of a predator) at time *t*. Note that the arguments hereunder hold also, given the updated form of the consumption equation (see Appendix Equation A17).

For a simple (static) case such that $w_A = \alpha_{A,t}(C_{A,t})$ = constant and with the prey biomass $B_{i,t}$ held constant, the above formulation is identical to a traditional Beverton-Holt stock-recruit relationship:

$$(R/S)_t = \frac{\alpha}{1+\beta S_t} \quad , \qquad (14)$$

where $$\alpha = w_A * {}^{c1\,c2}\!\big/_{2\,c_{A,0}}\, a_{ij} B_{i,t} \qquad (15)$$

and $$\beta = {}^{a_{ij}}\!\big/_{2\,v_{ij}} \quad . \qquad (16)$$

Note that the Beverton-Holt model shows compensation, i.e. as spawner abundance S_t decreases, the stock "compensates" by increasing its *per capita* birthrate. In a practical implementation, Equations (13) and hence (14) hold for the ECOPATH starting "equilibrium" with recruitment R_0^* and spawning biomass S_0. This provides one relation to determine the α and β parameters of Equation (14), *viz*.:

$$R_0^*\big/S_0 = \frac{\alpha}{1+\beta \cdot S_0} \quad . \qquad (17)$$

The further relation required to solve for α and β is provided by Equations (15) and (16). Input data determine some of the quantities involved, but the analyst has some flexibility of choice for the parameters *v*, *r* and W_g. Before adopting standard defaults for these quantities, it would seem to be important to check that the resultant value for α, the recruits per unit spawner biomass in the limit of low abundance, is consistent with values typical of the species concerned as determined by the analyses of Myers *et al.* (1999) of empirical recruitment/spawner biomass time-series.

Stock assessment scientists are typically more familiar with the steepness parameter (*h*) than α as characterizing the shape of a stock-recruitment function. Steepness is defined as the proportion of pristine recruitment (R_K) obtained when spawner biomass is reduced to 20% of its pristine level (K^{sp}). Therefore, from Equation (14):

$$\left.\begin{aligned} R_K/K^{sp} &= \alpha\big/\left(1+\beta\cdot K^{sp}\right) \\ hR_K\big/\left(0.2\,K^{sp}\right) &= \alpha\big/\left(1+\beta\cdot 0.2\,K^{sp}\right) \end{aligned}\right\} \quad , \qquad (18)$$

so values for α and β imply values for K^{sp} and *h* respectively. Essentially, therefore, the ECOSIM analyst's choices for *v*, *r* and W_g amount to independent specification of stock-recruitment steepness for the species concerned, rather than linking this to empirical data. (Myers *et al.* [1999] also provide estimates of *h* for the time-series they analysed.)

It is particularly important to appreciate the implications of the default choice $v_{ij}^* = 0.3$ for stock-recruit relationships. From Equations (7) and (16), it follows that

$$\beta = \frac{a_{ij}}{2\,v_{ij}} = 1\big/B_{A,0} = 1\big/S_0 \quad . \qquad (19)$$

Now the parameter β reflects the rate at which recruits per unit spawner biomass decline as abundance increases (from Equations 14 and 19):

$$\begin{aligned} (R/S)_t/(R/S)_{S=0} &= 1\big/\left(1+\beta\cdot S_t\right) \\ &= 1\big/1+S_t/S_0 \quad . \qquad (20) \end{aligned}$$

Therefore, the default choice for the vulnerability parameter corresponds to the initial spawning biomass being the sole determinant of this aspect of the slope (curvature) of the stock-recruitment function. However, the value of S_0 will be primarily determined by the prior exploitation history of the species, rather than (only) biological characteristics. This points to the unsatisfactory nature of adopting the default value for vulnerability for all species in ECOSIM applications. More generally and importantly, it serves to stress that vulnerability parameter values should not be set to the same constant for all species, nor be based on general biological aspects only, but need to take account also of species-specific exploitation histories, given the manner in which ECOSIM has been configured to depend upon the initial ECOPATH "equilibrium".

To better understand why EwE's "emergent" stock-recruitment function results in stock-recruitment patterns intermediate between the traditional Beverton-Holt and Ricker relationships, readers are referred to Figure 4. As is evident from Equation (15), α is linearly proportional to prey biomass in ECOSIM, so an increase in prey biomass results in an upward shift of the curve (Fig. 4a). The feeding interactions are such that prey abundance will tend to increase as predator numbers decrease. Hence, as predator spawner abundance decreases in Figure 4a, the change in prey sees

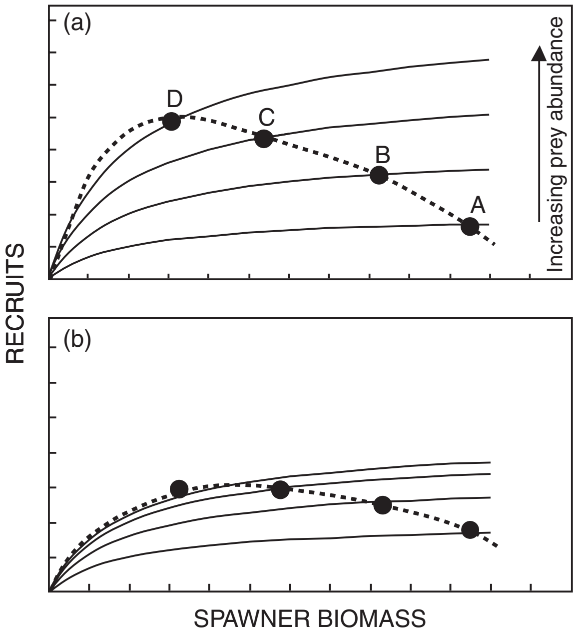

Fig. 4: (a) Illustration of the emergent predator spawner stock-recruitment relationship in EwE. The solid curves reflect the asymptotically flat Beverton-Holt relationships that apply for fixed prey biomass. However, as predator consumption (and hence recruitment under further assumptions) increases linearly with prey abundance in EwE, and because for equilibrium situations fewer predators will correspond to greater prey abundance, the emergent relationship (the dashed curve) shows non-monotonic Ricker-like behaviour with recruitment first increasing as spawner abundance declines. The four Beverton-Holt curves in (b) reflect the same prey abundance levels as in (a), but here *per capita* consumption is asymptotic rather than linear in prey abundance. In these circumstances the emergent stock-recruitment curve exhibits less compensation as spawner biomass decreases than it does for (a)

a move from point A to B to C to D, and thus a tendency towards an overcompensatory curve in which (unlike Beverton-Holt) recruitment initially increases as spawner abundance declines.

However, a problem with EwE is that consumption rates (in total or per predator) are essentially a linearly increasing function of prey abundance (see Appendix Equations A17–A19). In contrast to Figure 4a, Figure 4b shows a set of equilibria for which α is an asymptotic function of prey abundance (as would be expected given physiological upper bounds to *per capita* predator feeding rates). In this case, the resultant recruitment curve bears a closer resemblance to a Beverton-Holt than to a Ricker curve. Importantly, enhancement in recruitment as abundance declines is not as appreciable in this case as the EwE formulation in Figure 4a suggests.

THE PREDATION HYPOTHESIS

Some concerns regarding the inclusion and formulation of the predation hypothesis (the notion that animals spend less time foraging so as to decrease time at risk to predation) are discussed in Walters *et al.* (2000b). The inclusion of a routine that uses an optimization criterion for setting foraging time is an encouraging development (Christensen and Walters 2000). Moreover, the inclusion of the predation hypothesis routine in ECOSIM has played an important role in highlighting the risks of depensatory decreases in juvenile fish survival and recruitment (Walters and Kitchell 2001).

One criticism of the predation hypothesis is that, under changing conditions, for marine mammals in particular, adult natural mortality is conventionally considered one of the population parameters least liable to change. For long-lived mammals, density dependence is thought to affect first the rate of immature survival, then the age of sexual maturity and the birthrate, and only finally the adult survival rate (Boyd *et al.* 1995, Gaillard *et al.* 1998, Wade 2002). In pinnipeds, for example, pups may die as a result of being abandoned or separated for long periods from lactating females that are forced to compensate for reduced resources by increasing the duration of foraging trips (Boyd 1999). The primary compensatory mechanism is therefore not necessarily an increase in foraging time at lower food densities leading to increased predation risk, which brings into question whether or not EwE's predation hypothesis provides a reasonable proxy for the true underlying processes. For some marine mammals, this hypothesis may be adequate, given, for example, the effect of sharks in models of fishery impacts on monk seals *Monachus schauinslandi* (Stevens *et al.* 2000) in the Hawaiian Islands, and that Heithaus and Dill (2002) demonstrated that the distributions of foraging bottle-nose dolphins *Tursiops aduncus* in Shark Bay, Western Australia, reflect a trade-off between predation risk and food availability. However, it seems unlikely that this applies in the case of all marine mammals, particularly the widely ranging large whales.

Life history considerations

To model a life history response appropriately, it is important to assess not only *per capita* food availability, but also the relative rates of fishing mortality applied to the juvenile compared to the adult stock pool. Life history theory predicts that an increase in mortality during one age-class (*j*) selects for an increase in reproductive effort before and a decrease after the afflicted age-class.

Life history theory predictions have been most strongly tested in elegant field and laboratory experiments with guppies *Poecilia reticulata* (Reznick and Endler 1982, Reznick and Bryga 1987, Reznick *et al.* 1990). When guppies were introduced into streams with a pike cichlid *Crenicichla alta* and other predators that preyed mostly on adult guppies (similar to human fisheries that prey on adult age-classes), the guppies matured earlier (i.e. at smaller size), showed greater reproductive efforts/output, and produced more and smaller offspring, than did guppies introduced to streams with a predator that preyed mostly on juveniles. Reznick (1983) notes that fish that faced high juvenile predation and low adult predation invested in growth at the expense of reproduction, but selection was probably acting on growth rate (faster growth means that fish escape predation earlier), not reproductive rate.

Unlike most single-species models used to provide management advice, EwE simulations are often conducted over periods of several decades and may thus encompass several generations of shorter-lived species. Given a variety of different scenarios in which juvenile or adult predation pressure is high, it may be inadequate to model all life history responses in the same way, and some of the life history assumptions upon which the model is based may need to be revisited.

Complex trophic interactions and responses need to be included and tested in ecosystem frameworks, but it is important to bear in mind that, unless they are strongly supported and validated, they may well erroneously predict both the magnitude and direction of a population's response to a signal. Aydin and Friday (2001) and Aydin (2004) provide further examples of the need for caution in interpreting ECOSIM model outputs in the management arena before more thorough analyses regarding underlying metabolic/life history parameters have been conducted, because of the sensitivity of model outputs to the values of such parameters. In this sense, models such as EwE are quite different from the simpler single-species models often used to provide management advice, because the latter rely on an empirical representation of density dependence, with the associated parameters estimated by fitting to data on abundance levels rather than measured separately.

Cautions in applying EwE to marine mammals and seabirds

Models such as EwE are customarily constructed using a generic template tailored to fish species that generally produce thousands of eggs and can show dramatic annual differences in productivity. Marine mammals and seabirds (and also a few shark species) have very different life histories from most fish and have a restricted scope to increase reproductive outputs, given, for example, that they may produce an average of one young or less per year. Life history parameters such as fecundity and age-at-maturity differ dramatically between fish and marine mammals. Therefore, even though some fish may have the same expected growth rate as a marine mammal or seabird, differences in basic life history parameters mean that the range of distribution about the average is limited for this latter group, but can be much more extensive for fish.

Fowler (1981) provides evidence that in species, such as large mammals that have low reproductive rates and long lifespans, most density-dependent changes in vital rates occur at high population levels (close to carrying capacity), so the population levels providing the maximum sustainable yield tend to occur above the 50% of carrying capacity suggested by the Schaefer model. The reverse is true for species with life history strategies typical of most fish. In long-lived species such as marine mammals, one expects an appreciable change in natural mortality only when *per capita* prey availability falls below a low threshold value (see earlier discussion under predation hypothesis section). Notwithstanding that others (e.g. de la Mare 1994) have argued against some of the conclusions drawn by Fowler (1981), their posted counter-argument of hyper-compensation remains essentially speculative in nature (Butterworth and Punt 2003b).

Microscale to macroscale representation problems

ECOSIM's foraging arena model structure arises from biology and physics operating at the microscale (Walters and Kitchell 2001). Commendable though such insights and attempts to incorporate them in population models might be, there may nevertheless be problems in the associated necessary extrapolation from this microscale to the macroscale levels pertinent to populations.

As an example, Lindstrøm and Haug (2001) found that prey preferences determined at local levels by experiment may not be representative of inputs required for interaction models at the population level, because of spatio-temporal variations in predator-prey overlap over the region of interest. Even at the local level, estimates may be biased. Harbitz and Lindstrøm (2001) demonstrate the use of a stochastic spatial analysis framework to derive relationships between expected proportions of prey biomass in the sea and in the diet of minke whales *Balaenoptera acutorostrata*. They illustrate that, whereas minke whales in the Barents Sea appear to actively select capelin *Mallotus villosus* in preference to other species present, this is no longer the case once the preference of minke whales for foraging in the upper water layers is also taken into account. Interpreting results at the correct spatial scale, as in these examples, is the same kind of problem as ensuring that mechanisms in a model that are based on processes (and parameter) values operating at the microscale adequately represent these processes at larger scales.

From a mathematical viewpoint, extrapolations from the microscale to the macroscale require integrating the form of a functional response (the foraging arena model in this case) over the area concerned, with parameter values (such as those in Appendix Equation A17) changing over that area. When the form concerned is linear in the quantities integrated out, the functional form (i.e. shape) is preserved. However because this is not the case in this instance, there is no guarantee that the shape of the function at the macrolevel, and its predicted density-dependence, will fall within the range of emergent behaviours of ECOSIM's generalized foraging arena functional relationship. ECOSIM users should therefore be aware that, in some instances, model results based on careful representation of microscale processes may nonetheless fail adequately to capture broader-scale trends or may even translate into spurious functional response shapes when considered at the macroscale level. For the same reasons, independent estimates of parameters at the microscale will not necessarily remain appropriate if the same functional form is assumed to govern macroscale behaviour.

Modifying ECOSIM's functional response formulation on the basis of behaviour at the microscale to represent macroscale processes may be particularly problematic in instances where this is used as a surrogate for representing other processes. For example, as discussed earlier, consideration needs to be given to the extent to which behaviours such as seal pup deaths from abandonment by cows (under situations of reduced food resources) can reliably be represented by a model assuming that cows suffer extra mortality from predators because they are searching longer for food.

EwE IN A BROADER CONTEXT

Comparisons with single-species models

Three processes are primarily responsible for governing the dynamics of populations: I – competition, II – predation, III – environmental variation (Hollowed *et al.* 2000).

I. Single-species models applied as management tools typically ignore interspecific competition, but generally implicitly include the effects of intraspecific competition, for instance by including a logistic-type term in the equations to reflect density-dependence. Most commercially harvested species are well below pre-exploitation levels, and management is likely neither to try to rapidly recover nor to rapidly further deplete such resources, so change would be slow. Despite well-intended, but lofty-stated, general goals, such as that by the World Summit on Sustainable Development to "Maintain or restore stocks to levels that can produce the maximum sustainable yield with the aim of achieving these goals for depleted stocks on an urgent basis and where possible not later than 2015" (WSSD 2002), the socio-economic reality in most cases of resources below their *MSY* level is that the large short-term catch reductions needed to achieve anything other than a relatively slow rate of recovery would not be politically acceptable. This suggests that, at a first approximation, one can reasonably assume multispecies impacts not to change. Equally, however, it is not advisable to ignore interspecific competition in situations managed for rapid large changes.
II. Predation interactions are implicitly included in the mortality terms of most single-species models. This approach obviously fails in instances in which predation pressure varies dramatically over time, as may be the case for mid-trophic level species in particular. Ecosystem models have proved useful for exploring the relative importance of fishery and predation mortality effects (Link 1999).
III. Whereas single-species models generally ignore any effect of environmental variation on mortality, the effect of such variations on recruitment processes is often incorporated in a statistical (rather than a causal) framework. For example, by including stochastic fluctuations about a stock-recruitment curve in the model in contrast to the causal basis of the differential-equation-based EwE.

The above suggests that, in terms of describing the dynamics of a commercially harvested species, it is unlikely that approaches such as ECOSIM could afford much of an improvement on single-species management tools. The main potential would be to refine estimates (particularly on a temporal scale) of predation mortality. However, because of the greater uncertainty attached to input data required to estimate this source of mortality in ecosystem models (as well as uncertainty about the associated functional forms), this will not necessarily lead to an improvement. Christensen and Walters (2000) noted that, at that time, no substantial improvements in fits to data on population trends had been obtained with the use of ECOSIM (i.e. by explicitly accounting for variation owing to trophic interactions).

There are nevertheless a number of instances in which ecosystem approaches have greater utility than single-species approaches:

(1) to improve understanding of ecosystem functioning;
(2) to derive indices of ecosystem health, e.g. EwE's routine for computing the system particle size distribution (Christensen and Walters 2000);
(3) to try to quantify the impacts of harvesting on other species in the ecosystem, including those of little commercial value;
(4) to assess the effects of fishing on ecosystem stability (a key point being that ecosystem models introduce the possibility of multiple stable states; this raises the importance of the stability issue, which is trivially straightforward for conventional single-species models) and other ecosystem properties;
(5) to increase understanding of trophic cascade mechanisms (e.g. Daskalov 2002);
(6) for interpreting the effects of ecosystem-scale changes in productivity resulting from regime shifts (Christensen and Walters 2000);
(7) for highlighting complex nonlinear responses and interactions. An excellent example in this regard concerns the recommendations for fisheries management proposed by Walters and Kitchell (2001) on the basis of ECOSIM simulations that demonstrate the dangers of depensatory recruitment effects attributable to trophic interactions.

In earlier sections, criticism has been levelled at uncritical use of default values for certain parameters in many ECOSIM applications and their general lack of evaluations of sensitivity to such choices. Could not the same be said regarding practice in single-species assessment and management for parameters such as natural mortality M and stock-recruit steepness h? We consider, however, that some important differences apply:

(1) general (though admittedly not universal) practice in single-species analyses emphasizes the key importance of exploring sensitivity to input assumptions; such tests will usually be conducted prior to management advice being given, except perhaps in circumstances when experience with earlier analyses has shown such sensitivity to be low;
(2) there is already a large body of literature (e.g. Myers *et al.* 1999) available upon which to base choices of such input parameter values (or Bayesian priors) by analogy with existing estimates for other stocks of the same species or for similar species. In contrast, this is hardly the case at present (nor likely to shortly become so) for key ECOSIM parameters such as vulnerability v.

These current deficiencies in many ECOSIM applications will presumably be addressed once they come to be more closely considered in the formulation of management advice.

EwE as an operating model in an OMP/MSE context

One challenge for EwE users is to motivate the utility of this approach to provide the "operating models" of the underlying resource dynamics used to evaluate prospective management approaches to setting harvest limits in an Operational Management Procedure (OMP; Butterworth and Punt 1999), or analogously Management Strategy Evaluation (MSE; Smith *et al.* 1999) framework (Cochrane 1998). Although some encouraging attempts have been made explicitly to include multispecies models in MSE analyses (Schweder *et al.* 2000), practical applications involving fairly complex models such as ECOSIM are often limited by the paucity of data and insufficient system understanding to permit discrimination between radically different harvest policy options (such as whether or not predator culls would prove beneficial to harvesters of their prey; Butterworth and Punt 2003a). In principle, ECOSIM models based on good data could be used as operating models, although it remains to be seen whether or not the associated levels of uncertainty can be adequately constrained to yield scientifically defensible and practically useful conclusions (Cochrane 1998, 2002, Sainsbury *et al.* 2000). Whereas there is clearly an immediate role for ecosystem models as the operating models used to test OMPs, the development of tactical ecosystem models as the basis for computing harvest limits within the OMPs themselves still seems some time off (Butterworth and Plagányi 2004).

Increasingly complex management objectives (implicit in the frameworks indicated by Fig. 1b–d) generally require increasingly complex operating models. Apart from the associated dangers of model misspecification and inadequate parameter estimability, a major difficulty arises with the interpretation of simulation outputs. This is because of the need to consider the trade-offs between performance statistics (such as between average catch levels and interannual catch variability), not only for each resource separately, but now also between resources (Butterworth and Punt 2003a). It should therefore be understood that only relatively simple EwE models based on good data have *immediate* potential utility for this purpose.

Nonetheless, coupling the EwE and OMP approaches should be encouraged, because the latter can complement the former through the OMP approach's focus on the identification and modelling of uncertainties as well as in balancing different resource dynamics representations and associated trophic dependencies and interactions (Sainsbury *et al.* 2000). Even so, data limitations will likely mean that only a small subset of EwE models are likely to reach the stage of being considered viable operating models to assist in the management of target species. Following the lead from the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), attention should be focused on the need to account for key levels of uncertainty (Constable *et al.* 2000), preferably within a strategic and practical framework for developing an ecosystem approach to management.

Potential application of EwE as a management tool in southern Africa and the Southern Ocean

The potential of the EwE approach to assist in addressing five important multispecies management questions pertaining to the southern African (Cape fur seal – hake – fishery interactions; pelagic fish – seabird – fishery interactions, abalone – urchin – rock lobster interactions) and Antarctic marine ecosystems (post-exploitation recovery of whale stocks; Southern Ocean predators – krill – fishery interactions) is assessed by Plagányi (2004). Although EwE has some potential, especially if used in conjunction with ECOSPACE, problems are foreseen in all cases. The major limitations are as follows.

- The ECOPATH-based initial values are considered overly constraining for all five cases. The highly dynamic nature of some systems makes the choice of representative average values disputable. Moreover, although biomass values need not be at "equilibrium" for the reference year (or time period), because of an option to include a rate of biomass "accumulation" (or depletion, Christensen and Walters 2000), the pre-setting of a condition for increase or decrease (A. Bundy, Fisheries and Oceans Canada, pers. comm.) confounds the identification of the true underlying mechanism. The fact that extrapolations to situations far from "equilibrium" are considered tenuous in EwE (and indeed in any models) is problematic in an ecosystem management context, because it is generally extreme, and not average, ecosystem effects that are likely to be regarded as ecologically important variations to which managers must respond in setting regulations (Constable *et al.* 2000).
- The density-dependent EwE model formulations appear problematic in most instances, particularly when applied to marine mammals and seabirds.
- Complex trophic ontogenies are not always easily accommodated in the EwE framework because, for example, even if the diet composition of a juvenile group is well documented, there are problems in explicitly modelling prey species about which less is known. Size-dependent cannibalism interactions that span a number of age-classes are also problematic to include in the EwE framework (though recent development of EwE software may help to address this problem).
- Long-term average predictions, while improving understanding, are not always appropriate in management contexts, such as in instances where management decisions need to be sensitive to environmental processes operating at the mesoscale level.
- The utility of EwE depends in part on the relative roles of biotic and abiotic factors in mediating ecosystem change. EwE likely has limited predictive capability in systems characterized by high residual variability, in light of the predictions of Benedetti-Cecchi (2000) that, in such systems, even strong trophic interactions may be insufficient to increase the spatial and temporal variability in the abundance of a species. Foodweb and interaction-web models need to recognize the limits of explaining population dynamics in terms of the variance of trophic interactions in situations where the residual variability of a resource is high (and reflected, for example, by appreciable variations about a deterministic stock-recruitment relationship that results from environmental fluctuations).

DISCUSSION

It seems obvious that it will not always be effective or best to base fisheries management policies solely on single-species considerations. However, although the need for multispecies fisheries management has been recognized for a number of years, progress in this field has been impeded by the difficulties in building adequate models that can provide reliable scientific advice. This is on account of the complexity of the dynamics of, and interactions between, the various components of an ecosystem and the current, poor understanding of these. The EwE modelling approach is currently the most popular and widely applied one used to evaluate the ecosystem effects of fishing and to explore the consequences of different management policy options. One needs to ask, however, whether it is up to the task.

Advantages of EwE

Some of the main advantages of the EwE approach in this context include:

- the ECOPATH framework is useful to evaluate the compatibility of the various data inputs (Christensen and Walters 2000);
- the use of a common framework (generic model) is useful for making comparisons between systems studied by different researchers;
- the ECOPATH constraints act as a rigorous analytical framework (in contrast to an *ad hoc* type model);
- the level of detail included in the model structure and equations is a good attempt at including only those processes deemed most important;
- an improved understanding of ecosystem structure and functioning is achievable with EwE;
- given good input data, EwE has utility to provide a first-order perturbation analysis (Aydin and Friday 2001).

Shortcomings of EwE model structure

Some of the main shortcomings of EwE are summarized in Table I. The following have been identified as aspects of the actual EwE model structure that may merit further attention or are potentially problematic.

- There are some (apparently not far-reaching) mathematical inconsistencies underlying the ECOSIM interaction term (see Appendix).
- Predator consumption rates (in total or per predator) are essentially a linearly increasing function of prey abundance, despite the addition of a handling time term (see Appendix).
- The form of the ECOSIM interaction term involves the questionable assumption that prey vulnerable to one predator are distinct from those vulnerable to another. However, the complete prey population is vulnerable to a fishery (see Appendix and also comments in Walters *et al.* 2000b regarding the additivity of mortality components).
- The notion that predators are usually hungry and seeking food underlies the foraging arena formulation, but is open to debate and highlights the need to explore the consequences of alternative feeding interactions. By choosing appropriate parameter combinations, EwE can generate "emergent" functional response Types I and II, but not III.
- Model formulations based on behaviour at the microscale may fail adequately to represent macroscale processes, particularly in instances where these are used as surrogates for representing other processes.
- ECORANGER is likely computationally inefficient and could be improved.
- The absence of an energetic content parameter (see Equation 1) is problematic in scenarios in which there are substantial differences in the energy density of prey and hence in the food requirements of a predator as prey abundances change.
- The life history assumptions in EwE are flawed in some respects. Sadovy (2001) highlights the need for more work to evaluate compensatory, density-dependent responses to fishing and notes that such responses are highly variable and may be inadequate to allow full recovery.

In common with most other multispecies models, the constant suitability assumption (of EwE) may be violated under some circumstances, particularly when extrapolating to situations far from the initial model state.

Shortcomings of EwE – user applications

There are also some shortcomings of EwE applications that are attributable to user misuse (or insufficient use) rather than to the actual model structure. Greater focus on these issues may assist in trying to move the EwE suite closer to the sphere of practical fishery management.

- The development and implementation of statistical procedures for estimating model parameters is one of the major challenges facing ECOSIM (Aydin and Friday 2001). Model outputs need to be interpreted in a statistical framework that summarizes the confidence that can be attached to model results/predictions.
- Model properties and behaviour are currently insufficiently explored (particularly for simple scenarios for which such analyses are tractable).
- As noted by Larska and Wootton (1998), quantification of interaction strength (vulnerability settings in this context) permits the isolation of a few more likely possibilities from a vast range. Although far from perfect, the dynamic regression approach

Table I: Summary of key weaknesses of ECOPATH with ECOSIM (versions II–IV) in the context of its utility as a predictive multi-species tool for fishery management purposes. Weaknesses that are a consequence of the way in which the package is often used, rather than a problem or limitation of the model structure itself, are included at the end of the Table and are marked with an asterisk

Assumption/problem	Interpreting output in the management context	Possible solutions/developments
"Equilibrium"/"steady-state" as starting point for ECOSIM	Extrapolations tenuous when moved far from "equilibrium" (e.g. because of a change in fishing pressure); inappropriate constraints on parameter values	Full model fitting to datasets a partial solution
Life history assumptions	Not appropriate in all contexts. May generate e.g. overly strong compensatory responses (see text)	Thorough testing and validation of assumptions, or limit to inclusion of responses based on accepted state-of-the-art theory
Predator consumption rates a linearly increasing function of prey abundance (see Appendix)	Questionable degree of linearity assumed in the response of an aggregated taxonomic group to a change in food availability (see text)	Test the necessity to refine this aspect of the model
Expanding model complexity through addition of e.g. behavioural plasticity effects such as the predation risk avoidance hypothesis	Effect on model predictions may be disproportionately large relative to the importance of the behavioural response included	Careful *a priori* consideration of whether additional model complexity is justified for the case under consideration
Bioenergetic formulations	Sensitivity to these assumptions (see Aydin 2004) can result in overestimates of *MSY,* as demonstrated by Aydin and Friday (2001)	Suggestion by Aydin and Friday (2001) to merge bioenergetic models with population mass-balance models
Mesoscale gap	The effects on population dynamics of mesoscale spatial and temporal variations cannot safely be ignored in some fishery management contexts	Proxies could be used, such as the seasonal and long-term "shaper" interface in ECOSIM II (Walters *et al.* 2000b), but this is still inadequate in some contexts
Constant physical forcing	Physical forcing important in some contexts. Could result in incorrectly attributing ecosystem changes to predation/fishing effects. On the other hand, including physical forcing in the model is problematic because of constraints on "equilibrium"-based parameters	Inclusion of physical forcing possible with e.g. ECOSIM II "shaper" interface or by linking to e.g. climate models, but a differential-equation-based model will struggle to capture the response to strong physical forcing adequately. Biogeochemical models have been successful under these conditions, but this is partly a reflection of the focus of these models on the dynamics of low to middle trophic groups as compared with EwE, which concentrates more on the higher trophic groups (Fulton and Smith 2004)
Linear relationship between recruitment and consumption	Sensitivity to this function may result in overly optimistic recruitment predictions in some circumstances (see text for details). Caution is necessary in interpreting results for systems where other factors are presumed more important in determining recruitment levels	Explore the effect of introducing random fluctuations about the stock-recruit relationship
Constant/knife-edge selectivity function	Problematic in modelling fisheries with a history of large/frequent changes in fishing selectivity or where multi-fleet effects are considered important	Robustness to this formulation should be explored for "nonsplit pools" in particular. Fishing mortality rates F_i may need to be adjusted in an *ad hoc* manner to account for the disproportionately large effect on an aggregated taxonomic group's dynamics of selectively removing large, older individuals compared to juveniles
Unexplored properties (e.g. regions of dynamic stability)	Lack of sufficient explorations (preferably using simple model constructions) of model properties and behaviour. Aydin and Friday (2001) suggest that ecosystem models "must be built, examined and assembled piece by piece"	Model properties should be further explored using simple examples. The reconceptualization (to reduce structural uncertainty) of the ECOPATH approach as an iterative process (Pauly *et al.* 2000) is a promising development

(continued)

Table I: (continued)

Assumption/problem	Interpreting output in the management context	Possible solutions/developments
Prey-switching	Where important, leads to under- or overestimation of predicted responses to an environmental pulse	Introduction of stochastic component to dynamics; not important in all contexts
Parameter estimation in a rigorous statistical setting not routine; precision of parameter estimates seldom reported satisfactorily*	Garbage in–garbage out basic tenet of modelling	ECORANGER (Pauly *et al.* 2000); inverse methods (Savenkoff *et al.* 2001)
Aggregated functional groups*	Errors in choice of representative diet composition (because of complex spatial and temporal patterns and ontogenetic changes in feeding) may be important	Split pools only a partial solution. Model output must take into account uncertainty in diet compositions. Test sensitivity of models to varying levels of aggregation
Vulnerabilities of biomass pools*	Model results need to be interpreted taking account of their sensitivity to vulnerability settings (which determine the strength and direction of trophic flows)	If the degree of top-down vs bottom-up control is unknown, model sensitivity and robustness to this setting *must* be explored
Easily accessible user-friendly software (black-box approach)*	In the absence of alternatives and faced with strong pressures (and indeed the need for) multispecies advice, there is much potential for the misuse and misinterpretation of model applications. Preset parameter values are almost certainly not appropriate in all ecosystems. Users and managers need to bear in mind that all ECOSIM models are not created equally. The appropriate level of confidence to be attached to the predictions from one of these models is in large part a product of the quality of the input data and the level of statistical testing	Users should ensure they have a good understanding of what the approach can and cannot achieve (Pauly *et al.* 2000). Model applications destined for input into management decisions but without an assessment (statistical or otherwise) of the robustness of the results should be viewed with suspicion. The enabling of a "pedigree" model rating based on the quality of the input data is a step forward (Pauly *et al.* 2000)

proposed by Larska and Wootton (1998) may be a potentially useful method in some systems to narrow the uncertainty attached to vulnerability parameter estimates. The approach involves using multiple regression techniques to evaluate the relationship between empirically observed rates of change and species abundances (and thus works best for situations far from "equilibrium").

- Uncritical use of default parameter settings or setting of vulnerability values to the same constant for all species is unsatisfactory, because *inter alia* it assumes the same prior exploitation history for all species and may result in overcompensatory stock-recruitment relationships.
- Model applications that include marine mammals, seabirds and some species of shark need to account as far as possible for the different life histories of these species.

As emphasized by Walters and Kitchell (2000), there is a need to make ecosystem predictions, albeit sceptically, because the only "proof" of a proposed model is to check whether its predictions stand the test of time. Assumptions such as ECOSIM's additivity in mortality components (see Walters *et al.* 2000b) could similarly buckle or stand with confidence only if given a chance to be tested.

Suggestions for users regarding potential pitfalls

The user-friendly EwE interface introduces positive management possibilities, such as the potential to be highly community-based in the sense of fishing community groupings being afforded the opportunity to explore management options using the model (Okey and Pauly 1999). However, because of the potential for misuse of a "black-box type" model such as EwE, users are cautioned against some of the following potential pitfalls in model applications.

- The number of aggregated taxonomic groups included in the model should be a function not only of the need to include important groups, but also of the quality of the available data. The age-old model tenet of "start simple" is recommended. Yodzis (1998) provides a useful example of a way to simplify foodweb models through the removal of "weak links" that do not appreciably affect model predictions.

- Data should be input to the model in a form that, as best as possible, represents the chosen time- and space-scales of the model under construction. A common flaw (not necessarily avoidable) is the use of temporally non-representative diet composition data. This is particularly difficult to achieve if diets are highly diversified and in the case of aggregated taxonomic groups.
- The sensitivity of model results to vulnerability parameter settings is a critical factor to consider in establishing whether model predictions are robust. Given arguments presented here as to the unsatisfactory nature of adopting the default value for vulnerability for all species in ECOSIM applications, the following are suggested as some alternatives.
  (1) Group-specific values should be sought, rather than setting vulnerability to be the same for all species.
  (2) The model could be run to "equilibrium" under zero catch, followed by iteration on the vulnerability settings to get the inputs to give desired values at the pre-exploitation "equilibrium" stage, so that these are purely biologically determined /related and uninfluenced by catch histories.
  (3) Where time-series data are available, Christensen *et al.* (2000) suggest searching for vulnerability estimates that give better "fits" of ECOSIM to such series (e.g. Shannon *et al.* 2004).
  (4) Vulnerability values for marine mammals and other top predators should be set at or close to one (top-down control), unless there is evidence to suggest interference competition for food.
- Given the model complexity and the associated uncertainty in the data inputs, a single representation of a system's structure and dynamics is near meaningless. To be useful in the management context, models and their predictions should rather be presented in the form of a range of likely scenarios.

It is important to bear in mind EwE's limitations if it is to be used as the basis for management recommendations or decisions (e.g. Pitcher and Cochrane 2002). The details of foodweb structure can make a large difference in predicting the ecosystem effects of fishing (Yodzis 1998). Therefore, to be of use in managing a system, lack of knowledge needs to be acknowledged by calculating probability distributions for a response (Yodzis 1998). One way forward is to account for ecosystem considerations in fisheries management decisions through using statistically sound EwE model implementations as a basis for testing OMP candidates (Butterworth and Punt 2003a).

The most serious limitations for any multispecies or ecosystem modelling approach undoubtedly lie in the availability of good representative data and the need for improved understanding of the complexities of predator-prey interactions. The art of constructing a multispecies model for the purpose of contributing to fisheries management advice entails achieving an appropriate balance between the level of model complexity and the quality and quantity of available data. Marine science has undoubtedly progressed beyond the stage where only single-species assessments are deemed appropriate on the basis of data limitations. However, an immediate quantum leap into a melee of multispecies models is not justified either. An uncalibrated EwE model including hundreds of parameters with unknown values may have utility as a framework for a data gathering and cataloguing exercise, but it clearly should not be relied upon to underpin management advice. At the other extreme, prudent EwE applications that address uncertainty and are based on good data have the potential to make an important contribution to fisheries management advice in some situations.

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APPENDIX

Technical considerations in applying the "foraging arena" concept to develop the form of the interaction terms in ECOSIM

As discussed in the main text, for prey i and predator j, Walters and Kitchell (2001) model the dynamics of the vulnerable (V_{ij}) and non-vulnerable ($N_i - V_{ij}$) components of the prey abundance (by number) as:

$$\frac{d\left(N_i - V_{ij}\right)}{dt} = -v_{ij}\left(N_i - V_{ij}\right) + v'_{ij}\,V_{ij} \qquad \text{(A1)}$$

$$\frac{dV_{ij}}{dt} = +v_{ij}\left(N_i - V_{ij}\right) - v'_{ij}\,V_{ij} - a_{ij}V_{ij}N_j\,, \qquad \text{(A2)}$$

where the consumption rate Q_{ij} of prey i by predator j is $a_{ij}V_{ij}N_j$, and N_j represents the number of predators.

Summing these two equations yields

$$\begin{aligned}\frac{dN_i}{dt} &= -a_{ij}V_{ij}N_j \\ &= -Z_{ij}N_i \quad , \qquad \text{(A3)}\end{aligned}$$

where Z_{ij} is the instantaneous mortality rate effected by predator j on prey i.

Thus, $$a_{ij}N_j = \left(N_i / V_{ij}\right)\cdot Z_{ij} \quad . \qquad \text{(A4)}$$

Substituting into $V_{ij} = v_{ij}N_i/(v_{ij} + v'_{ij} + a_{ij}N_j)$ (Equation 4 in main text) yields

$$\frac{V_{ij}}{N_i} = v_{ij} \Big/ \left[v_{ij} + v'_{ij} + Z_{ij}\, {}^{N_i}\!/\!{}_{V_{ij}} \right]$$

or $$\frac{V_{ij}}{N_i}\left(v_{ij} + v'_{ij}\right) + Z_{ij} = v_{ij}$$

i.e. $$\frac{V_{ij}}{N_i} = \frac{v_{ij} - Z_{ij}}{v_{ij} + v'_{ij}} \quad . \qquad \text{(A5)}$$

The standard ECOSIM default

$$v_{ij} = v'_{ij} \quad , \qquad \text{(A6)}$$

$${}^{V_{ij}}\!\Big/\!{}_{N_i} = \tfrac{1}{2}\left(1 - \frac{Z_{ij}}{v_{ij}}\right) \quad . \qquad \text{(A7)}$$

Note that slow dynamics for the N_i compared to the V_{ij} implies

$$Z_{ij} << v_{ij} \quad ,$$

so that $${}^{V_{ij}}\!\Big/\!{}_{N_i} \approx {}^{1}\!/\!{}_{2} \quad . \qquad \text{(A8)}$$

Implications

(1) The default assumption of Equation A6 implies that about half the prey population numbers N_i are vulnerable to predator j, effectively irrespective of the value of v_{ij}. This hardly seems consistent with the idea of only a "small" proportion of the prey being vulnerable at any time. This suggests that one should default to a choice of v'_{ij} rather greater than v_{ij} to obtain a V_{ij}/N_i ratio well below 0.5.

A further difficulty of large V_{ij}/N_i ratios is that the standard ECOSIM interaction term (Equation 5 in main text) tacitly assumes that the prey vulnerable to predator j (V_{ij}) are distinct from those vulnerable to predators k (V_{ik}), l (V_{il}), etc. One cannot consistently maintain a large V_{ij}/N_i for all j when necessarily $V_{ij} + V_{ik} + V_{il} + \ldots < N_i$.

(2) Prey dynamics are governed by

$$\frac{dN_i}{dt} = -Z_iN_i = -\left(\sum_j Z_{ij} + F_i + M_i^0\right)N_i \quad , \qquad \text{(A9)}$$

where F_i is the fishing mortality and M_i^0 some residual natural mortality other than that caused by the predators j.

Thus, $$Z_{ij} < Z_i \qquad \text{(A10)}$$

and further, the assumption of slow dynamics for the prey overall (N_i) compared with its vulnerable component (V_{ij}) requires

$$Z_i << v_{ij} \quad , \qquad \text{(A11)}$$

so that

$$Z_{ij} < Z_i << v_{ij} \quad . \qquad \text{(A12)}$$

Now, the vulnerability v_{ij}^* as input to ECOSIM is a rescaling of the vulnerability parameter v_{ij} above, such that the recommended ECOSIM input default $v_{ij}^* = 0.3$ corresponds to (K. Y. Aydin, pers. comm.)

$$R_{ij} = {}^{2v_{ij}}\!\Big/\!{}_{a_{ij}N_j} = 1 \qquad \text{(A13)}$$

or $$a_{ij}N_j = 2v_{ij} \quad . \tag{A14}$$

However, by Equation A3, $$Z_{ij} = a_{ij}N_j \quad , \tag{A15}$$

so $$Z_{ij} = 2v_{ij} \quad . \tag{A16}$$

Inequality (Equation A12) and Equation A16 clearly contradict each other. This then seems to indicate that the derivation of the ECOSIM interaction term (Equation 5 in main text) is invalid for the standard defaults ($v'_{ij} = v_{ij}$; $v^*_{ij} = 0.3$) recommended for ECOSIM. The derivation would hold only in the limit of $v_{ij} >> Z_{ij}$, i.e. v^*_{ij} close to 1, corresponding to "top-down" control.

This suggests that ECOSIM should be integrating Equations A1 and A2 directly, rather than using Equation 4 of the main text. However, C. J. Walters (pers. comm.) advises that computations show that Equation 4 provides a reasonable surrogate for the behaviour of Equations A1 and A2 even when $v_{ij} \sim Z_{ij}$, i.e. v^*_{ij} is (possibly well) below rather than close to 1.

(3) Christensen and Walters (2000) report that the consumption equation has been amended in subsequent versions of ECOSIM to the form

$$Q_{ij} = \frac{a_{ij}v_{ij}B_iP_jT_iT_jS_{ij}M_{ij}/D_j}{v_{ij} + v_{ij}T_iM_{ij} + a_{ij}M_{ij}P_jS_{ij}T_j/D_j} , \tag{A17}$$

where

T_i is the prey (i) relative feeding time;
T_j is the predator (j) relative feeding time;
S_{ij} are the user-defined seasonal or long-term forcing effects;
M_{ij} represents mediation forcing effects; and
D_j accounts for handling time limitations on consumption rate by predator j as follows:

$$D_j = \frac{h_jT_j}{1 + \sum_k a_{kj}B_kT_kM_{kj}} \quad . \tag{A18}$$

Now, if some prey population becomes very large (some $B_k \rightarrow \infty$), Equation A18 implies that D_j becomes small. The final term in the denominator of Equation A17 will then dominate that denominator, with consequent cancellations yielding

$$Q_{ij} \rightarrow v_{ij}B_iT_i \quad . \tag{A19}$$

Therefore, handling time limitations appear not to restrict consumption rates (in total or per predator): these remain a linearly increasing function of prey abundance B_i. (Text under "Foraging time and predation risk" in Walters *et al.* (2000b) appears not to resolve this: seemingly, this suggests an inverse relationship between (time-dependent) v_{ij} and T_i, but such that $v_{ij}T_i$ would remain constant.)