Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries

Daniel Pauly, Villy Christensen, and Carl Walters

Since its development in the early 1980s, the mass-balance approach incorporated in the Ecopath software has been widely used for constructing food-web models of marine and other ecosystems. Generalizations on the structure and functioning of such ecosystems, relevant to the issue of fisheries impacts, have been developed and these have affected the evolution of the Ecopath approach. Thus, the description of the average state of an ecosystem, using Ecopath proper, now serves to parametrize systems of coupled difference and differential equations, which are used to depict changes in biomasses and trophic interactions in time (Ecosim) and space (Ecospace). The outcomes of these simulations can then be used to modify the initial parametrization, and the simulations are rerun until external validation is achieved. This reconceptualization of the Ecopath approach as an iterative process, which helps address issues of structural uncertainty, does not increase its input requirements markedly. Rather, it has become possible, through a Bayesian resampling routine, to explicitly consider the numerical uncertainty associated with these inputs. We present the key features of the reconceptualized approach, and two indices based thereon for quantifying the ecosystem impacts of fisheries. We conclude with a brief discussion of its limitations, both present and intrinsic.

D. Pauly, C. Walters: Fisheries Centre, 2204 Main Mall, University of British Columbia, Vancouver, BC, Canada V6T 1Z4 [tel: +1 604 822 1201; fax: +1 604 822 8934; e-mail: pauly@fisheries.com; walters@fisheries.com]. V. Christensen: ICLARM, M.C. PO Box 2631, 0718 Makati City, Philippines [e-mail: v.christensen@cgiar.org].

Introduction

That fishing should have an impact on ecosystems is obvious: removing biomass from a complex of species feeding on each other is bound to affect the food web. Evaluating the impact of fisheries, therefore, cannot consist only of demonstrating that fisheries do affect ecosystems. Rather, the task at hand, at least from the standpoint of research, is to assess whether the impact of a fishery (or of several) is likely to have indirect effects on the long-term viability of other fisheries. From a more conservation-orientated standpoint, the goal could also be formulated as ensuring that the exploitation of various resource species leaves the ecosystems with their biodiversity and structural integrity maintained, thus allowing for future services.

This implies that ecosystem representations (models) are required that can describe the biomass flows between the different elements of exploited ecosystems, and can provide answers to "what if" questions regarding the

likely outcomes of alternative fishing policies. Moreover, for such models to be effective in a management context, it should be possible to assemble them relatively quickly – even in data-sparse environments – so that they will be rejected equally quickly when they fail to match the known features and behaviour of the ecosystem that they aim to represent.

Several modelling approaches exist that meet some, or all of these requirements (Daan and Sissenwine, 1991; Silvert, 1993), and a balanced review cannot be provided in the space available here. Rather, we describe the Ecopath suite of software, now including Ecosim and Ecospace, and their various components, which do fulfil the above requirements. Elements of the Ecopath approach have been around since the early 1980s (Polovina and Tagami, 1980; Polovina and Ow, 1983; Polovina, 1984, 1985; Griggs *et al.*, 1984). However, as we will show, the recent development of Ecosim (Walters *et al.*, 1997) and Ecospace (Walters *et al.*, 2000) and the addition of various new routines have not only

increased the quantitative power of the approach (ease of manipulating data, explicit consideration of uncertainty), but have also allowed qualitatively new questions to be asked.

Ecopath proper

The master equation, originally proposed by Polovina (1984), requires that, for each functional group i in an ecosystem, mass balance should occur over a given time period such that:

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum_j B_j \cdot (Q/B)_j \cdot DC_{ij} \ldots, \qquad (1)$$

where B_i and B_j are biomasses (the latter pertaining to j, the consumers of i), P/B their production/biomass ratio, equivalent to total mortality rate under most circumstances (Merz and Myers, 1998), EE_i the fraction of production that is consumed within, or caught from the system, Y_i is the fisheries catch (Y = FB; F is fishing mortality rate), Q/B_j the food consumption per unit biomass of j, and DC_{ij} the contribution of i to the diet of j. Additional terms may be added on the left side to reflect a change in biomass over the time period studied, and/or net emigration (Christensen, 1995a).

Solving this system of linear equations is straightforward (Mackay, 1981). Once solutions are available, a quantified network of flows can be constructed from the biomass, production, and consumption estimates.

It must be emphasized that the logic of Equation (1) does not require equilibrium or steady state. Rather, all that is required is that the system, after for instance a seasonal cycle of changes in biomass and fluxes, returns to its earlier state (Jarre-Teichmann, 1995; Venier, 1997). When there is a seasonal cycle in B, P/B, Q/B, and/or diet composition, and when relative values of these parameters by season can be specified, appropriate integrated rates over a longer time step can be constructed so that the overall mass balance is maintained. In this case, the parameter estimates are interpreted as seasonal maxima of the relative rates specified by the model user (Walters, 1996).

Before the publication of Polovina (1984), Pauly (1982) had applied a piecemeal method for constructing trophic ecosystem models, which resulted in similar flowcharts (Nauen, 1984). However, the versatility of Equation (1) led Pauly et al. (1993) to concentrate on the Ecopath approach (see also Liew and Chan, 1987; Ulanowicz, 1986; Pauly, 1987). Christensen and Pauly (1992b) put the Ecopath II software on a solid footing, enabling its wide distribution. An early result of this was a poster session on "Trophic models of aquatic ecosystems" at the ICES Council Meeting in October 1990 in Copenhagen (Christensen and Pauly, 1993a). The

preface to the proceedings of that session describes much of the historic background.

Generalizations

Ecopath applications to ecosystems ranging from low latitude areas to the tropics, and from ponds, rivers, and lakes to estuaries, coral reefs, shelves, and the open sea, but all using the same metrics, allowed identification of several general features of aquatic ecosystems:

- Multivariate comparisons demonstrated the basic soundness of E. P. Odum's (1969) theory of ecosystem maturation (Christensen, 1995b), including a confirmation of his detailed predictions regarding ecosystems near carrying capacity (Christensen and Pauly, 1998). Conversely, this theory can now be used to predict the effect of fisheries on ecosystems, which tend to reduce their maturity, as illustrated by the comparison of Ecopath models for the Eastern Bering Sea in the 1950s and early 1990s (Trites et al., 1999a, b), and to guide ecosystem rebuilding strategies implied in "Back to the Future" approaches (Pitcher, 1998; Pitcher et al., 2000).
- The importance (relative to fishing) of predation by fish and marine mammals within marine ecosystems as suggested by complex models in a few areas (North Sea – Andersen and Ursin, 1977; North Pacific – Laevastu and Favorite, 1977) was confirmed globally by Ecopath models (Christensen, 1996; Trites et al., 1997).
- Identification of trophic levels as functional entities rather than as concepts for sorting species (Lindeman, 1942; Rigler, 1975) implied the use of non-integer values (computed as 1+ the mean trophic level of the preys, as proposed by Odum and Heald, 1975) that express degree of omnivory (Christensen and Pauly, 1992a), i.e., the extent to which feeding occurs at different trophic levels (Pimm, 1982). Also, trophic level estimated from analyses of stable isotopes of nitrogen has been shown to correlate well with estimates from Ecopath models (Kline and Pauly, 1998).

Estimates of transfer efficiencies between trophic levels (Christensen and Pauly, 1993b; Pauly and Christensen, 1995), previously a matter of conjecture usually pertaining to single-species populations or even to studies of a few individual animals (Slobodkin, 1972), differed radically from earlier guesses by ecosystem types (Ryther, 1969) used for inferences on the potential yields of fisheries (Pauly, 1996), even though the mean was unsurprising (about 10%; Morowitz, 1991).

Meta-analyses of published models

Combining calculated transfer efficiencies and estimates of trophic levels for major species in the world catches
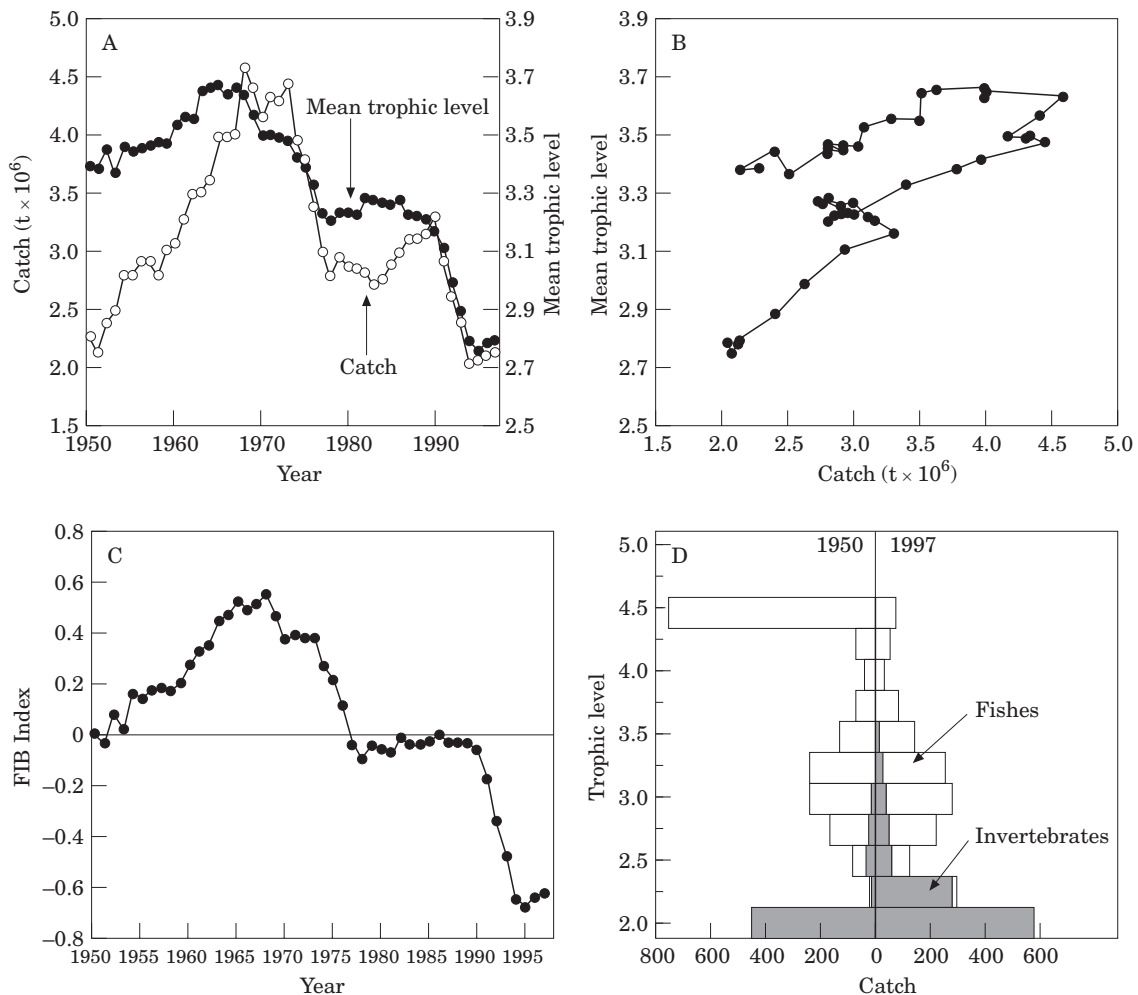
Figure 1. Representations of fishing down marine food webs in the North-west Atlantic (data for FAO Area 21): A. Trends in catch (circles) and their mean trophic level (dots), 1950–1997. B. Sequential plot of mean trophic level vs. catch. C. Trend in FIB index. D. Distribution of landings ('000 t) by trophic level in 1950 and 1997.

from a wide variety of Ecopath applications enabled computation of the primary production required (PPR) to sustain global fisheries (Pauly and Christensen, 1995), which is related to the emergy of H. T. Odum (Christensen, 1994) and to the ecological footprint concept (Folke *et al.*, 1998; Wackernagel and Rees, 1996). The PPR of global fisheries was estimated at 8% globally, four times higher than an earlier estimate (Vitousek *et al.*, 1986). More importantly, PPR was shown to reach 25–35% on continental shelves, from which the overwhelming majority of marine fish catches originate, close to the 35–40% range estimated by Vitousek *et al.* (1986) for the human appropriation of terrestrial primary production.

Subsequently, it was shown that the weighted mean trophic level of the fish landed (estimated for relevant species and species groups included in FAO fisheries statistics, 1950s to 1990s) has been declining in most areas for which sufficiently detailed data were available, a process identified as "Fishing down marine food webs" (Pauly *et al.*, 1998a; Fig. 1A). Large, slow-growing predators have been largely extirpated and replaced by small, fast-growing forage fish and invertebrates. Further, as impacts on key elements of the food webs increase, the upward transfer of production becomes impaired and plots of trophic levels versus catch bend backwards (Fig. 1B). Not only the mean of the trophic levels changes, but also their distribution (Fig. 1D). Caddy *et al.* (1998), while not disputing these processes, suggested that they cannot be documented based on FAO's series of landing statistics. A response may be found in Pauly *et al.* (1998b).

However, one problem with using a declining trend of mean trophic level of landings as evidence of the increasing impact on the ecosystem of a given fishery is that moving down the food web may be the result of a deliberate choice, for which justification may be found in the ever-increasing, world-wide demand for animal protein. After all, biological production does increase by a factor of around 10 as one moves down one trophic level in typical marine ecosystems. Thus, one could argue that a fair evaluation of the impacts of a fishery should not be based on an index which simply declines as the fishery moves down the food web of a particular ecosystem. Rather, such an index should decline only when catches do not increase as expected. Here, we propose an index that enables us to assess whether a fishery is balanced (FIB) in ecological terms or not. The FIB index for any year i in a series is defined by

$$FIB = \log(Y_i \cdot (1/TE)^{TL_i}) - \log(Y_0 \cdot (1/TE)^{TL_0}), \qquad (2)$$

where Y is the catch, TL the mean trophic level in the catch, TE the transfer efficiency, and 0 refers to any year used as a baseline.

Figure 1C illustrates a time series of the FIB index in the western North Atlantic, with TE = 0.10 (Pauly and Christensen, 1995). From 1950 to the mid-1960s, the index shows a steady upward trend owing to increases of both catches and mean trophic level, suggesting that the fishery was expanding to stocks previously not, or only lightly, exploited. Catches peaked in the late 1960s; thereafter, the index shows a stepwise decline, owing to the decrease in TL not being matched by a corresponding increase in catches, except in the 1980s. This analysis does not consider the aggravating effect of a decline in trophic level due to a reduction in mean size within species, which in fish is positively related to trophic level (Pauly et al., 1998b).

Ecosim

So far ecosystem simulation models have not been used much – if at all – for fisheries management. There are a number of causes for this, notably the difficulty in constructing, parametrizing, calibrating, and validating such models (Larkin and Gazey, 1982). Moreover, fisheries scientists and managers have until recently been almost exclusively concerned with single-species management issues.

The trends in Figure 1 clearly illustrate the need for fisheries policies that explicitly consider trophic interactions in an ecosystem context, as also recently emphasized by NRC (1999). Here, the task is not one of setting a total allowable catch in a given fishery, but one of exploring the ecosystem implications of a given policy, e.g., of targeting forage fish. Ecosim was developed to

address issues of this sort (Walters et al., 1997; Pauly, 1998).

The basics of Ecosim consist of biomass dynamics expressed in the form of coupled differential equations derived from Equation (1):

$$dB_i/dt = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_I, \qquad (3)$$

where dB/dt is rate of change in biomass, g is growth efficiency, F is fishing mortality rate, M is natural mortality rate (excluding predation), e is emigration rate, I is immigration rate, and C_{ij} (C_{ji}) is the consumption rate of type i (j) biomass by type j (i) organisms. Consumption rates are calculated by:

(a) dividing the biomass of each prey i into a vulnerable and an invulnerable component (Walters et al., 1997); the transfer rate (v_{ij}) between these two components (adjustable by the user) determines if control is top-down (Lotka-Volterra), bottom-up (donor-driven), or intermediate;
(b) keeping, in case of split pools (juveniles versus adults of the same species), account of the numbers that recruit from the juvenile to the adult stages (using the Deriso-Schnute delay-difference model, which leads to emergent stock–recruitment relationships) as part of the outputs.

These assumptions lead to the rate equation

$$C_{ij} = v_{ij}a_{ij}B_iB_j/(v_{ij} + v'_{ij} + a_{ij}B_j), \qquad (4)$$

where the v and v′ parameters represent rates of behavioural exchange between invulnerable and vulnerable states and a_{ij} represents rate of effective search by predator j for prey type i.

One interesting aspect is that Ecopath parametrizations can be quickly evaluated in terms of the dynamics they imply. For example, one can quickly identify over-aggregated groups, whose ability to consume a wide range of prey enables them, through ''unfair competition'', to drive other groups into extinction (Walters et al., 1997). This allows addressing, at least in part, some of the structural uncertainty associated with the definition of the pools in Ecopath models.

Several applications to policy exploration exist. Shannon et al. (2000) and Stevens et al. (2000) have applied Ecosim from a wider perspective on the Borguela upwelling system and on Chondrychthyans, respectively. Kitchell et al. (1999) used Ecosim to study the ecosystem effects of fishing down top predators in the Central Pacific, and Pitcher et al. (in press) evaluated the relative benefits of artificial reefs protected inside marine reserves to six sectors of the Hong Kong fishing industry.

Trites et al. (1999a, b), using detailed models of the Eastern Bering Sea, were unable to move from the

ecosystem state prevailing in the 1950s to that prevailing now solely on the basis of different exploitation patterns (e.g. fishing down whales or different fish groups). They interpreted this as indirect evidence for effects of mechanisms other than included in Ecosim (fishing+ predation) on the recruitment of the now very abundant Alaska pollack. The well-documented regime shift in the North Pacific in the 1980s comes to mind here (Beamish and Bouillon, 1993; Polovina *et al.*, 1995).

In contrast, Christensen (1998) showed that fishing alone could drive the Ecopath model of the Gulf of Thailand trawling grounds in 1963 (before the development of the trawl fishery) into the, independently estimated, 1983 configuration. Conversely, reduction of the trawling effort prevailing in 1983 led to a system configuration similar to that in 1963.

A simulation of the multispecies, multigear fisheries of San Miguel Bay, Philippines, by Bundy (1997) showed that Ecosim results depend strongly on the assumed vulnerabilities of the biomass pools. This allowed identification of a few robust policies that applied over a wide range of v_{ij} settings and their differentiation from policies whose outcome depended entirely on the setting of the v_{ij} and therefore would remain uncertain until subjected to rigorous testing under an adaptive management scheme (Walters, 1986).

Multisystem comparisons using Ecosim have involved policy evaluation for upwelling fisheries (Mackinson *et al.*, 1997). Vasconcellos *et al.* (1997) showed that increasing detritus recycling in ecosystems correlates with increased resilience to perturbations – as postulated by Odum (1969) – rather than being an expression of stress – as suggested by Baird *et al.* (1991).

We present another multisystem comparison dealing with the possible influence of the quality of the data used in constructing the models on their dynamic behaviour. This question is important because much of what has been written about ecosystem stability has been based on ecosystem models consisting of coupled differential equations with arbitrary or random parameters (May, 1972; Pimm, 1984). Yet it could be argued that, of the infinite number of potential values, only those combinations of parameters occur in nature that allow ecosystems to persist. Hence, models representing real ecosystems constructed from high quality data may be more stable than models constructed from low quality data (Walters *et al.*, 1997).

Three relevant indices were assembled for two groups of ecosystem models, coastal systems (n=8) and shelf systems (n=7): (1) ranked model "quality": derived by ranking the models within the two types of systems in terms of the amount of local data that went into the parameter estimation relative to the application of generic parameter estimates exported from other areas; (2) ranked ecosystem "persistence": refers to the level of vulnerability (v_{ij}) beyond which pools start to drop out

of the system, given a small perturbation (cf. Fig. 5 in Walters *et al.*, 1997); (3) ranked Finn's index of detritus recycling: expresses the amount of detritus that is recycled relative to the amount that flows through. This index was found earlier to correlate with system resilience (Vasconcellos *et al.*, 1997).

Table 1 summarizes the results. The (zero-order) rank correlation between persistence and quality is 0.45 for coastal systems (Fig. 2A) and 0.56 for shelf systems (Fig. 2B). The corresponding partial rank correlations, after accounting for the effect of detritus recycling, are 0.65 and 0.58. The former would be significant (p=0.05) if tested as a zero-order rank correlation, given the absence of a formal test for first-order rank correlation (Siegel, 1956). Thus, we suggest that a positive relationship between quality of Ecopath input data and the persistence of the Ecosim model based thereon might exist.

To follow up on this, we have recently enabled the entry of a "pedigree" (Funtowicz and Ravetz, 1990) for each Ecopath input (Equation [1]), identifying whether it is a mere guess, imported from a similar system, or represents a rough or a precise estimate based on local data. Each input is then linked to a (user-modifiable) default estimate of the associated confidence interval. This allows the computation of an overall index of model quality, and provides prior distributions for Ecoranger, which incorporates a Bayesian approach for explicitly considering uncertainty in Ecopath inputs (Fig. 3), based on McAllister *et al.* (1994) and Walters (1996).

The existence of a link between model quality and persistence, if confirmed by future work, would have profound implications for our understanding of ecosystem functioning and the research required for ecosystem-based management.

Ecospace

Real ecosystems are more complicated than massbalance fluxes in Ecopath models, however large the number of functional groups included. Real ecosystems also have dynamics far more complex than represented in Ecosim. However, in evaluating the realism of simulation software, the issue to consider is not how complex the processes represented therein are. Rather, the question is which structure allows a representation of the basic features of an ecosystem, given a limited amount of inputs. On such criteria, the major deficiency of the Ecopath/Ecosim approach was its assumption of homogeneous spatial behaviour. This was recently remedied through the development of Ecospace (Walters *et al.*, 2000), a dynamic version of Ecopath, incorporating all key elements of Ecosim.

Ecospace dynamically allocates biomass across a grid map (to be decided by the user but typically defined by 20×20 cells), while accounting for: (1) symmetrical

Table 1. Data for testing association between ranked indices of quality and persistence and Finn's index of Ecopath models (documented in Christensen and Pauly, 1992a, 1993; Liew and Chan, 1987; Pauly and Christensen, 1993). N: number of pools.

|	Quality	Persistence	Finn's index		N
			Ranked	%	
Coastal models					
Maputo Bay	1	2	7	5.8	10
Schlei Fjord	2	1	2	29.4	10
Etang de Thau	3	8	8	4.2	11
Gulf of Thailand, 10 m	4	6	3	21.5	15
Celestun Lagoon	5	3	4	14.6	15
Gulf of Mexico	6	5	5	9.5	15
Lingayen Gulf	7	4	1	38.4	16
Off Campeche	8	7	6	8.9	18
Shelf models					
North Sea	1	2	1	22.6	28
Venezuela	2	1	7	2.7	16
Off Yucatan	3	5	6	12.6	20
Gulf of Thailand, 50 m	4	6	2	19.1	15
Brunei Shelf	5	3	4	16.3	13
Malaysia	6	4	3	17.4	13
Northern Gulf of Mexico	7	5	5	12.8	23
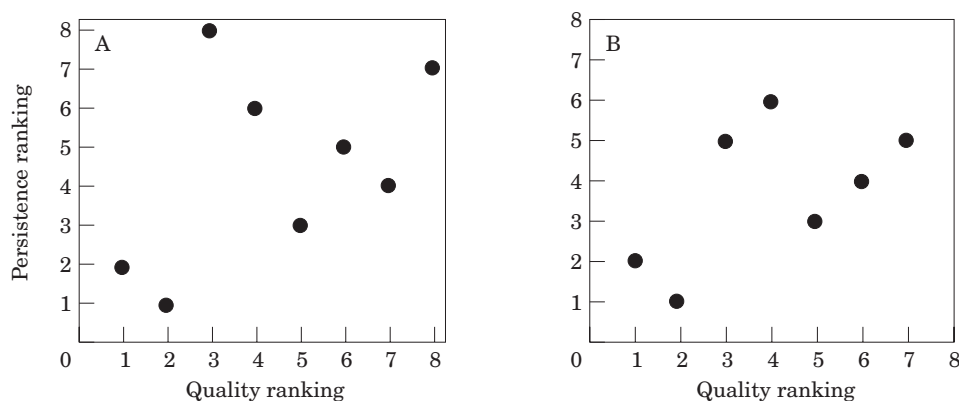
Figure 2. Relation between ranked indices of quality of input data to Ecopath models and of persistence of functional groups in Ecosim runs: A. Coastal systems. B. Shelf systems.

movements from a cell to its four adjacent cells, modified by whether a cell is defined as preferred habitat or not (running means over adjacent sets of five cells allows for smooth transitions between habitat types, which are also user defined); (2) user-defined increased predation risk and reduced feeding rate in non-preferred habitat; (3) levels of fishing effort by fleet in each cell that are proportional to the overall profitability of fishing in that cell, and whose distribution can also be made sensitive to costs (e.g. of sailing to certain areas).

As yet, few applications are available for evaluation. However, numerous test runs with a wide range of available files suggest that Ecospace, like Ecosim, can help resolve some of the structural uncertainty associated with the construction of Ecopath models. Thus,

predators assigned to a given habitat type must be able to encounter sufficient prey in that habitat. Indeed, this suggests that Ecopath models, though they do not explicitly consider space, always should contain implicitly spatial subsystems with distinct food webs, corresponding to habitat types to be defined in Ecospace (Okey, 1998; Pauly, 1998). Moreover, definition of such subsystems leads to more robust simulations under Ecosim (less self-simplification). This obviously reflects the fact that spatial patterns do generate refuges from predation. It is those refuges that bring us to marine protected areas (MPAs).

Given its structure, Ecospace allows users to explore the potential role of MPAs as a tool to mitigate, and perhaps reverse various ecosystem effects of fishing,
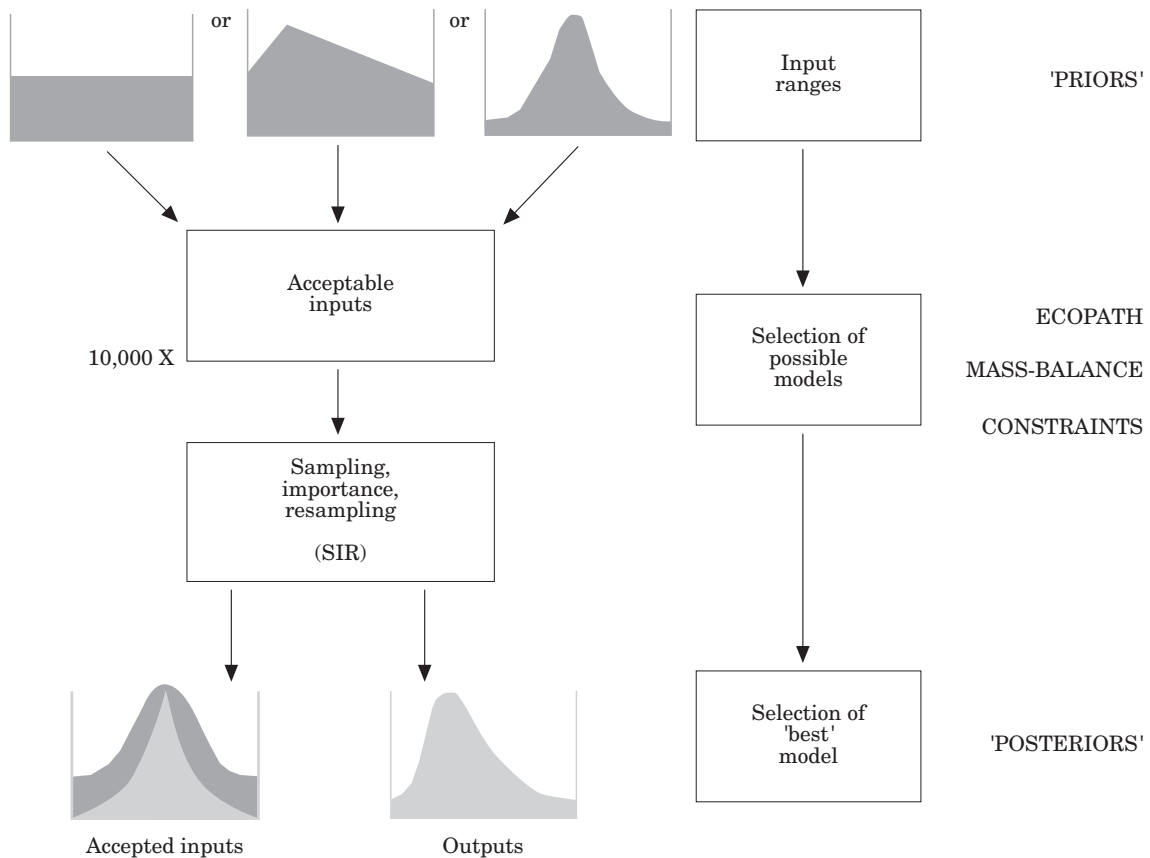
Figure 3. Schematic representation of the Bayesian approach incorporated in Ecoranger, a routine of Ecopath allowing explicit consideration of uncertainty in input values (prior distributions). Outputs include distributions of estimates and posterior distributions of acceptable inputs. A "best" model can also be identified by various criteria, including least squares.

notably the effects of fishing down marine food webs. The results obtained so far (Walters, 2000; Walters *et al.*, 1999) suggest that, due to trophic cascades within MPA owing to local protection of predators and to net movements of predators toward food concentrations outside the MPA, the net effect of small areas may be to increase the catch of fisheries because these will invariably concentrate their operation near their perimeter. Only large MPAs, with short perimeters relative to their surface areas, would solve this problem, as would MPAs in bays or gulfs with limited adjacency to exploited areas.

Some biomass pools may serve particular functions related to, but not directly involving, trophic flows. For example, macroalgae and sponges may act as critical mediators of trophic relationships by providing hiding places from predation and may be influenced both directly and indirectly by fishing (Sainsbury, 1988). Large predators may induce smaller fish to change their distribution and behaviour (risk-avoidance reactions) and thus alter their vulnerability to other predators. Such effects, while not invalidating the static flow estimates of Ecopath, call into serious question the dynamic

predictions from Ecosim/Ecospace. Thus, we recently included in Ecosim/Ecospace a routine called "Mediation", which allows sketching the assumed shape of the relationship between the biomass of a group, and the vulnerability of prey i to a predator j and running under the constraints generated by one or several such shape(s). This will allow to test for instance whether incorporating mediation effects resolves the apparent paradox of small MPAs being able to retain relatively large biomasses of predators (Roberts and Hawkins, 1997), despite the negative effects of trophic cascades within, and strong fishing effort around, their periphery (Walters *et al.*, 1999).

Ecospace still needs much work to make it a useful policy exploration tool for many ecosystems. Case experience suggests in particular that it needs to include representation of orientated migration (seasonal, ontogenetic) as well as simple dispersal, and a better way of specifying differences in trophic flows among habitat types than is offered by aggregate Ecopath analysis. Linkages of habitat type designations to variable features of the physical habitat are also required.

Conclusions

Some improvements are currently being implemented, but progress has been slow mainly due to requirements associated with making complex software accessible to a wide range of users. However, the key improvement, we believe, is not going to come from additional routines, but from a better understanding by users of what the approach can and cannot do. Properly used, it can lead, through successive iteration involving Ecopath, Ecosim, and Ecospace, to a reduction of structural uncertainty, or at least to models that are dynamically stable. Moreover, some of the inherent uncertainty in the input values may be accounted for by the Bayesian scheme (Fig. 3).

While Ecopath offers much promise as a tool for evaluating impacts of fishing on ecosystems, it is not fully capable of representing the trophic flows associated with the ontogeny of feeding relationships in many larger aquatic species: many fish begin life as tiny planktivores, feed later in different habitats on invertebrates, and finally emerge as piscivores. It is difficult to identify a representative diet composition for a pool labelled as a species or functional group with such characteristics, and to represent the flow of biomass across trophic levels represented by individuals graduating from one ontogenetic niche to the next. Ecosim and Ecospace attempt to deal with this problem by allowing users to split pools into juvenile and adult components, with accounting of age structure, but this partial solution may be inadequate for many situations.

Acknowledgements

References

Andersen, K. P., and Ursin, E. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Meddelelser fra Danmarks Fiskeri- og Havundersgelser, 7: 319–435.

Baird, D., McGlade, J. M., and Ulanowicz, R. E. 1991. The comparative ecology of six marine ecosystems. Philosophical Transactions of the Royal Society of London, 333: 15–29.

Beamish, R. J., and Bouillon, D. R. 1993. Pacific salmon trends in relation to climate. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1002–1016.

Bundy, A. 1997. Assessment and management of multispecies, multigear fisheries from San Miguel Bay, Philippines. Doctoral Thesis, University of British Columbia, Vancouver. 395 pp.

Burns, T. P. 1989. Lindeman's contradiction and the trophic structure of ecosystems. Ecology, 70: 1355–1362.

Caddy, J., Csirke, J., Garcia, S. M., and Grainger, R. J. R. 1998. How pervasive is "Fishing down marine food webs". Science, 282: 1839.

Christensen, V. 1994. Energy-based ascendency. Ecological Modelling, 72: 129–144.

Christensen, V. 1995a. A model of trophic interactions in the North Sea in 1981, the Year of the Stomach. Dana, 11(1): 1–19.

Christensen, V. 1995b. Ecosystem maturity – towards quantification. Ecological Modelling, 77: 3–32.

Christensen, V. 1996. Managing fisheries involving predator and prey species. Review in Fish Biology and Fisheries, 6(1): 1–26.

Christensen, V. 1998. Fishery-induced changes in a marine ecosystem: insights for models of the Gulf of Thailand. Journal of Fish Biology, 53(Suppl A): 128–142.

Christensen, V., and Pauly, D. 1992a. The ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, 61: 169–185.

Christensen, V., and Pauly, D. 1992b. A guide to the ECOPATH II program (version 2.1). ICLARM Software 6. International Center for Living Aquatic Resources Management, Manila, Philippines. 72 pp.

Christensen, V., and Pauly, D. (ed.) 1993a. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings, No. 26. 390 pp.

Christensen, V., and Pauly, D. 1993b. Flow characteristics of aquatic ecosystems. *In* Trophic Models of Aquatic Ecosystems, pp. 339–355. Ed. by V. Christensen, and D. Pauly. ICLARM Conference Proceedings, No. 26.

Christensen, V., and Pauly, D. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecological Applications, 8(1), (Suppl): 104–109.

Daan, N., and Sissenwine, M. P. (ed.) 1991. Multispecies Models Relevant to Management of Living Resources. ICES Marine Science Symposia, 193. 358 pp.

Folke, C., Kautsky, N., Berg, H., Jansson, A., and Troell, M. 1998. The ecological footprint concept for sustainable seafood production: a review. Ecological Applications, 8(1), (Suppl): 63–71.

Froese, R., and Pauly, D. (ed.) 1998. FishBase 98: Concepts, Design and Data Sources. ICLARM, Manila. 293 pp.

Funtowicz, S. O., and Ravetz, J. R. 1990. Uncertainty and Quality in Science for Policy. Kluwer, Dordrecht. 229 pp.

Griggs, R. W., Polovina, J. J., and Atkinson, M. J. 1984. Model of a coral reef ecosystem. III. Resource limitation, community regulation, fisheries yields and resources management. Coral Reefs, 3: 23–27.

Jarre-Teichmann, A. 1995. Seasonal mass-balance models of carbon flows in the central Baltic Sea, with emphasis on the upper trophic levels. ICES CM 1995/T: 6, 26 pp.

Kitchell, J. F., Boggs, C. H., He, Xi, and Walters, C. J. 1999. Keystone predators in the Central Pacific. *In* Ecosystem Approaches for Fisheries Management, pp. 665–689. Ed. by S. Keller. University of Alaska Sea Grant, Fairbanks.

Kline, T. C. Jr, and Pauly, D. 1998. Cross-validation of trophic level estimates from a mass-balance model of Prince William Sound using 15N/14N data. *In* Fishery Stock Assessment Models, pp. 693–702. Ed. by T. J. Quinn II, F. Funk. J. Heifetz, J. N. Ianelli, J. E. Powers, J. F. Schweigert, P. J. Sullivan, and C.-I. Zhang. Alaska Sea Grant, Fairbanks.

Laevastu, T., and Favorite, F. 1977. Preliminary report on the dynamical marine ecosystem model (DYNUMES) for Eastern Bering Sea. Manuscript Report, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Seattle.

Larkin, P. A., and Gazey, W. 1982. Application of ecological simulation models to management of tropical multispecies fisheries. *In* Theory and Management of Tropical Fisheries, pp. 123–140. Ed. by D. Pauly, and G. I. Murphy. ICLARM Conference Proceedings, 9.

Liew, H. C., and Chan, E. H. 1987. ECOPATH model of a tropical shallow-water community in Malaysia. Report of the International Development Research Centre (IDRC), Singapore.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology, 23(4): 399–418.

Mackay, A. 1981. The generalized inverse. Practical Computing, (Sept.): 108–110.

Mackinson, S., Vasconcellos, M., Pitcher, T., and Walters, C. 1997. Ecosystem impacts of harvesting small pelagic fish in upwelling systems: using a dynamic mass-balance model. *In* Proceedings of the Lowell Wakefield Symposium on Forage Fish in Marine Ecosystems, pp. 731–749. Alaska Sea Grant College Program, AS-SG-97-01.

McAllister, M., Pikitch, E. K., Punt, A. E., and Hilborn, R. 1994. A Bayesian approach to stock assessment and harvest decision using the sampling/importance resampling algorithm. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2673–2687.

May, R. M. 1972. Will a large complex system be stable? Nature, 238: 413–414.

Merz, G., and Myers, R. A. 1998. A simplified formulation for fish production. Canadian Journal of Fisheries and Aquatic Sciences, 55(2): 478–484.

Morowitz, H. J. 1991. The thermodynamics of pizza: essays on science and everyday life. Rutgers University Press, New Brunswick, New Jersey. 247 pp.

Nauen, C. 1984. The artisanal fishery in Schlei-Fjord, eastern Schleswig-Holstein, Federal Republic of Germany. *In* Management of Coastal Lagoon Fisheries, pp. 403–428. Ed. by J. M. Kapesky, and G. Lasserre. Studies & Reviews of the General Council of the Mediterranean. (61), Vol. 1. Rome.

NRC 1999. Sustaining marine fisheries. National Research Council, National Academy Press, Washington, D.C. 164 pp.

Odum, E. P. 1969. The strategy of ecosystem development. Science, 164: 262–270.

Odum, W. E., and Heald, E. J. 1975. The detritus-based food web of an estuarine mangrove community. *In* Estuarine Research, vol. 1, pp. 265–286. Academic Press, New York.

Okey, T. 1998. Constructing and balancing the PWS model. *In* A Trophic Mass-Balance Model of Alaska's Prince William Sound, for the Post-spill Period 1994–1996, pp. 71–86. Ed. by T. Okey, and D. Pauly. Fisheries Centre Research Reports 6(4).

Pauly, D. 1975. On the ecology of a small West African lagoon. Meeresforschung, 24(1): 46–62.

Pauly, D. 1982. Notes on tropical multispecies fisheries, with a short bibliography on the food and feeding habits of tropical fish. *In* Report of the Regional Training Course on Fisheries Stock Assessment, Samutprakarn, Thailand, 1 Sept.–9 Oct. 1981, Part II, Vol. 1, pp. 30–35 and 92–98. SCS/GEN/82/41 South China Sea Fisheries Development and Coordinating Program. Manila.

Pauly, D. 1987. Managing the Peruvian upwelling ecosystem: a synthesis. *In* The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Changes, pp. 325–342. Ed. by D. Pauly, and I. Tsukayama. ICLARM Studies and Reviews, 15.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution, 10(10): 430.

Pauly, D. 1996. One hundred million tonnes of fish, and fisheries research. Fisheries Research, 25(1): 25–38.

Pauly, D. (ed.) 1998. Use of Ecopath with Ecosim to evaluate strategies for sustainable exploitation of multi-species resources. Fisheries Centre Research Reports, 6(2). 49 pp.

Pauly, D., and Christensen, V. 1993. Stratified models of large marine ecosystems: a general approach, and an application to the South China Sea. *In* Stress, Mitigation and Sustainability of Large Marine Ecosystems, pp. 148–174. Ed. by K. Sherman, L. M. Alexander, and B. D. Gold. American Association for the Advancement of Science, Washington, D.C.

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

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. C. Jr 1998a. Fishing down marine food webs. Science, 279: 860–863.

Pauly, D., Froese, R., and Christensen, V. 1998b. How pervasive is "Fishing down marine food webs": response to Caddy *et al.* Science, 282: 1839.

Pauly, D., Soriano-Bartz, M. L., and Palomares, M. L. D. 1993. Improved construction, parameterization and interpretation of steady-state ecosystem models. *In* Trophic Models of Aquatic Ecosystems, pp. 1–13. Ed. by V. Christensen, and D. Pauly. ICLARM Conference Proceedings, No. 26.

Pimm, S. L. 1982. Food Webs. Population and Community Biology Series. Chapman and Hall, London. 219 pp.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature, 307: 321–326.

Pitcher, T. J. 1998. Back to the future: a novel methodology and policy goal in fisheries. *In* Back to the Future: Reconstructing the Strait of Georgia Ecosystem, pp. 4–7. Ed. by D. Pauly, T. J. Pitcher, and D. Preikshot. Fisheries Centre Research Reports, 6(5).

Pitcher, T. J., Watson, R., Haggan, N., Guénette, S., Kennish, R., and Sumaila, R. 2000. Marine Reserves and the Restoration of Fisheries and Marine Ecosystems in the South China Sea. Proc. Mote Symposium on Marine Protected Areas, Sarasota Springs, Florida. November 1998. Bulletin of Marine Science, 66(3) (in press).

Polovina, J. J. 1984. Model of a coral reef ecosystem. I: the ECOPATH model and its application to French Frigate Schoals. Coral Reefs, 3: 1–11.

Polovina, J. J. 1985. An approach to estimating an ecosystem box model. U.S. Fisheries Bulletin, 83(3): 457–460.

Polovina, J. J., Mitchum, G. T., and Evans, G. T. 1995. Decadal and basin-scale variation in mixed layer depth and the impact on biological production in the Central and North Pacific, 1960–88. Deep-Sea Research, 42(10): 1701–1716.

Polovina, J. J., and Ow, M. D. 1983. ECOPATH: a user's manual and program listing. National Marine Fisheries Service, NOAA, Honolulu, Hawaii, Administrative Report. H-83-23. 46 pp.

Polovina, J. J., and Tagami, D. T. 1980. Preliminary results from ecosystem modeling at French Frigate Shoals. *In* Proceedings of the Symposium on Status of Resource, pp. 286–298. Ed. by R. W. Griggs, and R. T. Pfund. Investigations in the Northwestern Hawaiian Islands, 24–25 April 1980. University of Hawaii, Honolulu. Sea Grant Misc. Reports UNIHI-SEAGRANT-MR-80-04.

Rigler, F. H. 1975. The concept of energy flows and nutrients flows between trophic levels. *In* Unifying Concepts in Ecology, pp. 15–26. Ed. by W. H. van Dobben, and R. H. Lowe-McConnel. Dr. W. Junk B.V. Publishers, The Hague.

Roberts, C. M., and Hawkins, J. P. 1997. How small can marine reserves be and still be effective? Coral Reefs, 16: 150.

Ryther, J. 1969. Photosynthesis and fish production in the sea. Science, 166: 72–76.

Sainsbury, K. 1988. The ecological basis of multispecies fisheries, and management of a demersal fishery in tropical Australia. *In* Fish Population Dynamics, pp. 349–382. Ed. by J. A. Gulland. Wiley, Chichester.

Shannon, L. J., Cury, P. M., and Jarre, A. 2000. Modelling effects of fishing in the Southern Benguela ecosystem. ICES Journal of Marine Science, 57: 720–722.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 pp.

Silvert, W. 1993. Size-structured models of continental shelf food webs. *In* Trophic Models of Aquatic Ecosystems, pp. 40–43. Ed. by V. Christensen, and D. Pauly. ICLARM Conference Proceedings, No. 26.

Slobotkin, L. B. 1972. Growth and Regulation of Animal Populations. Holt, Rhinehart and Winston, New York. 184 pp.

Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. 2000. The effects of fishing on sharks, rays and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476–494.

Trites, A., Christensen, V., and Pauly, D. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. Journal of Northwest Atlantic Fisheries Science, 22: 173–187.

Trites, A. W., Livingston, P. A., Vasconcellos, M. C., Mackinson, S., Springer, A., and Pauly, D. 1999a. Ecosystem considerations and the limitations of Ecosim models in fisheries management: insights from the Bering Sea. *In* Ecosystem Approaches for Fisheries Management, pp. 609–618. Ed. by S. Keller. University of Alaska Sea Grant, Fairbanks.

Trites, A. W., Livingston, P., Vasconcellos, M. C., Mackinson, S., Springer, A. M., and Pauly, D. 1999b. Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: testing ecosystem shift and commercial whaling hypotheses. Fisheries Centre Research Reports, 7(1). 106 pp.

Ulanowicz, R. E. 1986. Growth and development: ecosystem phenomenology. Springer-Verlag, New York. 203 pp.

Vasconcellos, M., Mackinson, S., Sloman, K., and Pauly, D. 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecological Modelling, 100: 125–134.

Venier, J. 1997. Seasonal ecosystem models of the Looe Key National Marine Sanctuary. Master's Thesis, University of British Columbia. 109 pp.

Vitousek, P. M., Ehrlich, A. M., Erhlich, A. H., and Matson, P. A. 1986. Human appropriation of the products of photosynthesis. Bioscience, 36: 368–373.

Wackernagel, M., and Rees, W. 1996. Our ecological footprint: reducing the human impact on the Earth. New Society Publishers, Gabriela Island. 160 pp.

Walters, C. 1986. Adaptive management of renewable resources. Macmillan, New York. 374 pp.

Walters, C. 1996. Suggested improvements for Ecopath modeling. *In* Mass-Balance Models of North-Eastern Pacific Ecosystems, pp. 82–86. Ed. by D. Pauly, and V. Christensen. Fisheries Centre Research Reports 4(1).

Walters, C. 2000. Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Proc. Mote Symposium on Marine Protected Areas, Sarasota Springs, Florida. November 1998. Bulletin of Marine Science 66(3) (in press).

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

Walters, C., Pauly, D., and Christensen, V. 2000. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems, 2: 539–554.