

CHAPTER 5

Ecopath with Ecosim: linking fisheries and ecology

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1 Why ecosystem modeling in fisheries?

Fifty years ago, fisheries science emerged as a quantitative discipline with the publication of Ray Beverton and Sidney Holt's [1] seminal volume *On the Dynamics of Exploited Fish Populations*. This book provided the foundation for how to manage fisheries and was based on detailed, mathematical analyses of the dynamics of individual fish populations, of how they grow and how they are affected by fishing. Fisheries science has developed and matured since then, and remarkably much of what has been achieved are modifications and further developments of what Beverton and Holt introduced.

Given then that fisheries science has developed to become one of the most data-rich, quantitative fields in ecology [2], how well has it fared? We often see fisheries issues in the headlines and usually in a negative context and there are indeed many threats to the sustainability of ocean resources [3]. Many, judging not the least from newspaper headlines, consider fisheries management a usual suspect in connection with fisheries collapses. This may lead one to suspect that there is a problem with the science, but I hold this to be an erroneous conclusion. It should be stressed that the main problem is not to be found in the computational aspects of the science, but rather in how management advice actually is implemented in praxis [4]. The major force in fisheries throughout the world is excessive fishing capacity; the days with unexploited resources and untapped oceans are over [5], and the fishing industry is now relying heavily on subsidies to keep the machinery going [6].

Yet, there is a growing interest worldwide for changing the way we evaluate fisheries management questions, notably for adopting ecosystem approaches to fisheries management as advocated by the UN Food and Agricultural Organization [7]. The main aspect of this is not, however, that we need to replace the standard assessment methodologies, but rather that we need to supplement them. We will continue to require evaluations of how much we can harvest of fisheries resources in a sustainable manner, but in addition, we must be able to evaluate, e.g., trade-offs between alternative uses, the impact of a potential protected area, or how competition between marine mammals and fisheries should be evaluated and managed. For this, we need a toolset different from that supplied by single-species assessment methodologies; we need ecosystem approaches to management. Tools such as these are described in this chapter.



2 The Ecopath with Ecosim (EwE) modeling approach

2.1 Model overview

The Ecopath mass-balance approach was developed by Jeff Polovina, NMFS, Hawaii, in the early 1980s to model an unexploited coral reef system, French Frigate Shoals, in the Hawaiian archipelago that was the subject of a 5-year, multidisciplinary study of its ecology. Polovina evaluated various ecosystem modeling approaches being developed at the time, decided that they were too complex and instead developed a simplified model inspired by the much more complex Bering Sea model of Taivo Laivastu, NMFS, Seattle. Polovina called the model Ecopath and he published it along with a detailed description and a User's Guide [8, 9].

The approach was subsequently further developed by Daniel Pauly at ICLARM, Manila, who started a re-programming and described its potential use in connection with a project in Kuwait [10]. Following this, the approach was further developed by the present author in co-operation with Pauly [11, 12], notably by linking the approach to network analysis [13] based on the work of Ulanowicz [14] and colleagues. The development has been continuous since then, with a focus on user support through distribution of the free software and through a large number of training courses and workshop. A notable result of this is that Ecopath has become the most widely used approach for ecosystem-based management of fisheries [15]. This is also illustrated by it recently being named as one of the 10 major scientific breakthroughs in the 200-year history of the US National Oceanographic and Atmospheric Administration (see <http://celebrating200years.noaa.gov/breakthroughs/welcome.html>).

The development of the Ecopath approach and software gained momentum when Carl Walters of the UBC Fisheries Centre, Vancouver, joined the project in 1995 and first developed the time-dynamic simulation model Ecosim [16, 17], and subsequently a spatial-dynamic simulation model, Ecospace [18]. The bottom line as of present is a well-developed approach with capabilities only few, if any users have explored fully [19].

2.2 Mass-balance

Ecopath by itself is chiefly an approach for parameterization of ecosystem models, i.e. for obtaining a well-described (and well-documented) initial model for dynamic simulations. Its core is that energy (or mass since mass can be measured using an energy unit, which may or may not be converted to a mass unit) is assumed to be conserved. We thus assume that the energy input to any group in a model must equal the energy output from the group (considering energy storage as part of the equation). This can be expressed as,

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated energy}, \quad (1)$$

where we subsequently can break down the production into its components:

$$\begin{aligned} \text{Production} = & \text{predation mortality} + \text{catches} + \text{net migration} \\ & + \text{biomass accumulation} + \text{other mortality}, \end{aligned} \quad (2)$$

or,

$$P_i = \sum_j Q_j \cdot DC_{ji} + (F_i + NM_i + BA_i + M0_i) \cdot B_i \quad (3)$$

where P_i is the production of prey group i , Q_j is the consumption of predator j (estimated from the predator biomass B_j times the consumption/biomass ratio Q_j/B_j for predator j), DC_{ji} is the diet



composition contribution of i to j 's diet (measured as a proportion by weight or rather energy), F_i is the fishing mortality expressed as an instantaneous rate (typically annual, along with other rates, NM_i is the net migration rate of prey group i , estimated from emigration less immigration, BA_i is the biomass accumulation rate for i , estimated from the group biomass at the beginning of the model time period (typically a year) less the biomass at the end of the time period and MO_i is the other mortality rate for i , expressing all other (i.e., non-predation, non-fishery) mortality, and B_i the biomass of i .

The equations above are illustrated in Fig. 1, which shows how consumption for a consumer must match the predation mortality it causes on its prey. The equations above also define the main input parameters for Ecopath, i.e. the biomass, B , the production/biomass ratio, P/B , the consumption/biomass ratio, Q/B , the catches, C , typically entered by fishing fleet, and the diet composition, DC , for each consumer group. The net migration rate, NM , and biomass accumulation rate, BA , are by default assumed to be zero, while the net migration rate, MO , most often is estimated so as to obtain mass-balance. This is done by estimating what in Ecopath is called "trophic transfer efficiency," EE , from eqn. (3), first calling the predation mortality rate from the equation for $M2 (= \sum_j Q_j \cdot DC_{ji} / B_i)$, which gives us,

$$P_i / B_i = (M2_i + F_i + NM_i + BA_i) + MO \tag{4}$$

We then define EE as the part of the mortality rate; we explain the fate of it in the Ecopath model, i.e. including all production terms but MO , the "other mortality,"

$$EE_i = (M2_i + F_i + NM_i + BA_i) / (P_i / B_i) \tag{5}$$

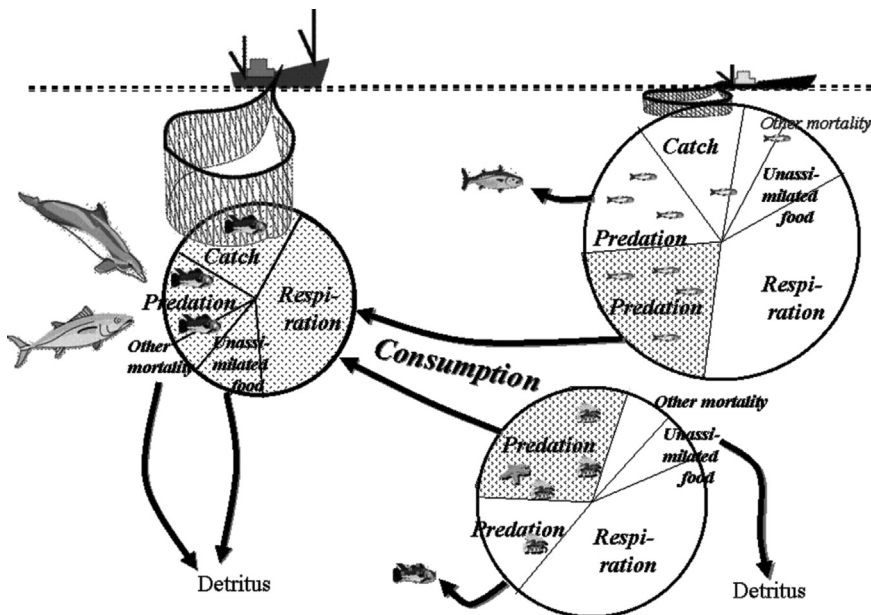


Figure 1: A schematic diagram to illustrate mass-balance in Ecopath. For the group to the left (an intermediate consumer), the total consumption (full pie, shaded) must equal its predation on the two prey groups to the right (shaded part of pies). For all groups, the consumption equals production + unassimilated food + respiration and production is further split into catch + predation + other mortality (based on Christensen *et al.*) [20].

By combining eqns. (4) and (5), we further have that the “other mortality” rate corresponds to,

$$MO_i = (1 - EE_i) \cdot P_i / B_i \quad (6)$$

When balancing a model, the most common approach is to leave the EE parameter unknown for all groups and letting the Ecopath mass-balance routine estimate this parameter, which is very difficult (or more often impossible) to estimate empirically. If needed, it is, however, also possible to estimate any other of the “basic input” parameters (B , P/B , Q/B) for any group where $EE > 0$, though we advise against estimation of Q/B , as this parameter can be estimated from P/B and an assumed gross food conversion efficiency, P/Q . Please see the EwE User’s Guide [20] for further information about data requirements and how the mass-balancing is performed.

The equations above outline a simple accounting scheme for mass flow in ecosystems, allowing for either estimation of “missing” parameters, e.g., using information about energy demands for consumers to conclude how big the production of the prey groups must be to meet the demands or for validation of estimates by comparing estimates for demand and supply. The simplicity and ease of parameterization of the approach has been a strong contributing factor to the widespread adoption of Ecopath.

2.3 The foraging arena

Ecosystem modeling has, back to the International Biological Program in the 1960s and 1970s, been marred by model self-simplification resulting in loss of species or functional groups over time. The reaction to this has been to introduce model-stabilizing mechanisms, notably functional relationships as pioneered by Holling [21], to limit prey uptake at low densities; yet, model capability to reproduce time trends across trophic levels in ecosystems has been lacking. This situation has, however, changed in recent years through Walters’ inclusion of prey behavior in predator–prey interactions, limiting predation mortality in what is termed the “foraging arena” [2, 22].

The key assumption in the foraging arena hypothesis is that a given prey can be either accessible or inaccessible to a given predator at any given point in time (see Fig. 2). Prey are (dependent on parameter settings) assumed to hide to reduce risk of predation, rather than feed at maximum capacity to optimize growth [23]. Furthermore, it is assumed that each predator–prey combination identifies a distinct foraging arena, though this assumption has recently been

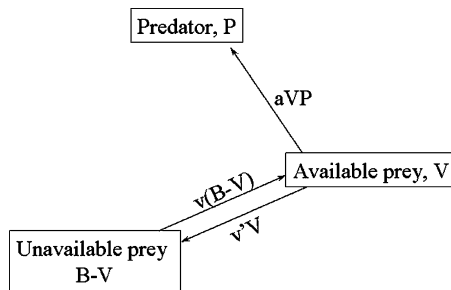


Figure 2: The foraging arena assumes that prey is only available to predation part of the time, typically this is when the prey themselves are feeding. It is a risky proposition to go on feeding (based on Christensen *et al.* [20]).

modified to optionally allow shared foraging arenas as well as to allow either bout feeding or continuous feeding [24].

In the foraging arena, predator–prey interactions scale from being top–down controlled when a predator is far from its carrying capacity to bottom–up when it is close to its carrying capacity [20]. This has strong implications for model and population stability as predator and prey behavior limits predation rates [25]. The mechanisms for this may (as for Type III functional response) be linked to spatial refuges as indicated in many studies [26, 27].

Stability in ecosystems has also been linked to other food web characteristics, e.g., connectivity [28, 29], alternative food [30] or rare species [31], each of which by themselves does not govern food web structure [32]. The foraging arena through its coupling with food web models [16] incorporates a number of such factors related to system and species stability, e.g., foraging time adjustment [23], effect of carrying capacity [33], and calls for further empirical testing [2] as well as contributes to the debate whether predation is prey- or ratio-dependent [34].

2.4 Ecosim

The Ecosim model in EwE incorporates the foraging arena as a key assumption (Fig. 3) with key initial parameters inherited from the base Ecopath model. The key computational aspects are in summary form: Use of mass-balance results (from Ecopath) for parameter estimation; Variable speed splitting enables efficient modeling of the dynamics of both “fast” (phytoplankton) and “slow” groups (whales); Effects of micro-scale behaviors on macro-scale rates: top–down vs. bottom–up control incorporated explicitly. Ecosim includes biomass and size structure dynamics

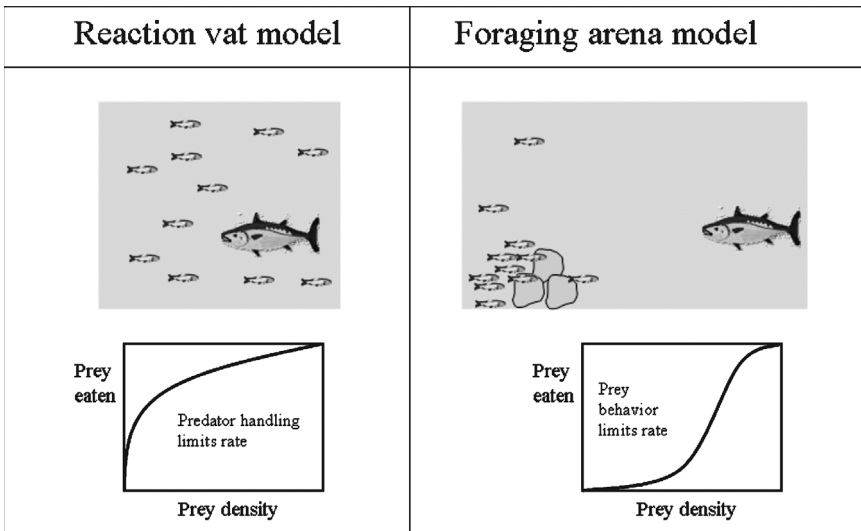


Figure 3: Relationship between prey eaten and prey density in classical predator–prey models (“reaction vats”) and in the foraging arena model. The basic thesis is that fish will minimize the risk of predation, even at the risk of reduced food uptake; it is better to be hungry than to be eaten. The foraging arena causes model stability as predation is reduced at low prey density, which is radically different from the behavior of the vat model (based on Walters and Kitchell [35]).

for key ecosystem groups, using a mix of differential and difference equations and it incorporates full age and number structure by monthly cohorts, density- and risk-dependent growth; accounting via delay-difference equations; stock–recruitment relationship as “emergent” property of competition/predation interactions of juveniles.

Ecosim uses a system of differential equations that express biomass flux rates among pools as a function of time varying biomass and harvest rates, (for equations see [16, 17, 36]). Predator–prey interactions are moderated by prey behavior to limit exposure to predation, such that biomass flux patterns can show bottom–up, top–down (trophic cascade) or mixed control [17]. Through repeated simulations, Ecosim allows for the fitting of predicted biomasses to time series data.

3 EwE modules and applications

The EwE approach and software includes a variety of models, requires a suite of information and has a range of applications (Fig. 4). Ecosystems and their embedded fisheries can be efficiently modeled using the mass-balance system of Ecopath [8, 11, 12]. The first stage of model building brings experts on different ecosystem components – plankton, invertebrates, demersal and pelagic fish, seabirds and marine mammals – together and requires them to standardize their data and agree on a model that is “possible” in terms of the production available and the demand by consumers.

Ecosim [16, 17] allows simulation of “what if” questions, e.g., what will the system look like in 5, 10, or 50 years, if we continue to harvest at the current rate? What if we double it? What if we start to harvest supposedly “under-utilized” species? This predictive capability allows fishers,

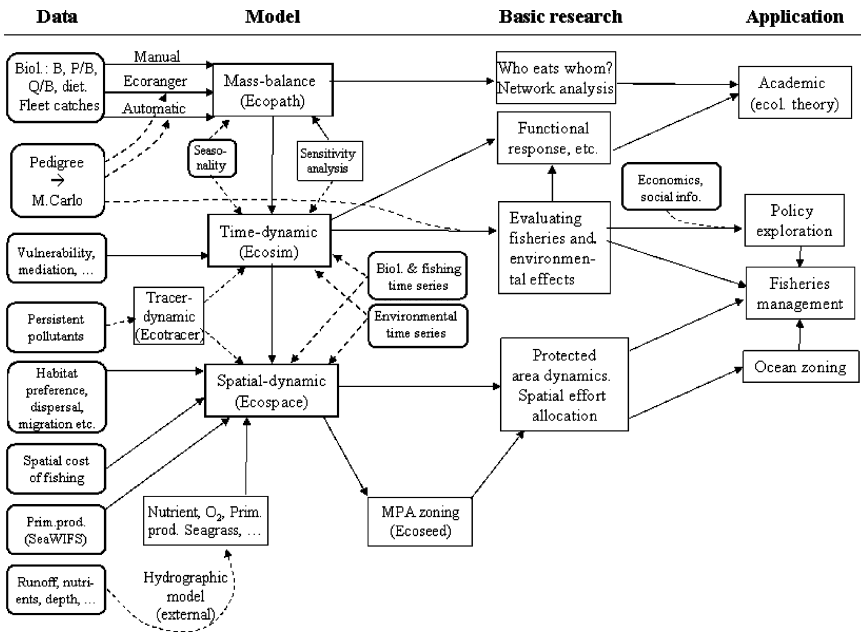


Figure 4: An overview of EwE data requirements, model types included as part of the software, and their application. Many of the modeling aspects are described in this chapter, but see Christensen and Walters [36] and Christensen *et al.* [20] for further information.

scientists, managers and policy makers to explore the ecological, economic and social costs and benefits of different conservation and harvest strategies.

Ecospace [18] introduces a capacity for explicit spatial modeling of ecosystems, which have been parameterized through Ecopath and analyzed for time-trends using Ecosim. This is useful in the modeling of sensitive coastal habitats such as mangrove swamps and sea grass beds and evaluation of the benefits of closed areas. Base maps for the simulations can be constructed by the user by using a drawing interface, or be read from Internet servers with spatial information. Integration of Ecospace maps with commercial GIS formats (using raster format) is also possible and there is currently considerable interest in developing such facilities further.

A module, Ecosed of Ecospace, is designed for zoning and optimizes placement of protected areas while evaluating economic and social considerations [37]. The module was developed for the EwE package in 2000–2001 as part of the student thesis project, but has never been made available or used further. Given the strong interest, notably in environmental NGOs, Ecosed is, however, currently being revived and updated to include a well-defined and flexible objectivity function, and it will be made available in the next release of EwE.

Ecopath with Ecosim also includes facilities for evaluating policy options for ecosystem-based management, notably for how to balance ecological, social, economic and legal constraints [38, 39]. Evaluation of benefits includes total catch, economic value, diversity of fishery products, social values such as food security and income for coastal communities, employment, biodiversity and reduction in sectoral conflicts. Using the policy optimization routines, the ecosystem and associated fisheries that maximize total benefit to society may be evaluated as potential policy goal, taking into account the costs of shifting from the current exploitation system [40].

There has been growing interest in modeling the fate of persistent pollutants and how these are transferred and accumulated through the food web. To that effect, EwE includes a module, Ecotrace, which is linked to the time-dynamic Ecosim model as well as to the spatial-dynamic Ecospace. The module has only been used for a handful of applications so far [41–43], but is likely to see more widespread use given the growing concern for the impact of persistent pollutants.

5 EwE applications

Ecopath (and its newer incarnation, EwE) has since its inception been an open-source, freely available software, the development of which was made possible through the 1990s by dedicated support from Danida, the Danish International Development Agency. Through widespread user support (including some 30 training courses conducted throughout the world), the approach has grown to have approximately 4000 registered users distributed over 124 countries; over the years, this has led to the construction of more than 325 models [44], many of which are available for downloading through www.ecopath.org. Most of the models (42%) have been constructed to describe the structure of ecosystems and their food webs, whereas 30% are aimed at fisheries management issues, 11% theoretical ecology, 9% has been to address policy questions and some 6% were constructed to address questions related to protected areas [44].

The models developed based on the EwE approach span in complexity over orders of magnitude, from very simple models (e.g., two imaginary models of the seas of Europa, the fourth moon of Jupiter [45]) to complex spatial models with hundreds of functional groups and life stages.

Trophic ecosystem models such as those developed based on the EwE approach and software have thus seen wide application. The applications were from the beginning aimed at fisheries biology and management with ecological studies aimed at describing the state of ecosystem being emphasized. The toolbox of choice was from the beginning based on network analysis [14],



and numerous applications have used network indicators to characterize ecosystem states (e.g., contributions in [46]), and notably, several contributions have indicated that it is feasible to quantify ecosystem maturity [47–50].

Recently, network analysis in EwE has been linked to the time-dynamic model, Ecosim, allowing evaluation of how a range of network indicators change over time, and in the process, opening a new approach to network analysis research [51].

The strength of the Ecopath approach relates to evaluating the impact of fisheries, while considering trophic interactions as well as environmental impact, notably related to system productivity [15].

In the early years of the Ecopath development, it was considered a major advantage by model developers that the Ecopath approach allowed for estimation of a “missing parameter,” it is like getting “data for free.” True, the model indeed requires that one basic parameter (B , P/B , Q/B or EE) is estimated for each functional group so as to obtain mass-balance in the model and this is an advantage when modeling data-sparse situations where, e.g. the biomass of a prey group can be estimated based on consumer demands. One does at least get an initial parameter estimate this way.

When moving on to the time-dynamic simulations, the situation changes somewhat, and to go beyond simple, exploratory analysis, the model becomes really data-hungry. To evaluate, e.g., the impact of changes in fishing pressure, we need to evaluate the level of density-dependent processes for key species. Strong density dependence (as typically occurs for a species when it is close to its carrying capacity) leads to compensation where a species will react less to changes in fishing pressure than is the case when density-dependent processes are more limited. We cannot predict the level of these processes based on readily measured parameters, but rather need to examine how the key species in the ecosystem have reacted to previous perturbations and how far the species are from their original abundance in the system. This calls for data! There is no way to over emphasize the importance of monitoring ecosystem changes.

Similarly, for spatial applications based on Ecospace or for that matter on any other ecosystem model, we need to know how species react to changes in external pressure, here notably fishing, and this calls for information about density-dependent processes – just as for the time-dynamic simulations. In addition, it is, however, necessary to predict spatial impacts, notably related to the rate of dispersal for each functional group or life stage. Dispersal rates represent the Holy Grail when it comes to describing the impact of marine-protected areas; at what rate do individuals within a protected area “spill-over” to supply the surrounding areas? Predictions hinge on this point, and it is one for which the empirical evidence is totally inconclusive.

Overall, the question of ecosystem models being data-hungry does indeed limit the extent to which we should trust predictions originating from such models. This becomes increasingly clear as ecosystem models are increasingly being introduced in the management process; when they were used for research only, it was possible to get away with more uncertain predictions, indeed with not even quantifying the associated uncertainty. Yet, we do not really have an alternative to using models, not using them, i.e. sticking to a non model-driven decision process represents a worse alternative. We do at least have the option in a model-driven process to quantify the associated uncertainty and to manage under the constraints given by uncertainty about processes and parameters.

6 Getting hold of the EwE software

The EwE software is freely available from the model website, www.ecopath.org, where a compiled version with a database with examples of models can be downloaded. The software, currently in its fifth generation, is currently available for use with Windows operating systems



(Windows 98 or later, though Windows XP or later is strongly encouraged to minimize the risk of encountering installation problems). The software has been reported to operate using Windows-emulation software on Macintosh computers as well.

The source code is available from the user on request, and we very much encourage scientists to examine the inner workings, as well as to develop alternative formulations, etc. The software is programmed primarily using Microsoft Visual Basic 6.0 in its present release (5.1), and we are currently re-programming it in a new programming environment based on Microsoft .Net (see www.lenfestoceanfutures.org for information). We expect that the new version (6) will be able to run on UNIX and Linux computers as well as on Windows, and we are again making software and code freely available. Please consult www.ecopath.org for further information about this.

7 Exercise: trawling cultivates the ocean bottom for squid

Before trawling became intensive on shelves, macro-algae, sponges, soft-corals and other large habitat-forming growth was abundant and provided shelter for juvenile fishes. Bottom trawling removes the habitat structure, opening for even more intensive trawling, and often a valuable squid fishery emerges (Fig. 5). Sainsbury *et al.* [52] described this process and found that fishers would actively promote this development (destruction of habitat structure) to cultivate squid fisheries. In this exercise, we will replicate the development based on a simple ecosystem model. Similar mechanisms are known to exist to promote shrimp fisheries.

To model such a development, we present here a simple model illustrating the use of EwE to analyze ecological issues of fisheries. I assume that you have already downloaded the EwE

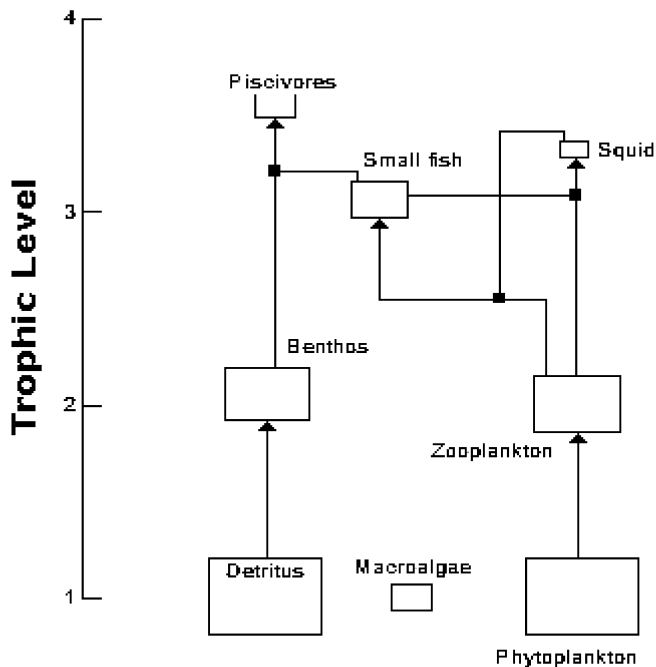


Figure 5: A simple flow chart of a food web model designed to demonstrate how trawling may cultivate the ocean bottom for squid.

set-up file from www.ecopath.org and that you have installed the software. Next, open EwE, and select “File,” “New” from the menu. Then select “Edit,” “Insert group, add multi-stanza” and you will have only one group (“Detritus”) listed in a spreadsheet as you start out. Now, click the row number in front of “Detritus” and a new blank row will be inserted, continue until you have at least eight rows. Then write the group names for each of the functional groups from Table 1, and click in the “Consumer” column for the first five groups, and the “Producer” column for the phytoplankton and macro-algae groups. Now select “OK” and the model will be saved and closed.

When you open the model again you may get a warning about “detritus fate”; select “yes” to send all detritus to the “Detritus” group. You should now have a model with eight groups listed and you should now enter the basic input parameter values from Table 2. Next, select “Input,” “Diet composition” and enter the diet compositions from Table 2.

Continue to the “Input,” “Fishery,” where you will have a blank page. Select “Edit,” “Add fleet,” to add a fleet, and once done, you can click the cell with the “Fleet1” name and change it

Table 1: Basic input parameters for the trawl-squid model. B is biomass (in $t\ km^2$), P/B is production/consumption ratio ($t\ km^2\ year^{-1}$), Q/B is consumption/biomass ratio ($t\ km^2\ year^{-1}$), and EE is the “ecotrophic efficiency,” expressing the proportion of the mortalities that are explained based on the model. The EE is typically used to check for mass-balance in the model.

	Group	B	P/B	Q/B	EE
1	Piscivores	0.5	0.3	1	
2	Small fish	1.5	1	4	
3	Squid	0.2	2	10	
4	Benthos	4	5	20	
5	Zooplankton	5	20	80	
6	Macro-algae	0.5	0.5		1
7	Phytoplankton	10	150		
8	Detritus	10			

Table 2: Diet composition for the trawl-squid model, given as proportions (by weight or volume). Predators are listed in columns.

Prey\Predator	1	2	3	4	5
Piscivores					
Small fish	0.50		0.30		
Squid		0.05			
Benthos	0.50			0.05	
Zooplankton		0.95	0.70		
Macro-algae					
Phytoplankton					1.00
Detritus				0.95	
Import					
Sum	1.00	1.00	1.00	1.00	1.00

to, for instance, “trawlers.” Next, click the “Landings” tab on the spreadsheet, and enter a landing of $0.05 \text{ t km}^{-2} \text{ year}^{-1}$ of piscivores; continue to the “Discards” tab and enter a discard of $0.3 \text{ t km}^{-2} \text{ year}^{-1}$ of macro-algae. Next, go to the “Discard Fate” tab on the “Fishery” screens, and specify that all the discards will go to the detritus box (i.e., enter 1.0 on the form).

You have now entered all the input parameters that are required for the model. You may notice on the “Basic input” form that all possible (i.e. not blocked as indicated with a yellow background color) input parameters have been entered for macro-algae, i.e., biomass (B), production/biomass (P/B) ratio and ecotrophic efficiency (EE). By entering all the basic input parameters, you are tweaking the Ecopath Master Equation (eqn. (2)). Whereas in most cases we seek to estimate either P/B (eqn. (4)) or EE (eqn. (5)), here we have for macro-algae entered as known EE , $M2$ (predation mortality), F (fishing mortality = catch/biomass), and P/B of eqn. (5), and the program will (to ensure mass-balance) instead estimate either the biomass accumulation (BA) or net migration term (NM) of eqn. (5).

The next step is to balance the model; select “Mass balance,” “Basic estimates” from the menu.

Having entered all basic input parameters for macro-algae will make EwE ask if you want to estimate BA for the group. You do, as macro-algae were being fished and discarded by the trawlers, and we expect their biomass to be declining in the base Ecopath-situation. This will open the results form, recognizable by the grid being red, and by parameters estimated through the Ecopath mass-balance calculations being shown in blue font.

In this example, the model balances as is. You can try, however, to see the impact of impossible or unlikely values, e.g. by going back to “Input,” “Basic input” on the menu, and change the biomass estimate for piscivores to 5 t km^{-2} . You will now get a warning that EE for small fish exceeds 1. Click the mortalities tab at the bottom. You can see that for small fish the instantaneous predation mortality rate is shown in red to indicate that it exceeds the total mortality rate. Click the “predation mortality” tab to see the breakdown of the predation mortality and it is clear that the problem with too high predation mortality is linked to the piscivores. No big wonder, we increased their biomass with an order of magnitude and this comes back now to haunt us. So, change the biomass for piscivores back to 0.5 t km^{-2} to re-balance the model.

When we next continue to the time-dynamic simulation model, Ecosim, it will pick up that there is a negative BA term for macro-algae. So, select “Ecosim,” “Start Ecosim” from the menu and enter a title for a scenario, e.g., “Base simulation.” Ecosim will save all parameters it requires for a run as part of this scenario and this way you can easily store alternative scenarios.

In Ecosim go to the “Run Ecosim” tab and click the “Run” command button, thus running Ecosim “as is,” i.e., with default parameter settings. The graph will show how biomasses are predicted to change relative to the Ecopath-baseline biomasses. You should see the biomass of macro-algae decreasing asymptotically. This is a consequence of us having “told” the model (by specifying a negative BA term) that in the baseline situation, the macro-algae were decreasing with a given rate.

Why don’t they just continue to extinction? The reason is that with the default parameter setting, there is assumed to be a density-dependent compensation for the producer group. As some are removed through fishing, those remaining get better conditions. You can change this prediction by going to “Ecosim,” “Group info” and change the assumption about “Max relative P/B ” for macro-algae from the default 2.0 to, e.g., 1.01, to indicate that there will not be any density-dependent compensation. Re-run Ecosim – and macro-algae will be heading toward extension.

What is then the “right” value to use for this parameter? Sorry, that is your problem; you are the one who needs to know what has happened with your groups in your systems, and I highlight this to strengthen what was stressed earlier: nothing substitutes data; at least not the kind of data that lead to knowledge.



In the simulation up to now (the “Base simulation”), only the macro-algae were impacted by the trawling; for the rest, a status-quo situation is predicted. We can modify this by invoking a process known as “mediation.” Mediation is here defined as a process where a group has a non-trophic impact on the trophic interaction of other groups in the system. In our case, the macro-algae serve as hiding places for small fish; they can hide for the piscivores and the squid that feed upon them.

Let us model this with a new scenario. Select “Ecosim,” “Load scenario” from the menu, and you will be asked if you want to save the scenario. Yes. Then enter a scenario title, e.g., “with mediation.”

Next, go to the “Mediation” tab in Ecosim. Click on the upper left plot (Mediation plot #1, MP1). Next, click “X-axis: Define mediating groups” and enter 1 (as a weight) for macro-algae. This defines the X-axis of MP1 as being the biomass of macro-algae. Next, change the shape of MP1 by clicking “Y-axis: Modify shape,” and enter 1 for “Y zero,” 0 for “Y end,” and then click “Sigmoid.” You should now have a sigmoid function similar to Fig. 6 defined.

We then have to define the Y-axis of MP1. Go to the “Apply FF” (for forcing functions, including mediation) tab. Click the colored cell indicating interaction between piscivores and small fish (column 1, row 2). On the “Apply FF and mediation functions” form that pops up, enter 1 for forcing function number, check “Mediation?,” and select the “vulnerability (v)” radio button. Close the form, and perform the same operation for the cell indicating interaction between squid and small fish.

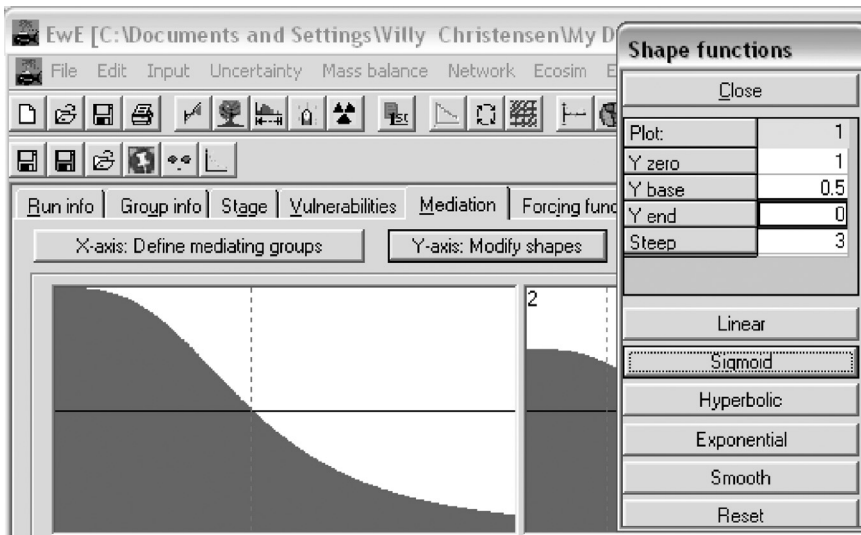


Figure 6: Screen shot from Ecosim showing a sigmoid mediation function that is used to impact the interaction between piscivores and their prey, small fish. The function is defined on the “Shape functions” accessible by clicking the “Y-axis modify shape” button. The “X-axis: Define mediating groups” button is used to define that the biomass of macro-algae is used as the one mediating. The stippled vertical line indicates the Ecopath baseline situation (and can be moved by clicking on the graph). Lower biomass of macro-algae will cause higher feeding interaction between piscivores and small fish, higher biomass lower.

We now have defined that if the biomass of macro-algae is lowered, there will be more interaction (higher predation rate) between piscivores and small fish, and also that this will lead to more predation by squid on small fish. Run the simulation again and see what happens now.

Macro-algae will decline as before; this will cause small fish biomass to go down because of increase predation from piscivores and squid. You can check that this is actually what is happening by clicking the “Plot” command button on the “Run Ecosim” form. Then select “small fish,” and see the plot with predation over time for the group. Next, the lower abundance of small fish causes their major predator, piscivores, to decline for lack of food, and the squid, which are released from the predation pressure caused by small fishes and which are losing a competitor in the form of the same group, increases their biomass.

To conclude, this simple model indeed demonstrates that trawl fisheries may cultivate the ground to improve the catches of squids. Let me stop by citing Keith Sainsbury as a good example of reversing common logic: “if you are considering a management intervention, and you cannot get it to work using a simple model, what is the chance that it will work in reality?”

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References

- [1] Beverton, R.J.H. & Holt, S.J., *On the Dynamics of Exploited Fish Populations*, Chapman & Hall: London, 1957; Facsimile reprint, 1993.
- [2] Walters, C.J. & Martell, S.J.D., *Fisheries Ecology and Management*, Princeton University Press: Princeton, 2004.
- [3] Christensen, V., Aiken, K.A. & Villanueva, M.C., Threats to the ocean: on the role of ecosystem approaches to fisheries. *Social Science Information*, **46(1)**, pp. 67–86, 2007.
- [4] Hilborn, R., Orensanz, J.M. & Parma, A.M., Institutions, incentives and the future of fisheries. *Philosophical Transactions of The Royal Society B – Biological Sciences*, **360(1453)**, pp. 47–57, 2005.
- [5] Pauly, D., *et al.*, The future for fisheries. *Science*, **302(5649)**, pp. 1359–1361, 2003.
- [6] Sumaila, U.R. & Pauly, D. (eds), *Catching More Bait: A Bottom-up Re-estimation of Global Fisheries Subsidies*, UBC Fisheries Centre Research Reports, Vol. 14(6), Second version, 2006.
- [7] FAO, *The Ecosystem Approach to Fisheries*, FAO Technical Guidelines for Responsible Fisheries, No. 4, Suppl. 2, FAO Fisheries Department: Rome, 2003.
- [8] Polovina, J.J., Model of a coral reef ecosystems: I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, **3(1)**, pp. 1–11, 1984.
- [9] Polovina, J.J. & Ow, M.D., *ECOPATH: A User’s Manual and Program Listings*, NOAA National Marine Fisheries Service Southwest Fisheries Center Honolulu Laboratory: Honolulu, HI, 1983.
- [10] Pauly, D., Soriano-Bartz, M. & Palomares, M.L., Improved construction, parametrization and interpretation of steady-state ecosystem models. *Trophic Models of Aquatic Ecosystems*,



- ICLARM Conference Proceedings No. 26., eds V. Christensen & D. Pauly, pp. 1–13, 1993.
- [11] Christensen, V. & Pauly, D., Ecopath II – a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, **61(3–4)**, pp. 169–185, 1992.
- [12] Christensen, V. & Pauly, D. (eds), *Trophic Models of Aquatic Ecosystems*, ICLARM Conference Proceedings No. 26, Manila, 1993.
- [13] Christensen, V., *Network Analysis of Trophic Interactions in Aquatic Ecosystems*, Royal Danish School of Pharmacy: Copenhagen, Denmark, 1992.
- [14] Ulanowicz, R.E., *Growth and Development: Ecosystem Phenomenology*, Springer Verlag: New York, 1986, reprinted by iUniverse, 2000..
- [15] Christensen, V. & Walters, C.J., Using ecosystem modeling for fisheries management: where are we? *ICES C.M.*, p. M:19, 2005.
- [16] Walters, C., Christensen, V. & Pauly, D., Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries*, **7(2)**, pp. 139–172, 1997.
- [17] Walters, C., *et al.*, Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems*, **3(1)**, pp. 70–83, 2000.
- [18] Walters, C., Pauly, D. & Christensen, V., Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems*, **2(6)**, pp. 539–554, 1999.
- [19] Plaganyi, É.E., Models for an ecosystem approach to fisheries. *GCP/INT/920/JPN: Capacity Building for an Ecosystem Approach to Fisheries*, FAO Fisheries Technical Paper, No. 477: Rome, 2007.
- [20] Christensen, V., Walters, C.J. & Pauly, D., *Ecopath with Ecosim: A User's Guide, November 2005 Edition*, Fisheries Centre, University of British Columbia: Vancouver, Canada, 2005.
- [21] Holling, C.S., The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canad. Entomol.*, **91**, pp. 293–320, 1959.
- [22] Walters, C.J. & Juanes, F., Recruitment limitation as a consequence of natural-selection for use of restricted feeding habitats and predation risk-taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **50(10)**, pp. 2058–2070, 1993.
- [23] Orpwood, J.E., Griffiths, S.W. & Armstrong, J.D., Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology*, **75(3)**, pp. 677–685, 2006.
- [24] Walters, C. & Christensen, V., Adding realism to foraging arena predictions of trophic flow rates in Ecosim ecosystem models: shared foraging arenas and bout feeding. *Ecological Modelling*, 209(2–4), pp. 342–350, 2007.
- [25] Wong, M.C., *et al.*, Behavioural mechanisms underlying functional response of sea stars *Asterias vulgaris* preying on juvenile sea scallops *Placopecten magellanicus*. *Marine Ecology-Progress Series*, **317**, pp. 75–86, 2006.
- [26] Finke, D.L. & Denno, R.F., Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia*, **149(2)**, pp. 265–275, 2006.
- [27] Harrison, S.S.C., Bradley, D.C. & Harris, I.T., Uncoupling strong predator–prey interactions in streams: the role of marginal macrophytes. *Oikos*, **108(3)**, pp. 433–448, 2005.
- [28] Beckerman, A.P., Petchey, O.L. & Warren, P.H., Foraging biology predicts food web complexity. *Proceedings of The National Academy of Sciences of The United States Of America*, **103(37)**, pp. 13745–13749, 2006.



- [29] Eklof, A. & Ebenman, B., Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, **75**(1), pp. 239–246, 2006.
- [30] van Baalen, M., *et al.*, Alternative food, switching predators, and the persistence of predator-prey systems. *American Naturalist*, **157**(5), pp. 512–524, 2001.
- [31] Yoshimura, J., *et al.*, The role of rare species in the community stability of a model ecosystem. *Evolutionary Ecology Research*, **8**(4), pp. 629–642, 2006.
- [32] Fox, J.W., Current food web models cannot explain the overall topological structure of observed food webs. *Oikos*, **115**(1), pp. 97–109, 2006.
- [33] Davoren, G.K., Montevecchi, W.A. & Anderson, J.T., Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Marine Ecology – Progress Series*, **256**, pp. 229–242, 2003.
- [34] Abrams, P.A. & Ginzburg, L.R., The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution*, **15**(8), pp. 337–341, 2000.
- [35] Walters, C. & Kitchell, J.F., Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, pp. 39–50, 2001.
- [36] Christensen, V. & Walters, C.J., Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, **172**(2–4), pp. 109–139, 2004.
- [37] Beattie, A., *et al.*, A model for the bioeconomic evaluation of marine protected area size and placement in the North Sea. *Natural Resource Modeling*, **15**(4), pp. 413–437, 2002.
- [38] Walters, C.J., Christensen, V. & Pauly, D., Searching for optimum fishing strategies for fisheries development, recovery and sustainability. *The Use of Ecosystems Models to Investigate Multispecies Management Strategies for Capture Fisheries*, eds T.J. Pitcher and K. Cochrane, Fisheries Centre Research Reports 10(2), pp. 11–15, 2002.
- [39] Christensen, V. & Walters, C.J., Trade-offs in ecosystem-scale optimization of fisheries management policies. *Bulletin of Marine Science*, **74**(3), pp. 549–562, 2004.
- [40] Ainsworth, C., Strategic marine ecosystem restoration in Northern British Columbia. *Resource Management and Environmental Studies*, University of British Columbia: Vancouver, Canada, 2006.
- [41] Booth, S. & Zeller, D., Mercury, food webs, and marine mammals: implications of diet and climate change for human health. *Environmental Health Perspectives*, **113**(5), pp. 521–526, 2005.
- [42] Coombs, A.P., *Marine Mammals and Human Health in the Eastern Bering Sea: Using an Ecosystem-based Food Web Model to Track PCBs*, MSc thesis, RMES, University of British Columbia, 2004.
- [43] Christensen, V. & Booth, S., Ecosystem modeling of dioxin distribution patterns in the marine environment (Chapter 6). *On the Multiple Uses of Small Pelagic Fishes: From Ecosystems to Markets*, eds J. Alder & D. Pauly, Report to the Pew Institute for Ocean Science, University of Miami, Miami, FL, 2006.
- [44] Morissette, L., *Ecosystem Models: Quality and Performance*, RMES, University of British Columbia, Vancouver, 2007.
- [45] Irwin, L.N. & Schulze-Makuch, D., Strategy for modeling putative multilevel ecosystems on Europa. *Astrobiology*, **3**(4): pp. 813–821, 2003.
- [46] Christensen, V. & Pauly, D., Flow characteristics of aquatic ecosystems. *Trophic Models of Aquatic Ecosystems*, eds V. Christensen & D. Pauly, ICLARM Conference Proceedings No. 26, Manila, pp. 338–352, 1993.
- [47] Christensen, V., Ecosystem maturity – towards quantification. *Ecological Modelling*, **77**(1), pp. 3–32, 1995.



- [48] Heymans, J.J., Shannon, L.J. & Jarre, A., Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s. *Ecological Modelling*, **172(2–4)**, pp. 175–195, 2004.
- [49] Brando, V.E., *et al.*, Assessment of environmental management effects in a shallow water basin using mass-balance models. *Ecological Modelling*, **172(2–4)**, pp. 213–232, 2004.
- [50] Villanueva, M.C., *et al.*, Comparative analysis of trophic structure and interactions of two tropical lagoons. *Ecological Modelling*, **197(3–4)**, pp. 461–477, 2006.
- [51] Heymans, J.J., Guénette, S. & Christensen, V., Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. *Ecosystems*, **10(3)**, pp. 488–502, 2007.
- [52] Sainsbury, K.J., Campbell, R.A. & Whitelaw, W.W., Effects of trawling on the marine habitat on the North West Shelf of Australia and implications for sustainable fisheries management. *Sustainable Fisheries through Sustainable Habitat*, ed. D.A. Hancock, Bureau of Rural Sciences Proceedings, AGPS: Canberra, pp. 137–145, 1993.

