The early development of Ecosim as a predictive multi-species fisheries management tool

KERIM AYDIN[1] AND NANCY FRIDAY[2]

[1]*School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 9818*
Contact e-mail: kerim@u.washington.edu
[2]*National Marine Mammal Laboratory, AFSC, 7600 Sand Point Way NE, Bldg. 4, Seattle, WA 98115, USA*
Contact e-mail: Nancy.Friday@noaa.gov

ABSTRACT

Ecosim is a recent addition to the family of surplus production fisheries models, and its multi-species nature raises the prospect of Large Marine Ecosystem (LME) management on the basis of predator/prey relationships. In particular, Ecosim appears to offer the promise of improved prediction of predator manipulations and their effects on exploited stocks, including the effects of removing a top predator from an ecosystem.

The development of Ecosim represents a considerable addition of the theory of predator/prey relationships in LME ecology; however, at present, it is an untested model in the management arena. In particular, the sensitivity of Ecosim to assumptions about energy dissipation, respiration, and top-down vs. bottom-up control may lead to models which predict the unrealistic sustainability of dangerously high fishing levels. This is not a problem with the model theory but its application: at present, little substantive work has been done to bring the statistical calibration of Ecosim parameters to the level of other fisheries models. As an example, a preliminary examination of Ecosim's sensitivities to assumptions about animal energetics is presented here.

Currently, Ecosim's primary role in ecosystem management is in exploratory analysis and developing the precautionary principle of ecosystem manipulations, and as such it shall continue to play a valuable role in increasing the understanding of ecosystem interrelations. However, in its current state of development, its results should not be used as a predictor for establishing large scale predator/prey manipulations as fisheries policy.

KEYWORDS: *MULTISPECIES FISHERIES MANAGEMENT; LARGE MARINE ECOSYSTEMS (LMES); FOOD WEB THEORY; BIOMASS DYNAMICS MODELS; SURPLUS PRODUCTION; BIOENERGETICS; ECOPATH; ECOSIM; TOP-DOWN; BOTTOM-UP; PREDATOR CONTROL.*

INTRODUCTION

"It is useful to test prospective management strategies against ecosystem models: if they don't work on simple models why should they work in reality" *Keith Sainsbury (ICES/SCOR Conference, Montpellier March 1999)*

A mandate for applying ecosystem management to Large Marine Ecosystems (LMEs) may be approached from two distinct and disparate angles.

First, the mandate may be taken as an extension of the precautionary principle in fisheries. This extension begins by noting that, in catching a species which is also consumed by a predator, the fishery has an effect on that predator. Furthermore, if the predator is also part of a fishery, the expected yields of the two fisheries managed will be higher than the actual sustainable yield of the two species, especially when large-scale environmental variability is taken into account. Viewed from this context, the continued data collection and exploration of predator/prey relationships, and their variability through time, may be greatly aided by the creation of quantitative food web models.

On the other hand, ecosystem management may be approached with a view towards tightening overall human control over the ecological interrelationships in the system. If a desired species (in terms of fisheries yield) is to be exploited in the maximum possible sustainable way, does it not make sense to remove any potential predators and competition? In the past, as is well-documented, many attempts to extend control have led to unexpected and occasionally disastrous consequences.

As our knowledge of LME ecological interactions increases, and the extent of our data collections extend in time and space, it is tempting to seek out potential yield improvements by simulating ecosystem control manipulations using newer and better-calibrated models. In the general sense, researchers should not be biased against such use of models. After all, if we believe a model when it warns us of danger, should we not also believe it when it suggests increased benefit through a manipulation? However, a first step, in all cases, must be a substantial evaluation of the predictive tools under consideration.

Ecopath (Polovina 1985; Christensen and Pauly 1993; Pauly et al. 2000), and its dynamic offshoot, Ecosim (Walters et al. 1997; Walters et al. 2000), is a relatively young ecosystems analysis tool (see the website http://www.ecopath.org for information and literature and the most recent freely-available model implementation). It has gained broad recognition as a tool for assembling and exploring data on marine food webs and currently over 100 food web models have been built using Ecopath as a tool.

Under the precautionary approach to ecosystem management, Ecopath allows investigators, by pulling together single-species data resources into a coherent food web, to perform exploratory data analysis on an ecosystem using a common framework. Uses of this exploratory analysis include comparing the food web of an ecosystem before and after fisheries manipulations (Pauly et al. 1998a), or using an ever-increasing collection of other Ecopath models to discover trends in human uses of LMEs that extend across the world (e.g. fishing down the food web, Pauly and Christensen 1995; Pauly et al. 1998b). Further, Ecopath and Ecosim may both serve as a first-order perturbation analysis, capable of answering questions, given *good* data, on which species are strongly linked to each other, are poorly understood keystone species, or are the most likely to change under specific manipulations.

Under the second, manipulative approach to ecosystem management, Ecosim is a dynamic, biomass-driven predator/prey surplus production model. Like single-species models before it, it projects the time trajectories of populations under differing management scenarios. It provides basic estimates of the sustainable yields (surplus production) which may be expected out of a species or group of species. Further, its projections provide, at a first glance, a fairly straightforward answer to questions like “if we remove marine mammals from an ecosystem, should we expect greater yields of fish?”

There is no theoretical reason why Ecosim should be poor at answering such questions, or at least poorer than many other models currently in use or development. Some of the criticisms of Ecosim; for example, are that it is an overly-stable equilibrium-based model, but such criticism misses the point. Ecosim, and the population production theory behind it, is in its own way no more or less complex than other fisheries management models. All such models have implied equilibrium points, species carrying capacities, and underlying model dynamics which cause them to differ from the reality, especially in the far-from-equilibrium hinterlands of extreme real world overfishing and depensation. Ecosim is not meant to be a detailed small-scale biophysical process model: its proper context for comparison is with other fisheries models currently in use.

The most important challenges facing Ecosim lie not in challenging detailed process models, but in comparison with these other relatively ‘simple’ fisheries population models. ‘Simple’ is used here to suggest the simplicity of the theory underlying the population dynamics, not the statistical procedures for calibrating the models: many fisheries models in current use are simple in their development of the dynamic theory of marine population behavior, while possessing extreme sophistication in the statistical analysis of their parameters.

To that end, there are at least two areas in which Ecosim must be carefully explored before it should be used as a predictive tool.

First of all, it is a relatively young model, and the ‘Arena’ predator/prey models that have been developed (Walters et al. 1997) as extensions to Lotka-Volterra predator/prey theory have not been examined to their full extent. Specifically, the parameter space of the models have not been explored in simple cases. Ecosim is built by default from a fully developed Ecopath food web model which may contain 20-50 species. It is possible that some pathological behavior of the model in certain parameter spaces may be cloaked by the complexity of interactions occurring in the larger models: Ecosim must perform reasonably well in the simplest of food chains before it is extended to a full web.

Moreover, even as these Ecosim formulae become more accepted as a method of modeling predator/prey dynamics, it should be realized that *Ecopath and Ecosim, like any other fisheries model*, may contain between 5-10+ parameters *per modeled species*, or 100-200+ parameters overall. The “out-of-the-box” Ecosim software contains many pre-set parameters. Although the parameters may be changed within the software, the current implementation is not meant to serve as an in-depth statistical tool for examining the parameter sensitivity of these models. Ecosim is a step forward, but it does not remove the need for statistical savvy in interpreting its results.

The quotation that begins this article points to the first and strongest argument for bringing Ecopath-style models into precautionary fisheries management. If a simple model confirms that we can get more out of a system than goes in, we take away a valuable lesson. However it is important to realize that these “simple” models, if built on the scale of an ecosystem, contain components and interactions that must be built, examined, and assembled piece by piece. It is a mistake to assume that by starting with a holistic, large-scale model, that each internal piece functions correctly, and that individual errors cancel each other out. It may be difficult to remember this if the first rounds of holistic results confirm some of our intuitive understandings of the ecosystem in question.

In designing any specific instance of a particular type of model, even a simple one, it is useful to begin with the simplest set of assumptions about limited pieces of the model, and build outwards, assuring that each piece functions as necessary. The Ecosim software, by starting with a complex food web model built through Ecopath, does not directly encourage such development. However, it is possible to take a step back and examine Ecosim as it functions for a simplified ecosystem; in this case, for a simple, linear food chain. It is possible to use simple comparisons with other models to gain insight into a model’s function.

In this case, we examine Ecosim’s prediction and estimation of the holy grail of fisheries management, Maximum Sustainable Yield (MSY), in comparison with the simplest of single-species models, the logistic (r-K) model. In doing so, we hope to focus on the function, sensitivities, and data explorations that will be eventually required to make Ecosim into a working ecosystem management tool.

METHODS-A BASIS FOR COMPARISON

For this experiment, we implemented a three compartment linear food chain with fixed primary production, shown in Figure 1. The biomasses of each box are normalized with respect to their carrying capacity: the production rates are typical of the order of magnitude found in temperate LMEs. In particular, the total natural mortality rate of the commercial fish species is 1.0/year in its virgin state: this is similar to many larger commercial fish species. 10% of the energy entering one trophic level passes onto the next trophic level.

This model is used in a simple experiment. Ecosim is a biomass-dynamics model extended to multiple species. The simplest single-species biomass dynamics model, the logistic model, formed the historical basis for developing the concept of maximum sustainable yield (MSY) based on the "intrinsic" growth rate (r) and carrying capacity (K) of the species.

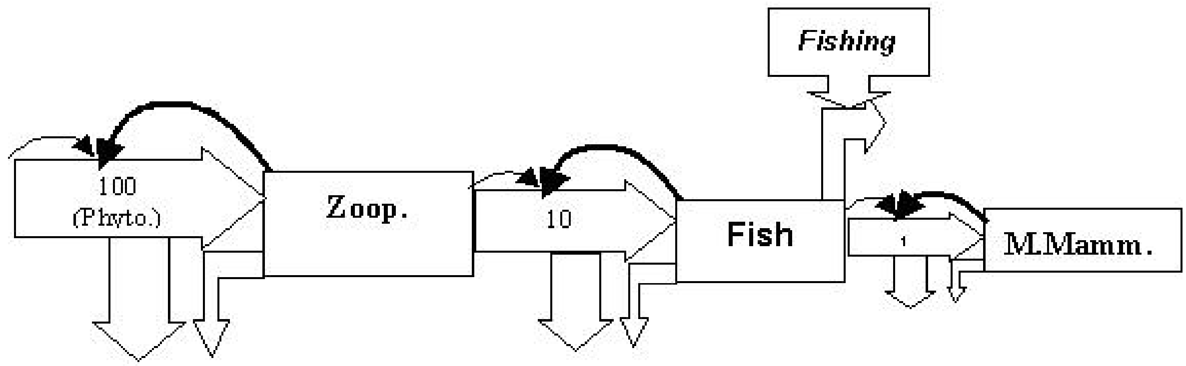

Figure 1. A simple 3 compartment model implemented in Ecosim. Arrows are described in the text.

The primary control factor for the experiment is fishing commercial fish, as shown in Figure 1. For testing the model, this fishing rate F (here assumed identical to fishing effort) is set at progressively higher values, and the model is allowed to come to an equilibrium biomass (B_{eq}) after each change of F. The equilibrium catch (C_{eq}) is plotted as a function of the equilibrium biomass. The plot will peak between the lowest and highest fishing rates at the MSY of the commercial fish (Figure 2).

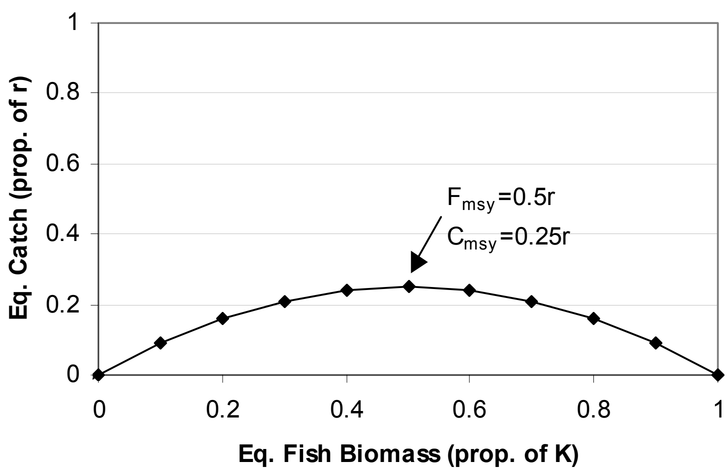

Figure 2. Catch as a function of equilibrium Biomass at differing constant fishing efforts (F), showing the fishing effort at maximum sustainable yield. The model assumes unchanging prey resources or predator populations, and a logistic model of production.

While the r-K logistic model is overly simplistic in itself, it is well-analyzed, and tellingly forms the basis of a widely-held general image of MSY as shown in Figure 2. In the original logistic model, r and K encompass predator/prey and other ecological interactions. The MSY for commercial fish in the logistic model occurs at the point where the equilibrium Biomass (B_{eq}) is equal to half the initial carrying capacity, or 0.5K (Hilborn and Walters 1992). If K is normalized to 1, the actual yield at MSY is 0.25r, and fishing effort required to maintain it is 0.5r.

More complex age-structured models may shift the values of F, and shift B_{msy} to the right or the left in Figure 2 or raise the level of C_{msy} or F_{msy} (Hilborn and Walters 1992). The values of F_{msy}, C_{msy}, and B_{msy} shown in Figure 2 will form the basis of comparison with the Ecosim model. Since r changes for a species in Ecosim with prey populations, the results will be normalized to r at K (r_0), or the gross per-biomass production of a species near carrying capacity. Progressively set fishing effort will be used to plot B_{eq} vs. C_{eq} and find B_{msy} and F_{msy}. This exercise was repeated while varying two sets of parameters for each of zooplankton, fish, and marine mammal groups.

Two parameters were tested for sensitivity for each of the three compartments on the food chain: the nonlinear top-down predator control (heavy curved arrows in Figure 1) and the balance of loss between active and passive metabolism (downward block arrows in Figure 1). Numbers in boxes are total mortality rates of prey in each predator/prey link. Fishing is the driving control for this experiment.

The first parameter, top-down predator control for a given predator/prey link, also called the prey "vulnerability" to predation, has received the most attention in Ecosim literature (e.g., Walters et al. 1997) and indeed, some first-order fitting routines for calibrating these values have been included in the most recent distributions of the software. This parameter is scaled between 0.01 (weak top-down control) and 1.0 (strong top-down control) with a default "mixed" control case occurring at 0.30 (the scale is logarithmic).

The second parameter is in reality a combination of two parameters from Ecopath itself: growth conversion efficiency (GE) of a predator and "other" mortality (1-Ecotrophic Efficiency, EE). Ecotrophic Efficiency is used as the primary "mass-balance" term in the Ecopath model, and reflects the difference between estimated production rates of a prey and consumption rates of a predator and fisheries, after GE loss (1-GE) is subtracted from prey production. Ecopath literature suggests that a "true" EE value of 0.80 for zooplankton, and 0.90 for higher trophic levels is appropriate, and GE levels of 0.01-0.50.

However, Ecosim itself uses this apportionment of loss between (1-GE) and (1-EE) to set the difference between active metabolism + loss (proportional to consumption) equal to the GE respiration loss of Ecopath, and passive metabolism + loss (proportional to biomass) equal to the (1-EE) loss in Ecopath, thus making the tool for measuring population mass-balance into a measure of the individual mass-balance of bioenergetics. For example, an EE of 0.90 and a GE of 0.10 implies, when translated into Ecosim terms, that 89% of energy lost by fish is proportional to their consumption, with only 1% lost in proportion to biomass (and the remaining 10% being passed on to the next trophic level). The implication here is that an animal could reduce its "metabolic cost of living" by 89% by ceasing to feed: in reality, passive (biomass-proportional metabolic loss, including reproduction) should be much more important.

It should be emphasized that this "error" may be corrected using simple accounting tricks in moving from Ecopath to Ecosim: it is possible to adjust the dynamic loss terms to reflect true, metabolic costs. However, the data to perform such calibration is difficult to obtain; more importantly, this operation is a "hidden" aspect of the model that has not been explored. To examine it here, the results of MSY are tested for sensitivity to a single parameter combining the two described above: this parameter is simply the proportion of metabolic + unexplained losses that are apportioned to passive vs. active metabolism.

The parameter space suggested above, by the set of two parameters for each species, will be examined in scenarios where both marine mammals and commercial fish are caught. In particular, we shall focus on the question: is it possible, using reasonable sets of parameters, to:

(a) Find a situation where fishing marine mammals improves fish yield (dominant top-down control).
(b) Find a situation where fishing marine mammals does not improve fish yield, but catching commercial fish hurts marine mammals (dominant bottom-up control).

The danger here is evident: if a hypothetical fishery is managed by removing marine mammals and expecting scenario (a), while in reality the "true" parameters favor scenario (b), one could easily harm the marine mammal population in two ways (fishing + removal of prey) while overfishing the commercial fish. Quite simply, it is important to examine your models to determine how much certainty you have about the world that you are in.

The model was implemented in C++ and Visual Basic using the Ecosim equations published in Walters et al. 1997 and code provided by Carl Walters and modified for parameter analysis by the primary author (K.A.). The complete equations and analysis of this Ecosim model's parameters is presented in Aydin (MS in prep.).

RESULTS

A few adjustments to the initial model of Figure 1 were required to examine the marine mammal/fish interaction: specifically, an additional constant food source for marine mammals, in addition to the commercial fish in the model, was necessary to stabilize the fish/marine mammal interaction. The extra import of marine mammal food was set so the complete elimination of the commercial fish was required to cause the complete elimination of the marine mammal population. This adjustment, as well as results in addition to those presented here, are discussed in greater detail in Aydin (MS in prep.).

Of the parameters tested overall, MSY, B_{msy} and F_{msy} was fairly invariant to changes in the parameters governing relationships between marine mammals and commercial fish. The two parameters with the strongest effect were the bottom-up parameters: the vulnerability of phytoplankton to zooplankton, and the proportion of active vs. passive metabolism occurring within zooplankton.

Figure 3A shows the changes in predicted MSY for commercial fish for the base case used in the model, and with an increase and decrease in the phytoplankton/zooplankton vulnerability. First of all, the "base case", (heavy lines in Figure 3A) as suggested by Ecosim defaults, occurs with "equally mixed" top-down and bottom-up relationship between phytoplankton and zooplankton (vulnerability=0.3) Compared with the logistic model, the MSY occurs at an equilibrium biomass B_{msy} of 18% of carrying capacity K compared to the B_{msy} at 50% of K in the logistic model (Figure 2). The fishing effort at MSY for this model is equal to $4.5r_0$ as opposed to $0.5r_0$ in the logistic model, as the per-biomass growth rate r of fish increased as commercial fish were fished down. The catch level $C_{msy}=0.7r_0$ is significantly higher than that of the logistic model where $C_{msy}=0.25r_0$.

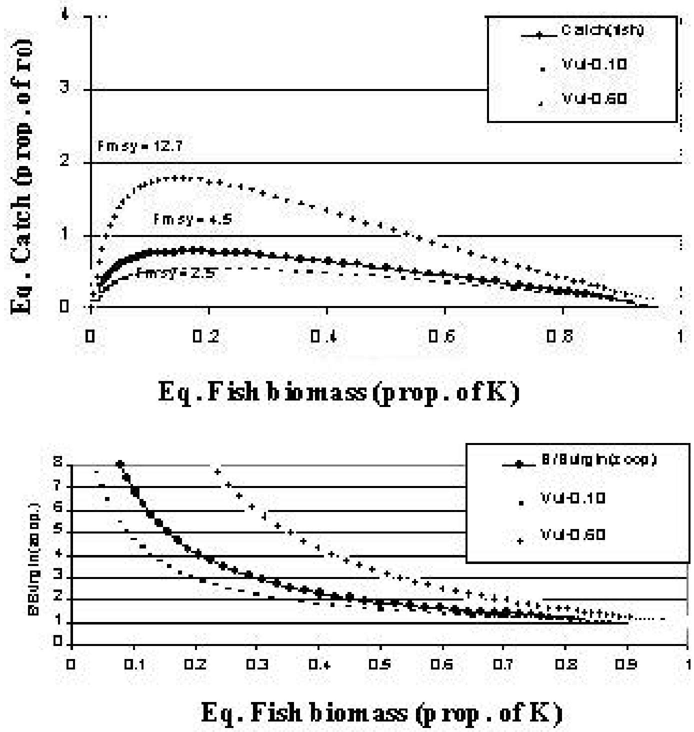

Figure 3. A. Equilibrium catch as function of equilibrium biomass for increasing fishing effort F. F values indicate fishing effort at MSY. Dark circles: "base case" in model. '+' symbols: phytoplankton/zooplankton vulnerability=0.60. '-' symbols: phytoplankton/zooplankton vulnerability=0.10.
B. Equilibrium zooplankton biomass as a function of equilibrium fish biomass for the three model runs in A.

This change in fish growth is due to the release of zooplankton, and as such is governed by the ability of zooplankton to increase their consumption of phytoplankton as mortality pressure on zooplankton decreases. If zooplankton exert strong top-down control on phytoplankton (phytoplankton/zooplankton vulnerability=0.6 as opposed to 0.3 in the base case), they are able to grow to proportionally higher levels as fish are removed from the system ('+' symbols in Figures 3A and 3B). In this case, the catch at MSY increases, but the B_{msy} is lower and requires a greater fishing effort to remove: in other words, in this case, fishing this system extremely hard (F near 12) would greatly increase the foraging opportunities of the remaining fish. Reducing phytoplankton/ zooplankton vulnerability to 0.10 has the opposite effect ('-' symbols in Figures 3A and 3B).

In the base case of Figure 3A, 89% of energy consumed by zooplankton leaves zooplankton as active metabolic loss, or proportional to its consumption of zooplankton. 10% of energy is passed to fish, while the remaining 1% is passive loss, proportional to zooplankton biomass. This represents a growth efficiency (GE) of 11% and an EE of 0.90, as is often suggested as a maximum top-down balancing default (with a 'typical' suggested value between 0.8 and 0.9).

Figure 4A again shows this base case, and then the change in the yield curve as the zooplankton respirative loss is shifted from active to passive. Case 1 is shown in which active metabolism is 80% and passive metabolism is 10%, corresponding to an EE of 0.5 for zooplankton. Case 2 is shown in which active metabolism is 70% and passive metabolism is 20% (EE=0.33).

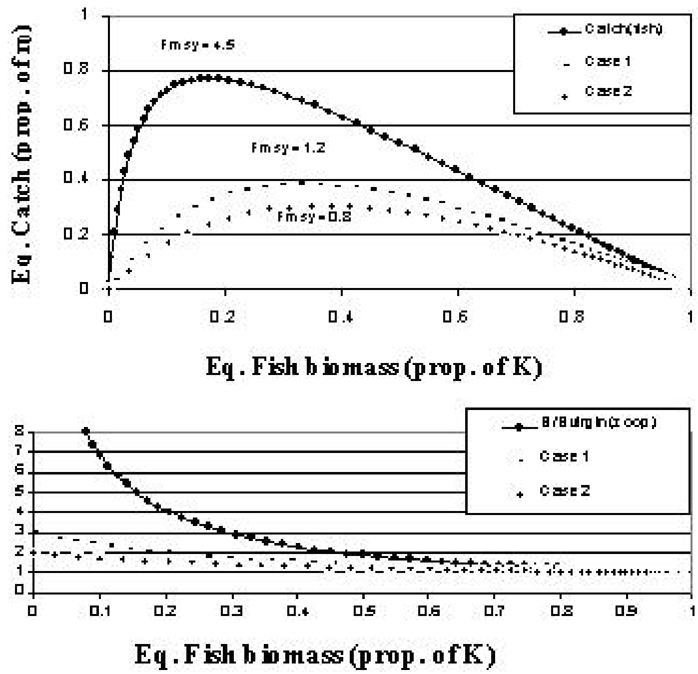

Figure 4. A. Equilibrium catch as function of equilibrium biomass for increasing fishing effort F. F values indicate fishing effort at MSY. Dark circles: "base case" in model: zooplankton dissipation 89% active/1% passive (EE=0.90). '-' symbols: zooplankton dissipation 80% active/10% passive (EE=0.50).. '+' symbols: dissipation 70% active/30% passive (EE=0.33) The remaining 10% of energy is passed to commercial fish in all scenarios.
B. Equilibrium zooplankton biomass as a function of equilibrium fish biomass for the three model runs in (A).

As the passive metabolism becomes greater and zooplankton loss as a proportion of its biomass increases, the loss serves as a stabilizer and prevents the zooplankton population from growing without bound (Figure 4B). As a result, the compensatory response of the commercial fish to fishing is drastically reduced. For Case 1, B_{msy} occurrs near 0.3K with a F_{msy}=1.2r_0, while for Case 2, B_{msy}=0.4 and F_{msy}=0.8r_0, which is very similar to the results of the initial logistic model.

Returning to the base case, removing marine mammals from the system via fishing did not greatly change the B_{msy} of C_{msy} of commercial fish, although it did substantially increase fish carrying capacity (Figure 5A). This result comes about as the actual production of fish remains set at the zooplankton level regardless of predation. However, if the zooplankton compensatory response is turned down as in Case 1 (Figure 4), removing marine mammals increases the commercial yield of fish, and also increases B_{msy} by more than 50% (Figure 5B).

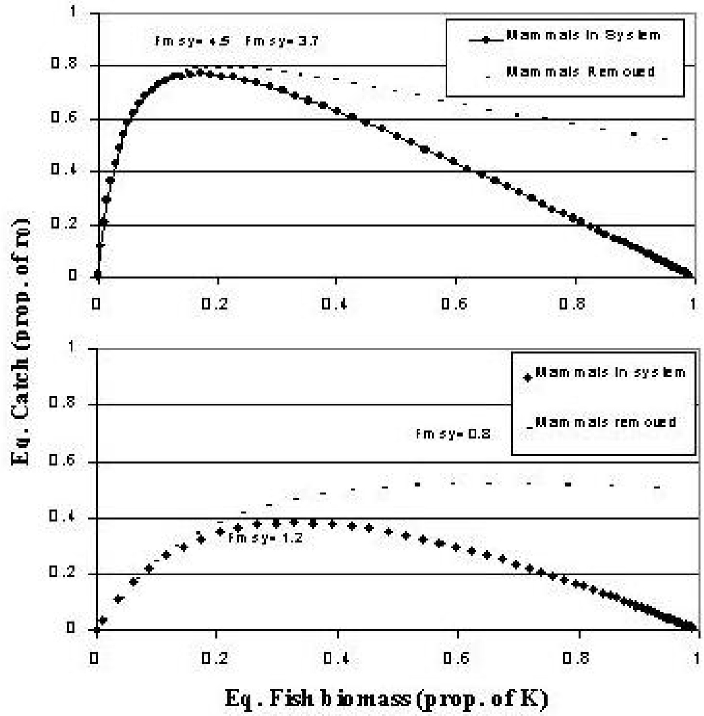

Figure 5. A. Commercial fishing in the base case both before and after removal of marine mammals; **B.** Commercial fishing in Case 1 (Figure 4) both before and after the removal of marine mammals.

DISCUSSION

Even with strong "top-down" vulnerabilities set in the model, bottom-up forces tended to dominate this model. The most important sensitivities determining MSY in the fish population came from changes in the bioenergetics of zooplankton (Figures 3 and 4); in other words, the apportionment between active and passive metabolism on the zooplankton level. While eliminated marine mammals from the ecosystem increased the carrying capacity for commercial fish, it did not increase the MSY appreciably (Figure 5), although it increased the B_{msy} in cases where zooplankton compensation was weak (Figure 5B). The removal of commercial fish resulted in decreased food for marine mammals except in cases where the marine mammals were buffered with "outside" prey sources.

The results presented here are limited, but illustrate the importance of a few metabolic/life history parameters on setting the behavior and predictions of Ecosim with respect to fishing. Generally, the balance between types of metabolism (active vs. passive) can greatly affect the predicted maximum sustainable yields of stocks. In particular, some of the default parameters in Ecosim lead to extreme overcompensation and the prediction of MSY at fishing rates which are perhaps unreasonably high. Additionally, the zooplankton metabolic link can affect the results of removing marine mammals: in other words, unless the model is correctly calibrated to zooplankton respiration, it may not be possible to tell if the "real" results of marine mammal removal will be as in Figure 5A or 5B.

This model behavior may be masked in a more complex food-web, such as those which are the results of many "real" Ecopath models. In particular, the over-increase of prey shown here as a fish is removed from a system may be "soaked up" by the fish's competitors, and may ultimately lead to predictions of overly high fishing rates for their competitors, or (if the competitors are not fished), an unrealistic maintenance of a top predator as one of its prey items is removed.

These results should not be taken as criticism of the Ecosim model or theory itself, but rather, simply lead to the results from these models being treated with the caution applied to all models: the results should neither be thrown out nor completely believed (Figure 6). Rather, the results should be subjected to continued and rigorous testing. In terms of predictive modeling, there are two distinct steps that should be taken to make Ecosim into a full-fledged management tool.

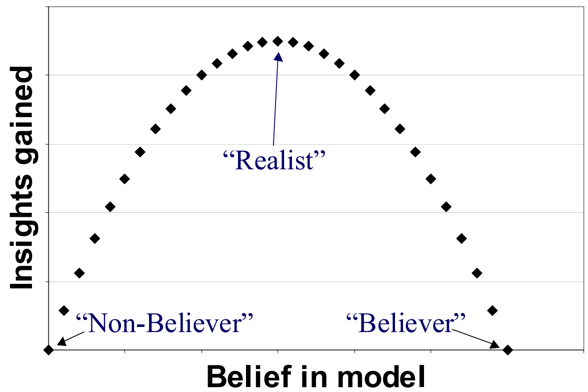

Figure 6. Learning from a model. There is a Maximum Yield to learning from a model, which lies somewhere between full belief and full skepticism.

To begin, examination of this model must merge individual mass balance models (bioenergetics) with population mass-balance (Ecopath). The development of marine animal energetics has been a key advance in fisheries science in the last 20 years: the results here show the critical importance of understanding sources of metabolism and correctly modeling fish energetics.

Furthermore, these results point to the continued importance of exploring empirical predator/prey interactions (especially through long-term food habits studies) to calibrate these interactions on an individual and population scale. Data, especially on diet and growth rates of fished species, is available in increasing quantities in many ecosystems, and could be put to good use.

More generally, the next step in establishing Ecosim as a predictive ecosystem management tool should be the implementation, by independent researchers, of the equations in a way that allows data assimilation into statistical parameter analyses for each Large Marine Ecosystem under consideration. The exploratory and educational nature that gives the current Ecopath with Ecosim software its power is not useful for such an exploration. Many fisheries models in use today contain 100+ parameters used for calibration: the existence of such a large parameter space does not degrade the utility of a model, but it points to the danger of accepting an uncalibrated one. The statistical standards for all developed fisheries models should be as high as the data allows.

Ecopath may or may not be a success in the establishment of sound ecosystem management: like all tools, it depends on how it is viewed and used (Figure 6). One of Ecosim's primary niches will continue to derive from developing the precautionary concept; in particular, it can show us where particular diet and predator/prey interactions may increase the sensitivity of a species to perturbation, or it can pinpoint environmental effects in cases where sudden changes in many fish populations cease to fit previously-measured predator/prey relationships. The theory of Ecosim is a sound development of predictive predator/prey theory and should be thoroughly explored. Extending that exploration through the combined use of general exploration with the current tools and extended data analysis through future tools can only increase Ecosim's utility to ecosystem management.

REFERENCES

Aydin, K.Y. MS in Prep. Reconciling individual and population scale mass-balance: bioenergetics and Ecopath/Ecosim.

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

Hilborn, R. and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment. Chapman and Hall, New York. 570p.

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

Pauly, D., T.J. Pitcher and D. Preikshot (Editors). 1998a. Back to the Future: Reconstructing the Strait of Georgia Ecosystem. Proceeding a of Workshop held at the First Nation House of Learning, University of British Columbia, Vancouver, B.C. November, 21-22, 1997. Fisheries Centre Research Reports 6(5), 99 p.

Pauly, D.; Christensen, V.; Dalsgaard, J.; Froese, R.; Torres, F., Jr. 1998b. Fishing down marine food webs, Science 279: 860-863.

Pauly, D., V. Christensen, and C.J. Walters. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. of Marine Science 57: 697-706 (available online at www.idealibrary.com as doi:10.1006/jmsc.2000.0726).

Polovina, J.J. 1985. An approach to estimating an ecosystem box model. U.S. Fish Bull. 83(3): 457-460.

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

Walters, C.J., J.F. Kitchell, V. Christensen and D. Pauly. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: Ecosim II. Ecosystems 3: 70-83.