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COMPUTER MODELLING OF MARINE ECOSYSTEMS

Applications to Pacific Salmon Management and Research

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LIST OF ABBREVIATIONS

AFMA	Australian Fisheries Management Authority
AFSC	Alaska Fisheries Science Center
AIET	Aleutian Islands Ecosystem Team
AIME	Aleutian Islands Marine ecosystem
CCAMLR	Convention for the Conservation of Antarctic Marine Living Resources
CGLRM	Council of Great Lakes Research Managers (Canada-US)
CSIRO	Commonwealth Scientific and Industrial Research Organisation (Australia)
DFO	Department of Fisheries and Oceans (Canada)
EwE	Ecopath with Ecosim
FMP	Fishery Management Plan
GLFC	Great Lakes Fishery Commission (Canada-US)
IAGLR	International Association of Great Lakes Research (Canada-US)
IATTC	Inter-American Tropical Tuna Commission
MSE	Management Strategy Evaluation
NEMURO	North Pacific Ecosystem Model for Understanding Regional Oceanography
NMFS	National Marine Fisheries Service (US)
NOAA	National Oceanographic and Atmospheric Administration (US)
NPFMC	North Pacific Fishery Management Council (US)
NZMoF	New Zealand Ministry of Fisheries
PPA	Primary Production Anomaly
SS	Sum of Squared differences
SSSAM	Single Species Stock Assessment Model

EXECUTIVE SUMMARY

Fisheries ecosystem modelling could be a useful tool to complement present approaches to salmon research and management on Canada's west coast. Ecosystem modelling refers to a computer application that simulates, through time, biological changes such as biomass, mortality, catch, feeding and competition in managed species. The models emulate such changes by considering factors like environment, predation, competition or fisheries effects. Because these models capture both ecosystem and species changes over time, they offer a potential guide to future changes.

This study examines ecosystem modelling and its relevance to fisheries management and research, and concludes that ecosystem modelling should be implemented alongside current salmon research and management techniques. To illustrate, a simple ecosystem modelling exercise using the Strait of Georgia displays the capabilities of ecosystem modelling.

The conclusion that ecosystem modelling be put into use for west coast salmon management is supported by three key facts. First, ecosystem modelling has developed into a discipline widely used by the research community. Second, British Columbia currently has local fisheries ecosystem models and model development taking place. Finally, fisheries ecosystem models are already in use by other jurisdictions to formulate research and management strategy.

INTRODUCTION

Simulation models of Pacific Ocean ecosystems can be applied to help develop management plans and research programs in order to conserve Canada's west coast salmon stocks. The use of ecosystem models to provide context for both researchers and management has already begun in other jurisdictions, e.g., Alaska (AIET 2007) and Australia (Fulton *et al*. In Press). For Canada, such modelling research can provide the basis upon which realistic and attainable targets are defined for sustainable harvest and recovery of salmon populations. A further benefit of using such models is to enable comparisons and trade-offs in different salmon management strategies to foster the development of policies that account for both biological and social needs within a realistic physical locale. Lastly, the use of ecosystem models fosters the development of ecosystem, rather than single species, indicators: a prerequisite for a true ecosystem-based management approach.

Crude and simplistic ecosystem models have been used as ways to conceptualise fundamental ecosystem principles for decades. Many readers will be familiar with the often seen 'food chain' or 'food web' illustrations in biology textbooks. These diagrams were products of early work seeking to understand how energy, i.e., food, is moved around in ecosystems. Thus, from the beginning of ecosystem modelling, the first question was: how do you define who eats who, with fisheries usually considered as a predator. Because early modellers (before the availability of both personal computers and the internet) were beset by limitations in computing power and a relative inability to share information, their models were often highly aggregated with species groups like 'top predators' or 'primary producers'. Further, most of these models were static acting merely as a snapshot of what was known about an ecosystem at a particular time.

WHAT IS AN ECOSYSTEM MODEL?

For the considerations of this paper, the term ecosystem model refers to a computer application that examines aquatic ecosystems with the ability to simulate, through time, biological changes in managed species, e.g., biomass, mortality, catch, feeding and competition, as influenced by, e.g., environment, predation, competition, fisheries, or some combination of such mechanisms. Crucial to this approach is the question of capturing ecosystem and species changes over time which suggests that these models not only reproduce changes in the past but also provide a guide to potential future changes. Starting from a know situation and based on updated information when required, the model can explain and predict what happens in the real world and support management decisions. The resulting system is "ecosystem-based" fisheries management. Also of significance is the ability to have the model resolve changes in particular species (and even life-history stages) thus providing a platform for truly managing species within an ecosystem context. Lastly, it must be remembered that managing the ecosystem *per se* is beyond current ambitions: it is fisheries and other economic/ social activities that are to be managed with the result of helping achieve targets within an ecosystem framework. Engaging ecosystem models would be a crucial part of placing these activities and their attendant effects on individual species in the context of their ecosystem and its constraints.

THE NEED FOR ECOSYSTEM MODELLING

The historic adoption of single-species management in many fisheries was an appropriate reflection of the best available contemporary biological science. The result, though, was research and management focused on life-history characteristics and behaviour of individual species. This work was typically done by groups of scientists and managers dedicated to one particular species, or even a particular stock. The goal of these species or stock teams would often be to achieve some sort of target to maximise a biological, economic or social aspect of that fishery, e.g., maximum sustainable yield. It is easy to see that by adopting such a framework it might be difficult for any particular species team to recognise that there may be limits on the capacity of the environment to provide maximum sustainable yield for *all* species or stocks at the *same* time. Furthermore, because each team would be focussed on managing its fishery to provide something to a community of users it would have been impossible to see trade-offs such as restricting 'their' fishery to provide a larger net benefit to all other fishers, or groups using that ecosystem. In the same manner it would have been difficult for such groups to explicitly account for effects like competition and predation between the species they were managing either in real time or as future projections.

A growing body of research has revealed the importance of ecosystem considerations such as interactions with other fish(ed) species, competition for prey species, mortality from predation, and environmental conditions. Towards understanding salmon biology the focus on stocks helped to emphasise the study and management of salmon during, or near to, their fresh water life-history phases. This resulted in a relative paucity of knowledge about what happened to many salmon once they entered the ocean environment. However, the migratory nature of salmon in the ocean and the continued inability of single-species management regimes to accurately forecast or anticipate salmon returns with sufficient accuracy have sparked interest in alternative approaches. This has been amplified by the desire to also account for changes in species other than salmon, e.g., forage species and marine mammals, which both influence, and are influenced by, changes in salmon populations and attendant management actions.

In a mechanistic sense many of these questions are related to classical debates over the influence of 'bottom-up' versus 'top-down' processes. For salmon populations bottom-up mechanisms can be thought of as those processes that change salmon populations by increasing or decreasing the food availability. For example, climate-driven changes in plankton populations could increase or decrease the capacity of ocean ecosystems to produce salmon biomass (as well as other fish and high trophic level species). Top-down mechanisms are effects like predator-driven trophic cascades in which the food web below a predator is shaped by the waxing or waning of its population. For example, seal predation may act directly on salmon populations (as prey) or indirectly (through a cascade in which seals may also eat salmon competitors) thus creating the potential for increased salmon populations if the competitor is more heavily predated upon by the seals. Such processes become easier to envision because the ecosystem model allows the placement of species within their food-web context.

Ecosystem-based management has become accepted by many fisheries agencies, including Canada's (DFO 2007), as a logical step towards better understanding and regulating human effects on fish and the marine environment. In the past, many fished marine ecosystems were managed under the general assumption that, by properly monitoring fished species, individually and separately, using sound research and responsible management policies, the system overall would take care of itself. Unfortunately, it has been observed that research and management, when applied to single species, have been disappointing in the achievement of targets for both fished and unfished species. Indeed, the declines of some species not of direct interest to fisheries or management appear to have been even more dire. Ecosystem-based management, therefore, has been proposed as a means to address the perceived shortcomings of current research and management paradigms.

In the process of developing ecosystem-based management and research, a question arises as to what, in fact, constitutes this approach. Marine ecosystem-based management measures can range from somewhat precautionary, e.g., establish marine reserves as a buffer against uncertainty (Hilborn *et al.* 2004) to highly interventionist, e.g., manipulate populations of non-fished species to enhance fished populations (Lessard *et al.* 2005). The apparent dichotomy of these two positions can be resolved through the application of ecosystem models. In the construction of an ecosystem model, researchers from different disciplines and backgrounds can be convened in workshops to share their knowledge. In the workshop process, key ecosystem functions, e.g., trophic linkages and ecological mechanisms, can be identified. The identification of these functions then allows modellers to see whether the scientific knowledge is sufficient to replicate ecosystem behaviour over time in the model, e.g., fishing effects, regime shifts, and biomass changes. Examples of models which have achieved the ability to replicate such ecosystem dynamics relevant to salmon and Pacific fisheries include Cox *et al.* (2002) (fishing effects), Preikshot (2007) (regime shifts), and Martell *et al.* (2002) (biomass changes). If a consensus can be realised regarding the realism of such models, managers and user groups can then engage in scenario gaming to examine the fisheries and ecosystem impacts of policies derived from precautionary or interventionist approaches (or anything in-between).

The discussion of ecosystem models has therefore moved from 'whether to use ecosystem models' to 'how to use ecosystem models'. This paper analyses how fisheries management agencies in several jurisdictions use ecosystem models as a crucial part of an integrated ecosystem-based management plan. A quick introduction to ecosystem models is provided to explain in general terms the capabilities of different models and literature that will provide further information on the related science and research. Ecosystems models are examined in terms of what they provide fisheries management agencies and how these experiences might be useful in the context of Canada's Pacific salmon resources.

MARINE ECOSYSTEM MODELS: CAPABILITIES

GENERAL PROPERTIES

The 1990s and early twenty-first century have been witness to the development of a suite of ecosystem modelling research tools. Computer-based ecosystem models have been developed by many governmental and academic research programs as a way to supplement traditional single species approaches. This paper is not meant to be a review of such developmental work. The reader is invited to consult reviews like Plagányi (2007) and Fulton *et al*. (2003) for thorough and cogent discussions of the development and theoretical basis of significant fisheries ecosystem models. Plagányi (2007) divides roughly two dozen different ecosystem modelling programs into the following categories:

- Whole ecosystem models,
- Dynamic ecosystem models,
- Biogeochemical models (often coupled to a biological sub-model),
- Minimum realistic models,
- Individual-based models,
- Bioenergetic models, and
- Models developed by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR).

What is apparent from such reviews is that one ecosystem model approach has been more widely adopted than others: Ecopath with Ecosim (EwE) (Christensen and Walters 2004, Pauly *et al*. 2000, Walters *et al*. 2000). EwE is both a whole and dynamic ecosystem modelling approach and is comprised of three components; Ecopath (a static, mass-based snapshot of the system), Ecosim (a time dynamic simulation module for policy exploration), and Ecospace (a spatial and temporal dynamic module primarily for exploring impact and placement of protected areas).

This reference is not to suggest that this model is inherently better than other approaches. Indeed, for ecosystem models to become a part of the management process it will be necessary to compare how they variously describe fished ecosystems and the mechanisms causing changes to the species therein. Complementing research with whole ecosystem models is oceanographic-based work which has produced environmentally-driven lower trophic web models, e.g., the North Pacific Ecosystem Model for Understanding Regional Oceanography (NEMURO) (Kishi *et al*. 2007). Such models can capture detailed information on the effects of physical processes on phytoplankton and zooplankton. The information derived from this work can then be used as information to help parameterise higher trophic level models like EwE. For instance, NEMURO estimates of changes in zooplankton have been used to estimate carrying capacity changes in oceanic habitats from 1950 to the present by a salmon modelling group (Mantua *et al*. 2007). Another group modelling changes in herring populations actually couples the fish growth model to the NEMURO model (Megrey *et al*. 2007). This shows that models from different disciplines can be used to inform each other. In term of the fisheries ecosystem models themselves, using different ecosystem models is desirable to provide cross-validation for predictions, whereas divergent model behaviour would help identify gaps in research and knowledge.

ECOPATH WITH ECOSIM

The EwE model suite and its spatial derivative, Ecospace, have been constructed for hundreds of ecosystems, several in Canada (Morissette 2007). EwE is now a component of the software suite for management advice systems for several of these ecosystems and their associated fisheries. Examples presented in the section below 'Organisations using ecosystem models for management' are mostly cases in which EwE, or a derivative, has been the ecosystem model of choice. Note, though, that research by Fulton *et al*. (2005) has led to the development of another ecosystem model software called ATLANTIS, used to aid fisheries management in Australia. The EwE model software may be more immediately applicable to the case of Canada's Pacific salmon, however, due to the proximity of the academic institute housing its development: the University of British Columbia Fisheries Centre. Further, as will be seen below, the EwE suite has become popular with federal fisheries research and management agencies in the United States, one of which (the North Pacific Fisheries Management Council) oversees a marine ecosystem similar to Canada's Pacific Coast. Such local sourcing of modelling capability, and initial application experience indicates the considerable interest and expertise in developing ecosystem models to help manage Canada's Pacific salmon resources.

The EwE model suite is the dominant software for ecosystem modelling because of its relatively long history, ease of use, and flexibility to address different ecosystem questions. As mentioned earlier, however, other modelling approaches must be used for cross validation. An excellent review of the most widely used ecosystem modelling programs is Plagányi (2007). That review identifies EwE and ATLANTIS as the two extant aquatic ecosystem modelling suites most suitable to investigating a wide variety of management policies and research questions. The first implementation of Ecopath was Polovina (1984), illustrating that this methodology has been used by the research community for more than 20 years. Because the EwE model suite has a graphic user interface, it is also applicable as a resource for working with managers and user groups, enabling them to participate in gaming scenarios to explore ecosystem behaviour (Plagányi 2007 and Christensen and Walters 2004). Gaming consist of users suggesting various scenarios for running the model to simulate different mechanisms, biological behaviours and fishing policies. These gaming scenarios can be done with historic data or to simulate possible future ecosystem responses to biological and/or human-driven changes, e.g., climate variation and fishing policies. Such a process can be part of an adaptive management process as an environmental assessment workshop as described in Walters (1986). Lastly, EwE models have modules that allow a variety of users to address different questions about ecosystem function, rather than create an 'everything model' which usually requires more resources than is practical for research and management agencies. By employing an ecosystem model, limited management and research resources can be directed more effectively by identifying which questions answer the biggest unknowns or provide the largest potential benefit-for-cost in any given biological, economic or social measure.

In a review of how the EwE models of marine ecosystems around the world had been used by researchers and applied to management, Christensen and Walters (2005) provide a look at what ecosystem models should do to be useful and what, in practice, has been achieved. In order for any model to be useful in helping make management decisions, it must at least be able to replicate known historical changes in the ecosystem. As discussed above, this has been achieved for many marine ecosystems for indicators including biomass fishing effects and regime shifts. A report card is provided in Christensen and Walters (2005) which assesses the capabilities of existing EwE models to capture various processes in fished marine ecosystems:

- Good: by-catch impacts, top-down effects of harvesting predators on valued forage species, multiple stable states, bottom-up effects of production regime changes.
- Fair: bottom-up effects of harvesting prey species on valued predators, regime shifts.
- Poor: top-down effects of harvesting predators on non-valued forage species, habitat damage effects, effects of selective fishing.

The not-so-surprising implication of this assessment is that the EwE models tend to perform more realistically when there is greater knowledge of population behaviours, usually as a result of prior fishing, research and management. This further suggests that in many cases it may be necessary to direct future research into programs on forage fish species, habitat, regimes (including climate change) and bottom-up effects. Note that, while some processes have not been as successfully modelled as others, this is not because they are inherently impossible to emulate. Rather, the deficiency of the model can be seen as a learning tool to help decide when management should be more precautionary. In turn, research can then be directed to help elucidate the sources of the uncertainty and contribute to more robust single species and ecosystem understanding of the marine ecosystem.

Some pessimism has also arisen from the potential for ecosystem models to contain, or even mask, false assumptions about life history processes or predator-prey mechanisms linking species in the model. Indeed, it also seems highly unlikely that any ecosystem model could actually be structured in such a way as to capture *all* processes driving changes in modelled species. Two responses may be noted here. The first is the general observation from Hilborn and Mangel (1997) that "...if our models are as complicated as nature itself then we may as well not bother with the model and focus only on the natural situation." That is to say: the point of modelling is to capture the *relevant* processes that best explain our hypotheses about why changes are occurring. Moreover, once a mechanism is deemed relevant it can then be incorporated into useful research and responsible management. In this way, ecosystem models would help us define which processes and mechanisms in the ecosystem are relevant to changes we can manage in the species we care about. Secondly, there is strong evidence that even if models get the mechanisms wrong they can still get the answer right. This result has been shown in an examination of ecosystem model outputs, e.g., historic changes in biomass, in which model parameter estimates are tuned to changes from extant assessment data (Essington 2004).

The degree to which a model can be tuned depends on the extent to which any one species population changes are constrained by its own life-history characteristics and the changes in the species it interacts with. In EwE models this is an explicit attribute (Christensen and Walters 2004). That is, population changes are bounded by a limited number of energetically possible configurations defined by the model. In a simple example imagine a predatory fished species that has experienced increases in its population. Three simple explanations of this might be, its prey has increased, fishing mortality has been relaxed, or recruitment processes have become more favourable. Regardless of the ability of the model to use one, or some combination of, these hypotheses to mimic actual changes in populations: the increase in that predator can not exceed some limit dependent on its supply of prey. Thus, if the changes in the prey are also known, we have an energetic envelope within which the predator's population is limited. In the end all three mechanisms could explain the population change. If no evidence in favour of one mechanism is forthcoming the ecosystem model has simply helped identify a useful field research question. In this fashion, ecosystem models can help identify likely mechanisms controlling both population changes and species interactions.

MARINE ECOSYSTEM MODELS: STRAIT OF GEORGIA EXAMPLE

The EwE model outputs have the capacity to be fitted to historic data. Figures 1a and 1b show outputs from an Ecosim model of the Strait of Georgia (Preikshot 2007). Each box compares the biomass values (lines) predicted by the model with those obtained from data based on historic stock assessments or other abundance indices (dots). The top nine boxes show how the model's predicted biomass changes compare to historic data when including fishing effects alone and no parameterisation of climate effects or changes to predator interaction with prey. The bottom nine boxes show that when the parameters for predator prey interactions and changes in primary production are tuned to historic data, the model generates a more satisfactory fit to the assessment data, as explained below.

An EwE model is tuned by minimising the weighted sum of squared differences (SS) between log reference and log predicted biomass (Christensen *et al*. 2005). SS can be influenced by changing predator-prey parameterisations at one of more of the trophic linkages to produce a predicted time series of biomass closer to the reference data. It is also possible to minimise the SS by creating a time series of primary production anomalies, e.g., changing phytoplankton production over the time period modelled. These methods allow the modeller the ability to compare the efficacy of top-down and bottom-up mechanisms to explain observed changes in species in an ecosystem. Figure 2 shows the Strait of Georgia EwE model hindcast of changes in annual phytoplankton production, or primary production anomaly (PPA) that produced the smallest SS between predicted and observed biomass changes in the biomasses of nine species; herring, orcas, seals, coho, chinook, pelagic-feeding birds, demersal-feeding birds, lingcod, and hake. This predicted PPA was generated *in conjunction with* trophic effects.

This PPA is not unfortunately comparable to any phytoplankton production times series collected in the Strait of Georgia. This is not because of a lack of research on phytoplankton production in the area. Rather, sampling periods and areas, over the time simulated are often disjointed. Further, there is no case of any continuous plankton time series which is integrated over the whole Strait of Georgia area for the simulated time period. The PPA shown is therefore a representation of what changes in primary production are most *likely* to have occurred to cause the observed biomass dynamics in the species modelled, given known trophic relationships and fishing regimes. To see a description of the Strait of Georgia model behaviour with trophic, or bottom-up forcing, effects only please refer to Preikshot (2007). In terms of the Strait of Georgia PPA having a link to environmental and ecosystem processes, Preikshot (2007) showed that there were strong correlations between the modelled PPA and climate time series like spring Fraser River discharge, Strait of Georgia salinity and West Coast upwelling. Thus, while the PPA can not be linked to an independent long-term phytoplankton data set, it can be linked to indices of environmental processes that are known to cause long-term changes in phytoplankton production over large areas. Given this linkage and the results shown in Figures 1a and 1b, we can illustrate several features of the value of ecosystem modelling.

FIGURE 1a. Biomass trends for nine species in a Strait of Georgia EwE model from 1950 to 2002 run in the Ecosim module, without tuning to climate and predator effects (Preikshot 2007).
Lines are estimations from the model and dots are abundance data from published research.

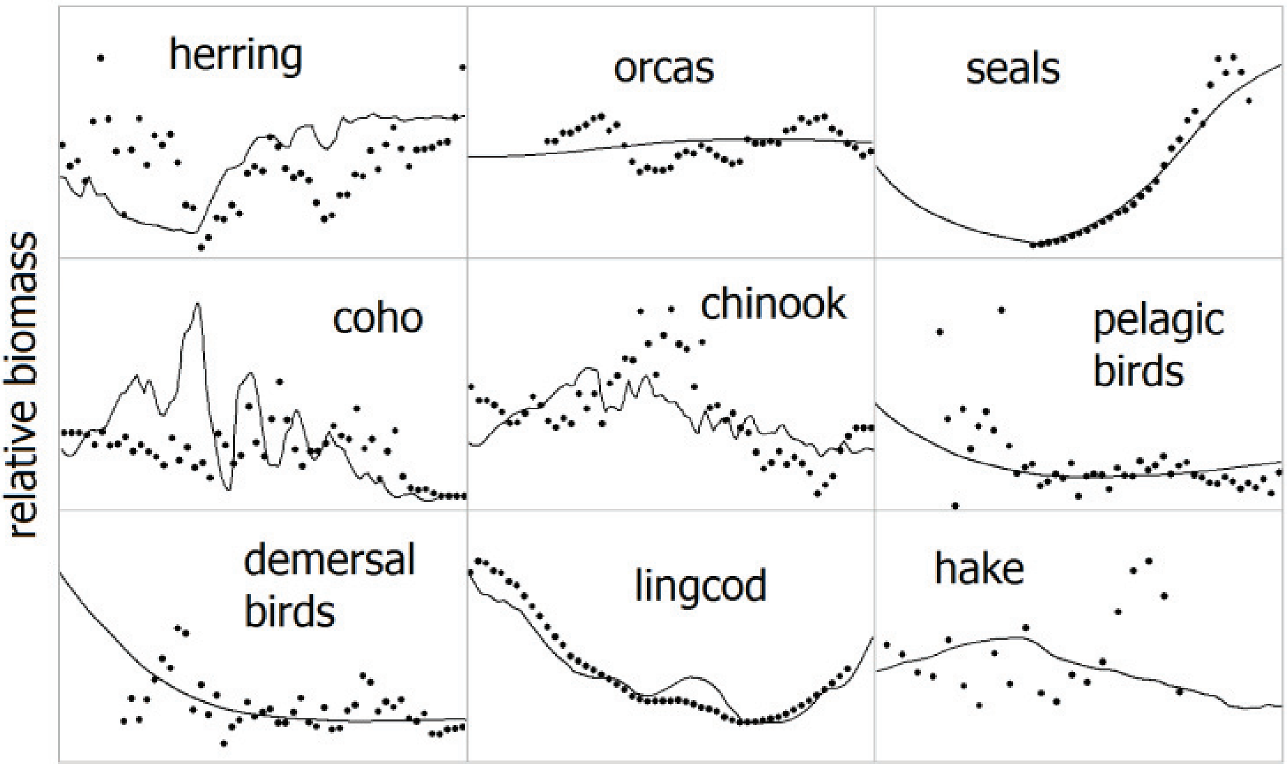


FIGURE 1b. Biomass trends for nine species in a Strait of Georgia EwE model from 1950 to 2002 run in the Ecosim module, with the model tuned to climate and predator effects (Preikshot 2007).
Lines are estimations from the model and dots are abundance data from published research.

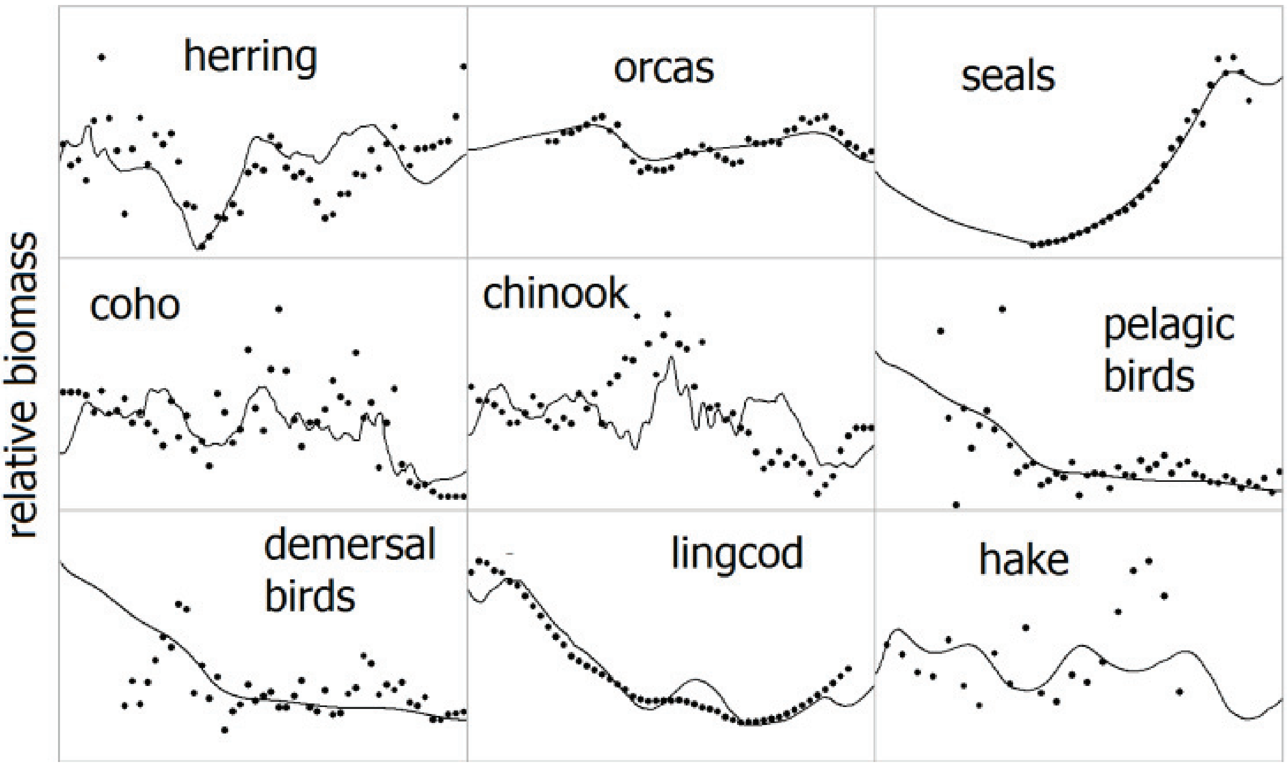
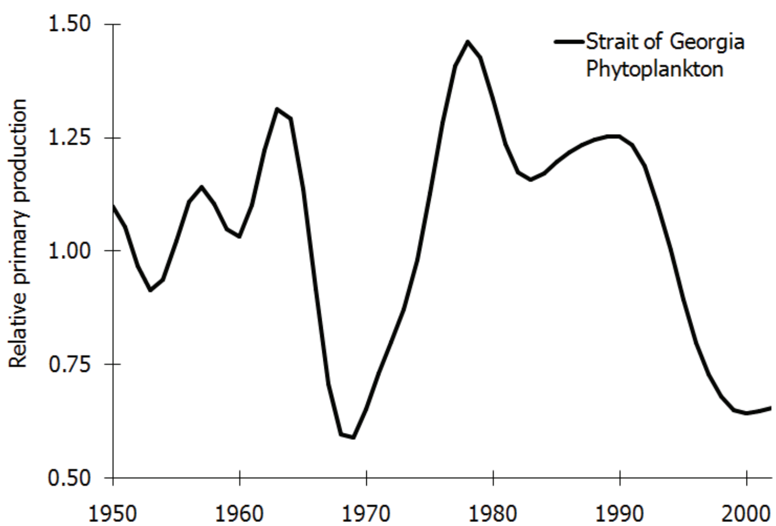


FIGURE 2. Relative changes of annual primary production (long term average = 1) in a Strait of Georgia EwE model from 1950 to 2002 run in the Ecosim module (Preikshot 2007).
These changes are estimated by the model to simulate 'bottom-up' dynamic effects that would result in better fits of modelled biomasses to reference time series, as in Figure 1b.



LINGCOD—FISHING DOMINANT EFFECTS

The species that are fished more heavily have dynamics that tend to be better explained than non-fished species. In Figures 1a and 1 b, it can be seen that lingcod dynamics are the same regardless of whether the model includes predatory prey dynamics and climate effects. This should not be surprising, given that Strait of Georgia lingcod supported a once-prosperous fishery that dwindled to nothing by the end of the twentieth century. Indeed, commercial Strait of Georgia lingcod fisheries were closed in 1990 and recreational fisheries were closed in 2002 (DFO 2005). Given that the 'fishing-effects-only' run of the EwE model produces the same decline in lingcod biomass as the tuned model run, it seems unlikely that the cause of the Strait of Georgia lingcod collapse was anything other than fishing. This result is similar to one reported for another Strait of Georgia model in Martell *et al*. (2002).

HERRING—EFFECTS OF PREDATION AND CLIMATE

The predicted biomass changes of herring, an important forage species, show strong effects of predation and climate. While the model run with fishing effects only explains some changes in herring biomass, the model that includes predation and climate effects performs much better. The tuned model appears to more accurately replicate changes in herring biomass especially in the early portion of the time modelled, up to the mid 1970s. This suggests that bottom-up and top-down mechanisms in the Strait of Georgia ecosystem are also important in determining what has happened to herring biomass from 1950 to 2002.

SALMON—REGIME SHIFTS

The bottom-up effects of harvesting prey (herring) on populations of chinook do not appear to be as strong as regime shift and climate effects (which influence the whole food web). The Strait of Georgia model shown here suggests that, surprisingly, the collapse in herring populations in the late 1960s did not have a great impact on chinook populations. This apparent lack of impact is predicted even though the model has herring as an important component of chinook diets. The health of chinook and coho stocks in the Strait of Georgia became a topic of great concern during the 1990s. Recent collapses in chinook and coho appear more likely to be linked to declining primary production (manifested as declines in almost all species after 1990 and several in the late 1960s). Figure 2 shows that the Strait of Georgia model predicted relative declines in primary production in the late 1960s and late 1990s. In fact changes in the Strait of Georgia PPA were strongly correlated to environmental indices like salinity, upwelling off Vancouver Island, and changes in Fraser River flow (Preikshot 2007). This climate/regime shift mechanism of changes in salmon populations is in keeping with recent work linking climate variation to declines in Strait of Georgia coho (Beamish *et al*. 1999) and Puget Sound chinook (Ruggerone and Goetz 2004). The inability of the model to fit particular changes in salmon biomasses, e.g., chinook increases in the 1970s, can also help in the exploration of new hypotheses to explain their dynamics. One example is the critical size idea of Beamish and Mahnken (2001) that sufficient growth early in the marine life of coho is crucial to first winter survival. Such mechanisms can be easily tied to production changes predicted by an ecosystem model. In such a feedback between modelling and research, our knowledge can be deepened about what is driving changes in salmon populations and how we can best respond with passive, proactive or reactive management policies.

HAKE—POORLY UNDERSTOOD DYNAMICS

What the model does not do well is explain why Pacific hake populations have changed in the latter half of the twentieth century. As might be suspected, this is due to the very uncertain nature of the biology of hake in the Strait of Georgia. Although they are likely the largest biomass of any fish species in the Strait of Georgia, there has been no stock assessment modelling done to explore how their populations may have changed from 1950 to 2000. There is only a small and irregular fishery on Strait of Georgia hake, so population estimates are based on hydro-acoustic surveys conducted at irregular times (Saunders and McFarlane 1999). As a result, the time series abundance data to which the model is compared is not from a formal stock assessment but is estimated from box core samples of hake scales in Saanich Inlet sediments (O'Connell 2000). Given the preponderant biomass of hake, even small changes in their biomass or feeding behaviour could have huge consequences as a competitor with, or predator/prey of, species like coho, chinook and herring in the Strait of Georgia ecosystem. Therefore, the ecosystem model provides an incentive to design research programs to better understand how hake populations have changed in the Strait of Georgia and what their interactions are with other species. This insight suggests that it is unlikely that an effective ecosystem-based management plan can be devised for the Strait of Georgia without a better understanding of the role of hake. In another exercise, we can also use the model to examine the potential value of the knowledge, e.g., what might the future profitability of fishing other species be, given differences in the cost of acquiring knowledge on hake through research.

BIRDS AND MAMMALS—SURPRISING OBSERVATIONS

Lastly, a word on the other 'non-fished' species in the model. One surprising result of the model is the apparent sensitivity of top-level predators to changes in primary production. The predicted biomass changes of orcas, seals and marine birds appear to be strongly affected by apparent declines in primary production in the late 1960s and 1990s, compare low points in these time series in both Figure 2 and Figure 1b. In Figure 1b model runs that include regime-type effects suggest that biomass changes of orcas, in particular, have been influenced by the waxing and waning of decadal primary production cycles. Note that both model runs account for orca removals by the aquarium trade in the early 1970s. This strong manifestation of a bottom-up mechanism in a top-level predator is quite interesting. Common wisdom on upper-level predators might suggest that the ability to switch prey would make them relatively immune to regime-type effects on carrying capacity. However, inspection of the tuned output for orcas shows that biomass declines in the 1960s and 1990s can be explained by regime-type changes. In the case of the other modelled marine mammal, the overwhelming influence on harbour seal population changes was fishing mortality, similar to lingcod. However, in the case of seals it was the removal of fishing, beginning with a ban on harvest in the early 1970s, that allowed their population to increase from about 3,000 to about 30,000 individuals by the end of the twentieth century (Olesiuk 1999).

ECOSYSTEM INDICATORS FOR RESEARCH AND MANAGEMENT

This brief discussion of modelling and the Strait of Georgia ecosystem model shows how even a cursory examination of the process raises issues relevant to moving research and management to a more solid footing to attain an ecosystem perspective. Models often fail to capture one or two species dynamics, but this does not negate the value of using the EwE modelling suite to explore parts of the ecosystem that it does replicate. Indeed, using the EwE model to examine portions of ecosystems is recommended by Christensen and Walters (2005), with the modelling process becoming one of enriching the data with portions of the ecosystem that are relevant to management and research needs. For example, in an expanded ecosystem model exploring Strait of

Georgia chinook and coho dynamics we likely do not need to track down the details of historic changes of sea stars, crabs, and rockfish populations. However, we might profit by devoting efforts to make the model enriched with better hake data and more detail in modelling chinook and coho salmon with two or three life history 'cohorts' to explore different mechanisms changing their populations.

Although qualitative ecosystem considerations have long been a part of management and research, in order to have true ecosystem-based management, quantitative ecosystem targets must be created. This can only be done by using ecosystem models. Many such ecosystem indicators were described at a conference in Paris, in 2004 (Daan *et al*. 2005). Examples of indicators included:

- Regime shifts,
- Changes in population characteristics across species,
- Changes in assemblages of fish species,
- Shifts in sizes of fished species, and
- Changes in the trophic structure of the ecosystem.

Useful ecosystem considerations will allow us to visualise what trade-offs there may be in the population levels of different managed species or what mixes of gear sectors we might use to foster some desired balance of species. For example, if we know the carrying capacity of an ecosystem changes and we can see when those changes happen, an ecosystem model of that system can help explore how species will respond to different fishing policies during different production regimes. In discussing hatchery policy for salmon in the North Pacific, Beamish *et al*. (1997) suggest it might be useful to explore the idea of decreasing hatchery production during less productive ocean regimes. An ecosystem model of the Strait of Georgia could address this very issue and thus help in the development of a research plan to develop hatchery practices to foster wild chinook and coho populations.

ORGANISATIONS USING ECOSYSTEM MODELS FOR MANAGEMENT

The organisations described in the following section do not represent an exhaustive review of all management agencies that are now using ecosystem models as an integrated component of planning. Rather, these organisations represent research and management contexts that are readily transferable to the milieu of salmon on the West Coast of Canada. The agencies and programs described below are staffed by scientists who have trained, workshopped and collaborated with other scientists and managers. The shared experiences mean that if ecosystem models can work in those other contexts, the marine salmon ecosystem of Canada’s Pacific Coast should benefit at least as much from a similar approach. What can be seen in most of these cases is a shared view of larger-scale, in terms of the area and time span, being examined when ecosystem considerations are assessed by modelling programs. This new strategic view is often seen as one of the boons of ecosystem-based management and ecosystem models (Christensen and Walters 2005). Ecosystem planning in the past has often been beset by short-term and small-scale thinking, a scale mismatch that stymies attempts to attain ecosystem targets. Short-term small-scale processes are often very well explained by classic single species approaches now commonly used. Therefore, the tendency to view research questions pertinent to management in terms of small time and area scales may simply be a product of our classical single species frame-of-reference. It is not surprising then to see studies most often devoted to single river basins or small coastal areas over periods of two years to only half a decade. The addition of a large-scale multi-species strategic approach would not nullify the value of the tactical single-species approaches of the past. Strategic thinking, fostered by transparent ecosystem models, simply adds more tools to the arsenal of researchers and managers.

INTERNATIONAL JOINT COMMISSION / INTERNATIONAL ASSOCIATION OF GREAT LAKES RESEARCH

The International Joint Commission was established in the early twentieth century as a Canada-US organisation to manage shared fresh water areas including the Great Lakes. It provides advice to both national governments and in 1997 introduced the International Watershed Initiative which included an ‘ecosystem approach’ as the means of guiding responses to trans-boundary water issues (IJC 1997). The International Joint Commission maintains a close relationship with the International Association of Great Lakes Research (IAGLR). One outcome of this alliance was two workshops on ecosystem models of the Lake Erie ecosystem and how to apply such models (CGLRM 2000). The concept of using ecosystem models to provide advice to management agencies in the Great Lakes area can be sees as early as recommendations in DePinto and Jain (1995) in which it was argued that models would provide the basis for sound advice through ecosystem indicators. There are many agencies with an interest in the Great Lakes. In the United States, the federal, state, and even county governments can all have an impact on fisheries management policy. In Canada, several agencies at both the federal and provincial level have a stake. When compared to the situation in the Strait of Georgia, there is thus a parallel in that many different agencies at different levels of governance, including First Nations, have a voice in managing the water body.

GREAT LAKES FISHERY COMMISSION

Much interest in the development of ecosystem models, as an aid to management and research, has arisen in the agency charged with the fish resources of the lakes, the Great Lakes Fishery Commission (GLFC). In addition to the extant ecosystem model work, the GLFC has requested a white paper on using ecosystem models to assess the health of ecosystems to aid in management of fisheries (Hecky 2008). It is proposed that ecosystem models have the ability to provide the GLFC with a quantitative basis upon which to determine the health of the lakes. Further, the indices developed through modelling would have the ability to not only guide management action but also to evaluate progress in attaining goals.

NATIONAL MARINE FISHERIES SERVICE

The National Marine Fisheries Service (NMFS), a division of the National Oceanic and Atmospheric Administration, (NOAA) has many offices that use ecosystem modelling as part of their management strategy, e.g., the Galveston Texas lab and the Alaska Fisheries Science Center. The overlap of regional NMFS science centers (also housing regional management) with readily definable ecosystems provides a strong motivation to employ ‘big picture’ research like ecosystem models. Science centres exist for Alaska (Gulf of Alaska, Bering Sea, Aleutian Islands), Northwest (Northern California Current), Southwest (Southern California Current), Southeast (Gulf of Mexico, Florida Bay, Florida to the Carolinas), Northeast (Virginia to Maine), and Pacific Islands (Hawaii and other US Pacific Islands). In many cases ecosystem models are established to create a framework within which managers and scientists can discuss ideas about a particular ecosystem. The original statement of the desire to achieve such goals can be found in NOAA (1999), in which the organisation outlined to the US Congress the steps necessary to achieve ecosystem-based management in marine environments. Murawski and Matlock (2006) provide some overview of the manner in which the National Oceanic and Atmospheric Administration and NMFS will get to ecosystem-based management and the manner in which ecosystem models will be used to achieve that goal. In their view ecosystem models are part of a research priority in developing new ecosystem-level approaches and shifting away from traditional small-scale management frameworks. From this perspective, ecosystem models provide management with regionally-based ecological forecasting tools that foster pro-active rather than reactive policies (Murawski and Matlock 2006).

At the Galveston lab, researchers in the fishery ecology branch are using the EwE models as a way to develop management strategies in ecologically complex coral reef communities. In this work, predictions of ecosystem configurations in marine reserves are used to develop targets for managing a fished ecosystem (Hill *et al*. 2005). Activities are also underway in the management of the Gulf of Mexico shrimp fishery to complement traditional single species assessments with ecosystem modelling that can help identify effects of by-catch, forecast harvests, and evaluate different management options.

The NOAA Alaska Fisheries Science Centre (AFSC) Resource Ecology and Ecosystem Modelling Group is specifically tasked with studying trophic interactions in North Pacific ecosystems and using the results to provide environmental assessments. The value of ecosystem models, and the EwE model in particular, to this work is immense. Ecosystem modelling activities at AFSC are reliant on data provided by field researchers and information from single-species and multispecies models. Numerous ecosystem models have been constructed by teams at the AFSC including the Eastern and Western Bering Sea (Aydin *et al*. 2002), Gulf of Alaska (Gaichas 2006), Aleutian Islands (AIET 2007), and Eastern and Western Subarctic Pacific Ocean Gyres (Aydin *et al*. 2003).

The Aleutian Islands marine ecosystem (AIME), in particular, is being used by the North Pacific Fishery Management Council as the test case for a Fishery Ecosystem Plan (FEP). The NPFMC is one of eight regional management agencies created by the Magnuson-Stevens Fishery Conservation and Management Act to manage

US fisheries in the North Pacific. Relative to the Bering Sea and Gulf of Alaska, the AIME is recognised as being complex and unpredictable. The FEP is regarded as a tool to help develop a proactive approach, rather than reactive, in the face of the complex and changing ocean conditions in the AIME. The FEP process is anticipated to be evolutionary in nature and its results are intended to be:

1. To integrate information from across the FMPs (fishery management plans) with regard to the Aleutian Islands, using existing analyses and reports such as the Groundfish PSEIS (preliminary supplemental environmental impact statement), the EFH EIS (essential fish habitat environmental impact statement), and the Ecosystem Considerations chapter
   NOTE: this integration should be user-friendly, i.e., short, simple, and avoiding redundancy
2. To identify a set of indicators for the Aleutian Islands to evaluate the status of the ecosystem over time
3. To provide a focal point to develop and refine tools, such as ecosystem models to evaluate the indicators
4. To identify sources of uncertainty and use them to determine research and data needs
5. To assist the Council in (1) setting management goals and objectives, and (2) understanding the cumulative effects of management actions (AIET 2007)

Note that point b is relevant to the science-driven facets of this paper and is predicated on the acceptance of the value of ecosystem indicators as described in Daan *et al*. (2005). The role of the FEP is to provide managers with a sound understanding of the physical, biological and anthropogenic factors that influence a marine ecosystem. An important part of this role is the identification of areas of uncertainty, i.e., so that these are taken into consideration and/or can be responded to with directed research programs. Point e is a powerful confirmation of the value the NPFMC attaches to ecosystem considerations and how the decisions regarding *any* species must be made in the context of how their effects will be manifested across *all* species.

CSIRO MARINE AND ATMOSPHERIC RESEARCH

The Commonwealth Scientific and Industrial Research Organisation (CSIRO) uses the ATLANTIS ecosystem modelling software to help in making management decisions for fisheries of the southeast coast. “A version of the model, ATLANTIS SE, has been developed to provide strategic advice to the Australian Fisheries Management Authority (AFMA) on management of the Southern and Eastern scalefish and shark fishery, which harvests some 150 species in a region covering a third of Australia’s Exclusive Economic Zone” (CSIRO 2008a). In addition to ATLANTIS the EwE model has also been used by the management authority as a way to evaluate management strategies (CSIRO 2008b). ATLANTIS differs from EwE in that its fundamental unit of currency is nutrient pools rather than biomasses, reflecting its integration of biology and chemistry in its approach (Plagányi 2007). ATLANTIS is similar to EwE with its incorporation of time and spatial dimensions and allowing the modeller to represent detail in managed or otherwise significant species, with age-structured population sub-models while other species can be aggregated into functional groups.

The CSIRO management strategy evaluation (MSE) is an extension of the adaptive management approach developed by Walters (1986). MSE, in the Australian context, was developed to evaluate management strategies on ecosystem oriented goals (Sainsbury *et al*. 2000). In using MSE each stage of the adaptive management process, planning, doing, evaluating, and adjusting, are subject to modelling (and even various models for each stage). This approach is outlined in Sainsbury *et al*. (2000) who argue that uncertainty in both ecosystem-based management and modelling is a reality that can be embraced. The MSE approach they describe relies on the identification of objectives, i.e., reference points and is iterative with feedback between objectives, models and results. The process therefore fosters recognition of different views regarding mechanisms driving the ecosystem and trade-offs between management policies. It is the conclusion of Sainsbury *et al.* (2000) that MSE has helped establish agreement on both monitoring protocols and management actions in Australia.

This tendency to be thinking with a strategic frame-of-reference has predisposed CSIRO and the Australian Fisheries Management Agency to incorporating information arising from ecosystem modelling exercises. Researchers at CSIRO have thus played a large role in the development of marine ecosystem models by figuring prominently in published studies using the EwE model and leading the development of ATLANTIS (Fulton *et al.* 2005).

NEW ZEALAND MINISTRY OF FISHERIES

The New Zealand Ministry of Fisheries (NZMoF) has initiated a project to use ecosystem models to study the Ross Sea ecosystem in general and the toothfish harvest in particular. Ecosystem models are seen as a way of understanding important mechanisms controlling the Ross Sea ecosystem determining how the toothfish fishery affects the ecosystem requirement of governments managing Southern Ocean fisheries under CCAMLR, the Convention for the Conservation of Antarctic Marine Living Resources (NZMoF 2004).

INTER-AMERICAN TROPICAL TUNA COMMISSION

The Inter-American Tropical Tuna Commission (IATTC) was established in 1950 between the US and Costa Rica. Since that time, its membership has expanded to include Panama in 1953, Ecuador in 1961, Mexico in 1964, Canada in 1968, Japan in 1970, France and Nicaragua in 1973, Vanuatu in 1990, Venezuela in 1992, El Salvador in 1997, Guatemala in 2000, Peru in 2002, Spain in 2003, and Republic of Korea in 2005, although Canada has since withdrawn. The Commission exists to provide scientific advice on the management of tuna and billfish resources and has also developed significant study on dolphins due to by-catch concerns (Bayliff 2007). Due to this multi-species large area responsibility, it is not surprising that ecosystem models have been adopted as part of it work. The IATTC has developed an EwE model to explore the ecosystem effects of different fishery policies (Olson and Watters 2003). The IATTC is a member of the Working Group on Models of Alternative Management Policies for Marine Ecosystems, a program of the National Center for Ecological Analysis and Synthesis at the University of California, Santa Barbara Campus. While this working group has purposes beyond the scope of the IATTC, the Commission has become involved to use models to identify robust management policies incorporating ecosystem consideration in the management of fisheries in five large Pacific marine ecosystems (Bayliff 2007).

CONCLUSION

Hollowed *et al*. (2000) argued that one limitation of ecosystem models was an inability to incorporate regime shifts, especially their role in varying recruitment and non-fishing mortality. However, recent work with the EwE model has shown that regime shifts can indeed be hindcast by ecosystem models, e.g., the primary production anomalies in Preikshot (2007) and similar work by Field *et al*. 2006. Information from Ocean-Atmosphere Coupled General Circulation Models on potential future ocean conditions could then also be used as input for future simulations in an ecosystem model for strategic planning. Christensen and Walters (2005) note that one source of hesitation, by managers and researchers, to using ecosystem models may be fear of adopting a long-term and large-scale strategic frame of reference. The ability to use oceanographic models in conjunction with ecosystem models may address such concerns.

Babcock and Pikitch (2004) outline three possible future routes along which ecosystem-based fisheries management might proceed:

1. Marine ecosystems are unknowable thus we are best advised to create large marine protected areas and use a highly precautionary approach.
2. Combine ecosystem modelling with single species modelling with control rules from the latter informed by information from the former.
3. Completely replacing single species management and modelling with indicators from ecosystem models.

Unfortunately, much of the literature seems to be focused on the apparent conflict between those advocating the use of single species stock assessment modelling (SSSAM) and those for the use of ecosystem models: the crux of point 3 in Babcock and Pikitch (2004). The tendency of many to see this dichotomy may be a by-product of the analytic mind to use the principle of falsification as the only means of addressing scientific questions, i.e., hypotheses. In the case of answering ecosystem questions one approach or the other must be wrong. Many of the successes of modern science have been based on applying Karl Popper's idea that a question is scientific if and only if it is falsifiable. Many graduates of biology programmes can point to the statistics classes and lab sessions where they learned to reject or accept the null hypothesis in applied science exercises. Note the conditionality of *accepting* rather than *confirming* the hypothesis. However it has become apparent that many natural systems, even the behaviour of individual fish stocks, can be so complex that a simple statement of rejecting or accepting one idea about them is simply insufficient. Indeed, we may often suspect that there may be more than one idea about how a system works. Thus, many practitioners of modern fisheries science and more generally, ecosystem modelling, have moved to the use of Bayesian inference to assess hypotheses, see, e.g., Punt and Hilborn (2002) and Walters and Martell (2004). In a Bayesian approach probabilities of a given hypothesis being true are calculated, implying a suite of ecosystem states rather than an either/or state.

Thus, advocates for only using SSSAMs can argue that ecosystem models do not provide robust predictability. Whereas those who argue for the use of ecosystem models point out that SSSAMs have failed to prevent fish stock collapses in the past. Based on the organisational review in this paper, it would seem that enough researchers and management agencies have confidence in both ecosystem models *and* SSAMs that the second path described by Babcock and Pikitch (2004) is being adopted. Evidence presented here suggests that marine fisheries management is evolving in such a way that ecosystem models are used to augment information from SSAMs and *vice versa,* e.g., as a component of a Management Strategy Evaluation-type process as described in Sainsbury *et al.* (2000), see above section on CSIRO.

SSAMs will not be replaced or lose relevance. However, it also seems unlikely they will be improved in such a way as to render moot the potential benefits from using ecosystem models. As an example, classical (AKA Newtonian) Mechanics has been shown to be not entirely correct, but it can be a very powerful tool to understand motions of bodies in space. However, general (Einsteinian) relativity can be used to address, in greater detail, questions about bodies in space though it is not practical to use it at all times. The point is that *both* approaches are used to model questions about the cosmos. The apparent precision of one does not mean it replaces the other. Models derived from these approaches to physics serve complementary purposes.

Another factor giving caution to ecosystem model sceptics may be based on experience with early work in the field. Walters and Martell (2004) describe how early ecosystem models tended to produce rather unrealistic dynamics in which competition between two species would lead to the extinction of one, biomasses of species would fluctuate wildly between different ecosystem states, and the only mechanism of trophic control would be predator-driven trophic cascades. In the evolution of the EwE modelling suite, these types of instability were seen to be due to the false assumption that predators and prey interact like randomly distributed chemicals in a reaction vat. Stable dynamics and realistic reproductions of biomass histories were achieved by EwE models after the introduction of so-called foraging arena dynamics to manage energy flows between predators and prey (Christensen and Walters 2004). This insight allows ecosystem models (large scale) to incorporate small scale phenomena (feeding events). Foraging arena theory incorporates known behaviours of prey: the use of strategies, e.g., schooling and hiding, to reduce their risk of predation when not feeding (Walters *et al.* 1997).

NRC (2007) warns that ecosystem modelling may not yet have advanced to the stage where it can be used as a tool to ‘steer’ ecosystems to desired states, dynamic or static. However, this assumes that currently used tools like SSSAMs are presently at a level of reliability and sophistication that they can ‘steer’ single species to desired states, dynamic or static. Indeed, one of the key realisations upon adopting an ecosystem-based approach is that the very goal of steering an ecosystem is a chimæra. Rather, ecosystem models should be thought of as a tool to help us understand just how wide the variation in an ecosystem can be from desired states and what robust approaches we might devise when unexpected changes happen in the future. Towards this view, NRC (2007) concludes that even if an ecosystem model is incapable of reproducing known dynamics, this fact does not preclude the exercise of beginning the iterative development (with feedback from field research) of useful ecosystem models.

Ecosystem modelling needs to be used as a strategic long-term approach to management. Ecosystem models do not replace single species models that are more useful for short-term tactical approaches. These short-term concerns have dominated the use of models by management up to the present. This may be a result of the perceived reliability of the predictions. While there have been some notable historic successes of these SSSAMs to provide predictions to help fisheries succeed over the long-term, e.g., North Pacific halibut, there are many more that have been of limited success.

In the case of Canada’s Pacific salmon, the activities of the AFSC and IATTC are particularly relevant to developing a Canadian ecosystem model program. In the case of the AFSC, one large marine ecosystem, the Aleutians, has been chosen as a test case for developing procedures for the use of ecosystem indicators. In the AFSC work, ecosystem models are a vital part of framing research and advice. While some managed species in the Aleutians may have populations in small areas, the life history of most of the managed groundfish and salmonids, and their predators (marine mammals) and prey (herring and other small pelagics), was on larger scales of time and space that could only be visualised by using ecosystem models. By using ecosystem models, the effects of long-term, large-scale processes like climate variation are seen as being soluble for the management agency. Similarly, the IATTC has been forced to respond to dealing with species moving over large areas with populations that change on long-time scales.

It is well known that Pacific Salmon undergo large scale movements in the ocean (Azumaya *et al*. 2007, Welch *et al*. 1995) and their populations respond to long-term changes in climate (Beamish and Bouillon 1993, Hare and Francis 1995, and Mantua *et al*. 1997). Researchers studying Canada's Pacific Coast have already constructed basic EwE models of relevant coastal and open ocean ecosystems, some with salmonids as one focus, e.g., Preikshot 2007 and Martell *et al*. 2002. The next logical step would appear to be establishing a team capable of taking this preliminary work and integrating it with the best data available from the Department of Fisheries and Oceans. Given the detailed knowledge of salmonids and most of the species interacting with salmonids, ecosystem models could easily to be tailored to specific questions and portions of the ecosystem while generalising more peripheral parts. Figure 3a and 3b show trophic linkages for two important species in the Strait of Georgia, adult chinook salmon and adult herring, respectively. These two species are significant for social and economic use and are known to be key players in the way energy is moved through the marine ecosystem.

Figures 3a and 3b show how we can use a model to quickly identify where the important interactions between key species might be. When looking at these linkages, keep in mind that they are meant represent the average state of affairs between 1950 and 2002. The width of connection between two species indicates the strength of the interaction. In the case of adult herring, the largest food item in the model is herbivorous zooplankton, followed by krill, with carnivorous zooplankton as the smallest portion of diet, Figure 3b. In Figure 3a it may surprise some to see that seals and sea lions exert at least as much mortality upon adult chinook as fisheries. Each species in the model can be illustrated in this fashion. One benefit of these visual representations is that researchers and users can examine different aspects of the model in an intuitive way to see if how the model behaves squares with their knowledge. Points of contention or agreement become the stepping stones to developing consensus among modelling participants like researchers, user groups and managers. In a similar fashion, dynamic outputs of the model can also be used to see if, for instance, biomasses in the model change in ways that 'make sense'. In the case of the biomass changes shown in Figure 1b any person can quickly identify how different species populations change in the model and use that information to form an opinion as to the validity of the model (or, indeed the reference data to which the ecosystem model outputs were compared).

FIGURE 3a. Trophic linkages to adult chinook salmon (in the centre of the figure) in an EwE model of the Strait of Georgia (Preikshot 2007).

The relative width of each connection indicates its magnitude. Blue lines indicate prey species, red lines predators and green lines are fisheries. The trophic level of each species, group or fishery in the model is indicated by the Y-axis.

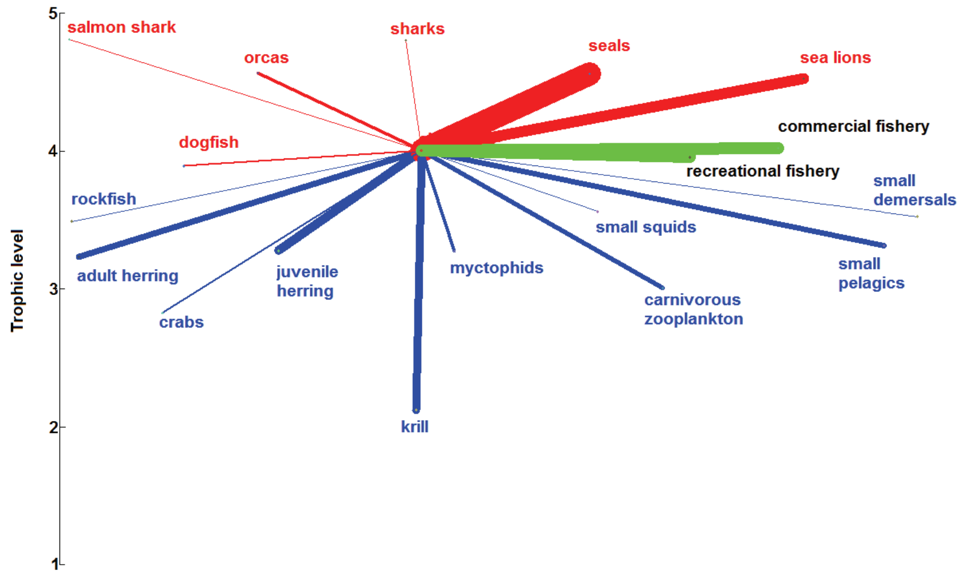
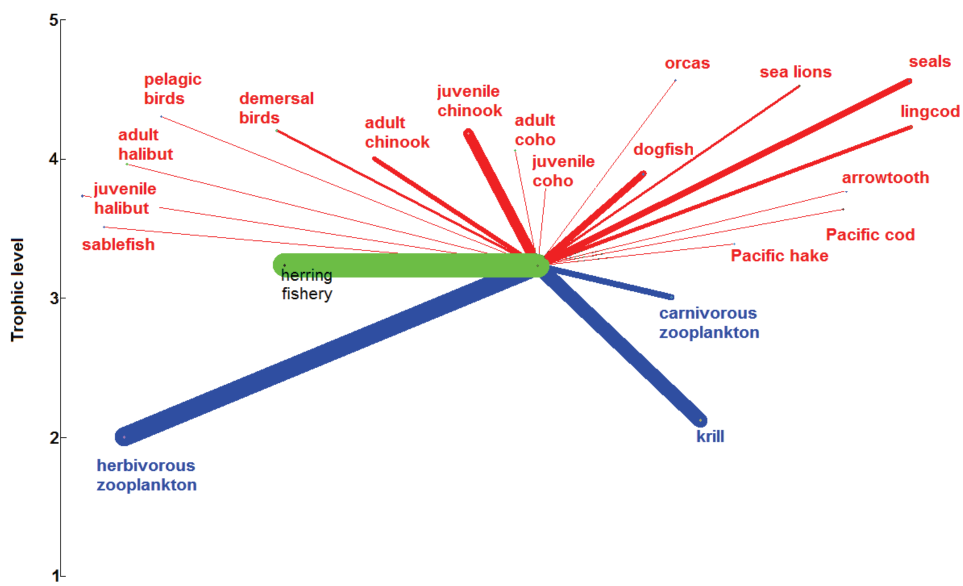


FIGURE 3b. Trophic linkages to adult herring (in the centre of the figure) in an EwE model of the Strait of Georgia (Preikshot 2007).

The relative width of each connection indicates its magnitude. Blue lines indicate prey species, red lines predators and green lines are fisheries. The trophic level of each species, group or fishery in the model is indicated by the Y-axis.



FUTURE STEPS TOWARDS SALMON-ECOSYSTEM MODELS

A practical first phase, then, would be defining species of interest to user groups, management and researchers and the natural ecosystem mechanisms to model. Using the Strait of Georgia again as an example, EwE models have been constructed with 15 species groups (Pauly *et al.* 1996), 26 species groups (Pauly *et al.* 1998), 27 species groups (Martell *et al.* 2002), 32 species groups (Beamish *et al.* 2001), and 55 species groups (Preikshot 2007). It is instructive to note that as time has gone by the level of detail in these models has increased. This illustrates the principle that there is never a final 'model'. All of these models were built with reference to pre-existing iterations, with subsequent research building upon the extant knowledge base. Detail in early versions of EwE Strait of Georgia models tended to be in marine mammals, with later versions often becoming more detailed in their approach to fished and other managed species, i.e., representing them with multiple life-history stages. In the case of building salmon-centric BC coastal models, like the Strait of Georgia, it may not be necessary to have a model with 55 species groups as in Preikshot (2007).

Table 1 shows the kinds of species groups that, for the Strait of Georgia, would be useful to explore management options and act as a knowledge bridge of scientific research on the ecosystem. Such a grouping could be easily modified to model other BC coastal ecosystems.

The inclusion of hatchery and wild stocks would enable us to replay the history of hatchery management policy. For example, Beamish *et al.* (1997) suggest that hatchery planning should be conducted with a view to the effect of regime shifts on oceanic salmon production. An EwE model including hatchery and wild chinook and coho could be used to explore what might have occurred to wild stocks given different hatchery policies between 1950 and the present. Because we now have a good idea of when production regimes have changed in the Strait of Georgia (Preikshot 2007 and Beamish *et al.* 2004) we could replay history in the model to see if other policies might have helped mitigate coho and chinook collapses in the 1990s. Knowledge from such an exercise could be valuable in advising on future hatchery management when regime shifts occur in the future. By adopting such a strategic modelling perspective, research and management on Canada's Pacific ecosystem would be able to develop more robust strategies to preserve our precious salmon resources.

TABLE 1. A list of potential EwE-type model species groups for that could be used to explore dynamics of chinook and coho salmon in the Strait of Georgia.
For chinook and coho W refers to wild stocks and H refers to stocks of hatchery origin.

High Trophic Vertebrates	Salmon	Other Fishes	Invertebrates
birds, pelagic pisciv	pink juv.	pollock	krill
birds, demer pisciv	chum juv.	rockfish	carn. zooplankton
birds, planktivores	sockeye juv	Pac. hake	herb. zooplankton
odontocetae	W. coho juv.	yellowfin sole	jellies
mysticetae	W. coho ad.	rock sole	large squids
sea lions	W. chinook juv.	flatfish other	small squids
seals	W. chinook ad.	myctophids	shrimps
dogfish	H. coho juv.	small demersals	crabs
rajidae / ratfish	H. coho ad.	small pelagics	bivalves
Pacific cod	H. chinook juv.	herring juv.	echinoderms
arrowtooth	H. chinook ad.	herring ad.	other benthos
lingcod			phytoplankton
predatory pelagics			macrophytes
			detritus

The benefits of this approach would also be immediate. Any exercise in which the research community has the chance to amass known information on the functioning of managed species must be *de facto* an informative exercise. By having researchers collaborate on ecosystem models and compare their outputs to past known changes we can identify what we know about mechanisms controlling valued species in the ecosystem. The identification of unknowns suggests areas in which we can design research programs to further complete our understanding of the ecosystem. In a more exacting way we can even use the model to help allocate limited research funding to the areas that will give us the most cost effective means of maximising ecosystem knowledge. The short-term benefits would also extend to creating a feedback loop between those using SSSAMs which to suggest different scenarios for *their* construction and, in turn, provide the ecosystem modellers with the best available knowledge of changes in individual species. This cycle of collaboration and feedback would, with the participation of management advice, help establish a world-class ecosystem modelling capacity to help us create sound salmon stewardship for both the present and the future.

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