Development of research methodology and quantitative skills for integrated fisheries management in Western Australia

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Australian Government

Fisheries Research and Development Corporation

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Fisheries Research and Development Corporation Report
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OBJECTIVES:

During the course of the project, the original objectives of this study were extensively modified by the Project Steering Committee to become:

1. To develop an ecosystem model of the West Coast Bioregion of Western Australia, employing the commercial fisheries data that are available for that system.
2. To develop more sophisticated and advanced quantitative techniques for analysing biological data so that more reliable information can be provided to fisheries managers and training in quantitative skills can be provided to postgraduate students.

NON TECHNICAL SUMMARY:

OUTCOMES ACHIEVED TO DATE

The Project has developed a relatively-simple but effective modelling approach that can be used to describe the changes in the abundance of the groups of exploited species within a marine ecosystem, and which can be applied using data that are typically collected by a fisheries agency. This modelling approach offers a less expensive alternative when the cost of developing a detailed ecosystem model is not justified or when the available data constrain the ability to fit a complex model. A method developed to resolve the apparent inconsistencies between estimates of natural mortality produced by different life history approaches has improved the reliability of these estimates and will lead to more reliable stock assessments. The Project has also produced postgraduate and Honours students with training in quantitative skills and two fisheries scientists with a sound understanding of the use of quantitative approaches for fisheries science. Such skills are in great demand as fisheries agencies address increasingly complex issues of ecosystem-based approaches to fisheries management and Western Australia's fishers will benefit from the contribution that these scientists are now making.

Fisheries managers are increasingly aware of the need to ensure that the impact of fishing does not cause major and unsustainable change to the species composition of the marine ecosystem on which the exploited fish stocks depend. However, in order to assess the impacts of fishing on the ecosystem and to predict the consequences of current levels of fishing effort, there is a need to subject the available fishery and biological data to detailed statistical analysis, and interpret the data using simplified descriptions (models) of the interactions between the different species and the effects of fishing. The ecosystem models that have typically been used in such analyses are

very complex, require the collection of extensive data sets for species that range from phytoplankton to seabirds, and usually demand sophisticated modelling skills. For the majority of Australia's fisheries, the cost of producing such complex models is unlikely to be justified. A relatively simple modelling approach that could use existing fisheries data to describe the interactions among different groups of exploited species in the ecosystem and the effect of fishing was urgently needed and has been developed in this Project.

The model produced in this study predicts the changes in abundance of each group of species as a consequence of the changes in fishing effort, and in response to the changes in abundance of the other groups of species that represent the predators or prey of the group of species for which the prediction is being made. The model was tested using synthetic data generated by EcoSim, a more complex model that is frequently used to describe ecosystems elsewhere in the world. The results of this test confirmed that the model was able to describe the behavior of the synthetic data and capable of producing relatively-reliable short-term predictions. The model was also fitted to data for the West Coast Bioregion. While it fitted the trends of a number of species well, it was unable to capture the inter-annual variation present in species such as the large migratory fish, suggesting that time series of environmental variables may need to be included to explain such variation. The increasing trends present in the relative abundance of many of the species groups were possibly the result of increasing efficiency of fishers, suggesting that this needs to be assessed and the data standardized before the model will be able to assess reliably the state of the various species groups in the West Coast Bioregion.

The requirement for fisheries managers to adopt an ecosystem-based approach to fisheries management and the adoption in Western Australia of integrated fisheries management has placed increasing demand on fisheries scientists for analyses to assess the status of fish stocks and quantify the allowable catch that the fishery can sustain. There is increasing need in Australia and elsewhere in the world for fisheries scientists with strong quantitative skills, *i.e.* skills to carry out such assessments, and an urgent need to train such scientists if the demands for complex analyses are to be met by fisheries agencies. The Project used the development of more sophisticated methods of analysis of existing data sets as the vehicle by which such training could be provided to a number of postgraduate students at Murdoch University. Two fisheries scientists with strong quantitative skills, who are now producing research results that are benefitting Western Australia's fishers, were trained during the course of the project.

Through the analyses used in training the students, the Project also provided the opportunity to develop a method for producing more reliable estimates of natural mortality (deaths due to natural causes such as predation, disease, etc.). Such estimates are crucial for stock assessment, as they allow estimation of the current level of exploitation, *i.e.* the proportion of the fish that are vulnerable to capture that are actually caught. The availability of a reliable estimate of natural mortality results in improved estimates of the allowable level of catch that can be sustained by a fish stock. Methods of analysis were also developed to improve our understanding of the variability of growth among individual fish and the imprecision of estimates obtained for growth, natural mortality and the lengths at which individual fish become mature. Such imprecision needs to be taken into account when assessing the quantity of fish that are available to be caught without affecting the sustainability of the fish stock.

KEYWORDS: **Ecosystem model, natural mortality, size-related movement, growth.**

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Background

The increasing size of the population of Western Australia, together with a rapid growth in the participation rate and adoption of modern technology by recreational fishers, makes it inevitable that the magnitude and efficiency of the recreational fishing sector in this state will continue to expand at a significant rate. Furthermore, the increasing modification of many fish habitats as a result of human activities will inevitably have an impact on fish abundance. For the above reasons, the Department of Fisheries Western Australia recognised that there is an urgent need to develop plans for an integrated approach to fisheries and ecosystem management that address the ways in which fisheries resources are allocated between recreational and commercial sectors and which, at the same time, take into account the need for ensuring that those resources are ecologically sustainable (Anon, 2000a, b). The need to adopt an integrated approach to fisheries management had been identified in the 2000-2005 Research and Development Plan of the FRDC as a major requirement for fisheries throughout Australia. The Western Australian

Department of Fisheries had recognised also that its fisheries needed to be managed in accordance with the principles of Ecologically Sustainable Development (ESD) (Fletcher, 2002) and had commenced to move towards adoption of an ecosystem-based approach to fisheries management. In addition, the operational reporting requirements for ESD from the Standing Committee on Fisheries and Aquaculture and Environment Australia (part of the Commonwealth Department of the Environment and Heritage, which is now the Department of the Environment and Water Resources) (Schedule 4 Guidelines of Environment Australia and the Environment Protection and Biodiversity Conservation Act 1999) require the development of improved assessments of the impacts of fishing on ecosystems.

The aim of this project proposal was to appoint an experienced quantitative biologist to undertake the research needed to develop new and innovative models required to facilitate the development of management plans aimed at ensuring the ecological sustainability of fisheries resources in Western Australia in the future. Such plans need to address the interrelated needs of the recreational and commercial fishing sectors, as well as those of conservation bodies and the community as a whole, and must also be based on sound quantitative assessments of biological data on fish and fish communities. This was seen as necessitating the development of new models which, by incorporating data on ecosystem interactions, would extend beyond traditional stock assessment approaches. The new ecosystem models would facilitate an understanding of the direct and indirect impacts of fishing on target species and an assessment of the impact of management controls on fish populations and biotic communities.

The proposed appointee would become an integral member of the Murdoch University Centre for Fish and Fisheries Research and would work with staff in the fields of biological sciences and mathematics at Murdoch University, postgraduate researchers, and fisheries scientists at the Department of Fisheries WA, to provide a collective approach to refining the methods for analysing traditional fish and ecosystem data series. The advantage of this approach was that it would provide more sophisticated data for use in fisheries and ecosystem models and would result in producing not only cutting-edge research but also young research scientists with the strong backgrounds in quantitative and modelling skills that are increasingly required in fisheries research. The very considerable commitment of Murdoch University to fisheries-related research is demonstrated by its recognition in 1999 of the above centre as one of its Centres of Research Excellence and by the continued financial support that it has provided to this Centre.

While the study originally envisaged the development of complex ecosystem models employing, for example, multi-agent and individual-based modelling approaches (DeAngelis and Gross, 1992; Reynolds, 1999) and cellular automata, it rapidly became apparent that the immediate need was for the development of models that could employ the types of data that had been collected traditionally by fisheries agencies and would not require the collection of vast quantities of additional biological data. For the majority of fisheries, the expense of such collection was likely to be prohibitive. Furthermore, a modelling approach was required that would represent a relatively simple extension to the types of fishery models currently employed in fisheries agencies. That is, the type of model that should be developed was required to be of a complexity that was appropriate for fisheries agencies to adopt and maintain with existing expertise. The paucity of highly-experienced fishery modellers and the expense of developing and maintaining sophisticated ecosystem models preclude the use of such models for many of Australia's less valuable fisheries.

The long time series of total catch and effort data, which are traditionally used to analyse the status of commercial fisheries, are usually lacking or incomplete for fisheries with a significant recreational catch. In the absence of such time series, it is difficult to develop dynamic models of the fisheries and, in any case, traditional fishery models are likely to be inappropriate. Furthermore, traditional models do not incorporate information on dietary interactions among fish species. Such data are required to assess the indirect effects of fishing and thereby allow evaluation of the effectiveness of management strategies that are aimed at meeting the objective of ecological sustainability. Greater emphasis has thus to be placed on utilising, in an optimal manner, the information obtained from existing biological and ecosystem data by developing appropriate new modelling approaches and more sophisticated quantitative methods of analysis for these data.

The study proposed to use the extensive biological data for the fisheries and the fish populations and communities in estuarine and near-shore marine waters that had been collected during other Murdoch University' studies, and also those that would be acquired during current studies. Dr Peter Rogers, who at the time of project submission was the Executive Director of the Department of Fisheries, had advised that his Agency would make available the relevant research data that had been collected by his agency under appropriate arrangements to preserve fishers' confidentiality. Initially, it had been intended that the focus of the ecosystem studies should be the Peel-Harvey Estuary. However, as the study evolved, it rapidly became clear that there was greater need to concentrate attention on the marine ecosystem of the West Coast Bioregion. This latter region is heavily exploited by recreational and commercial fishers, and some finfish species in the region, such as Dhufish and Pink Snapper, appear to be experiencing overfishing.

This project was intended to address the strategies identified in Program 1, Natural Resources Sustainability, of the FRDC R&D Plan 2000-2005. The proposed modelling would complement, rather than overlap, the standard stock assessments that are conducted on populations of species that are targeted, particularly by commercial fishers. The approach to be adopted would build on the high level of collaboration which had existed between Murdoch University and the Department of Fisheries WA for about 25 years and which had been effective in addressing important issues associated with the management of certain fisheries and habitats in Western Australia.

In order to develop the cutting-edge skills required by future fisheries scientists, Murdoch University needed to ensure that research students were subjected to a sound training in the analysis of the characteristics of fish populations and communities and the relationships of those populations and communities with the environment. The most effective form of training involves the research student applying the theory and research methodology to the data collected during his/her project and ensuring that the project undertaken is of high quality and of benefit to the Department of Fisheries WA and the Western Australian community. The Department of Fisheries WA and Murdoch University recognised that the ongoing implementation of integrated fisheries and ecosystem management, involving the use of new modelling approaches, would require the production of high-quality research scientists with the requisite quantitative skills. In this context, the Fish and Fisheries Research Centre at Murdoch University proposed the development of quantitative skills by employing the quantitative biologist to assist PhD students to explore quantitatively and in greater depth their own data. This was intended to complement, but not overlap, the work of the Quantitative Training Unit (QTU) at the University of Sydney, which focuses on the training of staff in fisheries research institutions in stock assessment. By aiding the acquisition of quantitative skills by research students, these future researchers would be better equipped to meet the emerging needs of fisheries and environmental managers and would assist in maximising the State's use of human capital resources. Without the development of such associated skills, effective management of the fishery resources of Western Australia in the future would be jeopardised.

Sound data on the size and age compositions, growth rates and length and age at first maturity of numerous fish and crustacean species in south-western region of Western Australia have been collected and are stored within the Murdoch and the Department of Fisheries WA data bases. These data would be subjected to more detailed and sophisticated analyses than had traditionally been the case, in order to extract further valuable biological information. For example, such analyses might include a description of variability in the length at age of individuals, rather than just of the population, and also the selectivity of fishing gear.

This project addressed specifically the objective and vocational development strategy of Program 3 (Human Capital Development) in the FRDC's Research and Development Plan for 2000-2005. Furthermore, involvement by postgraduate students was seen by the then Executive Director of Fisheries WA as an essential element of the State's strategy for developing the research structures, skills and training required for facilitating the implementation of integrated fisheries management plans.

This project complemented aspects of the biological and modelling research being conducted during other current FRDC projects, both at Murdoch University and within other institutions around Australia. The habitat project (FRDC 2000/159), that was being undertaken by Murdoch University, was directly relevant as it would provide improved data on the relationships between various invertebrate and fish species and their habitats, and thus also an understanding of the factors that influence fish populations and structure fish communities. The detailed and composite data that would be derived from that study would provide an excellent data base for developing quantitative predictive models for management and thus supplement the subjective results obtained during that study. The development of such models also complemented the study by Dr Rick Fletcher, which was aimed at developing methods for assessing fisheries against a background of ESD criteria (FRDC 2000/145). The Department of Fisheries WA was actively engaged in developing stock assessment and fishery models for many of Western Australia’s fisheries, and this included an analysis of the application of time series models to fisheries data (FRDC 1999/155). These assessments would be enhanced by the development at Murdoch University of models that describe aspects of the interactions between fish populations and communities, and which could be used to assist in planning for integrated fisheries management.

Dr Norman Hall, a fisheries scientist with considerable modelling experience, was appointed to Murdoch University in late January 2001 to lead the project. A Research Steering Committee was then established to provide research direction. This Committee comprised Professor Tony Tate (Chair), Dr Peter Rogers, Dr Rick Fletcher, Professor Ian Potter, Dr Rod Lenanton, Dr Norman Hall, Dr Chris Simpson, Dr Gary Morgan, and Professor George Kailis. Following his appointment to Murdoch University, Professor Neil Loneragan later joined the group. It should be noted that the FRDC advised early in this Project that precise specification of the project would need to be identified following a comprehensive review of methods in the first six months of the study and that the direction provided by such a Committee would be essential to ensure that the project focused on research needs.

A review of methods used in ecosystem modelling and data needs was undertaken, taking into account the requirements of fisheries agencies and managers. The methods that were proposed in the initial project application were modified by the Research Steering Committee following this review and in response to evolving knowledge as the study progressed.

Need

As the project progressed and was modified by the Research Steering Committee, the needs identified in the original project application became more sharply focused and may be summarized as the need for:

1. Developing a form of ecosystem model that, in combination with data on the biology and dietary interactions of the target species, could use existing fisheries data to assess the state of the marine ecosystem and thereby facilitate the production of high quality management plans aimed at ensuring the ecological sustainability of fisheries resources in Western Australia.
2. Developing the quantitative approaches for analysing, in a more sophisticated manner, the biological data on fish populations that are traditionally used for developing management plans for fish stocks.

3. Producing high-quality scientists, who have the quantitative skills required for understanding and developing ecosystem and fishery models, and who thus have skills suitable for their employment in areas related to the implementation of integrated fisheries and ecosystem management.

Objectives

The original project objectives listed in the project application were:

1. To use the extensive data set for the fishery, fish and invertebrate fauna, flora and environment of the Peel-Harvey estuary to develop models that are able to be used for developing plans for integrated fishery and ecosystem management in that estuary.
2. To develop the above models further, using data for other ecosystems, so that combined fisheries and ecosystem models then become available for a range of different ecosystems.
3. To develop more sophisticated and advanced quantitative techniques for analysing the biological data present in existing datasets so that more complex information, such as individual variability in growth and gear selectivity, can be provided to those managers responsible for developing the plans for an integrated approach to fisheries and ecosystem management.

During the course of the project, the original objectives of this study were extensively modified by the Project Steering Committee to become:

1. To develop an ecosystem model of the West Coast Bioregion of Western Australia, employing the commercial fisheries data that are available for that system.
2. To develop more sophisticated and advanced quantitative techniques for analysing biological data so that more reliable information can be provided to fisheries managers and training in quantitative skills can be provided to postgraduate students.

Both of the revised objectives were achieved during the course of the project.

Methods

Ecosystem study

An ecosystem may be defined as an integrated unit comprising the biota and their environment, which is dependent on the interactions among the individual species within the biota and of those species with their environment. The fundamental concept reflected in this definition is that multiple species are interacting with each other (through predation and competition) and with the environment.

When considering ecosystem-based approaches to fishery management, the effects of fishing on the biota and environment must also be considered. In describing the different approaches that have been applied to modelling such ecosystem effects of fishing, Plagányi (2007) discusses models that focus on interspecies interactions of a subset of the ecosystem, referring to these as Minimally Realistic Models, dynamic models that incorporate the environment and lower trophic levels of the ecosystem, models that include a representation of age and/or spatial structure, and whole-of-ecosystem models that "represent all trophic levels of the ecosystem in a balanced way".

In her review, Plagányi (2007) notes the trade-off between model complexity associated with improved biological realism and the resulting uncertainty associated with inadequate knowledge of functional relationships and imprecise estimates of parameters, and that the "choice of method depends on the question and research objectives". To this might be added the need to increase complexity incrementally, in order that a sound understanding of a simpler model is gained before a new level of complexity is introduced. The need to match model complexity with available data and with the objectives of the study requires that the representation of the ecosystem is far simpler than the system itself. Typically, such simplification involves grouping species into functional groups with similar characteristics, inclusion of only the key components of the system (e.g. some functional groups or environmental influences may be ignored), and ignoring detailed structure (e.g. age, sex, space, time).

Early in the study, staff from the Department of Fisheries advised that modelling of the West Coast Bioregion was more urgent that that of the Peel Harvey Estuary, which had been proposed originally as the focus of modelling in the project application. The former region had become the subject of increasing attention by Fishery Managers and there was increasing need for the development of appropriate reports on the finfish fisheries within this region for Environment Australia. The decision was subsequently made by the Research Steering Committee and endorsed by the FRDC that the West Coast Bioregion, off the south-western coast of Western Australia, would be the focus of the modelling activity in the project. The goal of this component of the study was identified as being the development of a method of modelling the marine ecosystems associated with the fish species that are the targets of fishing, such that traditional fisheries data available to fisheries agencies might be employed in these models and development of such models would not be constrained by the paucity of data for non-target species.

A preliminary set of fishery catch statistics provided by the Department of Fisheries Western Australia was explored to identify more precisely the format and content of the statistics that would be available for the project. The required commercial fishery catch statistics for each estuary and for the south and west coast bioregions of Western Australia (as defined by the Department of Fisheries) were then extracted by the Department of Fisheries for use in the study. The data were summarized and filtered by the Department prior to release to ensure that no confidential information was released. An Access database was created from these catch and effort data and routines were written to extract data from this database in a form suitable for use in the model that was developed in the study.

After considering the range of data available and the objectives of the study, a Minimally Realistic Model using a multi-species biomass-dynamics framework was selected for the ecosystem model of the West Coast Bioregion as this best suited the available data for the fish of this region. No environmental influences were considered to be necessary at this stage of model development. Essentially, the form of model selected for use in this study may be considered a modification of the generalised Lotka-Volterra model. This model, for *m* species in an unexploited system, may be described by the generalised system of differential equations

$$\frac{dB_i}{dt} = \left(a_i + \sum_j b_j B_j \right) B_i$$

where B_i is the biomass for species i and a_i and b_j are parameters that represent the per capita birth, consumption, growth and death (through predation or other factors).

In the simplest case, for an unexploited single species and rewriting the symbols used for the different parameters, this takes the form of the logistic model

$$\frac{dB}{dt} = (a + bB)B = rB\left(1 - \frac{B}{K}\right).$$

For a two species predator-prey system, again re-writing the symbols, the respective equations for the prey and predator species are

$$\begin{aligned}\frac{dB_1}{dt} &= rB_1 - dB_1B_2 \\ \frac{dB_2}{dt} &= edB_1B_2 - M_2B_2\end{aligned}$$

Such models may be extended to include exploitation by subtracting terms of the form, $q_iE_iB_i$, from the rate of change in biomass for each species, i, where q_i represents the catchability of that species and E_i is the effort employed to catch the species.

The Ecosim model has a similar formulation, but extends the representation of the system to include the possibility of immigration and emigration. Pauly *et al.* (2000) describe the structure of Ecosim as a set of coupled differential equations of the form,

$$\frac{dB_i}{dt} = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_i$$

where B_i, g_i, I_i, M_i, F_i and e_i are the biomass, growth efficiency (*i.e.* increase in biomass per unit of biomass consumed), immigration, natural mortality, fishing mortality and emigration rates for species i. The term C_{ij} represents the consumption rate of the biomass of species j consumed by species i, where

$$C_{ij} = \frac{v_{ij} a_{ij} B_i B_j}{v_{ij} + v'_{ij} + a_{ij} B_j}$$

and v_{ij} and v'_{ij} determine the rates of interchange between invulnerable and vulnerable states for the fish of species *i*, while a_{ij} is the rate of effective search by the predator species *j* for the prey species *i*.

The Ecosim model is commonly used to represent a large portion of the food web, ranging from primary producers and detritus to top predators, and thereby allows an initial estimate of parameters to be obtained from the assumption of mass balance that is employed by Ecopath. However, a subset of these equations for the individual species could be used to represent a multi-species subset of the fauna within the ecosystem. For this to provide an internally-consistent and complete representation of that multi-species component of the marine ecosystem, terms and factors representing the biomasses and consumption of species that are not considered in the multi-species model would need to be replaced by parameters or functions of the biomasses of those species included within the model.

Further alternative forms of biomass dynamics model may be defined. An extension of the generalised Lotka-Volterra multi-species model, which is proposed for use in this study, first describes the biomass dynamics of each species using single-species logistic models. These initial models may then be extended to multi-species models, and finally to a full ecosystem model, by progressively combining the various species in the representation. This model "borrows" from the Ecosim formulation in its representation of consumption and predation but avoids the use of states in which the biomass of a species is invulnerable to predation. Instead, as in the simple logistic or two-species Lotka-Volterra models, the model assumes that there is an additional resource that is solely available to each species and that each species is constrained by a carrying capacity, *i.e.* by density-dependent processes. A description of this model is presented below.

The fishing mortality rate on species *i*, *i.e.* F_i, is assumed to be proportional to the fishing effort *E*, and thus $F_i = q_i E$, where q_i is the catchability of species *i*. As with fishing, the mortality rate of species *i* that arises from its predation by species *j* may be assumed to be directly proportional to the biomass of species *j*. That is, if a_{ij} is the rate of effective search by the predator species *j* for a prey species *i*, then the resultant mortality rate is $a_{ij}B_j$, and the rate of consumption of species *i* by species *j* is $C_{ij} = a_{ij}B_iB_j$, where consumption is reduced proportionally if $\sum_{i=1}^{n} a_{ij}B_i > \frac{Q}{B_j}$ where $\frac{Q}{B_j}$ is the annual consumption per unit of biomass of species *j*. It is assumed that, in the absence of fishing or predation by those species included in the ecosystem model, other non-represented factors will constrain the growth of species *i*. This is represented in the model by a density-dependent mortality of species *i* that is written as $M_i = m_iB_i$, a simple linear function of biomass.

It is assumed that the rate of growth in biomass is related to the assimilation of the biomass of prey that is consumed. Thus, if g_i is the growth efficiency, then the contribution to the rate of growth of species *i* due to its predation of species *j* is g_iC_{ji}, *i.e.* $g_ia_{ji}B_iB_j$. Again, it is assumed that species *i* may consume species that are not represented within the equations of the ecosystem model, and thus an additional term, r_iB_i, is included in the model to represent such consumption.

The ecosystem is represented by the system of *n* differential equations

$$\frac{dB_i}{dt} = \left(r_i + g_i \sum_j a_{ji}B_j - \sum_j a_{ij}B_j - m_iB_i - F_i \right) B_i$$

where *n* is the number of functional groups of species that are represented by the model. In the simplest form, where a single species or functional group is considered, this model takes the form of the logistic equation, where $m_i = \frac{r_i}{K_i}$. The model represents a system that is closed to emigration and immigration, and is similar to the Ecosim formulation. However, rather than assuming that there is exchange between an invulnerable and vulnerable state for predation and that natural mortality is constant, all fish are considered vulnerable and "natural mortality" is assumed to be density dependent. The parameters of the model are r_i, g_i, K_i, B_{0_i}, q_i, $\frac{Q}{B_i}$, and a_{ij}, where $i = 1, \cdots, n$, and $j = 1, \cdots, n$. The number of parameters that must be estimated may be reduced, however, when, for example, diet composition data indicate that certain functional groups are unlikely to be predated by other functional groups, or reliable estimates of the parameters are available. In a future implementation of the model, penalty functions will be introduced to constrain predicted values of dietary composition to those recorded in dietary studies for the same years.

It should be noted that, in this sense, “natural mortality” represents the decline in the net per capita rate of biomass increase, *i.e.* $r_i - m_i B_i$, that accompanies the increase in biomass. Thus, in the logistic sense, this expression becomes zero when the biomass reaches the carrying capacity for the stock.

By representing the system in this form, which allows for species that are not represented within the system of equations, the model can be extended from a single species model to a multi-species model, and finally to a model that represents those aspects of the ecosystem for which data are available. It should be noted that, at this stage of development, the model has not been extended to consider the spatial distribution of the various species or of fishing effort, or the influence of environmental variables.

Application of biomass dynamics model to the marine ecosystem of south-western Australia

Commercial catch and fishing effort data for the West Coast Bioregion from 1975 to 2001 (Department of Fisheries Catch and Effort System) were extracted from the Access database for those species that contributed the greatest total catches over this period.

In forming functional groups of species to be represented in the model, the advice given by Christensen *et al.* (2000) was followed, *i.e.* species should be aggregated such that they have similar sizes, growth and mortality rates, and have similar diet compositions. The resulting “functional groups” are intended to represent taxonomically- or ecologically-related groups of species. Christensen *et al.* (2000) further advise that the parameters for EcoPath/EcoSim that should then be used for the groups are the weighted means of the parameters for the component species, where the biomass of each species is used as its weighting factor.

Thus, species for the West Coast Bioregion were classified into functional groups using such criteria as the habitat that they occupy, their size, and likely prey and predator species. Dietary details for these fish species were surprisingly sparse, considering the importance of the target species to the commercial and recreational fishers in this region. Qualitative information on the species composition of diets was drawn from reviews such as provided by Kailola *et al.* (1993) or extracted from FishBase (Froese & Pauly, 2003). A food web was derived from the available data on diets of the commercial fish species in this West Coast Bioregion. This web was extended to include plankton, detritus, birds and pinnipeds, however these latter functional groups are represented only implicitly in the model that was developed.

Implicitly, the functional groups should represent species that have similar trophic levels, diets, consumptions per unit of biomass, natural mortalities, and stock-recruitment relationships. Furthermore, they should display similar response to fishing mortality and experience similar time series of fishing mortalities. However, the catches per unit of effort (cpues) of the different species within each of the functional groups were often poorly correlated. Moreover, as the measures of effort used to calculate the catches per unit of effort were often based on different fishing gears and estimates of biomass were unavailable, it was not possible to calculate a weighted average based on the biomasses of the different species. The catches per unit of effort for the different species within each functional group were combined by selecting the effort time series for one of these species (usually that with the greatest average annual catch) as a "standard" for the group, then calculating a conversion factor for the effort measures used for each of the other species using the average of the ratios of the annual catch rates for that species and for the standard species. The annual effort for the other species was then "standardized" and the overall annual cpue was calculated as the sum of the catches of the different species in the functional group divided by the sum of the standardized efforts for these species. Note that this approach implicitly assumes that the amounts of fishing effort for each species were independent.

An initial version of the ecosystem model for the West Coast Bioregion was obtained by treating the cpue for each functional group as the dependent variable of a multi-species biomass dynamics model. The annual values of the intrinsic rate of increase and the instantaneous rate of natural mortality were calculated from the cpues of the other functional groups, which were taken, together with annual catch, as independent variables in this dynamic model. The cpues used in the calculation of the rate of increase were restricted to those of the functional groups considered to constitute the prey for the selected functional group, while those used in the calculation of natural mortality were restricted to the functional groups considered to be the predators for the selected group. An additional constant rate of increase and constant level of natural mortality were used to represent groups that had not been explicitly incorporated in the model. These, together with an assumption of a carrying capacity, ensured that the model for each group was reasonably "realistic".

The ecosystem model was then fitted simultaneously to the data and equations for the nine functional groups in the marine ecosystem of the West Coast Bioregion of WA. For this, 104 parameters were required to be estimated. Because of the inter-dependence of the functional groups, the resulting system is relatively stiff and parameter estimation is time consuming. After testing a number of approaches, the amoeba routine was adopted for use in parameter estimation. This function-minimization algorithm, which was described by Nelder and Mead (1965), "moves" a set of trial points over the multi-dimensional surface towards the minimum in a manner similar to the movement of an amoeba "flowing" over a three-dimensional surface. However, it was noted that, with this algorithm, the parameter set often became trapped at a local minimum (thereby producing biased parameter estimates) and that it was necessary to refit the model using numerous random starting points to determine the global minimum (*i.e.* the best parameter estimates), suggesting that a simulated annealing approach, which incorporates a progressively-refined random search over the parameter space in its algorithm and is thus less likely to become trapped at a local minimum, might be more appropriate for fitting the model. The data input to the model for the West Coast Bioregion was then modified by removing Dhufish from the "Large demersal fish" category and re-inserting it, together with other "Large demersal fish", as separate "functional groups", and the model was re-fitted.

To allow compilation and thereby improve performance, the routine used to fit the ecosystem model was converted to Visual Basic 6. Additional code was then added to enable fitting of the model to the time series of data while constraining the level of biomass for a specific functional group within a specified year to a particular value. For this, a penalty function was introduced to penalise estimates of biomass that deviated from the specified level. The objective function was changed to calculate and use log-likelihood rather than the sum of squared deviations of estimated from observed catches per unit of effort, where this log-likelihood was calculated separately for each time series of catch per unit of effort data and the results then summed over the various functional groups. While the fitted model used non-transformed cpues, a logarithmic or other transform could be easily applied. Using the modified routine, it was possible to fit the model while constraining the biomass of the selected group in the specified year to each of a series of distinct levels, thereby allowing the generation of an approximation to the likelihood profile, from which approximate values of the 95% confidence limits of the biomass could be estimated. The routine was applied to the estimate of biomass for Dhufish in 2000. Subsequently, on noting that the results of this analysis suggested that fitting had terminated prematurely, the fitting algorithm was modified further to incorporate a mixture of techniques and to allow more thorough exploration of the likelihood surface.

A copy of the Visual Basic source code for EcoPath/EcoSim, which was kindly provided by Villy Christensen (University of British Columbia), was examined to confirm that it possessed the ability to generate synthetic data, which could be used to assess the performance of the ecosystem model that had been developed at Murdoch University during the current FRDC study (termed the Murdoch model in the subsequent text). A number of existing models for different fisheries/systems are included in the database that is supplied with the EcoPath/EcoSim software and further models may be downloaded from the UBC site. These provide a range of "marine ecosystems" for which synthetic fisheries data may be generated. The EcoPath/EcoSim code has an option in the procedure, RunModel of Sim.bas, that allows the results of a simulation run to be saved, with the biomass of each functional group at each time step being output to a file and the catches of each functional group taken by each gear type during each time step being output to a separate file. Examination of the source code and results produced by EcoPath/EcoSim demonstrated that the biomass and catch data for each functional group, which are output by this software, could serve as a set of synthetic data with which to test the Murdoch model. That is, EcoPath/EcoSim could generate an index of abundance (to which "observation error" might be added) and total catch for each exploited functional group for a specified effort scenario, and for which the biomass of each functional group at each time step was known and responded in a manner consistent with the dynamics of the simulated ecosystem.

The Murdoch model was "validated" by fitting it to the first 20 years of simulated data generated by an EcoPath/EcoSim model then comparing the Murdoch model's predictions to the values of the simulated data from the subsequent 20 years. For this, an EcoPath/EcoSim model for "Canada, Northern Gulf of St. Lawrence - 1980s" was selected from those available on the EcoPath/EcoSim web site. The fishery described in this EcoPath/EcoSim model targets large Cod and, to a lesser extent, redfish. Small planktivorous pelagic fish and shrimp are also caught, together with a number of bycatch species. The ecosystem described by the model represents that which was present prior to the collapse of the Atlantic Cod fishery in the late 1980s. After balancing the model in EcoPath, a simulation spanning 40 years was run using EcoSim and applying an arbitrarily-selected fishing pattern that displayed two peaks in effort. The data resulting from this run were saved to be used as input to subsequent analyses using the Murdoch model. It should be noted that, with the exception of the cpues for Cod, the cpues generated by EcoPath/EcoSim typically remained relatively stable or increased as the Cod stock declined under the specified fishing effort regime.

The data produced by EcoSim are output in several files, two of which were used in this study. The first of these files provided details of the average biomass of each functional group and average time-dependent fishing mortality imposed on that group at each of the time steps within each year of the simulation. The second file contained the details of the annual fishing effort and landings of each functional group that were used in this study. The data produced by EcoSim were divided into two sets, each ranging over 20 years. The first 20 years of data were used in fitting the Murdoch model , while the second 20 years of data were used as the reference against which predictions produced by the Murdoch model were compared, thereby exploring the extent to which this model provided an adequate prediction of the ecosystem's response to fishing.

Only a subset of these functional groups included in the Gulf of St Lawrence model were analysed using the Murdoch model, as it is assumed that, in many cases, the data likely to be available in Australian fishery agencies for developing ecosystem models will be those collected during fishing operations. Thus, the data from the EcoPath/EcoSim functional groups were combined into a smaller number of groups for use in this study.

The Murdoch model was applied directly to the data produced by EcoPath/EcoSim, assuming no observation error, thereby determining the capability of the Murdoch model to reflect the trends in abundance of the different functional groups included in the analysis. While log-normal (or other) observation error could have been added to the synthetic data to allow exploration of the sensitivity of model predictions to such error, it was considered more important to determine whether the simplified model structure used in the Murdoch model was capable of representing the dynamics of the ecosystem as produced by the EcoPath/EcoSim model. It was thus assumed that the median values of the predictions that could have been obtained by fitting the Murdoch model to multiple data sets generated using different sets of randomly-selected observation errors would be likely to reflect the results obtained by fitting the

Murdoch model directly to the data generated by the EcoPath/EcoSim model without the addition of such observation error.

The starting values of the estimates of biomass used in fitting the Murdoch model were obtained through the use of single-species biomass dynamics models. For these analyses, the intrinsic rate of natural increase was set as twice the instantaneous rate of natural mortality for the various species. This latter figure was taken as the natural mortality of one of the more important species in the functional group or, in the case of the crustacea or molluscs was arbitrarily set to 0.8 $year^{-1}$. The Murdoch model was then fitted using the resulting starting values for the parameters.

Projections of the values of cpue predicted by the Murdoch model were plotted over the five years immediately following the twenty years of data to which the model was fitted, and then over the subsequent twenty years, to compare the extent to which projected values matched those generated by EcoPath/EcoSim over short and long terms. The values of effort used when generating the EcoPath/EcoSim data were also applied when calculating the projected values of cpue using the Murdoch model.

Development of quantitative techniques

The training that was offered to Postgraduate and Honours students was specifically tailored to the needs of the different students, and was related to the data analyses that those students were undertaking. A deficiency of many formal courses undertaken by students is that the courses provide information that is forgotten by the student before it can be used. By providing the information at a time when it is being applied, the training is more likely to be effective. The majority of postgraduate research students in the Centre for Fish and Fisheries Centre at the South Street Campus of Murdoch University were engaged in studies of the population biology of selected fish species, particularly in studies of the growth and reproduction of those species. Thus the focus of the quantitative approaches that were introduced to these students was the use of aspects of modelling that related to the analyses required in this field.

Note that the results of this component of the study are the methods that were developed or used when analyzing the students’ data. Accordingly, rather than including the descriptions of these in the Methods section of this report, they are reported in the Results section.

Results/discussion

Ecosystem study

Examination of the commercial fishery catch statistics that were kindly supplied by the Department of Fisheries, and preliminary exploration of these data using the EcoSim software, suggested that the ecosystem models for the south western bioregion of Western Australia would need to be based on the biological data that exist for the target species and tuned to the catch and effort data from the commercial fishery. Interactions between the species would need to be imposed through assumptions derived from the available dietary information, much of which comprised qualitative data on broad species composition rather than quantitative data, and the uncertainty associated with such assumptions would need to be explored. There were insufficient data on the non-target species to allow estimation of the many parameters that would be required to incorporate these species (or groups) explicitly within the models.

The commercial species that contributed most to the commercial fisheries landings of the West Coast Bioregion between 1975 and 2001 are listed in Table 1, together with the functional groups to which these species were assigned. The food web, which is represented by these functional groups and reflected in the species composition of their diets, is presented in Figure 1.

In classifying the species shown in Table 1 into functional groups, consideration was given to the habitats occupied by the species, their sizes, and likely prey species. Parameters such as consumption per unit of biomass, natural mortality and trophic level (where available) were also considered. In this, the values of trophic levels reported in FishBase were applied. When consumption per unit biomass was plotted against natural mortality or trophic level, species classified into the same functional groups appeared to cluster together. However, the catches per unit of effort (cpues) of the different species within each of the functional groups were often poorly correlated (for example, the correlation coefficient for the Pink Snapper and Dhufish time series shown in Fig. 4 was -0.41 (P>0.05)).

Other problems encountered in this analysis were that the data were influenced by management initiatives (*e.g.* Southern Bluefin Tuna), unusual events (*e.g.* mortality due to the Pilchard virus) and the fact that the catch and effort data recorded by commercial fishers are based on market categories rather than according to the scientific names of the different species.

The results obtained by fitting the initial version of the ecosystem model for the West Coast Bioregion are shown in Fig. 5, where this model treated the cpue of each functional group as the dependent variable and the cpues of the remaining functional groups as values of independent variables (without error). Unexpectedly, the observed cpues for almost all groups appear to have increased. While the trends of the estimates of cpue matched those of the observed cpues for cephalopods, crustaceans, small pelagic fish, benthic sharks and rays, and pelagic sharks, the fits for the other groups were poor. Similar trends were shown by the (re-scaled) cpues when the ecosystem model was fitted simultaneously to the data for the nine functional groups (Fig. 6). In neither case did the model have the ability to respond to the marked inter-annual changes in abundance shown by functional groups such as those displayed by the large pelagic fish.

Table 1. Fish, crustacean and mollusc species exploited by commercial fishers in the West Coast Bioregion of Western Australia and the associated functional groups in the marine ecosystem of this region to which these species have been assigned. These species are those that have contributed most to the commercial landings from 1975 to 2001.

Functional group	***Species***	***Trophic level***
Bivalve and gastropod molluscs	Saucer scallop	
	Mussels (aquaculture)	
	Roe's abalone	
	Scallop, pecten	
Cephalopods	Octopus	
	Squid	
Crustaceans	Western rock lobster	
	Blue swimmer crab	
	Western king prawn	
	Prawns (other)	
Large demersal fish	Pink snapper	3.3
	West Australian dhufish	4.3
	Cod	3.9
	Snapper - North-west (L.)	3.3
	Snapper - norwest/spangled emperor	3.3
	Queen snapper	
	Emperor, sweetlip	3.5
	Baldchin grouper	
Small pelagic fish	Pilchard	2.1
	Whitebait	3.4
	Anchovy	3.0
	Blue sprat	3.4
	Maray	3.5
	Scaly mackerel	2.5
Large pelagic/benthopelagic fish	Southern bluefin tuna	3.9
	Spanish mackerel	4.5
	Samson fish	
	Western Australian salmon	4.2
	Yellowtail kingfish	4.8
	Trevally, other (skippy)	3.2
Medium-sized fish (benthic/bentho-pelagic/pelagic)	Sea mullet	2.1
	Perth herring	3.4
	Western sand whiting	3.2
	Australian herring	4.3
	Yellowtail scad	
	Sea garfish	2.7
Benthic sharks, skates and rays	Skates and rays	
	Whiskery	3.8
	Wobbegong	4.2
	Gummy	4.3
Pelagic sharks	Bronze whaler	4.5
	Thickskin	4.5
	Hammerhead	4.5
	Blacktip	4.2
	Sharks (other)	

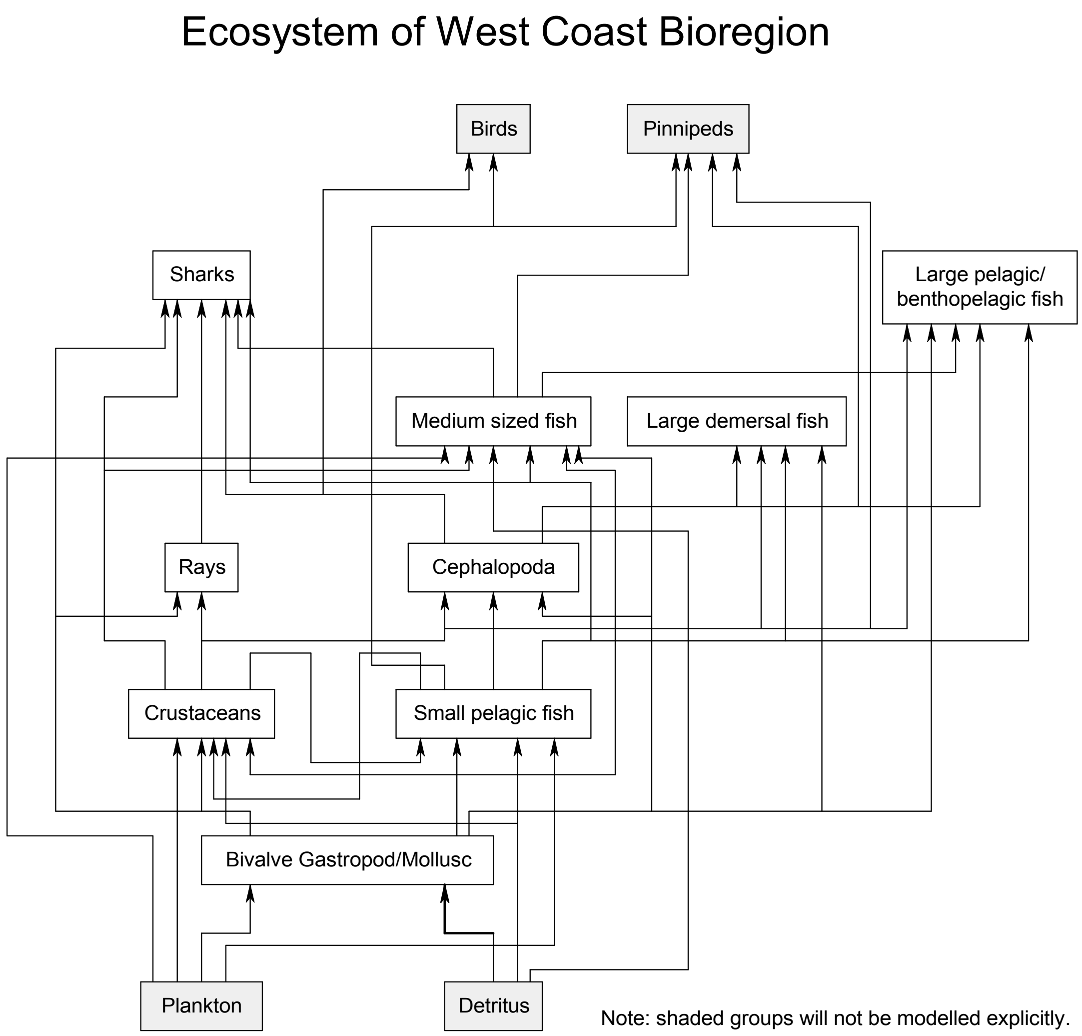


Figure 1. The marine ecosystem of the West Coast Bioregion of Western Australia. The non-shaded functional groups are those that are to be included within the proposed ecosystem model for this region.

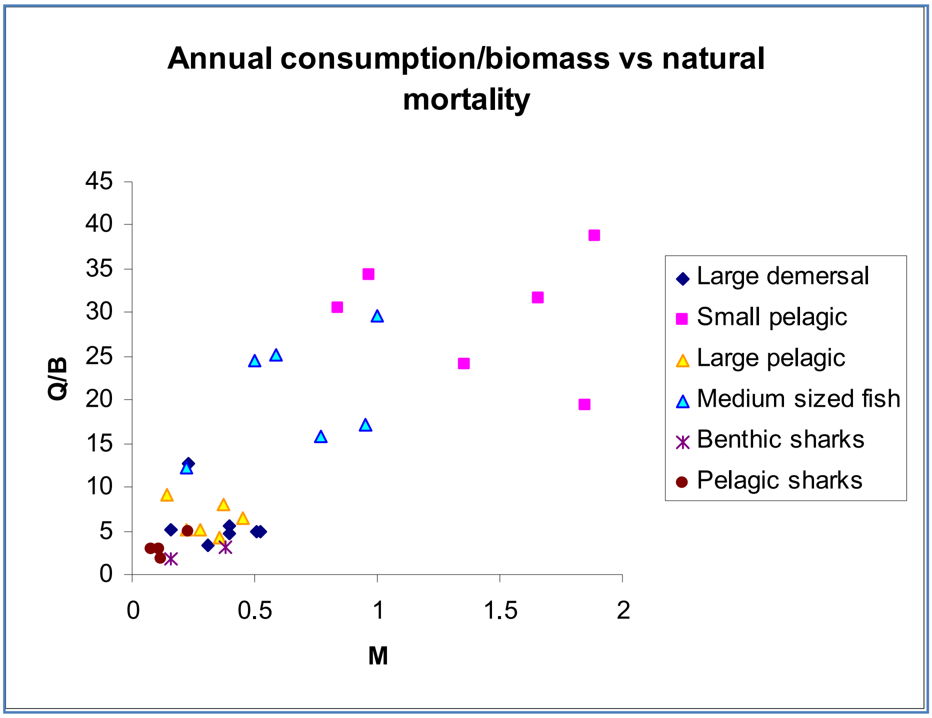


Figure 2. Plot of the consumption per unit of biomass, *Q*/*B*, versus natural mortality, *M*, for fish species from the West Coast Bioregion of Western Australia.

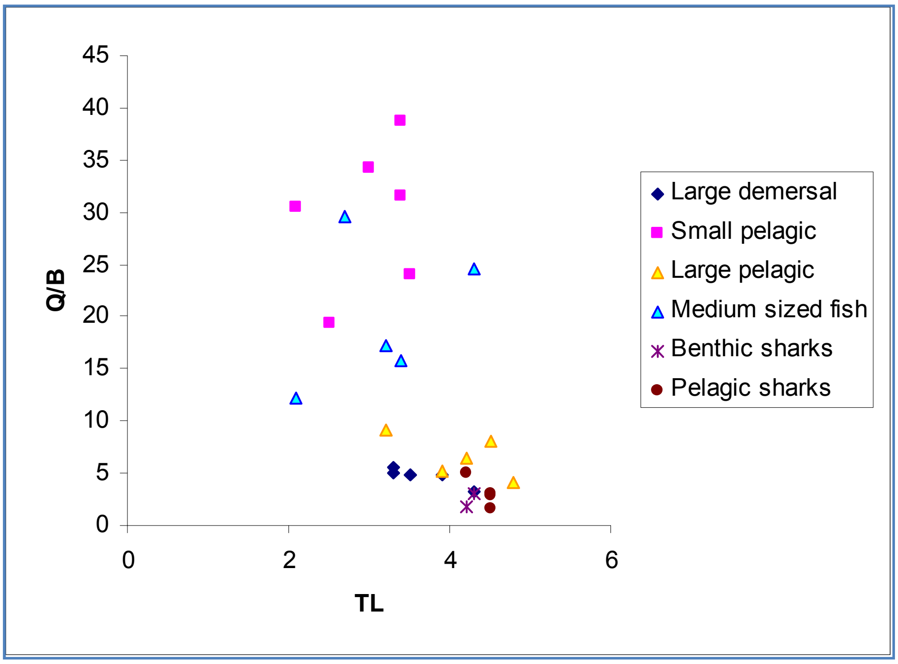


Figure 3. Plot of the consumption per unit of biomass, *Q*/*B*, versus trophic level, TL, for fish species from the West Coast Bioregion of Western Australia.

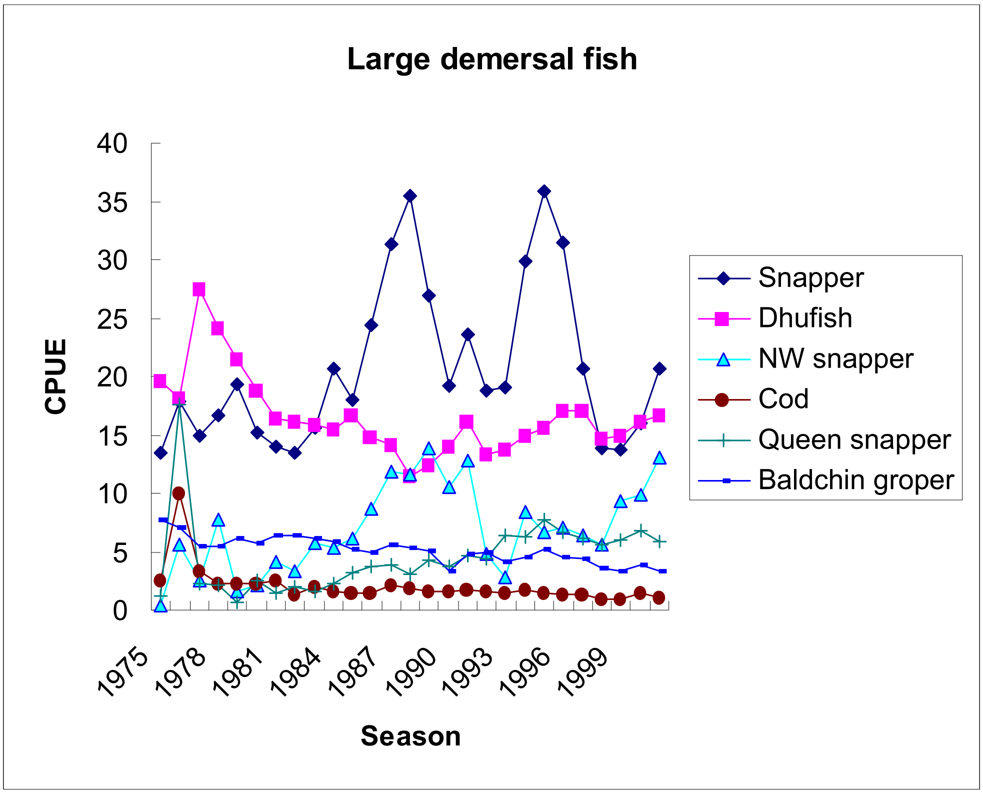


Figure 4. Annual catches per unit of effort (with various units) for six of the large demersal finfish species of the West Coast Bioregion of Western Australia. The measure of effort differs among the species and thus the figure displays trends in "abundance" of the individual species but does not allow comparison of the abundances of the different species.

The ecosystem model was fitted to data that had been modified by removing Dhufish from the "Large demersal fish" category and including it, together with "Large demersal fish", as a separate "functional group". The estimates of cpues for the functional groups were similar to those presented in Fig. 6. A good fit to the cpue data for Dhufish was obtained (Fig. 7). However, the trend of the estimates of cpue for large demersal fish was still a poor fit to the trend exhibited by the observed data, and was similar to that obtained when Dhufish were included in the functional group (*cf.* Figs 6 and 8).

The profile of relative likelihoods of a range of values of the biomass of Dhufish in 2000 was calculated and plotted (Fig. 9). The results suggested that the 95% confidence limits for the biomass ranged from 17,760 to 17,930 tonnes, with the annual commercial catch in 2000 being 194 tonnes. Note that the model was unable to produce feasible estimates when the biomass was

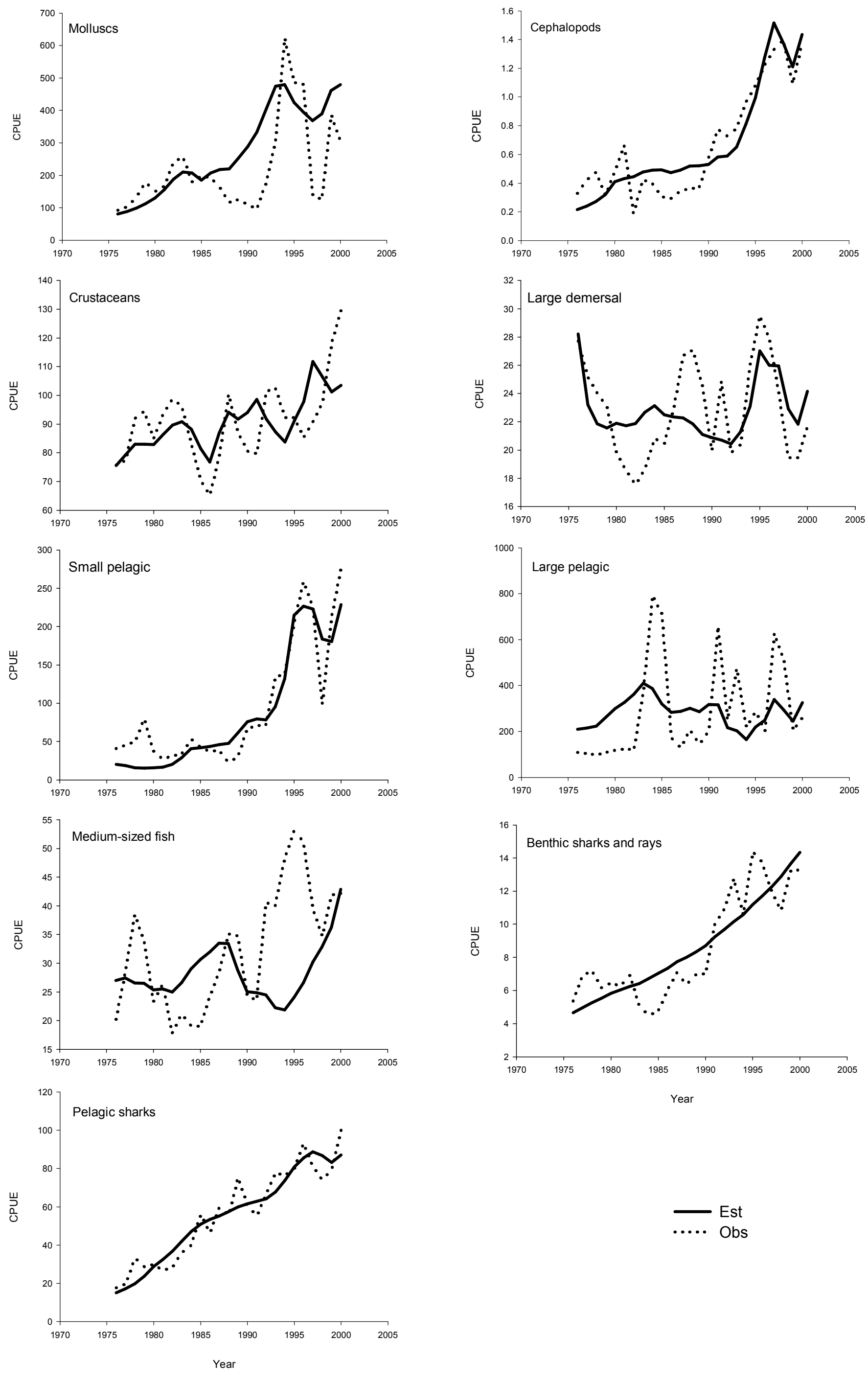


Figure 5. Results of fitting multi-species biomass dynamics models independently to each of the functional groups in the marine ecosystem of the West Coast Bioregion of Western Australia.

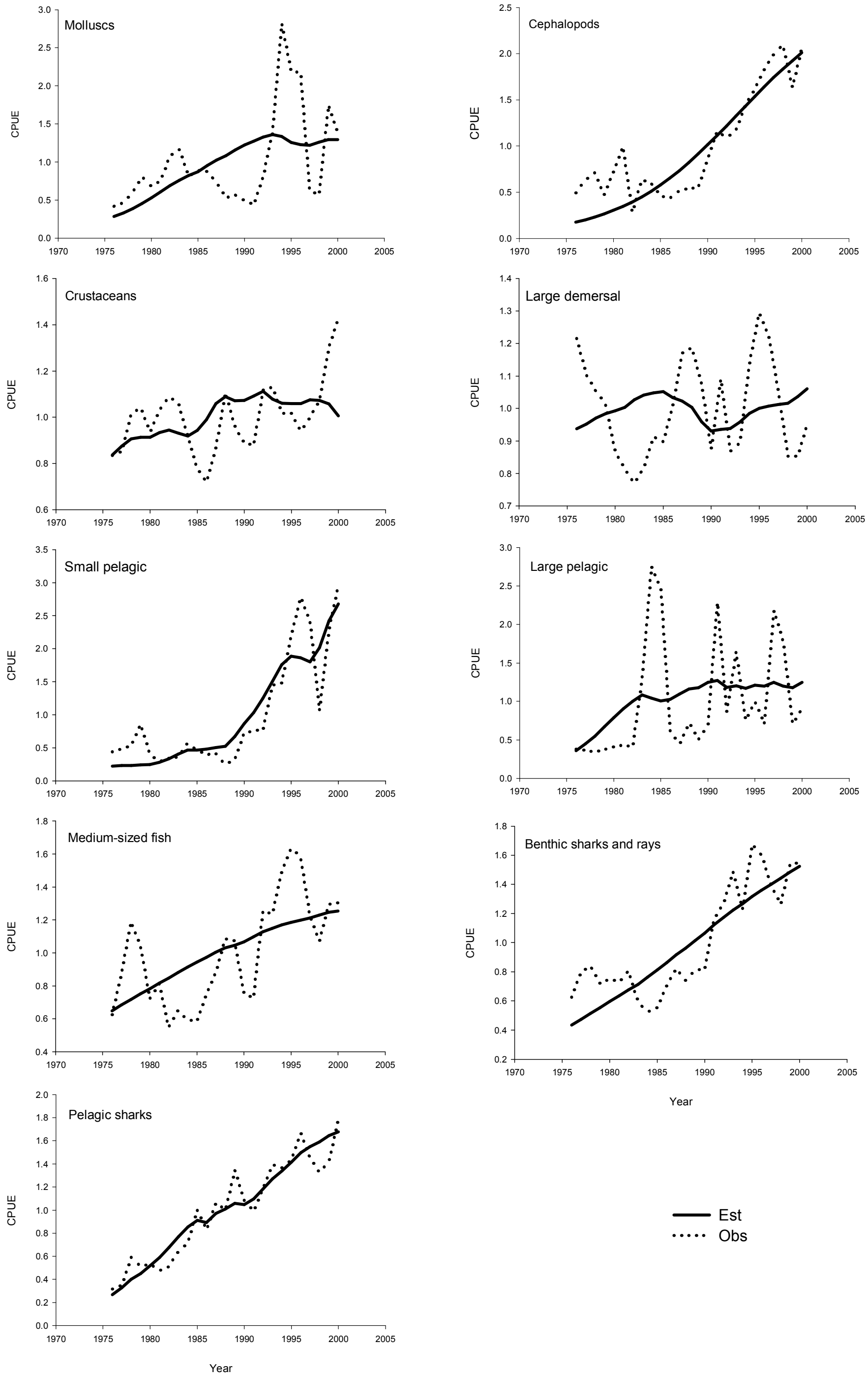


Figure 6. Results of fitting the marine ecosystem model for the West Coast Bioregion of Western Australia.

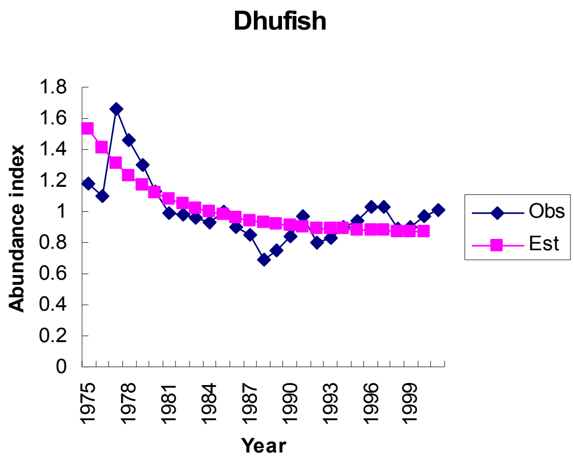


Figure 7. Time series of scaled catch per unit of effort data for Dhufish in the West Coast Bioregion and values of this index estimated by the model.

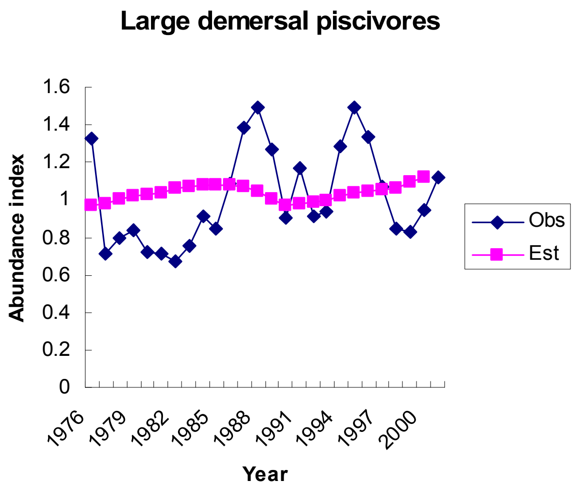


Figure 8. Time series of scaled catch per unit of effort data for large demersal piscivores in the West Coast Bioregion and values of this index estimated by the model.

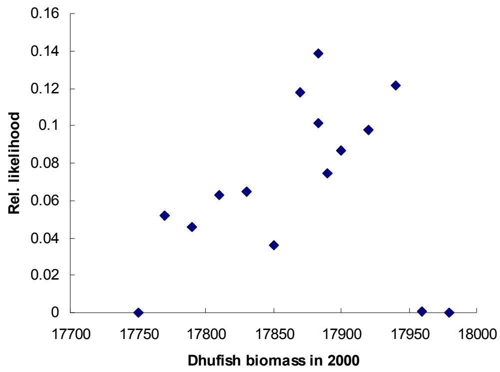


Figure 9. Plot of the relative negative likelihood of the time series of catch per unit of effort data for the different functional groups in the West Coast Bioregion when the Dhufish biomass in 2000 was constrained to different values.

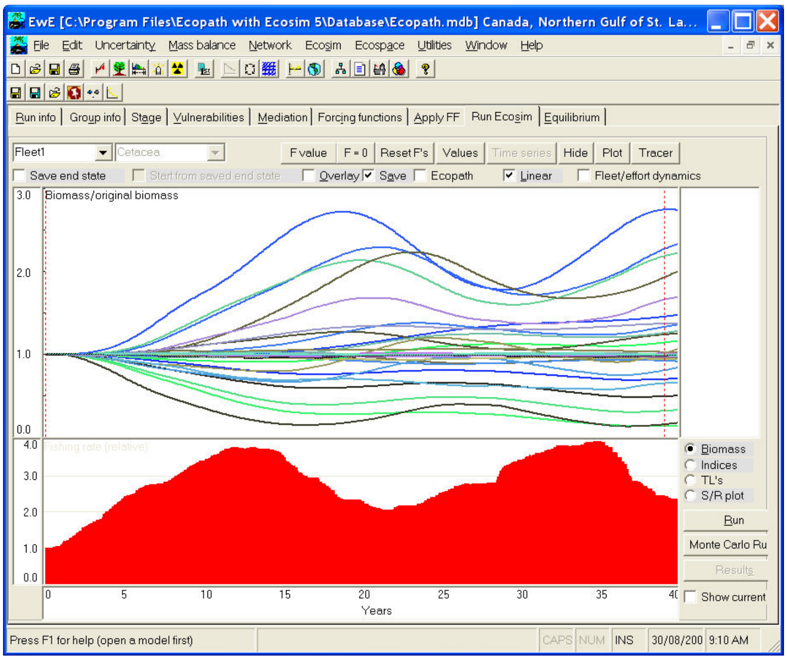


Figure 10. Plot of fishing effort time series used to generate 40 years of synthetic data for a "fishery" exploiting species from the ecosystem which was present in the northern Gulf of St Lawrence, Canada, in the 1980s.

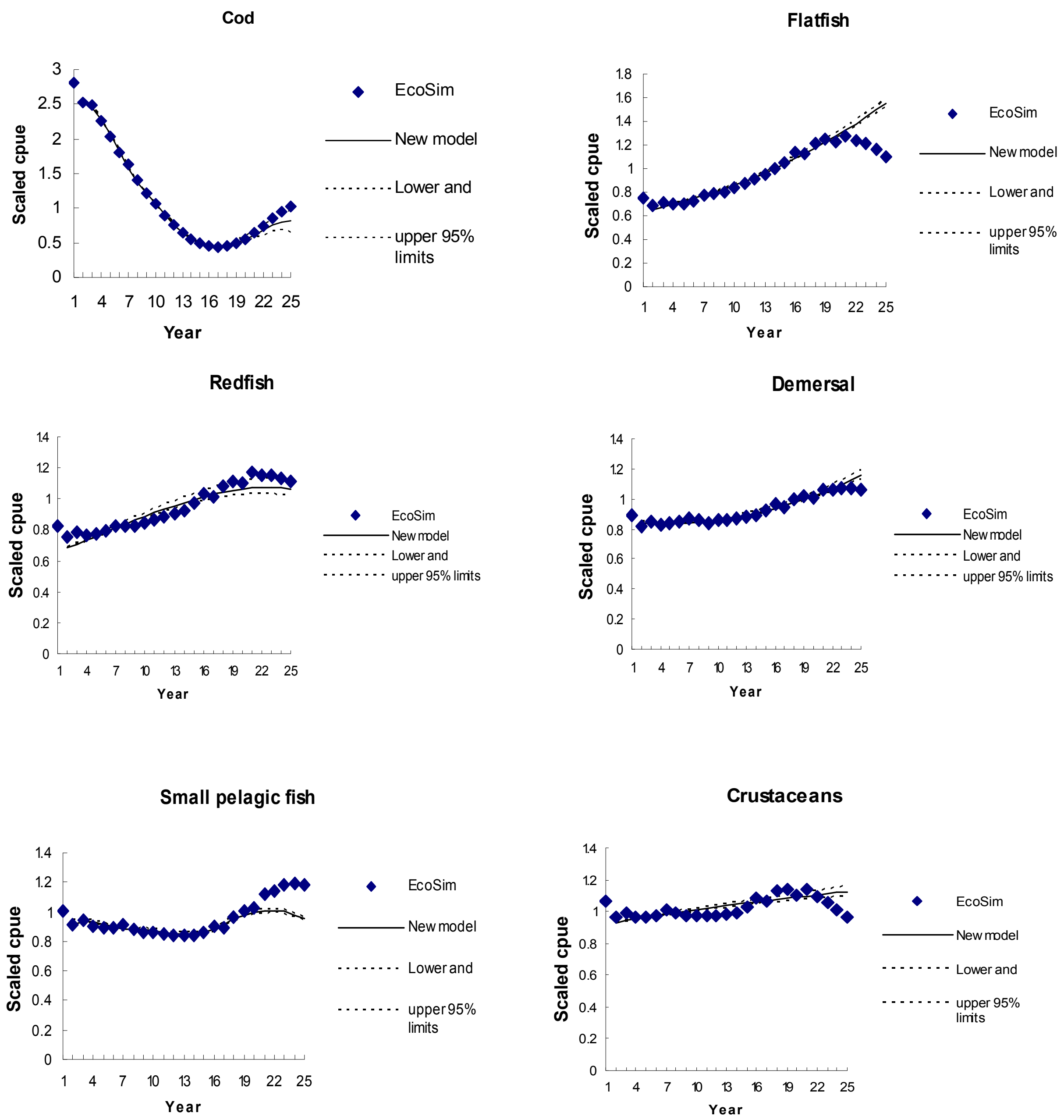
Table 2. Details of the functional groups used in the EcoPath/EcoSim and Murdoch models.

Functional groups used in EcoPath/EcoSim	***Functional groups used in Murdoch model***
Cetacea	
Harp seals	
Hooded seals	
Grey seals	
Harbour seals	
Seabirds	
Large cod	Cod (large and small)
Small cod	As above
L. Greenland halibut	Flatfish (L. and S. Greenland halibut, American plaice, Flounders and Skates)
S. Greenland halibut	As above
American plaice	As above
Flounders	As above
Skates	As above
Redfish	Redfish
L. demersals	Demersal (L. and S. demersal)
S. demersals	As above
Capelin	As above
Sand lance	As above
Arctic cod	As above
L. pelagics	
S. pisciv. pelagics	Small pelagics (piscivorous and planktivorous)
S. plankt. pelagics	As above
Shrimp	Crustacea (shrimp and large crustacean)
Large crustacea	As above
Echinoderms	
Molluscs	Molluscs
Polychaetes	
Other bent. invert.	
Large zooplankton	
Small zooplankton	
Phytoplankton	
Detritus	

set to 17,750 or values greater than 17,960 tonnes. However, the scatter of the points in this plot revealed that the routine was still difficult to fit and, in some cases, terminated prematurely. It is possible that, with further analysis, *e.g.* “jittering” the starting values of parameter estimates, values of the relative likelihood might be derived for these values of biomass. Subsequently, the fitting algorithm was modified to incorporate a mixture of techniques and to explore the likelihood surface more thoroughly.

The model, "Canada, Northern Gulf of St. Lawrence - 1980s" was downloaded from the EcoPath/EcoSim web site. After balancing the model in EcoPath, a simulation spanning 40 years was run using EcoSim and applying a fishing pattern that displayed two peaks in effort (Fig. 10). The data from this run for each of the functional groups used in the EcoPath/EcoSim model were saved and used to derive the input data for the functional groups used when fitting and projecting the Murdoch model (Table 2).

The Murdoch model provided an excellent representation of the trends in cpue data for the Cod, flatfish, demersal and small pelagic fish over the first twenty years and, although it failed to capture the trends for redfish, crustaceans and molluscs as faithfully as for the other species, the fit to the first twenty years of data was adequate (Fig. 11). In assessing the quality of fit, it should be noted that all data sets are fitted simultaneously, allowing for the interactions among the different species. Thus, the result should not be judged on the basis of the fit for a single functional group but must be assessed on the combination of the fits to all functional groups. Under this criterion, clearly the Murdoch model has provided a good representation of the data to which it was fitted. Predicted values for the first few years of the forward projection are adequate (Fig. 11). Projected values, however, begin to deviate from the values generated by EcoPath/EcoSim, with the deviation increasing as the lead time of the prediction is increased and becoming particularly evident as the lead time is extended from five to 20 years (*cf.* Figs 11 and 12).



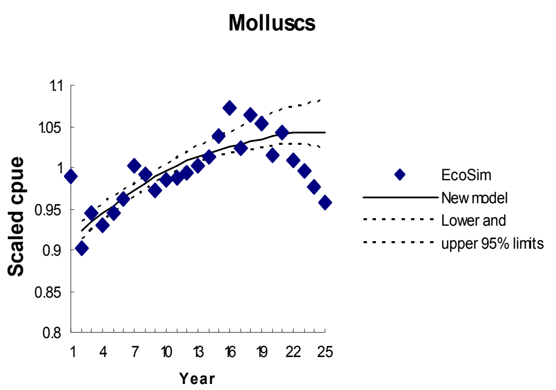
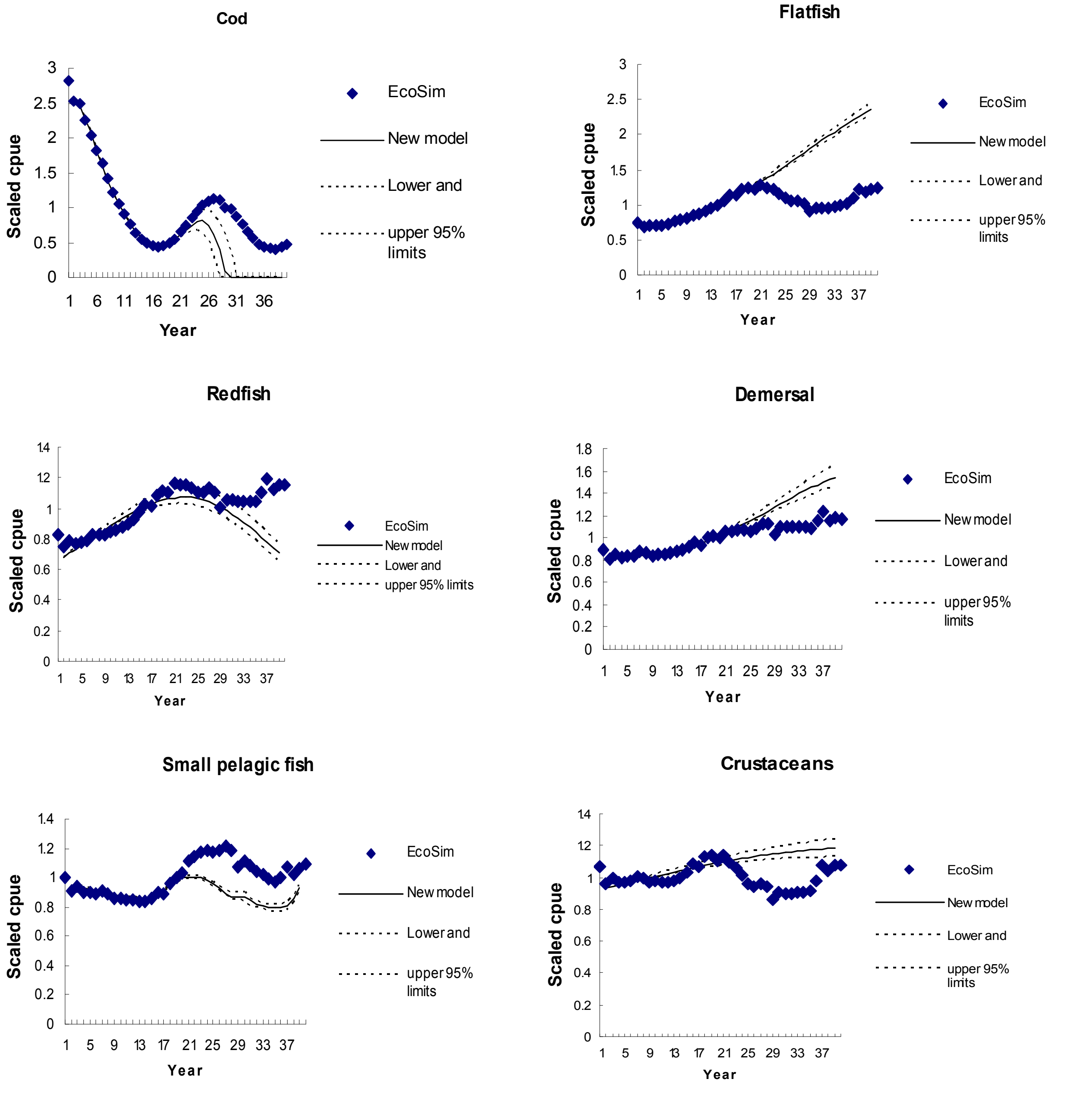


Figure 11. Comparison of the scaled values of cpue predicted by the Murdoch model with those values generated by EcoSim/EcoPath. The Murdoch model was fitted to the first 20 years of data to which the former model was fitted. Estimates of cpue for the next five years were predicted using the values of effort applied when generating the EcoSim/EcoPath data.



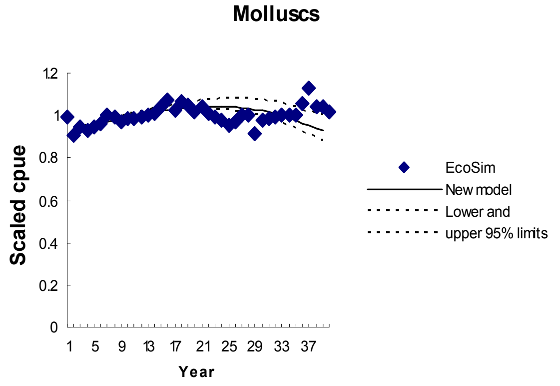


Figure 12. Comparison of the scaled values of cpue predicted by the Murdoch model with those values generated by EcoSim/EcoPath. The Murdoch model was fitted to the first 20 years of data to which the former model was fitted. Estimates of cpue for the next 20 years were predicted using the values of effort applied when generating the EcoSim/EcoPath data.

Discussion of ecosystem modelling

The biomass dynamic representation of the ecosystem presented by the Murdoch model may be regarded as providing a relatively-simplistic description of the dynamics of those components of the ecosystem for which adequate time series of data are available. The model differs from EcoPath/EcoSim in that it has a simpler model structure, deals with a smaller subset of the species and functional groups within the ecosystem, and requires less data. The lack of a detailed description of non-target species in the Murdoch model reflects the limitations of data rather than a limitation of the model. In the absence of quantitative dietary data for some functional groups, it would be impossible even for an ecosystem model such as EcoPath/EcoSim to extrapolate reliably for those functional groups the consequences of changes in exploitation for target functional groups. Even with reliable quantitative information on the interactions among functional groups (usually "snapshots" obtained over specific short time periods), the lack of time series of data for many of the non-target or non-piscivorous functional groups would preclude tuning to describe reliably how these groups had responded to the changes in species composition throughout the history of the fishery.

It would be appropriate to note that, for Ecosim, Christensen (1998) advises that "Parameterization of the model calls for input of three of the following four parameters: biomass, production/biomass, consumption/biomass, and other mortality, for all groups of living organisms discerned in the models. The fourth parameter is then calculated using a set of linear equations so as to ensure mass balance", where quantitative dietary data describe the interactions among the various functional groups of the model. Development of an EcoPath/EcoSim model for the West Coast Bioregion is constrained by the lack of biological data for many of the non-target or less important target species in this region. The lack of quantitative dietary data for many species would introduce considerable uncertainty into such a model. Although estimates of missing parameters for some species could be obtained from sources such as Fishbase, the values of these parameters are often derived from studies relating to stocks from different ecosystems and geographic regions.

A further cautionary note is provided by Larkin (1996), who, after reviewing the current state of ecosystem modelling, concluded that "Realistically, for some time to come, ecosystem models will not be successful in predicting individual species variations in abundance. But what they can provide is a depiction of the interdependencies between trophic levels, which may serve at least as gross indicators of major modifications". A preliminary examination of the catch and effort data from the West Coast Bioregion for some of the more important commercial species indicates that the information content of the available data is likely to be low. Thus, while it is likely that a model can be developed which describes the types of interactions that are occurring in the ecosystem of this region, which is sufficient to explore the effectiveness of alternative reference points and decision rules for management of such a system, this model will not provide the detail necessary to predict reliably the response of a particular species to large changes in the system. Such a conclusion is not unexpected when the food web is examined (Fig. 1), as it is the response of the functional group that is modelled rather than the response of a particular species.

Although the biomass dynamics model of the ecosystem demonstrates the potential of this approach for fisheries management, the limitations of the current data are becoming increasingly evident. A major deficiency of the current model is the lack of catch data for the recreational fishing sector. This lack has currently been ignored, and the model has been applied to the commercial fisheries data without recognition of the impact of the resulting bias in the model outputs. However, the data also reveal a further anomaly, in that the biomass for almost all groups appears to have increased. This appears at odds with reality as most authorities suggest that exploitation has increased considerably over recent decades. There appears to be no ecological basis for the apparent increases in biomasses of the majority of functional groups that are indicated by the data for the West Coast Bioregion. It appears very likely that catchability has increased over recent years, leading to an apparent increase in cpue despite the probable increase in exploitation. Consideration must be given to improving the data sets on which future assessments will rely.

The estimates of cpue produced by the model did not respond to the marked changes in inter-annual abundance of functional groups such as those of the large pelagic fish. The observed changes in cpue for long-lived fish such as the large pelagic fish appear likely to reflect changes in catchability (availability) and/or variability in inter-annual recruitment. While such variability could be allowed for by inclusion of environmental variables and additional parameters, consideration must also be given to the number of degrees of freedom and appropriate model complexity. Additional abundance indices from fishery independent surveys may be required to ensure the adequacy of the data to which the model is fitted.

The addition of an n'th functional group to this ecosystem model requires the use of an additional $2n + 6$ parameters, where $2n - 1$ of these reflect the interactions among species through predator-prey relations. Thus, as Dhufish represented the 10'th functional group, 27 degrees of freedom were lost by its introduction. The total number of parameters in the current model is $n^2 + 7n$, where the number of functional groups, *n*, is currently 10, *i.e.* 170 parameters. The model is fitted to the 10 time series of catch per unit of effort data covering the period from 1976 to 2000, *i.e.* 250 observations. With this number of parameters, it is not surprising that there is considerable similarity between the trends of the observed data and those of the estimated data. However, the quality of the observed data is reflected in the estimates that are obtained when the model is fitted. The model produces a relatively good fit to the input data, however it is crucial that the time series of observed data are as reliable as possible and that they represent good indices of the abundance of the different functional groups. It is also crucial that dietary data are collected such that, rather than estimating the extent to which the different groups prey upon the other groups, sound quantitative data can be input with the results of the model thereby becoming more reliable. Estimates of the efficiency creep of fishing effort are essential if this or any other model is to produce reliable predictions.

Predicted values for the first few years of the forward projection are adequate (Fig. 11) and would be sufficient to allow use of management strategy evaluation to produce reliable decision rules for the management of the fisheries of the various species. The Murdoch model bases its estimates of the future trajectory on the data that have been observed but the information content of the data resulting from only 20 years is limited and thus the predictions cannot be expected to be perfect. In effect, the model's estimate of the biomass of each functional group gradually drifts further and further from the "real" biomass if there is no feedback to correct for this deviation. In practice, in applying the model for fishery assessment, the model would be re-fitted to incorporate newly-acquired data, thereby continually refining the parameter estimates and providing relatively-reliable predictions for the immediate one or two future years.

The simulation using EcoPath/EcoSim has demonstrated that the Murdoch model can capture the observed dynamics of an ecosystem and describe the changes in abundance of the main targeted species fished in this system, provided the abundance data are sufficiently reliable (an issue affecting all stock assessment models). Short term projections are sufficiently accurate to allow the exploration and development of appropriate decision rules for the management of fisheries, within an ecosystem context.

Development of quantitative techniques

During the course of FRDC 2000/311 (and subsequently), approximately 20 postgraduate and Honours students have received training in various quantitative aspects of fisheries science, evidence of which is demonstrated in the fact that, since 2002, twenty scientific papers by these students and by the Principal Investigator reporting aspects of this work have been published or accepted for publication in peer-reviewed international journals and a contribution has been made by the Principal Investigator to the analyses reported in six FRDC final reports (Table 3). The project also saw the development of two fisheries biologists with strong quantitative skills, Drs Simon de Lestang and Alex Hesp. Dr de Lestang is now employed by the Department of Fisheries and has been taking a lead role in the development of a new model for the Western Rock Lobster fishery, while Dr Hesp, a Postdoctoral Fellow at Murdoch University, is about to complete an assessment of the abalone resources in the Capes region of south-western Australia, and has demonstrated considerable ability in training postdoctoral and Honours skills in the quantitative skills that he has developed. The effectiveness of the training offered by the Principal Investigator was multiplied by encouraging Drs de Lestang and Hesp to mentor other Honours and postgraduate students, while supporting them in this exercise.

To maximize uptake of knowledge, training was focused on the methods required for the analyses that the students required for their individual research studies, not on the approaches used to develop the model described in the earlier section of this report. Training was provided in one-on-one informal sessions, not in structured, formal lectures, and covered the following topics.

- The use of Excel and Visual Basic for Applications for analyzing data. Drs Alex Hesp and Simon de Lestang and Ms Colleen Greenwell were the primary recipients of training in this aspect of fisheries science. Subsequently, training has also been provided to approximately 30 postgraduate students who have undertaken a short course in Quantitative Resource Ecology. Since the current project has terminated, Dr Hesp has developed and presented a training unit focused on the advanced use of Excel and macros developed in Excel, which will be offered to postgraduates each year and run if numbers of enrolled students are sufficient.

- The use of logistic regression analysis for fitting maturity ogives. Initial concentrated training was provided to Dr Alex Hesp, and such further support was given to other Honours and Postgraduate students as was necessary to assist Dr Hesp in resolving issues relating to fitting and comparing models, and estimating the uncertainty of predictions. The methods have been used in all subsequent studies of fish and invertebrate reproduction at Murdoch University, by approximately 15 Honours and postgraduate students, and have been disseminated to the Department of Fisheries and other fisheries scientists outside Murdoch University.
- The use of more appropriate curves than the von Bertalanffy growth curve when the last model failed to provide an adequate fit to data, or more appropriate error structures. Drs William White, Alex Hesp and Bryn Farmer received guidance on the former issue, while Dr Hesp was provided with training on the latter.
- The development for Dr Simon de Lestang of improved techniques for fitting growth curves to modes in length frequency data. The approach was applied to data for *Portunus pelagicus*.
- Maximum likelihood approaches to estimating parameters and use of the likelihood-ratio test. While Drs Alex Hesp and Simon de Lestang were the principal recipients of training in these aspects, approximately 15 other Honours and postgraduate students have received advice on these topics and on aspects of model comparison.
- Bootstrapping approaches to estimating approximate 95% confidence intervals for parameters. Primary training on this was given to Drs Alex Hesp and Simon de Lestang, and the approaches have subsequently been applied by approximately 15 Honours and postgraduate students.
- Fitting curves to describe the relationships with length of the proportions of individuals of hermaphroditic species that become mature and that then change sex. The models, which were developed, were applied by Drs David Fairclough and Alex Hesp to their data.
- Methods of model comparison for non-nested models. Training in these approaches was provided to Dr Alex Hesp.

- Estimating natural and total mortality. The primary recipient of training in these methods was Alex Hesp, and the methods have subsequently been adopted and applied by approximately 15 Honours and postgraduate students.
- Use of yield-per-recruit and egg-per-recruit analyses and consideration of biological reference points based on Spawning Potential Ratio (SPR). Again the primary recipient of training in the methods was Alex Hesp, and through him, the approaches have been demonstrated to and applied by approximately 15 Honours and postgraduate students.

Other results included the following.

- Catch curve analyses were extended to encourage consideration of samples from multiple years through the use of relative abundance analysis, the extension to catch curve analysis that was developed by Deriso *et al.* (1985). This was applied by Dr Alex Hesp to samples of age composition data for the Western Yellowfin Bream from Shark Bay (FRDC 2000/137) and has been applied subsequently by approximately 5 other Honours and postgraduate students to age composition data for other species. The resulting estimates of total mortality obtained using this approach were considered to be of improved accuracy as the assumption required for catch curve analysis, that recruitment of each year class is constant, was no longer required. The computer routine was passed to the Department of Fisheries for application to other data sets.

Table 3. Publications reporting results of quantitative analyses undertaken while providing training to postgraduate and Honours students at Murdoch University.

Peer-reviewed papers		
Number	**Year**	**Details**
1.	2002	Hesp, S.A., Potter, I.C. and Hall, N.G. Age and size compositions, growth rate, reproductive biology, and habitats of the West Australian Dhufish (*Glaucosoma hebraicum)* and their relevance to the management of this species. *Fish. Bull.U.S.* **100**: 214-227.
2.	2002	White, W.T., Hall, N.G. and Potter, I.C. Reproductive biology and growth during pre- and postnatal life of *Trygonoptera personata* and *T. mucosa* (Batoidea: Urolophidae). *Mar. Biol*. **140**: 699-712.
3.	2002	White, W.T., Hall, N.G. and Potter, I.C. Size and age compositions and reproductive biology of the nervous shark *Carcharhinus cautus* in a large subtropical embayment, including an analysis of growth during pre- and postnatal life. *Mar. Biol.* **141**: 1153-1164.
4.	2003	de Lestang, S., Hall, N.G. and Potter, I.C. Do the age compositions and growth of the crab *Portunus pelagicus* in marine embayments and estuaries differ? *J. mar. Biol. Ass. U.K.* **83**: 971-978.
5.	2003	de Lestang, S., Hall, N. and Potter, I.C. Influence of a deep artificial entrance channel on the biological characteristics of the blue swimmer crab *Portunus pelagicus* in a large microtidal estuary. *J. Exp. Mar. Biol. Ecol.* **295**: 41-61.
6.	2003	de Lestang, S., Hall, N.G. and Potter, I.C. Reproductive biology of the blue swimmer crab (*Portunus pelagicus*, Decapoda: Portunidae) in five water bodies on the west coast of Australia. *Fish. Bull. U.S.* **101**: 745-757.
7.	2003	de Lestang, S., Hall, N. and Potter, I.C. Changes in density, age composition, and growth rate of *Portunus pelagicus* in a large embayment in which fishing pressures and environmental conditions have been altered. *J. Crust. Biol.* **23**: 908-919.
8.	2004	Partridge, G.J., Sarre, G.A., Hall, N.G., Jenkins, G.I., Chaplin, J. and Potter, I.C. Comparisons between the growth of *Acanthopagrus butcheri* cultured from broodstock from two estuarine populations that are reproductively isolated and differ markedly in growth rate. *Aquaculture* **231**: 51-58.
9.	2004	Hesp, S.A., Hall, N.G. and Potter, I.C. Size-related movements of *Rhabdosargus sarba* in three different environments and their influence on estimates of von Bertalanffy growth parameters. *Mar. Biol.* **144**: 449-462.
10.	2004	Hesp, S.A., Potter, I.C. and Hall, N.G. Reproductive biology and protandrous hermaphroditism in *Acanthopagrus latus*. *Env. Biol. Fish.* **70**: 257-272.
11.	2004	Hall, N.G., Hesp, S.A. and Potter, I.C. A Bayesian approach for overcoming inconsistencies in mortality estimates using, as an example, data for *Acanthopagrus latus*. *Can. J. Fish. Aquat. Sci.* **61**: 1202-1211.
12.	2004	Smith, K.D., Hall, N.G., de Lestang, S. and Potter I.C. Potential bias in estimates of the size of maturity of crabs derived from trap samples. *ICES J. Mar. Sci.* **61**: 906-912.
13.	2004	Smith, K.D., Hall, N.G. and Potter, I.C. Relative abundances and size compositions of champagne crabs, *Hypothalassia acerba* on two coasts and in different water depths and seasons. *Mar. Freshwat. Res.* **55**: 653-661.
14.	2005	Coulson, P., Hesp, S.A., Potter, I.C. and Hall, N.G. Comparisons between the biology of two co-occurring species of whiting (Sillaginidae) in a large marine embayment. *Env. Biol. Fish.* **73**: 125-139.
15.	2006	Hall, N.G., Smith, K.D., de Lestang, S. and Potter, I.C. Does the largest chela of the males of three crab species undergo an allometric change that can be used to determine morphometric maturity? *ICES J. Mar. Sci.* **63**: 140-150.
16.	2006	Mant, J.C., Moran, M.J., Newman, S.J., Hesp, A.S., Hall, N.G. and Potter, I.C. Biological characteristics and mortality of western butterfish (*Pentapodus vitta*), an abundant bycatch species of prawn trawling and recreational fishing in a large subtropical embayment. *Fish. Bull*. **104**: 512-520.

17.	2007	Moore, S.E., Hesp, S.A., Hall, N.G. and Potter, I.C. Age and size compositions, growth and reproductive biology of the breaksea cod *Epinephelides armatus*, a gonochoristic serranid. *J. Fish Biol.* in press.
18.	2007	Bird, D.J., Rotchell, J.M., Hesp, S.A., Newton, L.C., Hall, N.G. and Potter, I.C. To what extent are hepatic concentrations of heavy metals in *Anguilla anguilla* in a contaminated estuary related to body size and age and reflected in the metallothionein concentrations? *Env. Pollut*. In press.
19.	2007	Potter, I.C., French, D.J.W., Jenkins, G.I., Hesp, S.A., Hall, N.G. and de Lestang, S. Comparisons of the growth of black bream, *Acanthopagrus butcher*i, in an estuary with those of its wild stock. *Rev. Fish. Sci.* In press.
20.	2007	Jones, A.A., Hall, N.G. and Potter, I.C. Size compositions and reproductive biology of a heterodontid shark in waters in which it is an abundant bycatch species. *J. mar. Biol. Ass. U.K.* In press.
FRDC Final reports		
Number	**Year**	**Details**
1.	2003	Fairclough, D.V., Hesp S.A., Potter, I.C. and Hall, N.G. Determination of the biological parameters required for managing the fisheries of four tuskfish species and western yellowfin bream. FRDC Project No. 2000/137.
2.	2004	Smith, K.D., Potter, I.C. and Hall, N.G. Biological and fisheries data for managing the deep-sea crabs *Hypothalassia acerba* and *Chaceon bicolor* in Western Australia. Project Nos 1999/154 and 2001/055.
3.	2006	Pember, M.B., Newman, S.J., Hesp, S.A., Young, G.C., Skepper, C.L., Hall, N.G. and Potter, I.C. Biological parameters for managing the fisheries for Blue and King Threadfin Salmons, Estuary Rockcod, Malabar Grouper and Mangrove Jack in north-western Australia. FRDC Project No. 2002/003.
4.	2006	Farmer, B.M., French, D.J.W., Potter, I.C., Hesp, S.A. and Hall, N.G. Determination of the biological parameters for managing the fisheries for Mulloway and Silver Trevally in Western Australia. FRDC Project No. 2002/004.
5.	2006	Hoeksema, S.D., Chuwen, B.M., Hesp, S.A., Hall, N.G. and Potter, I.C. Impact of environmental changes on the fish faunas of Western Australian south-coast estuaries. FRDC Project No. 2002/017.
6.	2006	Jenkins, G.I., French, D.J.W., Potter, I.C., de Lestang, S., Hall, N.G., Partridge, G.J., Hesp, S.A. and Sarre, G.A. Restocking the Blackwood River Estuary with the Black Bream *Acanthopagrus butcheri*. FRDC Project No. 2000/180.

- Methods to determine the uncertainty of the mortality estimates derived from life history data were introduced. A major deficiency in reporting mortality estimates derived using these methods in most papers in international journals and in most stock assessment reports is that, typically, no confidence limits are provided. Instead, estimates of uncertainty are frequently derived from the wide range of parameter estimates resulting from the application of alternative life history approaches. In our study, the raw data used by Pauly (1980) and by Hoenig (1983) in developing their regression equations were re-analysed. The imprecision associated with an estimate of mortality obtained using either of these equations was calculated using the variance-covariance matrix of the resulting parameter estimates, the residual variance, and the deviations of the independent variables from the means of those variables for the data used when deriving the regression equations. The resulting estimates of the confidence intervals from the different methods are extremely broad. Such imprecision and the uncertainty relating to the estimates obtained using different life-history approaches clearly need to be considered when assessing the state of a fish stock or considering the implications of alternative harvest strategies. The primary recipient of training in this area was Dr Alex Hesp, who collaborated in the development of the methods, and has subsequently disseminated the approaches to approximately 10 Honours or postgraduate students for application to their data.

- Deep sea crabs
  Difficulties were encountered in the use of traditional approaches for the determination by Dr Kim Smith of the lengths at which the deep sea crabs *Hypothalassia acerba* and *Chaceon bicolor* attain maturity, an analysis required for the deep sea crab projects, FRDC 1999/154 and 2001/055. As resolution of these issues was critical to delivering reliable biological data for use in the subsequent management of the fisheries for these crabs, and as the development of such quantitative approaches fell directly within the scope of FRDC 2000/311, Professor Ian Potter requested assistance in the complex and demanding analyses that were required. Accordingly, in collaboration with Drs Simon de Lestang and Kim Smth, data for trawl, seine and trap-caught females of *Portunus pelagicus* were analysed. A bias in the size composition of trap-caught females was demonstrated, with mature females more likely to be caught than immature females. A similar bias was likely to be present in the data for the deep sea crabs *H. acerba* and *C. bicolor* as few small individuals of these species were caught, even with traps that were enclosed in a small mesh. Initially, a new method of analysis suggested by Dr Simon de Lestang was employed to overcome this bias. However, reviewers identified critical problems with the approach and we were obliged simply to acknowledge the implications of the bias in our estimates of the sizes at maturity of the females of *H. acerba* and *C. bicolor*. For male crabs, the change in the level of allometry of the length of the chelae with respect to the size of the crab has typically been used by crab biologists to provide an estimate of the size at which the males become "morphometrically" mature. We showed that it was essential to demonstrate that there was a distinct rather than continuous change in the level of allometry before estimates of the body size of the male crabs at the change in level could be accepted as reliable measures of morphometric mature. Neither *H. acerba* or *C. bicolor* revealed any distinct change in the level of allometry of their

chelae, and thus we concluded that physiological maturity, *i.e.* maturity determined from examination of the gonads, would be the appropriate measures to use when assessing the sizes at which the males of these species become mature.

- Use of WinBUGS.

  It has become increasingly apparent that fisheries scientists will require skills in Bayesian techniques of analysis if they are to meet the needs of fisheries agencies and to provide details of the uncertainty associated with the outputs of their analyses and the management advice that is derived from these results. Accordingly, Bayesian approaches for fitting growth curves, maturity at length data, catch curve data and dynamic fisheries models were explored using both WinBugs and an Excel macro that implements the Metropolis algorithm, where convergence was tested using the BOA package within R. A method was developed to analyse recreational catch per fishing trip data that estimates the average catch per fishing trip after correcting for the bias associated with bag limits and allowing for the "sharing" of catch among fishers within a group. An initial application of this approach in an analysis of fishing club competition data suggests that it may provide a reliable index of abundance from the recreational fishing sector. The approaches used by Dr Hesp at Murdoch University to study growth have been extended to incorporate the use of back-calculated data and WinBugs to take into account the variability of growth among individual fish. A generalised logistic curve and its inverse were employed to fit the relationships between otolith radius and fish length for both the males and females of *Epinephelus coioides* and *Epinephelus malabaricus*. These relationships were then used to derive back-calculated lengths for a number of fish, applying both the body and scale proportional assumptions described by Francis (1990). The resulting back-calculated lengths and estimates of parameters from the analysis of individual growth curves assisted our understanding of the relationships between sex change and size/age for these two hermaphroditic species. Since vulnerability to capture is often size-dependent, knowledge of the individual variability of growth derived using such data will be valuable in refining future assessment of stock status and risk associated with different harvest strategies. The information contained in the back-calculated data should assist in reducing the sample sizes required for growth studies and may allow the influence on growth of environmental variables to be assessed.

- Dr ALex Hesp and Ms Ashlee Jones have received training in the use of WinBugs, while Dr Neil Gribble was introduced to its use.
- Ways to reconcile the inconsistencies among different estimates of natural mortality were considered in collaboration with Dr Alex Hesp (see below). The approaches that were developed have subsequently been used by approximately 5 Honours and PhD students.
- A growth model applicable when fish move to different habitat types on the basis of length, and representative samples may be obtained from each habitat type but not for the population was developed in collaboration with Dr Alex Hesp (see below).

Reconciliation of the inconsistencies among different estimates of natural mortality

During the early stages of this study, it became apparent that the life-history methods usually employed for estimating important parameters of biological processes, such as mortality and growth, and which are fundamental to the development of appropriate models for this study, were frequently imprecise and/or inappropriate. In the context of natural mortality, the estimates of mortality of Dhufish, based on the excellent data collected during FRDC 1996/103 and using the Pauly (1980), Ralston (1987) and Hoenig (1983) methods, were found to differ markedly (Hesp *et al*., 2002). Although the widely-used Pauly equation was clearly inappropriate for estimating the mortality of Dhufish, in that it produced estimates that were inconsistent with the observed age composition, the results obtained by the other methods were also shown to be inadequate through comparisons with the results of catch curve analyses. A major failing of the Pauly (1980) and Ralston (1987) approaches is that, at least in the case of Dhufish, they produced what appeared to be highly biased results. However, it should also be recognised that all three methods lack precision. Similar problems in estimating natural mortality using the above three methods have also been noted in the scientific literature by other workers (see also Vetter, 1988, for a review of methods).

In the absence of more informative data and better approaches, and in common with other workers around the world, we are still obliged to use life history methods for obtaining estimates of natural mortality. Reliable estimates of this parameter are crucial for stock assessments and fisheries management as, through subtraction from estimates of total mortality, they allow determination of fishing mortality and the extents to which fish stocks are exploited. Accordingly, in this FRDC project, we sought to develop a new approach to the estimation of natural mortality which might reconcile the differences in the parameter estimates produced by the different approaches and thereby improve the resulting estimate of fishing mortality. A full description of this approach is presented by Hall *et al.* (2004)

The predicted value of the natural logarithm of total mortality, ln(*Z*), for the Western Yellowfin Bream *Acanthopagrus latus* in Shark Bay, which was calculated using Hoenig's (1983) regression equation for fish from the maximum age recorded in the samples taken by Alex Hesp, is assumed to be distributed as a Student's *t*-distribution with 80 degrees of freedom and with a mean value and standard error for the prediction, which are calculated from the value of the independent variable, maximum age. If *f*(ln(*Z*)) is the probability density function of ln(*Z*), then the probability density function of Z is $g(Z) = f(\ln(Z))/Z$. Thus, the likelihood associated with *Z* for *A. latus*, based on Hoenig'(s) regression equation, was calculated by dividing the likelihood of ln(*Z*), as determined from the *t*-distribution derived from Hoenig's (1983) regression equation, by *Z* (Fig. 13). Estimates of the likelihood distributions of *Z* for *A. latus* in Shark Bay were also obtained when the relative abundance model (Deriso *et al.* 1985) was fitted to the descending limbs of sets of annual age-composition data using assumptions based on both constant and variable recruitment (Fig. 13).

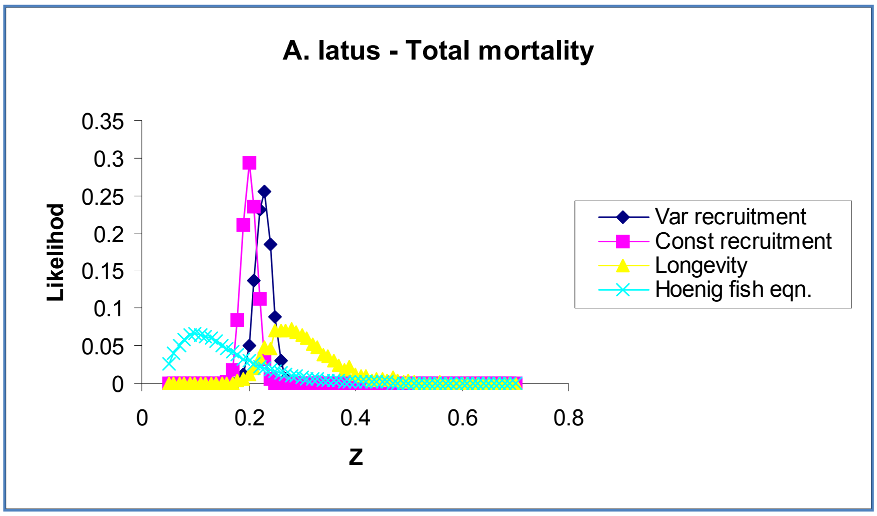


Figure 13. Estimated likelihood for total mortality, *Z*, for *Acanthopagrus latus* in Shark Bay, Western Australia.

The selection of random samples of a specified sample size from a fish stock, with constant total mortality following a specified age at which the fish are fully vulnerable to the fishing gear, may be simulated. By running this simulation a large number of times, it is possible to develop an approximation to the probability density function for the maximum age recorded in a random sample of a specified sample size, for a specified level of Z. The number of simulation runs will determine the precision of this approximation. Our analysis employed 100,000 runs. This process may be repeated to obtain similar approximations to the probability density function for each of a large number of discrete values of Z, covering the full range of feasible values for Z. Using these results, it is possible to determine the likelihood function for Z, by applying Bayes theorem to the maximum recorded age from such a sample, with the assumption of a uniform prior probability distribution function for Z. This method was applied to the age composition data obtained for the Western Yellowfin Bream in Shark Bay. Approximations of the probability density functions for the maximum age from random samples of fish of identical sample size to those collected by Alex Hesp were calculated from 5000 simulations for each value of Z ranging from 0.05 to 10 year^{-1} at 0.01 intervals. The resulting likelihood function of Z based on the longevity of *A. latus* in Shark Bay is presented in Fig. 13.

Although Hoenig's (1983) equation was developed using data for lightly fished stocks and his estimates of Z were therefore likely to have approximated estimates of the natural mortality, M, the maximum age for the Western Yellowfin Bream in Shark Bay was obtained from an exploited stock. Thus, rather than an estimate of M, Hoenig's equation is likely to yield an estimate of Z for this stock. The expected value derived from this method was considerably lower than that derived from the approximate distributions of maximum ages from simulated random samples and using the same value of maximum recorded age for the Western Yellowfin Bream (Fig. 13). However, the estimates of Z that were obtained from the relative abundance analysis were intermediate to those obtained from the other two estimates (Fig. 13). Interestingly, these estimates were far more precise, possibly as a consequence of using all of the data from age classes greater than the age at which the fish became fully vulnerable to the fishing gear, but also due to the assumptions imposed in this analysis. The two estimates of Z obtained by using the relative abundance analysis are not independent, however, as they were derived from the same data; the more reliable estimate is that produced under the variable recruitment hypothesis as this imposes less stringent conditions on the data. Although both Hoenig's regression equation and the calculation of Z from the approximate probability density functions derived from simulation make use of the same longevity data from the Western Yellowfin Bream fishery, the former method uses information contained in the set of data from the range of species and stocks to which Hoenig fitted his regression equation. Thus, the information that is used to develop these two estimates may be assumed to be almost independent, despite the fact that the same longevity data for the Yellowfin Bream was applied in both methods. Accordingly, we may consider that there are three independent estimates of Z for *A. latus*, namely those obtained from Hoenig's (1983) equation, the simulation method, and the relative abundance analysis under the assumption of variable recruitment. The likelihood functions for these three estimates of Z for *A. latus* were combined by calculating their product at each value of Z (Fig. 14). The resulting likelihood function of Z for this species in Shark Bay is dominated by the more precise estimates of Z derived from the relative abundance analysis.

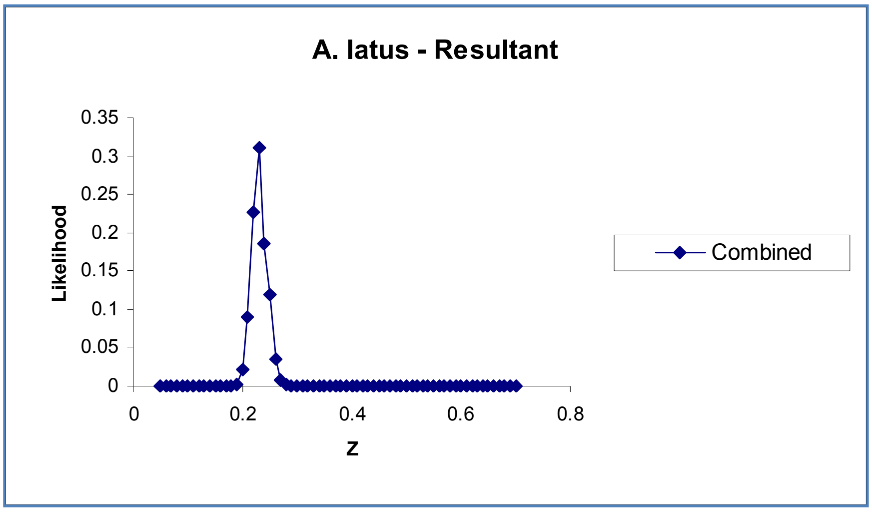


Figure 14. Combined likelihood function for *Z* for *Acanthopagrus latus* from Shark Bay.

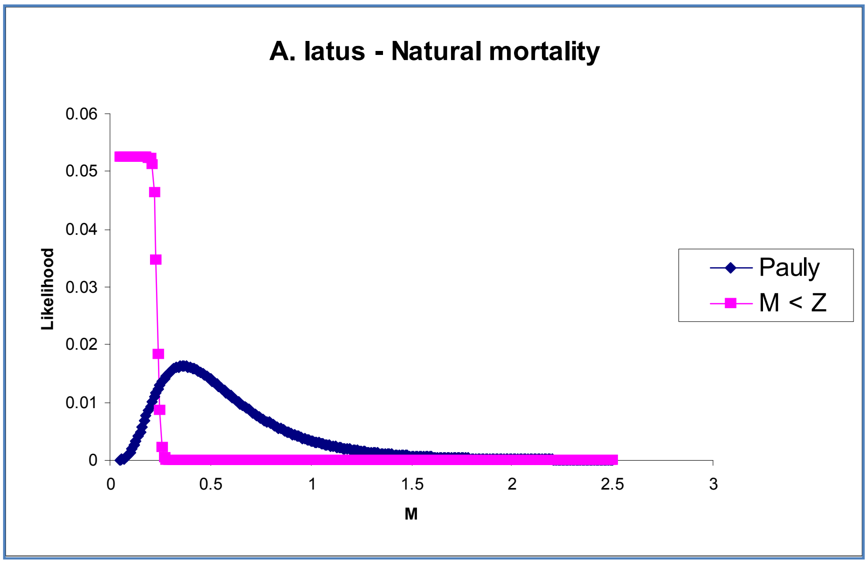


Figure 15. The likelihood functions for *M* for *Acanthopagrus latus* in Shark Bay that were derived from Pauly's (1980) method and from the combined likelihood function for estimates of *Z* determined from Hoenig's (1983) regression, simulation-derived estimates of the likelihood functions of the maximum age, and relative abundance estimates.

The likelihood of the natural mortality *M* may be calculated from the likelihood for *Z* by assuming that, for each value of *Z*, there is a uniform probability that $M < Z$. Thus, if $F(Z)$

represents the cumulative likelihood of Z and $\bar{Z}$ is the expected value of Z, the likelihood of M may be calculated as $(1-F(Z))/\bar{Z}$. The resulting likelihood function of M for *A. latus* in Shark Bay is presented in Fig. 15.

A further estimate of the likelihood function of M may be obtained from the application of Pauly's (1980) regression equation. It is assumed that the values of ln(M) for the Western Yellowfin Bream *Acanthopagrus latus*, which are predicted by Pauly's (1980) regression equation, are distributed as a Student's *t*-distribution with 171 degrees of freedom and with a mean value and standard error for the prediction, which are calculated from the values of the independent variables (for formulae, see Sokal and Rohlf, 1995). The calculation for the standard error uses the estimates of the variance of the residuals and the variance-covariance matrix for the parameter estimates that are output when the multiple regression equation is fitted to the data used by Pauly (1980). As with the case for the likelihood function for Z from Hoenig's (1983) regression, the likelihood associated with each value of ln(M) may be calculated by dividing the likelihood of ln(M), as determined from the *t*-distribution derived from Pauly's (1980) regression equation, by M (Fig. 15).

The resulting likelihood functions for M, which are shown in Fig. 15, may be combined by forming their product at each corresponding value of M (Fig. 16). From this, the expected value of M and its 95% confidence interval for *A. latus* in Shark Bay is estimated to be M = 0.20 (0.12 to 0.26) year^{-1} while Z=0.23 (0.21 to 0.27) year^{-1}.

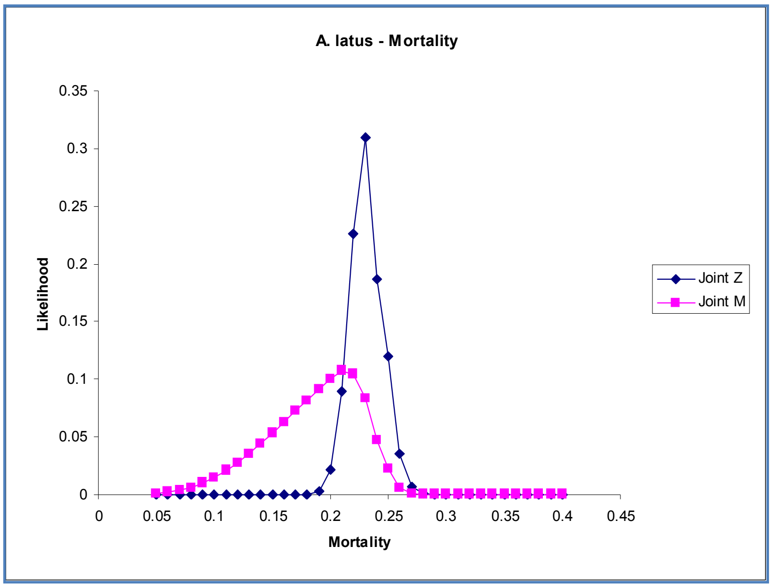


Figure 16. Estimated likelihood functions for *Z* and *M* for *Acanthopagrus latus* in Shark Bay, representing the combined likelihood function for estimates of *Z* determined from Hoenig's (1983) regression, simulation-derived estimates of the likelihood functions of the maximum age and relative abundance estimates, and the likelihood function of *M* derived from Pauly's (1980) method combined with the likelihood function of *M* based on the combined likelihood function for *Z*.

This approach, which has been outlined above and is described by Hall *et al.* (2004), reconciles the apparent inconsistencies between point estimates of *M* derived using the different methods. In essence, it represents an application of Bayes' theorem, allowing us to combine the information from different data sources and thereby to produce a combined estimate of *M*. The new technique is of considerable relevance to the stock assessment and management of other finfish species, for which estimates of natural mortality have been based on life history parameters such as those of the von Bertalanffy growth curve or maximum age within a sample of fish.

A growth model applicable when fish move to different habitat types on the basis of length

As with many other species of finfish, the Tarwhine, *Rhabdosargus sarba*, moves offshore as it becomes larger. This results in exploitation by shore-based anglers when the fish are young and by boat-based anglers when the fish are older. Obtaining a representative sample of fish, such that each individual in the population has an equal chance of inclusion in the sample, is difficult as the catches per unit of effort in the inshore and offshore regions are not directly comparable. Thus, sampling intensities for the different regions are likely to differ and the resulting set of length at age data is likely to be biased towards the assemblage in one or other of these regions. Failure to recognise this bias will affect the estimates of the parameters of the growth curve fitted to the resulting data. Furthermore, catch curve analysis of the resulting age composition data will produce a biased estimate of total mortality.

A plot of the length at age data for *R. sarba* collected by Alex Hesp, Murdoch University, from sheltered inshore, exposed inshore and offshore regions demonstrates clearly that older and larger fish are located in the offshore region (Fig. 17). It was assumed that the distribution of fish is length dependent, and that the probability that a fish from one region will move to the adjacent offshore region may be described by a logistic relationship. Through this assumption, a single von Bertalanffy growth equation has been fitted to the data, resulting in the three separate "growth" curves shown in Fig. 17. The method, which is described below and in Hesp *et al.* (2004a), accommodates the different sampling intensities in the different regions.

The lengths at age of male and female fish in each population of *R. sarba* were assumed to be normally distributed around von Bertalanffy growth curves, *i.e.* $L_t \sim N\left(\hat{L}_t, \sigma^2\right)$, where the probability density function for the length at age (over all habitats) is

$\phi(L_t) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[-\frac{\left(L_t - \hat{L}_t\right)^2}{2\sigma^2}\right]$. Because it is assumed that movement is size-related, separate component distributions will exist for the fish found within each habitat type. These distributions were assumed to be the product, for each length at age, of the probability of a fish having that specified length at age, $\phi(L_t)$, and the proportion of fish at length L_t within each habitat type, where the latter proportion was determined from separate logistic equations that were assumed to describe the movement of fish between each of the different habitat types. The likelihood of each observed length at age within each habitat type could thus be calculated from the probability distribution of lengths at age for the corresponding habitat type and the combined likelihood used to fit an adjusted von Bertalanffy growth curve which, through accounting for the different length at age distributions within each of the habitat types, describes the growth of fish in the population as a whole.

The probability that a fish of length L_t was present in the sample from habitat type *h* ($h = h_1$, h_2 or h_3) was determined by

$$p_h(L_t) = \begin{cases} 1-\psi(L_t, h_1 \to h_2) & \text{if } h = h_1 \\ \psi(L_t, h_1 \to h_2)\left[1-\psi(L_t, h_2 \to h_3)\right] & \text{if } h = h_2 \\ \psi(L_t, h_1 \to h_2)\psi(L_t, h_2 \to h_3) & \text{if } h = h_3 \end{cases}$$

where $\psi(L, h_1 \to h_2) = \dfrac{1}{1+\exp\left[-\ln(19)\dfrac{L - L_{50}^{h_1\to h_2}}{L_{95}^{h_1\to h_2} - L_{50}^{h_1\to h_2}}\right]}$ is the probability that a fish of length *L* has moved from habitat h_1 to h_2, and $L_{50}^{h_1\to h_2}$ and $L_{95}^{h_1\to h_2}$ are the lengths at which 50 and 95% of the fish have moved. $L_{95}^{h_1\to h_2}$ was constrained to exceed $L_{50}^{h_1\to h_2}$ by at least 1 mm. The probability density function of the lengths of fish of age *t* in habitat type *h* has been approximated by $f(L_t, h) = \dfrac{p_h(L_t)\phi(L_t)}{\int_{L=\hat{L}_t-5s}^{L=\hat{L}_t+5s} p_h(L)\phi(L)dL}$ where *s* is the estimated value of σ. The mean length at age within each habitat is calculated as $L_{t,h} = \int_{L=\hat{L}_t-5s}^{L=\hat{L}_t+5s} f(L,h)L\,dL$, where the integrals were evaluated using numerical quadrature. The likelihood of the observed lengths at age was calculated as $\lambda = \prod_{j=1}^{n} f(L_t, k)$. AD Model Builder (Fournier, 1994) was used to maximize the likelihood and estimate the parameters L_∞, k, t_0, σ, $L_{50}^{h1\to h2}$ $L_{95}^{h1\to h2}$, $L_{50}^{h2\to h3}$ and $L_{95}^{h2\to h3}$.

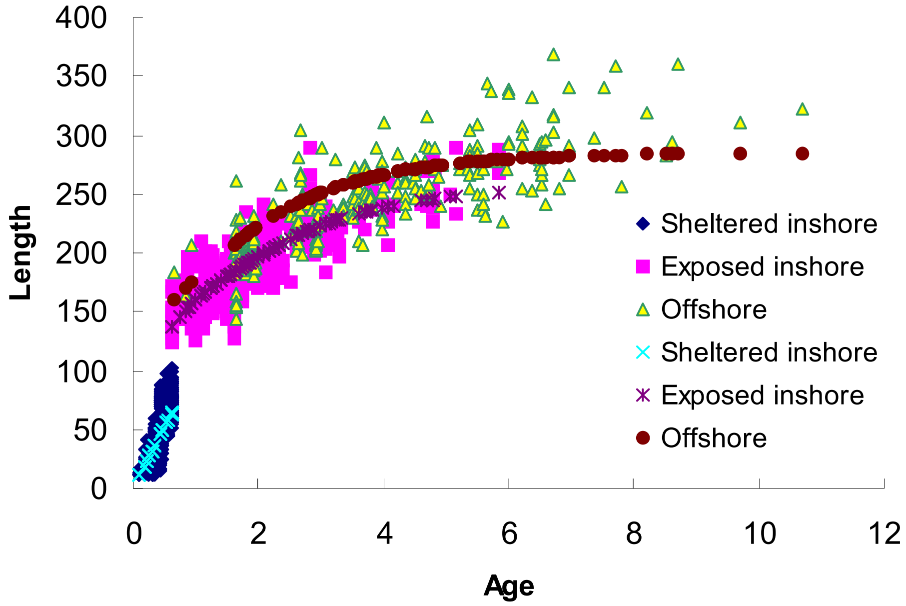


Figure 17. The apparent growth curves representing length at age for *Rhabdosargus sarba* in sheltered and exposed inshore regions and an offshore region. The three "growth" equations are derived from a single von Bertalanffy growth curve fitted to age at length data, where it is assumed that logistic curves determine the length at which fish move offshore.

This modelling approach, which is described in Hesp *et al.* (2004a) appears likely to prove useful in (a) providing an unbiased estimate of the parameters of the von Bertalanffy growth curve and (b) providing information on the proportions of fish of different length classes within each age class that are likely to be found in different regions for species where the individuals move offshore as they grow. It appears likely that the resulting estimates for the proportions of each length class in the different depths may be used to enable the determination of unbiased estimates of total mortality from catch curve analysis of age composition data collected from such stocks.

Discussion relating to development of quantitative techniques

The improved methods of analysis that were introduced during the course of this FRDC project continue to be used by students at Murdoch University and have been disseminated (through both responses to personal enquiries and through published scientific papers) to Fisheries scientists at the Department of Fisheries Western Australia and other fisheries agencies. For example, Dr Neil Gribble is using WinBugs to assess the state of two fish stocks in

Queensland. These methods and the accompanying use of Excel tools to explore data have raised the quality of the results that have been produced by postgraduate and Honours students at Murdoch over recent years and, as they have become accepted practice at the University, will continue to influence future research. In addition, the FRDC project provided the opportunity to increase the awareness of the postgraduate and Honours students to issues relating to statistical design and analytical power, moving students from least squares to likelihood estimates and to the associated likelihood-ratio tests, impressing on them the need for residual analysis, and introducing them to methods of comparing non-nested models.

The development of an approach that allows the estimates of natural mortality produced by different life-history approaches to be reconciled was an important achievement of the Project. The method thereby ensures that resulting estimates of natural mortality are feasible and do not exceed the estimates of total mortality for the stock. As the assessment and management of many of Australia's fisheries is dependent on the availability of a reliable estimate of natural mortality, the availability of such a method is of considerable importance.

Probably the greatest achievement of this component of the study was the training of Drs Simon de Lestang and Alex Hesp in aspects of programming and the use of EXCEL as a tool for analysis. Dr Hesp continues to develop the quantitative skills of students by passing on the training that he has received, thereby multiplying the benefits of this work. However, the nature of the analyses conducted at Murdoch, which do not include formal stock assessment and the development of dynamic fisheries models, precluded provision of training in the art of fisheries modelling and stock assessment. Dr de Lestang has demonstrated, however, that the skills that he developed at Murdoch allowed him to develop a new model for Western Rock Lobster fishery for the Department of Fisheries.

Benefits

This study has had the following major benefits.

1. Development of a multi-species biomass dynamics model to represent the components of an exploited marine ecosystem for which time series of data are available, that can be fitted to those data and used to assess the implications of alternative management strategies.

2. Development of an approach that reconciles the differences between estimates of natural mortality produced by different life-history methods and ensures that the estimates of natural mortality do not exceed the estimates of total mortality.

3. The training of a number of postgraduate and Honours students in quantitative aspects of data analysis and the development of two fisheries scientists with strong quantitative skills.

Use of the methods developed in this project will benefit both recreational and commercial fishers through the improved ability of fisheries scientists to assess the implications on exploited stocks of the indirect impact of fishing other stocks, and more reliable estimates of natural mortality. The contribution of Drs de Lestang and Hesp's improved quantitative skills to other fisheries studies is already providing benefit to fishers in the Western Rock Lobster, abalone and finfish fisheries of Western Australia.

Further development

An opportunity exists to refine the multi-species biomass dynamics model of an exploited marine ecosystem by constraining the values a_{ij}, the rate of effective search by the predator species j for prey species i, such that, for this predator, the proportion of the dietary biomass composition represented by this prey species, *i.e.* $a_{ij}B_i/\sum_i a_{ij}B_i$, is equal to the observed proportion of the prey species in the guts of individuals of the predator species in years in which such samples have been collected. Improvement to the reliability of the prediction of biomasses may be possible by reducing model complexity where such complexity fails to improve the precision of the prediction and by relating the rates of change of biomasses to time series of environmental variables that are considered to reflect changes in primary production, recruitment, or vulnerability. Use of the model in a harvest strategy evaluation framework would assist fishery managers in developing effective strategies for ecosystem-based fishery management.

The full realization of the benefits that flow from the multi-species biomass dynamics model of an exploited marine ecosystem developed during this study will depend on the refinement of the relative abundance data available for the various exploited species in each region and adjustment of these data for increasing efficiency of effective effort. The choice of ecosystem model used by fishery scientists will be determined by the appropriateness of the model for the data that are available for that ecosystem. The multi-species biomass dynamics model offers considerable benefits as it has a complexity that matches the types of data that are available in most fishery agencies.

Future training in quantitative approaches would be enhanced by the development of a closer linkage between Murdoch University and the Department of Fisheries, such that postgraduate students might obtain experience in applying models such as Stock Synthesis II or CASAL to actual fishery data, and gain valuable experience in the development of models using tools such as AD Model Builder. Such a linkage would assist the Department by providing additional modelling capacity.

This study continues to highlight the need to develop more reliable methods for determining natural mortality from life history characteristics such that we might derive better estimates of fishing mortality and stock status.

Planned outcomes

Modification to the project's original objectives by the Research Steering Committee also resulted in slight changes to expected outcomes. However, the fundamental outcome was still that there would be development of a model for use by resource and fisheries managers involved in integrated fisheries management. The Research Steering Committee sought to ensure also that this model would have a relatively simple structure employing typically-collected fisheries data, thereby facilitating its use by fisheries agencies to assess the indirect effects of fishing on other exploited fish species in the marine ecosystem. The cost of collecting detailed information on all aspects of a marine ecosystem is prohibitive for many fisheries. Similarly, the approaches used in assessing the indirect impacts of fishing need to be relatively simple as the cost of sophisticated modelling is not warranted for many fisheries. The Project has successfully achieved the outcome of developing a model that is relatively simple, uses the time series of data of the types typically collected by fisheries agencies, and allows exploration of the indirect effects on other exploited fish species of fishing for a target species.

A second outcome of the Project was to produce a greater number of fisheries scientists who have had experience in the advanced quantitative skills required to meet the needs for the continuing development of the models required for integrated fisheries management plans. This outcome has been achieved both by providing quantitative training to postgraduate and Honours students in the course of their studies, and by providing two recently-graduate fisheries scientists, Drs Simon de Lestang and Alex Hesp, with sound training in the use of quantitative approaches for fisheries science.

Conclusion

During the course of the project, the original objectives of this study were extensively modified by the Project Steering Committee. The resulting objectives were achieved.

The first of the modified objectives required the development of an ecosystem model of the West Coast Bioregion of Western Australia, employing the commercial fisheries data that are available for that system. For this element of the study, a multi-species biomass dynamics model of the exploited components of the marine ecosystem of the West Coast Bioregion was created. The resulting model reflects those functional groups of the ecosystem for which there were time series of fisheries data, allowing representation of the extent to which those components interact but avoiding extrapolation to other functional groups for which there were no fisheries data. The trends exhibited by the data for many of the functional groups suggested that fishing efficiency had increased markedly to the extent that, although the biomass dynamics model produced predictions that reflected those trends, the response of the ecosystem to the increasing fishing effort experienced in the West Coast Bioregion appeared unlikely to be realistic. There would be considerable value in reviewing the fisheries data and producing a refined series of relative abundance indices that have been adjusted for increase in efficiency to which the model could be refitted.

The biomass dynamics model was tested using data generated by an EcoSim model and produced a good fit to these data, with reasonably accurate short term predictions. Longer term predictions were imprecise, however, indicating that only short-term predictions are likely to useful for fisheries management. The fact that the model was able to reflect the behavior of the EcoSim-generated data and produce useful short-term projections indicates that, provided the input data are of reasonable quality, the model is likely to be of value to fisheries agencies in implementing an ecosystem approach to fisheries management. The model has the advantage to fisheries agencies that it requires use only of data that are typically collected by those agencies, and is relatively simple in structure, thereby facilitating its use by those agencies.

The second objective of the study, which was the development of more sophisticated and advanced quantitative techniques for analysing biological data so that more reliable information can be provided to fisheries managers and training in quantitative skills can be provided to postgraduate students, was also accomplished. The results of this modelling has been reported in twenty scientific papers and six final FRDC reports produced by the postgraduate and Honours students who received training in quantitative approaches to analyzing fisheries data. New methods of analyzing growth and maturity data were developed and postgraduate students were introduced to the use of WinBugs and Monte Carlo Markov Chain approaches to analysis, including use of these to explore and fit models describing individual variation in growth.

A model was developed to reconcile the differences in estimates of natural mortality produced by different life history approaches and ensure that the estimate of natural mortality does not exceed that for total mortality. This model has considerable potential for improving the reliability of estimates of natural mortality that are crucial for stock assessment. Another valuable result of this analysis was that the imprecision of the resulting estimates of mortality was calculated. Such imprecision needs to be taken into account when assessing stock status and exploring the effectiveness of alternative management strategies. Another result had potential benefit for analysis of the biological data collected from finfish stocks that progressively move offshore as their length increases. A von Bertalanffy growth curve was fitted to the lengths at age of fish in each of three different habitats under the assumption that logistic curves described the probabilities that a fish of a given length was likely to occupy each habitat. The estimates of the parameters of the logistic curves provide information relating to offshore movement thereby providing the opportunity to improve the stock assessment of species that exhibit such offshore movement.

The Project produced two scientists with sound training in the use of quantitative approaches to fisheries science, Drs Simon de Lestang and Alex Hesp. Each is now making his own contribution to understanding the population dynamics of Western Australia’s fish stocks, while Dr Hesp is passing his knowledge on to new Honours and postgraduate students.

References

Anon. 2000a. *Management directions for Western Australia's finfish fisheries*. Fisheries Western Australia, Fisheries Management Paper No. 134.

Anon. 2000b. *Protecting and sharing Western Australia's coastal fish resources. The path to integrated management*. Fisheries Western Australia, Fisheries Management Paper No. 135.

Bird, D. J., Rotchell, J. M., Hesp, S. A., Newton, L. C., Hall, N. G. and Potter, I. C. 2007. To what extent are hepatic concentrations of heavy metals in *Anguilla anguilla* in a contaminated estuary related to body size and age and reflected in the metallothionein concentrations? *Env. Pollut.* In press.

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

Christensen, V., Walters, C.J. and Pauly, D. 2000. *Ecopath with Ecosim: a User's Guide*, October 2000 Edition. Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia. 130 p.

Coulson, P., Hesp, S. A., Potter, I. C. and Hall, N. G. 2005. Comparisons between the biology of two co-occurring species of whiting (Sillaginidae) in a large marine embayment. *Env. Biol. Fish.,* **73**: 125-139.

DeAngelis, D. L., and Gross, L. J. (editors). 1992. *Individual-Based Models and Approaches in Ecology*, Routledge, Chapman and Hall, New York.

de Lestang, S., Hall, N. G. and Potter, I. C. 2003a. Do the age compositions and growth of the crab *Portunus pelagicus* in marine embayments and estuaries differ? *J. mar. Biol. Ass. U.K.,* **83**: 971-978.

de Lestang, S., Hall, N. and Potter, I. C. 2003b. Influence of a deep artificial entrance channel on the biological characteristics of the blue swimmer crab *Portunus pelagicus* in a large microtidal estuary. *J. Exp. Mar. Biol. Ecol.,* **295**: 41-61.

de Lestang, S., Hall, N. G. and Potter, I. C. 2003c. Reproductive biology of the blue swimmer crab (*Portunus pelagicus*, Decapoda: Portunidae) in five water bodies on the west coast of Australia. *Fish. Bull., U.S.,* **101**: 745-757.

de Lestang, S., Hall, N. and Potter, I. C. 2003d. Changes in density, age composition, and growth rate of *Portunus pelagicus* in a large embayment in which fishing pressures and environmental conditions have been altered. *J. Crust. Biol.,* **23**: 908-919.

Deriso, R. B., Quinn II, T. J., and Neal, P. R. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.,* **42**: 815-824.

Fairclough, D. V., Hesp, S. A., Potter, I. C. and Hall, N. G. 2003. *Determination of the biological parameters required for managing the fisheries of four tuskfish species and western yellowfin bream.* FRDC Project No. 2000/137.

Farmer, B. M., French, D. J. W., Potter, I. C., Hesp, S. A. and Hall, N. G. 2006. *Determination of the biological parameters for managing the fisheries for Mulloway and Silver Trevally in Western Australia.* FRDC Project No. 2002/004.

Fletcher, W. J. 2002. *Policy for the Implementation of Ecologically Sustainable Development for Fisheries and Aquaculture within Western Australia. Department of Fisheries, Western Australia.* Fisheries Management Paper No. 157, 70 pp.

Fournier DA (1994) AUTODIF, a C++ array language extension with automatic differentiation for use in nonlinear modelling and statistics. Otter Research, Sidney, Canada

Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. *Journal of Fish Biology* **36**: 883-902.

Froese, R., and Pauly, D. (Editors). 2003. *FishBase*. World Wide Web electronic publication. www.fishbase.org, version 16 June 2003.

Hall, N. G., Hesp, S. A. & Potter, I. C. 2004. A Bayesian approach for overcoming inconsistencies in mortality estimates, using, as an example, data for *Acanthopagrus latus*. *Can. J. Fish. Aquat. Sci.,* **61**: 1202-1211.

Hall, N. G., Smith, K. D., de Lestang, S. and Potter, I. C. 2006. Does the largest chela of the males of three crab species undergo an allometric change that can be used to determine morphometric maturity? *ICES J. Mar. Sci.,* **63**: 140-150.

Hesp, S. A., Potter, I. C. and Hall, N. G. 2002. Age and size compositions, growth rate, reproductive biology, and habitats of the West Australian Dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species. *Fish. Bull., U.S.,* **100**: 214-227.

Hesp, S. A., Hall, N. G. & Potter, I. C. 2004a. Size-related movements of *Rhabdosargus sarba* in three different environments and their influence on estimates of von Bertalanffy growth parameters. *Mar. Biol.,* **144**: 449-462.

Hesp, S. A., Potter, I. C. & Hall, N. G. 2004b. Reproductive biology and protandrous hermaphroditism in *Acanthopagrus latus*. *Env. Biol. Fish*., **70**: 257-272.

Hoeksema, S. D., Chuwen, B. M., Hesp, S. A., Hall, N. G. and Potter, I. C. 2006. *Impact of environmental changes on the fish faunas of Western Australian south-coast estuaries*. FRDC Project No. 2002/017.

Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull., U.S.,* **81**: 898-903.

Jenkins, G. I., French, D. J. W., Potter, I. C., de Lestang, S., Hall, N. G., Partridge, G. J., Hesp, S. A. and Sarre, G. A. 2006. *Restocking the Blackwood River Estuary with the Black Bream* Acanthopagrus butcheri. FRDC Project No. 2000/180.

Jones, A. A., Hall, N. G. and Potter, I. C. 2007. Size compositions and reproductive biology of a heterodontid shark in waters in which it is an abundant bycatch species. *J. mar. Biol. Ass. U.K.,* In press.

Kailola, P.J., Williams, M.J., Stewart, P.C., Reichelt, R.E., McNee, A. and Grieve, C. 1993. *Australian Fisheries Resources*. Bureau of Resource Sciences and the Fisheries Research and Development Corporation, Canberra.

Larkin, P.A. 1996. Concepts and issues in marine ecosystem management. *Reviews in Fish Biology and Fisheries,* **6**: 139-164.

Mant, J. C., Moran, M. J., Newman, S. J., Hesp, A. S., Hall, N. G. and Potter, I. C. 2006. Biological characteristics and mortality of western butterfish (*Pentapodus vitta*), an abundant bycatch species of prawn trawling and recreational fishing in a large subtropical embayment. *Fish. Bull., U.S.,* **104**: 512-520.

Moore, S. E., Hesp, S. A., Hall, N. G. and Potter, I. C. 2007. Age and size compositions, growth and reproductive biology of the breaksea cod *Epinephelides armatus*, a gonochoristic serranid. *J. Fish Biol*. In press

Nelder, J. A. and Mead, R. 1965. A simplex method for function minimization. Computer Journal, **7**: 308-313.

Partridge, G. J., Sarre, G. A., Hall, N. G., Jenkins, G. I., Chaplin, J. and Potter, I. C. 2004. Comparisons between the growth of *Acanthopagrus butcheri* cultured from broodstock from two estuarine populations that are reproductively isolated and differ markedly in growth rate. *Aquaculture*, **231**: 51-58.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer*, **39**:175-192.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science*, **57**: 697-706.

Pember, M. B., Newman, S. J., Hesp, S. A., Young, G. C., Skepper, C. L., Hall, N. G. and Potter, I. C. 2006. *Biological parameters for managing the fisheries for Blue and King Threadfin Salmons, Estuary Rockcod, Malabar Grouper and Mangrove Jack in north-western Australia.* FRDC Project No. 2002/003.

Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. FAO, Rome. *FAO Fisheries Technical Paper*, No. 477, 108 p.

Potter, I. C., French, D. J. W., Jenkins, G. I., Hesp, S. A., Hall, N. G. and de Lestang, S. 2007. Comparisons of the growth of black bream, *Acanthopagrus butcheri*, in an estuary with those of its wild stock. *Rev. Fish. Sci*. In press.

Ralston, S. 1987. Mortality rates of snappers and groupers. In: Polovina, J. J., and Ralston, S., eds. *Tropical snappers and groupers. Biology and fisheries management*. Colorado, Westview Press: 375-404.

Reynolds, C. 1999. Individual-based models. URL: http://www.red3d.com/cwr/ibm.html.

Smith, K. D., Hall, N. G. and Potter, I. C. 2004. Relative abundances and size compositions of champagne crabs, *Hypothalassia acerba* on two coasts and in different water depths and seasons. *Mar. Freshwat. Res*., **55**: 653-661.

Smith, K. D., Hall, N. G., de Lestang, S. and Potter, I. C. 2004. Potential bias in estimates of the size of maturity of crabs derived from trap samples. *ICES J. Mar. Sci*., **61**: 906-912.

Smith, K. D., Potter, I. C. and Hall, N. G. 2004. *Biological and fisheries data for managing the deep-sea crabs* Hypothalassia acerba *and* Chaceon bicolor *in Western Australia*. Project Nos 1999/154 and 2001/055.

Sokal, R. R., and Rohlf, F. J. 1995. *Biometry*, 3rd ed. Freeman: San Francisco, 887 pp.

Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: A review. *Fish. Bull., U.S.,* **86**: 25-43.

White, W. T., Hall, N. G. and Potter, I. C. 2002a. Reproductive biology and growth during pre- and postnatal life of *Trygonoptera personata* and *T. mucosa* (Batoidea: Urolophidae). *Mar. Biol*., **140**: 699-712.

White, W. T., Hall, N. G. and Potter, I. C. 2002b. Size and age compositions and reproductive biology of the nervous shark *Carcharhinus cautus* in a large subtropical embayment, including an analysis of growth during pre- and postnatal life. *Mar. Biol*., **141**: 1153-1164.

Appendix 1: Intellectual property

The information produced in the study is not suited to commercialization.

Appendix 2: Staff list

Staff employed on the project included:

Dr Norman Hall

Dr Alex Hesp