RISK ANALYSIS AND SUSTAINABILITY OF THE SOUTHERN ROCK LOBSTER (*JASUS EDWARDSII*) RESOURCES IN SOUTH AUSTRALIA

Y. XIAO AND J. PRESCOTT

JANUARY 2008

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Risk analysis and sustainability of the southern rock lobster (*Jasus edwardsii*) resources in South Australia.

Final Report to the Fisheries Research and Development Corporation

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NON-TECHNICAL SUMMARY

In this project, we reviewed the relevant models developed and used in other invertebrate fisheries; then developed a population dynamics model for *J. edwardsii* for the Northern and Southern Zone Rock Lobster Fisheries, and finally outlined future research needs.

In this review, we attempt to explain why, in the deterministic context, an age-dependent population model is the same as a size-dependent model, and discuss several other related issues that must be understood, in order to implement, correctly, a size-dependent population model. Our overall argument is most difficult to explain in non-technical terms, but it is based on some probability theory that is well understood only by a handful of researchers with a background of statistics and probability theory. Such argument starts to appear in primary journals of fisheries research (Wang and Ellis, 2005; Kristensen et al., 2006) and will soon prevail, if logic prevails. We did not follow the published descriptions of size-dependent models, including those used in Tasmania, Victoria, NSW, Queensland, WA, New Zealand, and South Africa, because they run into some problems, three of which are bypassed by our work. We believe that a better approach would be to condition on the underlying model and the distributions of the parameters. By developing an age-dependent population model, by using a growth curve between size and age, and by determining the variability of growth parameters, we are able to develop a theoretically justifiable model that we have.

Based on this reasoning, a sex-specific, age- and time-dependent population model was developed to assess the status of the Northern Zone Rock Lobster Fishery (NZRLF) from both commercial catch and effort and additional sources of biological data. The outputs from the stochastic model allowed us to evaluate several management strategies by accounting for the spatiotemporal expansion of the fishery. Overall, the outputs indicated that both the total and exploitable biomass of lobsters (at or above an age of 3.5 yr) in the population, all decreased from 100% in 1970 to slightly above 20% in 2002.

Similarly, a sex-specific, age- and time-dependent population model was developed to assess the status of the Southern Zone Rock Lobster Fishery (SZRLF) from both commercial catch and effort and additional sources of biological data. Model design and development was similar to that described for the NZRLF . Overall, the model outputs indicated that both the total biomass and the exploitable biomass (at or above an age of 3.5 yr) in the population, all varied from 100%

in 1970 to slightly above 40% in 1987. This then increased to 80% in 2004.

Several conclusions can be drawn from this study. Probably most importantly, the stock status of *J. edwardsii* differs substantially between the Northern and Southern Zones. In the Northern Zone, the total biomass and number, the exploitable biomass and number, and the spawning (mature female) biomass and number of lobsters (at or above an age of 3.5 yr) all decreased from 100% in 1970 to slightly above 20% in 2002. By contrast, those in the Southern Zone all varied from 100% in 1970 through slightly above 40% in 1987 to 80% in 2004. Such differences must have resulted partly from the differing patterns of fishing mortality and recruitment. The significant recruitment in biomass of lobsters in the Southern Zone around 1998 appears to have increased the population size. In the Northern Zone however, the continued poor recruitment partly explains the current status of the fishery.

Finally, some areas for future research become clear from this work. (1) The relationship between the size of spawning stock, the number of spawned eggs and their subsequent recruitment to the fishery and the effects of environmental factors all require further study in order to improve the performance the model outputs; (2) An extension to the model that should be implemented immediately is to refine the catch equation, so that it represents the fishing seasons precisely and incorporate all the missing terms. In 3–5 years of time, the numerical solution of a system of ordinary or partial differential equations, with fish catch and hence equation being its part, is essential in fish population dynamics; (3) More biological realism needs to be incorporated immediately. The time step in the models was one year. Monthly or even daily time step should be used immediately, to make full use of the catch and effort data. In 3–5 years of time, the problem of an arbitrary time step should be eliminated, by numerically solving a system of ordinary or partial differential equations, with fish catch and hence equation being its part; and (4) the models need to be improved in 2–5 years of time by collecting and explicitly incorporating data on the transformation of larval stages to refine the estimates of the number of recruits.

Risk analysis and sustainability of the southern rock lobster (*Jasus edwardsii*) resources in South Australia

FRDC PROJECT NUMBER: 2000/123

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Objectives:

1. Undertake a review of appropriate models developed and used in other invertebrate fisheries, including those in Tasmania and Western Australia.
2. Develop a spatial-, time- and age-dependent model (or equivalently a spatial-, time- and size-dependent model).
3. Use the model to evaluate various harvesting strategies.
4. Use the model to forecast catch and abundance for individual areas.
5. Use the model to answer the following questions:
   How much risk is associated with any particular TAC or level of effort?
   What are the economic benefits of various harvesting strategies?
   Which fishing strategy produces a sustainable fishery, while, at the same time, maximizes catch and revenue?
   How does the current harvesting strategy compare to the optimal harvesting strategy?
   How much more biological information is gained or lost by adopting various harvesting strategies?
   What are the implications of lobsters' aggregating behaviour for the assessment of the stock?

OUTCOMES ACHIEVED

- A review of current fishery models used in lobster stock assessment and other invertebrate fisheries was completed;
- An integrated, sex-specific, age- and time-dependent population dynamics model was parameterised that utilised data on the biology of the southern rock lobster *Jasus edwardsii* off southern Australia, including tagging data, log-book catch and effort data, and length-frequency data as input to an integrated stock assessment model;
- The model was used, as a simulation model, to evaluate various harvesting strategies.
- Outputs of management interest were provided for both the Northern and Southern Zones of the fishery;
- Several key questions in relation to management interest were addressed (see General Discussion); and
- Future research areas were identified.

Review of appropriate models developed and used in other invertebrate fisheries:

In this review we attempt to explain why, in the deterministic context, an age-dependent population model is equivalent to a size-dependent one, and discuss several other related issues that must be understood, in order to implement, correctly, a size-dependent population model. The published descriptions of size-dependent models, including those used in Tasmania, Victoria, NSW, Queensland, WA, New Zealand, and South Africa generally indicate that they have eight primary problems, three of which are addressed here. Firstly, the age-based instantaneous rates of fishing and natural mortalities (which must be used in an age-dependent model) are mistakenly used as size-based ones. Since both types of mortalities differ substantially in value and in dimension, this oversight is equivalent to assuming that a fish population is far more dynamic than real, the size of its population is far smaller than real, its recruitment strength is far greater than real, and its population (if depleted) recovers much faster than real. Thus, any assessments based on this assumption, will produce a far more optimistic picture than reality. Secondly, it can be shown that any attempt at constructing, from a set of tagging data, a growth function or a size-transition matrix that can account for the incremental change in the size of a crustacean as a function of its age is inappropriate, unless data are available on the moult number and the duration of the stages of individual animals. However, almost all size-dependent models use a growth function or a size-transition matrix derived from tag-recapture data without information on moult number or stage duration. Thirdly, there is a logical inconsistency in the way in which the stochasticity in the quantities of interest is introduced. We believe that a better approach would be to condition on the underlying model and the distributions of the parameters. By developing an age-dependent population model, and by not claiming that a growth function accounts for the incremental change in the size of a crustacean as a function of its age (as a result of an absence of necessary data), and by conditioning on the underlying model and the distributions of the parameters, at least three of the logical inconsistencies mentioned above are addressed.

A population dynamics model for *J. edwardsii*: The Northern Zone Rock Lobster Fishery:

A sex-specific, age- and time-dependent population model was developed to assess the status of the Northern Zone Rock Lobster Fishery (NZRLF) from both commercial catch and effort and additional sources of biological data. The model construction was undertaken in two stages. Firstly, a deterministic model was developed to produce estimates of recruitment (R) and fishing mortality (F). The model was conditioned on catch in weight (Cw) and fitted to catch in number (Cn) as derived from commercial catch and effort data. In the model, the lobster population was divided into age groups that were followed over time. Outputs of R and F from the deterministic model were then used as priors for the second model development phase i.e. the stochastic model.

As with the deterministic model, the stochastic model was age based. The number of lobsters of each sex in each age group were estimated by applying growth, fishing mortality, natural mortality, and annual recruitment to each year. Biomass estimates were then derived using, sequentially, an age-length and a length-weight relationship. The outputs of annual recruitment (R) and derived levels of fishing mortality (F), for each year, from the deterministic model were used as priors for these values in this model (with a 10% error applied through a uniform distribution) that were adjusted by fitting into the standardized catch rate, the abundance of undersized lobsters, length-frequency data, and an index of puerulus settlement. The variability in length and hence the variability in the whole model conditional on the variability of the growth parameters.

The goodness-of-fit of the model seemed reasonable for all sources of data. Despite its simplicity, the model seemed to be sufficiently robust for management purposes, particularly because it overcomes the common problem of constructing a size-transition matrix. The outputs from the stochastic model allowed us to evaluate several management strategies by accounting for the spatiotemporal expansion of the fishery. Overall, the outputs indicated that both the total and exploitable biomass of lobsters (at or above an age of 3.5 yr) in the population, all decreased from 100% in 1970 to slightly above 20% in 2002. From 1970 to 2002, the catch in biomass and number of lobsters, rate of exploitation in terms of biomass of individuals, and the instantaneous rate of fishing mortality were all near, at or above that at the maximum sustainable yield. The biomass and number of recruits varied considerably from 1970 to 2002, although the number of eggs produced by female lobsters steadily decreased, reaching its lowest level in 1994, before slightly increasing thereafter. Although those calculations are somewhat uncertain due to a lack of some biological data, the fishery seems to have declined steadily over this period. Finally, the study highlighted certain gaps in available data such as information on the temporal changes in lobster body weight (because of the variability in the body weight of the individuals of the same length), effects of gear selectivity, female fecundity and expansion and contraction of the fishery. Collection of these data in the future will allow for a more robust stock assessment in this zone.

A population dynamics model for *J. edwardsii*: The Southern Zone Rock Lobster Fishery

A sex-specific, age- and time-dependent population model was developed to assess the status of the Southern Zone Rock Lobster Fishery (SZRLF) from both commercial catch and effort and additional sources of biological data. Model design and development was the same as that described for the NZRLF.

Similarly, the goodness-of-fit of the model seemed reasonable for all sources of data. Despite its simplicity, the model seemed to be sufficiently robust for management purposes, particularly because it overcomes the common problem of constructing a size-transition matrix. Overall the model outputs indicated that both the total biomass and the exploitable biomass (at or above an age of 3.5 yr) in the population, all varied from 100% in 1970 to slightly above 40% in 1987. This then increased to 80% in 2004. The catch in biomass was above the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter. The rate of exploitation in biomass was above that at the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter. The number of recruits were variable but increased slightly with time, with a significant influx of 6.2×10^6 individuals in 1998. However, the number of eggs produced by female lobsters decreased somewhat, reached its lowest level of 422.5×10^9 in 1988, and its highest level of 876.4×10^9 in 2002. Calculations are somewhat uncertain, because of a lack of some biological data, and hence the results should be treated cautiously. Overall however, the fishery appears to be in a healthy state.

Several conclusions can be drawn from this study. Probably most importantly, the stock status of *J. edwardsii* differs substantially between the Northern and Southern Zones. In the Northern Zone, the total biomass and number, the exploitable biomass and number, and the spawning (mature female) biomass and number of lobsters (at or above an age of 3.5 yr) all decreased from 100% in 1970 to slightly above 20% in 2002. By contrast, those in the Southern Zone all varied from 100% in 1970 through slightly above 40% in 1987 to 80% in 2004. Such differences must have resulted partly from the differing patterns of fishing mortality and recruitment. The significant recruitment in biomass of lobsters in the Southern Zone around 1998 appears to have increased the population size. In the Northern Zone however, the continued poor recruitment partly explains the current status of the fishery.

Future Research Priorities

Several issues must be addressed, in order to improve the performance of the models.

- The relationship between the size of spawning stock, the number of spawned eggs and their subsequent recruitment to the fishery and the effects of environmental factors all require further study in order to improve the performance of the model. In particular, the following questions should be answered: (1) why is the fishery in the Southern Zone remarkably resilient, despite a high level of catches? (2) why is the fishery in the Northern Zone pessimistic, despite a low level of catches? (3) what are the relative contributions to recruitment from internal and external sources, for either Northern or Southern Zone? It is the answers to those questions that are the basis for formulating biologically realistic and mathematically sound curves of recruitment.

- An extension to the model that should be implemented immediately is to refine the catch equation, so that it represents the fishing seasons precisely and incorporate all the missing terms. In 3–5 years of time, the numerical solution of a system of ordinary or partial differential equations, with fish catch and hence equation being its part, is essential in fish population dynamics. Such a system of differential equations has already been formulated for a multi-species fishery, with a single-species fishery as a special case.

- More biological realism needs to be incorporated immediately. The time step in the models was one year. Monthly or even daily time step should be used, to make full use of the catch and effort data. In 3–5 years of time, the problem of an arbitrary time step should be eliminated, by numerically solving a system of ordinary or partial differential equations, with fish catch and hence equation being its part.

- The models need to be improved in 2–5 years of time by collecting and explicitly incorporating data on the transformation of larval stages to refine the estimates of the number of recruits.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 BACKGROUND

Southern Rock Lobster (*Jasus edwardsii*) are distributed from southwestern Western Australia to the south coast of New South Wales and around the North and South Islands of New Zealand. Fishing for rock lobster has been carried out in South Australia since early European settlement. In the early 1940's lobster processing for the United States 'lobster tail' market commenced, which proved to be a catalyst for the development of the fishery throughout South Australia. The fishery constitutes South Australia's most valuable commercial fishery, with the annual gross landed value of production (GVP) currently estimated to be $83 million (Morrison 2002). Production in the Northern and Southern Zones was 446 and 1,900 tonnes respectively in the 2004/05 fishing season. The Rock Lobster Fishery, like other State fisheries, generates export revenue for South Australia (approximately $110 million), creates employment in catching and handling operations (approximately 2,000 jobs, mostly in regional areas) and generates business in supporting fishing service and supply industries. The annual business turnover for both fisheries is estimated to be $230 million (Morrison 2002).

The South Australian Rock Lobster Fishery has been separated into two discrete fishing zones for the purposes of management since 1968 (Figure 1.1). This geographic separation recognises key differences in the physical and ecological character that exist between the eastern and western borders of South Australia. The climatic and oceanographic influences on each fishery are quite distinct because of the wide geographic separation between each zone.

The Northern Zone is generally characterised by patchy and discrete reef formations (mainly granite) that are separated by large expanses of sandy bottom. These characteristics are known to limit the amount of suitable habitat afforded to lobster and result in a generally more patchy distribution of lobster and higher inter-annual variability in recruitment strength. In contrast, the Southern Zone is characterised by more continuous and inter-connected limestone reef formations, strong upwelling and more reliable puerulus settlement and recruitment patterns (Lewis 1981).

Historically, different management arrangements have been adopted for the commercial fishery in each zone in response to these unique characteristics. In the Southern Zone, the fishery is managed primarily on the basis of an Individually Transferable Quota (ITQ) system introduced in 1993, which is complemented by a mix of input controls including limited entry, a closed season and gear restrictions. In the Northern Zone, the perceived difficulties associated with TAC setting and catch monitoring, that arise as a result of higher recruitment variability and the large geographic expanse, have underpinned the historical industry and Government support for a management system based primarily on input controls. Despite this, the fishery progressed to a different position in 2003, where the environmental carrying capacity and long term sustainable yield, was by then, much better understood. As a result, an ITQ system similar to the Southern Zone was introduced from 2003/04.

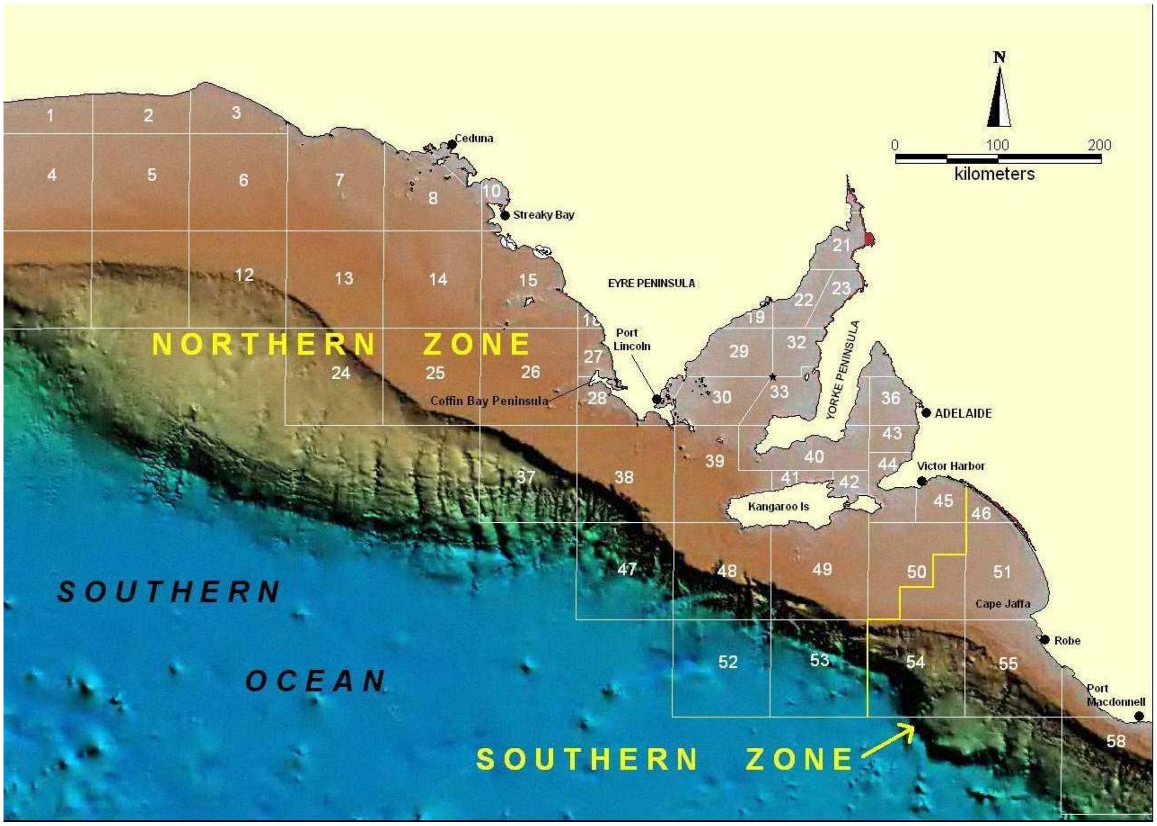

Figure 1.1. Marine Fishing Areas in the Northern and Southern Zones of the southern rock lobster fishery.

Both fisheries, while based principally on the capture of *J. edwardsii*, allow access to a range of other species. Key by-product species include octopus (*Octopus maroum*) and giant crab (*Pseudocarcinus gigas*).

Licence holders complete a compulsory daily logbook that has been regularly amended to accommodate changes in the fishery. During 1998, the logbook was modified to include specific details about giant crab fishing. In 2000/01, the logbook was amended so that the recording of numbers of undersize, spawning and dead lobsters, along with numbers of octopus, became voluntary. Logbook returns are submitted monthly and are entered into the South Australian Rock Lobster (SARL) database.

Since 1991, commercial fishers and researchers have collaborated in an at-sea voluntary pot-sampling program with the main aim of providing temporal and spatial data on pre-recruit indices, length-frequencies, reproductive status, sex ratios and estimates of lobster mortality. Fishers are encouraged to record the above data from 3 pots (in which the escape gaps are closed) per day. This sampling strategy can provide data from most vessels across many areas (McGarvey and Pennington, 2001).

Rates of puerulus and post-puerulus settlement have been monitored in the NZRLF since 1996 and the SZRLF since 1991 with 4 and 5 sites in each zone respectively. Data are utilised to calculate a puerulus settlement index (PSI) in order to estimate future biomass in the fishery using a 4–5 year time span between settlement and recruitment. A major tagging study was undertaken in the fishery between 1993 and 1996 (McGarvey et al., 1999; Linnane et al., 2005). The results highlighted spatial variation in movement rates, growth, size composition, and size at maturity.

Like many fisheries, the South Australian rock lobster fishery is characterized by a spatiotemporal expansion that is difficult to quantify. Although stocks have been assessed by various methods, including yield per recruit analysis, egg per recruit analysis and various production models of differing complexity, none of these assessments, nor assessments elsewhere, consider spatiotemporal expansion. There are also other difficulties in rock lobster assessments. One such difficulty is a false belief that an assessment can be length-based, without knowing the age (the sum of the intermoult periods). It can be shown that such assessments rest on the assumption that length is proportional to age, with proportionality constant of unity. In the case of the SA rock lobster fishery, no risk analysis has been conducted.

Two models have previously been developed for the South Australian Rock Lobster Fishery. The first model, the SARL model, was valuable in comparing alternative management strategies, but as it was never intended to be a stock assessment model, and hence cannot answer emerging questions regarding resource sustainability. The second model, the qR model, represented a major advance for the assessment of SA's lobster fisheries. However, limitations of the model include the absence of many sources of data (e.g. commercial catch-sampling data) as an input to the model.

This report has five chapters. Following this Chapter (General Introduction), Chapter 2 reviews some current fisheries models developed and used in lobster stock assessment and other invertebrate fisheries. In Chapters 3 and 4, integrated, sex-specific, age- and time-dependent population dynamics models for the Northern and Southern Zones of the fishery, respectively; are described. These models will utilize a broad range of data on the biology of the southern rock lobster *Jasus edwardsii* off southern Australia, including tagging data, log-book catch and effort data, and length-frequency data. Outputs of management interest are given for both the Northern and Southern Zones of the fishery. This report concludes in Chapter 5 with a general discussion of the findings and an identification of some areas for future research

1.2 NEED

The South Australian lobster fishery has a rich source of biological and fisheries-dependent data. However, to date, these data were not been fully exploited in a modelling sense. Although recent assessments provide useful information on the various aspects of the fishery, no risk analysis of management strategies have been undertaken.

The consequences of this are:

- The lobster industry is exposed and vulnerable to claims of over-fishing because it cannot respond with a defence of its management strategies and practices based on a formal risk assessment.
- Because the risk of over-fishing is not quantified, the fishery must be managed under the guidance of the precautionary principle. Hence, catches and revenues may be sub-optimal.
- The industry may not be able to capitalize on the opportunities for attracting premium prices for their product through certification of the fishery's sustainability, and meeting the export requirements from Australia's Environmental Protection and Biodiversity Conservation (EPBC) Act.

1.3 OBJECTIVES

1. Undertake a review of appropriate models developed and used in other invertebrate fisheries, including those in Tasmania and Western Australia.
2. Develop a spatial-, time- and age-dependent model (or equivalently a spatial-, time- and size-dependent model).

3. Use the model to evaluate various harvesting strategies.
4. Use the model to forecast catch and abundance for individual areas.
5. Use the model to answer the following questions:
   How much risk is associated with any particular TAC or level of effort?
   What are the economic benefits of various harvesting strategies?
   Which fishing strategy produces a sustainable fishery, while, at the same time, maximizes catch and revenue?
   How does the current harvesting strategy compare to the optimal harvesting strategy?
   How much more biological information is gained or lost by adopting various harvesting strategies?
   What are the implications of lobsters' aggregating behaviour for the assessment of the stock?

CHAPTER 2. A REVIEW OF SIZE-DEPENDENT POPULATION MODELS (Xiao, 2006a)

Objective 1: Undertake a review of appropriate models developed and used in other invertebrate fisheries, including those in Tasmania and Western Australia.

This objective was achieved by explaining, in broad terms, why, in the deterministic context, an age-dependent population model is equivalent to a size-dependent one, and discussing several other related issues that must be understood, in order to implement, correctly, a size-dependent population model. The published descriptions of size-dependent models, including those used in Tasmania, Victoria, NSW, Queensland, WA, New Zealand, and South Africa generally indicate that they have eight primary problems, three of which are addressed here. Firstly, the age-based instantaneous rates of fishing and natural mortalities (which must be used in an age-dependent model) are mistakenly used as size-based ones. Since both types of mortalities differ substantially in value and in dimension, this oversight is equivalent to assuming that a fish population is far more dynamic than real, the size of its population is far smaller than real, its recruitment strength is far greater than real, and its population (if depleted) recovers much faster than real. Thus, any assessments, based on this assumption, will produce a far more optimistic picture than real. Secondly, it can be shown that any attempt at constructing, from a set of tagging data, a growth function or a size-transition matrix that can account for the incremental change in the size of a crustacean as a function of its age is inappropriate, unless data are available on the moult number and the duration of the stages of individual animals. However, almost all size-dependent models use a growth function or a size-transition matrix derived from tag-recapture data without information on moult number or stage duration. Thirdly, there is a logical inconsistency in the way in which the stochasticity in the quantities of interest is introduced by manipulating the population model that was originally derived assuming that all the quantities were fixed. We believe that a better approach would be to condition on the underlying model and the distributions of the parameters. By developing an age-dependent population model, and by not claiming that a growth function accounts for the incremental change in the size of a crustacean as a function of its age (as a result of an absence of necessary data), and by conditioning on the underlying model and the distributions of the parameters, at least three of the logical inconsistencies mentioned above are addressed.

2.1 INTRODUCTION

Age- and time-dependent population models have been used extensively in many sciences since Lotka (1922, 1924), McKendrick (1926), Kermack and McKendrick (1927, 1932) and Hoppensteadt (1975). Interestingly, although such models pre-dated their work by more than two decades, Beverton and Holt (1957) used, in their now much cited work, ordinary differential equations instead of partial differential equations. While their use of ordinary differential equations popularised their work, it meant that many important processes and traits, such as recruitment and the initial age distribution of fish, could not be treated in an integral manner. Had they used first order partial differential equations, as in previous works, for example, these processes and traits would have fallen naturally as their initial and boundary conditions, and therefore would not have led to the utilization of yield-per-recruit analysis in future years.

The first order partial differential equations or their discrete versions are implied by all the dynamic-pool models, models for VPA (Virtual Population Analysis), and other age- and time-dependent models in fisheries science. These age-structured models, as they are commonly known as, became popular in the late 1980s. Initially, they were deterministic in nature, but soon, errors were added to their quantities in a particular application, in order to capture the "uncertainty". These models could be fitted into data from almost any source, as well as data on the size composition of the fish, provided that the expected values from the model can be computed, given the model structure, the data, and the estimated or specified parameters. They could be used for the prediction of a function of any single quantity or multiple quantities that are in a model, in a maximum likelihood or Bayesian context. This was undertaken for many species. Soon some fisheries scientists argued that certain species of animals, such as crustaceans, could not be aged, as a justification for the development of "size-structured models". This argument is appealing, and was accepted by many, and so are those models, which are now commonly used to underpin fisheries management. As with age-structured models, these models could also be fitted into data from almost any source, as well as data on the size composition of the fish, provided that the expected values from the model can be computed, given the model structure, the data, and the estimated or specified parameters. They could be used for the prediction of a function of any single quantity or multiple quantities that are in a model, in a maximum likelihood or Bayesian context. This was again undertaken for many species. However, in contrast with size-dependent models in other fields of science (e.g. ecology), the published descriptions of size-dependent models in fisheries journals, including those used in Tasmania (Punt and Kennedy, 1997), Victoria (Hobday and Punt, 2001), New Zealand (Bentley et al., 2001; Breen et al., 2001), South Africa (Bergh and Johnston, 1992; Johnston and Bergh, 1993), and North America (Chen et al., 2005) have some subtle conceptual problems.

Firstly, what is the difference between an age-dependent population model and a size-dependent one? In the deterministic context, the answer to this question is trivial to many, as it has been given, at least implicitly, on many occasions (e.g. Fournier and Doonan, 1987; Schnute, 1987; Beyer, 1989; Quinn and Deriso, 1999, p. 368; Xiao, 2003). The clearest description is provided by Quinn and Deriso (1999, p. 368). Nevertheless, despite Quinn and Deriso's elegant, down-to-earth, and very helpful style of presentation throughout their now classic book, and despite whatever logically sound models have been published before and after it, most model users still do not appreciate the somewhat subtle differences between a logically consistent age-dependent population model and a logically consistent size-dependent one. Indeed, quite frequently, the components of one are confused with those of the other.

In this chapter, I address this unfortunate oversight, by explaining, simply and in detail, Quinn and Deriso's (1999, p. 368) answer to the question, and by commenting on several other related issues that must be understood, in order to implement, correctly, a size-dependent population model. It will be shown that if the growth of an individual fish is deterministic, then age- and size-dependent population models are equivalent; if not, e.g. as a result of the variability among individuals in growth, the situation is very complicated. The simplest way in which this is done in a valid manner is exemplified, in a logically similar but practically different context, by Wang and Ellis (2005) and Kristensen et al. (2006).

2.2 AN AGE-DEPENDENT MODEL

For simplicity, suffice to consider the simple differential equation

$$dN(a)/da = -\left[F(a)+M(a)\right]N(a), \qquad a_0 \le a \tag{1}$$

where $N(a)$ is the number of fish of age a in a fish population, $F(a)$ is the instantaneous rate of fishing mortality of fish of age a, $M(a)$ is the instantaneous rate of natural mortality of fish of age a, and a_0 is the age, say, at birth or the age at recruitment. To solve this equation, divide both sides by $N(a)$, then "multiply" both sides of the resulting equation by da, and finally integrate both sides of the resulting equation with respect to age a (in whose place, I now use, for clarity, age s as the dummy variable of integration) from age a_0 to age a, such that

$$\int_{N(a_0)}^{N(a)} dN(s)/N(s) = -\int_{a_0}^{a} \left[F(s) + M(s)\right] ds$$

or equivalently

$$\ln(N(s))\Big|_{N(a_0)}^{N(a)} = \ln(N(a)) - \ln(N(a_0)) = \ln\left(\frac{N(a)}{N(a_0)}\right) = -\int_{a_0}^{a} \left[F(s) + M(s)\right] ds \tag{2}$$

Now, taking the exponential on both sides of Eq. (2), gives the well-known formula

$$N(a) = N(a_0)\exp\left(-\int_{a_0}^{a} \left[F(s) + M(s)\right] ds\right) \tag{3}$$

Eqs. (1)–(3) are (part of) an age-dependent model.

2.3 A SIZE-DEPENDENT MODEL

A size-dependent model can be easily derived from Eqs. (1)–(3), say, by changing the dummy variable of integration in Eq. (3) from age to size. To do this, we need to introduce a growth (in size) curve — the von Bertalanffy growth equation

$$dL(a)/da = K\left[L_\infty - L(a)\right] \qquad a_0^{'} \le a \tag{4}$$

or equivalently

$$da = \frac{dL(a)}{K\left[L_\infty - L(a)\right]} \qquad a_0^{'} \le a \tag{5}$$

where $L(a)$ is the size of a fish of age a, K and L_∞ are the two well-known parameters, and $a_0^{'}$ is a reference age. As a simple linear ordinary differential equation, Eq. (4) or (5) can be solved, as an initial value problem, to give

$$L(a) = L_\infty - \left[L_\infty - L(a_0^{'})\right]\exp\left(-K\left(a - a_0^{'}\right)\right) \tag{6}$$

which is slightly more general than, and hence is slightly different from, what most people are accustomed to. This curve is, of course, a deterministic model; I shall comment on stochastic growth models below.

Now, to get a size-dependent model, all that is needed to do is to substitute Eq. (5) into Eq. (3). This being done, we have

$$N(a) = N(a_0)\exp\left(-\int_{a_0}^{a} \frac{F(s)+M(s)}{K\left[L_\infty - L(s)\right]} dL(s) \right)$$

which can be rewritten as

$$N(L(a)) = N(L(a_0))\exp\left(-\int_{L(a_0)}^{L(a)} \frac{F(s)+M(s)}{K\left[L_\infty - L(s)\right]} dL(s) \right) \tag{7}$$

This is (part of) a size-dependent model, which has been derived on numerous occasions.

Therefore, in the deterministic context, an age-dependent population model is equivalent to a size-dependent one (Beyer, 1989; Quinn and Deriso, 1999, p. 368; Xiao, 2003), with one being deducible from the other, simply by changing the variable of integration. In other words, a size-dependent model is an age-dependent population model "plus" a growth curve, and conversely, an age-dependent population model is a size-dependent model "minus" a growth curve.

2.4 AGE-BASED INSTANTANEOUS RATES OF MORTALITIES VERSUS SIZE-BASED ONES

Eq. (7) does make sense, dimensionally or otherwise. Under the integral sign, for example, $dL(s)$ is the dummy variable of integration and has a dimension of size (e.g. mm) that matches, exactly, the dimension of $L_\infty - L(s)$; $F(s)$ and $M(s)$ are the instantaneous rates of fishing and natural mortalities and share a dimension of per unit of time (e.g. year^{-1}) with the growth parameter K. Therefore, the dimensions of all the quantities in Eq. (7) are matched up perfectly.

Now, I must mention a rather important but usually neglected fact that is absolutely essential for implementing, correctly, an age-dependent model, or a size-dependent one. The commonly known $F(a)$ and $M(a)$ are actually the age-based instantaneous rates of fishing and natural mortalities of fish of age a, both with a dimension of per unit of time (e.g. year^{-1}). By contrast, the terms $F_L(a) = \dfrac{F(a)}{K\left[L_\infty - L(a)\right]}$ and $M_L(a) = \dfrac{M(a)}{K\left[L_\infty - L(a)\right]}$ in Eq. (7) are the corresponding size-based instantaneous rates of fishing and natural mortality of fish of size $L(a)$, both with a dimension of per unit of size (e.g. mm^{-1}). For a general growth curve, $F_L(a) = \dfrac{F(a)}{dL(a)/da} = F(a)\dfrac{da}{dL(a)}$, and $M_L(a) = \dfrac{M(a)}{dL(a)/da} = M(a)\dfrac{da}{dL(a)}$. The age-based fishing and natural mortalities, which must be used in an age-dependent model, are rather different, both in dimension and in value, from size-based ones, which must be used in a size-dependent model. Unfortunately, this protocol has rarely been observed in published size-dependent population models in fisheries journals.

Just to see how different they are, let us have a simple example, based loosely on the male southern rock lobster *Jasus edwardsii*, where $F(a)$=0.4 year^{-1}, $M(a)$=0.1 year^{-1}, K=0.2135 year^{-1}, L_∞=198.90 mm, $a_0^{'}$=1 year, and $L(a_0^{'})$=11 mm. Substituting these values into the size-based fishing and natural mortalities $F_L(a)$ and $M_L(a)$, with $L(a)$ being calculated by use of Eq. (6), produces very interesting results (Figure 2.1). For a year 4 lobster, for example, its $F(4)$=0.4 year^{-1}, whereas its $F_L(4)$=0.0189 mm^{-1} (21.16 times smaller or larger if one is confused with the other); its $M(a)$=0.1 year^{-1}, whereas its $M_L(4)$=0.004723 mm^{-1} (21.14 times smaller or larger if one is confused with the other). Confusing one with the other is like confusing apples with oranges.

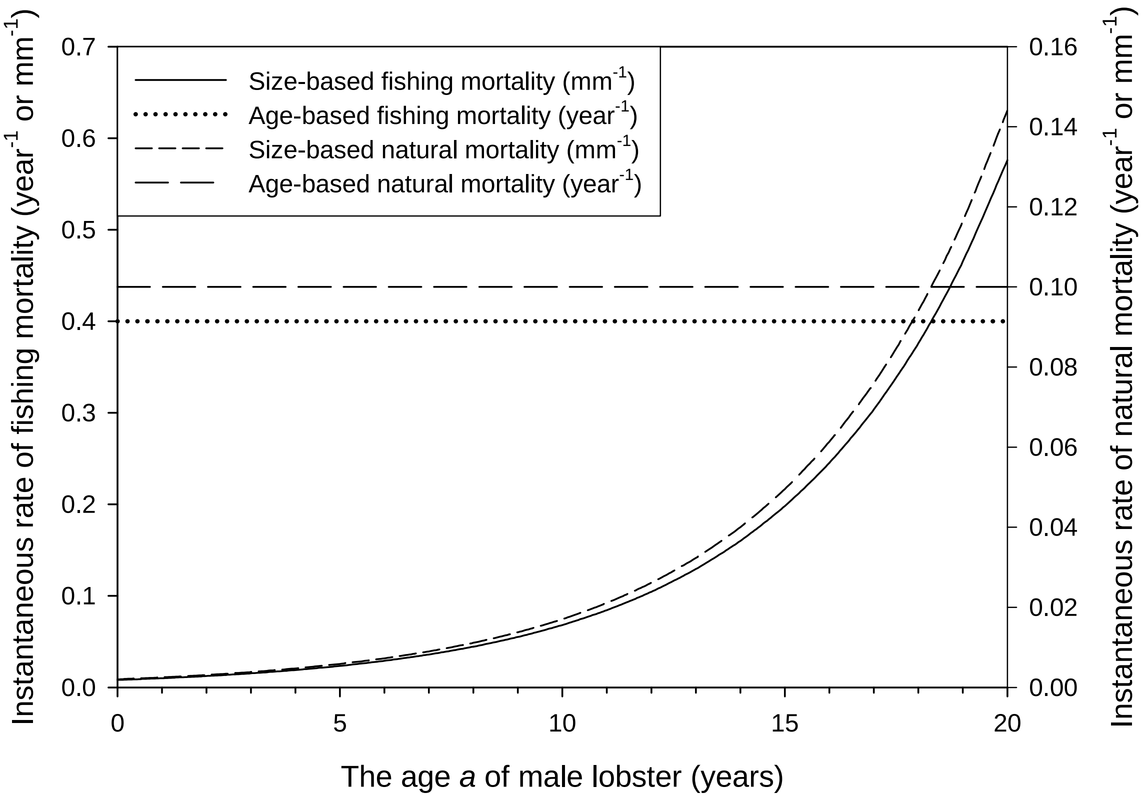

Figure 2.1. Calculations of the age-based instantaneous rates of fishing and natural mortalities.

($F(a)$ and $M(a)$), and size-based instantaneous rates of fishing and natural mortalities ($F_L(a)$ and $M_L(a)$), based loosely on the male southern rock lobster *Jasus edwardsii*, with $F(a)$=0.4 year^{-1}, $M(a)$=0.1 year^{-1}, K=0.2135 year^{-1}, L_∞=198.90 mm, a_0'=1 year, and $L(a_0')$=11 mm.

Such huge differences both in value and in dimension imply that any confusion of age-based instantaneous rates of fishing and natural mortalities with size-based ones, or vice versa, is bound to wreak havoc with the results of the models. This is because the instantaneous rates of fishing and natural mortalities are crucially important quantities in characterizing a fish population. Indeed, the instantaneous rate of natural mortality is a measure of how dynamic a fish population is. In the case of the lobster example above, use of the age-based instantaneous rate of natural mortality in place of the size-based one in a size-dependent model for a fish population is equivalent to assuming that its population is far more dynamic than real, the size of its population is far smaller than real, its recruitment strength is far greater than real, and its population (if depleted) recovers much faster than real. Thus, such an assessment will produce a far more optimistic picture than real. Unfortunately, age-based mortalities have invariably been used, in almost all published size-dependent models, as if they were size-based ones.

What should be done about this unfortunate oversight? If a size-dependent model is used, then size-based mortalities must be used in it, and many other age-based quantities must be converted into size-based ones. Many of these conversions can be difficult to output and require at least some elementary knowledge of calculus. The alternative, of course, is to use an age-dependent population model, where no such conversion is necessary and where most biological data are age-based. Clearly, however, these apply only to deterministic age- and size-dependent population models.

2.5 DOES AN AGE-DEPENDENT POPULATION MODEL APPLY TO ANIMALS THAT CANNOT BE AGED?

There is often the misconception among many fisheries biologists that as neither lobsters nor any other crustaceans can be aged, an age-dependent population model does not apply to them. Biological age aside, chronological age is just the time elapsed from the time of birth. Time is age, and age is time, so to speak. If time enters a model, so must age. What is important to recognize here is that, as far as age or time is concerned, what really matters is the change of time and the change of age, both of which are synonymous (up to a known multiplier at most). So, if a model is implemented on an annual time step, then the animal's age has an annual increment. If one knows the breeding season and hence the time of birth of a fish population, then one knows the age increment from it. Put in another way, age is rather like the "time at liberty" of a tagged fish in a tag-recapture study, where one does not have to know the absolute age of individual animals to estimate some of their growth parameters from a set of conventional tagging data. That lobsters, or indeed any other crustaceans, cannot be aged only implies that one cannot collect age-specific data on them. This limitation is common to both types of models. Therefore, as an equivalent of a size-dependent model in the case of deterministic population models, an age-dependent population model not only applies to populations of animals that can or cannot be aged, but also is much simpler to implement.

2.6 DETERMINISTIC GROWTH MODELS

There is often considerable variability among the individuals of an animal population in their growth trajectories. For a "continuously" or "smoothly" growing fish, however, such variability might be sufficiently small to be ignored in modelling their populations. For animals such as crustaceans, which grow during moulting, their size changes abruptly with moult number, and their age is the sum of their inter-moult periods. It is natural, then, to model this type of animal by modelling their change in size as a result of the change in moult number.

In this section, I deal with the implications of the absence of data on the moult number for modelling the growth of crustaceans. Specifically, I answer the question: can we really parameterize a growth model for crustaceans from a set of conventional tagging data, where we only know the time at release, the time at recapture, the size at release, and the size at recapture, but do not know the moult number?

As a simple (deterministic) example, we know very well that a linear relationship exists between the pre- and post-moult sizes of a crustacean, such that

$$L(n+1) = a + bL(n) \tag{8}$$

where $L(n)$ is the size of a crustacean at moult n, and a and b are the parameters that have been estimated for many species. Eq. (8) is a simple difference (as against differential) equation, with a solution

$$
\begin{aligned}
L(n) &= \frac{a}{1-b} - \left(\frac{a}{1-b} - L(n_0) \right) b^{n-n_0} \\
&= L_\infty - \left(L_\infty - L(n_0) \right) \exp\left(\ln(b)(n-n_0) \right)
\end{aligned} \qquad (9)
$$

where $L_\infty = a/(1-b)$ is the maximum size of a crustacean. A comparison of Eq. (9) with Eq. (6) reveals their identity, provided that $L_\infty = a/(1-b)$, and $K = -\ln(b)$. Therefore, the size $L(n)$ of a crustacean at moult n varies with moult number n in a von Bertalanffy manner.

But, how does the size $L(n)$ of a crustacean at moult n vary with its age? Is it also describable by a von Bertalanffy growth curve? In preparing to answer this question, we now derive a simple deterministic model for the age of a crustacean as a function of its moult number. For this purpose, we notice that the duration of a (moult) stage of a crustacean generally depends on the number of stages that it has already experienced. For example, the stage 1 of a phyllosoma of a lobster may last for 18 days, and stage 2 for 21 days, an increase of three days. This general observation can be described by a simple deterministic model, of the form

$$
\frac{\Delta D(n+1)}{\Delta D(n)} = 1 + \alpha \qquad (10)
$$

where $\Delta D(n) = D(n+1) - D(n)$ is the duration of stage n of an individual, $\sum_{i=n_0}^{n-1} \Delta D(i) = D(n) - D(n_0)$ is the cumulative duration of stages from stage n_0 to stage n, $n \geq n_0$, and α is the fractional change in stage duration at stage n. Eq. (10) implies that

$$
\Delta D(n) = \Delta D(n_0) \left(1 + \alpha \right)^{n-n_0} \qquad (11)
$$

and

$$
D(n) = D(n_0) + \Delta D(n_0) \frac{1}{\alpha} \left[\left(1 + \alpha \right)^{n-n_0} - 1 \right] \qquad (12)
$$

Now, Eq. (12) can be solved for $n - n_0$ to yield

$$
n - n_0 = \frac{1}{\ln\left(1 + \alpha \right)} \ln\left(1 + \frac{\alpha}{\Delta D(n_0)} \left[D(n) - D(n_0) \right] \right)
$$

which can be substituted into Eq. (9) to give

$$
L(n) = L_\infty - \left(L_\infty - L(n_0) \right) \exp\left(\frac{\ln(b)}{\ln\left(1 + \alpha \right)} \ln\left(1 + \frac{\alpha}{\Delta D(n_0)} \left[D(n) - D(n_0) \right] \right) \right) \qquad (13)
$$

Eq. (13) is the counterpart of, but is not the same as, Eq. (6). It says that the size $L(n)$ of a crustacean at its “time at liberty” (or age) $\left[D(n)-D(n_0)\right]$ increases in a quasi-von Bertalanffy manner. The prefix quasi- is used here, because of its intermittent nature.

From Eq. (13), a striking conclusion can be drawn. If we know the moult number n_0 of a crustacean at release, its “time at liberty” $\left[D(n)-D(n_0)\right]$, its size at release $L(n_0)$, its size at recapture $L(n)$, and its duration $\Delta D(n_0)$ of stage n_0, then we can hope to estimate all the parameters in Eq. (13), at least theoretically. In marked contrast, the estimation of all the parameters in Eq. (6) requires only three pieces of information — the time at liberty $\left(a-a_0'\right)$ of an animal, its size $L(a_0')$ at release, and its size $L(a)$ at recapture, two pieces of data fewer.

This simple example illustrates that any attempt at constructing, from a set of conventional tagging data, a growth function that can account for the incremental change in the size of a crustacean as a function of its age is doomed to failure, unless data are available on the moult number and the duration of the stages of individual animals. Without such data, the only thing that can be done is to fit Eq. (6) or something like it, but , in so doing, no claim can be made that the fitted growth equation accounts for the incremental change of the animal's growth, for we know that Eqs. (6) and (13) are very different. Why is this? The reason is quite simple. The growth of a crustacean is not describable by its size as a function of its age alone; it is describable, say, by a parametric growth function, with its size AND its age, each as a function of time — its parameter. A similar reasoning applies to stochastic growth models for crustaceans.

2.7 STOCHASTIC GROWTH MODELS

Can a size-transition matrix that accounts for the incremental change in the size of a lobster or any other crustacean be determined from a set of conventional tagging data? The answer is no. To see this, let us assume here that time flows continuously for a crustacean; its moulting occurs instantaneously at certain time-varying intervals. These biological characteristics can be approximated by a system of difference-differential equations, of the form

$$\begin{cases} dN(0,t)/dt = -\lambda N(0,t) \\ dN(i,t) = -\lambda N(i,t) + \lambda N(i-1,t), \qquad i = 1,2,3,\cdots \end{cases}, \qquad t_0 \le t \tag{14}$$

where $N(i,t)$ is the probability that a crustacean is in moult $i=0,1,2,\cdots$ at time t, λ is a parameter defining an infinitesimal transition matrix (not to be confused with the transition matrix in a finite period of time), and t_0 is its time at birth. Its solution is

$$N(i,t)=\frac{1}{i!}\left[\lambda(t-t_0)\right]^i \exp\left(-\lambda(t-t_0)\right), \qquad i=0,1,2,\cdots \tag{15}$$

or, in terms of any previous moult number $i_0=0,1,2,\cdots$ and of a previous time t_1, $t_0\le t_1\le t$, as a "transitional probability", is

$$N(i,t)=N(i_0,t_1)\frac{i_0!}{i!}\frac{\left[\lambda(t-t_0)\right]^i}{\left[\lambda(t_1-t_0)\right]^{i_0}}\exp\left(-\lambda(t-t_1)\right), \qquad i\ge i_0=0,1,2,\cdots;\ t\ge t_1\ge t_0 \tag{16}$$

Eqs. (14)–(16) say that one cannot compute the probability $N(i,t)$ that a crustacean is in moult $i=0,1,2,\cdots$ at time t, unless one knows the number i_0 of moults that a crustacean has already passed through at a previous time t_1, $t_0\le t_1\le t$, in exactly the same way that one simply cannot find the probability of having two heads in two throws of a coin, without knowing the probabilities of the events of the first throw! The situation is actually slightly worse here, for we cannot even eliminate the time at birth t_0 in Eq. (16) and hence cannot even construct a transitional matrix. This is not surprising, especially considering the fact that a transitional matrix cannot, in general, be constructed for an arbitrary stochastic process. Simple as this example may be, this conclusion is fairly general. As mentioned above, no information is available on the number of moults of a crustacean from a set of conventional tagging data; hence no length-transition matrix can, in general, be determined.

Therefore, it is impossible to determine the growth equations, deterministic or stochastic, that account for the incremental change in the size of a lobster or any other crustacean from a set of conventional tagging data.

2.8 HOW SHOULD STOCHASTICITY IN A POPULATION MODEL BE INTRODUCED?

In fisheries research, most people introduce variability into the quantities of interest in an age-dependent or size-dependent deterministic population model, which is derived by assuming that those very same quantities are deterministic. For example, one might assign a uniform prior to the instantaneous rate $M(a)$ of natural mortality, say, in Eq. (3), to make it stochastic. Such an approach to stochasticity is very common, but clearly is not self-consistent. This is because if $M(a)$ in Eq. (3) is a random variable, so is the same $M(a)$ in Eq. (1). But, if the $M(a)$ in Eq. (1) is a random variable, then Eq. (3) does not apply. Thus, one cannot introduce stochasticity whenever and wherever one wants to in an existing population model, simply to maintain its logical consistency and validity.

However, the instantaneous rate of natural mortality and many other quantities in a population model do vary with a great many environmental factors, and making them stochastic is fully justified biologically and statistically (Schnute, 1991). For logical consistency, however, their stochasticity must be introduced at the very beginning of the development of an age- or size-dependent population model, as basic assumptions. In the case of Eqs. (1)–(3), one must start with Eq. (1) and derive the analogue of Eq. (3). This is, of course, much easier said than done, depending on what sort of variability is to be introduced. For example, if the $M(a)$ in Eq. (1) follows a multivariate normal distribution, with an appropriate variance-covariance matrix, then Eq. (1) becomes a stochastic differential equation (Gardiner, 1985; Øksendal, 1998). In the case of individual variability in growth, Eq. (1), which applies to a sufficiently number of individuals as a single entity, no longer applies. A brand-new stochastic process model might be a natural representation.

Since the most commonly used population models (e.g. Eq. (1)) are, or the solutions of, ordinary or partial differential equations, for logical consistency of the resulting equations, a direct introduction of stochasticity into their quantities is likely to make them stochastic differential equations (Øksendal, 1998) or to yield new stochastic processes (Gardiner, 1985). Because of the considerable difficulties in handling stochastic ordinary or partial differential equations, few fisheries biologists are at ease with handling them. Nothing can be done about this enormous obstacle, except perhaps to improve the analytical competence of fisheries modellers. Nonetheless, much work has been done. The interested reader should consult Quinn and Deriso (1999, p. 363–397) and the references therein to get started. In a stochastic model, for instance, the instantaneous rate of natural mortality of fish can be modelled as a function of age or size, whereas that of fishing mortality as a function of size.

2.9 DISCUSSION

Although useful work was undertaken before the 1990s on size-dependent population models (e.g. Deriso and Parma, 1988), the last decade has seen the repeated publication of size-dependent population models with many logical inconsistencies, as a result of falling into one or more of the many traps mentioned above. It is high time to follow the examples of work undertaken before the 1990s on size- and age-dependent population models and move forward. Two recent published pieces of exemplary work in this regard are Wang and Ellis (2005) and Kristensen et al. (2006), who showed how easy it is to account for the variability in growth of animals, without ever constructing a length-transition matrix.

Several conclusions can be drawn from this review. The published descriptions of size-dependent models, including those used in Tasmania, Victoria, NSW, Queensland, WA, New Zealand, and South Africa generally indicate that these models have eight primary problems, three of which are mentioned here. Firstly, the age-based instantaneous rates of fishing and natural mortalities (which must be used in an age-dependent model) are mistakenly used as size-based ones. Since both types of mortalities differ substantially in value and in dimension, this oversight is equivalent to assuming that a fish population is far more dynamic than real, the size of its population is far smaller than real, its recruitment strength is far greater than real, and its population (if depleted) recovers much faster than real. Thus, any assessments, based on this assumption, will produce a far more optimistic picture than real.

Secondly, it can be shown that any attempt at constructing, from a set of tagging data, a growth function or a size-transition matrix that can account for the incremental change in the size of a crustacean as a function of its age is inappropriate, unless data are available on the moult number and the duration of the stages of individual animals. However, almost all size-dependent models use a growth function or a size-transition matrix derived from tag-recapture data without information on moult number or stage duration. Thirdly, there is a logical inconsistency in the way in which the stochasticity in the quantities of interest is introduced by manipulating the population model that was originally derived assuming that all the quantities were fixed. We believe that a better approach would be to condition on the underlying model and the distributions of the parameters.

By developing an age-dependent population model, and by not claiming that a growth function accounts for the incremental change in the size of a crustacean as a function of its age (as a result of an absence of necessary data), and by conditioning on the population dynamics model and the distributions of the parameters, the developed model reduces the logical inconsistencies by at least three. That is why deterministic and stochastic sex-, time- and age-dependent models were selected because, properly structured, these are equivalent to a size-structured model, and vice versa (see, for example, Quinn and Deriso 1999, pp 368).

CHAPTER 3. A POPULATION DYNAMICS MODEL FOR THE SOUTHERN ROCK LOBSTER, *JASUS EDWARDSII*, OFF SOUTHERN AUSTRALIA: THE NORTHERN ZONE ROCK LOBSTER FISHERY

Objective 2: Develop a spatial-, time- and age-dependent model (or equivalently a spatial-, time- and size-dependent model).

Objective 3: Use the model to evaluate various harvesting strategies.

Objective 4: Use the model to forecast catch and abundance for individual areas.

Objective 5: Use the model to answer several relevant questions. Namely:

- How much risk is associated with any particular TAC or level of effort?
- What are the economic benefits of various harvesting strategies?
- Which fishing strategy produces a sustainable fishery, while, at the same time, maximizes catch and revenue?
- How does the current harvesting strategy compare to the optimal harvesting strategy?
- How much more biological information is gained or lost by adopting various harvesting strategies?
- What are the implications of lobsters' aggregating behaviour for the assessment of the stock?

These objectives were achieved by parameterizing a sex-specific, age- and time-dependent population model to assess its stock from commercial catch and effort data and other biological data and to evaluate several management strategies. Notably, spatiotemporal expansion of the fishery was incorporated in the model. The total biomass and the exploitable biomass of lobsters (at or above an age of 3.5 yr) in the population all decreased from 100% in 1970 to slightly above 20% in 2002. From 1970 to 2002, the catch in biomass and number of lobsters, the rate of exploitation in terms of biomass of individuals, and the instantaneous rate of fishing mortality were all near, at or above that at the maximum sustainable yield. The biomass and number of recruits varied considerably from 1970 to 2002, although the number of eggs produced by female lobsters steadily decreased, reached its lowest level in 1994, and slightly increased thereafter. Although those calculations are somewhat uncertain because of a lack of some biological data, and hence the results should be treated cautiously, the fishery seems to have declined steadily. The study highlights gaps in the current data such as information on temporal changes in body weight of lobsters, gear selectivity and fecundity. Mapping of the spatial expansion and contraction of the fishery is also highlighted as being required in future assessments. Finally, the relatively small size of the stock does present a challenge for any attempt at its predictions.

Mathematically, almost all models in fisheries science are based on differential or difference equations, which work well if the size of a stock is sufficiently large. When a stock's size is reduced from a large value to a small value over time, although a prediction can be made, its accuracy deteriorates over time. In this sense, an intrinsically discrete model, such as a discrete stochastic process model, offers a much better prediction.

Also, the model was used, as a simulation model, to evaluate various harvesting strategies for SARDI staff members, for PIRSA and for the FMC. The outcomes of this were provided to the industry, managers and the FMC, for the Northern Zone of the fishery. Several questions of management interest are answered (see General Discussion); and future research areas were identified.

3.1 INTRODUCTION

Like many fisheries, the South Australian rock lobster fishery is characterized by a spatiotemporal expansion that is difficult to quantify. Although stocks have been assessed by various methods, including yield per recruit analysis, egg per recruit analysis and various production models of differing complexity, none of these assessments, nor assessments elsewhere, have considered spatiotemporal expansion. There are also other difficulties in rock lobster assessments. One such difficulty is a false belief that an assessment can be length-based, without knowing the age (the sum of the intermoult periods). It can be shown that such assessments rest on the assumption that length is proportional to age, with proportionality constant of unity. In the case of the SA rock lobster fishery, no risk analysis has been conducted.

In this chapter, we parameterize a sex-specific, age- and time-dependent population model (Xiao, 1997, 2000a) to assess stock status in the Northern Zone Rock Lobster Fishery (NZRLF) from both commercial catch and effort data and other biological data. This was used to evaluate several management strategies by accounting for spatiotemporal expansion of the fishery.

3.2 MATERIALS AND METHODS

3.2.1 Deterministic model

3.2.1.1 OVERVIEW

The model was developed in SAS statistical software. It is age based. The lower age limit is 3 years. There are 32 age classes. Sexes are distinguished, but recruitment is divided evenly between both sexes. The model runs on an annual time step. There are no spatial cells. Catches from commercial fishers were used in the model, through a derived gear selectivity curve.

In the model, the lobster population is divided into age groups that are followed over time. The numbers of lobster of each sex in each age group are estimated by applying growth, fishing mortality, natural mortality, and annual recruitment each year. Biomass estimates are then derived using, sequentially, an age-length and a length-weight relationship.

The model was conditioned on catch in weight (Cw) and fitted to catch in number (Cn) – both from commercial catch and effort data. Outputs from the model were the estimates of recruitment (R) and the levels of fishing mortality (F), for each year.

3.2.1.2 MODEL INPUTS AND ASSUMPTIONS

1. *Commercial catch data*: Total catch in weight and catch in number, aggregated by year, were obtained from commercial logbooks for the period 1970 – 2004.
2. *Spatiotemporal expansion:* von Bertalanffy curve fitted to the number of licences and the number of MFAs fished, by season, by the least-squares method.
3. *Gear selectivity*: The gear selectivity was determined from data obtained during escape gap experiments, fitted using the logistic curve. It was unchanged from 1970 to 2003, with a minor modification from 2003 onwards.
4. *Length at age:* von Bertalanffy growth curve fitted to tag-recapture data, by sex, by the least-squares method. All lobsters within each age group are of the same length.
5. *Weight at length:* Nonlinear, least-squares fit to length-weight data, by sex. As all lobsters within each age group are of the same length, they also have the same weight – although the values are different for each sex. This curve was based on data from Tasmania.
6. *Natural mortality*: Assumed to be 0.1 yr^{-1} (ages 3 – 30), but increases linearly from 0.1 yr^{-1} at age 30 to 20 yr^{-1} at age 35 (to ensure that every cohort of lobsters dies an age-wise smooth death).
7. *Sex ratio:* Recruitment in each year is divided evenly between both sexes.
8. *Sexual maturity:* Logistic curve fitted to maturity data using a likelihood function based on the binomial distribution.
9. *Fecundity:* Fixed relationship between size (age) and fecundity. Data from Bob Kennedy (personal communication to Jim Prescott. The method of analysis is unknown).
10. *Initial age distribution:* Specified for each age and sex, approximately as an exponential function obtained through the application of the maximum entropy principle.
11. *Recreational and illegal catches*: These were assumed to be zero in all years.

Note that, in this deterministic model (1) commercial catch size-frequency, effort, CPUE or standardised CPUE data are not used, (2) ‘growth’ is only incorporated as the relationship between age and length, and (3) the only parameters freely estimated are yearly R – the corresponding F in each year was calculated by solving the nonlinear catch equation.

3.2.1.3 FITTING

Annual estimates of recruitment were obtained using the maximum likelihood method, by maximizing the likelihood function:

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_N(t)} \exp\left(-\frac{1}{2\sigma_N(t)^2} \left(C_N(t) - \hat{C}_N(t) \right)^2 \right)$$

under the assumption that the catch in the number of lobsters at time t follows independent normal distributions, with a variance of $\sigma_N(t)^2$ and a model-predicted mean of $\hat{C}_N(t)$. This process uses the dual quasi-Newton optimization, using the modified VMCWD algorithm of Powell, with DBFGS update programmed in SAS.

3.2.1.4 SENSITIVITY ANALYSES

Sensitivity of the model outputs to natural mortality, length-at-age relationship, spatial expansion and level of illegal fishing were determined. This was achieved by setting natural mortality at 0.15 yr^{-1} and 0.2 yr^{-1} (for lobsters of ages 3 – 30 yr), deriving length at age from Wang (personal communication) rather than the von Bertalanffy growth curve, removing the effect of spatial expansion and setting levels of illegal catch (1) at 5, 10 and 20% of the commercial catch, and (2) decreasing from 25% to 5% (1970 – 1983) and then from 5% asymptotically to 0% (1983 onwards) of the commercial catch.

3.2.1.5 MODEL OUTPUTS

Outputs from the model are given in the figures below. These include the trajectories of the total and exploitable biomass and model fit to catch in number (Figure 3.1), egg production and recruitment (Figure 3.2), instantaneous rate of fishing mortality (Figure 3.3) and sensitivity of the model outputs to a range of sensitivity analyses conducted (Figure 3.4). The goodness-of-fit seemed reasonable (Figure 3.1), with a –log-likelihood value of 50041495.62. The parameters in the model were estimated in an increment of five (A similar idea is formalized in the software AD Model Builder), so that a global (rather than local) optimal point must have been found.

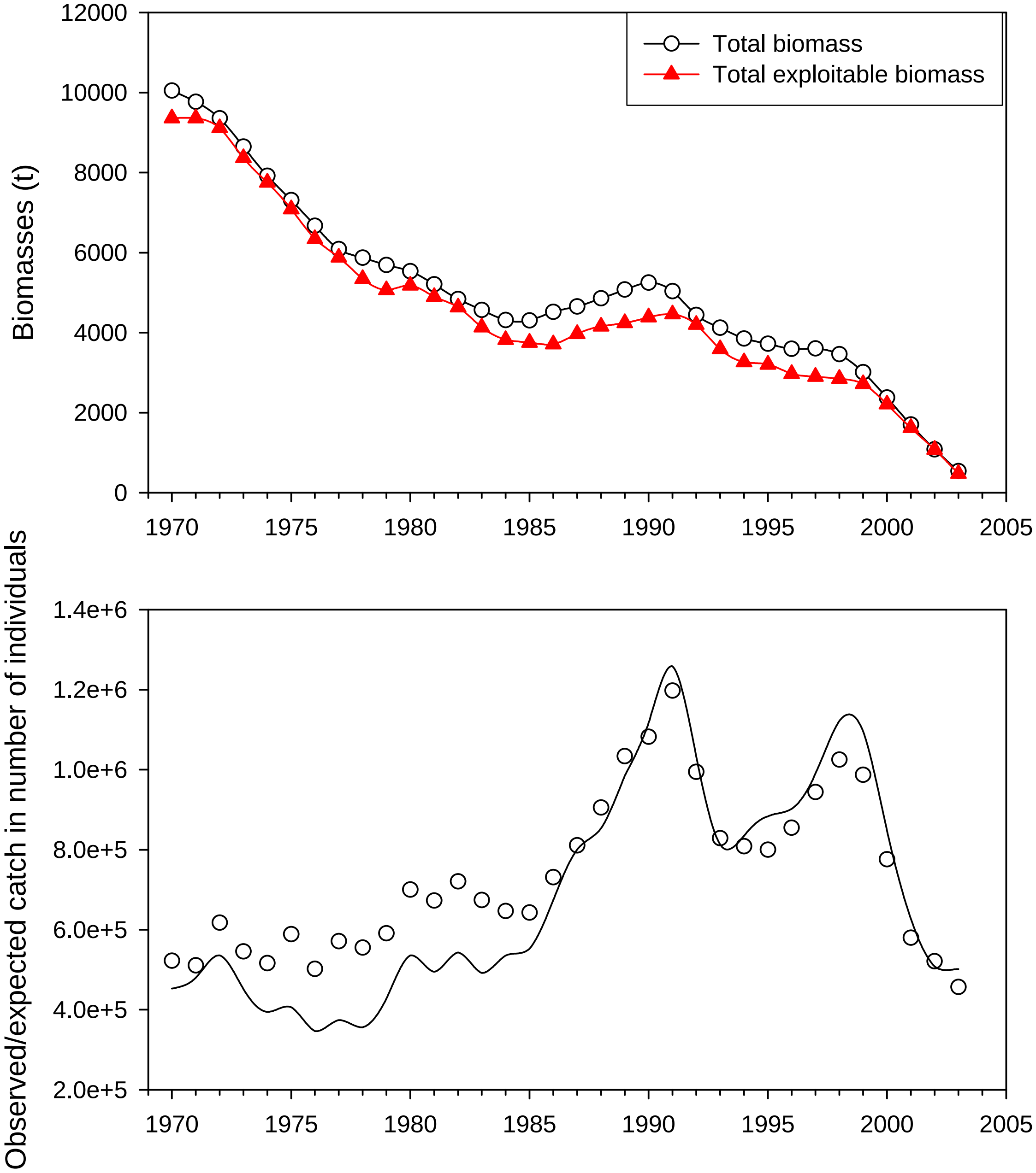

Figure 3.1. The total and exploitable biomass and model fit to catch in number.

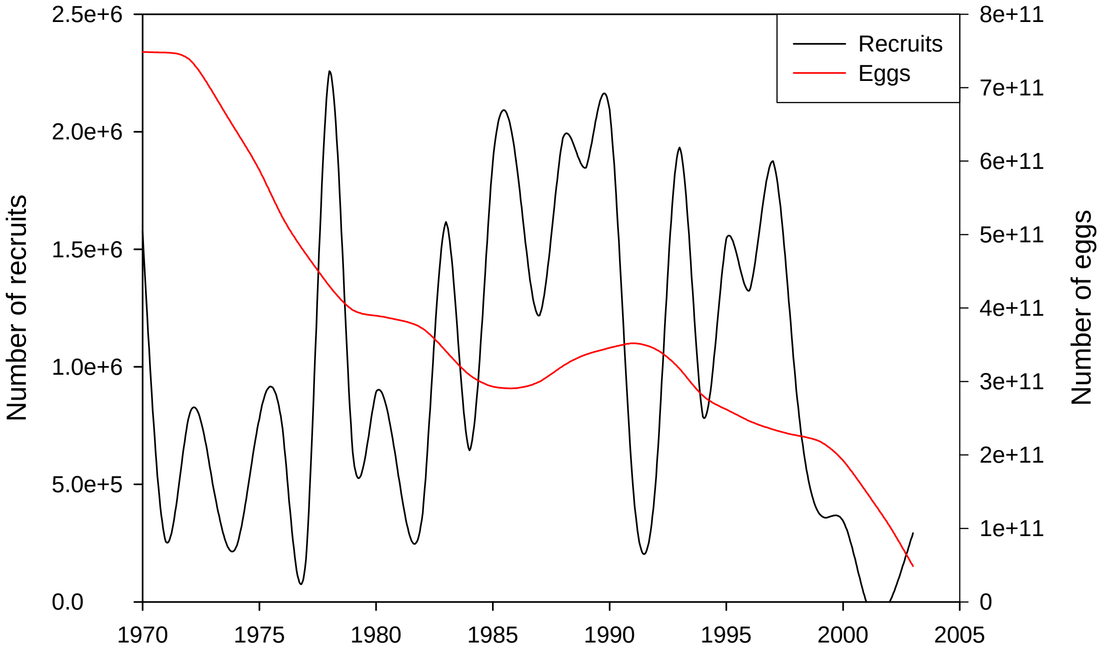

Figure 3.2. Egg production and the number of recruits.

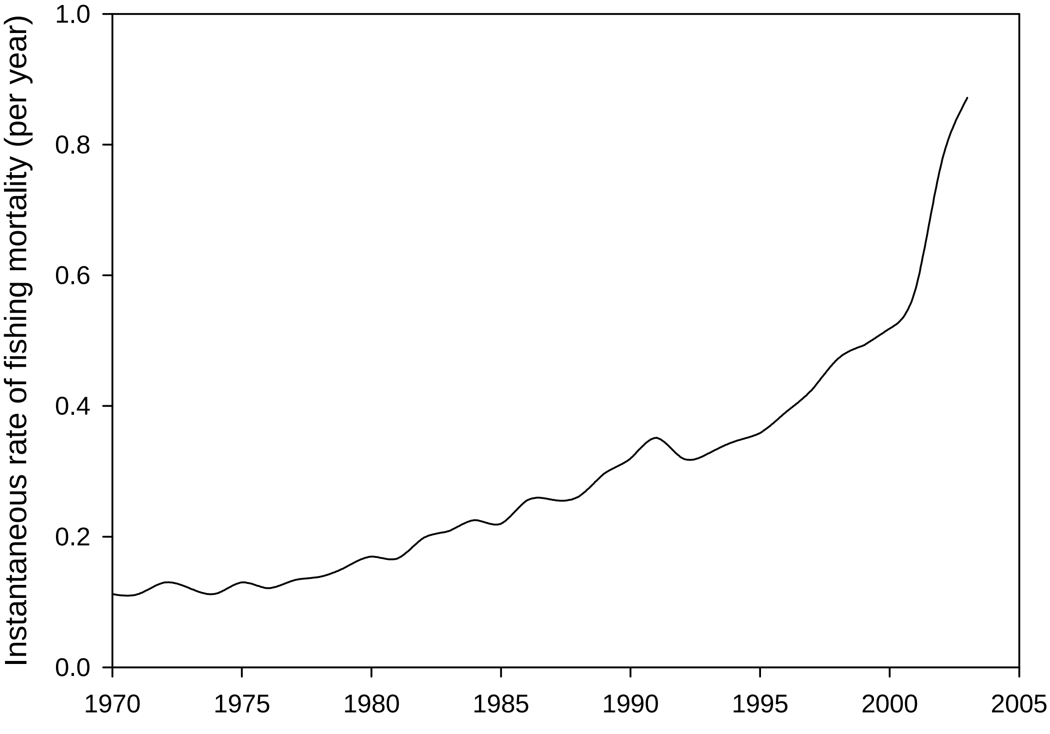

Figure 3.3. Instantaneous rate of fishing mortality.

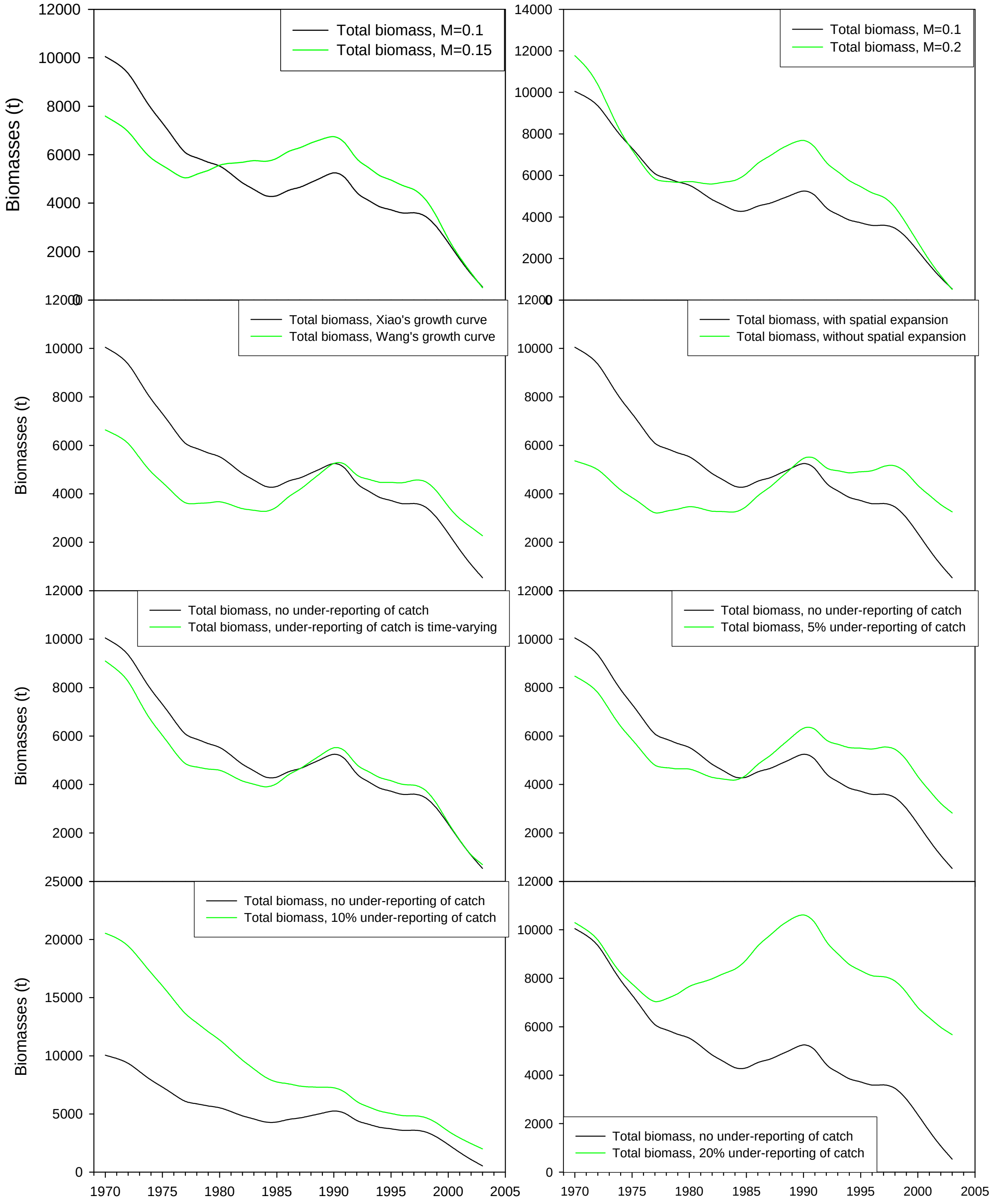

Figure 3.4. Results from a range of sensitivity analyses conducted.

3.2.2 Stochastic model

3.2.2.1 OVERVIEW

The stochastic model was developed in WinBUGS 1.4. As with the deterministic model, it is age based. The lower age limit is 3 years. There are 32 age classes. Sexes are distinguished, but recruitment is divided evenly between both sexes. The model runs on an annual time step. There are no spatial cells. The number of chains is two, burn-in rate is at least 10000 (against the recommended value of 4000), and thinning factor is 10. Such a burn-in rate are reasonable, as was confirmed by displaying the value of the deviance and the similarity of the results from the two chains. A thinning factor of 10 is more than enough to eliminate the serial correlations among values from different simulations.

As in the deterministic model, the lobster population is divided into age groups that are followed over time. The numbers of lobster of each sex in each age group are estimated by applying growth, fishing mortality, natural mortality, and annual recruitment each year. Biomass estimates are then derived using, sequentially, an age-length and a length-weight relationship.

The outputs of annual recruitment (R) and derived levels of fishing mortality (F), for each year from the deterministic model were used as priors for these values in this model (with a 10% error applied through a uniform distribution). They were adjusted by fitting into the standardized catch rate, the abundance of undersized lobsters, an index of puerulus settlement, and the length-frequency data. Bayesian posteriors for these parameters and other values of interest (***e.g.*** B/B0) were derived using Markov Chain-Monte Carlo simulation (MCMC).

3.2.2.2 MODEL INPUTS AND ASSUMPTIONS

3.2.2.2.1 *Annual recruitment*: Time series of R from the deterministic model. Stochasticity introduced through a log-normal prior in all years (±5% of value estimated in the deterministic model).

3.2.2.2.2 *Annual fishing mortality*: Time series of F from the deterministic model. Stochasticity introduced through a uniform prior in all years (±10% of value estimated in the deterministic model).

3.2.2.2.3 *Spatiotemporal expansion:* von Bertalanffy curve fitted to the number of licences and number of MFAs fished, by season. No stochasticity incorporated.

3.2.2.2.4 *Gear selectivity*: The gear selectivity was determined from data obtained during escape gap experiments, fitted using the logistic curve. It was unchanged from 1970 to 2003, with a minor correction (from a 2-d Taylor series expansion) from 2003 onwards. Stochasticity incorporated through normal priors (based on mean and SE) on both parameters from the logistic curve (Appendix A).

3.2.2.2.5 *Length at age:* von Bertalanffy growth curve fitted to tag-recapture data, by sex. Stochasticity introduced through normal priors (based on mean and SE) on K and $L\infty$ (Appendix A).

3.2.2.2.6 *Weight at length:* Nonlinear, least-squares fit to length-weight data, by sex. As all lobsters within each age group are of uniform length, they also have a uniform weight – although the values are different for each sex. No stochasticity was incorporated.

3.2.2.2.7 *Natural mortality*: Assumed to be 0.1 (ages 3–30), but increases linearly from 0.1 at age 30 to 20 at age 35. Stochasticity was introduced through a uniform prior (±10% of value).

3.2.2.2.8 *Sex ratio:* Recruitment in each year is divided evenly between both sexes. No stochasticity incorporated.

3.2.2.2.9 *Sexual maturity:* Logistic curve fitted to maturity data using a likelihood function based on the binomial distribution. Stochasticity incorporated through normal priors on both parameters from the logistic curve (Appendix A).

3.2.2.2.10 *Fecundity:* Fixed relationship between size (age) and fecundity. Data from Bob Kennedy (personal communication to Jim Prescott). No stochasticity incorporated.

3.2.2.2.11 *Initial age distribution:* Specified for each age and sex, approximately as an exponential function obtained through the application of the maximum entropy principle. Stochasticity incorporated through the stochasticity in natural mortality.

3.2.2.2.12 *Recreational and illegal catches*: These were assumed to be zero in all years.

3.2.2.2.13 *Standardised CPUE*: A relative index of the exploitable biomass at time *t* (from 1970) obtained by analysing commercial catch and effort data using a generalized linear model that accounts for the effects of the time of year, the differences in fishing efficiency among fishers, fishing area and fishing effort on catch rate.

3.2.2.2.14 *Abundance of under-sized lobsters*: The number of under-sized lobsters caught in the commercial catches, from 1983 onwards.

3.2.2.2.15 *Index of puerulus settlement*: The mean number of puerulus, per collector, from 1996 onwards.

3.2.2.2.16 *Length-frequency data*: The length-frequency data on lobsters of both sexes for the Northern Zone of the southern rock lobster fishery for 1995 and 2005.

3.2.2.2.17 *Process error*: Log-normal distribution with a mean of 1 and CV of 5% applied to R.

3.2.2.3 FITTING

Posterior distributions of each of the parameters estimated were obtained from Monte Carlo simulations on the basis of the five likelihood functions below by simultaneously fitting to all the data sources.

3.2.2.3.1 Fit to standardised cpue

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_{std}(t)} \exp\left(-\frac{1}{2\sigma_{std}(t)^2}\left(I(t)-\hat{I}(t)\right)^2\right)$$

where the standardized catch rate $I(t)$ at time t as a relative index of the exploitable biomass follows independent normal distributions, with a variance of $\sigma_{std}(t)^2$ and a mean of $\hat{I}(t) = C_B(t)/\hat{F}(t)$.

3.2.2.3.2 Fit to number of under-sized lobsters

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_s(t)} \exp\left(-\frac{1}{2\sigma_s(t)^2}\left(C_s(t)-\sum_g \sum_{a=a_0}^{a_0+1} C_N(g,a,t)\right)^2\right)$$

where the number of under-sized lobsters (at age a_0=3.5 yr) caught in the commercial catches at time t is assumed to follow independent normal distributions, with an expected value of $\sum_g \sum_{a=a_0}^{a_0+1} C_N(g,a,t)$ and with a variance of $\sigma_s(t)^2$.

3.2.2.3.3 Fit to number of puerulus per collector

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_p(t)P(t)} \exp\left(-\frac{1}{2\sigma_p(t)^2}\left(\ln\left(P(t)\right)-\mu(t)\right)^2\right)$$

where the mean number of puerulus on a collector at time t is assumed to follow independent log-normal distributions, with an expected value of $K_p R(t-3)$ and a variance of $V[K_p]R(t-3)^2$, where K_p is sampled from $U\left(0,\ 0.8569\times10^{-6}\right)$ and $V[K_p] = 6.1384\times10^{-14}$.

This implies that $\mu(t) = \ln\left(K_p R(t-3)\right) - \sigma_p(t)^2/2$ and $\sigma_p(t)^2 = \ln\left(1 + \mathrm{CV}(t)^2\right)$.

3.2.2.3.4 Fit to numbers of under-sized lobsters of both sexes from pot sampling

$$\prod_{t,g} \frac{1}{\sqrt{2\pi}\sigma_s(g,t)} \exp\left(-\frac{1}{2\sigma_s(g,t)^2} \left(C_s(g,t) - q_s(g) \frac{E_p(t)}{E(t)} \sum_{a=a_0}^{A(g)} C_N(g,a,t) \right)^2 \right)$$

where the number $C_s(g,t)$ of under-sized lobsters of sex g (at age a_0=3.5 yr) from pot sampling of commercial catches at time t is assumed to follow independent normal distributions, with an expected value of $q_s(g)\left(E_p(t)/E(t)\right)\sum_{a=a_0}^{A(g)} C_N(g,a,t)$ and with a variance of $\sigma_s(g,t)^2$. Here $E_p(t)$ is the number of pots-lifts associated with pot sampling, $E(t)$ is the total number of pot-lifts in the fishery, $A(g) = a_0 + 1$ for females and a_0 for males, and $q_s(g)$ is the catchability coefficient for lobsters of sex g.

3.2.2.3.5 Fit to the length-frequency data from pot sampling

$$\prod_{t,g} \frac{1}{\sqrt{2\pi}\sigma_l(g,t)} \exp\left(-\frac{1}{2\sigma_l(g,t)^2} \left(C_l(g,a(l(g)),t) - q_l(g,t) \frac{E_p(t)}{E(t)} \sum_{l(g)} \hat{C}_N(g,a(l(g)),t) \right)^2 \right)$$

where the number $C_l(g,a(l(g)),t)$ of lobsters of size $l(g)$ and sex g (at age a_0=3.5 yr) from pot sampling of commercial catches at time t is assumed to follow independent normal distributions, with an expected value of $q_l(g,t)\frac{E_p(t)}{E(t)}\sum_{l(g)} \hat{C}_N(g,a(l(g)),t)$ and with a variance of $\sigma_l(g,t)^2$. Here $E_p(t)$ is the number of pots-lifts associated with pot sampling, $E(t)$ is the total number of pot-lifts in the fishery, and $q_l(g,t)$ is the catchability coefficient for lobsters of size $l(g)$ and sex g.

3.2.2.4 MODEL OUTPUTS

Outputs from the model are provided in the figures below. These include model fit to the number of undersized lobsters (Figure 3.5), standardized CPUE (Figure 3.6), the number of puerulus per collector (Figure 3.7), the number of lobsters from pot sampling (Figure 3.8), and the length-frequency data on lobsters of both sexes for the Northern Zone of the southern rock lobster fishery from 1991 to 2004 (Figure 3.9), but with only two years (1995 and 2005) shown (there would otherwise be too many graphs to be clear). The goodness-of-fit seemed reasonable in all cases, as was confirmed by displaying the value of the deviance and monitoring the results from the two chains. The under-predicted catch-rates in the last two years (Figure 3.6) are well expected. The reason for this is that the standardized catch rates come from fisheries-dependent data. As a rule, catch rates almost always increase faster and decrease more slowly than does the size of the stock — a result of the fishers knowing what they are doing.

The outputs from the model also include a contrast between the prior and posterior probability density functions of the instantaneous rate of fishing mortality for 1970 and 2004 (Figure 3.10), a contrast between the prior and posterior probability density functions of the number of recruits for 1970 and 2004 (Figure 3.11), a contrast between the reported and expected catch (Figure 3.12), the trajectories of the total and exploitable biomass (Figures 3.13 and 3.14), the instantaneous rate of fishing mortality (Figure 3.15), the rates of exploitation (Figure 3.16), annual recruitment (Figure 3.17), annual egg production (Figure 3.18), and annual change of revenue (Figure 3.19).

Although somewhat variable, the total biomass of lobsters (at or above an age of 3.5 yr) in the population decreased from 10176.728±2077.137 tonnes in 1970 to 1132.982±160.841 tonnes in 2003. The exploitable biomass of individuals in the population decreased from 9477.810±2051.217 tonnes in 1970 to 1097.640±160.612 tonnes in 2003 (Figure 3.13). Thus, the total biomass decreased somewhat gradually, reached its lowest level in 2003 of 11.59±2.87% of that in 1970, and increased thereafter, probably as a result of the unreliable data on the mean number of pueruli per collector (Figure 3.7). A similar pattern was found in the total exploitable biomass (Figure 3.14).

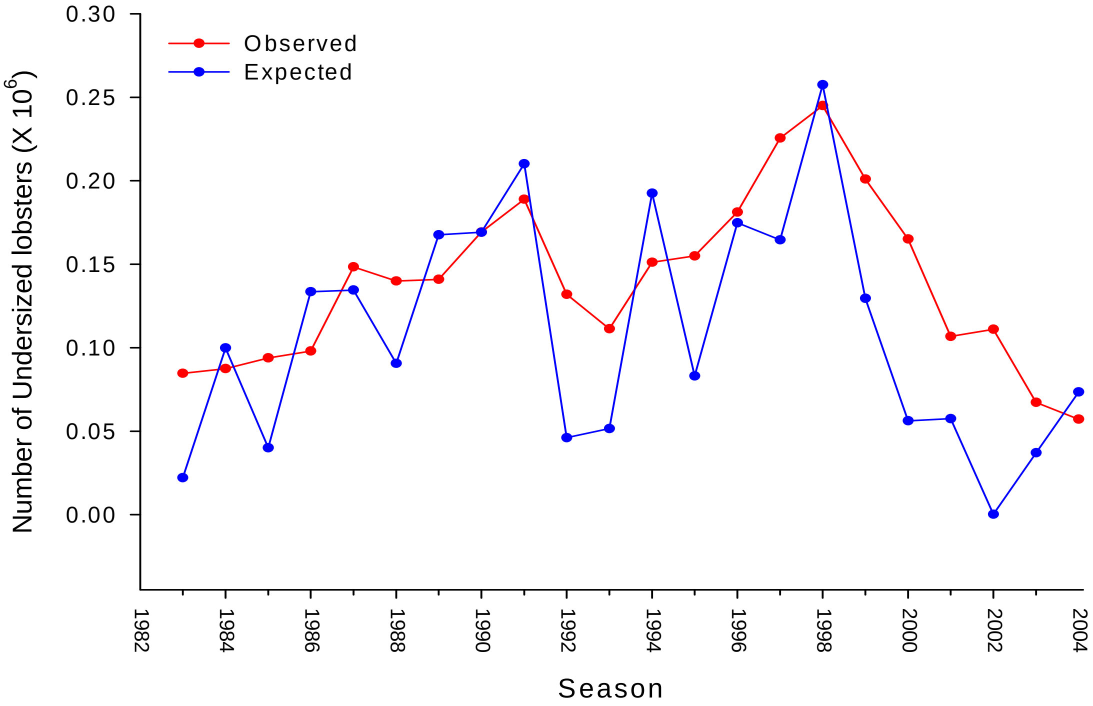

Figure 3.5. Model fit to the number of undersized lobsters for the Northern Zone of the southern rock lobster fishery.

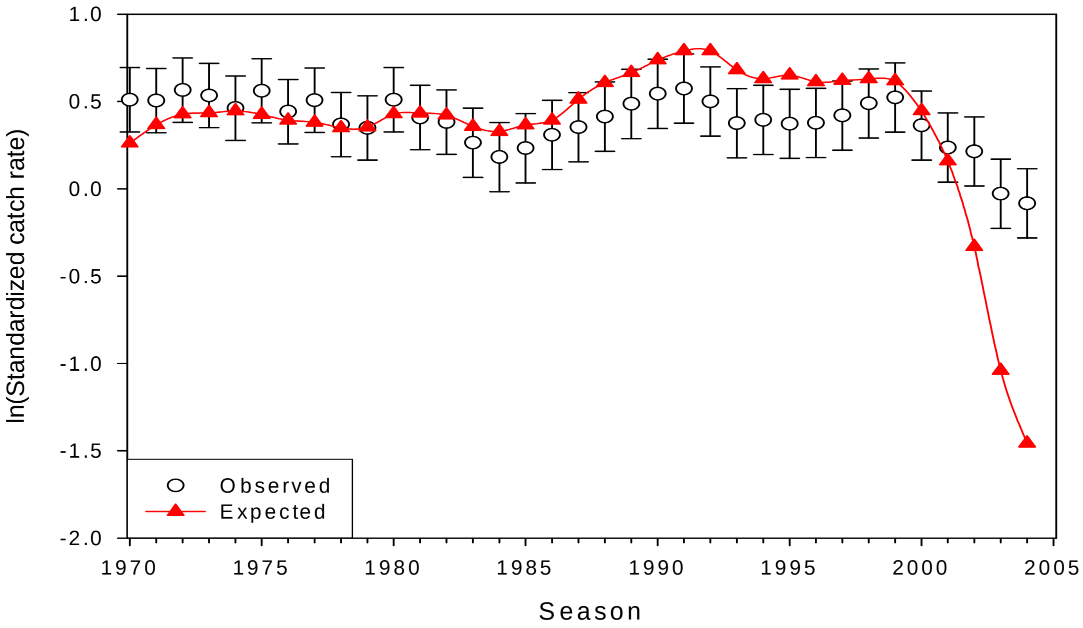

Figure 3.6. Model fit to the standardized CPUE for the Northern Zone of the southern rock lobster fishery.

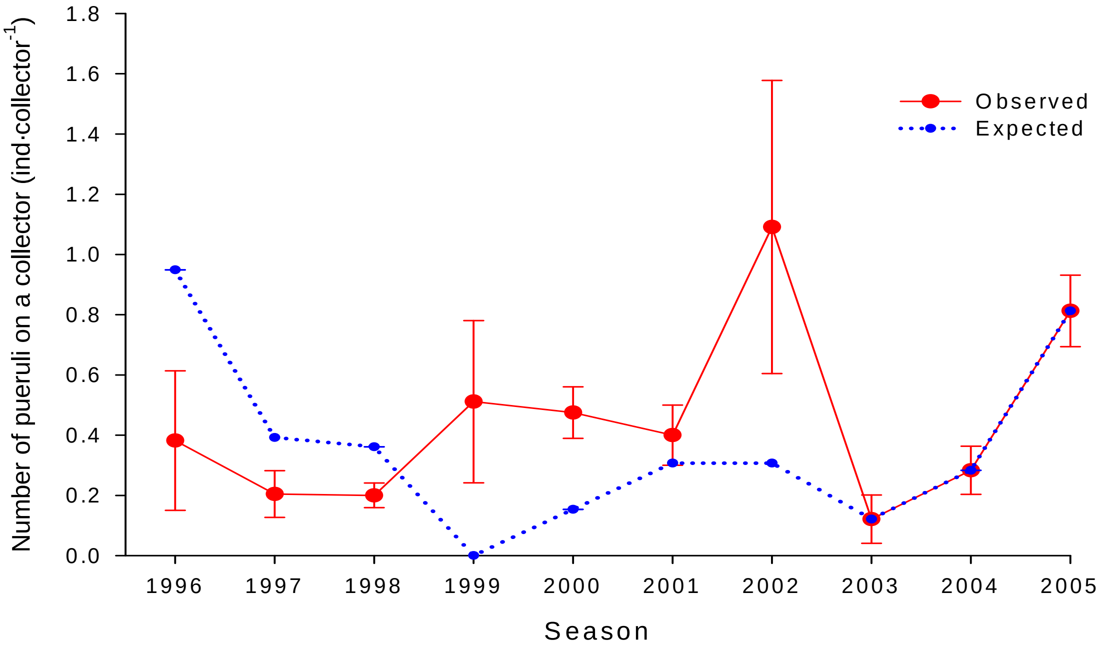

Figure 3.7. Model fit to the number of puerulus per collector for the Northern Zone of the southern rock lobster fishery.

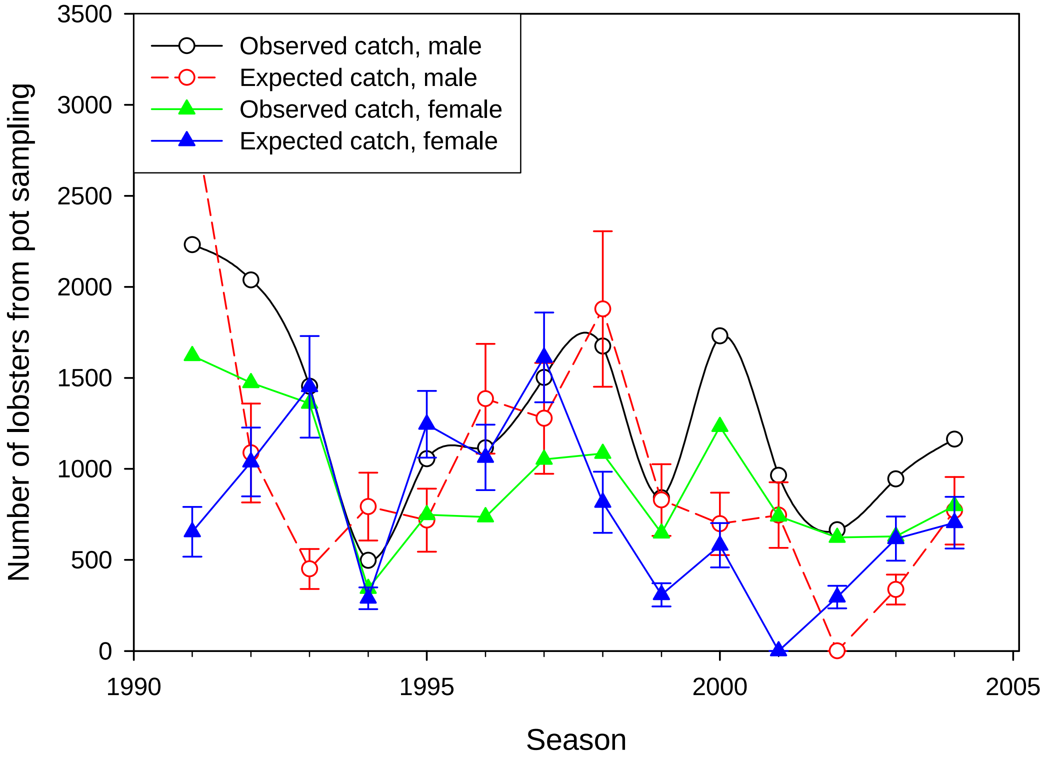

Figure 3.8. Model fit to the number of lobsters of both sexes from pot sampling for the Northern Zone of the southern rock lobster fishery.

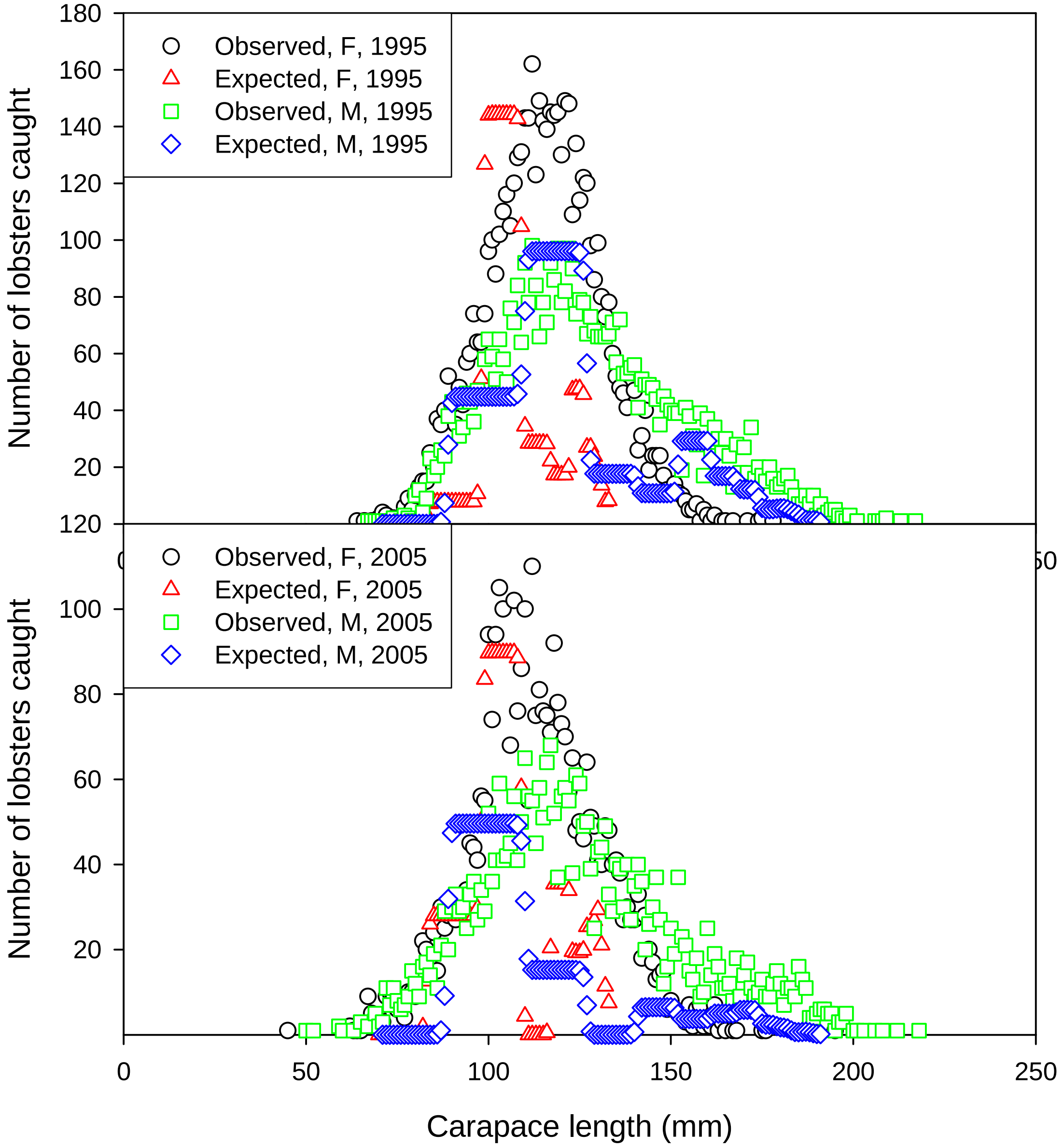

Figure 3.9. Model fit to the length-frequency data on lobsters of both sexes for the Northern Zone of the southern rock lobster fishery for 1995 and 2005.

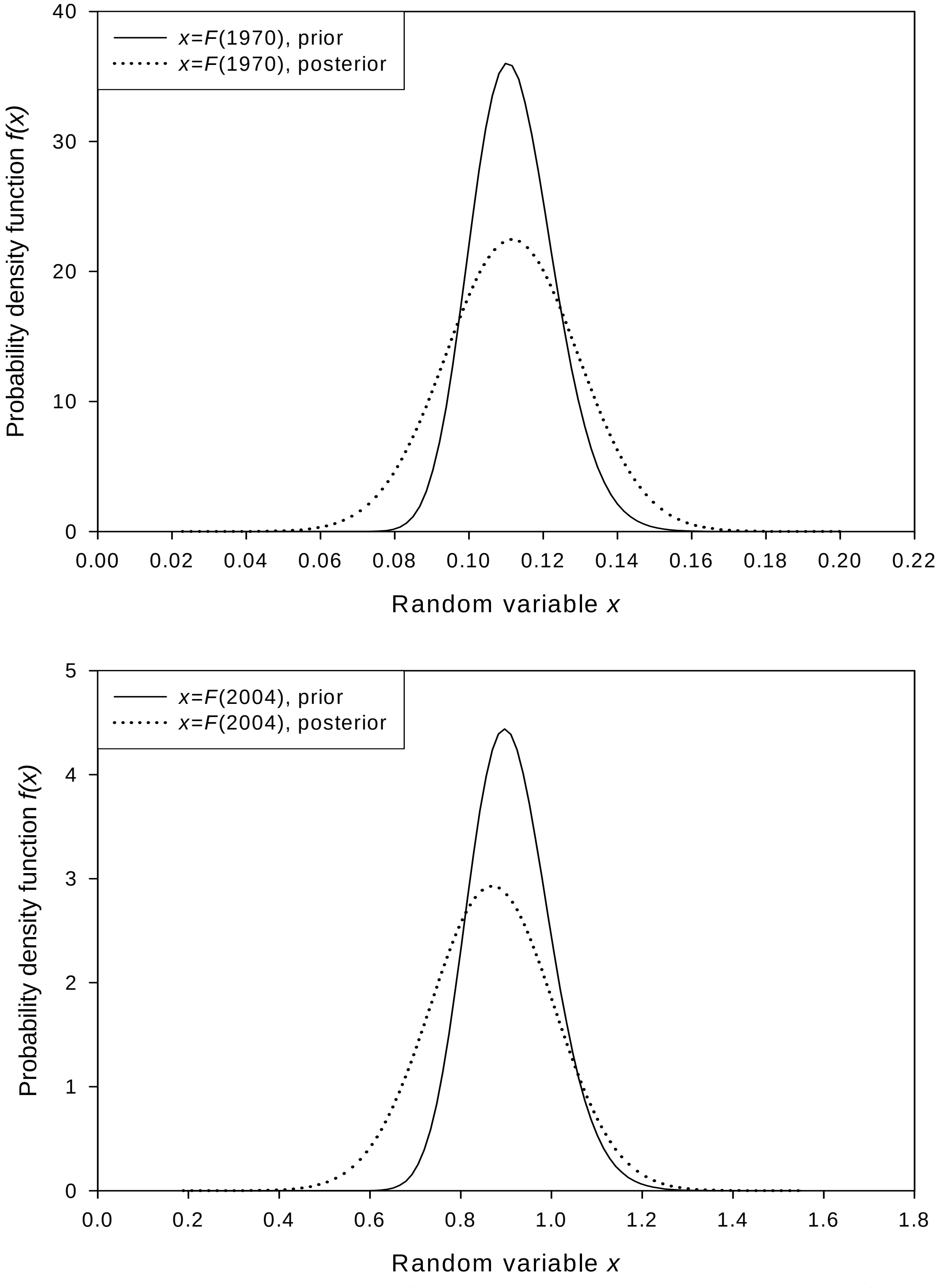

Figure 3.10. The prior and posterior probability density functions of the instantaneous rate of fishing mortality for the Northern Zone of the southern rock lobster fishery for 1970 and 2004.

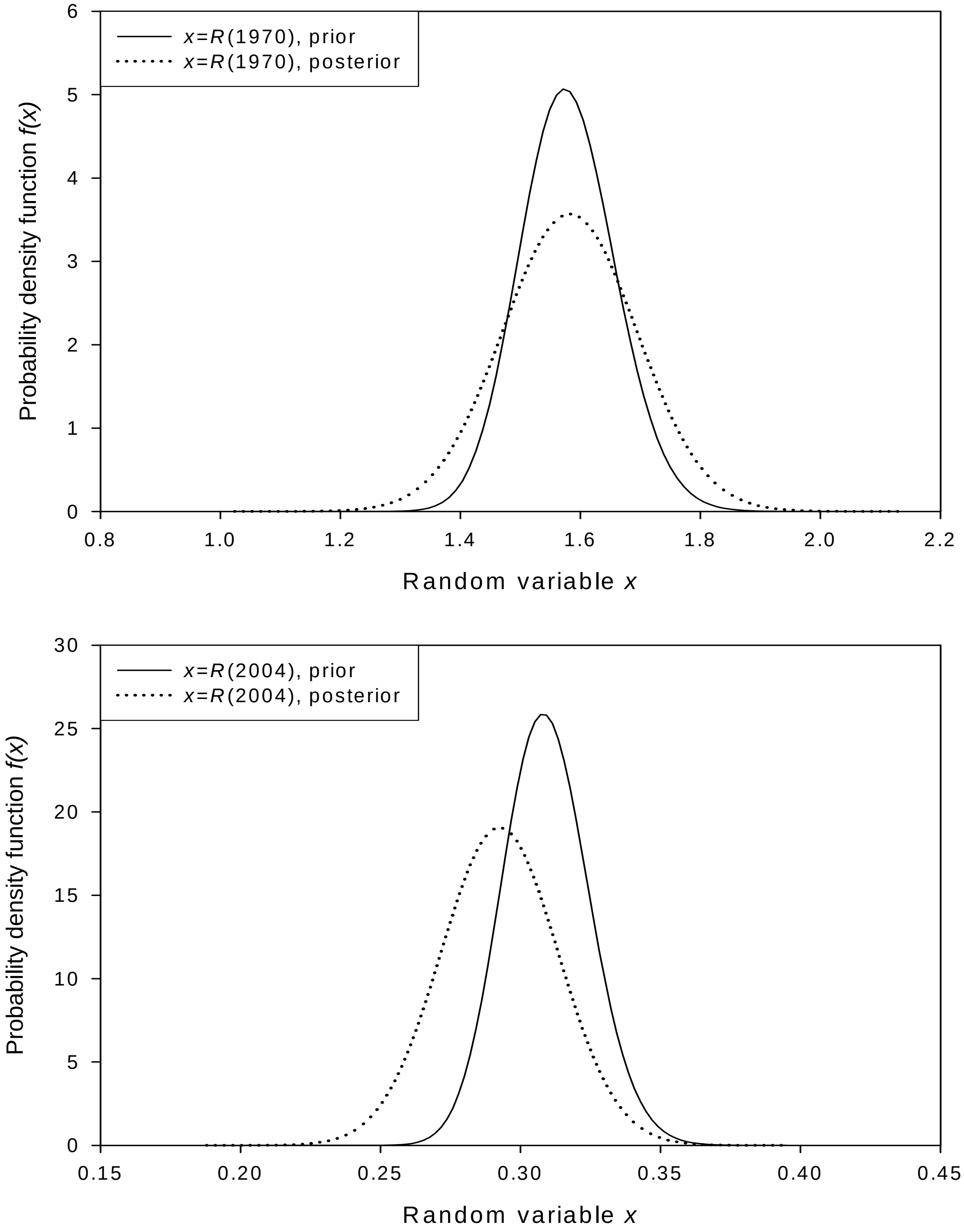

Figure 3.11. The prior and posterior probability density functions of the number of recruits in the Northern Zone of the southern rock lobster fishery for 1970 and 2004.

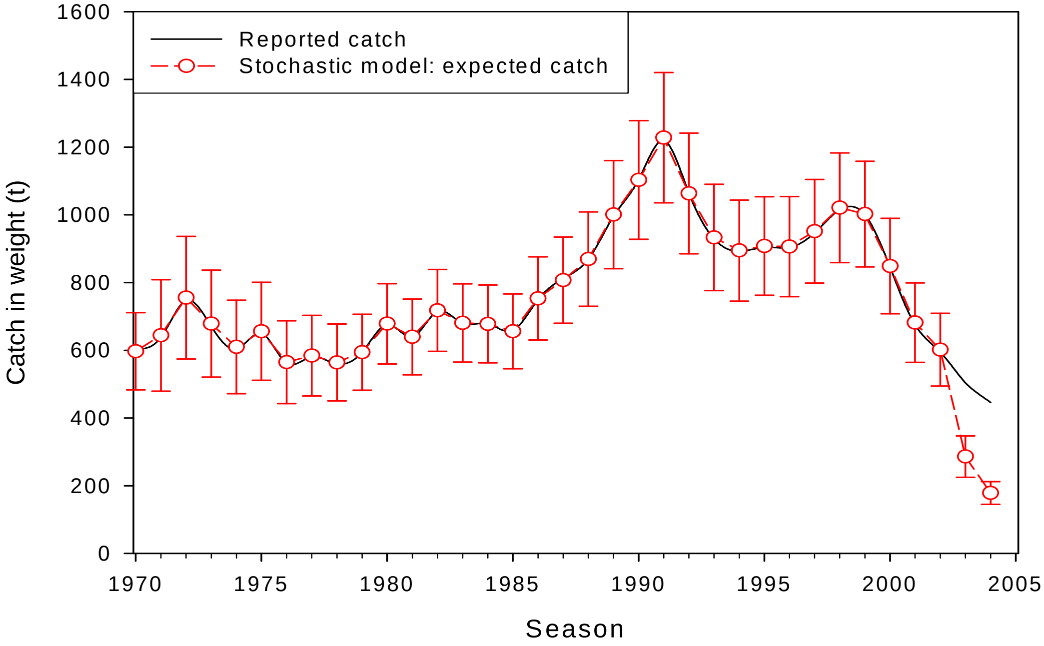

Figure 3.12. Observed and expected (commercial) catches in biomass of the adult lobsters in the Northern Zone of the southern rock lobster fishery from 1970 to 2004.

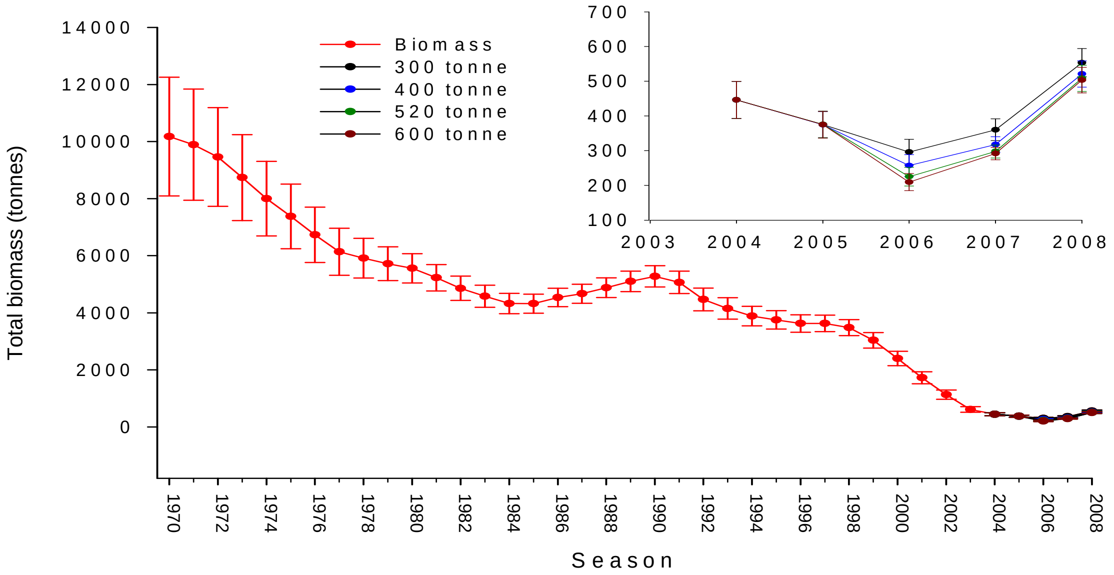

Figure 3.13. The total biomass for the Northern Zone of the southern rock lobster fishery from 1970 to 2004, and its expected value from 2005 to 2008 under four harvesting strategies (from top to bottom, catch in biomass equals 300, 400, 520, and 600 tonnes).

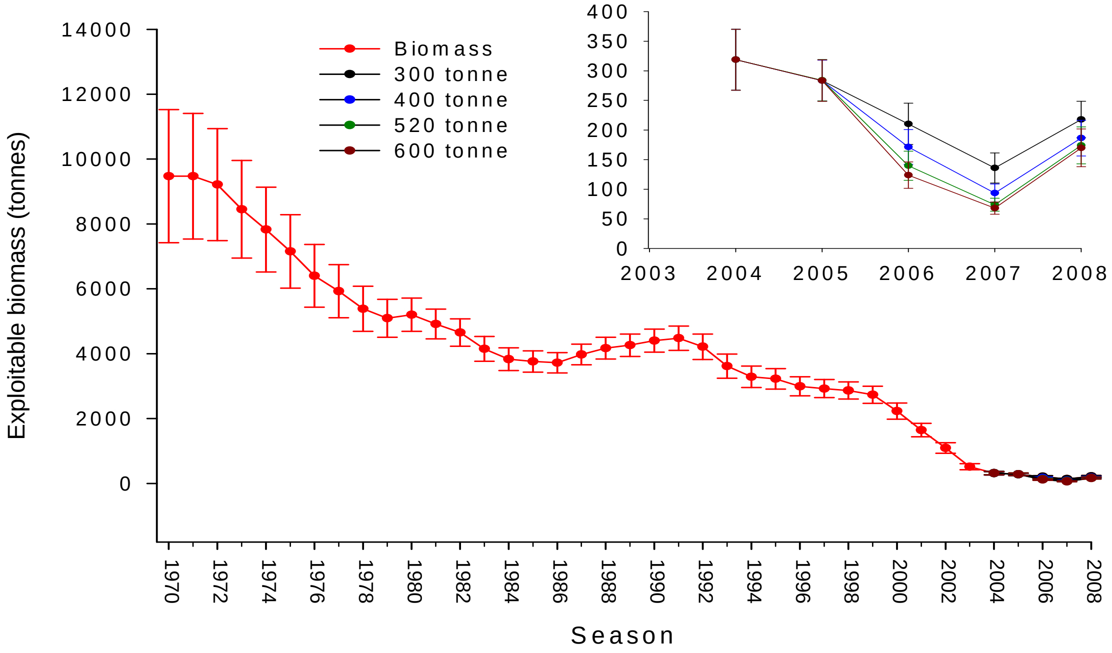

Figure 3.14. The exploitable biomass for the Northern Zone of the southern rock lobster fishery from 1970 to 2004, and its expected value from 2005 to 2008 under four harvesting strategies (from top to bottom, catch in biomass equals 300, 400, 520, and 600 tonnes).

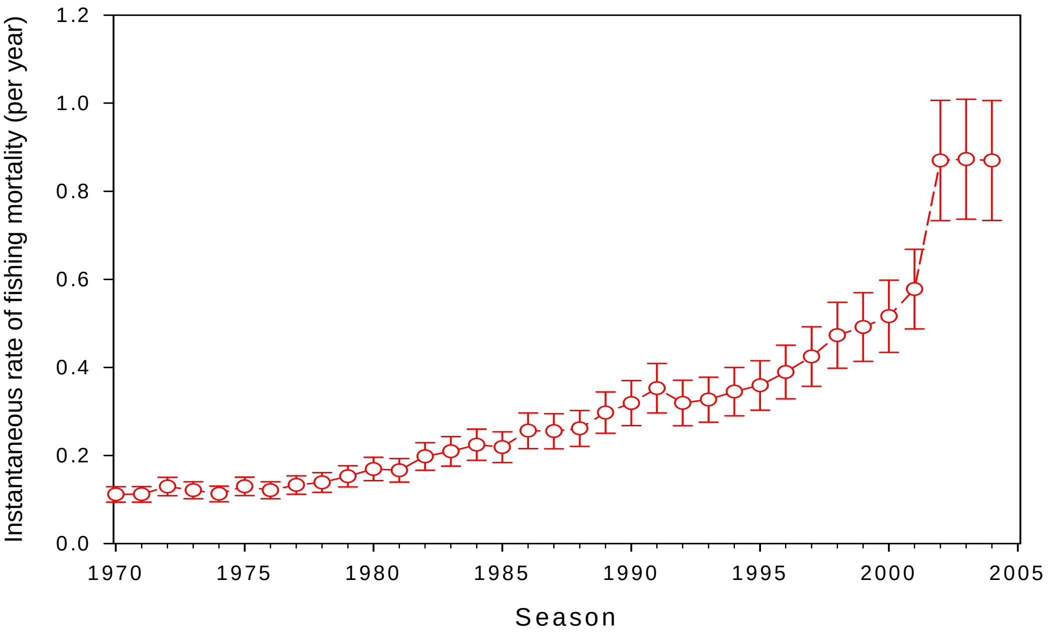

Figure 3.15. The instantaneous rate of fishing mortality for the Northern Zone of the southern rock lobster fishery from 1970 to 2005, and its expected value under four harvesting strategies from 2003 to 2005.

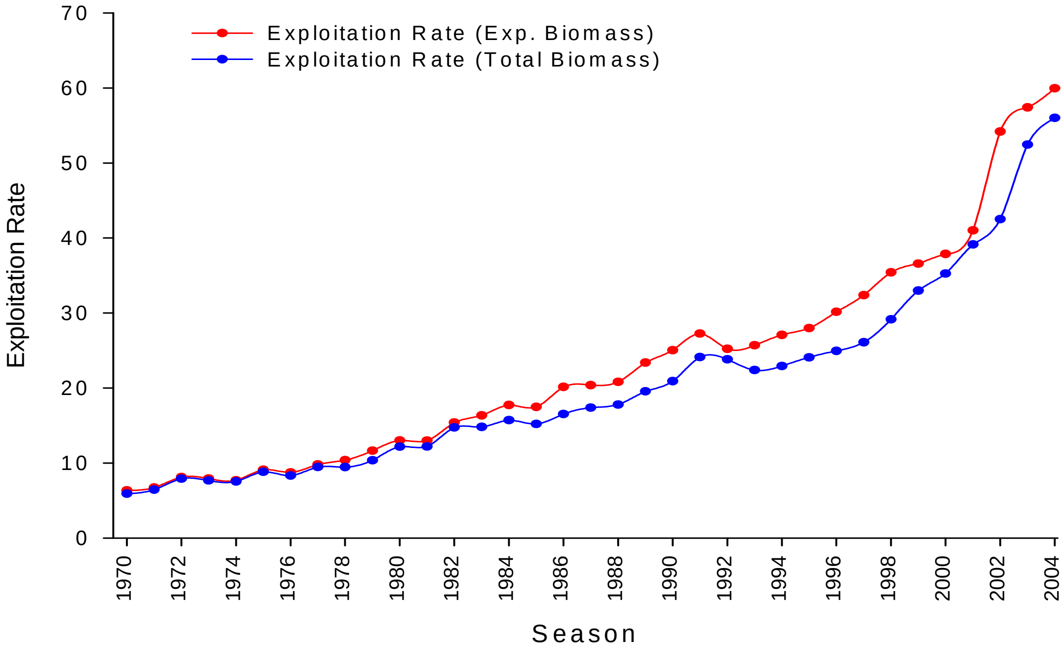

Figure 3.16. The rates of exploitation for the Northern Zone of the southern rock lobster fishery from 1970 to 2004.

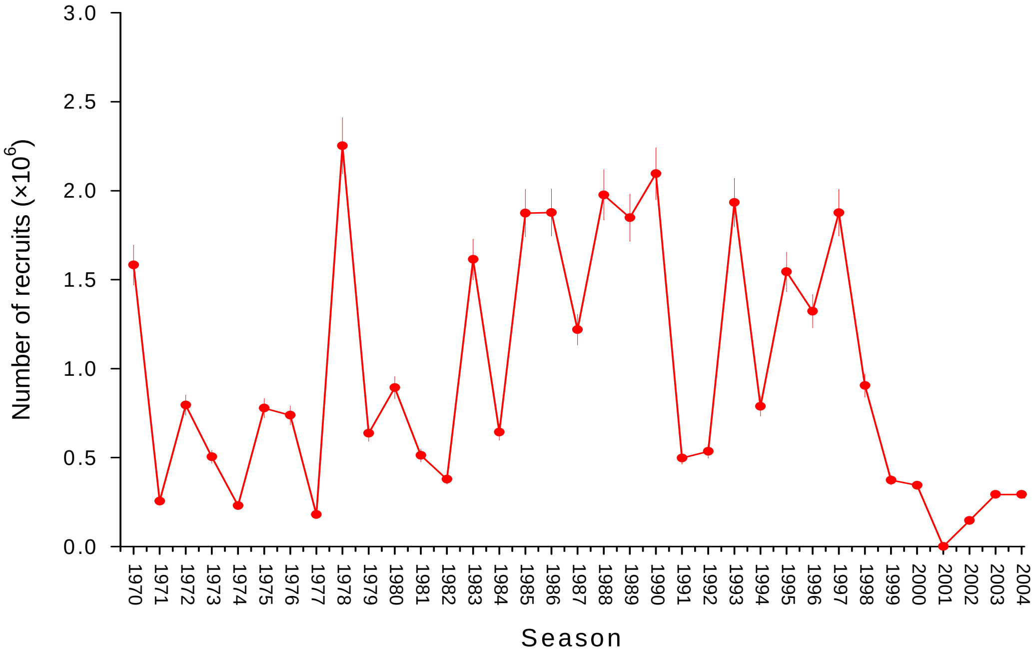

Figure 3.17. Temporal variation of the total number of recruits of lobsters in the Northern Zone of the southern rock lobster fishery from 1970 to 2004.

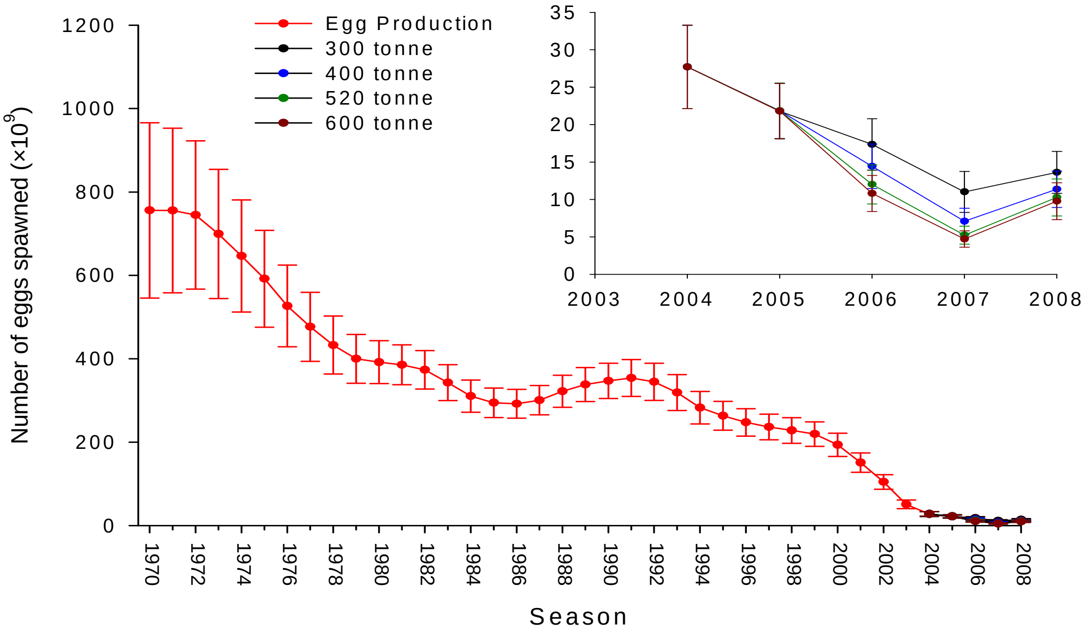

Figure 3.18. Temporal variation of the total number of eggs produced of lobsters in the Northern Zone of the southern rock lobster fishery from 1970 to 2004, and its expected value from 2005 to 2008 under four harvesting strategies (from top to bottom, catch in biomass equals 300, 400, 520, and 600 tonnes).

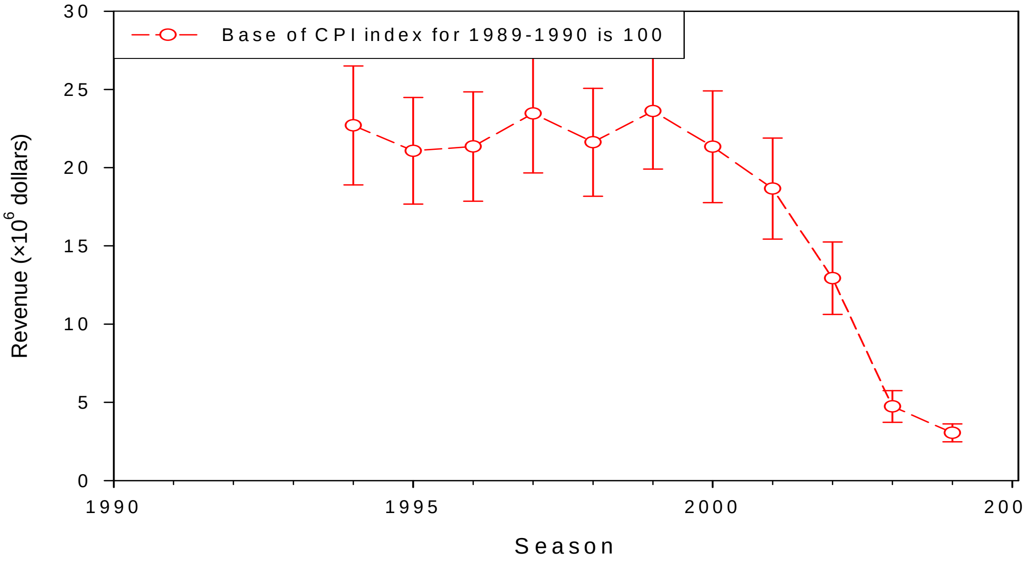

Figure 3.19. Revenue from expected (commercial) catches in biomass of the adult lobsters in the Northern Zone of the southern rock lobster fishery from 1993 to 2004. The base CPI index for food for 1989–1990 is 100.

3.3 DISCUSSION

In this chapter, we developed and used a sex-specific, age- and time-dependent population model to assess the stock status of lobsters from both commercial catch and effort data and other biological data, to evaluate, also as a simulation model, four management strategies by accounting for spatiotemporal expansion of the fishery. This model addresses at least three of the eight problems in the currently used size-dependent models, including those used in Tasmania, Victoria, NSW, Queensland, WA, New Zealand, South Africa, and North America: (1) problems in implementing size-based instantaneous rates of fishing and natural mortalities; (2) problems in constructing, from a set of tagging data, a size-transition matrix; and (3) a logical inconsistency in the way in which the stochasticity in the quantities of interest is introduced by manipulating the population model that was originally derived assuming that all the quantities were fixed. This was done by developing an age-dependent population model, and by not claiming that a growth function accounts for the incremental change in the size of a crustacean as a function of its age (as a result of an absence of necessary data), and by conditioning on the underlying model and the distributions of the parameters.

However, an important point must be appreciated in interpreting the results. From a mathematical point of view, a relatively small-sized stock of an animal population presents a challenge for any attempt at predictions of its various aspects of biology. As with many other sciences, almost all mathematical models in fisheries science are based on differential or difference equations. However, these models work well if the size of a stock is sufficiently large — the larger, the better. Although a prediction for a small-sized stock can be made by use of these models, its accuracy deteriorates as the size of the stock is reduced over time. In this sense, an intrinsically discrete model, such as a discrete stochastic process model, as a replacement of differential or difference equations, should offer much better predictions. But, developing such models is not a simple task and can be time-consuming and computationally intensive. Keeping these in mind, several conclusions can be drawn from this study as a general guide.

The population size of lobsters in the Northern Zone is at a low level. This is because several population characteristics, including the total biomass of lobsters (at or above an age of 3.5 yr) in the population, and the exploitable biomass of individuals in the population (Figures 3.13 and 3.14), all decreased from 100% in 1970 to slightly above 10% in 2002. The number of eggs produced by female lobsters also decreased somewhat steadily (Figure 3.18). The number of recruits were very variable with time, with a significant increase from 2003 onwards (Figure

3.17). However, the mean number of pueruli per collector that led to this apparent increase in recruitment (Figure 3.7) are based on so few pueruli that such a picture is overly optimistic and subject to chance events. Indeed, our calculations were based only on 22, 13, 8, 23, 19, 8, 52 and 4 pueruli caught from two sites from 1996 to 2003. For such data to be more useful as an index of the strength of recruitment in the Northern Zone, more sites should be chosen, more collectors deployed, and the process of pueruli landing on and moving out of a collector studied in detail. Therefore, it seems that the population of lobsters in the Northern Zone has declined substantially from its level in 1970.

Although recruitment varies considerably, such a decrease in the size of the population results partly from fishing. The number of recruits varied substantially with time (Figure 3.17), but showed no steady decrease. On the other hand, the 'observed' rate of exploitation in terms of biomass was relatively high (Figure 3.16). Therefore, the somewhat steady decrease in population size seems to have mirrored the changes in fishing intensity, although substantial variations in the instantaneous rate of natural mortality of the lobsters cannot be ruled out.

It should be noted that the above findings are subject to uncertainties in our model structure, the values of its parameters, and the quality of data. Indeed, many quantities were treated as fixed and many assumptions made about their values. These include data on the growth in the body weight of the lobster. The spatial expansion and contraction of the fishery was modelled, but a more detailed mapping is necessary. The collection of these biological data is essential for improving a stock assessment and for reducing the uncertainties in the results. Another major uncertainty that was not taken into account is the changing practice of reporting. The catch may have been mis-reported before and after the introduction of some management measures. The extent of this under-reporting reflected directly in the possible over- or under-estimation of certain quantities and should be studied to reduce this source of uncertainty. Of course, this also highlights the importance of reliable catch and effort data, and indeed, any sources of data. Consequently, the results obtained should be treated with caution.

Finally, the model developed above is amenable to improvements and extensions to incorporate more biological realism. For example, the time step in it was one year. Monthly or even daily time step should perhaps have been used, to make full use of the catch and effort data. However, this would lengthen the time of computations.

CHAPTER 4. A POPULATION DYNAMICS MODEL FOR THE SOUTHERN ROCK LOBSTER, *JASUS EDWARDSII,* OFF SOUTHERN AUSTRALIA: THE SOUTHERN ZONE

Objective 2: Develop a spatial-, time- and age-dependent model (or equivalently a spatial-, time- and size-dependent model).
Objective 3: Use the model to evaluate various harvesting strategies.
Objective 4: Use the model to forecast catch and abundance for individual areas.
Objective 5: Use the model to answer several relevant questions (as in Chapter 3).

These objectives were achieved by parameterizing a sex-specific, age- and time-dependent population model to assess its stock from the commercial catch and effort data and other biological data and to evaluate several management strategies. The total biomass and the exploitable biomass (at or above an age of 3.5 yr) in the population, all varied from 100% in 1970 through slightly above 40% in 1987 to 80% in 2004. The catch in biomass was above the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter; the rate of exploitation in biomass was above that at the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter. The number of recruits were fairly variable but increased slightly with time, with a significant influx of 6.2×10^6 individuals in 1998. However, the number of eggs produced by female lobsters decreased somewhat, reached its lowest level of 422.5×10^9 in 1988, and its highest level of 876.4×10^9 in 2004. Although those calculations are somewhat uncertain, because of a lack of some biological data, and hence the results should be treated cautiously, the fishery seems to have remained healthy. Finally, there is a need for collecting data on the temporal changes in the body weight of the lobsters, gear selectivity, and fecundity for a more robust stock assessment.

Also, the model was used, as a simulation model, to evaluate various harvesting strategies for SARDI staff members, for PIRSA and for the FMC. The outcomes of this were provided to the industry, managers and the FMC, for both the Southern Zone of the fishery. Several questions of management interest are answered (see General Discussion); and future research areas were identified.

4.1 INTRODUCTION

In this chapter, we parameterize a sex-specific, age- and time-dependent population model (Xiao, 1997, 2000a) to assess stock status in the SZRLF from both commercial catch and effort data and other biological data. This was used to evaluate several management strategies.

4.2 MATERIALS AND METHODS

4.2.1 Deterministic model

4.2.1.1 OVERVIEW

The model was developed in SAS statistical software. It is age based. The lower age limit is 3 years. There are 32 age classes. Sexes are distinguished, but recruitment is divided evenly between both sexes. The model runs on an annual time step. There are no spatial cells. Catches from commercial fishers were used in the model, through a derived gear selectivity curve.

In the model, the lobster population is divided into age groups that are followed over time. The numbers of lobster of each sex in each age group are estimated by applying growth, fishing mortality, natural mortality, and annual recruitment each year. Biomass estimates are then derived using, sequentially, an age-length and a length-weight relationship.

The model was conditioned on catch in weight (Cw) and fitted to catch in number (Cn) – both from commercial catch and effort data. Outputs from the model were the estimates of recruitment (R) and the levels of fishing mortality (F), for each year.

4.2.1.2 MODEL INPUTS AND ASSUMPTIONS

1. *Commercial catch data*: Total catch in weight and catch in number, aggregated by year, were obtained from commercial logbooks for the period 1970 – 2004 (n = 998 015 records).
2. *Gear selectivity*: The gear selectivity was determined from data obtained during escape gap experiments, fitted using the logistic curve. It was unchanged from 1970 to 2003, with a minor modification from 2003 onwards.
3. *Length at age:* von Bertalanffy growth curve fitted to tag-recapture data, by sex, by the least-squares method. All lobsters within each age group are of the same length.

4. *Weight at length:* Nonlinear, least-squares fit to length-weight data, by sex. As all lobsters within each age group are of the same length, they also have the same weight – although the values are different for each sex. This curve was based on data from Tasmania.
5. *Natural mortality*: Assumed to be 0.1 yr^{-1} (ages 3 – 30), but increases linearly from 0.1 yr^{-1} at age 30 to 20 yr^{-1} at age 35 (to ensure that every cohort of lobsters dies an age-wise smooth death).
6. *Sex ratio:* Recruitment in each year is divided evenly between both sexes.
7. *Sexual maturity:* Logistic curve fitted to maturity data using a likelihood function based on the binomial distribution.
8. *Fecundity:* Fixed relationship between size (age) and fecundity. Data from Bob Kennedy (personal communication to Jim Prescott. The method of analysis is unknown).
9. *Initial age distribution:* Specified for each age and sex, approximately as an exponential function obtained through the application of the maximum entropy principle.
10. *Recreational and illegal catches*: These were assumed to be zero in all years.

Note that, in this deterministic model (1) commercial catch size-frequency, effort, CPUE or standardised CPUE data are not used, (2) 'growth' is only incorporated as the relationship between age and length, and (3) the only parameters freely estimated are yearly R – the corresponding F in each year was calculated by solving the nonlinear catch equation.

4.2.1.3 FITTING

Annual estimates of recruitment were obtained using the maximum likelihood method, by maximizing the likelihood function:

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_{std}(t)} \exp\left(-\frac{1}{2\sigma_{std}(t)^2} \left(I(t) - \hat{I}(t) \right)^2 \right)$$

under the assumption that the standardized catch rate $I(t)$ at time t as a relative index of the exploitable biomass follows independent normal distributions, with a variance of $\sigma_{std}(t)^2$ and a mean of $\hat{I}(t) = C_B(t) / \hat{F}(t)$. This process uses the dual quasi-Newton optimization, using the modified VMCWD algorithm of Powell, with DBFGS update programmed in SAS.

4.2.1.4 SENSITIVITY ANALYSES

Sensitivity of the model outputs to natural mortality, length-at-age relationship, and level of illegal fishing were determined. This was achieved by setting natural mortality at 0.15 yr^{-1} and 0.2 yr^{-1} (for lobsters of ages 3 – 30 yr), deriving length at age from Wang (personal communication) rather than the von Bertalanffy, and setting levels of illegal catch (1) at 5, 10 and 20% of the commercial catch, and (2) decreasing from 25% to 5% (1970 – 1983) and then from 5% asymptotically to 0% (1983 onwards) of the commercial catch.

4.2.1.5 MODEL OUTPUTS

Outputs from the model are given in the figures below. These include the trajectories of the total and exploitable biomass and model fit to catch in number (Figure 4.1), egg production and recruitment (Figure 4.2), instantaneous rate of fishing mortality (Figure 4.3) and sensitivity of the model outputs to a range of sensitivity analyses conducted (Figure 4.4). The goodness-of-fit seemed reasonable (Figure 4.1), with a –log-likelihood value of 8.2488120. The parameters in the model were estimated in an increment of five (A similar idea is formalized in the software AD Model Builder), so that a global (rather than local) optimal point must have been found.

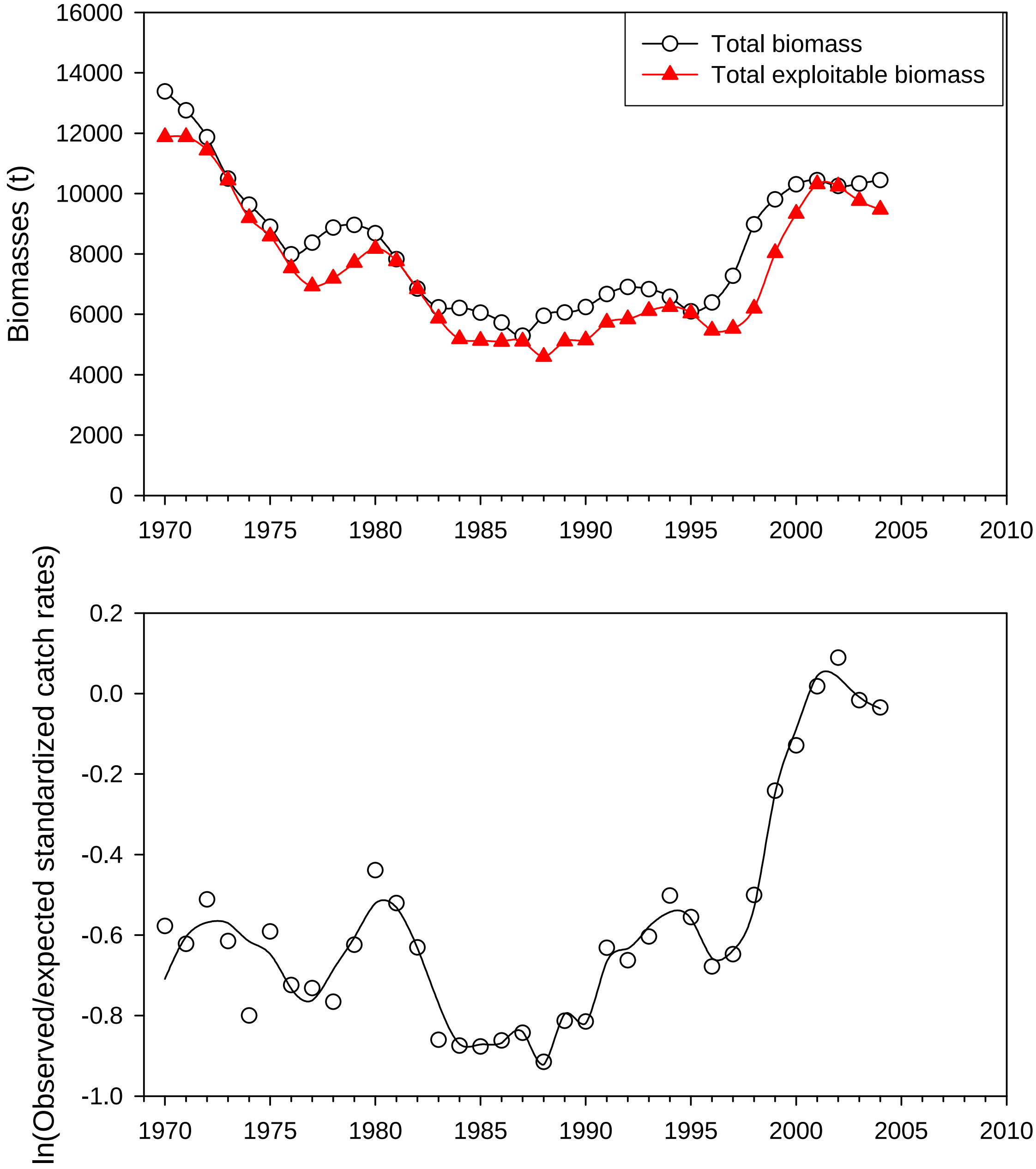

Figure 4.1. The total and exploitable biomass and model fit to catch in number.

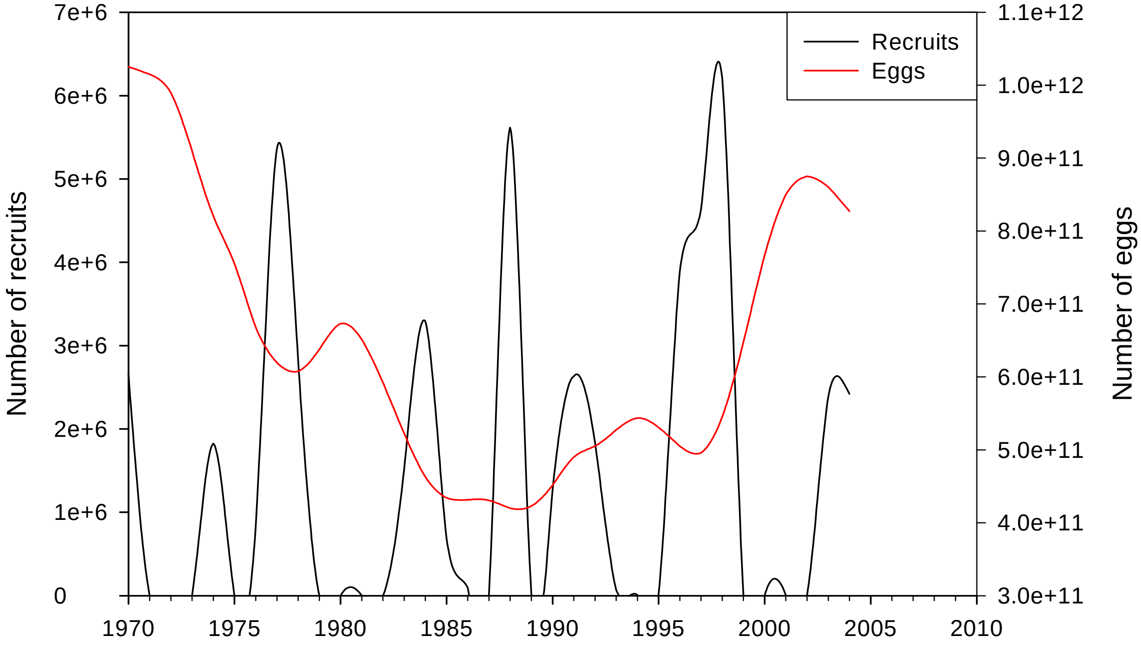

Figure 4.2. Egg production and the number of recruits.

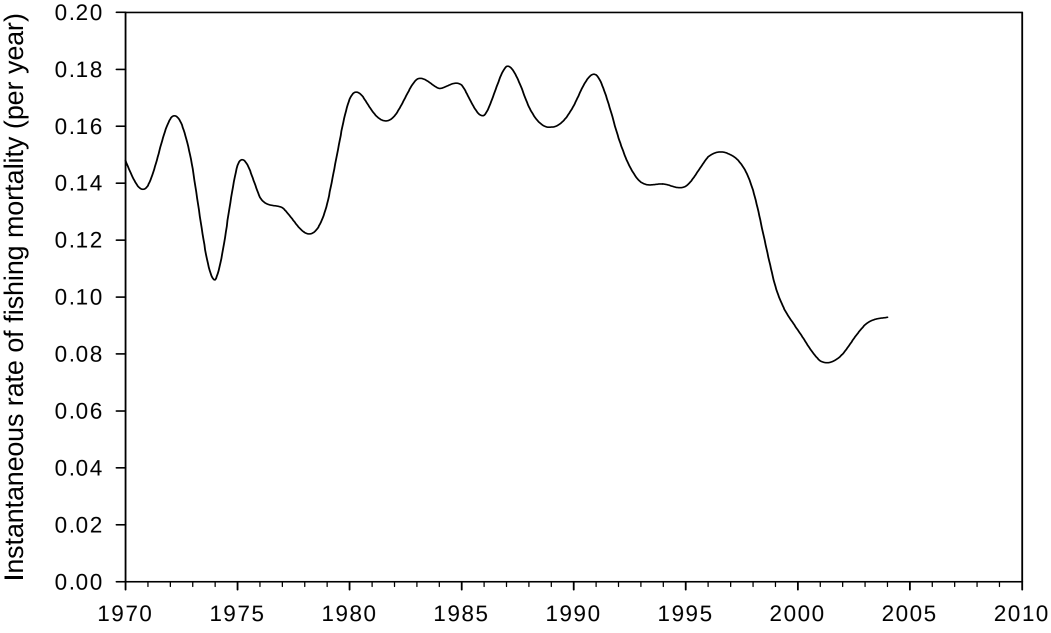

Figure 4.3. Instantaneous rate of fishing mortality.

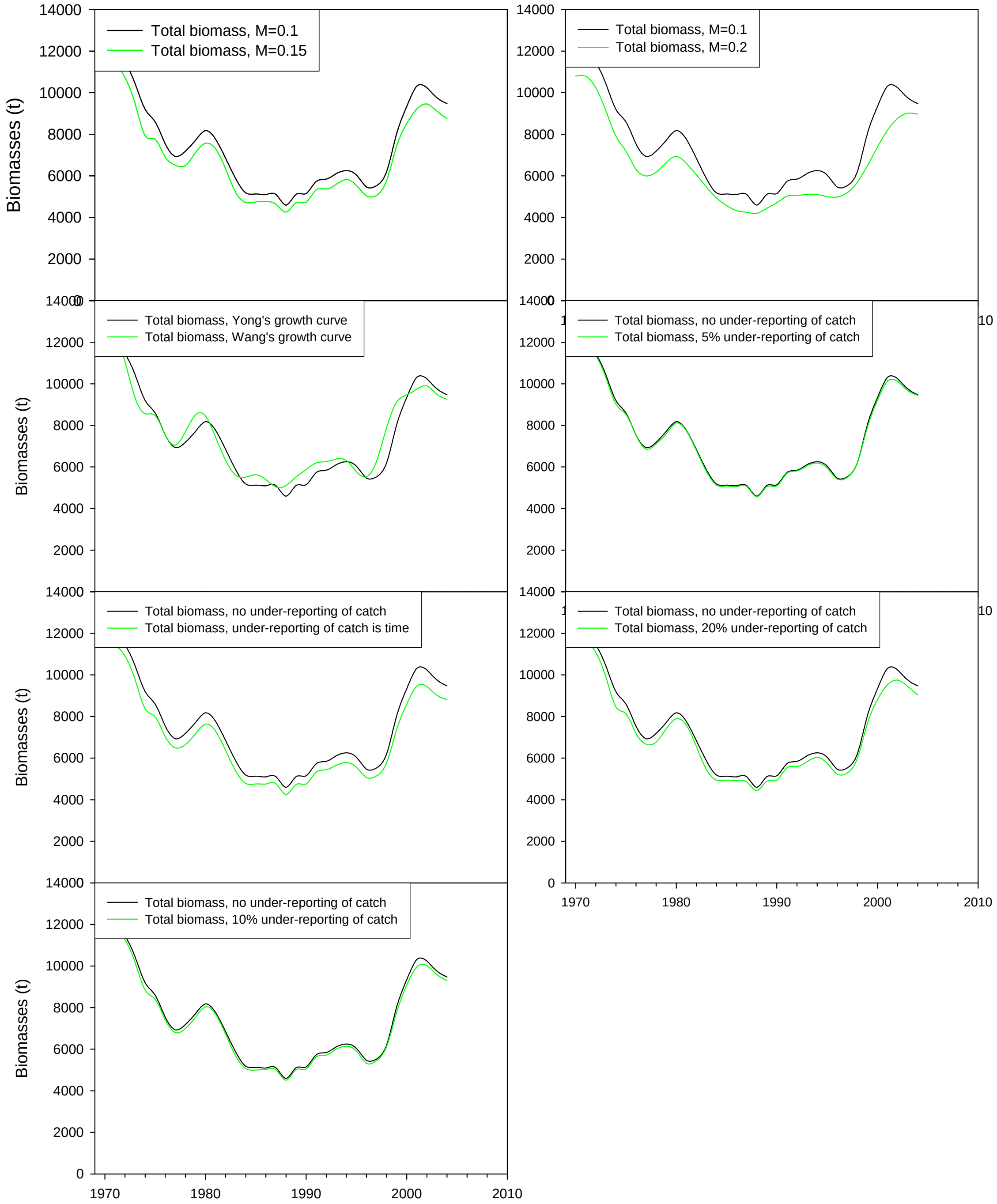

Figure 4.4. Results of a range of sensitivity analyses conducted.

4.2.2 Stochastic model

4.2.2.1 OVERVIEW

The stochastic model was developed in WinBUGS 1.4. As with the deterministic model, it is age based. The lower age limit is 3.5 years. There are 32 age classes. Sexes are distinguished, but recruitment is divided evenly between both sexes. The model runs on an annual time step. There are no spatial cells. The number of chains is two, burn-in rate is at least 10000, and thinning factor is 10. Such a burn-in rate are reasonable, as was confirmed by displaying the value of the deviance and the similarity of the results from the two chains. A thinning factor of 10 is more than enough to eliminate the serial correlations among values from different simulations.

As in the deterministic model, the lobster population is divided into age groups that are followed over time. The numbers of lobster of each sex in each age group are estimated by applying growth, fishing mortality, natural mortality, and annual recruitment each year. Biomass estimates are then derived using, sequentially, an age-length and a length-weight relationship.

The outputs of annual recruitment (R) and derived levels of fishing mortality (F), for each year, from the deterministic model were used as priors for these values in this model (with a 10% error applied through a uniform distribution) that were adjusted by fitting into the standardized catch rate, the abundance of undersized lobsters, an index of puerulus settlement, and length-frequency data. Bayesian posteriors for these parameters and other values of interest (*e.g.* B/B0) were derived using Markov Chain-Monte Carlo simulation (MCMC).

4.2.2.2 MODEL INPUTS AND ASSUMPTIONS

1 *Annual recruitment*: Time series of R from the deterministic model. Stochasticity introduced through a lognormal prior in all years (±5% of value estimated in the deterministic model).

2 *Annual fishing mortality*: Time series of F from the deterministic model. Stochasticity introduced through a uniform prior in all years (±10% of value estimated in the deterministic model).

3 *Gear selectivity*: The gear selectivity was determined from data obtained during escape gap experiments, fitted using the logistic curve. It was unchanged from 1970 to 2003, with a minor correction (from a 2-d Taylor series expansion) from 2003 onwards. Stochasticity

incorporated through normal priors (based on mean and SE) on both parameters from the logistic curve (Appendix A).

4 *Length at age:* von Bertalanffy growth curve fitted to tag-recapture data, by sex. Stochasticity introduced through normal priors (based on mean and SE) on K and $L\infty$ (Appendix A).

5 *Weight at length:* Nonlinear, least-squares fit to length-weight data, by sex. As all lobsters within each age group are of uniform length, they also have a uniform weight – although the values are different for each sex. No stochasticity incorporated.

6 *Natural mortality*: Assumed to be 0.1 (ages 3–30), but increases linearly from 0.1 at age 30 to 20 at age 35. Stochasticity introduced through a uniform prior (±10% of value).

7 *Sex ratio:* Recruitment in each year is divided evenly between both sexes. No stochasticity incorporated.

8 *Sexual maturity:* Logistic curve fitted to maturity data using a likelihood function based on the binomial distribution. Stochasticity incorporated through normal priors on both parameters from the logistic curve (Appendix A).

9 *Fecundity:* Fixed relationship between size (age) and fecundity. Data from Kennedy. No stochasticity incorporated.

10 *Initial age distribution:* Specified for each age and sex, approximately as an exponential function obtained through the application of the maximum entropy principle. Stochasticity incorporated through the stochasticity in natural mortality.

11 *Recreational and illegal catches*: These were assumed to be zero in all years.

12 *Standardised CPUE*: A relative index of the exploitable biomass at time *t* (from 1970) obtained by analysing commercial catch and effort data using a generalized linear model that accounts for the effects of the time of year, the differences in fishing efficiency among fishers, time of day, fishing area and fishing effort on catch rate.

13 *Abundance of under-sized lobsters*: The number of under-sized lobsters caught in the commercial catches, from 1983 onwards.

14 *Index of puerulus settlement*: The mean number of puerulus, per collector, from 1996 onwards.

15 *Length-frequency data*: The length-frequency data on lobsters of both sexes for the Northern Zone of the southern rock lobster fishery for 1995 and 2005.

16 *Process error*: Log-normal distribution with a mean of 1 and CV of 5% applied to R.

4.2.2.3 FITTING

Posterior distributions of each of the parameters estimated were obtained from Monte Carlo simulations on the basis of the five likelihood functions below by simultaneously fitting to all the data sources.

4.2.2.3.1 Fit to number of lobsters

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_N(t)} \exp\left(-\frac{1}{2\sigma_N(t)^2}\left(C_N(t) - \hat{C}_N(t) \right)^2 \right)$$

where the catch in the number of lobsters at time t follows independent normal distributions, with an expected value of $\hat{C}_N(t) = \sum_g \sum_{B(g)}^{a_\infty} C_N(g,a,t)$ and a variance of $\sigma_N(t)^2$, and $B(g) = a_0 + 2$ for females and $B(g) = a_0 + 1$ for males.

4.2.2.3.2 Fit to number of under-sized lobsters

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_s(t)} \exp\left(-\frac{1}{2\sigma_s(t)^2}\left(C_s(t) - \hat{C}_s(t) \right)^2 \right)$$

where the number of under-sized lobsters (at age a_0=3.5 yr) caught in the commercial catches at time t is assumed to follow independent normal distributions, with an expected value of $\hat{C}_s(t) = \sum_g \sum_{a=a_0}^{A(g)} C_N(g,a,t)$ and a variance of $\sigma_s(t)^2$, and $A(g) = a_0 + 1$ for females and a_0 for males.

4.2.2.3.3 Fit to number of puerulus per collector

$$\prod_t \frac{1}{\sqrt{2\pi}\sigma_p(t)P(t)} \exp\left(-\frac{1}{2\sigma_p(t)^2}\left(\ln\left(P(t)\right) - \mu(t) \right)^2 \right)$$

where the mean number of puerulus on a collector at time t is assumed to follow independent log-normal distributions, with an expected value of $K_pR(t-3)$ and a variance of $V[K_p]R(t-3)^2$, where K_p is sampled from $U\left(8.6422\times10^{-8}, 4.5184\times10^{-7}\right)$ and $V[K_p] = 1.1128\times10^{-14}$. This implies that $\mu(t) = \ln\left(K_pR(t-3)\right) - \sigma_p(t)^2/2$ and $\sigma_p(t)^2 = \ln\left(1 + \mathrm{CV}(t)^2\right)$.

4.2.2.3.4 Fit to numbers of under-sized lobsters of both sexes from pot sampling

$$\prod_{t,g} \frac{1}{\sqrt{2\pi}\sigma_s(g,t)} \exp\left(-\frac{1}{2\sigma_s(g,t)^2} \left(C_s(g,t) - q_s(g) \frac{E_p(t)}{E(t)} \sum_{a=a_0}^{A(g)} C_N(g,a,t) \right)^2 \right)$$

where the number $C_s(g,t)$ of under-sized lobsters of sex g (at age a_0=3.5 yr) from pot sampling of commercial catches at time t is assumed to follow independent normal distributions, with an expected value of $q_s(g)\left(E_p(t)/E(t)\right)\sum_{a=a_0}^{A(g)} C_N(g,a,t)$ and with a variance of $\sigma_s(g,t)^2$. Here $E_p(t)$ is the number of pots-lifts associated with pot sampling, $E(t)$ is the total number of pot-lifts in the fishery, $A(g) = a_0 + 1$ for females and a_0 for males, and $q_s(g)$ is the catchability coefficient for lobsters of sex g.

4.2.2.3.5 Fit to the length-frequency data from pot sampling

$$\prod_{t,g} \frac{1}{\sqrt{2\pi}\sigma_l(g,t)} \exp\left(-\frac{1}{2\sigma_l(g,t)^2} \left(C_l(g,a(l(g)),t) - q_l(g,t) \frac{E_p(t)}{E(t)} \sum\nolimits_{l(g)} \hat{C}_N(g,a(l(g)),t) \right)^2 \right)$$

where the number $C_l(g,a(l(g)),t)$ of lobsters of size $l(g)$ and sex g (at age a_0=3.5 yr) from pot sampling of commercial catches at time t is assumed to follow independent normal distributions, with an expected value of $q_l(g,t)\frac{E_p(t)}{E(t)}\sum\nolimits_{l(g)} \hat{C}_N(g,a(l(g)),t)$ and with a variance of $\sigma_l(g,t)^2$. Here $E_p(t)$ is the number of pots-lifts associated with pot sampling, $E(t)$ is the total number of pot-lifts in the fishery, and $q_l(g,t)$ is the catchability coefficient for lobsters of size $l(g)$ and sex g.

4.2.2.4 MODEL OUTPUTS

Outputs from the model are provided in the figures below. These include model fit to the number of undersized lobsters (Figure 4.5), standardized CPUE (Figure 4.6), the number of puerulus per collector (Figure 4.7), the number of lobsters from pot sampling (Figure 4.8), and the length-frequency data on lobsters of both sexes for the Southern Zone of the southern rock lobster fishery from 1991 to 2005 (Figure 4.9), but with only two years (1995 and 2005) shown (there would otherwise be too many graphs to be clear). The goodness-of-fit seemed reasonable in all cases, as was confirmed by displaying the value of the deviance and monitoring the results from the two chains.

The outputs from the model also include a contrast between the prior and posterior probability density functions of the instantaneous rate of fishing mortality for 1970 and 2004 (Figure 4.10), a contrast between the prior and posterior probability density functions of the number of recruits for 1970 and 2004 (Figure 4.11), a contrast between the reported and expected catch (Figure 4.12), the trajectories of the total and exploitable biomass (Figures 4.13 and 4.14), the instantaneous rate of fishing mortality (Figure 4.15), the rates of exploitation (Figure 4.16), annual recruitment (Figure 4.17), annual egg production (Figure 4.18), and annual change of revenue (Figure 4.19).

Although somewhat variable, the total biomass of lobsters (at or above an age of 3.5 yr) in the population (Figure 4.16) decreased from 14114.8580±4008.0742 tonnes in 1970 through 5341.4887±677.8641 tonnes in 1987 to 10513.6705±1201.9291 in 2004, the exploitable biomass of individuals in the population decreased from 12600.9928±3963.6537 tonnes in 1970 through 4652.3901±648.9217 tonnes in 1988 to 9534.6456±1196.9953 in 2004 (Figure 4.13). Thus, the total biomass decreased somewhat gradually from 100% in 1970, reached its lowest level in 1987 of 40.64±11.84%, and increased thereafter, probably as a result of the unreliable data on the mean number of pueruli per collector (Figure 4.7), to 80.45±24.74% in 2004 of that in 1970. Similarly, the total exploitable biomass decreased somewhat gradually from 100% in 1970, reached its lowest level in 1988 of 40.44±13.63%, and increased thereafter, probably as a result of the unreliable data on the mean number of pueruli per collector (Figure 4.7), to 83.29±29.01% in 2004 of that in 1970 (Figure 4.14). The total biomass and exploitable biomass of the population will be similar or increase slightly at all levels of future catches (1770, 1900, 2000 and 2100 tonnes) (Figure 4.14).

The catch in biomass (Figure 4.12) was above the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter; the rate of exploitation in biomass (Figure 4.16) was above that at the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter. Such temporal changes of catches and exploitation mirrored those of the instantaneous rate of fishing mortality (Figure 4.15).

The number of recruits were fairly variable but increased slightly with time, with a significant influx of $6.2067\times10^6\pm0.4629\times10^6$ individuals in 1998 (Figure 4.17), probably as a result of the increased recruitment, as indicated by the mean number of pueruli per collector (Figure 4.7). The number of eggs produced by female lobsters decreased from $1.06653\times10^{12}\pm0.3544\times10^{12}$ in 1970 to $0.4225\times10^{12}\pm0.0652\times10^{12}$ in 1988, and then increased to $0.8306\times10^{12}\pm0.1355\times10^{12}$ in 2004 (Figure 4.18). Thus, the number of eggs produced by female lobsters decreased from 100% in 1970, reached its lowest level in 1988 of 43.65±15.28%, and increased thereafter, probably as a result of the unreliable data on the mean number of pueruli per collector (Figure 4.7), to 86.27±32.12% in 2004 of that in 1970.

The revenue from expected (commercial) catches in biomass of the adult lobsters in the Southern Zone of the southern rock lobster fishery decreased from $452.15\times10^6\pm143.06\times10^6$ A\$ in 1993 to $389.72\times10^6\pm126.00\times10^6$ A\$ in 1994, gradually increased to $492.78\times10^6\pm159.59\times10^6$ A\$ in 2001, and finally decreased to $365.45\times10^6\pm122.38\times10^6$ A\$ in 2004.

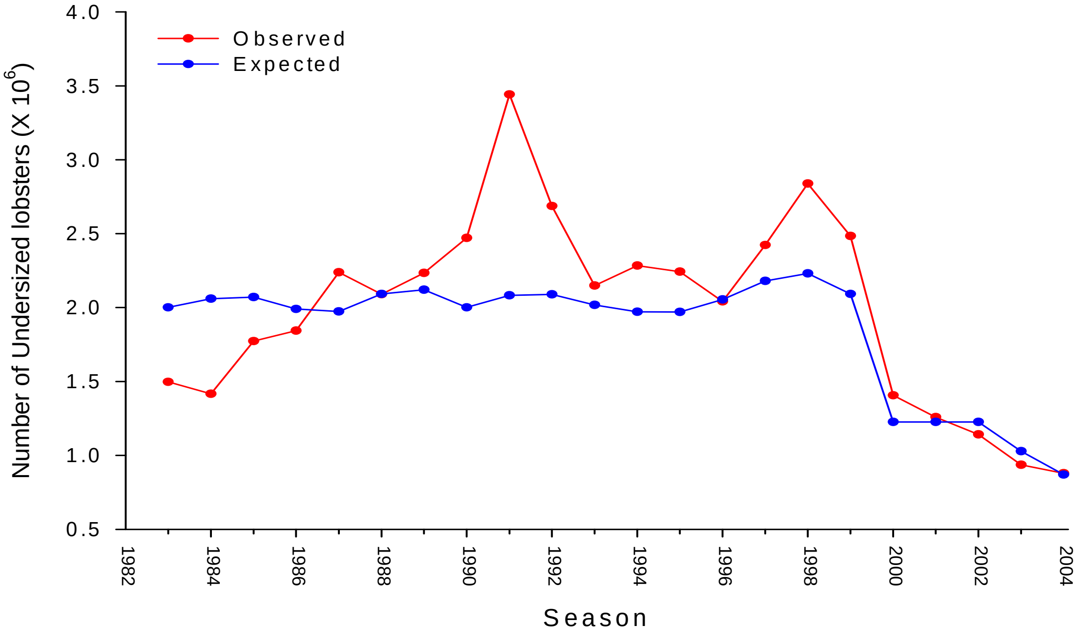

Figure 4.5. Model fit to the number of undersized lobsters for the Southern Zone of the southern rock lobster fishery.

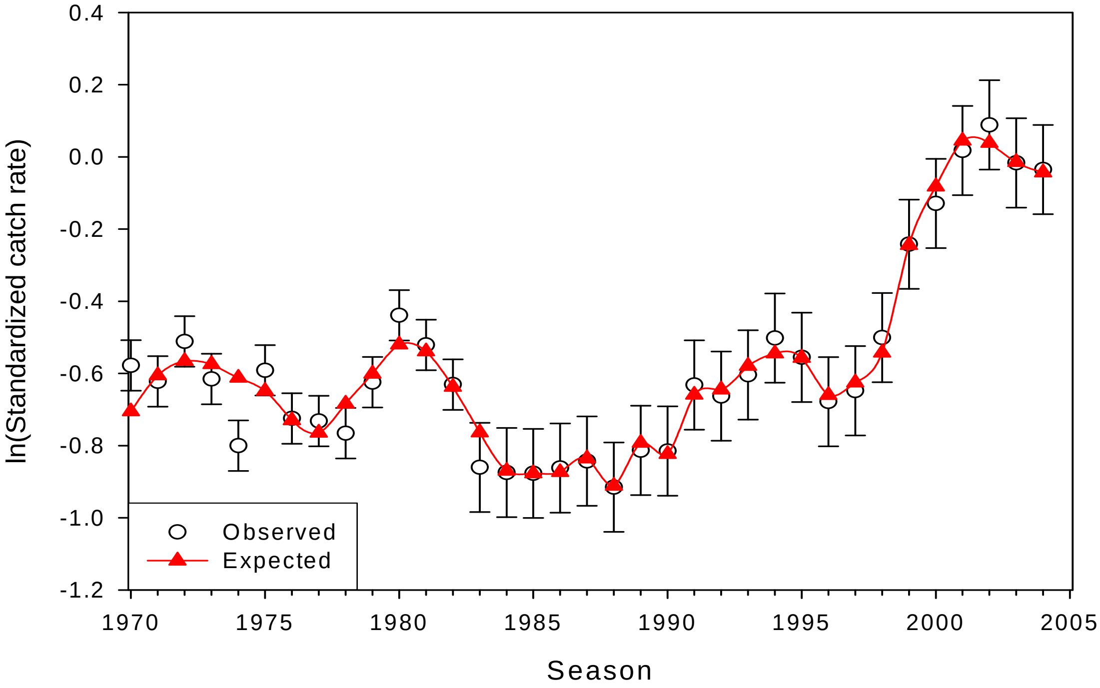

Figure 4.6. Model fit to the standardized CPUE for the Southern Zone of the southern rock lobster fishery.

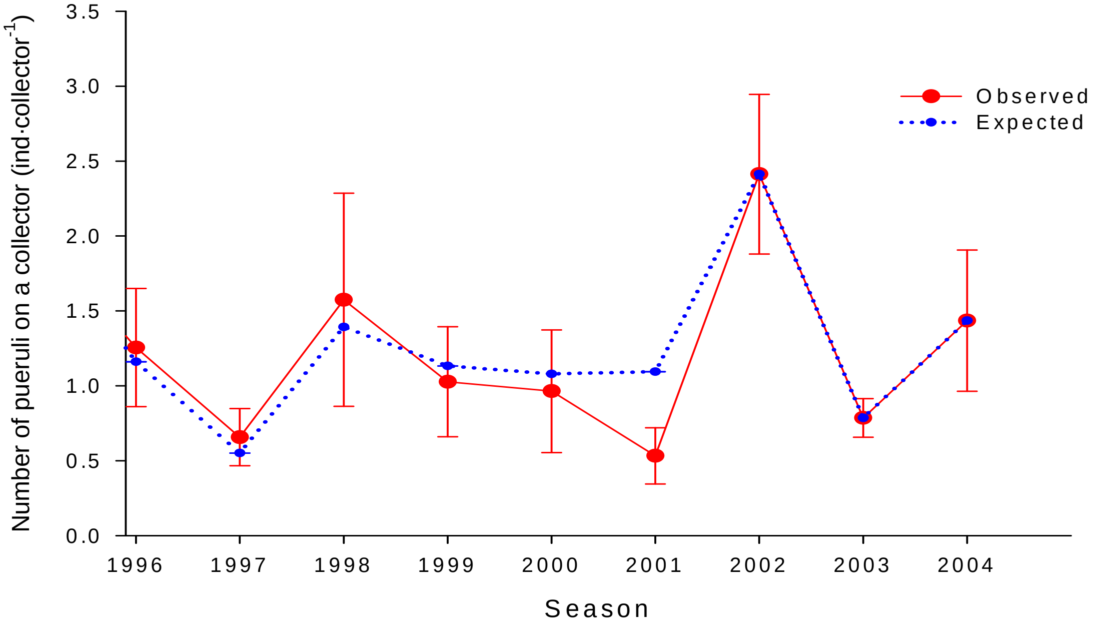

Figure 4.7. Model fit to the number of puerulus per collector for the Southern Zone of the southern rock lobster fishery.

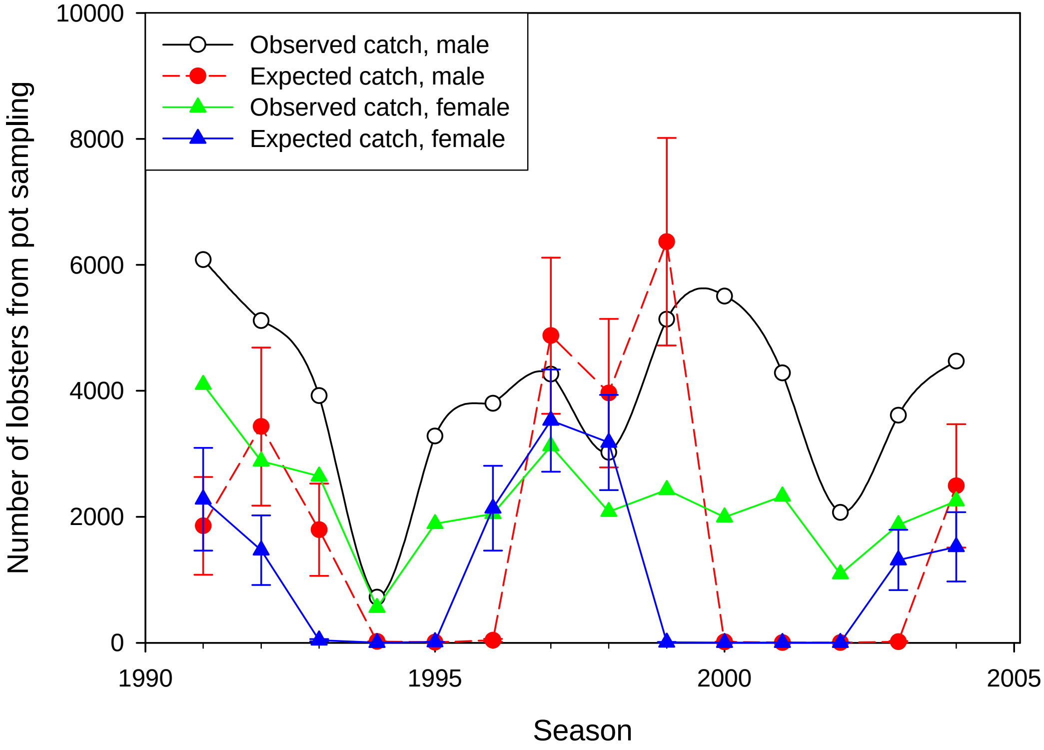

Figure 4.8. Model fit to the number of lobsters of both sexes from pot sampling for the Southern Zone of the southern rock lobster fishery.

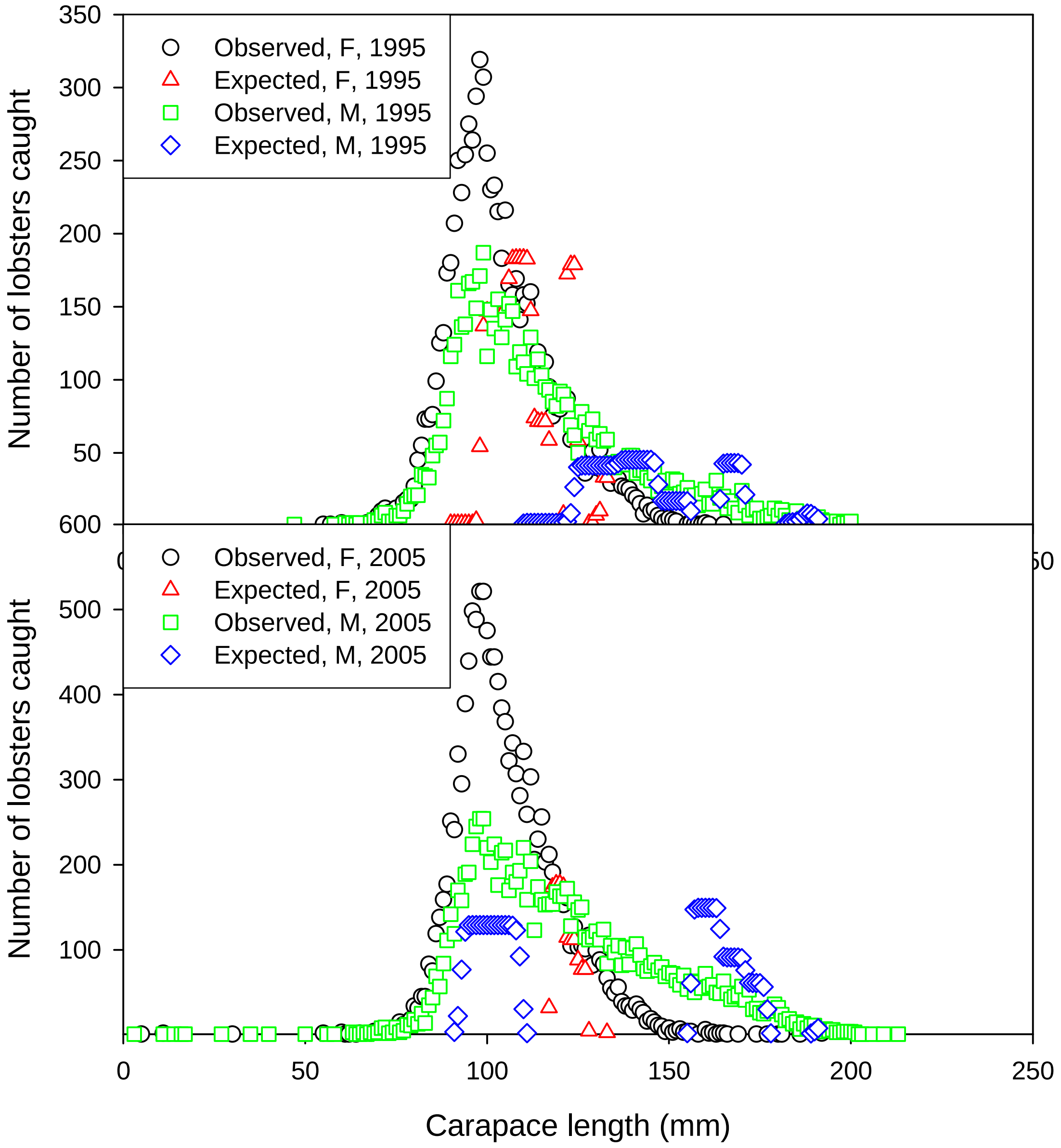

Figure 4.9. Model fit to the length-frequency data on lobsters of both sexes for the Southern Zone of the southern rock lobster fishery for 1995 and 2005.

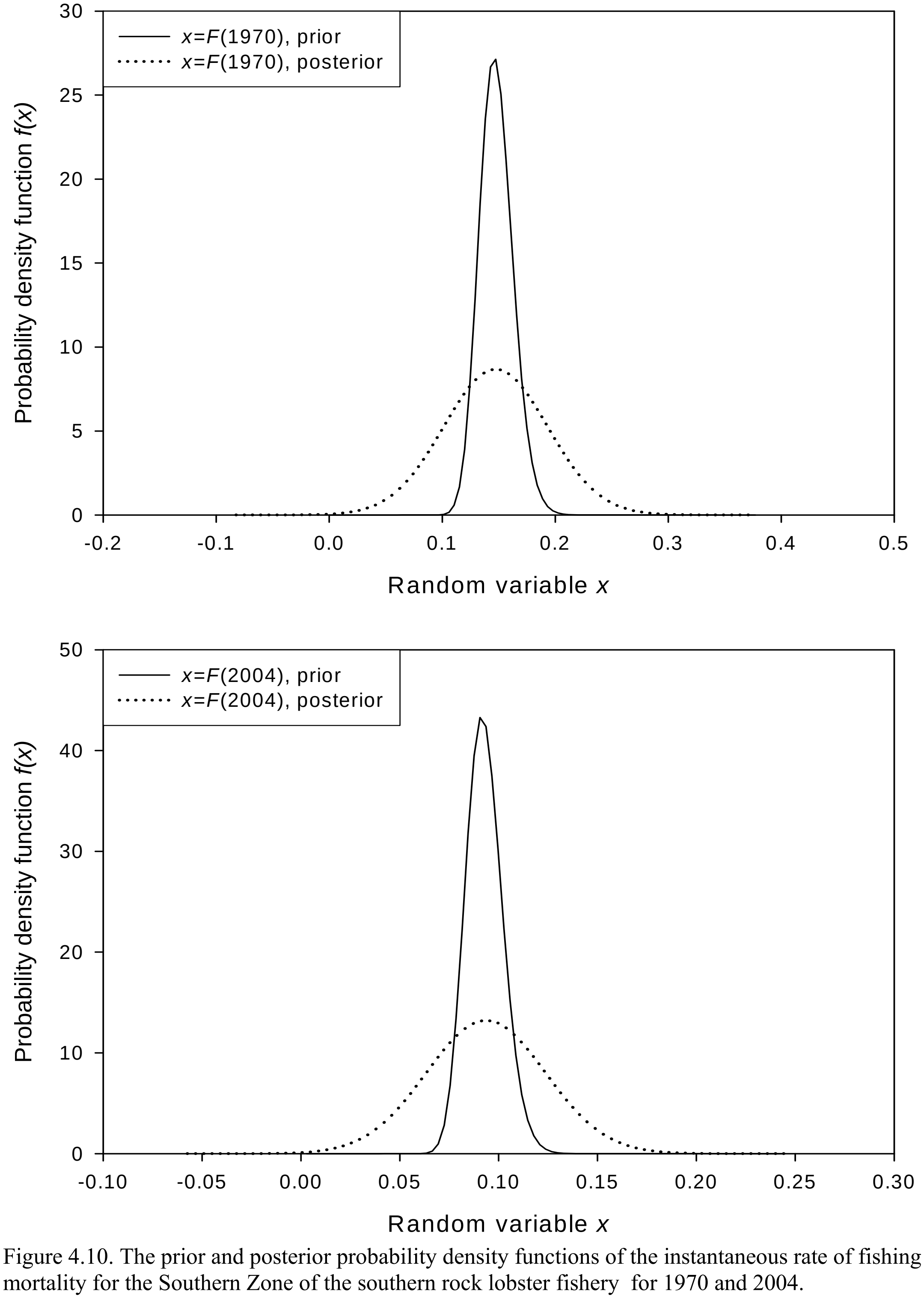

Figure 4.10. The prior and posterior probability density functions of the instantaneous rate of fishing mortality for the Southern Zone of the southern rock lobster fishery for 1970 and 2004.

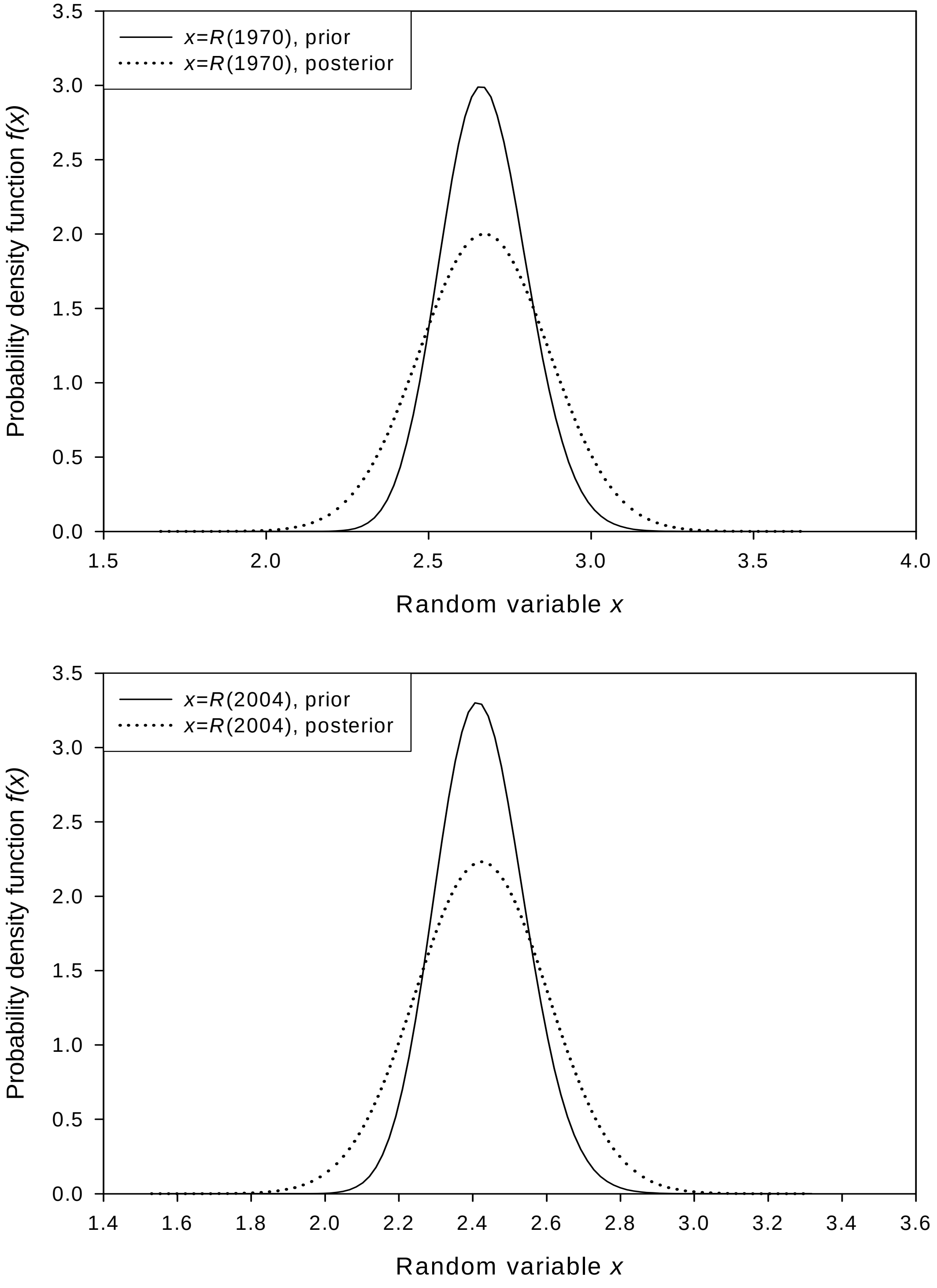

Figure 4.11. The prior and posterior probability density functions of the number of recruits in the Northern Zone of the southern rock lobster fishery for 1970 and 2004.

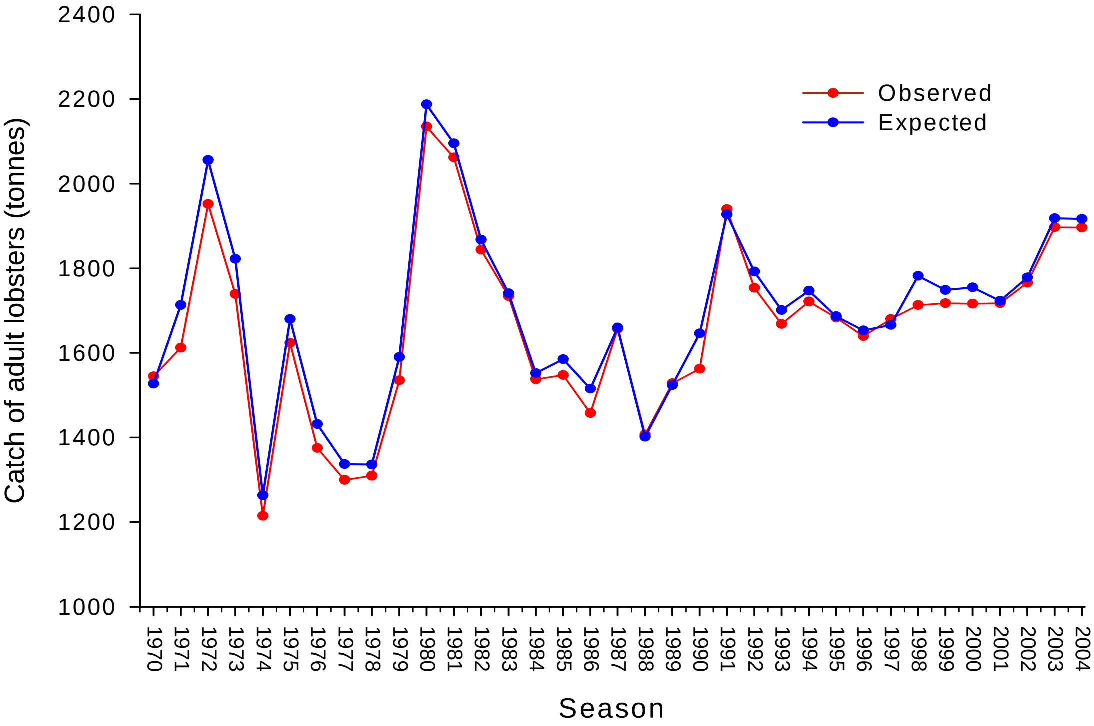

Figure 4.12. Observed and expected (commercial) catches in biomass of the adult lobsters in the Southern Zone of the southern rock lobster fishery from 1970 to 2004.

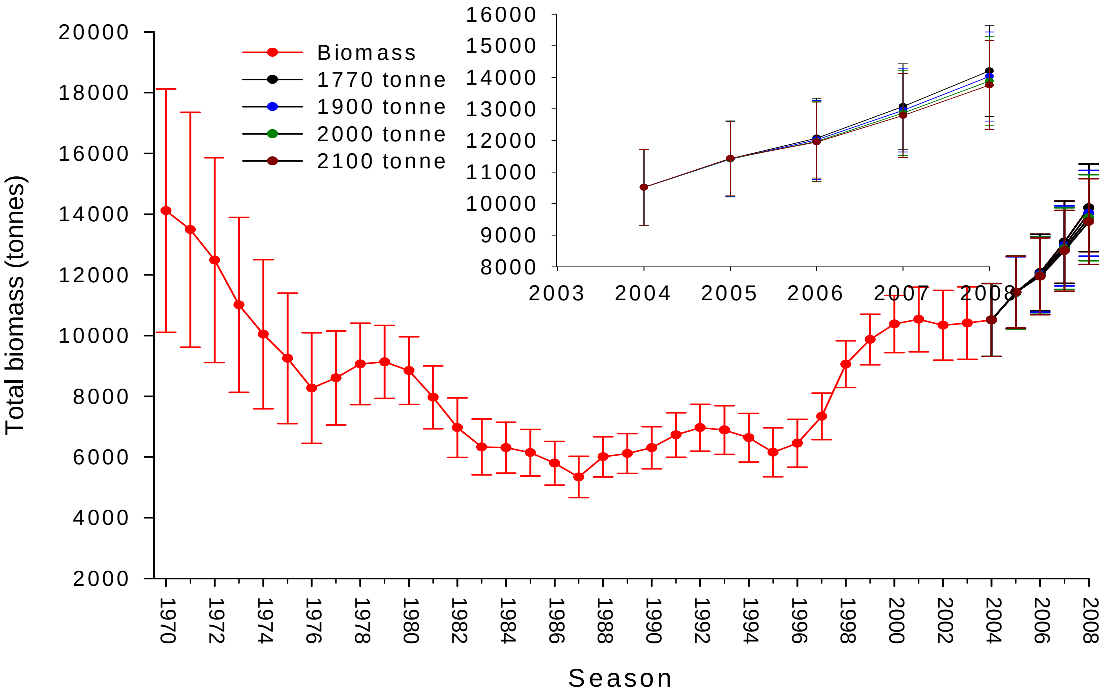

Figure 4.13. The total biomass for the Southern Zone of the southern rock lobster fishery from 1970 to 2004, and the expected biomass from 2005 to 2008 under four harvesting strategies (from top to bottom, catch in biomass equals 1770, 1900, 2000, and 2100 tonnes).

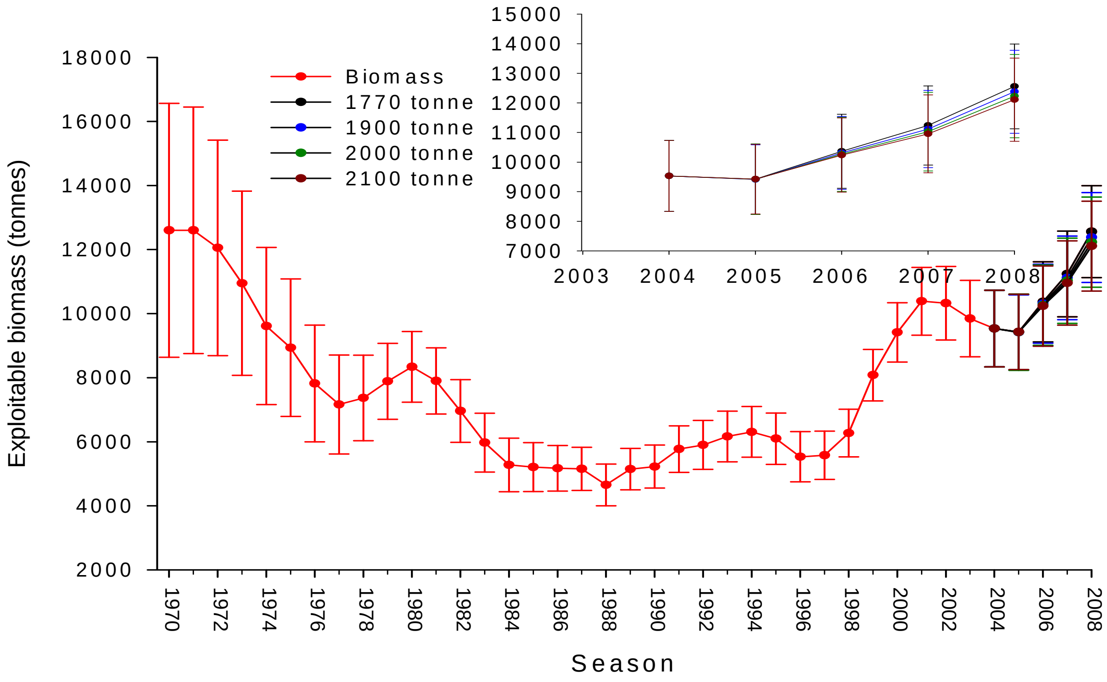

Figure 4.14. The exploitable biomass for the Southern Zone of the southern rock lobster fishery from 1970 to 2004, and its expected value from 2005 to 2008 under four harvesting strategies (from top to bottom, catch in biomass equals 1770, 1900, 2000, and 2100 tonnes).

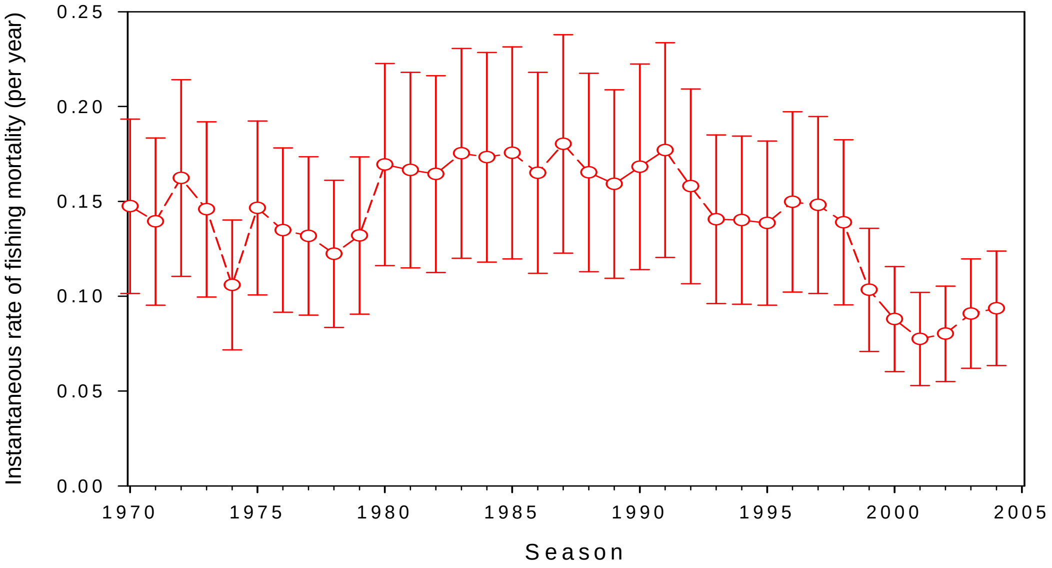

Figure 4.15. The instantaneous rate of fishing mortality for the Southern Zone of the southern rock lobster fishery from 1970 to 2004, and its expected value under four harvesting strategies from 2003 to 2005.

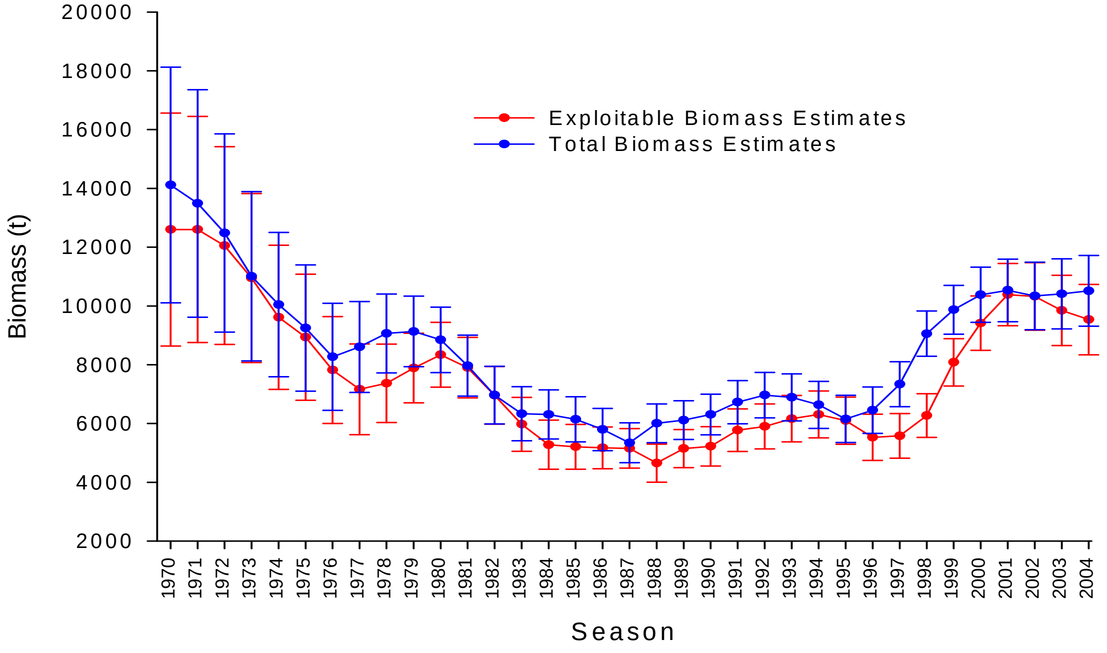

Figure 4.16. The rates of exploitation for the Southern Zone of the southern rock lobster fishery from 1970 to 2004.

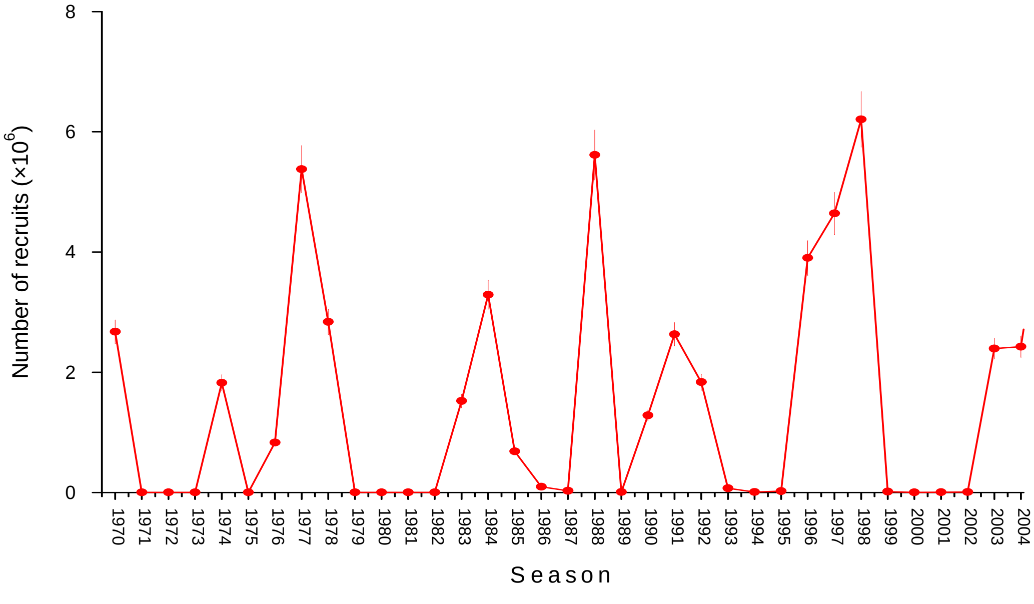

Figure 4.17. Temporal variation of the total number of recruits of lobsters in the Southern Zone of the southern rock lobster fishery from 1970 to 2004.

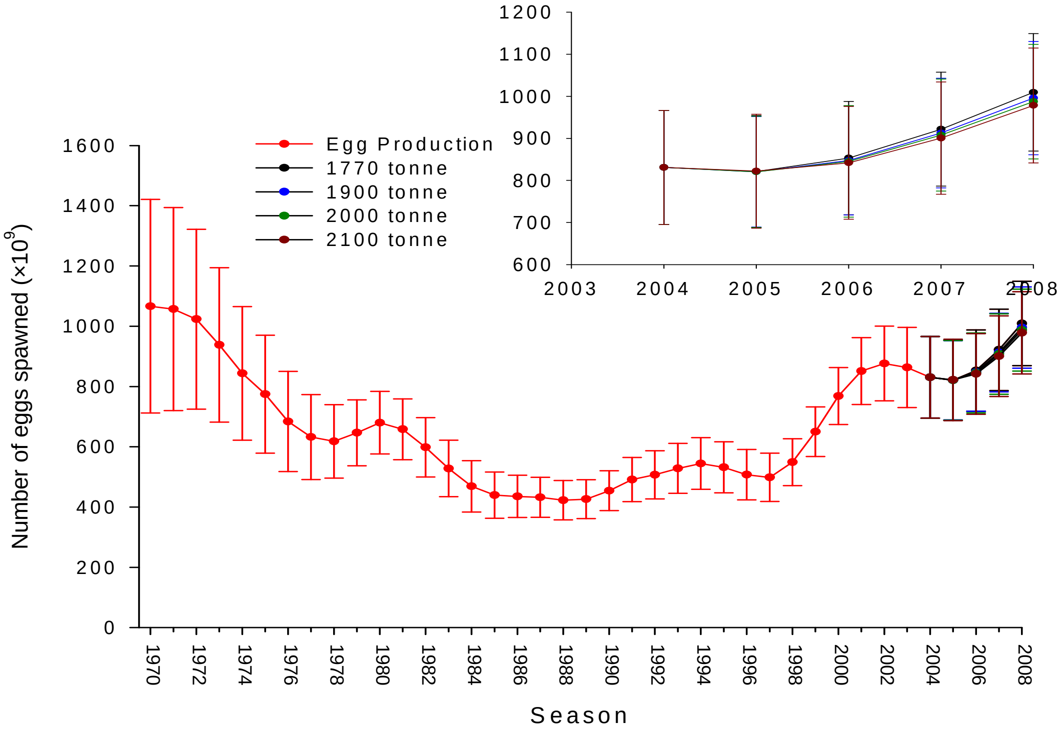

Figure 4.18. Temporal variation of the total number of eggs produced of lobsters in the Southern Zone of the southern rock lobster fishery from 1970 to 2004, and its expected value under four harvesting strategies from 2005 to 2008 (from top to bottom, catch in biomass equals 300, 400, 520, and 600 tonnes).

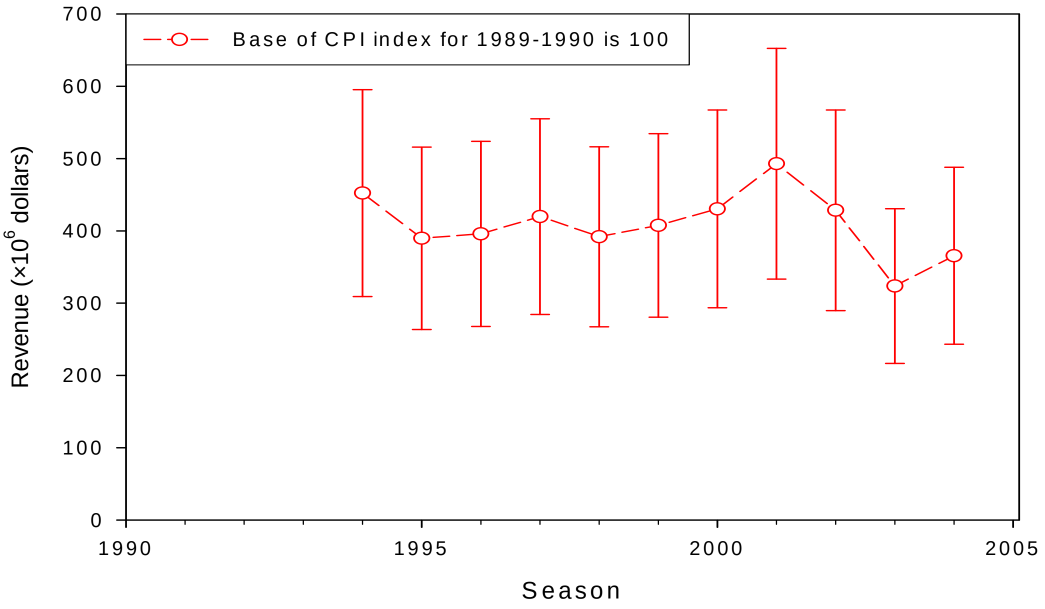

Figure 4.19. Revenue from expected (commercial) catches in biomass of the adult lobsters in the Southern Zone of the southern rock lobster fishery from 1993 to 2004. The base CPI index for food for 1989–1990 is 100.

4.3 DISCUSSION

In this chapter, we developed and used a sex-specific, age- and time-dependent population model to assess the status of the stock of lobsters from the commercial catch and effort data and other biological data, to evaluate, also as a simulation model, the risks of various quantities under four levels of future TACC's (1770, 1900, 2000 and 2100 tonnes). The good 'goodness-of-fit' indicates that the model is a fairly robust tool for assessing the fishery. Several conclusions can be drawn from this study.

This model addresses at least three of the eight problems in the currently used size-dependent models, including those used in Tasmania, Victoria, NSW, Queensland, WA, New Zealand, and South Africa: (1) problems in implementing size-based instantaneous rates of fishing and natural mortalities; (2) problems in constructing, from a set of tagging data, a size-transition matrix; and (3) a logical inconsistency in the way in which the stochasticity in the quantities of interest is introduced by manipulating the population model that was originally derived assuming that all the quantities were fixed. This was done by developing an age-dependent population model, and by not claiming that a growth function accounts for the incremental change in the size of a crustacean as a function of its age (as a result of an absence of necessary data), and by conditioning on the underlying model and the distributions of the parameters.

The population size of lobsters in the Southern Zone is at a high level. This is reflected in the temporal changes of several population characteristics, including the total biomass of lobsters (at or above an age of 3.5 yr) in the population, and the exploitable biomass of individuals in the population. Although somewhat variable, these characteristics all decreased from 1970 to 1988 and recovered substantially from 1988 to 2004. From 2004 onwards, they are similar or decrease slightly at all levels of future TACC's (1770, 1900, 2000 and 2100 tonnes). The temporal variations of the number of recruits, and of the number of eggs produced by female lobsters all indicate that the fishery is in a strong position.

That the fishery seems to be 'sustainable' even if the fishing mortalities have been above that at the maximum sustainable yield can be readily explained. The seemingly complex, but regular temporal patterns of the number of recruits, and the number of eggs produced by female lobsters were weakly related to the size of parental stocks. This suggests that the strength of recruitment to the fishery is environmentally driven so much so that the variations in recruitment are affected more by environmental factors than fishing. Consequently, both aspects of the recruitment should be studied more closely to better predict the temporal changes of any population characteristics. Such studies would comprise developing mechanistic models as well as collecting appropriate biological data.

Of crucial importance here is a close monitoring of the early stages of the lobster and an interpretation of their temporal variations by an appropriate mechanistic model. The reliable prediction of any characteristics of the fishery depends, inter alia, on our knowledge of the mechanisms of the seemingly complex temporal patterns of the biomass and number of recruits, and of the number of eggs produced by female lobsters. The predictability can be improved substantially, if such patterns are better understood. But, this requires the development of a mechanistic model for the number of recruits at a particular time as a function of the number of pueruli and hence of the eggs produced in previous years, as well as a continued collection of data on the number of pueruli as a function of time. Therefore, the data on the early stages of the lobster need to be collected and analyzed by a mechanistic model, to improve model predictions.

It should be noted that the above findings are subject to uncertainties in our model structure, the values of its parameters, and the quality of data. Indeed, many quantities were treated as fixed and many assumptions made about their values. These include data on the growth in the body weight of the lobster, fecundity of females, and changes of gear selectivity with time. The collection of these biological data is essential for improving a stock assessment and for reducing the uncertainties in the results. Another major uncertainty that was not taken into account is the changing practice of reporting. The catch may have been mis-reported before and after the introduction of some management measures. The extent of this under-reporting reflected directly in the possible over- or under-estimation of certain quantities and should be studied to reduce this source of uncertainty. Of course, this also highlights the importance of reliable catch and effort data, and indeed, any sources of data. Consequently, the results obtained should be treated with caution.

Finally, the model developed above is amenable to improvements and extensions to incorporate more biological realism. For example, the time step in it was one year. Monthly or even daily time step should perhaps have been used, to make full use of the catch and effort data. But, this would greatly lengthen the time of computations and would require substantially more computing resources.

CHAPTER 5. GENERAL DISCUSSION

Following a careful review of appropriate models developed and used in other invertebrate fisheries, including those in Tasmania and Western Australia (Chapter 2), we have analyzed almost all the data on the biology of the southern rock lobster *Jasus edwardsii* off southern Australia, including tagging data, log-book catch and effort data and length-frequency data. Some analyses were based on simple models, and others sophisticated ones. This was used to develop an integrated, sex-specific, age- and time-dependent population dynamics model, for the Northern and Southern Zones of the fishery. Originally, a spatially-explicit, sex-specific, age- and time-dependent population dynamics model was to be developed. However, analysis of the tagging data by use of Xiao's (2000b) individual-based approach to evaluating experimental designs for estimating the rates of fish movement from tag recoveries indicated little movement among the Marine Fishing Areas. The movement rates were underestimated, for three reasons: (1) the actual times of the movement of individuals between areas are unknown, (2) the actual times of their natural deaths are unknown, and (3) data on the great majority of individuals are right censored. Also, from the point of view of management, the fishery is divided into Northern and Southern Zones, with very different characteristics. Consequently, an integrated, sex-specific, age- and time-dependent population dynamics model was developed for both Zones (Chapters 3 and 4), both as an estimation model and as a simulation model. 'Fitting' of both models to various sources of data gave a good goodness-of-fit. This and other considerations suggest that both models are sufficiently robust for managing the fisheries in both Zones. Several conclusions can be drawn from this study.

The stock status of *J. edwardsii* differs between the Northern and Southern Zones. In the Northern Zone, the total biomass and number, the exploitable biomass and number, and the spawning (mature female) biomass and number of lobsters (at or above an age of 3.5 yr) all decreased from 100% in 1970 to slightly above 20% in 2002. By contrast, those in the Southern Zone all varied from 100% in 1970 through slightly above 40% in 1987 to 80% in 2004. Such differences would have resulted partly from the different patterns of fishing mortality and recruitment. Clearly, the significant recruitment in the biomass of lobsters in the Southern Zone around 1998 had increased the size of the population. For the Northern Zone, however, the poor recruitment in successive years explains, at least partly, the current status of the fishery. These findings suggest that although the variations in recruitment strength are related to environmental variations, fishing exacerbates them. More work is needed to understand the relationship between the size of the parental stock, the number of spawned eggs and the subsequent recruitment of lobsters to the fishery, as well as the effects of environmental factors.

The developed models were used as simulation models to evaluate various harvesting strategies for SARDI staff members, for PIRSA and for the FMC, for both Northern and Southern Zones. The outcomes of this were provided to the industry, managers and the FMC, thereby empowering the fishing industry and managers to make better informed decisions and to answer general questions of management interest. Also, the models were used to answer the following questions:

a) How much risk is associated with any particular TAC or level of effort?
b) How much more can fishers gain in revenue terms under alternative strategies while demonstrating long term sustainability with a quantified risk?
c) Which fishing regime produces a sustainable fishery, while, at the same time, maximises catch and revenue?
d) How does the current harvesting strategy compare with the optimal harvesting strategy?
e) How much more biological information is gained or lost by adopting various harvesting strategies?
f) What are the implications for lobsters' aggregating behaviour for the assessment of the stock?

a) The risk of an action may be characterized by its chance of success, or failure, or both, and can be described completely by its associated probability density function or distribution function. Any particular TAC or level of effort constitutes an action and hence has a risk associated with it. This risk is reflected in the changes of the probabilities of a great many quantities, which can all be computed. In this project, the probability density functions were computed only for the total exploitable biomasses at the start, and at the current season of the fishery, but any others are trivially computable. Because the total exploitable biomasses are such large numbers that come from a large number of simulations, and, by the Central Limit Theorem, must necessarily follow asymptotic normal distributions, which are describable by only two parameters: the mean and the standard error. Therefore, the risk here is given not only by the pdfs of the total exploitable biomasses associated with each TAC, but also by their means and standard errors.

b) The revenues from expected (commercial) catches in biomass of the adult lobsters in both Zones of the southern rock lobster fishery from 1993 to 2004 were calculated (Chapters 3 and 4), assuming that the base CPI index for food for 1989–1990 is 100. The future revenues can also be easily calculated, if the CPI Index and the prices can be forecast. However, the values of the CPI Index and the prices of the lobsters and their associated commodities were not forecast because of our very limited abilities.

c) It is well known that, if the recruitment of a fish stock does not depend on its size, then one may choose to fish as hard as possible on the stock to maximize catch. Such a drastic action, in the face of many uncertainties, is unlikely to be acceptable for a variety of reasons. Equally well known is that, for the Maximum Sustainable Yield (MSY) to exist and hence to be computed, a relationship must exist between the size of a fish stock and its strength of recruitment. In the case of the Northern Zone lobster fishery, its recruitment varies with year, such that it is most difficult to discern or even surmise such a relationship, to such extent that the number of recruits must be estimated for each year. Of course, this does not imply that there is not a relationship as such, but doing so makes it impossible to find a fishing regime that produces a sustainable fishery, while, at the very same time, maximize catch and hence revenue.

Nonetheless, we calculated, under the assumption that the base CPI index for food for 1989–1990 is 100, the revenues from expected (commercial) catches in the biomass of the adult lobsters in both Zones of the southern rock lobster fishery from 1993 to 2004 (Chapters 3 and 4). These calculations should give some indication of how the current fishing regime fares, in terms of producing a sustainable fishery, while maintaining existing catch and hence revenue. The future revenues could also have been calculated, if the CPI Index and the prices had been available from the Bureau of Statistics. Unfortunately, the Bureau did not produce any forecast of the values of the CPI Index and the prices of the lobsters and their associated commodities.

d) As with many fisheries scientists, the optimal strategy that we had envisaged was based on the common assumption that a recruitment curve is fitted explicitly in the model — an approach that was elegantly elaborated by Deriso (1987). We have tried Ricker curve, Beverton and Holt curve, generalized Ricker curve, difference equations of 1st, 2nd and 3rd orders, and superimposition of periodic functions, before we decided to compute annual levels of recruitment. Thus the optimal harvesting strategy for this fishery follows the so-called bang-bang policy, where fishing should cease if the size of the stock falls below a certain level, only resuming when that level is exceeded. Such a policy is neither sensible nor optimal, however, when the fixed costs of fishing businesses are considered (aside from market impacts). Consequently, we calculated, by assuming that the base CPI index for food for 1989–1990 is 100, the revenues from expected (commercial) catches in the biomass of the adult lobsters in both Zones of the southern rock lobster fishery from 1993 to 2004 (Chapters 3 and 4). These calculations should indicate how the current fishing regime fares, in terms of producing a sustainable fishery, while maintaining existing catch and hence revenue. We did not compute the future revenues, because the Bureau of Statistics did not produce any forecast of the values of the CPI Index and the prices of the lobsters and their associated commodities.

e) The information about a fishery comes from both fishery-dependent data and fishery-independent surveys. Driving the stock to very different levels undoubtedly provides valuable information about it. However, there is always a risk of over-fishing. For the Northern Zone, adopting a larger TAC will generate slightly more information on the size of the stock than a smaller one. However, such an increase in information may not be detectable, given that the levels of TAC are quite similar. Also, adopting a larger or smaller minimum size limit will skew the size distribution of the catch, and the mean weight at size. But, this problem can be corrected externally or internally in a model. Finally, assessments would be improved if quota enables commercial data to be collected over shorter fishing seasons, as this will give more intra-annual contrasts.

f) As with the aggregating behaviour of many other animals, the aggregation of lobsters causes the variances of the estimates of the abundance indices to be extremely large (over-dispersion or hyper-dispersion). Such large variances have been taken into account in fitting into the standardized catch rates.

The models developed above for both Northern and Southern Zones are amenable to improvements and extensions to incorporate more biological realism. For example, it currently uses a one-year time step. Monthly or even daily time step should perhaps have been used, to make full use of the catch and effort data. But, this would have lengthened the time of computations, would require substantially more computing resources. Another far more important improvement, that can be implemented immediately, would be to refine the catch equation, so that it represents the fishing seasons more precisely. A similar improvement could be made if the relationship between the size of parental stock, the number of spawned eggs and their subsequent recruitment of lobsters to the fishery, as well as the effects of environmental factors was better understood. Specifically, the following questions should be answered: (1) why is the fishery in the Southern Zone remarkably resilient, despite a high level of catches? (2) why is the fishery in the Northern Zone pessimistic, despite a low level of catches? (3) what are the relative contributions to the recruitment from internal and external sources, for either Northern or Southern Zone? Finally, the models can be improved by explicitly incorporating information on the transformation of larval stages to refine the estimates of the number of recruits.

In Chapter 2, we mentioned some potential problems with the use of size-dependent models. Specifically, it is not that simple to determine a size-transition matrix, if the stochastic process concerned is not Markovian. For an example of a stochastic process model that deals with growth through multiple moults, see Xiao (in press). It is important to note that although one can somehow compute, numerically, a size-transition matrix, one cannot assume that a simple size-transition matrix exists for one to fit it into a conventional tagging data set. The method of the size-transition matrix in some size-dependent models, i.e., $x(L+1)=A\ x(L)$ is taken from models for fish movement $x(t+1)=A\ x(t)$. Although both have exactly the same functional form, they are very different. For fish movement, Matrix A operates on the numbers of fish in different areas; for the individual growth of a fish, matrix A operates on the probability of a fish in a particular size category. In fitting the model to the data, $x(t)$ is known precisely for fish movement (because the areas of release are known), $x(L)$ is not known (because it is a probability, which is not a proportion and must be calculated from the probability of a previous size by using the same equation).

Why was the deterministic model used first, instead of implementing a full stochastic model? The ideal system would utilise all the data in a single analysis. However, this only works if one can specify sensible priors for its parameters. In the present case, it is not possible even to guess the order of magnitude for some quantities. Simply giving each random variable a wide range is not going to work, as errors propagate and go out of bounds very quickly, as a consequence of Gauss's Law of error propagation. Also, a single analysis approach never really exists in practice, as some sort of "empirical Bayes" must be applied. As a maximum likelihood model, the deterministic model was used to gauge the unknown order of magnitude of the parameter estimates to be used as priors for the stochastic model. This practice is not ideal, but is justifiable through the use of empirical Bayes methods for data analysis (Carlin and Louis, 2000). Here, one must appreciate that both a maximum likelihood estimator and a Bayesian estimator maximize the same generalized likelihood function, with the latter having the extra integration to calculate the estimates of the means of the parameters and the means of their functions.

Another source of uncertainty in the model is our reliance on the index of settlement and on the linearity assumption arising from the difficulty in incorporating a stock recruitment curve. If one investigates the levels of recruitment computed for each year, one will conclude that fitting a recruitment curve is very difficult. Indeed, we have tried Ricker's curve, Beverton and Holt curve, generalized Ricker curve, difference equations of 1st, 2nd and 3rd orders, and compositions of periodic functions, before we decided to compute annual levels of recruitment. Clearly, the low number of pueruli in the NZ dataset may account for these difficulties. We also tried to fit various recruitment curves to the data on the number of pueruli in the SZ dataset, without much success.

The results from the sensitivity analyses (Figures 3.4 and 4.4) can be readily explained. Take the values of M for example. Since M is the reciprocal of the mean age of all the individuals in a stable population (Xiao, 2001), a change of M from 0.1 to 0.15 means a change of the mean age of all the individuals in the population from 10 years to 6.67 years; a change of M from 0.1 to 0.2 means a change of the mean age of all the individuals in the population from 10 years to 5 years. Such seemingly small changes in the values of M imply appreciable changes in the structure of the population and hence appreciable changes in its trajectories. Much more significant changes come from structural changes, as in the case of including or excluding spatial expansion.

What does a single "curve" for the length-at-age of crustaceans do in explaining some aspects of their moulting growth? The parameters of any model are just “summarized data". Indeed, whatever "curve" is fitted to a set of data on crustaceans, its parameters will have information about its biology. As mentioned above, a single "curve" for the length-at-age only applies to the deterministic model; the "curve" becomes stochastic in the stochastic model, with its length-transition matrix being calculated from the unconditional pdf of the lengths of lobsters are generated from the pdfs of K and L_∞. This approach to the modelling of the growth of lobsters, albeit not ideal, does not assume the existence of a simple transition matrix, which does not exist for a general random process (Xiao, 2006). The deterministic model is used to estimate the means of R and F, without which it is impossible to guess the order of magnitude of the recruitment levels of the fishery.

Why were more sources of data, such as CPUE, not used in the deterministic model (maximum likelihood model) in estimating yearly fishing mortality and level of recruitment? CPUE, raw and/or standardized, contains information on the changes in the levels of "fishable" stock biomass in a fish population, and the levels of its recruitment and fishing mortality. Neither was used for this purpose, because, as econometricians have found out after decades of searching for the ideal way of weighting up data from different sources, the only logical approach is to adopt the Bayesian approach. The number of data sets used in the deterministic model should then be such that no specification of their respective weights is necessary. All other sets of data are incorporated with the stochastic model. Thus, two sets of data are used by the deterministic model, i.e. the annual catch in the weight of lobsters, and the annual catch in the number of lobsters. Therefore, the point estimates for the annual recruitment and annual fishing mortality of the lobsters are determined from total catch in weight and total catch in number by the deterministic model, whereas the stochastic model is fitted into all other sources of data (standardized catch rates, catch in the number of the under-sized lobsters, and the number of puerulus per collector), where the priors centred about those point estimates are adjusted.

SUMMARY AND CONCLUSIONS

Review of appropriate models developed and used in other invertebrate fisheries:

In the review we attempt to explain why, in the deterministic context, an age-dependent population model is equivalent to a size-dependent one, and discuss several other related issues that must be understood, in order to implement, correctly, a size-dependent population model. The published descriptions of size-dependent models, including those used in Tasmania, Victoria, NSW, Queensland, WA, New Zealand, and South Africa generally indicate that they have eight primary problems, three of which are addressed here. Firstly, the age-based instantaneous rates of fishing and natural mortalities (which must be used in an age-dependent model) are mistakenly used as size-based ones. Since both types of mortalities differ substantially in value and in dimension, this oversight is equivalent to assuming that a fish population is far more dynamic than real, the size of its population is far smaller than real, its recruitment strength is far greater than real, and its population (if depleted) recovers much faster than real. Thus, any assessments based on this assumption, will produce a far more optimistic picture than reality. Secondly, it can be shown that any attempt at constructing, from a set of tagging data, a growth function or a size-transition matrix that can account for the incremental change in the size of a crustacean as a function of its age is inappropriate, unless data are available on the moult number and the duration of the stages of individual animals. However, almost all size-dependent models use a growth function or a size-transition matrix derived from tag-recapture data without information on moult number or stage duration. Thirdly, there is a logical inconsistency in the way in which the stochasticity in the quantities of interest is introduced. We believe that a better approach would be to condition on the underlying model and the distributions of the parameters. By developing an age-dependent population model, and by not claiming that a growth function accounts for the incremental change in the size of a crustacean as a function of its age (as a result of an absence of necessary data), and by conditioning on the underlying model and the distributions of the parameters, at least three of the logical inconsistencies mentioned above are addressed.

A population dynamics model for *J. edwardsii*: The Northern Zone Rock Lobster Fishery:

A sex-specific, age- and time-dependent population model was developed to assess the status of the Northern Zone Rock Lobster Fishery (NZRLF) from both commercial catch and effort and additional sources of biological data. The model construction was undertaken in two stages. Firstly, a deterministic model was developed to produce estimates of recruitment (R) and fishing mortality (F). The model was conditioned on catch in weight (Cw) and fitted to catch in number (Cn) as derived from commercial catch and effort data. In the model, the lobster population was divided into age groups that were followed over time. Outputs of R and F from the deterministic model were then used as priors for the second model development phase i.e. the stochastic model.

As with the deterministic model, the stochastic model was age based. The number of lobsters of each sex in each age group were estimated by applying growth, fishing mortality, natural mortality, and annual recruitment to each year. Biomass estimates were then derived using, sequentially, an age-length and a length-weight relationship. The outputs of annual recruitment (R) and derived levels of fishing mortality (F), for each year, from the deterministic model were used as priors for these values in this model (with a 10% error applied through a uniform distribution) that were adjusted by fitting into the standardized catch rate, the abundance of undersized lobsters, length-frequency data, and an index of puerulus settlement. The variability in length and hence the variability in the whole model conditional on the variability of the growth parameters.

The goodness-of-fit of the model seemed reasonable for all sources of data. Despite its simplicity, the model seemed to be sufficiently robust for management purposes, particularly because it overcomes the common problem of constructing a size-transition matrix. The outputs from the stochastic model allowed us to evaluate several management strategies by accounting for the spatiotemporal expansion of the fishery. Overall, the outputs indicated that both the total and exploitable biomass of lobsters (at or above an age of 3.5 yr) in the population, all decreased from 100% in 1970 to slightly above 20% in 2002. From 1970 to 2002, the catch in biomass and number of lobsters, rate of exploitation in terms of biomass of individuals, and the instantaneous rate of fishing mortality were all near, at or above that at the maximum sustainable yield. The biomass and number of recruits varied considerably from 1970 to 2002, although the number of eggs produced by female lobsters steadily decreased, reaching its lowest level in 1994, before slightly increasing thereafter. Although those calculations are somewhat uncertain due to a lack of some biological data, the fishery seems to have declined steadily over this period. Finally, the study highlighted certain gaps in available data such as information on the temporal changes in lobster body weight (because of the variability in the body weight of the individuals of the same length), effects of gear selectivity, female fecundity and expansion and contraction of the fishery. Collection of these data in the future will allow for a more robust stock assessment in this zone.

A population dynamics model for *J. edwardsii*: The Southern Zone Rock Lobster Fishery:
A sex-specific, age- and time-dependent population model was developed to assess the status of the Southern Zone Rock Lobster Fishery (SZRLF) from both commercial catch and effort and additional sources of biological data. Model design and development was the same as that described for the NZRLF.

Similarly, the goodness-of-fit of the model seemed reasonable for all sources of data. Despite its simplicity, the model seemed to be sufficiently robust for management purposes, particularly because it overcomes the common problem of constructing a size-transition matrix. Overall the model outputs indicated that both the total biomass and the exploitable biomass (at or above an age of 3.5 yr) in the population, all varied from 100% in 1970 to slightly above 40% in 1987. This then increased to 80% in 2004. The catch in biomass was above the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter. The rate of exploitation in biomass was above that at the maximum sustainable yield from 1970 to 1999, below it from 2000 to 2003, and above it thereafter. The number of recruits were variable but increased slightly with time, with a significant influx of 6.2×10^6 individuals in 1998. However, the number of eggs produced by female lobsters decreased somewhat, reached its lowest level of 422.5×10^9 in 1988, and its highest level of 876.4×10^9 in 2002. Calculations are somewhat uncertain, because of a lack of some biological data, and hence the results should be treated cautiously. Overall however, the fishery appears to be in a healthy state.

Several conclusions can be drawn from this study. Probably most importantly, the stock status of *J. edwardsii* differs substantially between the Northern and Southern Zones. In the Northern Zone, the total biomass and number, the exploitable biomass and number, and the spawning (mature female) biomass and number of lobsters (at or above an age of 3.5 yr) all decreased from 100% in 1970 to slightly above 20% in 2002. By contrast, those in the Southern Zone all varied from 100% in 1970 through slightly above 40% in 1987 to 80% in 2004. Such differences must have resulted partly from the differing patterns of fishing mortality and recruitment. The significant recruitment in biomass of lobsters in the Southern Zone around 1998 appears to have increased the population size. In the Northern Zone however, the continued poor recruitment partly explains the current status of the fishery.

CHALLENGES AND LIMITATIONS IDENTIFIED

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Continuous-time formulation

This project had set as its original objective the ambitious goal of building a model based on continuous rather than discrete time. Most fishery models used in stock assessment assume discrete time steps of year, season or month. In these dynamic fishery models, the population array, which quantifies the model-predicted number of animals, specifies one set of population numbers per time step. Specifically, these models fit available data to estimate the number of lobsters in the stock at the start of each yearly, seasonal, or monthly time period. A major obstacle to progress during the early stages of this project was the challenge of trying to develop an entirely new method of representing lobster population numbers, not just in yearly or monthly steps, but as a continuously varying function of time. In the end, no practical means to represent such a formulation was found to be technically feasible.

Continuous distribution of lobster carapace lengths

Similarly, while the lobster numbers by body length generally vary continuously in real populations, because real population numbers are large, many length-based fishery models in current use approximate these continuous probability densities of length frequency by breakdown into discrete length bins, of fixed or variable width. For example, the model adopted in South Australia, that of Punt and Kennedy (1997), uses fixed length bins of 4-mm CL. This approach is also used throughout Australia and New Zealand for lobster modelling. Other length- and age-based stock assessment models (Fournier et al. 1990; Frøysa et al. 2002) also use fixed bins, within each age group. While some methods in the literature do describe approachs that represent the spread of body sizes in each cohort as a continuous density or distribution function (Banks et al. 1991; Smith and Botsford 1998), these are rarely employed in fishery stock assessment practice, being difficult to generalise to the wide array of assumptions for selectivity and growth. A range of alternative growth descriptions have been developed, notably ‘transition matrices’ (Sainsbury 1982; Punt et al. 1997), which grow model lobsters among fixed bins. This method permits growth model flexibility by generalising the von Bertalanffy model, thereby accounting for the slowing in growth of female lobsters at maturity which was the principal challenge in growth modelling of South Australian rock lobster.

Partial differential equations

Some mathematical approximation is inherent when breaking up continuous variables of time and body length into discrete bins. This approximation has been widely applied in current fishery modelling because it makes computation and programming much more straightforward than if one attempts to retain a continuous description of lobster numbers in time and body size. Thus, an early goal of this project was to attempt to avoid the mathematical simplifications of discrete bins in the hope of obtaining a more accurate model description. In formal terms, the model was seeking to base the population dynamics on a von Foerster partial differential equation formulation, rather than a finite difference formulation. In the end, little progress was achieved in this direction, numerical computation being an inherently discrete process.

Integrating maximum likelihood and Bayesian approaches

At later stages of the project development, the objective of representing time and lobster carapace length continuously was abandoned, and a yearly discrete time model was adopted. However, an attempt was made to retain stochasticity within the approach. To account for uncertainty in a Bayesian framework, the lobster modelling was undertaken with two models, rather than one. The first 'deterministic', i.e. maximum likelihood model from which the estimates were obtained of F and absolute population numbers via yearly recruitment, used logbook catch and effort. The second 'stochastic' model, was a WinBugs Bayesian model with priors that were not taken from the output of the first model. This WinBugs model applied priors of various forms, to incorporate stochasticity, and thus represent uncertainty in model estimates. It was found that the construction of two models also posed major limitations, in that many of the features of more generalised integrated models were difficult or impractical to implement. In particular, lobster carapace length sample data were not fitted, and a rigorous growth description could not be formalised.

NEED FOR FURTHER RESEARCH

Several issues must be addressed, in order to improve the performance of the models.

The relationship between the size of spawning stock, the number of spawned eggs and their subsequent recruitment to the fishery and the effects of environmental factors all require further study in order to improve the performance of the model. In particular, the following questions should be answered: (1) why is the fishery in the Southern Zone remarkably resilient, despite a high level of catches? (2) why is the fishery in the Northern Zone pessimistic, despite a low level of catches? (3) what are the relative contributions to recruitment from internal and external sources, for either Northern or Southern Zone? It is the answers to those questions that are the basis for formulating biologically realistic and mathematically sound curves of recruitment.

An extension to the model that should be implemented immediately is to refine the catch equation, so that it represents the fishing seasons precisely and incorporate all the missing terms (Xiao, 2005, 2006b). In 3–5 years of time, the numerical solution of a system of ordinary or partial differential equations, with fish catch and hence equation being its part, is essential in fish population dynamics. Such a system of differential equations has already been formulated for a multi-species fishery, with a single-species fishery as a special case (Xiao, 2006c).

More biological realism needs to be incorporated immediately. The time step in the models was one year. Monthly or even daily time step should perhaps have been used, to make full use of the catch and effort data. In 3–5 years of time, the problem of an arbitrary time step should be eliminated, by numerically solving a system of ordinary or partial differential equations, with fish catch and hence equation being its part.

The models need to be improved in 2–5 years of time by collecting and explicitly incorporating data on the transformation of larval stages to refine the estimates of the number of recruits.

REFERENCES

Banks, H.T., Botsford, L.W., Kappel, F., and Wang, C. 1991. Estimation of growth and survival in size-structured cohort data: an application to larval striped bass (Morone saxatilis). J. Math. Biol. 30: 125-150.

Bentley, N., Breen, P.A., Starr, P.J., Kendrick, T., 2001. Assessment of the CRA 3 and NSS substocks of red lobster (*Jasus edwardsii*) for 2000. New Zealand Fisheries Assessment Report 2001/69, 84 p.

Bergh, M.O., Johnston, S.J., 1992. A size-structured model for renewable resource management with application to resources of rock lobster in the south-east Atlantic. *S.A. J. Mar. Sci.* **12**, 1005–1016.

Beyer, J., 1989. Recruitment stability and survival — simple size-specific theory with examples from the early life dynamics of marine fish. *Dana* **7**, 45–147.

Carlin, B.P., Louis, T.A., 2000. Bayes and Empirical Bayes Methods for Data Analysis. 2nd ed, Chapman and Hall/CRC, London, 419 pp.

Breen, P.A., Starr, P.J., Bentley, N., 2001. Rock lobster stock assessment for the NSN substock and the combined CRA 4 and CRA 5 areas. New Zealand Fisheries Assessment Report 2001/7, 73 p.

Chen, Y., Kanaiwa, M., Wilson, C., 2005. Developing and evaluating a size-structured stock assessment model for the American lobster, *Homarus americanus*, fishery. *N.Z. J. Mar. Freshwater Res.* **39**, 645–660.

Deriso, R.B., 1987. Optimal $F_{0.1}$ criteria and their relationship to maximum sustainable yield. *Can. J. Fish. Aquat. Sci.* **44** (suppl. 2), 339–348.

Deriso, R.B., Parma, A.M., 1988. Dynamics of age and size for a stochastic population model. *Can. J. Fish. Aquat. Sci.* **45**, 1054–1068.

Frøysa, K.G., Bogstad, B., Skagen, D.W. 2002. Fleksibest—an age-length structured stock assessment model. Fish. Res. 55: 87-101.

Fournier, D.A., Doonan, I.J., 1987. A length-based stock assessment method utilizing a generalized delay-difference equation. *Can. J. Fish. Aquat. Sci.* **44**, 422–437.

Fournier, D., Sibert, J.R., Majkowski, J., and Hampton, J. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (Thunnus maccoyii). Can. J. Fish. Aquat. Sci. 47: 301-317.

Gardiner, C.W., 1985. Handbook of Stochastic Methods for Physics, Chemistry and the

Natural Sciences, 2nd ed, Springer-Verlag, London, 444 pp.

Gardner, C., Frusher, S.D., Kennedy, R.B., Cawthorn, A., 2001. Relationship between settlement of southern rock lobster pueruli, *Jasus edwardsii*, and recruitment to the fishery in Tasmania, Australia. *Mar. Freshw. Res.* **52**, 1271–1275.

Hobday, D., Punt, A.E., 2001. Size-structured population modelling and risk assessment of the Victorian southern rock lobster, *Jasus edwardsii*, fishery. *Mar. Freshwater Res.* **52**, 1495–1507.

Hoppensteadt, F., 1975. Mathematical theories of populations: demographics, genetics and epidemics. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania.

Johnston, S.J., Bergh, M.O., 1993. Size-based estimates of survivorship for the South African rock lobster *Jasus lalandii*. *Fish. Res.* **18**, 277–304.

Kermack, W.O., McKendrick, A.G., 1927. Contributions to the mathematical theory of epidemics. II. The problem of endemicity. *Proc. R. Soc., Series* A **115**, 55–83.

Kermack, W.O., McKendrick, A.G., 1932. Contributions to the mathematical theory of epidemics. III. Further studies of the problem of endemicity. *Proc. R. Soc., Series A* **138**, 94–122.

Kristensen, K., Lewy, P., Beyer, J.E., 2006. How to validate a length-based model of single-species fish stock dynamics. Can. J. Fish. Aquatic Sci. **63**: 2531–2542.

Lewis, R.K., 1981. Southern rock lobster *Jasus novaehollandiae*: Zone N Review, South Australian Department of Fisheries.

Linnane, A., Dimmlich, W., Ward, T., 2005. Movement patterns of the southern rock lobster, *Jasus edwardsii*, off South Australia. *N.Z. J. Mar. Freshwater Res.* 39, 335–346.

Lotka, A.J., 1922. The stability of the normal age distribution. *Proc. Nat. Acad. Sci.* **8**, 339–345.

Lotka, A.J., 1924. Elements of physical biology. Reprinted in 1956 as "Elements of mathematical biology". Dover Publications, Inc., N.Y.

Lyons, W.B., and J.H. Hunt. 1991. Catch rates of spiny lobsters (*Panulirus argus*) in traps equipped with escape gaps and potential benefits to the south Florida fishery. *Proceedings of the Gulf and Caribbean Fisheries Institute, Miami FL*, **40**, 452–470.

McGarvey, R., Ferguson, G.J., Prescott, J.H., 1999. Spatial variation in mean growth rates of rock lobster, *Jasus edwardsii*, in South Australian waters. *Mar. Freshwater Res.* **50**, 333–342.

McGarvey, R., Pennington, M., 2001. Designing and evaluating length-frequency surveys for trap fisheries with application to the southern rock lobster. *Can. J. Fish. Aquat. Sci.* **58**, 254–261.

McKendrick, A.G., 1926. Applications of mathematics to medical problems. *Proc. Edinburgh*

Math. Soc. **44**, 98–130.

Øksendal, B., 1998. Stochastic Differential Equations: An Introduction with Applications. 5th ed, Springer-Verlag, Berlin, 324 pp.

Punt, A.E., Kennedy, R.B., 1997. Population modelling of Tasmanian rock lobster, *Jasus edwardsii*, resources. *Mar. Freshwater Res.* **48**, 967–980.

Punt, A. E., Kennedy, R. B., and Frusher, S. D. (1997). Estimating the size-transition matrix for Tasmanian rock lobster, Jasus edwardsii. *Mar. Freshwater Res.* **48**, 981–92.

Quinn, II, T.J., Deriso, R.B., 1999.Quantitative Fish Dynamics. Oxford University Press, Oxford, 542 pp.

Sainsbury, K. J. (1982). Population dynamics and fishery management of the paua, Haliotis iris II. Dynamics and management as examined using a size class population model. New Zealand Journal of Marine and Freshwater Research 16, 163–73.

SAS Institute, 1988. SAS/STAT User's guide, Release 6.03 Edition. Cary NC, SAS Institute Inc, 1028 pp.

SAS Institute, 1996. SAS/STAT Software: changes and enhancements through Release 6.11. Cary NC, SAS Institute Inc, 1094 pp.

Schnute, J., 1987. A general fishery model for a size-structured fish population. *Can. J. Fish. Aquat. Sci.* **44**, 924–940.

Schnute, J.T., 1991. The importance of noise in fish population models. *Fish. Res.* **11**, 197–223.

Seber, G.A.F., Wild, C.J., 1989. Nonlinear regression. John Wiley & Sons, NY, 768 pp.

Smith, B.D., and Botsford, L.W. 1998. Interpretation of growth, mortality, and recruitment patterns in size-at-age, growth increment, and size frequency data. In Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management. Edited by G.S. Jamieson and A. Campbell. Can. Spec. Pub. Fish. Aquat. Sci. 125: 125-139.

Spiegelhalter, D.J., Thomas, A., and Best, N.G., 2000. WinBUGS Version 1.3 User Manual. Medical Research Council Biostatistics Unit, Institute of Public Health, Cambridge, UK, http://www.mrc-bsu.cam.ac.uk/bugs

Wang, Y.-G., Ellis, N., 2005. Maximum likelihood estimation of mortality and growth with individual variability from multiple length-frequency data. *Fish. Bull.* **103**: 380–391.

Xiao, Y., 1997. Subtleties in, and practical problems with, the use of production models in fish stock assessment. *Fish. Res*. **33**, 17–36.

Xiao, Y., 2000a. A general theory of fish stock assessment models. *Ecol Model.* **128**, Nos. 2 & 3, 165–180.

Xiao, Y., 2000b. An individual-based approach to evaluating experimental designs for estimating rates of fish movement from tag recoveries. *Ecol. Model.* **128**, Nos. 2 & 3, 149–163.

Xiao, Y., 2001. Formulae for calculating the instantaneous rate of natural mortality of animals from its surrogates. *Math. Comp. Model.* **33**, Nos. 6 & 7, 783–792.

Xiao, Y., 2003. Doppler effect in larval biology: theory and applications. *Ecol. Model.* **165**, 1–22.

Xiao, Y., 2005. Catch equations: restoring the missing terms in the nominally generalized Baranov catch equation. *Ecol. Model.* **181(4)**, 535–556.

Xiao, Y., 2006a. Several traps in size-dependent population models published in fisheries journals. *Fish. Res.* **77**, No. 3, 265–270.

Xiao, Y., 2006b. Catch equations: calculating the instantaneous rate of fishing mortality from catch and back. *Ecol. Model.* **193(3&4)**, 225–252.

Xiao, Y., 2006c. The fundamental equations of multi-species virtual population analysis and its variants. *Ecol. Model.* doi:10.1016/j.ecolmodel.2006.10.014).

Xiao, Y., in press. A stochastic model for the duration of a larva with multiple stages applied to the larval development of the dungeness crab *Cancer magister* Dana. *Fish. Res.*

Young, C.M., 2000. Atlas of Marine Invertebrate Larvae. Academic Press, New York, 626 pp.

APPENDIX A MODEL FOR THE NORTHERN ZONE

MODEL

Let $N(g,a,t) \geq 0$, $B(g,a,t) \geq 0$ and $W(g,a,t) \geq 0$, $0 \leq a_0 \leq a < \infty$, $-\infty < t_0 \leq t < \infty$, denote, respectively, the number, biomass and the average body weight of individuals, of lobsters of age a and sex g ($g = f, m$) at time t, with the average age at recruitment a_0 and reference time t_0. The change in $N(g,a,t)$ in a small time interval $[t, t+\Delta t]$ of length Δt is assumed to satisfy the modified first order partial differential equation of Xiao (1997, p. 21–25, 2000b)

$$\frac{\partial N(g,a,t)}{\partial a}\frac{da}{dt} + \frac{\partial N(g,a,t)}{\partial t} = -Z_e(g,a,t)N(g,a,t) \tag{1}$$

where da/dt is the derivative of age a with respect to time t (da/dt=1 if both age a and time t have the same unit, say, year); $Z_e(g,a,t) = F(g,a,t) + M(g,a,t) - \kappa(g,a,t)$ is the total instantaneous rate of mortalities of lobsters of age a and sex g at time t corrected for the spatiotemporal expansion of the fishery; $F(g,a,t) \geq 0$ is the instantaneous rate of fishing mortality of lobsters of age a and sex g at time t; $M(g,a,t) \geq 0$ is the instantaneous rate of natural mortality of lobsters of age a and sex g at time t; $\kappa(g,a,t) \geq 0$ is the specific rate of the spatiotemporal expansion of the fishery for lobsters of age a and sex g at time t. Thus, $\kappa(g,a,t) = \frac{1}{P_e(g,a,t)}\left[\frac{\partial P_e(g,a,t)}{\partial a}\frac{da}{dt} + \frac{\partial P_e(g,a,t)}{\partial t}\right]$, where $P_e(g,a,t)$ is the number of areas fished by a licence. In this formulation, we have implicitly assumed that the spatiotemporal expansion increases the number of fishable lobsters of age a and sex g at time t by a multiplier $\gamma P_e(g,a,t)$, such that $N(g,a,t) = \gamma P_e(g,a,t)N_-(g,a,t)$, where $N_-(g,a,t)$ is the number of fishable lobsters of age a and sex g at time t ignoring the effect of spatial expansion; γ is the proportionality constant (a nuisance parameter).

Eq. (1) describes the dynamics of a closed (to immigration, emigration, and any other processes that change $N(g,a,t)$) population. For useful perspectives on age-dependent models in non-fisheries contexts, see Lotka (1922, 1924), McKendrick (1926), Kermack and McKendrick (1927, 1932), and Hoppensteadt (1975).

To solve Eq. (1), two boundary conditions must be specified. The number of lobsters of age at recruitment a_0, $N(g,a_0,t)$, depends on the number of eggs spawned at time $t-\tau$, and hence those of pueruli and spawning females at an earlier time, and on environmental conditions. In this work, their values are first estimated as separate parameters by use of Eq. (1) as a deterministic model by use of one set of data and then used as priors in a corresponding stochastic model by use of other sources of data. In the latter, the number of recruits is driven by data on the numbers of under-sized lobsters and pueruli (chapter 4). The other boundary condition is the age distribution of a population of lobsters at time t_0, assumed to be of the form

$$N(g,a,t_0)=R_0(g)\exp\left(-\int_{a_0}^{a}Z_e(g,s,t_0)ds\right)$$

where $R_0(g)>0$ is the number of lobsters of age a_0 and sex g at time t_0 and $Z_e(g,s,t_0)$ is specified partly by solving the catch equation for $F(g,s,t_0)$.

The solution of Eq. (1) under both boundary conditions is

$$N(g,a,t)=\begin{cases} N\left(g,a_0,t-\frac{1}{\alpha}(a-a_0)\right)\exp\left(-\int_{t-\frac{1}{\alpha}(a-a_0)}^{t}Z_e(g,a-\alpha(t-s),s)\right)\varepsilon(g,a,t), & a-a_0\le(t-t_0)\\ N\left(g,a-\alpha(t-t_0),t_0\right)\exp\left(-\int_{t_0}^{t}Z_e(g,a-\alpha(t-s),s)\right)\varepsilon(g,a,t), & a-a_0>(t-t_0)\end{cases} \qquad (2)$$

where $\varepsilon(g,a,t)$ follows a log-normal distribution, with an expected value of unity, a variance of 0.05^2 and a coefficient variation of 0.05.

INPUTS

Use of Eqs. (1)–(2) in data analysis requires specification of many quantities. Because age a and time t have the same unit (in years), da/dt=1. In our calculations, we set the age at recruitment of lobsters a_0=3.5 yr (equal to a mean phyllosomal duration of 360.6784 d from spawning to metamorphosis into a puerulus plus a growth period of 2.5142 yr until recruitment) (chapter 3), a maximum age of 35 yr, a projection period of 2 yr, a time span of the fishery of 33 yr from 1970 to 2002, a time of the start of the fishery t_r=1, and a 1:1 sex ratio for eggs ($R(f,a,t)$=1/2, $R(m,a,t)$=1/2).

The carapace length $L(g,a,t)$ of a lobster of age a and sex g at time t is assumed to satisfy the von Bertalanffy growth equation

$$L(g,a,t)=L_{g,\infty}-\left(L_{g,\infty}-L(g,a'_{g,0},t)\right)\exp\left(-K_g\left(a-a'_{g,0}\right)\right)$$

where $L_{f,\infty}$=135.8029±0.4793 mm, K_f=0.3435±0.0069 ·yr^{-1}, $a'_{f,0}$=12/12.0 yr, and $L(f,a'_{f,0},t)$=11.0 mm; $L_{m,\infty}$=198.9020±2.0529 mm, K_m=0.2135±0.0057 ·yr^{-1}, $a'_{m,0}$=12/12.0 yr, and $L(m,a'_{m,0},t)$=11.0 mm. In the stochastic model, $L_{f,\infty} \sim N(135.8029, 0.4793^2)$, $K_f \sim N(0.3435, 0.0069^2)$; $L_{m,\infty} \sim N(198.9020, 2.0529^2)$, $K_m \sim N(0.2135, 0.0057^2)$. This set-up makes it possible to account for the variation in the length-at-age of the lobsters for each sex.

Carapace length (mm) and average body weight (tonnes) relationship is given by

$$W(f,a,t) = 8.4869\times10^{-4} L(f,a,t)^{2.8917} / 1.0\times10^{6}$$

for females, and

$$W(m,a,t) = 5.3142\times10^{-4} L(m,a,t)^{2.9813} / 1.0\times10^{6}$$

for males. The relative gear selectivity as a function of carapace length (mm) is given by

$$S(g,a,t) = \left(1+\exp\left(-\left(L(g,a,t)-\alpha\right)/\beta\right)\right)^{-1}$$

for both sexes, with α=97.0137±1.3762 mm and β=2.3305±0.3663 mm (chapter 2). In the stochastic model, $\alpha \sim N(97.0137, 1.3762^2)$ and $\beta \sim N(2.3305, 0.3663^2)$.

The fecundity of (the number of eggs produced by) an average female lobster of age a at time t $\beta(a,t)$ is given by

$$\beta(a,t) = 0.226 L(f,a,t)^{2.912}$$

and the proportion of sexual maturity of female lobsters at age a at time t $m(a,t)$ by

$$m(a,t) = \max\left(\left(1+\exp\left(\alpha-\beta\, L(f,a,t)\right)\right)^{-1}, 0\right)$$

where parameters α=−11.7373±0.1426 mm and β=0.1085±0.0012 mm for NZ and α=−6.9485±0.0972 mm and β=0.0736±0.0009 mm for SZ. In the stochastic model, $\alpha \sim N(\text{-}11.7373, 0.1426^2)$ and $\beta \sim N(0.1085, 0.0012^2)$ for NZ, and $\alpha \sim N(\text{-}6.9485, 0.0972^2)$ and $\beta \sim N(0.0736, 0.0009^2)$ for SZ.

The catch in the number of lobsters of age a and sex g at time t $C(g,a,t)$ is calculated by partitioning sex and age aggregated catch in biomass at time t by approximating the catch in biomass of lobsters of age a and sex g at time t by

$$C_B(g,a,t) = \frac{F(t)S(g,a,t)B(g,a,t)}{F(t)S(g,a,t)+M(g,a,t)}\left\{1-\exp\left[-\left(F(t)S(g,a,t)+M(g,a,t)\right)\Delta t\right]\right\}.$$

Under this assumption, the sex and age aggregated catch in biomass at time t

$$C_B(t) = \sum_{g,a} C_B(g,a,t) = \sum_{g,a} \frac{F(t)S(g,a,t)B(g,a,t)}{F(t)S(g,a,t)+M(g,a,t)}\left\{1-\exp\left[-\left(F(t)S(g,a,t)+M(g,a,t)\right)\Delta t\right]\right\}$$

where $F(t)S(g,a,t)$ is the instantaneous rate of fishing mortality of lobsters of age a and sex g at time t; $S(g,a,t)$ is the relative gear selectivity as a function of carapace length (mm). Thus, $F(t)$ can be solved for from (known) $C_B(t)$ and other (known) quantities, and hence $C(g,a,t)$ and $C_B(g,a,t)$ can be readily calculated.

The instantaneous rate of natural mortality $M(g,a,t)$ ($\cdot\text{yr}^{-1}$) of lobsters of age a and sex g at time t is given by

$$M(g,a,t) = \begin{cases} 0.1 & a \le 30 \\ 0.1 + \dfrac{20.0-0.1}{35-30}\left(a-30\right) & a > 30 \end{cases}$$

This implies that few lobsters remain after their age reaches 35 yr, for $M(g,35,t)$=19.9 ($\cdot\text{yr}^{-1}$). In the stochastic model, 0.1 ($\cdot\text{yr}^{-1}$) is replaced by $N(0.1, 0.01^2)$.

In our calculations, we also considered spatial expansion of the fishery by regressing the number of areas fished per active licence against time t, so that the relative spatial expansion of the fishery as a function of time t is approximated by

$$P_e(t) = \begin{cases} 1-(1-A_0/A_\infty)\exp\left(-\lambda_e\left(t-t_r\right)\right) & t_r < t \\ 0 & t_0 \le t \le t_r \end{cases}$$

where A_0=22.7594, A_∞=35.7097, and λ_e=0.1110 $\cdot\text{yr}^{-1}$. Such a simple treatment of spatiotemporal expansion is necessary because of time constraints; a sophisticated treatment would be based on diffusion and advection models, which is beyond the scope of this study.

Data on lobster (sex and age aggregated) catch in biomass $C_B(t)$ and relative exploitable biomass $I(t)$ at time t are also required as inputs. $C_B(t)$=0 for $t_0 \le t < t_r$; $C_B(t)$ is equal to the sum of commercial catches for $t_0 \le t_r \le t$. Recreational and illegal catches are not taken into account, because of a lack of information. The relative exploitable biomass $I(t)$ at time t was obtained by analyzing commercial catch and effort data by use of a generalized linear model by considering the effects of time of year, differences in fishers, time of day, fishing areas and fishing effort (SAS Institute, 1988, 1996). This (separate) analysis for a relative index of lobster abundance can, of course, be imbedded in the present work, but it will substantially complicate the calculation.

APPENDIX B MODEL FOR THE SOUTHERN ZONE

MODEL

Let $N(g,a,t) \geq 0$, $B(g,a,t) \geq 0$ and $W(g,a,t) \geq 0$, $0 \leq a_0 \leq a < \infty$, $-\infty < t_0 \leq t < \infty$, denote, respectively, the number, biomass and the average body weight of individuals, of lobsters of age a and sex g ($g = f, m$) at time t, with the average age at recruitment a_0 and reference time t_0. The change in $N(g,a,t)$ in a small time interval $\left[t, t+\Delta t\right]$ of length Δt is assumed to satisfy the modified first order partial differential equation of Xiao (1997, p. 21–25, 2000a)

$$\frac{\partial N(g,a,t)}{\partial a}\frac{da}{dt} + \frac{\partial N(g,a,t)}{\partial t} = -Z_e(g,a,t)N(g,a,t) \tag{1}$$

where da/dt is the derivative of age a with respect to time t (da/dt=1 if both age a and time t have the same unit, say, year); $Z_e(g,a,t) = F(g,a,t) + M(g,a,t) - \kappa(g,a,t)$ is the total instantaneous rate of mortalities of lobsters of age a and sex g at time t corrected for the spatiotemporal expansion of the fishery; $F(g,a,t) \geq 0$ is the instantaneous rate of fishing mortality of lobsters of age a and sex g at time t; $M(g,a,t) \geq 0$ is the instantaneous rate of natural mortality of lobsters of age a and sex g at time t; $\kappa(g,a,t) \geq 0$ is the specific rate of the spatiotemporal expansion of the fishery for lobsters of age a and sex g at time t. Thus, $\kappa(g,a,t) = \frac{1}{P_e(g,a,t)}\left[\frac{\partial P_e(g,a,t)}{\partial a}\frac{da}{dt} + \frac{\partial P_e(g,a,t)}{\partial t}\right]$, where $P_e(g,a,t)$ is the number of areas fished by a licence. In this formulation, we have implicitly assumed that the spatiotemporal expansion increases the number of fishable lobsters of age a and sex g at time t by a multiplier $\gamma P_e(g,a,t)$, such that $N(g,a,t) = \gamma P_e(g,a,t)N_{-}(g,a,t)$, where $N_{-}(g,a,t)$ is the number of fishable lobsters of age a and sex g at time t ignoring the effect of spatial expansion; γ is the proportionality constant (a nuisance parameter).

Eq. (1) describes the dynamics of a closed (to immigration, emigration, and any other processes that change $N(g,a,t)$) population. For useful perspectives on age-dependent models in non-fisheries contexts, readers may wish to consult Lotka (1922, 1924), McKendrick (1926), Kermack and McKendrick (1927, 1932), and Hoppensteadt (1975).

To solve Eq. (1), two boundary conditions must be specified. The number of lobsters of age at recruitment a_0, $N(g,a_0,t)$, depends on the number of eggs spawned at time $t-\tau$, and hence those of pueruli and spawning females at an earlier time, and on environmental conditions. In this work, their values are first estimated as separate parameters by use of Eq. (1) as a deterministic model by use of one set of data and then used as priors in a corresponding stochastic model by use of other sources of data. In the latter, the number of recruits is driven by data on the numbers of under-sized lobsters and pueruli. The other boundary condition is the age distribution of a population of lobsters at time t_0, assumed to be of the form

$$N(g,a,t_0) = R_0(g)\exp\left(-\int_{a_0}^{a} Z_e(g,s,t_0)ds\right)$$

where $R_0(g) > 0$ is the number of lobsters of age a_0 and sex g at time t_0 and $Z_e(g,s,t_0)$ is specified partly by solving the catch equation for $F(g,s,t_0)$.

The solution of Eq. (1) under both boundary conditions is

$$N(g,a,t) = \begin{cases} N\left(g,a_0,t-\dfrac{1}{\alpha}(a-a_0)\right)\exp\left(-\displaystyle\int_{t-\frac{1}{\alpha}(a-a_0)}^{t} Z_e(g,a-\alpha(t-s),s)\right)\varepsilon(g,a,t), & a-a_0 \le (t-t_0) \\ N\left(g,a-\alpha(t-t_0),t_0\right)\exp\left(-\displaystyle\int_{t_0}^{t} Z_e(g,a-\alpha(t-s),s)\right)\varepsilon(g,a,t), & a-a_0 > (t-t_0) \end{cases} \tag{2}$$

where $\varepsilon(g,a,t)$ follows a log-normal distribution, with an expected value of unity, a variance of 0.05^2 and a coefficient variation of 0.05.

INPUTS

Use of Eqs. (1)–(2) in data analysis requires specification of many quantities. Because age a and time t have the same unit (in years), da/dt=1. In our calculations, we set the age at recruitment of lobsters a_0=3.5 yr (equal to a mean phyllosomal duration of 360.6784 d from spawning to metamorphosis into a puerulus plus a growth period of 2.5142 yr until recruitment), a maximum age of 35 yr, a projection period of 2 yr, a time span of the fishery of 33 yr from 1970 to 2002, a time of the start of the fishery t_r=1, and a 1:1 sex ratio for eggs ($R(f,a,t)$=1/2, $R(m,a,t)$=1/2).

The carapace length $L(g,a,t)$ of a lobster of age a and sex g at time t is assumed to satisfy the von Bertalanffy growth equation

$$L(g,a,t) = L_{g,\infty} - \left(L_{g,\infty} - L(g,a'_{g,0},t)\right)\exp\left(-K_g\left(a-a'_{g,0}\right)\right)$$

where $L_{f,\infty}$=139.8047±0.5961 mm, K_f=0.2055±0.0040 ·yr^{-1}, $a'_{f,0}$=12/12.0 yr, and $L(f,a'_{f,0},t)$=11.0 mm; $L_{m,\infty}$=214.8277±3.1223 mm, K_m=0.1466±0.0047 ·yr^{-1}, $a'_{m,0}$=12/12.0 yr, and $L(m,a'_{m,0},t)$=11.0 mm. In the stochastic model, $L_{f,\infty} \sim N(139.8047, 0.5961^2)$, $K_f \sim N(0.2055, 0.0040^2)$; $L_{m,\infty} \sim N(214.8277, 3.1223^2)$, $K_m \sim N(0.1466, 0.0047^2)$. This set-up makes it possible to account for the variation in the length-at-age of the lobsters for each sex.

Carapace length (mm) and average body weight (tonnes) relationship is given by

$$W(f,a,t) = 8.4869 \times 10^{-4} L(f,a,t)^{2.8917} / 1.0 \times 10^6$$

for females, and

$$W(m,a,t) = 5.3142 \times 10^{-4} L(m,a,t)^{2.9813} / 1.0 \times 10^6$$

for males. The relative gear selectivity as a function of carapace length (mm) is given by

$$S(g,a,t) = \left(1 + \exp\left(-\left(L(g,a,t) - \alpha\right)/\beta\right)\right)^{-1}$$

for both sexes, with α=97.0137±1.3762 mm and β=2.3305±0.3663 mm. In the stochastic model, $\alpha \sim N(97.0137, 1.3762^2)$ and $\beta \sim N(2.3305, 0.3663^2)$.

The fecundity of (the number of eggs produced by) an average female lobster of age a at time t $\beta(a,t)$ is given by

$$\beta(a,t) = 0.226 L(f,a,t)^{2.912}$$

and the proportion of sexual maturity of female lobsters at age a at time t $m(a,t)$ by

$$m(a,t) = \max\left(\left(1 + \exp\left(\alpha - \beta\, L(f,a,t)\right)\right)^{-1}, 0\right)$$

where parameters α and β are estimated for different areas. The mean value of $m(a,t)$ among all areas was used in the calculations.

The catch in the number of lobsters of age a and sex g at time t $C(g,a,t)$ is calculated by partitioning sex and age aggregated catch in biomass at time t by approximating the catch in biomass of lobsters of age a and sex g at time t by

$$C_B(g,a,t) = \frac{F(t)S(g,a,t)B(g,a,t)}{F(t)S(g,a,t) + M(g,a,t)} \left(1 - \exp\left(-\left(F(t)S(g,a,t) + M(g,a,t)\right)\Delta t\right)\right).$$

Under this assumption, the sex and age aggregated catch in biomass at time t

$$C_B(t) = \sum_{g,a} C_B(g,a,t) = \sum_{g,a} \frac{F(t)S(g,a,t)B(g,a,t)}{F(t)S(g,a,t)+M(g,a,t)} \left(1-\exp\left[-\left(F(t)S(g,a,t)+M(g,a,t)\right)\Delta t\right]\right)$$

where $F(t)S(g,a,t)$ is the instantaneous rate of fishing mortality of lobsters of age a and sex g at time t; $S(g,a,t)$ is the relative gear selectivity as a function of carapace length (mm). Thus, $F(t)$ can be solved for from (known) $C_B(t)$ and other (known) quantities, and hence $C(g,a,t)$ and $C_B(g,a,t)$ can be readily calculated.

The instantaneous rate of natural mortality $M(g,a,t)$ $(\cdot\mathrm{yr}^{-1})$ of lobsters of age a and sex g at time t is given by

$$M(g,a,t) = \begin{cases} 0.1 & a \le 30 \\ 0.1 + \dfrac{20.0-0.1}{35-30}\left(a-30\right) & a > 30 \end{cases}$$

This implies that few lobsters remain after their age reaches 35 yr, for $M(g,35,t)$=19.9 $(\cdot\mathrm{yr}^{-1})$.

In our calculations, we could also have considered spatial expansion of the fishery by regressing the number of areas fished per active licence against time t, so that the relative spatial expansion of the fishery as a function of time t is approximated by

$$P_e(t) = \begin{cases} 1-(1-A_0/A_\infty)\exp\left(-\lambda_e\left(t-t_r\right)\right) & t_r < t \\ 0 & t_0 \le t \le t_r \end{cases}$$

where A_0, A_∞ and λ_e are parameters to be estimated or specified. Such a simple treatment of spatiotemporal expansion is necessary because of time constraints; a sophisticated treatment would be based on diffusion and advection models, which is beyond the scope of this study. Since the fishery has expanded spatially, we set parameters A_0=0, A_∞=1, and λ_e=0 $\cdot\mathrm{yr}^{-1}$.

Data on lobster (sex and age aggregated) catch in biomass $C_B(t)$ and relative exploitable biomass $I(t)$ at time t are also required as inputs. $C_B(t)$=0 for $t_0 \le t < t_r$; $C_B(t)$ is equal to the sum of commercial catches for $t_0 \le t_r \le t$. Recreational and illegal catches are not taken into account, because of a lack of information. The relative exploitable biomass $I(t)$ at time t was obtained by analyzing commercial catch and effort data by use of a generalized linear model by considering the effects of time of year, differences in fishers, time of day, fishing areas and fishing effort (SAS Institute, 1988, 1996). This (separate) analysis for a relative index of lobster abundance can, of course, be imbedded in the present work, but it will substantially complicate the calculation.

APPENDIX C — INTELLECTUAL PROPERTY

No patentable inventions or processes were developed as part of this project. The work presented in this report remains the intellectual property of the authors, and they should be acknowledged when citing this work.

APPENDIX D — STAFF

Staff directly involved in this project were
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