Predicting the impacts of shifting recreational fishing effort towards inshore species

Fisher, E.A., Hesp, S.A., Hall, N.G. and Sulin, E.H.







Government of Western Australia Department of Fisheries

Project No. 2010/001

Title: Predicting the impacts of shifting recreational fishing effort towards inshore species

Authors: Fisher, E.A., Hesp, S.A., Hall, N.G. and Sulin, E.H.

FRDC Project No. 2010/001

© Copyright Fisheries Research and Development Corporation and Murdoch University, 2014.

This work is copyright. Except as permitted under the Copyright Act 1968 (Cth), no part of this publication may be reproduced by any process, electronic or otherwise, without the specific written permission of the copyright owners. Information may not be stored electronically in any form whatsoever without such permission.

Disclaimer: The authors do not warrant that the information in this document is free from errors or omissions. The authors do not accept any form of liability, be it contractual, tortious, or otherwise, for the contents of this document or for any consequences arising from its use or any reliance placed upon it. The information, opinions and advice contained in this document may not relate, or be relevant, to a reader's particular circumstances. Opinions expressed by the authors are the individual opinions expressed by those persons and are not necessarily those of the publisher, research provider or the FRDC.

The Fisheries Research and Development Corporation plans, invests in and manages fisheries research and development throughout Australia. It is a statutory authority within the portfolio of the federal Minister for Agriculture, Fisheries and Forestry, jointly funded by the Australian Government and the fishing industry.

ISBN 978-1-921877-05-6

TABLE OF CONTENTS

1. NON-TECHNICAL SUMMARY	4
2. ACKNOWLEDGEMENTS	8
3. BACKGROUND	9
Shifting recreational fishing effort	9
Focus on Silver Trevally and King George Whiting	9
Assessing stocks of fish species that undertake size-related movements	
Proposed new method for estimating rates of mortality and movement	12
Development of a guide to temperate WA fish species	
Variations to project	14
4. NEED	15
5. OBJECTIVES	16
6 MATERIALS AND METHODS	17
Cich sampling	17
Fish sampling	1/ 10
Evoloration of age and length data	10
Exploration of individual growth of fish	21 21
Description of offshore movement model	21
Fitting the offshore movement model	
Further analyses for <i>Pseudocaranx aeoraianus</i>	
Per-recruit analysis	
Decision table analysis	
7. RESULTS	36
Age and length data for Pseudocaranx georgianus	
Growth of Pseudocaranx georgianus accounting for individual variation	
Explorations of the robustness of the offshore movement model using simulated data for <i>Pseudoc</i> aeorgianus.	aranx: 39
Fits of offshore movement model to real data for <i>Pseudocaranx georgianus</i>	
Estimates of the rates of decline of fully-recruited <i>Pseudocaranx georgianus</i> from inshore waters 2001-2004 vs. 2009-2012	in 44
Per-recruit and decision table analyses (for exploring management implications, for	
Ago and longth data for Silloginodes nunctota	44 50
Age and length data for sindyinodes punctata accounting for individual variability	50 50
Explorations of the robustness of the offshore movement model using simulated data for <i>Sillaging</i>	odes
punctata	
Pris of offshole movement movel to red udid for <i>Sindymouts punctula</i>	
Sillaginodes punctata, of model uncertainty)	60
8. DISCUSSION	65
Size-dependent offshore movements of fish	
Patterns of individual growth of fish	

Robustness of the offshore movement model Value of per-recruit and decision table analyses for exploring implications of size-do movements for management	ependent, offshore 71
9. BENEFITS AND ADOPTION	73
10. FURTHER DEVELOPMENT	75
11. PLANNED OUTCOMES	77
12. CONCLUSION	79
REFERENCES	80
APPENDIX 1: INTELLECTUAL PROPERTY	86
APPENDIX 2: STAFF	86
APPENDIX 3: JITTER TESTS	86

1. NON-TECHNICAL SUMMARY

2010/001: Predicting the impacts of shifting recreational fishing effort towards inshore species

Principal Investigator: Address: Dr S. Alex Hesp Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Government of Western Australia, P.O. Box 20, North Beach, Western Australia 6920 (previously, Murdoch University) Telephone: 08 9203 0145 Fax: 08 9203 0199

Objectives:

- (1) To develop a method for estimating mortality in species which exhibit sizerelated movements.
- (2) To predict impacts of shifting effort towards certain temperate, inshore WA fish species.
- (3) To produce a guide to key temperate WA fishes, for all industry stakeholders.

OUTCOMES ACHIEVED TO DATE

The project outputs have led to the following outcomes:

- 1. A model has been developed enabling reliable estimation of mortality of fish species that undertake size-related, unidirectional, offshore movements from age and length data. This new modelling approach is likely to be applicable to stocks of a number of fish species with this life history attribute, for which current stock status information may be very limited due to the difficulty of obtaining a representative sample for an overall stock.
- 2. Current age and length composition data and estimates of key stock assessment parameters, including selectivity, movement and fishing mortality, are now available for Silver Trevally and King George Whiting in coastal waters near Perth in Western Australia. Managers are aware that the study results have provided preliminary evidence that Silver Trevally and King George Whiting in waters near Perth are not currently experiencing overfishing.
- 3. This project has provided managers with information about the relative extents to which the stocks of Silver Trevally and King George Whiting in coastal waters near Perth might be expected to be impacted if fishing pressure were to increase by specified amounts. Managers are thus aware that King George Whiting stocks are likely to be more vulnerable than Silver Trevally to increases in fishing pressure in inshore waters.
- 4. Detailed summaries of the biology, stock assessment and management for 30 of Western Australia's most important and/or well-known temperate fish species are now accessible to fishery stakeholders in the form of a species guide (published separately as Fisheries Research Report No. 242 by the Department of Fisheries, Western Australia). The guide provides a comprehensive "go to" source of information for anyone who wishes to find key facts and/or literature relating to these species.

Between 2007 and 2010, substantial changes to management were introduced to provide increased protection for a suite of demersal fish species in coastal waters of southwestern Australia. There was a concern, however, that, as a consequence of those management measures, recreational fishing effort for those species may become redirected towards some other species such as Silver Trevally and King George Whiting, thereby placing them at increased risk from overfishing. Furthermore, information on the levels of fishing mortality experienced by these two species was very limited and researchers had also recognised that the types of assessment approaches available for estimating fishing mortality from size and age composition data were not suitable for these species.

As with several other fish species, Silver Trevally and King George Whiting undertake a pronounced, unidirectional offshore movement during life. In coastal waters near Perth, Silver Trevally caught around reefs in "inshore" waters at depths of up to ~ 60 m deep are therefore typically smaller and younger than those caught in deeper waters. In the same region, King George Whiting first settle as very small juveniles in shallow (less than 1.5 m deep) nearshore estuarine or coastal waters and then, as they grow larger, move to deeper waters (6-15 m deep) in estuaries, or to sand/seagrass habitats in coastal waters. Once King George Whiting approach sexual maturity, they then

move to coastal reefs. The offshore movements undertaken by these species make it virtually impossible to obtain representative age and length data for an overall population of these species, as required by traditional stock assessment approaches such as catch curve analysis.

Estimating fishing mortality rates for fish species that exhibit large movements from size and age composition data (or from tagging data) is inherently difficult. This study has developed a novel modelling approach for estimating movement and mortality rates for such species from size and age composition data. The approach relies on the assumptions that 1) offshore movement is related more to size than to age, whereas 2) fishing mortality (for individuals that are large enough to be fully vulnerable to being caught by the fishing gear), is largely age dependent. The finding in this study that, for a given age, the individuals of each species are typically larger in offshore than inshore waters provides strong evidence to support the former assumption and the latter assumption is one that is routinely made in stock assessments.

The model requires size and age composition data for fish in each habitat, an estimate of natural mortality and parameters describing the pattern of growth of the species. In the latter case, it is necessary that the variation in growth patterns among individual fish is accounted for, as was done in this study using a random effects model similar to that described by Pilling *et al.* (2002). This requirement reflects the fact that larger individuals of a given age in the inshore habitat are more likely to move offshore than are smaller individuals.

Prior to its application to real data for Silver Trevally and King George Whiting, the reliability of the modeling approach was tested by fitting the model to simulated (computer-generated) data that were consistent with the assumptions of the model and certain values for each of the model parameters. This testing demonstrated that the model was reliable in that, on average, it was able to "recover" the same values of the parameters specified to generate those data. In other words, the model would be expected to be able to find the true values of the parameters when being fitted to real data if the various assumptions made by the model are true for the species. "Jitter" analyses, which involve running the model multiple times using different initial guesses of the true values of the parameters, always resulted in the same results, thereby further demonstrating the reliability and "robustness" of the model. In order to achieve this level of robustness for King George Whiting, it was necessary, however, to use two model fitting algorithms in tandem, a technique which substantially increased the time taken to obtain a single set of results.

The simulation study results also showed that estimates of fishing mortality in inshore waters are generally less precise than those for the fish in offshore waters, a result repeated when the model was next fitted to real data. Further explorations involving the use of simulated data sets highlighted the fact that inshore fishing mortality estimates are least precise when the size and age ranges over which fish remain in inshore waters are small. This reflects the fact that, if fish remain in the inshore region only briefly, the information content within the size and age sample data, for estimating rates of mortality and movement, is small.

Sampling during this study aimed to collect representative samples of the individuals of species in each of the habitats occupied by the two species. Most fish were obtained from catches taken by recreational fishers, but some (mainly small individuals) were also collected by researchers to provide a description of the growth of the two species as required by the model. Although, overall, sampling for King George Whiting was successful, the number of Silver Trevally collected from offshore waters was very low and insufficient to allow the type of modelling proposed for this species in this study. Thus, another data set for this species, collected during FRDC project 2002/004, was used to test the applicability of the model for Silver Trevally. The low number of Silver Trevally in offshore waters in recent years is apparently due to markedly reduced targeting of these fish by recreational anglers and charter boat operators.

For King George Whiting, fitting the model to real data proved more difficult than for Silver Trevally. "Realistic" results for King George Whiting could thus only be obtained if the inshore age composition data, which covered only a very narrow age range but were highly influential on the analyses, were excluded from the objective function when fitting the model.

When fitting the model to real data for each species, it was necessary to impose additional assumptions regarding the size ranges over which fish move offshore. For Silver Trevally, it was assumed that before fish typically move offshore, they become fully vulnerable to being caught by the fishing gear. For King George Whiting, it was assumed that fish move offshore over the range of lengths for which the frequencies of fish in samples from offshore waters were increasing or had just peaked. Although these assumptions appeared justifiable, the fact that small modifications to these assumptions influenced the resultant model estimates for fishing mortality in inshore waters demonstrated that this aspect of the model fitting process was highly uncertain.

Recognising that the estimates of fishing mortality for inshore waters are uncertain, the results indicated that, at the time of data collection, fishing pressure on Silver Trevally and King George Whiting near Perth was low in offshore waters and moderate in inshore waters. Comparisons of age compositions for Silver Trevally in inshore waters determined during this study (2009-2012) and previously (2002-2004) did not provide evidence that fishing pressure on this species in that region has increased markedly during recent years.

A per-recruit analysis, modified to account for size-related, offshore movements of fish, was used to explore the relative impacts of different levels of change in fishing pressure on the reproductive potential (spawning potential ratio) of the stocks of two species in coastal waters near Perth. The per-recruit analyses indicated that 1) neither species in this region is currently overfished and 2) any future increase in fishing mortality in inshore waters is likely to impact King George Whiting more than Silver Trevally, reflecting the fact that the former species does not mature until it moves offshore. The likely consequences of alternative management actions, taking into account a range of modelling uncertainties, were explored using "a decision table approach". The results of this analysis indicate that the stock of Silver Trevally is likely to be robust to moderate (< 40%) increases in fishing mortality in the inshore region, whereas a similar increase for King George Whiting would be likely to result in the spawning potential ratio falling to about 30% (which is often considered as a threshold or limit that should not be exceeded).

KEYWORDS: Silver Trevally, King George Whiting, size-related movement, fishing mortality, uncertainty, model assumptions

2. ACKNOWLEDGEMENTS

We are very thankful to Kim Smith, Joshua Brown and Chris Dowling (Department of Fisheries, DoF) for helpful discussions and incorporating King George Whiting as a species within the Department's "Research Angler" and "Send Us Your Skeletons" sampling programs, which greatly enhanced data collection for this species. We thank Brett Molony and Brent Wise (DoF) for their valuable feedback throughout the project and to Peter Stephenson, Tim Nicholson and Martin Holtz (DoF) for helpful comments on a draft of this report.

We thank Peter Coulson at Murdoch University for ageing the Silver Trevally samples collected for this project and Ben French, Lauren Veale and Michael Taylor for their help with sampling. Thanks to Dan French for providing us the data he collected for Silver Trevally in 2001-2004 when at Murdoch University (FRDC project 2002/004).

We are grateful to the many recreational and commercial fishers who supplied us with samples of fish, without which this project would not have been possible. A special thanks to the members of the Marmion Angling and Aquatic Club, Hillarys Yacht Club, Ocean Reef Sea Sports Club, Melville Amateur Angling Club and Mandurah Offshore Fishing and Sailing Club for providing us with fish frames from weigh-ins on their fishing competition days. Thanks also to Saltwater Charters and Mills Charters for donating frames of Silver Trevally.

We thank all of the fisheries researchers and managers who attended a workshop at Murdoch University in June 2011 to provide feedback on the content of the fish species guide developed as part of this project funded by FRDC (published as part of FRDC project 2010/001, by the Department of Fisheries, Western Australia as Fisheries Research Report No. 242,). We are also very grateful to the researchers and managers who reviewed the summary documents on the 30 fish species covered by that guide.

We wish to express our sincere gratitude to the FRDC for providing the funding necessary to be able to undertake this project. We further thank Carolyn Stewardson (FRDC) for her kind administrative support/advice throughout the project. Thanks also to Murdoch University for providing Emily Fisher with a Murdoch International Postgraduate Scholarship for her PhD studies which were focused, in part, on this project.

3. BACKGROUND

Shifting recreational fishing effort

This study was initiated by Recfishwest in response to concern that changes to the management of demersal finfish stocks in waters off south-western Australia were likely to result in a shift in targeting by recreational boat-based fishers from several iconic demersal fish species, including the West Australian Dhufish (Glaucosoma hebraicum) and Snapper (Chrysophrys auratus), to inshore species such as Silver Trevally (*Pseudocaranx georgianus*, formerly considered as *P. dentex*) and King George Whiting (Sillaginodes punctata). On advice that fishing mortality for demersal species in the West Coast Bioregion needed to be reduced by at least 50%, a two-month seasonal closure of the recreational fishery (15 October - 15 December) was introduced in 2009, together with a range of other recreational management measures. These included changes to bag and boat limits and the requirement, when fishing for demersal species, to carry a release weight for returning fish back to the seabed as guickly as possible following capture to help minimise barotrauma-related injuries (Department of Fisheries, 2012). In addition to the introduction of a fishing licence for boat-based recreational fishers in March 2010, these changes complemented the full closure of the commercial fishery for several demersal fish species in the Perth Metropolitan zone (Lancelin to Mandurah) in November 2007. There was concern, however, that several other fish species which were already abundant in recreational catches, might be placed under increased exploitation pressure as a consequence of fishers re-directing their fishing effort towards those species in response to the management changes.

Discussions among fisheries scientists from the Department of Fisheries, WA, and Murdoch University, aimed at identifying research directions to address the needs for assessing the status of several recreationally important coastal and estuarine fish species, identified *P. georgianus* and *S. punctata* as two of the key recreational fish species for which research was needed. Other key species included Australian Herring (*Arripis georgianus*), Tailor (*Pomatomus saltatrix*) and other whiting (*Sillago*) species, the majority of which are targeted by shore-based fishers in nearshore coastal waters. Importantly, the group noted that little information was available on the stock status of any of these fish species. Furthermore, as these species were abundant in catches, it was possible that these fish species might already be heavily fished. To allow the potential impact of a shift in fishing effort towards inshore fish species to be assessed, information on the status of the stocks of each of these species in south-western Australia was thus urgently needed.

Focus on Silver Trevally and King George Whiting

In response to the above-mentioned discussions, the Department of Fisheries, WA, began monitoring of the stocks of several key fish species in south-western Australia at about the same time as this FRDC project started. These species included *A. georgianus*, *P. saltatrix* and *Sillago* species (supported by a research grant funded by NRM). That research program does not, however, extend to

P. georgianus and *S. punctata*. The two latter species are among the most commonly targeted species by recreational fishers on the lower west coast of Australia (Henry and Lyle, 2003; Department of Fisheries, 2011a). For example, between Kalbarri and Augusta, *Pseudocaranx* spp. (including Sand Trevally *P. wrightil*) and *S. punctata* ranked fourth and fifth in terms of biomass (34 and 19 tonnes, respectively) of the estimated catches taken by recreational boat-based fishers in estuaries and coastal waters (< 20 m deep) in 2005/2006 (Sumner *et al.*, 2008).

Biological studies of *P. georgianus* and *S. punctata* in Western Australia have indicated that these species, which attain maximum ages 18 and 14 years, respectively, undertake pronounced offshore movements associated with an increase in the age and size of fish (Hyndes et al., 1998; Farmer et al., 2005). As with some other species (e.g. Hesp et al., 2004; Russell and McDougall, 2005; Platell et al., 2007), P. georgianus occupy estuaries and relatively shallow (< 60 m deep) coastal waters as juveniles or young adults and apparently move into deeper waters (60-120 m deep) as they become older and larger (Farmer et al., 2005). Similar patterns in the distributions of fish are also evident in the age and length data for the closely related P. dentex in the central North Atlantic (Afonso et al., 2008) and in Japan (Masuda and Tsukamoto, 1999). In Western Australia, P. georgianus are known to mature at lengths of ~ 300 mm and are often targeted at around and above this size by recreational line-fishers mainly in "inshore" waters < 60 m deep (Farmer et al., 2005). The larger P. georgianus in "offshore" waters have been targeted, at least in the past, mainly by charter boat operators, particularly over artificial reefs (sunken barges) at ~ 110 m deep waters off Rottnest Island, where they have been found to aggregate between September and December (Farmer et al., 2005).

The patterns of offshore movements of S. punctata are better understood and documented than those of P. georgianus. Small 0+ juveniles of S. punctata occupy shallow (< 1.5 m) waters over sand or sand/seagrass, in either estuaries or in sheltered, coastal embayments, *i.e.* in "nearshore" waters (Jones et al., 1990; Fowler and Short, 1996; Hyndes et al., 1998; Fowler et al., 2002). As they become larger and older, the juveniles move offshore into deeper (2-15 m) "inshore" waters over sandy habitats in estuaries or sand/seagrass habitats in coastal waters (Hyndes et al., 1998). Finally, as individuals approach maturity at a total body length of about 400 mm (Hyndes et al., 1998; Jenkins et al., 1998; Fowler et al., 1999; Fowler et al., 2000), they move onto reefs, and generally to deeper (15-60 m), "offshore" waters (Hyndes et al., 1998; Fowler et al., 2000; Fowler et al., 2002). The minimum legal length for capture and retention of S. punctata is 280 mm and thus well below the length at which individuals of this species typically mature. Juveniles of this species are thus caught by fishers in both estuaries and shallow (6-15 m) coastal waters over seagrass/sand habitats, and the adults are also caught, over coastal reefs.

To maintain consistency between this report and previous scientific literature on *P. georgianus* and *S. punctata* in Western Australia, in this report, the meaning of the terms "inshore" and "offshore" are different for these species. Note also that the above terms, and the term "nearshore", differ from the descriptions now routinely employed by the Department of Fisheries, Western Australia, to describe

"suites" of fish species within different bioregions (Department of Fisheries, 2011b).

Assessing stocks of fish species that undertake size-related movements

Due to the lack of an extended time series of catch and effort data for many recreational and small-scale commercial fisheries, assessments of fish stocks targeted by these fishing sectors commonly focus on relatively simple mortality-based methods, such as catch curve and per-recruit analyses, which have relatively-limited data requirements (Dowling *et al.*, 2008; Coulson *et al.*, 2009; Wayte and Klaer, 2010). These methods rely on "basic" information about the biological characteristics of the targeted fish species, and age and/or length composition data from fishery-dependent or fishery-independent sampling (*e.g.* Wise *et al.*, 2007; Wayte and Klaer, 2010). Although catch curve analyses continue to be used extensively in fisheries assessments, and particularly for data-limited fisheries (*e.g.* Grandcourt *et al.*, 2008; Smith *et al.*, 2008; Griffiths, 2010), these methods are also frequently criticised because of their strong assumptions (Deriso *et al.*, 1985; Hilborn and Walters, 1992). Consequently, the use of traditional catch curve methods is likely to be inappropriate if their key assumptions are not satisfied.

Most stock assessment methods, including conventional catch curve analysis, rely on the simplifying assumption that fish stocks constitute homogenous collections of individuals that are evenly distributed across the area of the fishery and have equal probabilities of being caught by fishers (Hilborn and Walters, 1992). In reality, however, this is rarely the case. Fish species such as P. georgianus and S. punctata, which undertake pronounced offshore movements, present a challenge to stock assessment scientists, particularly if those movements are sizedependent. This is largely related to the fact that differences in sampling methods, catchability and in the abundances of fish among the different regions can all impact on the randomness of sample data (Morales-Nin and Ralston, 1990; Walters, 2003; Hesp et al., 2004). Thus, depending on the extent to which fish sample data used in assessment models fail to constitute a random sample from the overall fish population, measures of stock status derived using these models may be heavily biased (McGarvey et al., 2010). This, in turn, can lead to highly uncertain or incorrect management advice (Hilborn and Walters, 1992; Welch et al., 2010).

As traditional sampling methods are likely to be deficient for providing the necessary representative age composition samples to estimate fishing mortality for *P. georgianus* and *S. punctata* for traditional catch curve analysis, clearly, an alternative assessment approach was needed. Although, for a number of larger-scale commercial fisheries, spatially-explicit assessment models are now becoming increasingly applied to deal with non-random spatial distributions of fish (*e.g.* Hampton and Fournier, 2001; Gardner *et al.*, 2003; Aires-da-Silva *et al.*, 2009), these types of models typically employ data derived from tagging studies (Punt *et al.*, 2000), which are expensive and time-consuming to collect. Following discussions among scientists at the Department of Fisheries, WA, Murdoch University and FRDC, it became clear that an extensive, large-scale tagging study

was not a viable option for these species. There was, however, considerable support for the development of a modelling approach that could estimate the rates of offshore movements and mortality through employing age and length data for *P. georgianus* and *S. punctata*. It was also agreed that it was important to understand the extent to which the stocks of these species might be at increased risk if recreational fishing effort were to be re-directed towards these species, following the management changes introduced to protect demersal fish species.

Proposed new method for estimating rates of mortality and movement

To estimate the overall mortality of the stock of a fish species which exhibits a pronounced, size-related offshore movement, it first needs to be recognised that fishing mortality in the inshore and offshore habitats may differ markedly (Chen *et al.*, 1998). This may occur, for example, if catchability is much greater in one habitat than the other. Furthermore, as discussed above, even if researchers have made every effort to obtain good samples from each of the habitats occupied by the individuals of such species, the overall sample may not adequately represent the relative abundances of fish of different sizes and ages in the overall population (*e.g.* Hesp *et al.*, 2004). As demonstrated in this project, however, it is possible to estimate the levels of fishing mortality in each habitat if the sample data adequately represent the abundances of fish (from the same stock) of different sizes and ages *within* each habitat.

A key feature of the age and length composition data for fish species which undertake a pronounced offshore movement is that the descending right-hand limb of the age and length frequency data for fish in the inshore region reflects not only the loss of fish through fishing and natural mortality, but also that resulting from the movement of fish from the inshore to offshore region. In this regard, the effects of these two processes on the inshore age composition are very similar and thus very difficult to "disentangle" (see also McGarvey *et al.*, 2010). The offshore data will subsequently reflect an increase in abundance with age and length (left-hand limb) as fish move to join the proportion of the stock that inhabit these deeper waters, and then a decline in abundance with age and length (righthand limb), reflecting the mortality of fish in offshore waters (*i.e.* the terminal habitat).

The method developed in this study for estimating mortality and movement requires the assumption that, among the ages and sizes over which the species is exploited, mortality is related solely to age, whereas movement is more strongly associated with size. The method is applicable to stocks for which it can be demonstrated that their individuals undertake a pronounced unidirectional, size-related movement between habitats or areas, and for which age and length composition data are available that are representative of those habitats or areas in which they are targeted by fishers. The study then aimed to apply the new modelling approach to produce estimates of fishing mortality for the inshore and offshore components of a stock of each species. As neither *P. georgianus* nor *S. punctata* had been intensively sampled for about a decade (*i.e.* since FRDC projects 2002/004 and 93/082, respectively), age and length data were collected for both species during this study.

Earlier attempts during this study to develop the model for estimating mortality in fish species that exhibit offshore, size-related movements, as described in the original FRDC application, highlighted issues with the model fitting process and reliability of results. The model was insensitive to the mortality parameters, and some of the parameter estimates produced by the model were shown through simulation to be biased. Various attempts were made to overcome these problems, which included completely re-constructing the model several times, with various simplifying assumptions and the use of alternative approaches for fitting the model. For example, several optimisation algorithms (other than Solver in Excel) were trialled, including the Nelder and Mead (1965) simplex algorithm, particle swarm optimisation and a simulated annealing algorithm, combined with the use of a phased approach to fitting the model. Unfortunately, none of these processes could be shown to be successful in producing reliable results.

In a final attempt to improve the robustness of the method, the model was restructured to account for variability in growth among individual fish, noting that an understanding of individual variability in the growth of fish allows for more realistic, individual-based simulations of fish populations (Martínez-Garmendia, 1998; Challier et al., 2006). Thus, rather than estimating the average growth of fish in the population, as originally proposed, a random effects model similar to that of Pilling et al. (2002) was fitted to back-calculated, length-at-age data to provide a description of growth that accounts for variability among individuals. The resultant growth parameters also provided information on the extent of correlation between the asymptotic length and growth coefficient parameters of the fitted von Bertalanffy growth model (see results for more details). Employing the parameters estimated by this random effects model for describing growth, the re-structured model could be shown through simulation testing to produce far more robust estimates of mortality (and selectivity and movement parameters) than any previous version. The model was, however, still difficult and time consuming to fit. In some cases, the use of two optimisation algorithms (Excel's Solver and a VBA implementation of the Nelder-Mead simplex algorithm) interchangeably was necessary to obtain a robust solution. Using the new version of the model, it typically took about 10 hours for it to converge to a solution when fitting a single model. The on-going issues regarding the modelling component of the study had implications for achieving certain objectives related to the original milestones listed for this project (see below section on "Variations to project" for further details).

Development of a guide to temperate WA fish species

While preparing the project application, discussions were held between Murdoch University and the Department of Fisheries, WA, regarding the development of a guide (book) to summarise current understanding of the biology and known stock status of important and/or well-known temperate recreational fish species in southwestern Australia. It was agreed that such a guide would be very valuable and thus the development of this species guide was included as part of the original application to FRDC. This guide, entitled "Biology, stock status and management summaries for selected fish species in south-western Australia" has been published separately by the Department of Fisheries, WA, as Fisheries Research Report No. 242.

Variations to project

For the original project application, it was proposed that the offshore movement model developed during the study would be implemented into the management strategy evaluation (MSE) framework produced in a previous FRDC project (FRDC 2008/006), which was developed for relatively data poor fisheries employing fishing mortality-based assessments. Such implementation would allow, through using MSE simulations, an exploration of the likely effectiveness of using different sets of management controls under alternative scenarios of future fishing pressure.

As described above, during the early stages of developing and testing the model for estimating mortality in species that exhibit offshore size-related movements, it became clear that the model was more difficult to fit than envisaged, and the fitting process was very time consuming. It was thus determined that it was not feasible to use the model within the MSE testing framework developed in FRDC 2008/006 and run large numbers of simulations, as such an approach was too computationally intensive. Moreover, it was considered important that most focus be placed on developing strategies for improving the robustness of the model, combined with approaches for assessing the implications, for management, of uncertainty in model parameters.

Following meetings between the project investigators and representatives of the Department of Fisheries, WA, including Dr Brett Molony (Supervising Scientist, Finfish) and Lindsay Joll (Director of Aquatic Mangement), it was considered that per-recruit analyses which account for the offshore movement of fish could provide a more appropriate and much less time-consuming approach for "predicting" the effects of different levels of fishing mortality on the inshore and offshore components of the stocks of *P. georgianus* and *S. punctata*. Coupled with the use of decision table analysis (*e.g.* Hilborn and Walters, 1992), this approach would enable the likely consequences of alternative management changes, for the states of the two species, to be determined under alternative scenarios of mortality levels. The decision table approach would also be able to account for uncertainty in model parameters, such as may occur due to confounding between the parameters for movement and mortality, for example.

The proposed variations to the modelling component of the project received strong support from scientists and managers at the Department of Fisheries, WA, and were formally submitted to the FRDC as part of the fourth milestone report for this project (30 November 2011) and subsequently approved. The variations to the project still enabled the project objectives, as outlined in the original application, to be achieved.

4. NEED

Prior to this study, representatives of the Department of Fisheries, WA, and Recfishwest, in particular, expressed concern that exploitation of several marine fishes near Perth, including Silver Trevally (Pseudocaranx georgianus) and King George Whiting (Sillaginodes punctata) may be expected to increase substantially. This was because new fishing regulations introduced to protect iconic demersal fish species, such as West Australian Dhufish (Glaucosoma hebraicum) and Snapper (Chrysophrys auratus), were expected to result in at least some fishing effort being re-directed towards other species, including P. georgianus and S. punctata. At the time, no reliable information was available on the stock status of these two species, which may already have been over-exploited. Furthermore, the available fishing mortality-based assessment methods were inadequate for P. georgianus and S. punctata because size-related offshore movements of the individuals of these species, combined with their different catchabilities in inshore and offshore habitats, make it virtually impossible to obtain a representative age composition sample for an overall stock of these species. This problem can be addressed through developing a new approach that accounts for size-related movements between habitats. The new approach is also likely to be applicable to other recreational and/or commercial species, e.g. Estuary Cod (Epinephelus coioides) and Mangrove Jack (Lutianus argentimaculatus), which share this life history characteristic.

The biological information published in reports and papers on commercial and recreational fish species in south-western Australia is often inaccessible to fishers and researchers may not be aware of all available information for those species. A book explaining key concepts in fisheries science and outlining key information for important temperate Western Australian fish species would be invaluable for engaging fishers and a valuable reference for researchers and managers. Such a book was produced during this project for 30 of Western Australia's most important and/or widely-known fish species which occur in temperate waters. That book is not presented as part of this report.

This project directly addresses an urgent need of the Department of Fisheries, WA, and the recreational fishing sector to assess the likely impacts of recreational effort transfer from offshore to important inshore species. The assessment approach and species guide are also very relevant to the commercial fishing sector.

5. OBJECTIVES

The overall objectives of this study were to:

- (1) develop a method for estimating mortality in species which exhibit size-related movements,
- (2) predict impacts of shifting effort towards certain temperate, inshore WA fish species, and
- (3) produce a guide to key temperate WA fishes, for all industry stakeholders.

6. MATERIALS AND METHODS

Fish sampling

Silver Trevally (*Pseudocaranx georgianus*) and King George Whiting (*Sillaginodes punctata*) were collected at regular intervals (at least monthly) during 2009-2012 and 2010-2012, respectively. Both species were sampled from coastal marine waters of south-western Australia between Lancelin (31°S, 115°E) and Mandurah (32°S, 115°E), and in the case of *S. punctata*, also from the Peel-Harvey Estuary at Mandurah.

Most *P. georgianus* were collected from recreational fishing competitions and had been caught by line-fishing for this species in shallower (< 60 m deep) "inshore" coastal marine waters. Some line-caught *P. georgianus* from deeper (\geq 60 m deep) "offshore" waters were obtained from these fishers and also from charter boat operators, who sometimes target aggregations of this species over artificial reefs (sunken barges) in waters of ~ 110 m depth between September and December (Farmer *et al.*, 2005). This study has also used samples of *P. georgianus* collected during a previous study in 2001-2004 (FRDC 2002/004, see Farmer *et al.*, 2005). The sampling regime in that former study was similar to the current study except that a substantial number of fish had also been collected by line-fishing during research fishing trips.

Samples of *S. punctata* were collected from over (i) sand in shallow (< 1.5 m deep) coastal and estuarine nearshore waters, (ii) sand or sand/seagrass in slightly deeper (~ 2-15 m) coastal and estuarine inshore waters, and (iii) reefs at depths varying from 4 to 60 m in more offshore, marine waters. Small *S. punctata* from nearshore waters were collected by seine netting in Mangles Bay, near Rockingham (32°S, 115°E) and in the Peel-Harvey Estuary. Larger individuals of this species were sampled from catches taken in inshore and offshore waters by commercial gillnet and haul net fishers, and recreational line fishers. Recreationally-caught *S. punctata* had either been donated to the Department of Fisheries, WA, as part of their ongoing "Research Angler" and "Send Us Your Skeletons" sampling programs, or sampled from anglers' catches taken during monthly local fishing club competitions. Details of the numbers of each species caught by different methods in each region are provided in the Results.

Note that the definitions used to distinguish between "inshore" and "offshore" samples for *P. georgianus* differ from those used for *S. punctata*. Hereafter, the terms inshore and offshore are used interchangeably for the two fish species to refer to samples of fish collected in the different regions specified above. Note also that the above terms, and the term "nearshore", differ from the descriptions now routinely employed by the Department of Fisheries, Western Australia to describe "suites" of fish species within different bioregions (Department of Fisheries, 2011b).

Biological measurements and ageing procedures

The total length (TL) of each sampled fish was measured to the nearest 1 mm and, wherever possible, their whole weights were measured to the nearest 0.1 g. Unless they had already been removed by fishers during filleting, the gonads of each fish were used to classify individuals, on the basis of macroscopic examination, as unsexed juveniles (very small fish), females or males.

Sagittal otoliths of sampled fish were extracted, cleaned, dried and stored in labelled paper envelopes prior to processing. Previous biological work has shown that although, for *P. georgianus*, the opaque growth zones in otoliths of this species are always far more visible after the otoliths have been sectioned (Farmer *et al.*, 2005), for *S. punctata*, this is only the case for larger/older individuals (Hyndes *et al.*, 1998). To determine the length of *S. punctata* at which it is necessary to section the otoliths to reliably detect all of their opaque zones, the number of opaque zones in a sub-sample of 200 otoliths from fish covering essentially the full size range of this species were counted prior to and after section in all fish < 400 mm, the otoliths of all *S. punctata* below that length were read whole whilst those of larger fish were read from sectioned otoliths.

When examining the whole otoliths of *S. punctata*, the left sagittal otolith of each fish was placed in a black dish containing methyl salicylate, which was positioned under a dissecting microscope. Sectioning otoliths involved embedding these structures in clear epoxy resin and cutting them transversely through their primordia, at a thickness of ~ 0.3 mm using an Isomet Buehler low-speed diamond saw (Buehler Ltd., Lake Bluff, IL). The otolith sections were then rinsed and cleaned in water, dried and mounted on labelled microscope slides with either a mounting medium or casting resin using a cover slip. For both species, the sections were examined under reflected light against a black background using the same type of dissecting microscope as was used for reading the whole otoliths of *S. punctata*. The number of opaque zones visible on each whole or sectioned otolith was determined by examining an image of the otolith (Fig. 1) taken by employing a digital camera connected to the microscope.

The opaque zones in otoliths of *P. georgianus* and *S. punctata* were counted at least twice, with the latter count(s) being made without knowledge of any previous count. For each species, the coefficient of variation for the successive counts was determined as

$$CV_j = 100 \% \frac{\sqrt{\sum_{i=1}^{R} \frac{(x_{ij} - x_j)^2}{R - 1}}}{x_j}$$
(1)

where CV_j is the "age-reading" (*i.e.* opaque zone count) precision estimate for the j^{th} fish, x_{ij} is the i^{th} age determination of the j^{th} fish, x_j is the mean opaque zone count estimate of the j^{th} fish, and *R* is the number of times each fish in the sample



(c)

(d)



19

was aged (Campana, 2001). The values of CV_j were averaged to produce mean values of 2.2 and 0.25% for the full samples of *P. georgianus* and *S. punctata*, respectively.

The age at capture of each sampled fish was estimated from 1) its date of capture, 2) the number of opaque zones on its otolith, 3) the time of the year when the most recently-formed opaque zone typically becomes delineated from the otolith margin (determined as 1 November for both fish species) and 4) the assigned birth date for each species (1 October and 1 August for *P. georgianus* and *S. punctata*, respectively), which corresponded to the approximate mid-point of the spawning season for each of the two species.

To facilitate the correct assignment of ages to fish, each otolith was categorised according to the distance of the outer edge of the outermost opaque zone to the otolith periphery. The otolith was assigned as category 0 if an opaque zone was forming on its outer edge, as category 1 if the most recently formed opaque zone was delineated from the otolith edge by a narrow translucent margin, and as category 2 if that zone was delineated by a wide translucent margin.

For fish caught within two months prior to 1 November, the recorded number of opaque zones was adjusted downwards by one if their otoliths possessed a narrow translucent edge. Conversely, the number of opaque zones in otoliths of fish caught up to two months after 1 November was adjusted upwards by one if their otoliths possessed a wide translucent edge or an opaque edge. For each individual with one or more opaque zones on their otolith, its age at capture, a_c (years), was calculated, for *P. georgianus*, as

$$a_c = \begin{cases} i + [(m+2)/12] + (d/365.25) & \text{if } m < m_d \\ i + [(m-10)/12] + (d/365.25) & \text{if } m \ge m_d \end{cases}$$
(2)

and for S. punctata, as

$$a_c = \begin{cases} i + [(m+4)/12] + (d/365.25) & \text{if } m < m_d\\ i + [(m-8)/12] + (d/365.25) & \text{if } m \ge m_d \end{cases}$$
(3)

where *i* is the number of opaque zones detected on the otolith, *m* is the month of capture, *d* is the day of the month of capture and m_d is the month during which opaque zones typically become delineated from the edge of the otoliths. As the first annual growth zone in *S. punctata* otoliths is formed during the second year of life (Hyndes *et al.*, 1998), the ages of fish with zero opaque zones were assigned to the 0+ and 1+ age categories based on their size, *i.e.* whether individuals were below or above < 70 mm). Marginal increment analysis has been previously employed to validate that the opaque zones on the otoliths of *P. georgianus* and *S. punctata* are formed annually (Hyndes *et al.*, 1998; Farmer *et al.*, 2005).

Exploration of age and length data

To explore whether the offshore movements of *P. georgianus* and *S. punctata* are more strongly related to the size of fish than age, the mean lengths at ages were calculated for each fish species and region in which they were sampled. The mean lengths were then compared for those ages that were represented in samples from two consecutive regions, *i.e.* for *P. georgianus*, the inshore *vs.* offshore regions and, for *S. punctata*, the nearshore *vs.* inshore regions and the inshore *vs.* offshore regions.

Estimation of individual growth of fish

Back-calculation of lengths at age

The pattern of growth of each species was described using a random effects model (Pilling *et al.*, 2002) that accounts for variability in growth among individual fish and is fitted to back-calculated length-at-age data. The data to which the model was fitted thus comprised estimates of the lengths of individuals at several ages throughout their lives, *i.e.* corresponding to the ages at the formation of each successive opaque zone in their otoliths, and their ages on their dates of capture.

Back-calculated lengths at ages were produced for each species from measurements of the widths between successive opaque zones in sectioned sagittal otoliths. For *P. georgianus*, a total of 445 lengths at ages were calculated from measurements taken from otoliths of 58 fish. Note that as Farmer *et al.* (2005) had demonstrated that the patterns of growth of female and male *P. georgianus* were almost identical, the growth model for this species was fitted to pooled data for both sexes.

For *S. punctata*, 126 and 129 lengths at ages, respectively, were calculated using measurements taken from the otoliths of 24 females and 22 males. As the results of Hyndes *et al.* (1998) indicated that females grow slightly larger than males, the random effects growth model was initially fitted separately to the data sets for the two sexes of this species. However, as the growth curves for the two sexes were almost the same (see results), the data for females and males were subsequently pooled to produce a single set of growth parameter estimates for *S. punctata*.

A key assumption of back-calculation methods is that there is a direct (linear or non-linear) relationship between somatic growth of the fish and otolith growth (or other structures used for ageing) (Campana, 1990; Francis, 1990; Francis *et al.*, 1993). For this study, back-calculation was based on the widely-used approach referred to by Francis (1990) as the body proportional hypothesis (BPH). Following the BPH, the relationship between the TL, L_c (mm), and otolith radius, R_c (mm), of individual fish at their dates of capture was described for *P. georgianus* by the power function:

$$L_c = a R_c^{\ b} \tag{4}$$

where *a* and *b* are parameters that determine the form of the relationship (*e.g.* Morita and Matsuishi, 2001). For *S. punctata*, the relationship between L_c and R_c was best described by a generalised logistic curve, often referred to as the Richard's curve, *i.e.*

$$L_c = \alpha + \frac{\beta}{(1 + \gamma \exp[-\delta(R_c - \varepsilon)])^{1/\gamma}}$$
(5)

where the parameters α and β specify the lower and upper asymptotes of the curve, respectively, γ influences near which asymptote the maximum growth occurs, δ is the growth rate and ε specifies the value of R_c at maximum growth. This relationship for *S. punctata* was determined using fish length and otolith measurements for 49 female and 48 male fish, which thus constitutes a larger sample size than that used to fit the random effects growth model. The difference in sample size reflected the need, when fitting the growth model to data for *S. punctata*, to restrict the sample to fish containing \geq 2 opaque zones (to ensure that the data for individual fish contained information on the curvature of the growth trajectories of those individuals).

Back-calculated lengths at ages, L_i , for individuals of each species were derived by using measurements (to the nearest 0.01 mm and along the same axis of the otolith as the radius measurements were taken, near the sulcus and which were always perpendicular to the opaque zones) of the distances from the primordium of each otolith to the outer edge of each successive opaque zone, R_i . The estimated length (mm) of each fish corresponding to its age when opaque zone *i* was fully formed was then calculated from the BPH (Morita and Matsuishi, 2001), for *P. georgianus*, as

$$L_i = L_c \left(R_i / R_c \right)^b \tag{6}$$

and, for S. punctata, as

$$L_i = L_c \ (R_i/R_c). \tag{7}$$

where *b* is the constant obtained from the non-linear (power) regression of L_c on R_c for the former of these species. The model fitted to the back-calculated data for *P. georgianus* and *S. punctata* was

$$L_{i,x} = L_{\infty x} \left(1 - e^{-k_x (a_{i,x} - t_{0x})} \right) + \varepsilon_{i,x}$$
(8)

where $L_{i,x}$ denotes the estimated lengths for x = 1, 2 ..., n fish of each species, at ages $a_{i,x}$ when opaque zones $i = 0, 1 ..., I_x$ were formed. $L_{\infty x}$, k_x and t_{0x} are the estimated von Bertalanffy growth parameters for the x^{th} fish and $\varepsilon_{i,x}$ are assumed to be independent, normally distributed error terms with a mean of zero and a common variance σ_{ε}^2 , *i.e.* $\varepsilon_{i,x} \sim N(0, \sigma_{\varepsilon}^2)$. In contrast to the random effects model described by Pilling *et al.* (2002), which assumes that the individual growth parameters are sampled independently from a trivariate normal probability distribution, the model fitted in this study to the back-calculated data for *P. georgianus* and *S. punctata* assumes that $L_{\infty x}$ (mm) and k_x (year⁻¹) have a bivariate normal distribution with a mean μ and covariance Σ . That is,

$$\begin{pmatrix} L_{\infty \chi} \\ k_{\chi} \end{pmatrix} \sim N_{2}(\mu, \Sigma) \qquad \text{for } \chi = 1, 2 \dots, n.$$
 (9)

where the prior probability distributions for t_{0x} (years) were assumed to be normal with a mean of zero and a specified precision (= 1/ variance) of 0.001. Note that the above simplification of the growth model described by Pilling *et al.* (2002) was made with the intent of reducing the complexity of the model developed to estimate mortality of fish that undertake size-related, offshore movements.

As with the method described by Pilling *et al.* (2002; see also Helser and Lai, 2004), the random effects model was fitted using a Bayesian approach with uninformative prior probability distributions for the estimated parameters (μ , Σ and σ_{ε}^2) (Smith and Wakefield, 1994). The model was fitted to the back-calculated lengths at ages for the two species using Markov Chain Monte Carlo (MCMC) simulation methods employing the WinBUGS software package (Bayesian inference using Gibbs sampling, version 1.4.3; Spiegelhalter *et al.*, 2003). Estimates of the von Bertalanffy growth parameters, the correlation between L_{∞} and k, and standard deviations for each parameter were estimated from the results of a large number of iterations (10,000,000) from each of two Markov chains, after discarding the first 50,000 iterations and thinning the remaining 9,950,000 samples at a rate of 1 in 4,000. Note that diagnostic plots in WinBUGS indicated that, by following this procedure, convergence of each of the two chains was likely to have been achieved.

Description of offshore movement model

The model developed in this study to account for the size-related, offshore movements of fish classifies individuals into a number of age classes j (1 < j < J), where the upper bound of the maximum (integer) age class J corresponds to the integer age A + 1, and where A is the maximum age for the species (specified as 18 and 14 years for *P. georgianus* and *S. punctata*, respectively). Recruitment to the population is considered as the number of fish of age zero, *i.e.* the individuals that recruit to the first age class (j = 1). All age classes have a common age class interval of 0.05 years, which also corresponds to the age step Δa used in this model. The lower bound of the j^{th} age class is denoted by a_j , where $a_j = 0.05(j - 1)$ years, and the upper bound of the age class interval is 0.05j years. No separation was made between females and males in the model.

The use of a small step size facilitated the "discretization" of lengths at age for successive age classes, *i.e.* justifying the use of an assumption that the length of

each fish remained constant during the age step with relatively small length increments between age steps. (Note that a trade-off exists between the size of the age step and the computational demand when subsequently fitting the model). The model assumes that the age and length distributions of fish in inshore and offshore waters are determined by the size-related movements of individuals between these waters, the mortality experienced by the fish in each region, and by the variability in growth exhibited by fish in the population. For this calculation, the bivariate normal distribution of values for L_{∞} and k calculated using the parameters estimated when fitting the random effects model (see above) was divided into a bivariate grid of discrete class intervals for each of these two parameters, *i.e.* the range for each parameter was "discretized". The distribution for L_{∞} was divided into $n_{L_{\infty}}$ classes ($1 \le \omega \le n_{L_{\infty}}$), where the mid-point of the ω^{th} class and the lower and upper bounds of that class were determined, respectively, as

$$L_{\infty}^{\omega} = \left\{ \omega - \left(\left\lfloor n_{L_{\infty}}/2 \right\rfloor + 1 \right) \right\} \left[\frac{R\sigma_{L_{\infty}}}{n_{L_{\infty}} - 1} \right]$$
(10)

$$L_{\infty}^{\omega-} = L_{\infty}^{\omega} - \left[\frac{R\sigma_{L_{\infty}}}{2(n_{L_{\infty}} - 1)}\right]$$
(11)

$$L_{\infty}^{\omega+} = L_{\infty}^{\omega} + \left[\frac{R\sigma_{L_{\infty}}}{2(n_{L_{\infty}} - 1)}\right]$$
(12)

where $\sigma_{L_{\infty}}$ is the standard deviation for the asymptotic length, and the multiplier *R*, which was used to specify the range of values of asymptotic length (or growth coefficient *k*) to be considered when fitting the model, was specified as 8 for *P. georgianus* and 3 for *S. punctata* (which grows to a much smaller size). The notation $\lfloor x \rfloor$ represents the "floor" function, which is the largest integer less than or equal to *x*. Likewise, the values of *k* were divided into n_k classes $(1 \le \kappa \le n_k)$, where the respective mid-point, lower bound and upper bound of the κ^{th} interval of the *k* distribution were determined as

$$k^{\kappa} = \{\kappa - (\lfloor n_k/2 \rfloor + 1)\} \left[\frac{R\sigma_k}{n_k - 1} \right]$$
(13)

$$k^{\kappa-} = k^{\kappa} - \left[\frac{R\sigma_k}{2(n_k - 1)}\right] \tag{14}$$

$$k^{\kappa+} = k^{\kappa} + \left[\frac{R\sigma_k}{2(n_k - 1)}\right] \tag{15}$$

where σ_k is the standard deviation for the asymptotic length. The values of the two parameters at the centre of each of the resulting grid cells, denoted by L_{∞}^{ω} and k^{κ} , were used as the specific values for L_{∞} and k associated with that grid cell. The proportion of fish which lie within the grid cell, $p_{L_{\infty},k}$, was calculated from the bivariate normal distribution. The bivariate-normal distribution was assumed to be

truncated for values of asymptotic length or $k \le 0$. The following calculations were then undertaken for each pair of values of L_{∞}^{ω} and k^{κ} .

The lengths of fish in each age class, L_j , were assumed to be described by a von Bertalanffy growth curve:

$$L_j = L_{\infty}^{\omega} \left\{ 1 - \exp\left[-k^{\kappa} \left(a_j - t_0 \right) \right] \right\}.$$
(16)

Movement of fish from inshore to offshore waters was modelled as a logistic function with two parameters, where the probability that a fish in age class j (and thus of length L_j) has moved to the offshore region was determined as

$$P_{j}^{\text{offshore}} = \left\{ 1 + \exp\left[-\log_{e}(19) \frac{L_{j} - L_{50}^{\text{Move}}}{L_{95}^{\text{Move}} - L_{50}^{\text{Move}}} \right] \right\}^{-1}$$
(17)

and where L_{50}^{Move} and L_{95}^{Move} represent the lengths at which 50 and 95% of fish, respectively, have moved offshore. The model assumes that none of the fish recruit to the offshore region and that fish become fully selected prior to moving offshore. Thus, the probability that a fish in age class *j* still remains in inshore waters was calculated as

$$P_i^{\text{inshore}} = 1 - P_i^{\text{offshore}}.$$
 (18)

The proportion of inshore fish in age class j that are expected to move offshore during age step Δa was determined as

$$\psi_j^{\text{move}} = \left(P_j^{\text{inshore}} - P_{j+\Delta a}^{\text{inshore}} \right) / P_j^{\text{inshore}}.$$
 (19)

It was assumed that (i) all fish are destined to move offshore at some moment in life, if they do not die first, (ii) fish which have moved offshore do not return to inshore waters, and (iii) the selectivity of fish, *i.e.* their vulnerability to capture by the fishing gear, is the same in inshore and offshore waters. S_j , the selectivity of fish in age class j, which was assumed to be length-related, was determined as

$$S_j = \left\{ 1 + \exp\left[-\log_e(19) \frac{L_j - L_{50}^{\text{sel}}}{L_{95}^{\text{sel}} - L_{50}^{\text{sel}}} \right] \right\}^{-1}$$
(20)

where L_{50}^{Sel} and L_{95}^{Sel} represent the lengths of fish at which 50 and 95% are vulnerable to capture, respectively. As the model recognises that fishing mortality can differ between regions, the fishing mortality of fully selected fish in region r (1 = inshore, 2 = offshore) was denoted F_r . Thus, $F_{j,r}$, the instantaneous rate of fishing mortality (year⁻¹) of fish of length L_j in region r was calculated as

$$F_{j,r} = S_j F_r. \tag{21}$$

The instantaneous rate of total mortality (year⁻¹) for fish of length L_j in region r, denoted $Z_{i,r}$, was determined as

$$Z_{j,r} = F_{j,r} + M.$$
 (22)

where *M* is the instantaneous rate of natural mortality (year⁻¹). *M* was assumed to be constant for all fish and was estimated from the maximum age of the fish species using Hoenig's (1983) mortality equation for fish:

$$M = \exp \left[1.46 - 1.01 \log_e A \right]. \tag{23}$$

The proportion of fish of length L_j in region r that survive to the end of age step Δa , denoted $s_{i,r}$, was determined as

$$s_{j,r} = \exp\left[-Z_{j,r}\,\Delta a\right].\tag{24}$$

The relative number of fish (with the growth parameters associated with the current grid cell of discretized values of asymptotic length L_{∞} and growth coefficient k) in age class j in inshore waters, $n_{j,1}$, was calculated from the expected proportion of fish with those growth parameters $p_{L_{\infty},k}$ as

$$n_{j,1} = \begin{cases} p_{L_{\infty},k} & \text{for } j = 1\\ n_{j-1,1} s_{j-1,1} \left(1 - \psi_{j-1}^{\text{move}} \right) & \text{for } j > 1. \end{cases}$$
(25)

Likewise, the expected relative number of fish in age class j in offshore waters, $n_{j,2}$, was determined as

$$n_{j,2} = \begin{cases} 0 & \text{for } j = 1\\ (n_{j-1,2} s_{j-1,2}) + (n_{j-1,1} s_{j-1,1} \psi_{j-1}^{\text{move}}) & \text{for } j > 1. \end{cases}$$
(26)

The two latter equations rely on the assumption that fish in the population are unlikely to grow to ages greater than the specified maximum age for the species. For each region, the expected catch from age class j (and thus length L_j) for fish that had the specific growth parameters L_{∞}^{ω} and k^{κ} was calculated using the Baranov catch equation:

$$C_{j,r} = \frac{F_{j,r}}{Z_{j,r}} \left(1 - s_{j,r}\right) n_{j,r}.$$
(27)

and accumulated over all pairs of growth parameters, thus producing an estimate of the relative numbers of fish in each age or length class within the overall catch.

As the above model was intended to be fitted to age and length data for fish collected from inshore and offshore waters, the observed data represent numbers at integer ages rather than decimal ages of fish. To fit the model, therefore, the expected catch for each age class and region predicted by the model was now expressed in terms of integer ages and the expected length composition for each such integer age was determined. It was thus necessary to move from the earlier definition of age classes, which, to give the required precision of calculations, were based on an age interval of Δa , to an expression of the age distribution in terms of integer age τ ($0 \le \tau \le A$). The length classes are denoted by the subscript v, where the lower bound of the v^{th} length class is L_v , and the number of length classes and the size of the class intervals were those used for the observed length composition data.

The expected catch within each length class v, for each integer age τ and region r, denoted $C_{v,\tau,r}$, was calculated by summing the catches for that particular length class at age over all values of ω and κ . That is,

$$C_{\nu,\tau,r} = \sum_{\omega} \sum_{\substack{\kappa \\ a_{\tau} \le a_{j} \le a_{\tau+1} \\ L_{\nu} \le L_{j} \le L_{\nu+1}}} C_{j,r}^{\omega,\kappa}$$
(28)

Subsequently, $C_{\tau,r}$, the expected number of fish caught from each integer age class τ and region r was determined as

$$C_{\tau,r} = \sum_{\upsilon} C_{\upsilon,\tau,r} \,. \tag{29}$$

The total expected catch in region r was calculated as

$$C_r = \sum_{\tau=0}^{A} C_{\tau,r}$$
 (30)

The expected proportion of fish in the catch that belong to length class v from region r, denoted $\psi_{v,\tau,r}$, was determined as

$$\psi_{\nu,\tau,r} = \frac{C_{\nu,\tau,r}}{C_{\tau,r}}.$$
(31)

Similarly, the expected proportion of fish in the catch that belong to integer age class τ from each region, $\psi_{\tau,r}$, was calculated as

$$\psi_{\tau,r} = \frac{C_{\tau,r}}{C_r}.$$
(32)

Fitting the offshore movement model

Fitting the model requires the values for the various growth parameters estimated by the random effects model (see Tables 3 and 8 for *P. georgianus* and *S. punctata*, respectively), and an estimate for the instantaneous rate of natural mortality for that species. The values assumed for natural mortality were 0.23 year⁻¹ for *P. georgianus* and 0.30 year⁻¹ for *S. punctata*, as determined from Hoenig's (1983) equation for fish (see equation 23) and the maximum recorded ages of those species in Western Australia, *i.e.* 18 and 14 years, respectively (Hyndes *et al.*, 1998; Farmer *et al.*, 2005).

When the offshore movement model is fitted to age and length data, estimates are produced for six model parameters. These include two parameters of a logistic function describing the size-related selectivity of fish (L_{50}^{Sel} and L_{95}^{Sel}), two parameters of another logistic function describing the offshore movement of fish (L_{50}^{Move} and L_{95}^{Move}), and the instantaneous rates of fishing mortality of fish in the inshore and offshore regions (F_1 and F_2 , respectively). The six parameters are estimated by minimising an objective function which comprised the sum of the log-likelihoods calculated for the age compositions and lengths at ages from the two regions.

Denoting the observed frequency of fish in length class v as $f_{v,\tau,r}$, the loglikelihood associated with length-at-age data from inshore and offshore waters was calculated as

$$\lambda_{1} = \sum_{r=1}^{2} \sum_{\tau=0}^{A} \sum_{v} f_{v,\hat{o},r} \log_{e}(\psi_{v,\tau,r}).$$
(33)

Likewise, denoting the observed frequency of fish in integer age class τ as $f_{\tau,r}$, the log-likelihood associated with the age composition data from the two regions was calculated as

$$\lambda_{2} = \sum_{r=1}^{2} \sum_{\tau=0}^{A} f_{\tau,r} \log_{e}(\psi_{\tau,r}).$$
(34)

An estimate of the overall log-likelihood was calculated as the sum of the individual log-likelihoods associated with the age compositions and lengths at ages of fish in the catch. That is,

$$\lambda = \lambda_1 + \lambda_2. \tag{35}$$

The model was fitted using Solver in Microsoft Excel. Prior to the first fitting phase, random starting values were generated, within specified bounds, for each of the parameters. The parameter estimates resulting from each phase were then used as the starting values for subsequent fitting phases, thus progressively helping the model find a solution. Several penalty functions were implemented to ensure that a number of constraints necessary for fitting the model were satisfied:

- (i)
- (ii)
- (iii)
- $$\begin{split} & L_{95}^{\text{Sel}} > (L_{50}^{\text{Sel}} + x), \\ & L_{95}^{\text{Move}} > (L_{50}^{\text{Move}} + x), \\ & L_{50}^{\text{Move}} > (L_{95}^{\text{Sel}} + x), \text{ and} \\ & F_1 \text{ and } F_2 \text{ lie between 0.0001 and 1 year}^{-1}, \end{split}$$
 (iv)

where x denotes the minimum difference allowed between the respective parameters, which was specified as 20 mm for P. georgianus and 10 mm for S. punctata. The third penalty was used to satisfy the assumption that inshore fish become fully selected prior to 50% of their individuals moving to offshore waters. For S. punctata, three additional penalty functions were necessary for fitting the model to simulated and real data for this species. They included specifying: (1) a lower boundary for L_{50}^{Sel} of 275 mm, which was required to help the model fit to the very steep ascending limb of the inshore length composition data, (2) a lower boundary for L_{50}^{Move} of 390 mm, *i.e.* where fish first start appearing in offshore waters, and (3) an upper limit for L_{95}^{Move} to 460 mm, *i.e.* just after the peak of the offshore length composition data for this species.

To ensure that Solver provided a robust solution, "jitter tests" were undertaken which involved fitting the model on multiple occasions to the same data set, using different initial starting values for the parameters that were being estimated (see Myung, 2003). Although this exploration demonstrated that model fits to simulated and real data for P. georgianus yielded robust log-likelihoods when Solver was used, initially, this was not the case when fitting the model to data for S. punctata (Appendix 3). Further "jitter testing" using data for S. punctata demonstrated that use of the Nelder and Mead (1965) simplex algorithm, (implemented in Visual Basic for Applications) in tandem with Solver provided robust optimisation when the best of three consecutive model fits to the same data set (*i.e.* the fit with the smallest log-likelihood) was selected (Appendix 3). Moreover, extensive explorations using different versions of the model showed that, to improve the model fit to real data for S. punctata, it was also necessary to exclude the loglikelihood component of the objective function that related to the inshore age composition data (see results and discussion for more details).

Fitting the model to simulated data

To test the robustness of the model for reliably estimating the parameters describing the length-related selectivity and offshore movement of fish, and inshore and offshore fishing mortality, the model was first fitted to simulated age and length data for *P. georgianus* and *S. punctata*. The data were generated using an operating model that essentially comprised the same formulas as described in the model specifications provided above. The same values for the growth parameters and natural mortality were assumed when generating synthetic data sets for each fish species, as when fitting the model to either simulated data or "real" data for that species.

Cumulative frequency distributions of the expected age and length compositions, denoted $F(\psi_{\tau,r})$ and $F(\psi_{v,\tau,r})$, respectively, were calculated from values of $\psi_{\tau,r}$ and $\psi_{v,\tau,r}$ generated by the operating model for each fish species. Using the inverse method of random number generation described by Zelen and Severo (1965), observed samples of fish were then drawn from these two cumulative distributions. That is, to obtain an "observed age" for each simulated fish, a random number d was drawn from a uniform distribution with values ranging between zero and one, *i.e.* $d \sim U(0,1)$. The integer age τ , for which the value of d was such that $F(\psi_{\tau+1,r}) \leq d < F(\psi_{\tau,r})$, was then assigned to the fish, and the process repeated until samples of the required sample size for fish from region r had been generated.

The model was first fitted to 100 simulated data sets for *P. georgianus* and *S. punctata*, respectively, where each data set had been generated by the operating model using the parameters specified for a base case scenario (Table 1). The specified values for the selectivity and movement parameters, which represent "guesses" of the unknown true values for each species, were based on biological data presented in French (2003) and Farmer *et al.* (2005) for *P. georgianus* and in Hyndes *et al.* (1998) and Sulin (2012) for *S. punctata.* The values for fishing mortality in inshore and offshore waters (0.3 and 0.1 year⁻¹, respectively) that were specified to simulate size and age data for the base case scenario were also "guesses", but selected to not exceed the values of natural mortality for those species.

The resultant estimates of the selectivity and movement parameters and inshore and offshore mortality were then compared to the "true" parameter values used to simulate the data to determine how well the model could recover those true parameter values. Note that, for *P. georgianus* in particular, as it takes a long time (~ 10 h) to produce a single model fit, it was not possible within the time frame of the study to undertake a greater number of model fits to simulated data sets.

Parameter	Pseudocararanx georgianus	Sillaginodes punctata
Selectivity parameters		
L ^{Sel} (mm)	300	280
L ^{Sel} (mm)	400	300
Movement parameters		
L ^{Move} (mm)	450	400
L ^{Move} (mm)	600	450
Mortality parameters		
F_1 (inshore; year ⁻¹)	0.3	0.3
F_2 (offshore; year ⁻¹)	0.1	0.1

Table 1. Model parameters used for simulating age and length data for *Pseudocaranx georgianus* and *Sillaginodes punctata* (*i.e.* for base case scenarios).

To determine whether the amount of data available for fitting the model has a marked influence on parameter estimation, for each species, the model was fitted to a relatively small and then a larger data set. For *P. georgianus*, the model was fitted to synthetic data for a sample of 247 inshore fish and 107 offshore fish (*i.e.* corresponding to the amount of real data available for *P. georgianus* in Western Australia, collected between 2001 and 2004 for FRDC 2002/004), and a larger sample of 1000 inshore fish and 500 offshore fish. For *S. punctata*, the model was first fitted to a synthetic sample of 100 inshore fish and 200 offshore fish, and then to a larger sample of 500 inshore fish and 1000 offshore fish.

For *P. georgianus*, the reliability of the model was also tested against additional simulated data sets produced by specifying a value for the "true" inshore fishing mortality of 0.1 year⁻¹ (base case scenario = 0.3 year⁻¹) and 0.3 year⁻¹ for the offshore mortality (base case scenario = 0.1 year⁻¹). For *S. punctata*, the model was further tested to explore the influence on model parameter estimation of excluding, from the overall objective function, the log-likelihood component associated with inshore age compositions (as this was required to fit the model to real data for this species, see Results and Discussion).

Further model explorations were undertaken using simulated data to determine how different assumptions about the underlying data may influence parameter estimation. Four different scenarios, including the base case scenario for *P. georgianus*, were considered in the analysis to simulate hypothetical fish stocks for which the size range over which individuals of this species remained in inshore waters after becoming vulnerable to fishing varied. For example, in situations where the lengths at which fish begin moving offshore are only slightly greater than the lengths at which fish become selected by the fishing gear, the information content in the inshore age and length data for estimating movement and mortality will be less than when the offshore movement occurs at a larger size. Therefore, by varying the values specified for the parameters L_{50}^{Sel} , L_{50}^{Sel} , L_{50}^{Move} and L_{95}^{Move} when simulating data for *P. georgianus*, the ability of the model to deal with more or less informative data sets was explored. As above, the model was fitted to 100 simulated data sets (comprising 1000 inshore fish and 500 offshore fish) generated for each of the three additional scenarios considered in these explorations, where the fishing mortalities of *P. georgianus* in inshore and offshore waters were specified as 0.3 and 0.1 year⁻¹, respectively.

Fitting the model to real data

The model was fitted to "real" age and length data collected for both *P. georgianus* and *S. punctata* near Perth in south-western Australia. Although data for both species were collected during this study, for *P. georgianus*, those collected for the offshore region were insufficient for fitting the model. Thus, for this species, the model was fitted to data collected in 2001-2004 during a previous FRDC study. These data, which comprised 247 fish from inshore waters and 107 fish from offshore waters, were resampled and used in the model to produce 1000 sets of bootstrap estimates for each of the six model parameters. The medians of the estimates for each parameter, as well as the lower and upper 95% confidence levels, taken as the 2.5 and 97.5 percentiles, respectively, were then calculated.

The offshore movement model was also fitted to real data for *S. punctata* (collected in the current study), comprising the lengths and ages for 93 fish in inshore waters and 193 fish in offshore waters. Preliminary model fits to these data demonstrated that the model did not provide realistic results when it was fitted in the same manner as for *P. georgianus*. That is, the estimates of inshore mortality were consistently zero and further exploration of the model demonstrated that this was mainly due to the influence of one of the four components of the overall objective function, *i.e.*, that associated with the inshore age composition. Thus, when analysing the real data for *S. punctata*, the model was fitted to only the offshore age composition data and length-at-age data for both inshore and offshore waters (see Discussion for further explanation and rationale). Due to time limitations, only 100 bootstrap estimates of the six model parameters were produced for *S. punctata* to provide preliminary estimates of the model parameters for this species.

Further analyses for *Pseudocaranx* georgianus

As it was not possible, because of the paucity of samples of *P. georgianus* from the offshore region, to fit the model to the data collected for this species in this study, the following approach was employed to ascertain whether the inshore component of the stock of this species is likely to have experienced a significant change in mortality since data were last collected for this species in 2001-2004 (for FRDC 2002/004). Regression-based catch curves (*e.g.* Ricker, 1975) were fitted to the logarithms of the frequencies of fish at age in the inshore regions from each period. Although the decline in numbers of fully-recruited fish with increasing age in the inshore region for this species reflects the movement of fish to the offshore region as well as mortality, any difference between the catch curve estimates for the two sampling periods will reflect a change in mortality alone (if the rate of offshore movement of fish has not changed since the previous study). Catch curves were fitted to resampled inshore data from the two sampling periods to produce 1000 bootstrap estimates of "the rate of decline" of fish in this region. The catch curves were fitted to the logged frequencies of fish of ages above that at which fish are assumed to be fully selected, which was considered in this study to be one year older than the peak age. Following recommendations by Murphy (1997), the effect on catch curve estimates of specifying two different "threshold levels" (1 and 5 fish), representing the minimum allowed frequency of fish in the oldest age class to which the curve was fitted, was also explored. For each scenario, the median estimate of decline and the associated 95% confidence levels were calculated from the 1000 catch curve estimates from each of the two sampling periods.

Per-recruit analysis

Per-recruit analyses that account for the size-related movement of fish from inshore to offshore waters were used to explore the implications of different levels of fishing mortality in these two regions for the overall stock status of P. georgianus and S. punctata. For simplicity, only the females of the two fish species were considered in these analyses (noting that neither species is hermaphroditic). As the per-recruit analyses were intended to provide an indication of the likely consequences of differing mortality of fish in inshore and offshore waters, rather than to produce precise estimates of current yield and spawning biomass per recruit for *P. georgianus* and *S. punctata*, a simplified version of the offshore movement model was employed. For this, it was assumed that the lengths at ages of all fish were represented by the expected lengths at the midpoints of each age class *j* (as before, assuming a common age interval of 0.05 vears). These were calculated from the von Bertalanffy growth curve, using the mean growth parameters for *P. georgianus* and *S. punctata* estimated by the random effects model (see Tables 3 and 8), *i.e.* the growth model employed in the per-recruit analysis is deterministic and does not allow for variability in growth among individual fish. The values specified for other parameters used in the perrecruit analysis to determine the numbers at age in each of the inshore and offshore regions, $n_{i,r}$, were those obtained by fitting the offshore movement model to the real data available for the two species (see Tables 4 and 9 for parameter values for *P. georgianus* and *S. punctata*, respectively).

Yield per recruit, YPR, and spawning biomass per recruit, SBPR, were calculated for different specified values of fishing mortality in each region, F_r , ranging between zero and 0.6 for *P. georgianus* and between zero and 0.8 year⁻¹ for *S. punctata*. Assuming a maximum age of 18 and 14 years for *P. georgianus* and *S. punctata*, respectively, the YPR (g recruit⁻¹) for females of each species in inshore (r = 1) and offshore (r = 2) waters was calculated as

$$YPR_{r} = \sum_{j=1}^{J} \left[\frac{F_{j,r}}{Z_{j,r}} \left\{ 1 - \exp\left(-Z_{j,r} \Delta a\right) \right\} n_{j,r} W_{j} \right]$$
(36)

where W_j is the weight of fish (in g) at length L_j , (in mm) as estimated from the weight-length relationship for *P. georgianus* as $\log_e(W) = 2.992 \log_e(L) - 11.331$ (Farmer *et al.*, 2005), and for *S. punctata* as $W = 1.1 * 10^{-6} L^{3.29}$ (Gaughan *et al.*, 2006). For each species, the SBPR (g recruit⁻¹) for females in inshore and offshore waters was determined as

$$SBPR_r = \sum_{j=1}^{J} [\psi_j^{\text{mat}} n_{j,r} W_j]$$
(37)

where ψ_j^{mat} represents the proportion of fish of length L_j that are mature, which was determined as

$$\psi_j^{\text{mat}} = \left\{ 1 + \exp\left[-\log_e(19) \frac{L_j - L_{50}^{\text{mat}}}{L_{95}^{\text{mat}} - L_{50}^{\text{mat}}} \right] \right\}^{-1}.$$
 (38)

 L_{50}^{mat} and L_{95}^{mat} represent the respective lengths (mm) at which 50 and 95% of females are mature, *i.e.* 310 and 378 mm for *P. georgianus* (Farmer *et al.*, 2005) and 413 and 450 mm for *S. punctata* (Hyndes *et al.*, 1998). Values of the overall YPR and SBPR for fish in inshore and offshore waters were determined by summing the values for the two regions.

The spawning potential ratio, SPR, of *P. georgianus* and *S. punctata* (*i.e.* the level of spawning biomass of each stock at the estimated level of exploitation relative to the un-fished level) was calculated from the SBPR for different specified values of inshore fishing mortality (F_1) and offshore fishing mortality (F_2) as:

$$SPR_{F_1,F_2} = SBPR_{F_1,F_2}/SBPR_{0,0}.$$
(39)

Decision table analysis

A decision table approach (*e.g.* Cochrane, 2000) was used to examine how different management strategies are likely to perform given uncertainty in parameter estimates produced by the offshore movement model. One such source of uncertainty in the model outputs resulted from the necessity, when fitting the model, to implement penalties to ensure that the model parameters remained within what were considered biologically feasible bounds (specified prior to the model being fitted). When the model was fitted to the real data for *P. georgianus*, the penalty implemented to satisfy the assumption that inshore fish become fully selected before moving offshore (*i.e.* to ensure that $L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} + 20 \text{ mm}$) was found to impact on the resultant estimates of these parameters, causing them to be constrained by the specified bounds for these. For *S. punctata*, model fits to the real data for this species resulted in the estimates of L_{50}^{Move} and L_{95}^{Move} being constrained by their specified lower (390 mm) and upper (460 mm) bounds, respectively, which were implemented to ensure that the parameters

approximately conformed to the ascending limb of the offshore length composition data.

To explore the implications, for the effectiveness of alternative management measures, of the imposed penalty assumptions relating to the lengths at which fish move from inshore to offshore waters, the offshore movement model was fitted to the real data for each of the two species nine times, where each fit represented a certain "penalty scenario". For *P. georgianus*, these scenarios represented different minimum specified amounts by which L_{50}^{Move} was allowed to differ from L_{95}^{Sel} , ranging from -40 to +40 mm (Table 2). For *S. punctata*, the nine penalty scenarios represented different values for specified lower bounds for L_{50}^{Move} and upper bounds for L_{95}^{Move} , respectively (Table 2).

For each penalty scenario, estimates of the six parameters produced by the offshore movement model when fitted to the data for *P. georgianus* and *S. punctata* were used to calculate the YPR and SPR for the two species, using the per-recruit model that accounts for the size-related movements of fish to offshore waters. The per-recruit analyses were repeated for five alternative management measures explored in the decision analysis. For both fish species, these constituted reducing the estimated inshore fishing mortality by 25 and 50%, leaving it at its estimated level, or increasing the estimate for this parameter by 25 and 50%.

Table 2. Penalty scenarios used to explore the implications for management of different assumptions regarding the parameters for size-related selectivity and offshore movement of *Pseudocaranx georgianus* and *Sillaginodes punctata*, employing decision table and per-recruit analyses.

Penalty scenarios	Pseudocararanx georgianus	Sillaginodes punctata
1	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} - 40 \text{ mm}$	$L_{50}^{\text{Move}} > 350 \text{ mm}, L_{95}^{\text{Move}} < 460 \text{ mm}$
2	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} - 30 \text{ mm}$	L_{50}^{Move} > 360 mm, L_{95}^{Move} < 460 mm
3	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} - 20 \text{ mm}$	L_{50}^{Move} > 370 mm, L_{95}^{Move} < 460 mm
4	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} - 10 \text{ mm}$	L_{50}^{Move} > 380 mm, L_{95}^{Move} < 460 mm
5	$L_{50}^{\rm Move} > L_{95}^{\rm Sel}$	L_{50}^{Move} > 390 mm, L_{95}^{Move} < 460 mm
6	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} + 10 \text{ mm}$	L_{50}^{Move} > 390 mm, L_{95}^{Move} < 470 mm
7	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} + 20 \text{ mm}$	L_{50}^{Move} > 390 mm, L_{95}^{Move} < 480 mm
8	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} + 30 \text{ mm}$	$L_{50}^{\text{Move}} > 390 \text{ mm}, L_{95}^{\text{Move}} < 490 \text{ mm}$
9	$L_{50}^{\text{Move}} > L_{95}^{\text{Sel}} + 40 \text{ mm}$	L_{50}^{Move} > 390 mm, L_{95}^{Move} < 500 mm
7. RESULTS

Age and length data for *Pseudocaranx* georgianus

A total of 521 *P. georgianus* were collected between 2009 and 2012 from catches taken by recreational boat anglers (n = 511) and charter boat fishers (n = 10 fish), who had been rod and line fishing in coastal marine waters near Perth. Approximately 81% (420) of these fish were able to be aged. Most of these aged *P. georgianus* (76%, 320 fish) were between 2 and 4 years old and the maximum age of fish in samples was 9 years (Fig. 2a). The total lengths of sampled fish ranged from 215 to 582 mm, with 98% of the individuals having lengths between 250 and 400 mm (Fig. 2b).

93% (n = 486) of sampled *P. georgianus* were caught in inshore waters (< 60 m deep), and the remaining 7% (n = 35) were caught in deeper, offshore waters (Fig. 2). Of these inshore and offshore samples, 391 and 29 fish, respectively, could be aged. The reason for the limited sample from offshore waters appears to be that recreational fishers and charter boat operators rarely targeted this species in deeper waters in 2009-2012, with the result that very few individuals from those waters appeared in the catches weighed in at recreational angling competitions attended by researchers from Murdoch University or the Department of Fisheries, WA, or in catches from charter boat operators. Due to the paucity of *P. georgianus* collected in this study from the offshore region, most analyses presented below were undertaken using data for P. georgianus collected in 2001-2004 (for FRDC 2002/004). In that study, 247 fish collected from inshore waters and 107 fish from offshore waters were caught by line fishing (Fig. 3). The majority of these line caught fish were taken by recreational fishers, although some were caught by researchers and, in the case of offshore waters, by researchers onboard a charter vessel (exact numbers of fish caught by each source not specified).

The data for *P. georgianus* collected during FRDC project 2002/004 show that, for each of the ages at which individuals of this species occurred in both inshore and offshore waters, the lengths of fish in the latter region were typically greatest (Fig. 4). For example, at 5, 7, 9 and 11 years of age, the mean lengths of *P. georgianus* were 414, 459, 556 and 646 mm, respectively, in offshore waters, compared with 371, 389, 442 and 530 mm, respectively, in inshore waters.

Growth of Pseudocaranx georgianus accounting for individual variation

The total lengths of 58 *P. georgianus* on their dates of capture, L_c , which ranged between 230 and 885 mm, were strongly related to the radii of their otoliths, R_c , as described by the following power relationship: $L_c = 822.73 R_c^{1.538}$ (R² = 0.725; Fig. 5).

Fitting the non-linear random effects growth model to the back-calculated lengths at age (Fig. 6) for *P. georgianus* from both inshore and offshore waters produced mean estimates of the von Bertalanffy growth parameters L_{∞} , *k* and t_0 of 1246 mm, 0.075 year⁻¹ and -0.201 years, respectively (Table 3).



Fig. 2. (a) Age and (b) length-frequency distributions for line-caught *Pseudocaranx georgianus* collected between 2009 and 2012 in inshore (light blue bars) and offshore (dark blue bars) coastal waters of south-western Australia. Age frequency distributions; n = 391 fish for inshore waters and n = 29 fish for offshore waters. Length frequency distributions; n = 486 fish for inshore waters and n = 35 fish for offshore waters.



Fig. 3. (a) Age and (b) length frequency distributions for line-caught *Pseudocaranx georgianus* collected between 2001 and 2004 in inshore (light blue bars) and offshore (dark blue bars) coastal waters of south-western Australia (data collected for FRDC 2002/004). The data presented in (a) and (b) are restricted to the 247 and 107 fish from inshore and offshore waters, respectively, that could be aged in that study.



Fig. 4. Mean (± 1SE) total lengths (TL; mm) of *Pseudocaranx georgianus* in inshore and offshore coastal waters of south-western Australia, for those ages that were represented in both regions. Age classes (years) and corresponding sample sizes for inshore waters; 4 + (n = 79), 5 + (n = 58), 6 + (n = 33), 7 + (n = 22), 8 + (n = 5), 9 + (n = 2) and 11 + (n = 2). Age classes and corresponding sample sizes for offshore waters; 4 + years (n = 7), 5 + (n = 13), 6 + (n = 13), 7 + (n = 16), 8 + (n = 16), 9 + (n = 12) and 11 + (n = 3). Numbers on plot refer to age classes (years).



Fig. 5. Relationship between the total length (mm) and otoliths radius (mm) of 58 *Pseudocaranx georgianus* caught in inshore (light blue circles) and offshore (dark blue circles) coastal waters of south-western Australia.



Fig. 6. Back-calculated lengths at ages for 58 *Pseudocaranx georgianus* caught in inshore (light blue squares) and offshore (dark blue squares) coastal waters of south-western Australia. Note that each fish is represented by multiple data points, *i.e.* which correspond to the estimated lengths at the ages at which each successive opaque zone in its otolith were formed (and became delineated from the otolith edge), and at the age when the fish was caught.

Table 3. Estimated means and associated standard deviations (SD) of the von Bertalanffy growth
parameters, and the correlation between L_{∞} and k, for Pseudocaranx georgianus, derived by fitting
a non-linear random effects growth model to back-calculated lengths at ages.

Parameter	Mean	SD
Asymptotic length, L_{∞} (mm)	1246	85
Growth coefficient, k (year ⁻¹)	0.075	0.007
Theoretical age at length zero, t_0 (years)	-0.201	4.161
Correlation L_{∞}/k	-0.829	0.070

Outputs from the MCMC simulations demonstrated that the prior distributions specified for the three growth parameters were very broad relative to the respective distributions for the parameter estimates (Fig. 7), and thus would have been very unlikely to inform the estimation process. The correlation between L_{∞} and k estimated by the random effects model was highly negative (-0.829; Table 3).

Explorations of the robustness of the offshore movement model using simulated data for *Pseudocaranx georgianus*

Fitting the size-dependent, offshore movement model, developed for estimating mortality in inshore and offshore waters, to simulated data for *P. georgianus*

generated for the base case scenario (see Table 1) yielded model parameter estimates that were similar to the "true" values, *i.e.* as specified in the operating model (Fig. 8). For example, when the true fishing mortalities in inshore (F_1) and offshore (F_2) waters were specified as 0.1 and 0.3 year⁻¹, respectively, and the specified sample size was 247 inshore fish and 107 offshore fish, the respective medians of the estimates for F_1 and F_2 were 0.10 and 0.32 year⁻¹. For that scenario, the median values of the estimates for the two movement parameters L_{50}^{Move} and L_{95}^{Move} (451 and 601 mm, respectively) also were very close to the respective specified true values (450 and 600 mm). Increasing the sample size to 1000 inshore fish and 500 offshore fish likewise yielded median parameter estimates that were close to the true, specified values for those parameters (Fig. 8).

Whilst the level of accuracy of parameter estimates produced by the model was high for all six parameters estimated by the model, the precision of estimates of those parameters differed substantially among the parameters (Fig. 8). Thus, for example, when the specified true fishing mortalities were $F_1 = 0.3$ and $F_2 = 0.1$ year⁻¹ and the specified sample sizes were 247 and 107 fish, respectively, for inshore and offshore waters, the CVs calculated for the 100 estimates of F_1 (0.89) and F_2 (0.51) were substantially larger than those for L_{50}^{Sel} (0.06) and L_{95}^{Sel} (0.07). Increasing the sample size of the data to which the model was fitted generally led to improved precision of parameter estimates (Fig. 8). For example, when the true fishing mortalities in inshore and offshore waters were specified as 0.1 and 0.3 year⁻¹, respectively, the CV calculated from the estimates of F_2 for the larger sample size scenario (1000 inshore fish and 500 offshore fish) was 0.15,

compared with 0.31 for the small sample size scenario (247 inshore fish and 107 offshore fish). Increasing the sample size did not, however, dramatically improve the levels of precision for the estimates of inshore mortality (Fig. 8).

Further model explorations showed that the robustness of the model for reliably estimating fishing mortality for fish species that undertake size-dependent movements from inshore to offshore waters varies substantially depending on the lengths at which fish become selected by fishing gear, and the length range over which individuals move offshore (Fig. 9). Analyses of alternative scenarios of specified values for the selectivity and movement parameters demonstrated that the precision of estimates for inshore mortality is greatest when fish become selected at relatively small lengths and move offshore at relatively large lengths, *i.e.* which results in the length range of fish in inshore waters being larger (*cf.* scenarios 1 and 4 in Fig. 9). Conversely, the precision of estimates of inshore mortality is least when fish become selected at a relatively large length and move offshore soon thereafter (Fig. 9).



Fig. 7. Probability distributions (a, c, e) for the three von Bertalanffy growth parameters, L_{∞} , k and t_0 , for *Pseudocaranx georgianus*, when estimated by the non-linear random effects model fitted to back-calculated lengths at ages, and the prior probability distributions (b, d, f) specified for each of these parameters. Results are based on data for 58 fish and 445 lengths at ages.



Fig. 8. Model estimates of (a, b) selectivity parameters, (c, d) movement parameters, and (e, f) inshore and offshore fishing mortality (*F*) when fitted to simulated data for *Pseudocaranx* georgianus. The model was fitted to data for two scenarios of differing fishing mortalities, *i.e.* 0.1 year^{-1} for inshore *F* vs. 0.3 year^{-1} for offshore *F* (left hand side of each graph), and 0.3 year^{-1} for offshore *F* (right hand side of each graph), and two scenarios of differing sample sizes, *i.e.* 247 and 107 fish in inshore and offshore waters, respectively (white boxes), and 1000 inshore fish and 500 offshore fish (grey boxes). The line inside each box represents the median value, the bottom and top of the box show the 25th and 75th percentiles, and the lower and upper bars show the minimum and maximum values for 100 model fits. The true values for the parameters are represented as the dashed lines.



Fig. 9. Model estimates of inshore (light blue boxes) and offshore (dark blue boxes) fishing mortality (*F*) when fitted to simulated data for *Pseudocaranx georgianus* generated for four scenarios of differing specified sizes at which fish become selected by fishing gear and move offshore. For each scenario, the line inside the box shows the median value, the bottom and top of the box show the 25^{th} and 75^{th} percentiles, and the lower and upper bars show the minimum and maximum values for 100 model fits. The true values of inshore/offshore *F* were specified as 0.3/0.1 year⁻¹ and are represented as the dashed lines.

Fits of offshore movement model to real data for *Pseudocaranx* georgianus

The offshore movement model provided a relatively good fit to the real data for *P. georgianus* collected between 2001 and 2004 (n = 247 inshore fish and 107 offshore fish) (Fig. 10). Bootstrap estimates of F_1 and F_2 , obtained by fitting the model to resampled data, indicate that the mortality of this species differed substantially between the two regions (Table 4). Although the median estimate obtained for F_2 (0.02 year⁻¹) indicates that fishing mortality of *P. georgianus* in the offshore region at the time of sampling was negligible, the larger value for F_1 (0.30 year⁻¹) suggests that the fishing pressure on this species in inshore waters was more substantial, *i.e.* at about the level of estimated natural mortality for this species.

Estimates of the parameters that describe the size-dependent selectivity and offshore movement of *P. georgianus* (Table 4) are consistent with the observed size composition data. For example, the resulting estimate of L_{50}^{Sel} corresponds to a point approximately halfway up the ascending limb of the observed length-frequency distribution for *P. georgianus* in the inshore region, and the estimated value for L_{95}^{Sel} is close to the peak of this distribution. Likewise, the estimate for L_{50}^{Move} is close to the halfway-point of the ascending limb in the offshore length frequency distribution, and the estimate for L_{95}^{Move} is close to the path of the ascending limb in the offshore length frequency distribution, and the estimate for L_{95}^{Move} is close to the path of the ascending limb in the offshore length frequency distribution (Fig. 10c, d).

Estimates of the rates of decline of fully-recruited *Pseudocaranx georgianus* from inshore waters in 2001-2004 *vs.* 2009-2012

The rate of decline of *P. georgianus* with increasing age in inshore waters (due to a combination of mortality and offshore movement, as determined using linear catch curve analysis, was not markedly different between 2001-2004 and 2009-2012. When fitting the catch curve to all age classes in the sample data beyond the age corresponding to the peak frequency, and to all subsequent age classes with one or more fish, the median annual "rate of decline" of fish from the inshore region was 0.72 year⁻¹ (95% CIs, 0.49-0.92 year⁻¹) for the earlier sampling period, compared with 0.63 year⁻¹ (95% CIs, 0.51-0.78 year⁻¹) for the more recent period. Following truncation of the data sets so that the minimum frequency of fish to which the catch curves were fitted was at least five, the estimated annual "rate of decline" of fish from the inshore region for the 2001-2004 sampling period of 0.42 year⁻¹ (95% CIs, 0.28-0.67 year⁻¹) was about two thirds of that calculated for the 2009-2012 period as 0.60 year⁻¹ (95% CIs, 0.51-0.74 year⁻¹).

Per-recruit and decision table analyses (for exploring management implications, for *Pseudocaranx georgianus*, of model uncertainty)

Per-recruit analyses showed that the levels of mortality experienced by *P. georgianus* in inshore waters can influence, conspicuously, the overall yield and



Fig. 10. Observed and expected relative (a, b) age and (c, d) length frequency distributions for *Pseudocaranx georgianus* in inshore (a, c) and offshore (b, d) waters. The expected frequency distributions were produced by fitting the model to data for *P. georgianus* collected between 2001 and 2004.

Parameter	Median (95% CIs)
L ₅₀ ^{sel} (mm)	338 (328-348)
L ^{Sel} (mm)	414 (396-432)
L ^{Move} (mm)	434 (416-452)
L ^{Move} (mm)	593 (536-630)
F_1 (year ⁻¹)	0.30 (0.20-0.39)
F_2 (year ⁻¹)	0.02 (0.0001-0.11)

Table 4. Median values of model parameter estimates and associated 95% confidence intervals (CIs; in parentheses) obtained by fitting the model to 1000 sets of resampled "real" age and length data for *Pseudocaranx georgianus* collected between 2001 and 2004 in south-western Australia (n = 247 and 107 fish from inshore and offshore waters, respectively).

spawning potential of the stock. As would be expected, when the level of offshore fishing mortality was negligible, the value of overall YPR for *P. georgianus* increased markedly as the inshore mortality increased from 0 to 0.3 year⁻¹ (Fig. 11a). For any given level of inshore mortality, the maximum values of YPR were obtained at an offshore fishing mortality of about 0.3 year⁻¹ (Fig. 11a). At this level of mortality, the values of overall YPR were 4419, 4319, 4234 and 4096 g recruit⁻¹ when the rate of inshore fishing mortality was 0, 0.1, 0.2 and 0.3 year⁻¹, respectively.

For any of the specified values for inshore fishing mortality, the overall SPR for *P. georgianus* decreased as offshore mortality increased (Fig. 11b). Even at a relatively low offshore fishing mortality of 0.1 year⁻¹, increasing the inshore fishing mortality from 0 to 0.1, 0.2 and 0.3 year⁻¹ resulted in the overall SPR declining from 0.66 to 0.57, 0.50 and 0.44 (equivalent to percentage declines of 14, 24 and 33%), respectively. As the level of inshore fishing mortality was increased from 0 to 0.1, 0.2 and 0.3 year⁻¹, the often-used limit reference point for SPR of 0.3 (*e.g.* Goodyear, 1993; Mace and Sissenwine, 1993), is reached, *i.e.* as the respective values of offshore fishing mortality are approximately 0.47, 0.36, 0.28 and 0.22 year⁻¹.

Multiple fits of the offshore movement model to the same (2001-2004) data for *P. georgianus*, using different assumptions regarding the relationship between the size at which fish become fully-selected by the fishing gear and the size at which they move offshore (*i.e.* imposing different "penalties" to ensure they remain within biologically feasible bounds when fitting the model) affected the estimates of the various model parameters (Table 5). As the specified minimum difference between L_{95}^{Sel} and L_{50}^{Move} was increased from -40 to +40 mm, estimates of the two selectivity parameters declined, whilst the L_{50}^{Move} estimate subsequently increased (Table 5). Differences between the estimates obtained for the nine penalty scenarios explored in this analysis (see Table 5) varied more for some parameters than others. For example, the resulting estimates of inshore mortality ranged from 0.27



Fig. 11. Relationships between offshore fishing mortality and overall (a) yield per recruit (YPR; g recruit⁻¹), and (b) spawning potential ratio (SPR), based on spawning biomass per recruit for female *Pseudocaranx georgianus* in south-western Australia, given four alternative levels of inshore fishing mortality (F; year⁻¹).

Table 5. Estimates of model parameters describing the size-dependent selectivity of fish (L_{50}^{Sel} and L_{95}^{Sel}), movement of fish to offshore waters (L_{50}^{Move} and L_{95}^{Move}), and for the fishing mortality in the inshore and offshore regions (F_1 and F_2 , respectively), produced by fitting the offshore movement model to observed data for *Pseudocaranx georgianus* collected between 2001 and 2004, for a range of alternative scenarios in which the penalty implemented to ensure that then minimum difference between L_{95}^{Sel} and L_{50}^{Move} differed (see Table 2). Estimates in red highlight the two parameters which are constrained by the specified penalty.

	Parameter estimates						
– Penalty scenario	L ^{Sel} (mm)	L ^{Sel} (mm)	L ^{Move} (mm)	L ^{Move} (mm)	F ₁ (year ⁻¹)	F ₂ (year ⁻¹)	
-40	358	446	406	553	0.27	0.0002	
-30	353	442	412	568	0.29	0.0001	
-20	352	437	417	585	0.34	0.0062	
-10	350	437	427	590	0.34	0.0001	
0	347	429	429	569	0.35	0.0039	
10	345	428	438	609	0.37	0.0001	
20	340	414	434	590	0.33	0.0001	
30	336	410	440	592	0.30	0.0233	
40	334	402	442	604	0.31	0.0109	

to 0.37 year⁻¹, whilst the estimates of the offshore fishing mortality varied only between 0.0001 and 0.023 year⁻¹ (Table 5).

Given the estimates of the model parameters for *P. georgianus* produced for the nine penalty scenarios, results from the per-recruit calculations undertaken using these values also varied among the different scenarios (Table 6). When no change in the inshore fishing mortality was considered, the values for YPR for the different penalty scenarios were generally reflected by the values of inshore and offshore fishing mortality estimated by the offshore movement model, where the yields increased with an increasing mortality in the two regions (Tables 5 and 6). The largest YPR were obtained for the scenarios in which the minimum difference between L_{95}^{Sel} and L_{50}^{Move} was greatest, *i.e.* when estimates indicated that *P. georgianus* became selected at a smaller size and moved offshore at a larger size (Tables 5 and 6). For the management scenarios in which the inshore fishing mortality estimate was changed, the resulting mean value of YPR across the nine penalty scenarios showed some response to these changes. For example, increasing the inshore fishing mortality by 40% resulted in a 12% increase in the mean YPR (from 698 to 783 g recruit⁻¹), whilst a 40% reduction of inshore fishing mortality led to a 20% decrease in the mean yield (to 558 g recruit⁻¹).

The values of SPR for *P. georgianus* for the different penalty scenarios corresponded well with the fishing mortality estimates produced by the offshore movement model. As the sum of the fishing mortality of this species in inshore and

Table 6. Decision table showing the consequences of alternative management decisions to reduce and increase the inshore fishing mortality (F, year⁻¹) on the expected overall yield per recruit (YPR) and spawning potential ratio (SPR; based on the spawning biomass per recruit), calculated using the parameter estimates produced when fitting the offshore movement model to real available data for *Pseudocaranx georgianus*. The model fits were repeated for different penalty scenarios in which the specified minimum difference allowed between the model parameters L_{95}^{Sel} and L_{50}^{Move} ranged between -40 and 40 (see Tables 2 and 5).

Managamant	Penalty scenario ($L_{50}^{\text{Move}} - L_{95}^{\text{Sel}}$; mm)									
scenario	-40	-30	-20	-10	0	10	20	30	40	Mean
YPR										
F -40%	298	342	579	454	559	546	489	986	766	558
F -20%	366	417	651	542	643	641	583	1044	844	637
No change	423	479	707	611	708	711	656	1085	903	698
F +20%	472	530	750	665	759	763	713	1115	946	746
F +40%	514	573	783	707	799	801	756	1134	977	783
SPR										
F -40%	0.86	0.83	0.76	0.78	0.75	0.73	0.76	0.65	0.70	0.75
F -20%	0.82	0.79	0.71	0.72	0.69	0.67	0.70	0.60	0.64	0.70
No change	0.78	0.75	0.67	0.68	0.64	0.62	0.65	0.56	0.59	0.66
F +20%	0.75	0.72	0.63	0.64	0.60	0.58	0.61	0.52	0.55	0.62
F +40%	0.72	0.68	0.60	0.60	0.56	0.54	0.57	0.48	0.51	0.58

offshore waters increased, the SPR decreased (Tables 5 and 6). For the management scenario in which the inshore fishing mortality was increased by 40%, the mean SPR across the nine penalty scenarios decreased by 12% (from 0.66 to 0.58), whilst reducing the fishing mortality by 40% resulted in the mean value of SPR increasing by 13% (to 0.75).

Age and length data for Sillaginodes punctata

In total, 624 *Sillaginodes punctata* were collected by multiple fishing methods (*i.e.* seine netting, haul netting, gillnetting and line fishing) from estuarine and coastal marine waters near Perth, including 187 fish from the nearshore region (< 1.5 m deep, over sand in estuaries and coastal embayments), 244 fish from the inshore region (~ 2-15 m deep over sand or sand/seagrass in coastal waters), and 193 fish from the offshore region (4-60 m deep around reefs). All of the *S. punctata* collected from nearshore waters were caught (by researchers) by seine netting. In inshore waters, 97 fish were caught by commercial haul netting, 33 were caught by commercial gillnetting and 114 fish were caught by recreational line fishing. All offshore fish were caught by recreational line fishing.

All of the *S. punctata* in the sample were able to be aged. Virtually all fish in the nearshore region were < 2 years old and the vast majority of fish in inshore waters were < 4 years old. Fish in the offshore region ranged widely in age, *i.e.* 2-13 years (Fig. 12a). *Sillaginodes punctata* in nearshore waters were generally < 250 mm in length, those in inshore waters were typically between 250 and 350 mm, and those in offshore waters were mainly > 400 mm (Fig. 12b).

Of the total sample of *S. punctata*, 93 and 193 fish from inshore and offshore waters, respectively, were caught by line-fishing and above the minimum legal length for retention for this species of 280 mm (Fig. 13). These were the data subsequently used when fitting the offshore movement model to estimate mortality of this species.

The mean length of one year old *S. punctata* in the inshore region (*i.e.* 283 mm) was substantially larger than that for fish at this age in the nearshore region (*i.e.* 204 mm) (Fig. 14a). Likewise, the mean lengths of fish at comparable ages in the offshore region were always larger than those in nearshore waters, *i.e.* 393, 432 and 462 mm *vs.* 310, 412 and 427 mm at ages 2, 3 and 4 years, respectively (Fig. 14b).

Growth of Sillaginodes punctata accounting for individual variability

The relationships between total length, L_c , and otolith radius, R_c , at capture for the 49 female and 48 male *S. punctata* from nearshore, inshore and offshore waters were described well by the generalised logistic function (Fig. 15). Fitting the non-linear random effects model to the sex-specific back-calculated length-at-age data sets (Fig. 16) produced estimated mean values of the von Bertalanffy growth parameters L_{∞} , k and t_0 that were 543.1 mm, 0.446 year⁻¹ and 0.395 years, respectively, for females and 526.5 mm, 0.514 year⁻¹ and 0.568 years, respectively, for males (Table 7). Note that, when fitting growth curves for



Fig. 12. (a) Age and (b) length frequency distributions for *Sillaginodes punctata* caught by a combination of seine netting, haul netting, gillnetting, trawling and line fishing) between 2010 and 2012 in nearshore (white bars), inshore (light blue bars) and offshore (dark blue bars) coastal waters of south-western Australia. Age and length frequency distributions; n = 187 fish for nearshore waters, n = 244 fish for inshore waters and n = 193 fish for offshore waters.



Fig. 13. (a) Age and (b) length frequency distributions for line-caught *Sillaginodes punctata* that were collected between 2010 and 2012 in inshore (light blue bars) and offshore (dark blue bars) coastal waters of south-western Australia and above 280 mm in total length. Age and length frequency distributions; n = 93 fish for inshore waters and n = 193 fish for offshore waters.



Fig. 14. Mean (±1SE) total lengths (mm) of *Sillaginodes punctata* in (a) nearshore *vs.* inshore waters and (b) inshore *vs.* offshore waters, for ages that were represented in the two respective regions for each comparison. Age classes (years) and corresponding sample sizes for nearshore waters; 1 + (n = 60). Age classes and corresponding sample sizes for inshore waters; 1 + (n = 64), 2 + (n = 136), 3 + (n = 10), 4 + (n = 4). Age classes and corresponding sample sizes for offshore waters; 2 + (n = 10), 3 + (n = 61), 4 + (n = 37). Numbers on plot refer to age classes (years).



Fig. 15. Relationships between the total length (mm) and otoliths radius (mm) of (a) 49 female and (b) 48 male *Sillaginodes punctata* caught in nearshore (white circles) inshore (light blue circles) and offshore (dark blue circles) coastal waters of south-western Australia.



Fig. 16. Back-calculated lengths at ages of (a) 22 female and (b) 24 male *Sillaginodes punctata* caught in inshore (light blue squares) or offshore waters (dark blue squares) of south-western Australia. Note that each fish is represented by multiple data points, *i.e.* which correspond to the estimated lengths at the ages at which each successive opaque zone in its otolith were formed (and became delineated from the otolith edge), and at the age when the fish was caught.

Table 7. Means and standard deviations (SD) for estimates of the von Bertalanffy growth parameters and the correlation between L_{∞} and k for individual female and male *Sillaginodes punctata*. The estimates were obtained by fitting a non-linear random effects growth model to back-calculated lengths at age for female and male *S. punctata*, estimated using the body proportional hypothesis.

	Fem	ales	Males		
Parameter	Mean	SD	Mean	SD	
Asymptotic length, L_{∞} (mm)	543.1	12.5	526.5	14.4	
Growth coefficient, k (year ⁻¹)	0.446	0.021	0.514	0.025	
Theoretical age at length zero, t_0 (years)	0.395	6.189	0.568	6.408	
Correlation L_{∞}/k	-0.364	0.290	-0.483	0.326	

S. punctata, the length-at-age data were restricted to individuals whose otoliths contained at least 2 opaque zones.

Although the growth parameters differed between the two sexes, the estimated growth curves for female and male *S. punctata* were virtually the same for fish < 7 years of age, beyond which the lengths of fish increased only marginally as age increased further (Fig. 17). Moreover, the respective values for L_{∞} for the two sexes differed by only ~3% (17 mm), indicating that the difference at the upper ends of the growth curves for females and males was too small to be considered biologically important (Table 7). Thus, the length-at-age data for the two sexes were pooled to produce a single set of growth parameters which were then used when fitting the mortality model for this species (Table 8). As with *P. georgianus*, the prior distributions specified in the random effects model for the three growth parameters for *S. punctata* were very broad relative to the posterior distributions for those parameters (Fig. 18). For *S. punctata*, the estimated correlation between L_{∞} and *k* was -0.392 (Table 8).

Explorations of the robustness of the offshore movement model using simulated data for *Sillaginodes punctata*

Fitting the offshore movement model to data simulated for *S. punctata* (using a combination of Solver in Excel and the Nelder-Mead (1965) simplex optimisation algorithm for minimising the objective function) produced estimated means for the six model parameters that were similar to the "true" values of those parameters specified when simulating the data (Fig. 19). When fitting the model, as for *P. georgianus*, to both age and length data for the inshore and offshore regions, and the specified sample sizes for the two respective regions were 100 and 200 fish, the median values for estimates of F_1 (0.27 year⁻¹) and F_2 (0.10 year⁻¹) were close to or the same as the specified "true" values for these parameters of 0.3 and 0.1 year⁻¹. For that same scenario, the median values of the estimates for the two movement parameters L_{50}^{Move} and L_{95}^{Move} (400 and 454 mm, respectively) were also either very close to or the same as the respective specified true values for these



Fig. 17. von Bertalanffy growth curves of female and male *Sillaginodes punctata* given estimates of the growth parameters produced using the individual growth model fitted to back-calculated length at age data for each of the two sexes.

Table 8. Means and standard deviations (SD) for estimates of the von Bertalanffy growth parameters and the correlation between L_{∞} and k for *Sillaginodes punctata*. The estimates were obtained by fitting a non-linear random effects growth model to back-calculated lengths at age for *S. punctata* (sexes combined), estimated using the body proportional hypothesis.

Parameter	Mean	SD
Asymptotic length, L_{∞} (mm)	528.8	8.6
Growth coefficient, k (year ⁻¹)	0.487	0.016
Theoretical age at length zero, t_0 (years)	-0.510	4.566
Correlation L_{∞}/k	-0.392	0.296

parameters (400 and 450 mm). Fitting the model to simulated data for *S. punctata* of a larger sample size (500 inshore fish and 1000 offshore fish) yielded median parameter estimates that were also near the true, specified values for those parameters (Fig. 19).

As was the case with *P. georgianus*, the precision of parameter estimates produced by the offshore movement model when fitted to simulated data for *S. punctata* differed substantially among the six parameters (Fig. 19). For example, when the specified sample sizes for inshore and offshore waters were 100 and 200 fish, respectively, the CVs calculated from the 100 estimates of F_1 (0.80) and F_2 (0.35) produced by the original version of the model were substantially larger than those for L_{50}^{Sel} (0.02) and L_{95}^{Sel} (0.04). Increasing the sample



Fig. 18. Probability distributions (a, c, e) and prior probability distributions (b, d, f) for the three von Bertalanffy growth parameters, L_{∞} , k and t_0 , for *Sillaginodes punctata* when estimated using the non-linear random effects model fitted to back-calculated lengths at ages (for both sexes combined) estimated using the body proportional hypothesis. Results are based on data for 45 fish and 255 lengths at ages.



Fig. 19. Model estimates of (a, b) selectivity parameters, (c, d) movement parameters, and (e, f) inshore and offshore fishing mortalities (*F*) when fitted to simulated data for *Sillaginodes punctata*. The model was fitted to data for two scenarios of differing sample sizes, *i.e.* 100 and 200 fish in inshore and offshore waters, respectively (white boxes), and 500 inshore fish and 1000 offshore fish (grey boxes). The scenarios were repeated employing two fitting approaches, *i.e.* including the inshore age composition data in the overall log-likelihood (left hand side of each graph), and excluding the inshore age composition data (right hand side of each graph). The line inside each box represents the median value, the bottom and top of the box show the 25th and 75th percentiles, and the lower and upper bars show the minimum and maximum values for 100 model fits. The true values for the parameters are represented as the dashed lines.

sizes typically led to improved precision of parameter estimates (Fig. 19). For example, increasing the sample size of the data to which the original version of the model was fitted (to 500 inshore fish and 1000 offshore fish) produced estimates of F_2 with a CV of 0.17, corresponding to a 51% decrease in variation. Excluding the log-likelihood component associated with the inshore age composition data when fitting the model to simulated data (which was subsequently necessary to produce realistic estimates of the mortality parameters when the model was fitted to real data for *S. punctata*), did not markedly influence on the accuracy or precision of estimates of model parameters (Fig. 19).

Fits of offshore movement model to real data for Sillaginodes punctata

The offshore movement model provided a good fit to the real data for *S. punctata* collected between 2010 and 2012 (n = 93 inshore fish and 193 offshore fish) (Fig. 20), noting that all fits to the re-sampled observed data for this species were undertaken excluding the log-likelihood associated with the inshore age composition data in the overall objective function. The median values of the bootstrap estimates for F_1 and F_2 produced by the model indicate that the fishing mortality of this species in inshore waters (0.55 year⁻¹) is larger than that in the offshore region (0.06 year⁻¹). The relatively large confidence levels around these point estimates, however, particularly for estimates of the inshore fishing mortality, demonstrate that these estimates are far less precise than for the offshore fishing mortality (Table 9).

As with *P. georgianus*, estimates of the selectivity and movement parameters for *S. punctata* were consistent with the patterns exhibited by the observed length composition data for this species (*cf.* Table 9 and Fig. 20). This partly reflected, however, the values of certain parameters being bounded by constraints that were imposed when fitting the model, to ensure that the selectivity and movement parameters remained within feasible bounds. The key constraints that influenced the estimates of the two movement parameters were the limit imposed to ensure L_{50}^{Move} remained above 390 mm and another that ensured L_{95}^{Move} was less than 460 mm. These values corresponded to the length range over which the frequencies in the offshore region were increasing or had just peaked (Fig. 20d). The estimates of the selectivity parameters were influenced by a constraint which ensured that the value for L_{95}^{Sel} was at least 10 mm greater than L_{50}^{Sel} , *i.e.* as estimated mean value for L_{95}^{Sel} was exactly 10 mm above that for L_{50}^{Sel} .



Fig. 20. Observed and expected relative (a) age and (b) length frequencies of *Sillaginodes punctata* in inshore (a, c) and offshore (b, d) waters, indicating a good fit of the model to the data collected for this species between 2010 and 2012.

Table 9. Median values of model parameter estimates and associated 95% confidence intervals (CIs; in parentheses) obtained by fitting the model to 100 sets of resampled real age and length data for *Sillginodes punctata* collected between 2010 and 2012 in south-western Australia (n = 93 and 193 fish from inshore and offshore waters, respectively).

Parameter	Median (95% CIs)
L ^{Sel} (mm)	285 (282-290)
L_{95}^{Sel} (mm)	295 (292-300)
L ^{Move} (mm)	390 (390-403)
L ^{Move} (mm)	460 (457-460)
F_1 (year ⁻¹)	0.55 (0.11-1.00)
F_2 (year ⁻¹)	0.06 (0.004-0.12)

Per-recruit and decision table analyses (for exploring management implications, for *Sillaginodes punctata*, of model uncertainty)

The per-recruit analyses for *S. punctata* indicated that the level of inshore mortality can markedly influence the overall yield and spawning potential of the stock. Given a low value of fishing mortality in the offshore region, the overall YPR for *S. punctata* increased substantially as the inshore mortality increased from 0 to 0.6 year⁻¹ (Fig. 21a). Regardless of the value of inshore mortality, the overall YPR increased with increasing offshore mortality up to a maximum level of 0.52 year⁻¹, after which the overall YPR then declined (Fig. 21a). At this level of offshore mortality, the values of overall YPR were 1236, 1238, 1191 and 1123 g recruit⁻¹ when the rate of inshore fishing mortality was 0, 0.2, 0.4 and 0.6 year⁻¹, respectively.

For any of the specified levels of inshore fishing mortality, the overall SPR for *P. georgianus* decreased substantially as offshore mortality increased (Fig. 21b). Even at a relatively low offshore fishing mortality of 0.1 year⁻¹, increasing the inshore fishing mortality from 0 to 0.2, 0.4 and 0.6 year⁻¹ resulted in the overall SPR declining from 0.70 to 0.54, 0.43 and 0.35 (equivalent to percentage declines of 23, 39 and 50%), respectively. As the inshore fishing mortality is increased from 0 to 0.2, 0.4 and 0.6 year⁻¹, the limit reference point for SPR of 0.3 is reached as the respective values of offshore fishing mortality are approximately 0.48, 0.33, 0.23 and 0.15 year⁻¹.

Fitting the offshore movement model multiple times to the same real data for *S. punctata* and using different specified penalties to ensure that the movement parameters remained within biologically feasible bounds did not markedly influence estimation of the model parameters (Table 10). As the specified lower limit for L_{50}^{Move} was reduced from 390 to 350 mm, the estimate of this parameter only went as low as 387 mm, indicating that this penalty could have been relaxed without this having much impact on parameter estimation (Table 10). In contrast, as the specified upper limit for L_{95}^{Move} was increased from 460 to 500 mm, the estimate of this parameter were always constrained by these bounds (Table 10). Estimates of the offshore fishing mortality were very similar across the nine penalty scenarios, ranging in only between 0.04 and 0.06 year⁻¹. Inshore fishing mortality estimates were also relatively stable for scenarios in which the specified upper limit for this movement parameter was increased to 490 and 500 mm, however, the inshore mortality increased to 0.71 and 0.66 year⁻¹, respectively.

Given the limited impact of the imposed penalty functions for *S. punctata* on the estimates of the model parameters, results from the per-recruit calculations undertaken using these values differed only slightly between the nine different scenarios (Table 11). As was the case for *P. georgianus*, when no change in the inshore fishing mortality was considered the YPR values for the different penalty scenarios were generally reflected by the values of fishing mortality estimates produced by the offshore movement model (Tables 10 and 11).



Fig. 21. Relationships between offshore fishing mortality and overall (a) yield per recruit (YPR; g recruit⁻¹), and (b) spawning potential ratio (SPR), based on spawning biomass per recruit for female *Sillaginodes punctata* in south-western Australia, given four alternative levels of inshore fishing mortality (F; year⁻¹).

Table 10. Estimates of model parameters describing the size-dependent selectivity of fish (L_{50}^{Sel} and L_{95}^{Sel}), movement of fish to offshore waters (L_{50}^{Move} and L_{95}^{Move}), and fishing mortality in the inshore and offshore regions (F_1 and F_2 , respectively). The estimates were produced by fitting the offshore movement model for estimating mortality to real data for *Sillaginodes punctata* collected between 2010 and 2012, using different penalties to constrain the bounds of the two movement parameters (see Table 2). Estimates in red highlight the two parameters which were constrained by the specified penalties.

	Parameter estimates						
– Penalty scenario	L ^{Sel} (mm)	L ^{Sel} (mm)	L ^{Move} (mm)	L ^{Move} (mm)	<i>F</i> 1 (year⁻¹)	F_2 (year ⁻¹)	
1	285	295	389	460	0.53	0.04	
2	285	295	388	460	0.49	0.04	
3	285	295	387	460	0.45	0.04	
4	285	295	388	460	0.53	0.05	
5	285	295	390	460	0.54	0.05	
6	285	295	390	470	0.53	0.06	
7	285	295	398	480	0.58	0.05	
8	284	294	405	490	0.71	0.04	
9	284	294	408	500	0.66	0.04	

Table 11. Decision table showing the consequences of alternative management decisions to reduce and increase the inshore fishing mortality (F, year⁻¹) on the expected overall yield per recruit (YPR) and spawning potential ratio (SPR; based on the spawning biomass per recruit), calculated using the parameter estimates produced when fitting the offshore movement model to real available data for *Sillaginodes punctata*. The model fits were repeated for different penalty scenarios in which the specified minimum difference allowed between the model parameters L_{50}^{Move} and L_{95}^{Move} differed (see Tables 2 and 10).

	Penalty scenario									
Management	$L_{50}^{Move} > 350$	$L_{50}^{Move} > 360$	$L_{50}^{Move} > 370$	$L_{50}^{Move} > 380$	$L_{50}^{ m Move} > 390$	$L_{50}^{Move} > 390$	$L_{50}^{Move} > 390$	$L_{50}^{Move} > 390$	$L_{50}^{Move} > 390$	Mean
scenario	$L_{95}^{Move} < 460$	$L_{95}^{Move} < 460$	$L_{95}^{Move} < 460$	$L_{95}^{Move} < 460$	$L_{95}^{ m Move} < 460$	$L_{95}^{Move} < 470$	$L_{95}^{Move} < 480$	$L_{95}^{Move} < 490$	$L_{95}^{Move} < 500$	
YPR										
F -40%	619	651	602	626	653	702	693	703	704	661
F -20%	654	651	637	660	685	729	723	728	733	689
No change	675	673	661	680	702	742	737	733	742	705
F +20%	686	685	676	690	710	746	739	725	737	711
F +40%	689	690	684	693	710	742	734	710	725	709
F -40%	0.58	0.53	0.61	0.58	0.56	0.54	0.53	0.48	0.49	0.54
F -20%	0.52	0.53	0.55	0.52	0.50	0.48	0.46	0.40	0.42	0.49
No change	0.47	0.48	0.50	0.46	0.44	0.43	0.40	0.34	0.36	0.43
F +20%	0.42	0.43	0.46	0.41	0.40	0.39	0.36	0.29	0.31	0.39
F +40%	0.38	0.39	0.42	0.37	0.36	0.35	0.32	0.25	0.27	0.35

For the management scenarios in which the fishing mortality in the inshore region was reduced, the mean value of YPR for the overall stock decreased accordingly for all penalty scenarios (Table 11). Increasing the inshore fishing mortality, however, only increased the YPR up to a maximum value of 746 g recruit⁻¹, after which increasing the mortality further resulted in a reduced overall yield (Table 11). Increasing the inshore fishing mortality by 20% only resulted in an increase of the mean value of YPR across the nine penalty scenarios of less than 1% (from 705 to 711 recruit⁻¹), whilst a 40% increase in the inshore mortality resulted in a mean YPR of 709 recruit⁻¹.

Values of SPR for *S. punctata* for the nine penalty scenarios generally showed a similar pattern to the values of YPR, however, decreased with increasing levels of mortality (Table 10 and 11). Increasing the inshore fishing mortality by 40% resulted in a decrease in the mean SPR across the nine penalty scenarios by 20% (from 0.43 to 0.35), whilst reducing the fishing mortality by 40% resulted in the mean value of SPR increasing by 26% (to 0.54).

8. DISCUSSION

This study has described a method for estimating growth and mortality of fish species, such as Pseudocaranx georgianus and Sillaginodes punctata, which undertake pronounced (unidirectional), size-dependent movements during life, e.g. from shallower, inshore waters to deeper, more offshore waters. By fitting the new model to simulated age and length data for *P. georgianus* and *S. punctata*, it could be demonstrated that, on average, the model can reliably estimate parameters describing size-dependent gear selectivity, offshore movement and inshore and offshore mortality. Model explorations employing simulated data also indicated, however, that mortality estimates for the inshore region, in particular, are likely to be very imprecise for fish species that, like S. punctata, only occur in this region for a short period (and thus over a small size and age range). In such cases, the "information content" in the data that can be used to estimate this parameter is very limited. The model has also been fitted to real data for P. georgianus and S. punctata, thereby further demonstrating the applicability of the approach, and providing, for the first time, (preliminary) estimates of fishing mortality for these two fish species in both inshore and offshore coastal waters near Perth, in south-western Australia.

Per-recruit analyses accounting for size-dependent, offshore movements of fish have demonstrated the importance of being able to reliably estimate mortality of species like *P. georgianus* and *S. punctata* in each of the regions in which they are exploited by fishers. As with any model, the one developed in this study has several assumptions and specific (but relatively modest) data requirements. These aspects are now discussed, together with an illustration of its application using data for *P. georgianus and S. punctata*.

Size-dependent, offshore movements of fish

A key assumption of the model developed in this study for estimating fishing mortality is that the fish species exhibits a unidirectional offshore movement. In a previous study, Farmer et al. (2005) concluded that P. georgianus in coastal waters of south-western Australia move from inshore waters (< 60 m deep) to offshore waters (\geq 60 m deep). This conclusion was based on the observation that fish were typically larger and older in offshore waters, as also reflected in the maximum age and size of fish in offshore waters (18 years, 885 mm) being greater than for fish in inshore waters (11 years, 568 mm). Likewise, this type of movement is also suggested by length composition data for the closely-related P. dentex in the northeastern Atlantic (Afonso et al., 2008; 2009) and in Japan (Masuda and Tsukamoto, 1999). For S. punctata, the results of previous biological studies on this species in South Australia and Western Australia provided very strong evidence that the individuals of this species undertake a pronounced, unidirectional movement from shallow (<1.5 m deep), nearshore waters in estuaries or coastal waters to deeper (2-15 m deep) waters in those environments, respectively, and finally to coastal reefs as individuals approach maturity (Hyndes et al., 1998; Fowler et al., 2000; Fowler et al., 2002). With the exception of the shallow, nearshore environment for S. punctata,

both *P. georgianus* and *S. punctata* are targeted by anglers in each of the "habitats" occupied by these species throughout life.

The finding in this study that, for any given age, the respective mean lengths of *P. georgianus* and *S. punctata* are consistently larger for fish sampled in offshore waters provides strong evidence that the movements of these species in Western Australia are strongly size-dependent. The fact that, at a given age, fish in offshore waters were typically larger than those in inshore waters implies that, at any time, it is the largest individuals of these species (of this age) in the inshore region that are most likely to move offshore. The above attributes of these species have important implications for obtaining reliable estimates of fishing mortality for these species.

Firstly, as fishing mortality may differ between inshore and offshore waters, it is important to obtain an estimate of mortality for each of the environments occupied by individuals of these species in which they are fished. Secondly, at corresponding ages, the length distributions of fish in inshore and offshore waters differ, which means that age composition data, on its own, is unlikely to be sufficient for estimating the rates at which fish move offshore. Thirdly, if mortality of fish can be assumed to be age-dependent and if movement can be shown to be largely size-dependent, these two variables will impact on the age and length compositions of this species differently. This difference, *i.e.* in the ways in which the processes of movement and mortality influence age and length composition data, provided a basis for allowing these two parameters to be estimated for *P. georgianus* and *S. punctata* from such data.

The age and size compositions of fish in a population are strongly influenced by the growth patterns of its individuals and hence, any attempt to estimate movement and mortality will require a reliable description of growth for the fish species being studied. As the probability of an individual of a specified age moving from inshore to offshore waters, as described above, differs depending on its length, it is also necessary to account for variability in the growth of fish when estimating parameters that describe this movement process. In more recent years, approaches have been developed for estimating the individual variability in the growth of fish (*e.g.* Pilling *et al.*, 2002), which were able to be adopted for this study.

Patterns of individual growth of fish

This study is the first to describe the overall pattern of growth of *P. georgianus* throughout its depth range by accounting for the size-related movement of this species from inshore to offshore waters. For *S. punctata*, a recent study on this species in south-western Australia described the growth of this species using a model that accounted for size-dependent, offshore movements by this species, which yielded robust estimates of von Bertalanffy growth parameters (Sulin, 2012). That study employed the modified von Bertalanffy growth model described by Hesp *et al.* (2004), which was developed to describe the growth of the Tarwhine (*Rhabdosargus sarba*), another species which exhibits size-related offshore movements. That method, however, does not provide any information about the extent to which growth patterns vary among individuals of a species.

Although the recent study by Sulin (2012) demonstrated that, by accounting for offshore, size-related movement of fish, the growth model of Hesp *et al.* (2004) provided a better description of growth of *S. punctata* than the traditional von Bertalanffy growth model, the offshore movement parameter estimates produced by that model were very imprecise. Thus, the growth model of Hesp *et al.* (2004) did not, on its own, provide sufficient information on the growth of King George Whiting (*i.e.* it did not account for individual variation or provide sufficiently precise estimates of parameters describing its offshore movement) for subsequent use in the model developed in this study for estimating fishing mortality. Thus, for King George Whiting, an alternative approach to describing growth (and movement parameters) was required.

The statistical method applied in this study for describing growth of individual *P. georgianus* and *S. punctata* is based on data derived using back-calculation methods. As pointed out by Campana (1990), growth back-calculations assume that (i) the periodicity of the deposition of growth increments on otoliths is constant over time, as has been verified for *P. georgianus* by Farmer *et al.* (2005) and for *S. punctata* by Hyndes et al. (1998) using marginal increment analysis, and (ii) the distance between these increments relates directly to the somatic growth of fish. The observation that, for fish caught in both inshore and offshore waters, the total lengths of individual *P. georgianus* and *S. punctata* were related strongly and in the same manner to their otolith radii, suggests that, for each species, an otolith-based back-calculation approach was appropriate for describing their growth.

The growth estimates obtained by fitting a slightly-modified version of the random effects model of Pilling *et al.* (2002), *i.e.* which assumed a bivariate distribution for L_{∞} and k among individual fish and a common t_0 for all fish compared with a trivariate distribution for L_{∞} , k and t_0 among individual fish, demonstrated that the growth of *P. georgianus* varies considerably among individuals. This has also been shown for a number of other fish species, *e.g.* the Sand-smelt (*Atherina presbyter*, Moreno and Morales-Nin, 2003) and Red Snapper (*Lutjanus campechanus*; White and Palmer, 2004). The substantial variability in growth of individual *P. georgianus* is illustrated, for example, by the finding that the estimates of L_{∞} for different individuals ranged by as much as from ~ 900 to 1400 mm. Fitting the same model to back-calculated lengths at ages for *S. punctata* indicated that the growth of *P. georgianus* is much less variable among individuals (*cf.* Figs. 6 and 16; Tables 3 and 8), *e.g.* L_{∞} ranged only from ~ 500 to 570 mm.

In discussing the growth characteristics of *P. georgianus* and *S. punctata*, it may also be worth noting that the values obtained for the extent of correlation between L_{∞} and *k* differed markedly between the two species. Whilst the mean estimate of this parameter for *P. georgianus* (-0.829) is consistent with the general perception in the fisheries ecology literature that, among species, these two parameters are strongly negatively correlated (*i.e.* often in the range of -0.8 to -0.9; see Quinn and Deriso, 1999), the correlation between these parameters for *S. punctata* was only -0.392.

Robustness of the offshore movement model

To our knowledge, our model is the first to produce, for fish species that undertake a size-dependent offshore movement, estimates of fishing mortality in inshore and offshore waters, and of parameters describing the movement of fish between these waters and size-based selectivity to the fishing gear, using age composition and length-at-age data, a specified value for natural mortality and parameters that describe individual variation in growth. As size and age data are collected in many fish biological studies, the model may be widely-applicable in situations where targeted fish species exhibit an offshore, size-related movement. The model calculates the probabilities of sampled individuals occurring in inshore and offshore waters based on their ages and their sizes at those ages, and according to the specified value of natural mortality and patterns of growth. It is assumed that, for the age and size ranges over which the fish species is exploited, mortality is related solely to age whereas movement is strongly size-dependent. As described above, the age and length composition data for P. georgianus and S. punctata provide strong evidence that the offshore movement by these species is strongly sizerelated. It may also be noteworthy that a number of other fish species have been shown to exhibit offshore, size-related movements, e.g. Tarwhine (Rhabdosargus sarba; Hesp et al., 2004) and Mangrove Jack (Lutjanus argentimaculatus; Russell and McDougall, 2005). The assumption that mortality is age dependent is one that is commonly made in fisheries stock assessments, including those involving conventional catch curve analyses (Ricker, 1975). The modelling approach also requires (as assumed in this study for *P. georgianus* and *S. punctata*) that the samples across all habitats for a species are all derived from the same stock and that they adequate represent the relative abundances of individuals of different sizes and ages within each habitat.

The finding that, when fitting the model to simulated data for both *P. georgianus* and S. punctata, the values of the model parameters specified for simulating those data could (on average) be recovered, demonstrated the potential of the approach for providing robust parameter estimates for these fish species. The simulations thus indicated that, if substantial sample sizes for P. georgianus and S. punctata could be obtained from inshore and offshore waters, and if the values used to simulate data are within the "ball park" of the actual values of fishing mortality, and movement and gear selectivity parameters for these species, on average, the model is likely to yield reliable estimates of those parameters. The simulation testing also demonstrated, however, that if sample sizes are relatively small, as is the case with the data for both P. georgianus and S. punctata used in this study, then the estimated value of inshore mortality, in particular, is likely to be imprecise. Model explorations using simulated data for *P. georgianus* also showed that, if fish only reside in the inshore region for a short period (and thus over a very narrow age and size range), the amount of information in the inshore data may be insufficient for the model to "tease out" the differential effects of movement and mortality. In this regard, it may be worth noting that the value of simulation testing as an approach for assessing the robustness of fisheries assessment models is now widely recognised among fisheries stock assessment scientists (e.g. Cope and Punt, 2009; Wetzel and Punt, 2011). For any future use of the model developed in this study with other fish species, it is thus recommended that the likely robustness of the model first be investigated by simulating data using parameters appropriate for those species.

Another issue encountered when testing the robustness of the offshore movement model was that, although Solver alone was adequate to find a robust solution when fitting the model to simulated data for P. georgianus, this was not the case with S. punctata. Preliminary jitter tests using identical simulated age and length data for S. punctata, which closely resembled the real data collected for this species, produced estimates of the six model parameters and associated values of the overall log-likelihood (objective function) that varied substantially. Additional model explorations involving jitter tests (see Appendix 3) using alternative optimisation procedures demonstrated that stable values of the parameters and associated loglikelihood could be obtained by using the Nelder-Mead (1965) simplex algorithm in combination with Solver when fitting the model for this species. As S. punctata spends a very limited time in the inshore habitat before moving offshore, there was less information in the data (than for *P. georgianus*) for estimating movement and mortality, thereby making the model more difficult to fit. It is thus likely to be important, when applying this model to other species, to also trial different optimisation algorithms for determining which are likely to constitute the most optimal approach for fitting the model to data for that particular species.

Fitting the model to real data for Pseudocaranx georgianus

Estimates of fishing mortality for *P. georgianus* produced by fitting the model to real data collected for this species in south-western Australia (Farmer et al., 2005) indicated that fishing pressure in the early 2000s was substantially greater in inshore waters (0.3 year⁻¹, 95% CIs = 0.20-0.39 year⁻¹) compared with offshore waters (0.02) year⁻¹, 95% CIs = 0.00-0.11 year⁻¹). Although it must be recognised that these data for *P. georgianus* were collected about a decade ago, and that the situation with this species may have changed, the mortality estimates are consistent with anecdotal evidence from recreational anglers and charter boat fishers that they more frequently target and catch this species in inshore waters (E. Fisher, pers. obs., from discussions with recreational boat fishers and charter boat operators). As access to deeper (> 60 m), offshore waters is strongly weather-dependent and mainly limited to fishers with large boats, it might be expected that the levels of fishing mortality to which this mainly recreationally-targeted fish species is exposed in offshore waters is less than in the more easily accessible inshore region. Furthermore, fishers are known to catch offshore *P. georgianus* only during a few months of the year, at times when these fish have been found to aggregate over artificial reefs (sunken barges) in waters that are ~ 110 m deep. Such catches of *P. georgianus* often result from these fishers targeting other fish species, including Samson Fish (Seriola hippos).

When the model was fitted to resampled (*i.e.* bootstrapped) real data for *P. georgianus*, the resultant mortality estimates were less variable than those produced when the model was fitted to simulated data. This result may reflect the influence of one of the penalty terms imposed when fitting the model to keep certain parameters within feasible ranges. When fitting the model to real data, resultant estimates were constrained by the assumption imposed in the model that the mean length at which fish become selected by the fishing gear (L_{95}^{Sel}) is at least 20 mm less than the typical size at which the fish move offshore (L_{50}^{Move}). This assumption, which was necessary to be able to fit the model to the real data for *P. georgianus*, appeared consistent with the length compositions for this species in inshore and offshore waters. Although this resulted in estimated length and age compositions

that closely-matched the observed length and age compositions for *P. georgianus*, the need for this assumption represented a key source of uncertainty in the modelling, which therefore warranted further exploration (see section on decision table analyses for *P. georgianus*, below).

Fitting the model to real data for Sillaginodes punctata

Preliminary attempts to fit the model to real data for S. punctata demonstrated that, to obtain realistic parameter estimates, the model objective function needed to be modified to exclude one of the components that (for *P. georgianus*), contributed to the value of the model objective function, *i.e.* the log-likelihood associated with the inshore age composition data. The decision to modify the objective function was based on an exploration of the effect of modifying the value for inshore mortality on the values of each of the components of the objective function (i.e. the loglikelihoods associated with the age compositions and length-at-age distributions for inshore and offshore waters). This exploration demonstrated that, of the four components that contribute to the overall value of the objective function (prior to any modification of that function), the log-likelihood associated with the inshore age composition had, by far, the greatest influence on the overall value of the objective function when the value for inshore fishing mortality was changed. When its value was reduced from 0.6 to 0 year⁻¹, the change in value of the log-likelihood associated with the inshore age composition led, unexpectedly given that fishing is known to occur, to a substantial improvement in the value for the overall objective function. As the same type and strength of signal was not provided by the other three loglikelihood components of the model objective function, this indicated that, for S. punctata, "tension" existed between the different data sets when fitting the model, with the inshore age composition, *i.e.* as it provided a different "signal" to the other components with regards to the true value of inshore fishing mortality.

As *S. punctata* only reside in inshore waters (*i.e.* in waters 2-15 m deep, within estuaries or in sand/seagrass habitats in coastal waters) for a very short period (typically, no more than 2 years), the inshore age composition data should contain relatively limited information for estimating fishing mortality and yet the log-likelihood associated with these data exerted a strong influence on the data. Simulation testing, involving fitting the model to simulated data with the original objective function (all four components of the objective function included) and a modified objective function (without the log-likelihood associated with the inshore age composition) indicated that the model could still reliably estimate the "true" value of the inshore fishing mortality when the modified objective function was used. The precision did, however, reduce slightly. The above-described difficulties in fitting the model to real data when the inshore age composition was included in the analysis is considered to reflect a combination of the very short period over which *S. punctata* resides in inshore waters (limiting the information content in the inshore age composition data) and the limited sample size of 93 individuals that was able to be obtained during the study.

As with *P. georgianus*, when fitting the model (to real data, in particular) for *S. punctata*, it was necessary to constrain several of the parameter values to within "feasible" bounds. In some cases, the final estimates of parameters were the same as the values of the constraints imposed on those parameters. This included the movement parameters, which were constrained so that L_{50}^{Move} remained above

390 mm and another that ensured L_{95}^{Move} was less than 460 mm. These values corresponded to the length range over which the frequencies in the offshore region were increasing or had just peaked (Fig. 20d), *i.e.* the range over which the data indicated that fish were moving offshore. The estimates of the selectivity parameters were influenced by a constraint which ensured that the value for L_{95}^{Sel} was at least a small amount (10 mm) greater than L_{50}^{Sel} , *i.e.* as would be expected if size-based selectivity followed a logistic pattern. As indicated by the data, the selectivity curve for *S. punctata* is very steep, presumably due to the minimum legal length for capture and retention of this species (280 mm) being greater than the lengths at which individuals start becoming vulnerable to being caught by the gear. The above constraints, which enabled the model to provide good visual fits to the data, are thus considered appropriate.

Model fits to the real data collected for S. punctata between 2010 and 2012 from coastal waters near Perth yielded preliminary estimates of inshore and offshore fishing mortality for this species. Although the point estimate for fishing mortality in the inshore region (0.55 year⁻¹) was substantially greater than the estimated value of natural mortality of this species (0.3 year⁻¹), the estimated value for fishing mortality in the offshore region, where this species occurs for the majority of life, was very low (0.06 vear⁻¹). The above indication that fishing mortality is lighter in offshore waters may reflect the increased difficulty in catching this species in this environment (as S. punctata tend to be far more dispersed than in inshore waters), and the fact that, in more offshore waters, boat fishers typically target larger fish species such as the West Australian Dhufish (Glaucosoma hebraicum) and Snapper (Chrysophrys auratus). It must be noted, however, that although the estimate for fishing mortality was relatively precise (95% CIs, 0.00-0.12 year⁻¹) the opposite was true for the estimated level of fishing mortality in inshore waters (95% CIs, 0.11-1.00 year⁻¹). Although the model explorations involving simulated data for S. punctata indicated that the level of precision for the estimated of inshore mortality could be improved substantially by obtaining a larger sample (particularly for the inshore region), even with such a sample, the precision of this parameter is still likely to be relatively low.

Value of per-recruit and decision table analyses for exploring implications of size-dependent, offshore movements for management

This study has demonstrated the value of using a modified per-recruit analysis for fish species that exhibit offshore size-related movements, such as *P. georgianus* and *S. punctata*. Although the level of sophistication/realism of the per-recruit analyses used in this study could be enhanced through incorporating information on individual variability in growth among individual fish (as used in the offshore movement model), the approach clearly highlights its usefulness for understanding the relative impacts of fishing on such species in each of the regions in which they are targeted by fishers.

For both *P. georgianus* and *S. punctata*, the per-recruit analyses indicated that if exploitation of fish in inshore waters were to increase markedly, this alone could reduce the spawning potential ratio (estimated in terms of spawning biomass per recruit) of the stocks of these species near Perth to a relatively low level (*i.e.* \sim 30% of the unfished level). The importance of accounting for potentially different levels of
exploitation on the various components of a stock, which may be targeted by different fisheries, has been highlighted for some other fish species, including Redfish (*Centroberyx affinis*) and Tiger Flathead (*Neoplatycephalus richardsoni*) (Chen *et al.*, 1998). Although those authors demonstrated that changes to inshore fishing mortality can have a pronounced effect on the overall yield per recruit of a fish species, the results of this current study have highlighted the importance of also evaluating the impacts of such changes on the reproductive potential of its stocks. This is likely to be particularly important for *S. punctata*, which is targeted by fishers in inshore waters at sizes considerably smaller (as small as 280 mm, *i.e.* the minimum legal length for capture and retention) than that at which it becomes mature (about 400 mm).

Decision table analyses provided a valuable tool for "predicting" the likely impacts of potential future changes in fishing effort, *e.g.* as may occur 1) if fishing effort became re-directed away from demersal species such as West Australian Dhufish hebraicum) Snapper (Chrysophrys (Glaucosoma and auratus) towards P. georgianus and S. punctata, or 2) if management actions were taken to provide increased protection for P. georgianus and/or S. punctata. A major benefit of these analyses is that they are suited towards accounting for key uncertainties associated with model parameter estimates (Hilborn and Walters, 1992; Cochrane, 2000). The analyses demonstrated that although some of the penalty functions used when fitting the model to real data for the two species did, to some extent, constrain the estimates of certain model parameters (*i.e.* for movement and/or selectivity), this did not have a major impact on estimates of yield and spawning potential, as presented in the respective decision tables for the two species. The decision table analysis did demonstrate, however, that if recreational fishing on the inshore components of the stocks of either P. georgianus and (more particularly) S. punctata were to increase substantially, this would be likely to reduce their overall spawning stocks to a level (i.e. a spawning potential ratio of 0.3 or below) that would be of concern to managers.

It must also be noted that the decision table analyses employed in this study were based on point estimates for fishing mortality under a range of alternative modelling assumptions (penalties for selectivity and movement parameters). Thus, this analysis did not account for other important factors leading to uncertainty in estimates for fishing mortality. As pointed out above, the fishing mortality estimate for *S. punctata* in the inshore region, in particular, was very imprecise. Although this partly reflected the relatively small sample to which the model was fitted, it also reflected the fact that *S. punctata* resides in the inshore region for a very short period during life, which, in turn, limits the potential of any sample of size and age data to distinguish between the similar effects of mortality and movement on those data. Thus, in any future assessments for these species, results produced by this modelling approach for *S. punctata* (and *P. georgianus*) would need to be considered together with other "weight of evidence" information regarding stock status, *e.g.* trends in catches and catch rates.

9. BENEFITS AND ADOPTION

The offshore movement model developed during this study is novel and innovative, and overcomes a major issue that, in the past, has made it virtually impossible for fisheries scientists in Western Australia to produce an appropriate fishing mortalitybased assessment of the exploitation status of Silver Trevally and King George Whiting. The model accounts for unidirectional, size-related movements of fish from inshore to offshore waters and has been shown using simulation methods to produce robust estimates of fishing mortality, and selectivity and movement parameters for these species if substantial size and age composition data are available. The model is not restricted to the two species on which the current study was focused, but has potential to be applied or enhanced to assist in assessing the status of many other fish stocks for species that exhibit a pronounced, unidirectional (and relatively rapid) size-related movement from one region to another.

The study has produced a range of results that are likely to be of benefit to researchers and managers for studying and assessing stocks of Silver Trevally and King George Whiting. These include i) the first descriptions of the patterns of growth of these species which account for individual variability in growth, ii) estimates of selectivity and movement parameters, iii) estimates of fishing mortality for the "inshore" and "offshore" components of the stocks of these species in areas near Perth, iv) estimates of yield per recruit, spawning biomass per recruit and spawning potential ratio which take into account the different estimated levels of exploitation in inshore and offshore waters and v) results of decision table analyses, which present "predictions" of the relative impacts of different levels of potential changes in exploitation on these species. The project results have thus provided information that, when combined with additional data, such as on estimated catches and effort (from recreational fishing surveys) and commercial catch data, will assist managers in ascertaining the current levels of exploitation on these species, and the associated implications. The project has also provided valuable data on the size and age compositions of Silver Trevally and King George Whiting in different habitats, which will be of benefit to future research on these species.

The guide to the biology and stock status of 30 key temperate WA fish species (Fisheries Research Report No. 242) that was developed as a part of this study will be of benefit to scientists, managers, fishers and other interested stakeholders by identifying the scientific information available for each of these species. The guide has already been used extensively by researchers at the Department of Fisheries to assist in producing documentation associated with Marine Stewardship Council (MSC) pre-assessments for several finfish fisheries in Western Australia. It has also been used by other researchers in helping to validate certain aspects of recreational survey data. Managers have also provided positive feedback.

This project has been of great benefit to early-career scientists at Murdoch University, through introducing to them a range of concepts related to fisheries modelling and simulation. The study has formed part of the basis of a Research Masters by Training (RMT) degree (Miss Elena Sulin) and a PhD research degree (Dr Emily Fisher), both of which were completed in 2012.

10. FURTHER DEVELOPMENT

The following aspects related to this study could benefit from further development.

- 1) Continued data collection. Additional data collection for King George Whiting is likely to lead to more precise estimates of fishing mortality, and thus an improved understanding of overall stock status. Although the same is likely to be true Silver Trevally in offshore waters, experience from this study indicates that such collection would be likely to require fishery-independent sampling (as fishers apparently rarely currently target this species in those waters). Such sampling would be likely to be expensive and logistically difficult. Alternatively, the use of available benchmark information to produce comparisons of "rates of decline" in the frequencies of fully-recruited fish in inshore waters at different ages, by fitting catch curves, may provide a practical means of gauging, in the future, whether fishing pressure on this species in inshore waters has changed. In this respect, it may be relevant that the estimates of offshore fishing mortality for 2002-2004 were very low and apparently few fishers are currently targeting this species offshore. Furthermore, unlike King George Whiting, Silver Trevally reside in inshore waters for several years where they also become mature and spawn.
- 2) Application of the model to data for King George Whiting in other areas. This study has focused on these two species in waters near Perth. Substantial samples of this King George Whiting are currently being collected by the Department of Fisheries in different regions of south-western Australia (where growth has been shown to differ markedly, Sulin, 2012). In the future, the model is likely to be beneficial for gauging, in particular, the relative impacts of fishing pressure on King George Whiting in Geographe Bay, where this species is targeted by many fishers.
- 3) Increase the speed of the model fitting process. The offshore-movement model developed in this study, which was implemented in Excel VBA, takes a long time to fit, and this prohibited us undertaking larger numbers (1000s) of simulations when exploring the model. To help overcome this issue, the model is now being implemented in another software platform (AD Model Builder). This will make it easier for researchers to apply the model to updated sets of data (or data for other species), and/or undertake additional sensitivity analyses using actual or simulated data sets.
- 4) Incorporate additional data. An implication of the results of this study (imprecise mortality estimates for the inshore region) is that, as researchers aim to extract increasing amounts of information from limited data sets, assessment results can become increasingly less precise and thereby also less informative. In such situations, including additional sources of information in an assessment model (*i.e.* in an "integrated assessment model") can be highly beneficial. For example, if sufficient resources were to become available for a tagging study on one or both of these species, such data may provide valuable information that could assist in producing more precise/reliable estimates of fishing mortality. The extent to which such data might assist in providing improved estimates of fishing mortality could be explored using a desktop study, in which simulated tag-recapture experiments are undertaken. Mortality estimates produced from such experiments could be

combined with mortality values estimated by the offshore movement model (from simulated age and length composition data) to explore whether the combined use of these data sets can lead to improved mortality estimates. Such a study could provide a cost-benefit analysis accounting for different levels of initial tagging and then in effort towards obtaining data for recaptured fish.

11. PLANNED OUTCOMES

The planned outcomes for this project, as stated in the original application, and descriptions as to how they have been met, are as follows.

(1) A model enabling assessments of fish species which undertake size-related offshore movements.

The project has led to the development of a model for estimating fishing mortality of fish species such as Silver Trevally and King George Whiting, which exhibit a size-related movement from relatively shallower, inshore waters, to deeper, more offshore waters and which are exploited in each of these environments. The model provides estimates of fishing mortality in both environments, based on size and age data for fish in inshore and offshore waters, and pre-determined estimates of natural mortality and growth (accounting for individual variation). A "decision table" approach, employing model estimates of fishing mortality based on different assumptions regarding uncertain model parameters (for selectivity and/or movement), combined with the use of per-recruit analyses accounting for offshore movement, has provided "predictions" as to the likely impacts of potential future shifts (upward or downward) in fishing effort towards Silver Trevally and King George Whiting. A draft publication has been submitted to an international journal.

(2) Robust mortality estimates for specified fish species.

Current age and length data have been collected for Silver Trevally (2009-2012) and King George Whiting (2010-2012) in coastal waters off south-western Australia for estimating the levels of fishing mortality for these two species in inshore and offshore waters (*i.e.* the two regions in which they are targeted by fishers). For P. georgianus, the number of fish from offshore waters that were obtained from fishers during this study was not sufficient for fitting the offshore movement model to these data. To test the applicability of the model for P. georgianus and provide an historical "benchmark" for the levels of fishing mortality of this species, the model was fitted to data collected for this species during an earlier sampling period (2001-2004, for FRDC Project No. 2002/004). The results indicated that, at the time, fishing pressure on this species was substantially greater in inshore waters than in offshore waters, but only at a rate approximating that of natural mortality for this species. To assess whether fishing mortality in inshore waters is likely to have changed, linear catch curves were fitted to the frequencies at age of fully-recruited fish in inshore waters. As the "rates of decline" of fish from inshore waters were similar between the two periods (2009-2012 vs 2002-2004), this indicated that the level of fishing mortality directed towards this species in inshore waters is not likely to have changed markedly since the early 2000s. This conclusion assumes, however, that the rate at which fish move offshore has not changed between the two sampling periods.

As with Silver Trevally, the model was able to provide estimates of mortality for King George Whiting for both inshore and offshore waters. These mortality estimates derived for King George Whiting have been incorporated within a broader "weight of evidence" assessment of stock status of this species, documented by Brown et al. (2013). Due to the nature of the data (i.e. limited size and age range of fish in inshore waters, reflecting the short period individuals of this species occur in this environment), and the relatively small sample size for fish collected in inshore waters in this study, the estimate of inshore mortality is very imprecise. As sample collection for King George Whiting is ongoing, it is likely, as indicated by simulation testing of the model using different sample sizes for synthetic data sets, that the precision in the estimate of inshore mortality can be increased. As a result of this project, the sampling regime used by the Department of Fisheries, WA for King George Whiting, has been modified to incorporate more information on the habitats from which fish are caught, as needed to inform the model developed in this study for estimating mortality.

(3) A guide to the biology of key temperate WA fish species.

As part of this project, guide has been developed that summarises information about the biology, management history and stock status of 30 fish species in temperate waters of Western Australia. The guide makes reference to many hundred references, thus providing very comprehensive "go to" resource on available information on these species, for fisheries scientists, managers, fishers, students and other interested members of the community. Copies of the species guide have been provided to interested stakeholders, including representatives of RecFishWest, WAFIC, the WA Department of Fisheries, researchers at various universities, and interested anglers. The WA Department of Fisheries recognised the usefulness of the information contained within the species guide and agreed to publish it in their *Fisheries Research Report* series (number 242). The guide has since been used by the Department of Fisheries as a key source of information on the biology of a number of WA temperate finfish species, particularly when preparing documentation for MSC pre-assessments.

12. CONCLUSION

In conclusion, this study has developed and evaluated the robustness of a new and novel modelling approach for providing estimates of fishing mortality (and selectivity and movement parameters) for species such as Silver Trevally (Pseudocaranx georgianus) and King George Whiting (Sillaginodes punctata), which exhibit a sizerelated movement from inshore to offshore waters. The first step was to employ a slightly modified version of an existing random effects model (Pilling et al., 2002) for describing variability in growth among individual fish. The new model developed in this study for estimating fishing mortality requires the above information on growth of a species, and a specified value of natural mortality. This model was demonstrated to provide reliable estimates for size-dependent selectivity parameters and parameters describing the size-dependent rate of movement of individuals to offshore waters, and rates of fishing mortality for fish in those two regions. The simulation testing also demonstrated, however, that the estimates of fishing mortality in inshore waters are typically imprecise. Finally, the consequences for overall stock status of different levels of fishing mortality of fish in inshore and offshore waters were successfully explored using a decision table analysis, based on per-recruit analyses that employed values of fish mortality estimated by the model. The decision table approach accounted for key uncertainties in the modelling.

The model for estimating mortality was able to be fitted to the available data for Silver Trevally or King George Whiting. Estimates of mortality indicated that the fishing pressure on both species is greater in inshore waters than offshore waters. The mortality, per-recruit and decision table analyses, however, provided no indication that the current level of fishing pressure on these species in coastal waters near Perth is excessive. The analyses did suggest, however, that if fishing pressure on King George Whiting in these waters were to increase by a moderate amount (40%), the reproductive potential (spawning potential ratio) of the stock would decline to a level (0.3) that would become of concern to managers. The results produced by this project will, in conjunction with additional data, such as historic and current levels of fishing effort and catch by different sectors (as is currently being analysed by the Department of Fisheries for King George Whiting, Dr Josh Brown, pers. comm.), be of benefit to managers in assessing the current state of the stocks of these two species.

REFERENCES

- Afonso, P., Fontes, J., Holland, K. N. and Santos, R. S. (2009). Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally *Pseudocaranx dentex*, and their implications for marine reserve design. *Marine Ecology Progress Series* **381**, 273-286.
- Afonso, P., Fontes, J., Morato, T., Holland, K. N. and Santos, R. S. (2008). Reproduction and spawning habitat of white trevally, *Pseudocaranx dentex*, in the Azores, central north Atlantic. *Scientia Marina* **72**, 373-381.
- Aires-da-Silva, A. M., Maunder, M. N., Gallucci, V. F., Kohler, N. E. and Hoey, J. J. (2009). A spatially structured tagging model to estimate movement and fishing mortality rates for the blue shark (*Prionace glauca*) in the North Atlantic Ocean. *Marine and Freshwater Research* 60, 1029-1043.
- Brown, J., Dowling, C., Hesp, A., Smith, K. and Molony, B. (2013). Status of nearshore finfish stocks in south-western Australia. Part 3. Whiting (Sillaginidae). Fisheries Research Report No. 248. Department of Fisheries, Western Australia. 128 pp.
- Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 2219-2227.
- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197-242.
- Challier, L., Orr, P. and Robin, J.-P. (2006). Introducing inter-individual growth variability in the assessment of a cephalopod population: application to the English Channel squid *Loligo forbesi*. *Oecologia* **150**, 17-28.
- Chen, Y., Liggins, G. W. and West, R. J. (1998). A yield-per-recruit model for sequential fisheries and its application in evaluating the management strategy of changing incidental inshore fishing mortality. *Aquatic Sciences* **60**, 130-144.
- Cochrane, K. L. (2000). Reconciling sustainability, economic efficiency and equity in fisheries: the one that got away? *Fish and Fisheries* **3-21**.
- Cope, J. M. and Punt, A. E. (2009). Length-based reference points for data-limited situations: applications and restrictions. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **1**, 169-186.
- Coulson, P. G., Hesp, S. A., Hall, N. G. and Potter, I. C. (2009). The western blue groper (*Achoerodus gouldii*), a protogynous hermaphroditic labrid with exceptional longevity, late maturity, slow growth, and both late maturation and sex change. *Fishery Bulletin* **107**, 57-75.

- Department of Fisheries, WA. (2011a). *State of the Fisheries and Aquatic Resources Report 2010/11.* Department of Fisheries, Western Australia, 359 pp.
- Department of Fisheries, WA. (2011b). *Resource assessment framework (RAF) for finfish resources in Western Australia*. Fisheries Occasional Publication No. 85. Department of Fisheries, Western Australia. 28 pp.
- Deriso, R. B., Quinn, T. J. and Neal, P. R. (1985). Catch-age analysis with auxiliary information. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 815-824.
- Dowling, N. A., Smith, D. C., Knuckey, I., Smith, A. D. M., Domaschenz, P., Patterson, H. M. and Whitelaw, W. (2008). Developing harvest strategies for low-value and data-poor fisheries: case studies from three Australian fisheries. *Fisheries Research* 94, 380-390.
- Farmer, B. M., French, D. J. W., Potter, I. C., Hesp, S. A. and Hall, N. G. (2005). Determination of biological parameters for managing the fisheries for mulloway and silver trevally in Western Australia. Final Report to the Australian Fisheries Research and Development Corporation on Project No. 2002/004. Murdoch University, Western Australia, 150 pp.
- Fowler, A., McLeay, L. and Short, D. (1999). Reproductive mode and spawning information based on gonad analysis for the King George whiting (Percoidei: Sillaginidae) from South Australia. *Marine and Freshwater Research* **50**, 1-14.
- Fowler, A. J. and Short, D. A. (1996). Temporal variation in the early life-history characteristics of the King George Whiting (*Sillaginodes punctata*) from analysis of otolith microstructure. *Marine and Freshwater Research* **47**, 809-818.
- Fowler, A. J., Jones, G. K. and McGarvey, R. (2002). Characteristics and consequences of movement patterns of King George Whiting (Perciformes: *Sillaginodes punctata*) in South Australia. *Marine and Freshwater Research* 53, 1055-1069.
- Fowler, A. J., McLeay, L. and Short, D. A. (2000). Spatial variation in size and age structures and reproductive characteristics of the King George Whiting (Percoidei: Sillaginidae) in South Australian waters. *Marine and Freshwater Research* 51, 11-22.
- Francis, M. P., Williams, M. W., Pryce, A. C., Pollard, S. and Scott, S. G. (1993). Uncoupling of otolith and somatic growth in *Pagrus auratus* (Sparidae). *Fishery Bulletin* **91**, 159-164.
- Francis, R. I. C. C. (1990). Back-calculation of fish length a critical review. *Journal* of Fish Biology **36**, 883-902.
- French, D. J. W. (2003). The biology of the silver trevally *Pseudocaranx dentex* on the lower west coast of Australia. Honours thesis. Murdoch University, Western Australia.

- Gardner, C., Frusher, S., Haddon, M. and Buxton, C. (2003). Movements of the southern rock lobster *Jasus edwardsii* in Tasmania, Australia. *Bulletin of Marine Science* **73**, 653-671.
- Gaughan, D. J., Ayvazian, S., Nowara, G., Craine, M. and Brown, J. (2006). The development of a rigorous sampling program for a long term annual index of recruitment for finfish species from south-western Australia. Final report to the Australian Fisheries Research and Development Corporation on Project No. 1999/153. Fisheries Research Report No. 154. Department of Fisheries, Western Australia, 135 pp.
- Goodyear, C. P. (1993). Spawning stock biomass per recruit in fisheries management: foundation and current use. In *Risk evaluation and biological reference points for fisheries management.* (Smith, S. J., Hunt, J. J., and Rivard, D., eds) pp. 67-81, Canadian Special Publication of Fisheries and Aquatic Sciences 120, NRC Research Press, Ottawa.
- Grandcourt, E. M., Hecht, T., Booth, A. J. and Robinson, J. (2008). Retrospective stock assessment of the emperor red snapper (*Lutjanus sebae*) on the Seychelles Bank between 1977 and 2006. *ICES Journal of Marine Science* **65**, 889-898.
- Griffiths, S. P. (2010). Stock assessment and efficacy of size limits on longtail tuna (*Thunnus tonggol*) caught in Australian waters. *Fisheries Research* **102**, 248-257.
- Hampton, J. and Fournier, D. A. (2001). A spatially disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. *Marine and Freshwater Research* **52**, 937-963.
- Helser, T. E. and Lai, H.-L. (2004). A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, *Micropterus salmoides. Ecological Applications* **178**, 399-416.
- Henry, G. W. and Lyle, J. M. (2003). *The national recreational and indigenous fishing survey*. Australian Government Department of Agriculture, Fisheries and Forestry, Canberra, 188 pp.
- Hesp, S. A., Hall, N. G. and Potter, I. C. (2004). Size-related movements of *Rhabdosargus sarba* in three different environments and their influence on estimates of von Bertalanffy growth parameters. *Marine Biology* **144**, 449-462.
- Hilborn, R. and Walters, C. J. (1992). *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall, New York, 570 pp.
- Hoenig, J. (1983). Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* **82**, 898-903.

- Hyndes, G. A., Platell, M. E., Potter, I. C. and Lenanton, R. C. J. (1998). Age composition, growth, reproductive biology, and recruitment of King George whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia. *Fishery Bulletin* **96**, 258-270.
- Jenkins, G. P., Welsford, D. C., Keough, M. J. and Hamer, P. A. (1998). Diurnal and tidal vertical migration of pre-settlement King George whiting *Sillaginodes punctata* in relation to feeding and vertical distribution of prey in a temperate bay. *Marine Ecology Progress Series* **170**, 239-248.
- Jones, G. K., Hall, D. A., Hill, K. M. and Staniford, A. J. (1990). *The South Australian Marine Scalefish Fishery: stock assessment, economics, management.* Report (Green Paper) to the South Australian Department of Primary Industries and Regions. SARDI, Adelaide, 186 pp.
- Mace, P. M. and Sissenwine, M. P. (1993). How much spawning per recruit is enough? In *Risk evaluation and biological reference points for fisheries management* (Smith, S. J., Hunt, J. J., and Rivard, D., eds) pp. 101-118, Canadian Special Publication of Fisheries and Aquatic Sciences 120, NRC Research Press, Ottawa.
- Martínez-Garmendia, J. (1998). Simulation analysis of evolutionary response of fish populations to size-selective harvesting with the use of an individual-based model. *Ecological Modelling* **111**, 37-60.
- Masuda, R. and Tsukamoto, K. (1999). School formation and concurrent developmental changes in carangid fish with reference to dietary conditions. *Environmental Biology of Fishes* **56**, 243-252.
- McGarvey, R., Linnane, A. J., Feenstra, J. E., Punt, A. E. and Matthews, J. M. (2010). Integrating recapture-conditioned movement estimation into spatial stock assessment: a South Australian lobster fishery application. *Fisheries Research* **105**, 80-90.
- Morales-Nin, B. and Ralston, S. (1990). Age and growth of *Lutjanus kasmira* (Forskål) in Hawaiian waters. *Journal of Fish Biology* **36**, 191-203.
- Moreno, T. and Morales-Nin, B. (2003). Age determination and validation on otoliths of the sand-smelt *Atherina presbyter* (Cuvier, 1829) (Pisces: Atherinidae) from the central-east Atlantic. *Fisheries Research* **62**, 77-87.
- Morita, K. and Matsuishi, T. (2001). A new model of back-calculation of growth backcalculation incorporating age effect based on otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1805-1811.
- Murphy, M. D. (1997). Bias in Chapman-Robson and least-squares estimators of mortality rates for steady-state populations. *Fishery Bulletin* **95**, 863-868.
- Myung, I. J. (2003). Tutorial on maximum likelihood estimation. *Journal of Mathematical Psychology* **47** 90-100.

- Nelder, J. A. and Mead, R. (1965). A simplex method for function minimization. *The Computer Journal* **7**, 308-313.
- Pilling, G. M., Kirkwood, G. P. and Walker, S. G. (2002). An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 59, 424-432.
- Platell, M. E., Ang, H. P., Hesp, S. A. and Potter, I. C. (2007). Comparisons between the influences of habitat, body size and season on the dietary composition of the sparid Acanthopagrus latus in a large marine embayment. Estuarine, Coastal and Shelf Science **72**, 626-634.
- Punt, A. E., Pribac, F., Walker, T. I., Taylor, B. L. and Prince, J. D. (2000). Stock assessment of school shark, *Galeorhinus galeus*, based on a spatially explicit population dynamics model. *Marine and Freshwater Research* **51**, 205-220.
- Quinn, T. J. and Deriso, R. B. (1999). *Quantitative fish dynamics*. Oxford University Press, Oxford, 542 pp.
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada No. 191, Ottawa, 382 pp.
- Russell, D. J. and McDougall, A. J. (2005). Movement and juvenile recruitment of mangrove jack, *Lutjanus argentimaculatus* (Forsskål), in northern Australia. *Marine and Freshwater Research* **56**, 465-475.
- Smith, A. and Wakefield, J. C. (1994). The hierarchical Bayesian approach to population pharmacokinetic modelling. *International Journal of Bio-Medical Computing* **36**, 35-42.
- Smith, A. D. M., Smith, D. C., Tuck, G. N., Klaer, N., Punt, A. E., Knuckey, I., Prince, J., Morison, A., Kloser, R., Haddon, M., Wayte, S., Day, J., Fay, G., Pribac, F., Fuller, M., Taylor, B. and Little, L. R. (2008). Experience in implementing harvest strategies in Australia's south-eastern fisheries. *Fisheries Research* 94, 373-379.
- Spiegelhalter, D., Thomas, A., Best, N. and Lunn, D. (2003). *WinBUGS User Manual, version 1.4*. Medical Research Council Biostatistics Unit, Institute of Public Health, Cambridge, 60 pp.
- Sulin, E. H. (2012). Size and age compositions, and growth of King George Whiting (Sillaginodes punctata) in south-western Australia. MSc thesis. Murdoch University, Western Australia.
- Sumner, N. R., Williamson, P. C., Blight, S. J. and Gaughan, D. J. (2008). A 12month survey of recreational boat-based fishing between Augusta and

Kalbarri on the West Coast of Western Australia during 2005-06. Fisheries Research Report No. 177. Department of Fisheries, Western Australia, 44 pp.

- Walters, C. (2003). Folly and fantasy in the analysis of spatial catch rate data *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 1433-1436.
- Wayte, S. E. and Klaer, N. L. (2010). An effective harvest strategy using improved catch-curves. *Fisheries Research* **106**, 310-320.
- Welch, D. J., Mapstone, B. D., Davies, C. R. and Russ, G. R. (2010). Spatial and fishing effects on sampling gear biases in a tropical reef line fishery. *Marine* and Freshwater Research 61, 1134-1146.
- Wetzel, C. R. and Punt, A. E. (2011). Performance of a fisheries catch-at-age model (Stock Synthesis) in data-limited situations. *Marine and Freshwater Research* 62, 927-936.
- White, D. B. and Palmer, S. M. (2004). Age, growth, and reproduction of the red snapper, *Lutjanus campechanus*, from the Atlantic waters of the southeastern U.S. *Bulletin of Marine Science* **73**, 335-360.
- Wise, B. S., St John, J. and Lenanton, R. C. (2007). Spatial scales of exploitation among populations of demersal scalefish: implications for management. Part 1: Stock status of the key indicator species for the demersal scalefish fishery in the West Coast bioregion. Final report to the Australian Fisheries Research and Development Corporation on Project No. 2003/052. Fisheries Research Report No. 163. Department of Fisheries, Western Australia, 130 pp.
- Zelen, M. and Severo, N. C. (1972). Probability functions. In *Handbook of mathematical functions with formulas, graphs and mathematical tables* (Abramowitz, M., and Stegus, I. A., eds) pp. 925-995, Wiley, New York.

APPENDIX 1: Intellectual property

The information produced in this study is not intended for commercialisation.

APPENDIX 2: Staff

The following researchers have been involved with the work on this project: Dr Alex Hesp Prof Norm Hall Dr Emily Fisher Ms Elena Sulin Dr Claire Smallwood Prof Lynnath Beckley Dr Peter Coulson Ms Lauren Veale

APPENDIX 3: Jitter tests

Estimates of model parameters and the associated negative log-likelihoods (NLL) resulting from jitter tests, in which the offshore movement model was fitted ten times to identical age and length data, using different randomly-selected starting values for the parameters in each of these trials. The parameters estimated by the model include those describing the length at which fish become selected by the fishing gear (L_{50}^{Sel} and L_{95}^{Sel}), the length at which fish move from inshore to offshore waters (L_{50}^{Move} and L_{95}^{Move}) and the fishing mortality in inshore and offshore waters (F_1 and F_2 , respectively).

The jitter tests demonstrated that, although Solver in Excel provided a robust solution when the model was fitted to simulated data for *Pseudocaranx georgianus* and Sillaginodes punctata (see Tables A3.1 and A3.3, respectively), as well as to real data for the former species (Table A3.2), the same model fitting approach was not adequate when using real data for Sillaginodes punctata (Table A3.4). For S. punctata, fitting the offshore model to simulated and real data using Solver in tandem with the Nelder-Mead (1965) simplex algorithm (and selecting the best of three consecutive fits to the same data) resulted in improved values of NLL and more stable estimated parameters (cf. Tables A3.3, A3.4 with A3.5, A3.5). This fitting approach did still not, however, provide a good fit to the real data for S. punctata. For example, the most robust solution always resulted in the inshore fishing mortality estimate being equal to zero, which is highly unlikely for this species. Further exploration showed that, when the log-likelihood component associated with the inshore age composition data was excluded from the objective function, model fits to the real data for S. punctata yielded a solution that demonstrated a minimum overall log-likelihood that corresponded with an estimate of the inshore mortality that appeared reasonable (Table A3.7).

Parameters	L ^{Vuln} (mm)	L ^{Vuln} (mm)	L ^{Move} (mm)	L ₉₅ ^{Move} (mm)	<i>F</i> ₁ (year ⁻¹)	F ₂ (year ⁻¹)	NLL
Specified true values	300	400	450	600	0.3	0.1	
Trial							
1	309.7	412.2	446.8	589.2	0.364	0.111	-2401.8
2	309.7	412.2	446.8	589.2	0.364	0.111	-2401.8
3	309.7	412.2	446.8	589.2	0.364	0.111	-2401.8
4	309.7	412.2	446.8	589.2	0.364	0.111	-2401.8
5	309.7	412.3	446.9	589.3	0.365	0.111	-2401.8
6	309.7	412.2	446.8	589.2	0.364	0.111	-2401.8
7	309.7	412.2	446.8	589.2	0.364	0.111	-2401.8
8	309.7	412.3	446.9	589.2	0.365	0.111	-2401.8
9	309.7	412.3	446.8	589.2	0.364	0.111	-2401.8
10	309.7	412.2	446.8	589.2	0.364	0.111	-2401.8

Table A3.1. Estimates of parameters produced by fitting the model to the same simulated data (using different random starting values) for *Pseudocaranx georgianus* (n = 247 inshore and 107 offshore fish) using Solver.

Table A3.2. Estimates of parameters produced by fitting the model to the same real data (using different random starting values) for *Pseudocaranx georgianus* (n = 247 inshore and 107 offshore fish) using Solver.

Parameters	L ^{Vuln} (mm)	L ^{Vuln} (mm)	L ^{Move} (mm)	L ^{Move} (mm)	<i>F</i> ₁ (year ⁻¹)	F_2 (year ⁻¹)	NLL
Trial							
1	343.3	425.8	445.8	590.0	0.331	0.079	-3231.8
2	339.0	413.5	433.5	583.5	0.304	0.028	-3229.8
3	339.7	417.7	437.7	589.1	0.296	0.024	-3229.7
4	337.7	411.8	431.8	592.5	0.340	0.056	-3231.7
5	340.4	419.6	439.6	597.4	0.310	0.065	-3231.2
6	340.9	415.7	435.7	587.7	0.325	0.023	-3230.2
7	337.6	414.7	434.7	584.3	0.223	0.043	-3229.0
8	338.3	416.5	436.5	587.9	0.289	0.025	-3229.5
9	336.9	411.6	431.6	584.8	0.277	0.055	-3230.2
10	341.7	416.0	436.0	594.2	0.335	0.057	-3231.6

Parameters	$L_{50}^{ m Vuln}$ (mm)	$L_{95}^{ m Vuln}$ (mm)	L ^{Move} (mm)	L ^{Move} (mm)	<i>F</i> ₁ (year ⁻¹)	F ₂ (year ⁻¹)	NLL
Specified true values	280	300	400	450	0.3	0.1	
Trial							
1	277.1	307.6	392.2	448.3	0.302	0.106	-3308.5
2	280.0	307.1	390.7	446.3	0.301	0.100	-3308.5
3	280.6	311.6	390.1	447.9	0.274	0.077	-3308.9
4	275.5	298.4	390.0	443.5	0.000	0.137	-3308.7
5	284.9	322.0	390.1	445.4	0.242	0.126	-3307.6
6	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6
7	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6
8	285.6	323.2	391.3	447.0	0.295	0.126	-3307.6
9	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6
10	284.9	322.0	390.1	445.4	0.242	0.126	-3307.6

Table A3.3. Estimates of parameters produced fitting the model to the same simulated data (using different random starting values) for *Sillaginodes punctata* (n = 100 inshore and 200 offshore fish) using Solver.

Table A3.4. Estimates of parameters produced fitting the model to the same real data (using different random starting values) for *Sillaginodes punctata* (n = 100 inshore and 188 offshore fish) using Solver.

Parameters	L ^{Vuln} (mm)	L ^{Vuln} (mm)	L ^{Move} (mm)	L ^{Move} (mm)	<i>F</i> ₁ (year ⁻¹)	F_2 (year ⁻¹)	NLL
Trial							
1	244.2	264.2	422.7	529.5	0.352	0.099	-2220.2
2	240.7	261.0	388.6	483.7	0.000	0.060	-2212.2
3	242.3	262.3	388.1	483.2	0.000	0.059	-2212.3
4	241.5	261.5	411.4	521.2	0.288	0.048	-2218.4
5	242.8	262.8	387.6	482.9	0.000	0.057	-2212.3
6	243.4	263.4	421.7	531.2	0.283	0.101	-2218.8
7	242.5	262.5	416.5	525.1	0.294	0.070	-2218.5
8	242.5	262.5	387.9	483.2	0.000	0.058	-2212.3
9	243.7	263.7	412.9	521.3	0.281	0.074	-2218.2
10	240.8	260.8	388.5	483.7	0.000	0.059	-2212.2

Table A3.5. Estimates of parameters produced fitting the model to the same simulated data (using different random starting values) for *Sillaginodes punctata* (n = 100 inshore and 200 offshore fish) using Solver in conjunction with the Nelder-Mead (1965) simplex algorithm, and selecting the best of three consecutive fits.

Parameters	L ^{Vuln} (mm)	L ^{Vuln} (mm)	L ^{Move} (mm)	L ^{Move} (mm)	F ₁ (year ⁻¹)	F_2 (year ⁻¹)	NLL
Specified true values	280	300	400	450	0.3	0.1	
Trial							
1	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6
2	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6
3	285.0	322.2	390.4	445.8	0.253	0.126	-3307.6
4	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6
5	284.9	322.0	390.1	445.4	0.242	0.126	-3307.6
6	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6
7	284.9	322.0	390.1	445.3	0.241	0.126	-3307.6
8	284.9	322.0	390.1	445.4	0.242	0.126	-3307.6
9	285.6	322.7	390.0	445.9	0.296	0.100	-3307.9
10	285.0	322.2	390.4	445.7	0.252	0.126	-3307.6

Table A3.6. Estimates of parameters produced fitting the model to the same real data (using different random starting values) for *Sillaginodes punctata* (n = 100 inshore and 188 offshore fish) using Solver in conjunction with the Nelder-Mead (1965) simplex algorithm, and selecting the best of three consecutive fits.

Parameters	L ^{Vuln} (mm)	L ^{Vuln} (mm)	L ^{Move} (mm)	L ^{Move} (mm)	<i>F</i> ₁ (year ⁻¹)	F_2 (year ⁻¹)	NLL
Trial							
1	240.9	261.1	388.1	483.5	0.000	0.058	-2212.2
2	242.3	262.3	388.7	484.2	0.000	0.058	-2212.3
3	241.2	261.2	388.6	484.3	0.000	0.059	-2212.2
4	241.1	261.1	392.1	484.9	0.000	0.094	-2212.6
5	241.9	262.0	387.6	483.3	0.000	0.058	-2212.2
6	241.9	261.9	387.9	480.9	0.000	0.057	-2212.3
7	240.4	260.5	388.7	483.9	0.000	0.060	-2212.2
8	241.1	261.1	387.9	482.7	0.000	0.059	-2212.2

using Solver in conjunction with the Nelder-Mead (1965) simplex algorithm, and selecting the best of three consecutive fits.									
Parameters	L ^{Vuln} (mm)	L ^{Vuln} (mm)	L ^{Move} (mm)	L ₉₅ ^{Move} (mm)	F ₁ (year ⁻¹)	F_2 (year ⁻¹)	NLL		
Trial									
1	284.5	294.5	390.0	460.0	0.544	0.048	-10149.0		
2	284.6	294.7	390.0	459.9	0.493	0.046	-10149.1		
3	284.6	294.6	390.9	459.4	0.527	0.079	-10149.5		
4	284.2	294.2	390.9	459.0	0.497	0.059	-10149.2		
5	285.9	295.9	390.0	459.9	0.535	0.048	-10149.2		

390.0

392.2

390.0

390.5

390.0

460.0

459.8

460.0

460.0

460.0

0.532

0.593

0.499

0.490

0.576

0.062

0.090

0.049

0.079

0.048

-10149.1

-10150.0

-10149.0

-10149.5

-10149.0

284.7

284.1

284.7

284.5

284.8

294.7

294.1

294.7

294.5

294.8

6

7

8 9

10

Table A3.7. Estimates of parameters produced fitting the model (after removing the log-likelihood component associated with the inshore age composition data) to the same real data (using