

STOCK STRUCTURE AND REGIONAL VARIATION IN POPULATION DYNAMICS OF THE RED THROAT EMPEROR AND OTHER TARGET SPECIES OF THE QUEENSLAND TROPICAL REEF LINE FISHERY.

Principal Investigator

Campbell R. Davies

Authors

C.R. Davies, A.J. Williams, B.D. Mapstone, J. Benzie, L. van
Herwerden, J.H. Choat, S. Adams, C.D. Murchie, K. Bean, G.
Carlos, A. Tobin, J. Ackerman



Australian Government
**Fisheries Research and
Development Corporation**

Project No. 98/131

© Cooperative Research Centre for the Great Barrier Reef World Heritage Area, Fisheries Research and Development Corporation and Great Barrier Reef Marine Park Authority.

Stock structure and regional variation in population dynamics of the Red Throat Emperor and other target species of the Queensland tropical reef line fishery.

National Library of Australia Cataloguing-in-Publication entry

Bibliography.

Includes index.

ISBN 1876054786

1. Fishing – Queensland – Great Barrier Reef. 2. Fishery management – Queensland - Great Barrier Reef. I. Davies, Campbell R. (Campbell Robert). II. CRC Reef Research Centre. (Series: CRC Reef Research Centre technical report; no. 61)

This publication should be cited as Davies, C.R., Williams, A.J., Mapstone, B.D., Benzie, J., van Herwerden, L., Choat, J.H., Adams, S., Murchie, C.D., Bean, K., Carlos, G., Tobin A., Ackerman, J. (2005). Stock structure and regional variation in population dynamics of the Red Throat Emperor and other target species of the Queensland tropical reef line fishery. CRC Reef Research Centre Technical Report No 61. CRC Reef Research Centre, Townsville, Australia.

This work is copyright. The Copyright Act 1968 permits fair dealing for study, research, news reporting, criticism or review. Although the use of the PDF format causes the whole work to be downloaded, any subsequent use is restricted to the reproduction of selected passages constituting less than 10% of the whole work, or individual tables or diagrams for the fair dealing purposes. In each use the source must be properly acknowledged. Major extracts, or the entire document may not be reproduced by any process whatsoever without written permission of the Chief Executive Officer, CRC Reef Research Centre.

While every effort has been made to ensure the accuracy and completeness of information in this report, CRC Reef Research Centre Ltd accepts no responsibility for losses, damage, costs and other consequences resulting directly or indirectly from its use.

In some cases, the material may incorporate or summarise views, standards or recommendations of a third party. Such material is assembled in good faith but does not necessarily reflect the considered views of CRC Reef Research Centre Ltd or indicate a commitment to a particular course of action.

Published by the Cooperative Research Centre Ltd, PO Box 772, Townsville, Qld, 4810, Australia.

Non-Technical Summary

1998/131	Stock structure and regional variation in population dynamics of the Red Throat Emperor and other target species of the Queensland Tropical Reef Line Fishery.
----------	---

Principal Investigator Dr Campbell Davies

Address CRC Reef Research Centre – School of Tropical
Environmental Studies and Geography
James Cook University
Townsville, QLD 4811
Telephone: 07 47815113
Fax: 07 47814099

Objectives

- I. Establish regional variation in stock abundance, age, growth and mortality of the red throat emperor (*L. miniatus*).
- II. Establish stock abundance, age, growth and mortality for maori wrasse (*C. undulatus*) and barramundi cod (*C. altivelis*).
- III. Establish regional and seasonal variation in reproduction of *L. miniatus*, Maori wrasse, *C. altivelis*, *P. leopardus* and *P. laevis*, including size at first maturity, age at sex transition and sex-specific growth characteristics.
- IV. Develop stock discrimination techniques, based on genetic and otolith microchemistry approaches, for *L. miniatus*, and use them to determine the stock structure of *L. miniatus* in the Great Barrier Reef region.

Outcomes achieved to date

Outputs from this project have been used directly in the development of new management arrangements and regulatory measures for the Coral Reef Fin Fish Fishery and planning for activities within the Great Barrier Reef Marine Park.

Outcomes directly linked to outputs of this project include:

- Confirmation that the current minimum size limits for common coral trout, red throat emperor and stripey bass are appropriate;
- Information indicating that the timing of the spawning closure for the fishery is consistent with the timing of peak spawning activity for common coral trout for central GBR;
- Changes in the minimum size limit for blue-spot coral trout and introduction of a maximum size;

- Inclusion of a minimum size limit for small serranids (rock cods).

In the case of the red throat emperor, the project has also provided validated age and length based estimates of key population parameters, and the regional variation in them, as a basis for developing quantitative stock assessment models for quota setting. The significant regional variation in some parameters identified through this project may require these models to be spatially structured.

In contrast to the common coral trout we found the peak spawning period for red throat emperor not to coincide with that of the common coral trout, or the current spawning closure for the fishery. The current management arrangements for red throat emperor may need to be considered in light of this. The major outstanding questions with respect to the biology and ecology of red throat emperor include: the distribution and abundance of juveniles and the relative importance of bio-physical factors and historical and current levels of fishing in determining the observed regional differences in populations.

The lack of evidence for genetic stock structure in the red throat emperor is consistent with results for a range of other marine taxa on the GBR. This suggests, in the context of fisheries management, that the primary concern should be one of avoiding growth overfishing and localised depletion, as opposed to the potential for recruitment overfishing of multiple stocks. In the context of the Representative Areas Program, it would suggest that the current arrangement is likely to provide for considerable mixing of larva among highly protected areas and among protected areas and areas open to fishing as a mechanism for avoid the potential for selective effects of harvest.

The first age-based estimates of population parameters for Maori wrasse and barramundi cod have provided the basis for more comprehensive studies and a more informed debate on the potential vulnerability of these species to over harvest. These outputs are now being used directly in the development of management measures for these species in the Eastern Torres Straits.

Finally, this project, in conjunction with other elements of the ELF project, provided support for six PhD projects, and thereby made a contribution to increasing the number of well trained fisheries professionals available.

The Great Barrier Reef Marine Park (GBRMP) is the largest and, arguably, most pristine marine park in the world. Commercial, charter and recreational fishing have occurred on the Great Barrier Reef (GBR) for many decades. Since the late 1980's, there has been growing concern about the sustainability of fishing on the GBR and the potential for it to have impacts on the broader ecosystem.

The Queensland Coral Reef Fin Fish Fishery (CRFFF) is one of the larger fisheries operating within the GBRMP and includes significant commercial, charter and recreational sectors. The need to better understand the impacts of line fishing on the GBR and sustainable levels of fishing was identified during the early 1990's and was followed by a series of pilot and methodological studies. The outcomes of these studies and continuing concern lead to the establishment of the Effects of Line Fishing (ELF) Project in 1994 within the CRC Reef Research Centre. The centrepiece of the ELF Project is the Effects of Line Fishing Experiment and Management Strategy Evaluation (MSE) project (FRDC 97-124). The ELF Experiment involves monitoring the response of target and non-target species to

changes in fishing pressure on six reefs in each of four regions of the GBR by manipulating the amount of fishing pressure on individual reefs within each region. The outcomes of the first two phases of the ELF Experiment (1995-2000) and the first round of management strategy evaluations are reported in Mapstone *et al.* (2004).

Research on population dynamics within the ELF Project prior to this project (98-131) focussed on the common coral trout (*Plectropomus leopardus*). Samples of other target and bycatch species of the fishery were collected as part of the monitoring program for the experiment for population dynamics research. This project was designed to provide information on the population dynamics, stock structure and basic biology of several target and bycatch species of the CRFFF by capitalising on the samples available from the ELF Experiment. In particular the project aimed to provide:

- i) Estimates of regional variation in population parameters of red throat emperor; and determine the extent to which regional variation was likely to be the result of genetically distinct populations in different regions of the GBR;
- ii) Estimates of longevity, growth, mortality and reproductive parameters for three large, high profile species taken in the fishery, the maori wrasse (*Chelinus undulatus*), barramundi cod (*Cromileptes altivelis*) and blue-spot coral trout (*Plectropomus laevis*); and
- iii) Estimates of the regional variation in reproduction and sex structure of the common coral trout.

The red throat emperor was determined to be a protogynous hermaphrodite (changing sex from female to male) of moderate longevity (20 years), which is consistent with results from earlier studies.

Population parameters of red throat emperor were found to differ consistently between the Townsville, Mackay and Storm Cay clusters of reefs involved in the ELF Experiment from the years 1995-2000 inclusive. The differences in population parameters from closed reefs were consistent among years with higher productivity (higher mortality, larger maximum size, lower maximum age) in the Mackay region than in the Townsville region (lower natural mortality, smaller maximum size, higher maximum age), with the Storm Cay region generally being intermediate between the two northern regions. This regional pattern was consistent with that identified by Williams *et al.* (2003), which was the initial impetus for this component of the project. There were also significant regional differences in reproductive status that indicate the potential for a disproportionate contribution to total spawning stock biomass from the northern part of the range, due to a high proportion of mature but reproductively inactive females in the southern region.

We successfully isolated and applied genetic markers (nuclear microsatellites) and examined whether the observed regional differences in population parameters may have been the result of genetically isolated populations (stocks), with intrinsic population differences. The results of these analyses were consistent with red throat emperor being a single (panmictic) stock on the GBR. It appears most likely that the observed differences among regions are the result of contemporary spatial processes operating on a single stock. We consider the following factors to be the most likely potential influences: i) Regional variation in environmental conditions resulting in more favourable conditions for growth in the Mackay region; ii) A

combination of northward spawning migration and net southward drift of larvae resulting in a bias toward older mature fish in the north and younger, immature (and/or reproductively inactive) fish in the south; and iii) Regional differences in historical (pre-closure) impacts of fishing meaning that populations in different regions are currently at different stages of recovery towards unfished status. We provide recommendations on future research that may assist in distinguishing between the relative importance of these potential sources of regional difference. The introduction of quota management for red throat emperor will require the development of stock assessment methods to assist in setting sustainable levels of harvest. Given the results we have presented, it would seem appropriate that future development of stock assessments consider the implications of including the potential for such spatial differences in productivity, connectivity and/or status relative to unfished conditions and are evaluated to be robust to including, or not, assumptions relating to them.

We trialled otolith microchemistry techniques in an attempt to understand the regional differences in red throat emperor population parameters, in addition to the population genetics study. In this study we used both whole otolith techniques, which provide an integrated signal over the whole life of a fish, and juvenile and adult sections of otoliths, in an attempt to identify potential differences related to the juvenile and adult stages of the life-cycle. The results for barium (Ba) and strontium (Sr) for the whole otolith work did not indicate any consistent variation among regions. The results for the juvenile-adult otolith sections were more complicated, although they too did not indicate a regional pattern consistent with that observed in the population parameters. While the results from the otolith microchemistry were inconclusive, in terms of assisting with the interpretation of the spatial patterns of the adult component of the red throat emperor population, they may prove more useful in attempts to understand the distribution of juvenile component. Our preliminary results demonstrate a clear difference in the concentration of Sr between the adult and juvenile sections of the otolith. This may be evidence in support of the contention that for the first year or two of their life-cycle red throat emperor inhabit substantially different habitats to the adult phase. Further detailed work is required to establish whether this extrapolation based on these preliminary findings holds.

The maori wrasse, barramundi cod and blue-spot coral trout are all large reef fish that are highly prized by fishers, tourists and conservationists. At the initiation of this study, harvest of maori wrasse and barramundi cod was permitted in the CRFFF. Providing the necessary understanding of the basic biology of these species to support the development of management approaches for them was a priority objective for the project. We have provided age-based estimates of longevity, rates of growth and mortality and size and age at first reproduction and sex change for each of these species. In the case of maori wrasse we have also validated the periodicity of the bands in the otoliths as annual, providing a robust foundation for age-based parameter estimates, and confirmed its sex-changing reproductive strategy (protogynous hermaphrodite). Our initial results suggest maori wrasse is an "outlier" in terms of tropical wrasses with a combination of biological parameters (large size, fast growth, moderate longevity and mortality) that indicate a higher rate of population turnover than might be expected based on their large size alone. Notwithstanding this, we consider maori wrasse to be vulnerable to over harvest, principally because of its low natural abundance, shallow habitat distribution, nocturnal nesting habit and predictable location of spawning aggregations. This combination of characteristics, some of which are shared with a range of large serranids, including the barramundi cod, will make implementation of conventional harvest strategies that ensure sustainable levels of harvest difficult in any multi-species fishery. The implementation of the new management plan for the reef line

fishery prohibits the harvest of maori wrasse and barramundi cod and institutes a new minimum size limit for blue-spot coral trout and all small serranids. The outcomes for blue-spot coral trout indicate that will be more susceptible to over-fishing than the common coral trout, in particular due to its lower abundance, slower growth and higher age at maturity and sex change and shared distribution with the common coral trout over most of its range. In the absence of species specific measures to limit harvest of blue spot coral trout, it is likely that this species will be over-exploited and potentially prone to sperm limitation in the areas open to harvest.

We have confirmed that all five species examined in this project are protogynous hermaphrodites. In the case of the common coral trout and red throat emperor, we demonstrated there is significant variation in sex structure and reproductive parameters among regions of the GBR and the fishery. The implications of these differences for the management of the fishery will require evaluation via management strategy evaluation and assessment models. Notwithstanding the need for this work, the outcomes of this project strongly suggest that future approaches to assessment and management of the fishery will need to incorporate regional differences in the population structure of the principle target and bycatch species. In addition, further theoretical and empirical research on the protogynous reproductive strategy (a feature of many species of tropical reef fish) and the response of protogynous populations to harvest should be a high priority.

In addition to the primary outputs reported here, the project provided logistic, technical and supervisory support for several students who completed PhD research projects on red throat emperor (Williams 2003), reproductive biology of coral trout (Adams 2002), population biology and ecology of stripey bass (Kritzer 2001) and biology of the blue-spot rock cod (Mosse 2001). Readers are referred to the respective thesis and publications for details of these projects.

Key words: red throat emperor, coral trout, blue-spot trout, barramundi cod, maori wrasse, Great Barrier Reef, fisheries management, population biology, reproductive biology, stock structure, genetics, otolith microchemistry, regional variation, age, growth, mortality, abundance

Table of Contents

Non-Technical Summary	i
Objectives.....	i
Outcomes achieved to date	i
Key words.....	v
Table of Contents	vi
Acknowledgements	ix
Need	x
QFMA Research Priorities:	x
<i>Stock Assessment:</i>	x
<i>Biology:</i>	x
<i>Management:</i>	x
GBRMPA information requirements:	x
Objectives	xi
1. General Introduction	1
Management context in the Great Barrier Reef World Heritage Area	1
The Queensland Coral Reef Finfish Fishery	2
The Effects of Line Fishing Project	3
The Effects of Line Fishing Experiment.....	3
Preliminary evidence of regional variation in population dynamics of red throat emperor	4
This project.....	4
The structure of this report.....	5
2. General Methods	7
The Effects of Line Fishing Experiment.....	7
<i>Experimental Design</i>	7
Research Catch Surveys	8
<i>Swains survey</i>	10
Sampling for seasonal patterns in reproductive parameters.....	11
<i>Bramble Surveys</i>	11
<i>Samples of red throat emperor from the Commercial Fleet</i>	11
<i>Additional sampling for red throat emperor</i>	13
<i>Additional sampling for maori wrasse and barramundi cod</i>	13
Sample Processing.....	13
<i>Otolith processing</i>	13
<i>Sectioned otoliths</i>	13
<i>Whole otoliths</i>	16
<i>Otolith reading protocol and age determination</i>	16
<i>Sectioned otoliths</i>	16
<i>Whole otoliths</i>	17
<i>Gonad processing and histology</i>	18
<i>Reproductive staging</i>	18
3. Regional patterns in stock abundance, age, growth, mortality and reproductive biology of red throat emperor (<i>Lethrinus miniatus</i>) on the Great Barrier Reef	19

3.1 Introduction.....	19
3.2 Methods.....	20
<i>Sample collection</i>	20
<i>Effects of Line Fishing Experiment</i>	20
<i>Additional sampling</i>	20
<i>Relative abundance and biomass</i>	21
<i>Age structure</i>	21
<i>Growth</i>	22
<i>Mortality</i>	22
<i>Reproductive biology</i>	23
<i>Spawning season</i>	23
<i>Size and age at maturity</i>	25
<i>Size and age at sex change</i>	25
<i>Sex ratio</i>	26
3.3 Results.....	26
<i>Relative abundance and biomass</i>	26
<i>Age structure</i>	26
<i>Growth</i>	29
<i>Mortality</i>	30
<i>Spawning season</i>	33
<i>Size and age at maturity</i>	36
<i>Size and age at sex change</i>	36
<i>Sex ratios</i>	38
3.4 Discussion.....	39
4. Stock structure of red throat emperor (<i>Lethrinus miniatus</i>) in the Great Barrier Reef Region based on microsatellite and otolith microchemistry analyses.....	43
4.1 Introduction.....	43
4.2 Methods.....	45
<i>Sample collection</i>	45
<i>Microsatellite genetics</i>	45
<i>Otolith microchemistry</i>	46
<i>Whole otolith analyses</i>	47
<i>Adult-Juvenile section analyses</i>	48
4.3 Results.....	48
<i>Population Structure from microsatellite markers</i>	48
<i>Genetic variation</i>	48
<i>Deviations from Hardy-Weinberg and linkage equilibrium</i>	48
<i>Inter-population genetic structure</i>	48
<i>Microchemistry</i>	52
<i>Whole otoliths</i>	52
<i>Adult and juvenile sections of otoliths</i>	53
4.4 Discussion.....	57
<i>Microsatellite genetics</i>	57
<i>Otolith microchemistry</i>	58
5. Age, growth, mortality, and reproduction for maori wrasse (<i>Chelinus undulatus</i>), barramundi cod (<i>Cromileptes altivelis</i>) and blue-spot coral trout (<i>Plectropomus laevis</i>) on the Great Barrier Reef.....	60
5.1 Introduction.....	60
5.2. Methods.....	61
<i>Maori wrasse</i>	61
<i>Validation of periodicity of otolith increments</i>	62
<i>Age and growth</i>	63

<i>Mortality</i>	63
<i>Reproductive biology</i>	63
<i>Diet</i>	63
<i>Barramundi cod and blue-spot coral trout</i>	64
5.3. Results.....	64
<i>Summary of biological samples</i>	64
<i>Maori wrasse</i>	64
<i>Validation of periodicity of otolith increments</i>	64
<i>Age and Growth</i>	66
<i>Visual surveys</i>	66
<i>Mortality</i>	68
<i>Reproductive biology</i>	69
<i>Diet</i>	69
<i>Barramundi Cod</i>	70
<i>Age and Growth</i>	70
<i>Mortality</i>	71
<i>Reproductive biology</i>	72
<i>Blue-spot coral trout</i>	73
<i>Age and Growth</i>	73
<i>Mortality</i>	75
<i>Reproductive biology</i>	75
Discussion	78
<i>Maori wrasse</i>	79
<i>Barramundi cod</i>	82
<i>Blue-spot coral trout</i>	83
6. Regional patterns in the reproductive biology of common coral trout (<i>Plectropomus leopardus</i>)	85
6.1 Introduction	85
6.2 Methods.....	86
<i>Sample collection</i>	86
<i>Effects of Line Fishing Experiment</i>	86
<i>Additional sampling</i>	87
<i>Reproductive staging</i>	87
<i>Spawning season</i>	90
<i>Size and age at maturity</i>	91
<i>Size and age at sex change</i>	91
<i>Sex ratio</i>	91
6.3 Results.....	91
<i>Spawning season</i>	91
<i>Size and age at maturity</i>	93
<i>Size and age at sex change</i>	94
<i>Sex ratio</i>	96
6.4 Discussion	97
Conclusion	99
Benefits	100
Further Development	100
References	101
Appendix A: Intellectual Property	110
Appendix B: Staff	110

Acknowledgements

This project would not have been possible without the commitment and contribution of a large range of people. In addition to the project team we would like to thank Melita Samoily, Dave Welch, Stephanie Slade, Belinda Boyce and Lesa Peplow for their contributions at various stages of this project.

Many fishers contributed directly and indirectly to the information presented in this report and we are grateful to them all. In particular we thank Robin Stewart and Mary Peterson, of the *Peri*, who made invaluable contributions to the Catch Surveys and the collection of samples for the ELF Project and this project in particular. We also thank the skippers and crew from the *Vana*, *Hobo*, *Orpheus*, *El torito*, *Sharma*, *Bundy R*, *Cat Angler*, *Peggy Vee*, *Somerset*, *Battersea*, *Dorothy B*, *Peri* and *Catchalot* for providing monthly samples of red throat emperor, and Rick and Lyn Hack from the *Coimbra* for their generous hospitality and assistance in collecting red throat emperor samples from the Capricorn Group. We acknowledge the contribution of samples provided by a number of recreational spear and line fishers and the support of SUNFISH and the Queensland Commercial Fisheries Organisation for the project.

Finally we would like to thank the Fisheries Research and Development Corporation, the CRC Reef Research Centre, the Great Barrier Reef Marine Park Authority, the Australian Institute of Marine Science, the Queensland Department of Primary industries and Fisheries (formerly Queensland Fisheries Management Authority) and James Cook University for their support and funding for the project.

Need

QFMA Research Priorities:

This project addressed the following QFMA (now QDPI&F) research priorities (relevant objective in parentheses):

Stock Assessment:

Determine the size and distribution of the stock of red throat emperor *Lethrinus miniatus* ** (I).

Assess regional catch rates of red throat emperor *Lethrinus miniatus* ** (I).

Determine the habitat preferences of juvenile red throat emperor *Lethrinus miniatus* ** (IV).

Biology:

Basic biology of red throat emperor *Lethrinus miniatus* and maori wrasse *Cheilinus undulatus*** (I, II & III).

Management:

Identify appropriate units or indices on which to measure performance of stocks and the fisheries based on these stocks. *** (IV).

Determine the spawning period for major species other than coral trout *Plectropomus leopardus* and the red throat emperor *Lethrinus miniatus* ** (III, this objective includes research on the reproduction of red throat emperor and coral trout also).

GBRMPA information requirements:

This project will address both immediate and strategic research priorities of the GBRMPA.

There is very limited information available on the effects of fishing on target species of the reef line fishery other than common coral trout, even though some may be more susceptible to fishing. This project will provide information on population dynamics of the four reef fish species (red throat emperor, maori wrasse, barramundi cod and blue-spot coral trout) most likely to be impacted by reef line fishing. The need for this information has become more urgent given the recent and rapid development of fishing for live reef fish on the GBR to supply the Asian live reef fish trade, and the high value placed on maori wrasse and barramundi cod. There is considerable public and international concern to ensure that the harvest of these species does not compromise the conservation and World Heritage values of the GBR.

The GBRMPA has recently developed a system of representative highly protected areas. The primary objective of these areas is to protect a broad range of habitat types and reef communities from extractive use, including fishing, and conserve regional marine biodiversity within the GBRMP. Knowledge of the connectivity (larval and adult dispersal) among populations will be fundamental to an effective system of representative areas. This project, if successful, will provide information on the

connectivity among regions of the GBR for red throat emperor, and the technical basis to extend the approach to other species of reef fish.

This project will provide priority information for red throat emperor, maori wrasse, barramundi cod and the common and blue-spot coral trout, which will directly address immediate and long-term information requirements for the management of fishing on the GBR.

In doing so it will:

i) Through the application of genetic and otolith microchemistry techniques, provide information on the stock structure of red throat emperor within the GBR and the technical basis to extend these approaches to other species.

Evidence of the existence of regional structure (multiple stocks) on the GBR will have direct and substantial implications for future management of fishing on the GBR (ie. should a particular management tool be applied uniformly over the entire GBR, or to separate management units?).

ii) By focussing on species from three important families of reef fish (serranids (barramundi cod and coral trout), lethrinids (red throat emperor) and labrids (maori wrasse)), it will provide the empirical and conceptual basis required to develop age-based multi-species population dynamics models for tropical fish stocks.

iii) Maximise the R&D benefits obtained from the substantial logistic support and expertise currently available through the Effects of Line Fishing (ELF) Project, and the ELF Experiment in particular. The coordinated logistics and focussed collaboration provide a rare opportunity to obtain a cohesive set of information for a complex multi-species system at a scale appropriate to its management. This project will add a substantial dimension to the outcomes of the ELF Project by providing data on population dynamics of several high priority target species and essential information on the stock structure of red throat emperor.

Objectives

- I. Establish regional variation in stock abundance, age, growth and mortality of the red throat emperor (*L. miniatus*).
- II. Establish stock abundance, age, growth and mortality for maori wrasse (*C. undulatus*) and barramundi cod (*C. altivelis*).
- III. Establish regional and seasonal variation in reproduction of *L. miniatus*, *C. undulatus*, *C. altivelis*, *P. leopardus* and *P. laevis*, including size at first maturity, age at sex transition and sex-specific growth characteristics.
- IV. Develop stock discrimination techniques, based on genetic and otolith microchemistry approaches, for *L. miniatus*, and use them to determine the stock structure of *L. miniatus* in the GBR Region.

1. Background

Management context in the Great Barrier Reef World Heritage Area

The Great Barrier Reef Marine Park (GBRMP) is the largest and, arguably, most pristine marine park in the world (Wachenfeld *et al.* 1998). It is managed for conservation and reasonable use by the Great Barrier Reef Marine Park Authority (GBRMPA), a statutory authority established under the *Great Barrier Reef Marine Park Act 1975*, and was enshrined on the World Heritage List in 1981 in recognition of its unique natural and cultural values (UNESCO 2003).

Fishing is one of few extractive activities permitted within the GBRMP, and is principally managed by the Queensland Department of Primary Industries and Fisheries (QDPI&F) (formerly the Queensland Fisheries Management Authority). There has been sustained pressure to ensure that fishing activities within the GBRMP do not impact on the integrity of the ecosystems which support them. This is reflected in the Queensland Government's commitment to ensure that all fisheries are managed in an ecologically sustainable manner under the *Queensland Fisheries Act 1994*. This increased emphasis on the management of the broader impacts of fishing requires an understanding of the dynamics of species, other than the principle target species of the fishery, and their likely response to the potential impacts of fishing. This information has been lacking for the Queensland Coral Reef Fin Fish Fishery (CRFFF) (Williams and Russ 1994, Mapstone *et al.* 1997).

The GBRMPA has recently developed a system of representative highly protected areas as a conservation management tool to ensure, to the extent possible, that the entire biodiversity of the Great Barrier Reef (GBR) is protected from extractive activities within "no-take" marine protected areas (MPA). The primary objective of these highly protected areas is to set aside a broad range of habitat types and reef communities to conserve regional marine biodiversity. The system of areas will provide a pool of biodiversity which is protected from exploitative activities, such as fishing, and serve as a source of larval and post-settlement dispersal to other areas that are exploited. Dispersal from representative areas will also assist in maintaining biodiversity in areas of the GBRMP in which extractive activities are permitted by alleviating the potentially selective effects of harvest.

The available evidence suggests that most species of large reef fish have relatively restricted ranges of movement (Beinssen 1989, Davies 1995, 2000, Samoily 1997a, Zeller 1997, Zeller and Russ 1998). It is likely, therefore, that the majority of dispersal, and subsequent gene flow, can be expected to occur during the pelagic larval phase that is a feature of most reef fish life history cycles (Doherty 1991). At present, there is limited information available on the extent of dispersal of reef fish larvae within or among regions of the GBR, and none on the important commercial and recreational species of reef fish. The available evidence does suggest, however, that patterns of larval dispersal and gene flow are likely to be effected by the complex spatial structure of the individual reefs that constitute the GBR and the ability of reef fish larvae to actively influence their dispersal by swimming (Stobutzki and Bellwood 1994, 1997, Doherty *et al.* 1995, Shulman and Bermingham 1995, Wolanski *et al.* 1997, Stobutzki 1998, Leis and Carson-Ewart 1999, Fisher *et al.* 2000, Fisher and Bellwood 2002). As a result, the extent of dispersal among regions of the GBR is likely to be more restricted than would be expected on the basis of gross time-averaged hydrodynamics (James *et al.* 2002). Given this uncertainty in the current understanding of genetic connectivity on the GBR, improving the knowledge of the extent of gene flow, and by inference larval dispersal, among regions of the GBR

would be a valuable contribution to the design of the representative areas system, and future management of fisheries in the region.

The Queensland Coral Reef Finfish Fishery

A coral reef finfish fishery has operated in the GBR region for several decades (Mapstone *et al.* 2004). The present fishery makes a substantial contribution to the region through export and domestic sales of reef fish products and charter and recreational fishing activities targeting local, national and international tourism markets. Collectively, the commercial and recreational sectors of the fishery have been estimated to contribute directly over \$100 million dollars to the Queensland economy (Driml 1997, KPMG Consulting 2000, Williams 2002).

The Coral Reef Finfish Fishery (CRFFF) is a multi-species fishery with over 125 species or species groups reported as catch from the QDPI&F commercial logbook system (see Mapstone *et al.* 1996a,b,c for detailed review of commercial catch and effort). Two species groups dominate the demersal line catch from the fishery; i) coral trout, and ii) red throat emperor. The species group "coral trout" consists of at least four species (*Plectropomus leopardus*, *P. laevis*, *P. maculatus* and *P. areolatus*) with the common coral trout, (*P. leopardus*) and the blue-spot coral trout (*P. laevis*) constituting the majority of coral trout catch. These two species groups, coral trout and red throat emperor (*Lethrinus miniatus*), have comprised approximately 35-45% and 15-20%, respectively, of the total commercial line catch of demersal species between 1988 and 2000 (Mapstone *et al.* 1996a,b, Williams 2002). They are also the most popular target species for the majority of recreational reef fishers (Williams and Russ 1994, Higgs 1999, 2001).

A new management plan for the CRFFF was implemented in July 2003 (QFS 2003). The main changes to fishing regulations were the introduction of catch quotas for commercial fishers, the revision of many legal size and bag limits, and a prohibition on the taking of several coral reef fish species. Among the prohibited species is the maori wrasse (*Cheilinus undulatus*) and barramundi cod (*Cromileptes altivelis*), which were two species previously harvested in the fishery. Both species are highly valued in the live food fish trade, and are of significant conservation value (Lee and Sadovy 1998, Lau and Parry-Jones 1999). They are highly rated by dive tourist operators as an attraction for national and international tourists.

There is also considerable concern within the international conservation and scientific community about the viability of populations of maori wrasse and barramundi cod on south-east Asian coral reefs, where they are heavily targeted as part of the Asian live reef fish trade, often using destructive fishing practices (Johannes and Riepen 1995, Lee and Sadovy 1998). This concern led to the listing of maori wrasse as "endangered" (Cornish 2004) and barramundi cod as "data deficient" (Samoilys and Pollard 2000) on the World Conservation Union's (IUCN) Red List. A proposal for maori wrasse to be included on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) list was submitted in 2002, but later rejected. In October 2004 the proposal was successful and maori wrasse were listed in Appendix II of CITES, which means a permit is required for any trading of this species.

Currently, however, there is extremely limited information available on the abundance, distribution, or biology of maori wrasse and barramundi cod on the GBR, or elsewhere. Although both species are now listed as 'no take' species for the CRFFF, they will remain a bycatch species in the fishery, as the fishing gear used in the CRFFF will continue to catch both species. Issues relating to the survival of these

species after being captured and released will be important to consider, particularly with respect to the recent requirements under the *Environmental Protection and Biodiversity Conservation Act 1999* for all export fisheries to be conducted in a manner that does not threaten bycatch species.

The Effects of Line Fishing Project

The Effects of Line Fishing (ELF) Project is a large multi-faceted project focussed on improving our understanding of the response of reef fish populations to fishing with the objective of improving management of line fishing in the GBR. The ELF project is jointly funded by the Cooperative Research Centre for the Great Barrier Reef World Heritage Area (CRC Reef), the Fisheries Research and Development Corporation (FRDC), and the GBRMPA, and consists of a range of tasks which individually address the range of questions raised by the projects goal. The most widely recognised of these is the experimental manipulations of fishing pressure (The ELF Experiment) and quantitative evaluations of alternative management strategies for fishing on the GBR. The range of other tasks in the project, include: examination of the effort dynamics of the commercial fleet, analyses of QFS commercial logbook data, development of statistical analytical methods for catch and effort data from commercial multi-species fisheries, studies of the catch and effort characteristics of the recreational small boat fleet, examination of the length and age selectivity of line fishing, economic analyses of the aquarium and live food fish trades, and liaison with the fishing community, which will contribute significantly to the management strategy evaluations. The outcomes of the first set of management strategy evaluations for the fishery and the first two phases of the ELF Experiment are reported on in the final report of the related FRDC project (FRDC Project 97-124, Mapstone *et al.* 2004)

The Effects of Line Fishing Experiment

The ELF Experiment is a central component of the ELF Project and provides the focus, scale and logistic support required to address questions of regional variation in fishing, the population dynamics of key target species of the reef line fishery, and their response to changes in fishing pressure. The experimental design for the ELF experiment involves a total of 24 reefs divided into clusters of six reefs located in four regions of the GBR that span over 7° of latitude. Within each cluster, four reefs had been closed to all forms of fishing for 10-12 years prior to the start of the experiment, and the other two reefs had been open to fishing historically (see Mapstone *et al.* 2004 for more details on the experimental design). The response of target and non-target species to changes in fishing pressure was monitored in each region by manipulating the amount of fishing pressure on individual reefs within each region (Mapstone *et al.* 2004).

Research on population dynamics of reef fish in the ELF Project prior to this project had focussed on the common coral trout (*P. leopardus*), with an emphasis on the effects of fishing on rates of growth and mortality for this species for the 24 reefs involved in the ELF Experiment. Samples for the population dynamics research have been provided from the ELF research catch surveys. The main objectives of these surveys are to provide: i) research catch rate data as one source of relative abundance information for the ELF Experiment and, ii) samples of common coral trout for estimates of growth and mortality rates, for the reefs involved in the ELF Experiment. The funding for the principle objectives of these tasks is provided by contributions from CRC Reef (Task 2.4.12), FRDC (Project No: 97/124) and the GBRMPA.

Common coral trout have been the focus of resources for the Age Determination task (CRC Reef Task 2.4.12/4) within the ELF Project, and for the modelling and management strategy evaluations, to date. Samples of a variety of other species, including red throat emperor, maori wrasse, barramundi cod and blue-spot coral trout, are collected routinely as part of the research catch surveys concurrently with the common coral trout samples. This project provided the necessary operational resources to preserve, catalogue, process and analyse these samples and report on the biology and population dynamics of these other main target species of the fishery. It also supported the development and application of contemporary methods (genetic and microchemical) to examine the stock structure of reef fish on the GBR and elsewhere.

In the process of completing this research the project also provided valuable opportunities and support for the training of a number of post-graduate students whom have benefited from the experience of participating in a large collaborative project. The project has provided access to samples and data sets that allow significant questions in the fields of population biology and ecology, conservation ecology and fisheries science to be addressed in post-graduate research projects (Adams 1996, 2002, 2003, Adams *et al.* 2000, Kritzer *et al.* 2001, Kritzer 2001, 2002, 2004, Kritzer and Davies 2005, Mosse 2001, Williams 1997, 2003, Williams *et al.* 2003).

Preliminary evidence of regional variation in population dynamics of red throat emperor

Initial work on the age, growth and mortality of red throat emperor was completed with samples collected in 1995 as part of the baseline surveys for the ELF Experiment (Williams 1997, Williams *et al.* 2003). The results from this early work indicated significant differences in the age structure, rates of natural mortality and rates of growth of red throat emperor among the three experimental reef clusters in the central and southern GBR (the range of red throat emperor does not extend to the northern cluster of reefs included in the ELF Experiment). Subsequent analysis of samples collected during the 1996 surveys corroborated these results (see Chapter 3 of this report and Williams 2003). These patterns may reflect regional differences in productivity, responses to present or historical harvest patterns or the existence of separate isolated populations (stocks). Any of these alternative explanations has important implications for the assessment of the stock(s), the potential effects of fishing on the stock(s), and management of the fishing and conservation of regional biodiversity on the GBR. The population dynamics and stock structure components of this project built on these initial outcomes, made possible by the substantial sampling program in place for the ELF Experiment, using samples collected from the research catch surveys over the period 1995-2000.

This project

This project was designed to address key research priorities for the management of the reef line fishing (Anon 1997) in the GBRWHA. Specifically it was designed to: i) expand and consolidate initial work on the regional variation in abundance, distribution and population dynamics of red throat emperor; ii) initiate comprehensive studies of the key population parameters for maori wrasse and barramundi cod; iii) implement a study on important reproductive parameters of the five most important target species of the fishery, and; iv) using red throat emperor as a pilot species, commence a program aimed at applying genetic and otolith microchemistry

techniques of stock discrimination to commercially important species of reef fish within the GBR region.

The bulk of the samples (otoliths, gonads, tissue samples) required to address these objectives were collected from research catch surveys as part of the sampling program associated with the ELF Experiment (Davies *et al.* 1998, Mapstone *et al.* 2004). In addition to those samples, significant proportions of the samples were obtained from two other sources: i) commercial fishers provided the bulk of the samples used to examine seasonal and regional variation in reproduction of red throat emperor, and a proportion of the maori wrasse and barramundi cod samples, and; ii) targeted research sampling under permits provided specific size individuals of red throat emperor, blue-spot coral trout, maori wrasse and barramundi cod.

The structure of this report

The report is structured around the four objectives of the project and is intended to compliment the companion report on the ELF Experiment and Management Strategy Evaluations (Mapstone *et al.* 2004). Additional analyses and more detailed consideration of each of the chapters can be found in the related post-graduate theses and corresponding publications in the peer reviewed scientific literature.

Chapter 2, the general methods, provides an overview of the ELF experiment and the design and implementation of the research catch surveys. It also describes the other sample collection programs and the sample collation, processing and data management methods common to all aspects of the project.

Chapter 3 addresses regional variation in the population structure of red throat emperor (objectives I and III). This chapter draws on the considerable work done as part of the ELF Experiment (Mapstone *et al.* 2004) and the PhD research of Ashley Williams (Williams 2003), and focuses on the regional patterns in age, growth, sex structure and abundance. More detailed examination of the spatial and temporal variation in population structure can be found in Williams (2003) and associated publications. The effects of fishing and marine protected areas on red throat emperor are addressed in the companion report (Mapstone *et al.* 2004).

Chapter 4 describes the rationale and development of genetic and micro-chemical methods for examining the stock structure of reef fishes on the GBR and the results of applying these methods to red throat emperor (objective IV). Detailed descriptions of the genetic markers and their application to the stock structure of red throat emperor and the phylogenetic relationship among the five species of coral trout on the GBR can be found in van Herwerden *et al.* (2000, 2003) and van Herwerden *et al.* (2002) respectively.

The biology and population structure of maori wrasse, barramundi cod and blue-spot coral trout are presented in chapter 5 (objectives II and III). This chapter validates that increments in the otoliths (ear bones) are annual and can be used to provide reliable estimates of age for maori wrasse, and describes the reproductive biology of each species. Age-based growth curves are provided for each species, including estimates of sex-specific growth pattern, in the case of maori wrasse.

The final chapter describes the regional variation in reproduction and sex structure of the common coral trout. This chapter draws on the comprehensive Honours and PhD research done by Samantha Adams on the reproductive biology and effects of fishing on sex structure of coral trout on the GBR (Adams 1996, 2002, 2003, Adams *et al.* 2000) and includes additional analyses focussed on the specific objectives of this

project. As with red throat emperor, the effects of fishing and marine protected areas on common coral trout are addressed in the companion report (Mapstone *et al.* 2004) and in Adams (2002)

2. General Methods

The Effects of Line Fishing Experiment

Experimental Design

The experimental design of the ELF Experiment consists of six reefs in each of four regions of the GBR (Figure 2.1). The four regions extend over 7° latitude from the northern GBR (Cape Flattery) to the southern GBR (Swain Reefs). Field work for the experiment commenced in 1995 and is expected to conclude in 2006. Prior to 1995, four reefs in each region had been zoned Marine National Park B and closed to all forms of fishing for 10-12 years (hereafter 'closed' reefs). The other two reefs in each region were zoned General Use B and were open to line and spear fishing (hereafter 'open' reefs). Two of the closed reefs in each region represented the 'closed control' reefs of the ELF Experiment and will remain closed for the duration of the experiment.

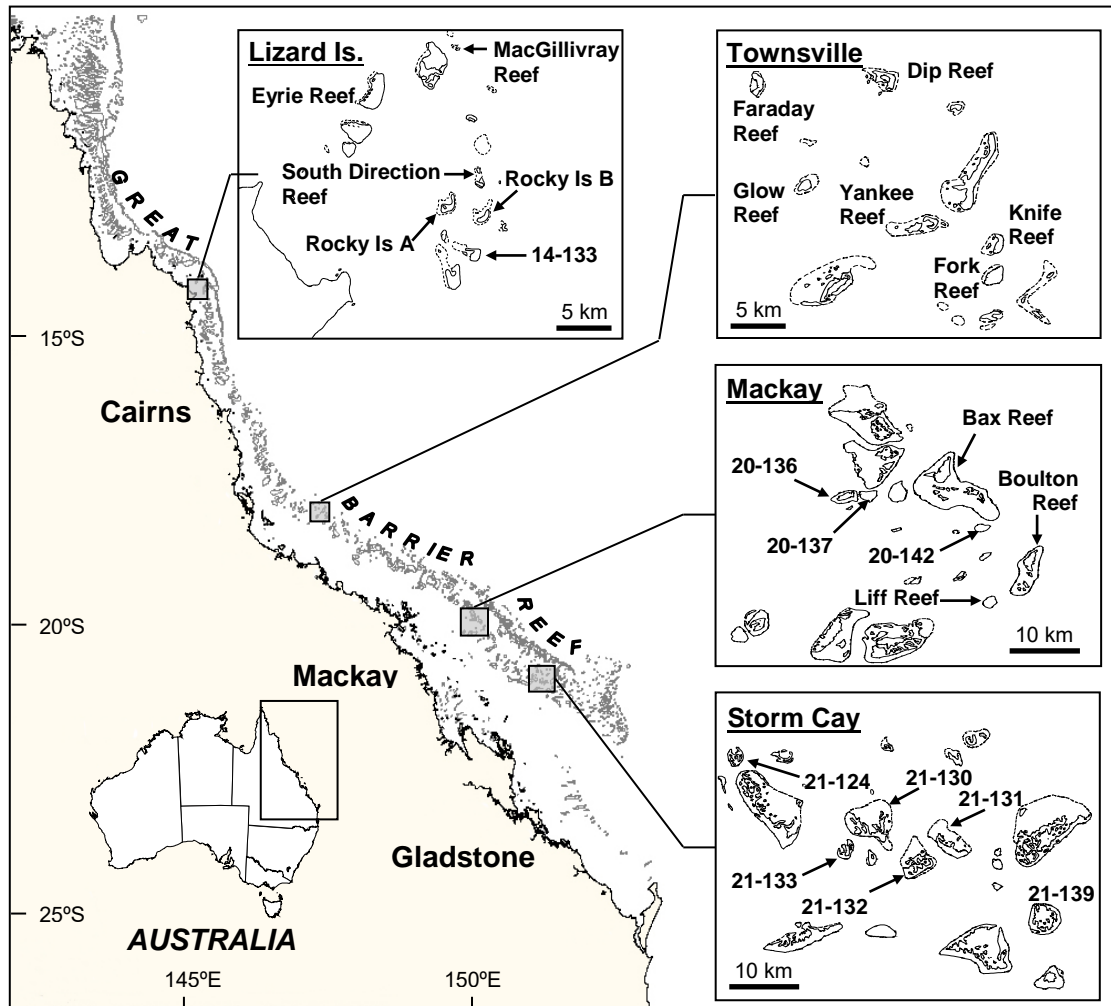


Figure 2.1. Location of the six reefs within four regions of the Great Barrier Reef sampled for the Effects of Line Fishing Experiment. Maps of reefs indicate the relative position and size of the six reefs in each region.

The other four reefs in each region (2 closed, 2 open) represented the 'treatment' reefs of the ELF Experiment. In March of 1997 one open and one closed treatment reef in each region were subjected to increased (manipulative) fishing pressure. These reefs were closed to fishing in March 1998 for a period of five years. This manipulation of fishing pressure was repeated for the remaining treatment reefs in each region in March 1999 (Mapstone *et al.* 1998a, Davies *et al.* 1998, Punt *et al.* 2001, Mapstone *et al.* 2004).

Research Catch Surveys

Line fishing catch surveys were done in the Austral Spring of each year to coincide with the spawning period of common coral trout (*Plectropomus leopardus*). The spring surveys are designed to sample fish during their spawning period when gonads are active and provide most information about the reproductive status of local populations. The surveys are timed around the full moons, however, to avoid the times of peak spawning activity that occur predominantly around the spring new moons (Samoilys and Squire 1994, Samoilys 1997b), and avoid potential biases incurred from sampling fish when they are aggregated for spawning¹.

Catch surveys were done via the charter of an active commercial line fishing operation with master fisherman and four dorymen (fishers), accompanied for the surveys by four research staff. Whenever possible, at least some of the dorymen were constant among surveys. The high turnover of crew among vessels in the reef line fishing fleet, however, meant that considerable changes in dorymen occurred among surveys. The same master fisherman was used for all surveys between 1995 and 2000, but different master fishermen had to be employed thereafter.

Fishing gear was standardised among fishers and over time to be comparable with standard contemporary gear used in the commercial line fishery on the GBR. We used 80lb monofilament fishing line with a "running sinker" rig, consisting of a bean sinker rigged on the main line above a single 8/0 hook (Mustard pattern 4279). Western Australian pilchards were used as the standard bait, as is the case in the commercial fishery. The use of "hard bait" (strips of freshly caught fish fillet) was not permitted, again to standardise methods among fishers and over time. Each fisher uses only one line at any time.

¹ Studies of the spawning behaviour of common coral trout indicates that for 3-4 days either side of the Spring new moons they aggregate daily to spawn (at dusk) but disperse between new moons, and sometimes disperse each day after spawning within the spawning period (Samoilys and Squire 1994, Samoilys 1997b, Zeller 1998).

Sampling at each reef involved the same general design, as follows. Each reef is divided into six approximately equal sized, contiguous 'blocks', three on the windward aspect of the reef and three on the leeward aspect (Figure 2.2). Block boundaries were located by GPS during each survey. Each reef is sampled on a single day on each sampling occasion², with sampling being stratified into morning (AM) and afternoon (PM) 'sessions' of 4-5 hours duration. One commercial doryman was allocated randomly to each of the three most up-stream blocks (as dictated by tidal flow³) in the AM session of each sampling day, and then again to one of the remaining three blocks in the PM session of that day. A fourth doryman 'roved' over all three blocks being fished in each session. Each doryman was required to distribute their fishing effort approximately evenly over the block, doing at least four 'hangs' (defined as a single location where a fisher sets anchor and commences to fish) in water less than 12 m deep and four hangs in depths greater than 12 m to extend the range of data to the margin of reef habitat. Each hang was between five and 20 minutes duration. Hangs were separated by at least 100m.

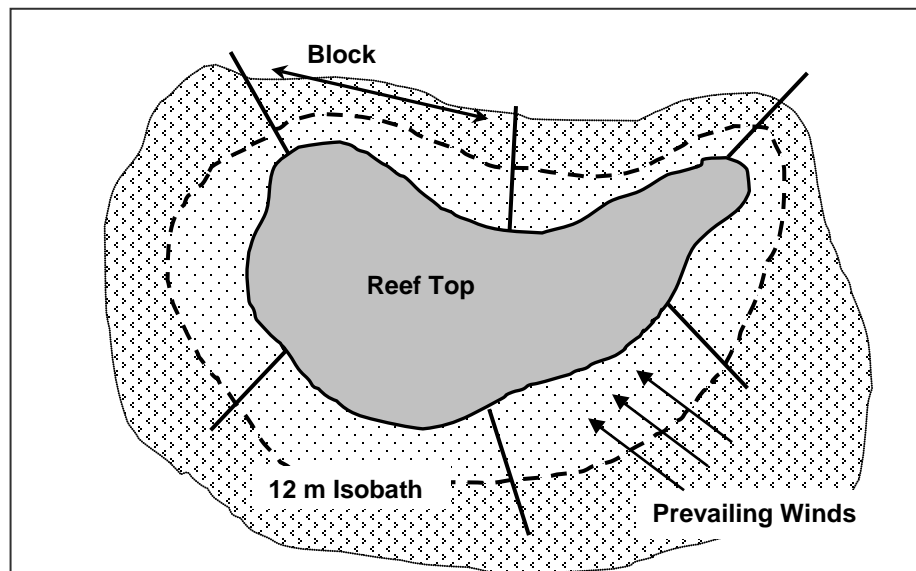


Figure 2.2. Diagram illustrating sampling stratification at each reef. Underwater Visual Surveys (UVS) were done within the 12m isobath, whilst Catch Surveys (CS) sampled equally in both depth strata (> and < 12m). Lines extending from reef perimeter indicate boundaries of 'blocks' within which UVS transects and CS 'hangs' were distributed. **Key:** - - - 12m Isobath; – Margin of reef habitat.

² In Spring 1995, each reef was sampled on two days, about one week apart. One day involved the structured fishing described here, whilst the second involved 'at will' fishing, monitored by researchers in each dory. This work was done to compare the catch characteristics and fishing behaviour of our structured surveys with 'normal' fishing conditions in the commercial fleet.

³ It is a common contention among experienced line fishers that the direction of "run" (tidal current) is a dominant determinant of catches at a particular location (Davies 1995, 2000). This is most likely related to the feeding behaviour of the target species and their interaction with the gear. Thus, catches are generally higher when fishing the "run on" side of a reef, where the prevailing current is flowing onto and over the reef, than the "run off" side, where the water flows off the reef into deeper water. We stratified sampling effort by tidal flow to standardise for this potential effect, wherever possible fishing each block during the "run on" phase of the tidal cycle for that block.

Each doryman was accompanied by a researcher who ensured that the designated sampling regime was adhered to and recorded a range of information about fishing locations (GPS location, depth, arrival and departure times), fishing practice (searching and anchoring times, line-reset times, time of each retrieval and result – e.g., no bait, species caught, etc), and characteristics of the catch (species, length). All fish caught up to the limits imposed by GBRMPA and QFMA/QFS permit conditions⁴ were tagged and kept for weighing and extraction of gonads and otoliths that evening. Fishing continued for the full day on each reef irrespective of whether the permit limits had been reached, with any fish caught beyond the permit limits being measured and held in live fish tanks in the dories and then released at the end of each hang.

In the evening of each day, the catch was processed for sale⁵ and the collection of biological samples. Each fish was identified (independently of its identification in the dory), weighed, gonads and otoliths removed, labelled and stored and then filleted or frozen in gilled and gutted form for sale. Most fish were processed completely at sea, but where this could not be done, 'frames' (head, viscera and skeleton) were frozen and processed on return to the laboratory. Gonads from common coral trout and blue-spot coral trout were collected in all surveys from 1995, whereas gonads were only collected from red throat emperor since the 1998 catch survey, and for barramundi cod and maori wrasse since the 1997 catch survey. Gonads were fixed in FAACC (Formaldehyde 4%, Acetic Acid 5%, Calcium Chloride 1.3%, Winsor 1984) prior to May 1999 and 4% Formaldehyde thereafter⁶. Removed otoliths were stored in labelled seed envelopes which were packed in plastic storage boxes for each reef on each sampling occasion. Tissue samples for genetic analyses were taken from red throat emperor collected during the 1999 catch surveys and frozen in liquid nitrogen.

Swains survey

One new location, in addition to the four regions involved in the ELF Experiment, was sampled to incorporate the southern extreme of the distribution of red throat emperor within the GBR for the stock discrimination component of the project. A dedicated sampling trip in August 1999 to Sweetlip and Sandshoe reefs in the south-east Swain Reefs collected additional red throat emperor samples. A total of 100 individuals were collected from each of the two reefs using the 'normal' fishing method outlined above. Fish were processed at sea in exactly the same way as during ELF Experiment catch surveys, and tissue samples for genetic analyses were taken and frozen in liquid nitrogen.

⁴ The permit limit was 300 common coral trout per reef per survey, with up to 90 undersized common coral trout (<38cm TL), and up to 350 individuals of all other species combined, also with various species-specific limits on the numbers of sub-legal sized fish that could be retained.

⁵ Following extraction of biological samples, all catch was processed on the main vessel as in the commercial fishery and product from legal-sized fish sold, with the proceeds of the sale returned to the ELF Project to partially off-set the costs of chartering the fishing operation for the catch surveys.

⁶ This change in fixative midway through the project was prompted by the discovery of deleterious effects of long term storage of gonads in FAACC on the staining properties of histological sections. Both whole (macroscopically or with stereomicroscope) and histological sections (microscopically) of gonad material were examined to define sex and reproductive status.

Sampling for seasonal patterns in reproductive parameters

It was necessary to implement a more frequent sampling program to explore seasonal patterns in some reproductive parameters of common coral trout and red throat emperor, as the ELF catch surveys only sampled once per year in Spring. A monthly sampling program was initiated specifically to verify the spawning season of coral trout and red throat emperor.

Bramble Surveys

Monthly samples of common coral trout were collected from a group of mid-shelf reefs located north of Townsville in the Central Section of the GBR, within a 7 day period surrounding the new moon from September 1998 to December 2000. The majority of samples were collected from Bramble Reef with relatively few coming from neighbouring Trunk and Britomart Reefs. Not all months were sampled due to bad weather and amendments to the university boating policy midway through the project. Two or occasionally three fishers collected monthly samples of common coral trout using standardised hook-and-line gear, with the exception of some samples sourced from the recreational fishing sector, which were collected by both hook-and-line and spear fishing. Samples were collected from a single day of fishing within the sampling window around the new moon. Fork length (FL) of all individuals was recorded to the nearest millimetre immediately after capture, and fish were kept on ice prior to processing. All individuals were weighed to the nearest gram for a measure of whole body weight (BW), except samples sourced from the recreational fishing sector which had been filleted and frozen. Gonads were removed, weighed (GW) to the nearest 0.1g and fixed in 4% Formaldehyde.

Samples of red throat emperor from the Commercial Fleet

A total of 1767 samples of red throat emperor were collected from the commercial fishing fleet, primarily for the estimation of the spawning season of red throat emperor. Samples were collected in the form of frozen fish frames (head, skeleton and viscera) from 14 commercial line fishing vessels operating from approximately 18°S to 22.5°S within the Central and Mackay/Capricorn sections of the GBR (Figure 2.3).

Samples were collected monthly from December 1998 to December 2000 from a total of 91 reefs. Samples collected north and south of 20°S latitude were divided into 'northern' and 'southern' areas respectively (Figure 2.3). These areas were treated as discrete for several reasons. First, there was a clear separation (of approximately 100 km) between the two nearest reefs sampled on the north and south sides of 20°S latitude. Second, 20°S latitude marks a significant change in the structure of the reefs on the GBR⁷; and third, this latitude is approximately the midpoint of the distribution of red throat emperor on the GBR. A total of 726 fish from 27 reefs were sampled from the northern area and 1041 fish were taken from 64 reefs in the southern area. For a comparison with the locations sampled during the ELF Experiment catch surveys, the Townsville region is located within the northern area, and the Mackay and Storm Cay regions are located within the southern area.

⁷ South of 20°S the reefs on the GBR are typically located further from the Queensland coastline and consequently further from terrestrial influences than reefs north of 20°S (Figure 2.1). The reefs south of 20°S are also spread over a larger distance across the continental shelf than reefs north of 20°S (Figure 2.1). Finally, the outer-shelf reefs between 20°S and 21°S are located much closer together than outer-shelf reefs between 18°S and 20°S forming what is known as the 'hardline' of reefs.

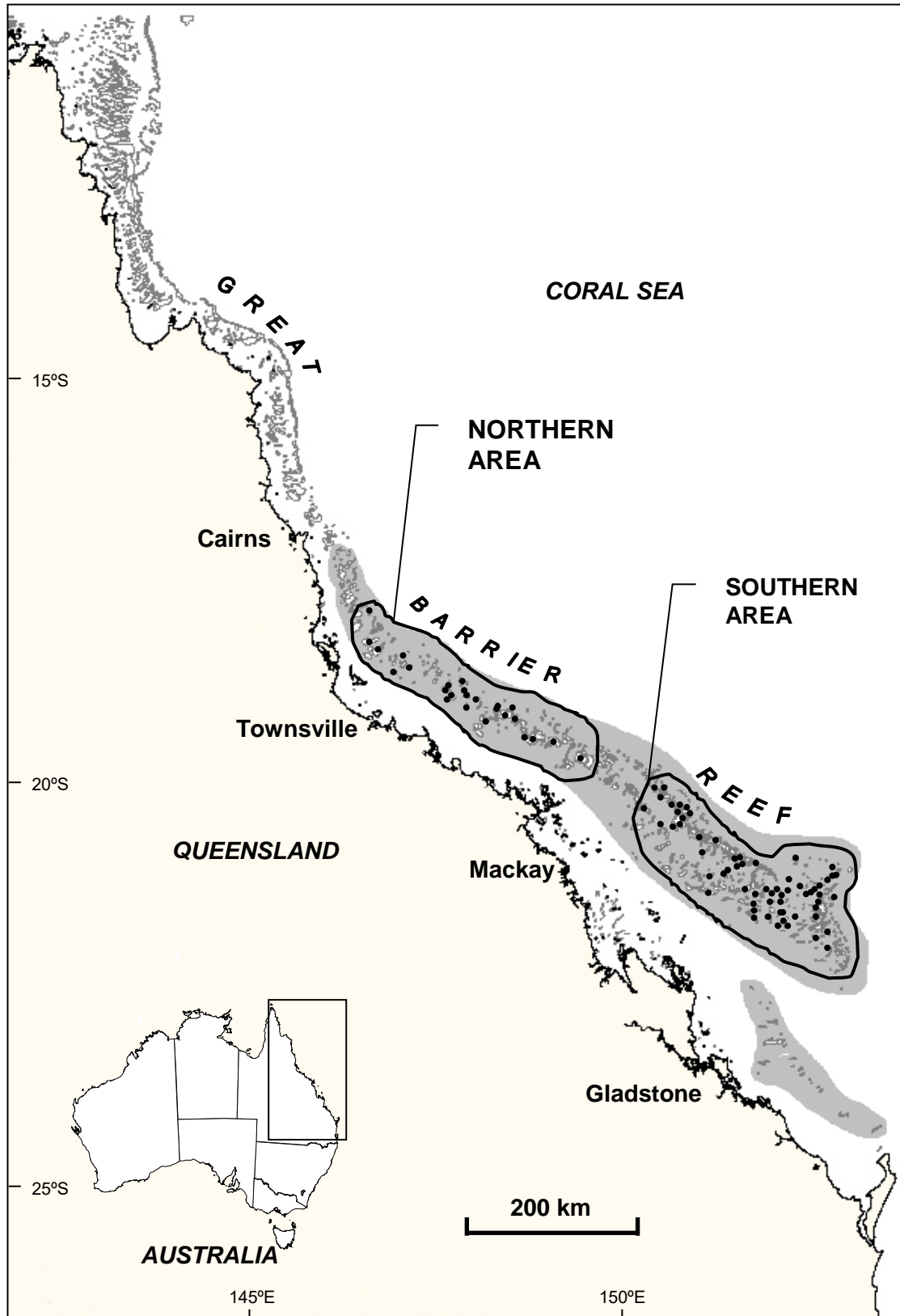


Figure 2.3. Distribution of red throat emperor on the Great Barrier Reef (shaded area) and the location of reefs sampled (•) within the northern and southern areas from which red throat emperor were collected by commercial line fishing vessels.

After thawing the fish frames, the FL of all samples was measured to the nearest millimetre. Sagittal otoliths were removed and cleaned of any residual material, then dried. Gonads were removed and the sex determined for each sample macroscopically. Gonads were preserved in FAACC. After fixation, each ovary or testis was dried of residual FAACC and weighed to the nearest 0.01g.

Additional sampling for red throat emperor

Very few red throat emperor less than 300 mm FL were collected from ELF catch surveys or the commercial line fishing fleet, due to the selectivity of the sampling gear (size 8/0 hooks). As a result, there were relatively few immature individuals identified in the sample collected. The estimation of size and age at maturity requires the collection of size and age data from immature individuals. Therefore, an additional sample of 92 red throat emperor containing relatively small (<300 mm FL) individuals was collected from reefs within the Capricorn Group in the far southern region of the GBR (Figure 2.4). These fish were collected in September 2002, which coincided with the peak spawning period in this region (Brown *et al.* 1994) and therefore maximised the contrast between mature and immature individuals. Samples were collected using hook and line (size 6 hooks) and were used only in the analysis of maturity schedules. Gonads from these samples were removed within one hour of capture and preserved in 4% Formaldehyde.

Additional sampling for maori wrasse and barramundi cod

Sample sizes for maori wrasse and barramundi cod were relatively low from ELF catch surveys. To increase sample sizes and obtain individuals to complete size distributions, additional samples were sourced from dedicated sampling trips to various reefs in the northern and central regions of the GBR. A small number of maori wrasse and barramundi cod were obtained from retail outlets, recreational spearfishers, and the aquarium trade.

Sample Processing

Otolith processing

The right sagittal otolith was used to estimate the age of all fish except if it was missing or damaged, in which case the left otolith was used. Methods for estimating age from otoliths differed among species, depending on the characteristics of the otoliths. Most age estimates for red throat emperor were obtained from whole otoliths, as initial trials showed that whole otoliths provided the same age estimates as sectioned otoliths (Williams *et al.* 2003). Age estimates for all other species were obtained from sectioned otoliths.

Sectioned otoliths

Otoliths to be sectioned were embedded in epoxy resin and cut transversely, adjacent to the anterior side of the nucleus, using a Buehler Isomet low-speed saw. The posterior portion of the otolith was retained and mounted on a glass microscope slide with Crystal Bond 509 adhesive. A second transverse cut adjacent to the posterior side of the nucleus resulted in a thin section, incorporating the otolith nucleus, remaining on the slide. Otolith sections were then ground on 800- and 1200-grade sandpaper and polished with 0.3 μm alumina micropolish to remove saw marks. A single drop of immersion oil was placed on sections to fill any remaining

surface irregularities. Otolith sections for red throat emperor, blue-spot coral trout and barramundi cod were examined under a stereo dissecting microscope at 40X magnification with reflected light and a black background.

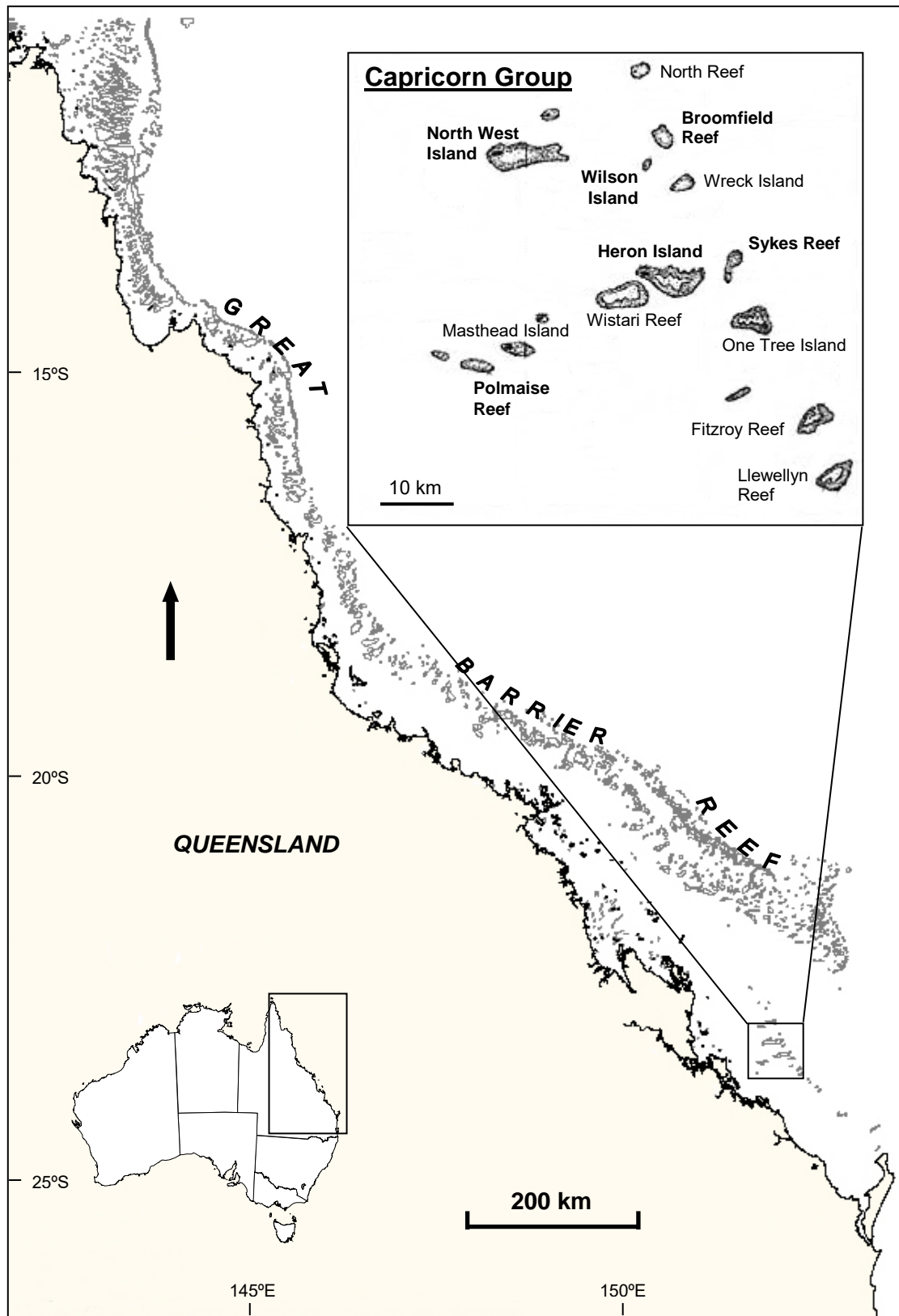


Figure 2.4. Location of reefs sampled for 'small' red throat emperor in the Capricorn Group within the Great Barrier Reef. Specific reefs sampled (in bold) were North West Island, Wilson Island, Broomfield Reef, Heron Island, Sykes Reef and Polmaise Reef.

Sectioned otoliths for maori wrasse were examined under both high power and dissecting microscopes using transmitted light.

Whole otoliths

Otoliths to be read whole were placed in a small black dish of immersion oil and examined under reflected light using a stereo dissecting microscope at 40X magnification.

Otolith reading protocol and age determination

Age estimates obtained from otoliths have been validated previously for common coral trout (Ferreira and Russ 1994) and red throat emperor (Williams 2003, Williams *et al.* in press). The age validation techniques for maori wrasse and barramundi cod are outlined in detail in Chapter 5.

Sectioned otoliths

All sectioned otoliths were examined in random order with no prior knowledge of location of capture or fish length. Interpretation of increments in otoliths and methods for age determination varied among species. Counts of opaque increments in sectioned otoliths were made from the nucleus to the proximal surface, along the ventral (common coral trout, blue-spot coral trout, maori wrasse, barramundi cod) or dorsal (red throat emperor) margin of the sulcus acousticus (Ferreira and Russ 1994, Williams *et al.* 2003) (Figure 2.5). The opaque increment closest to the margin of the otolith was only included in the count when the reader interpreted the increment as completely formed and with discernible translucent material between that opaque increment and the otolith margin.

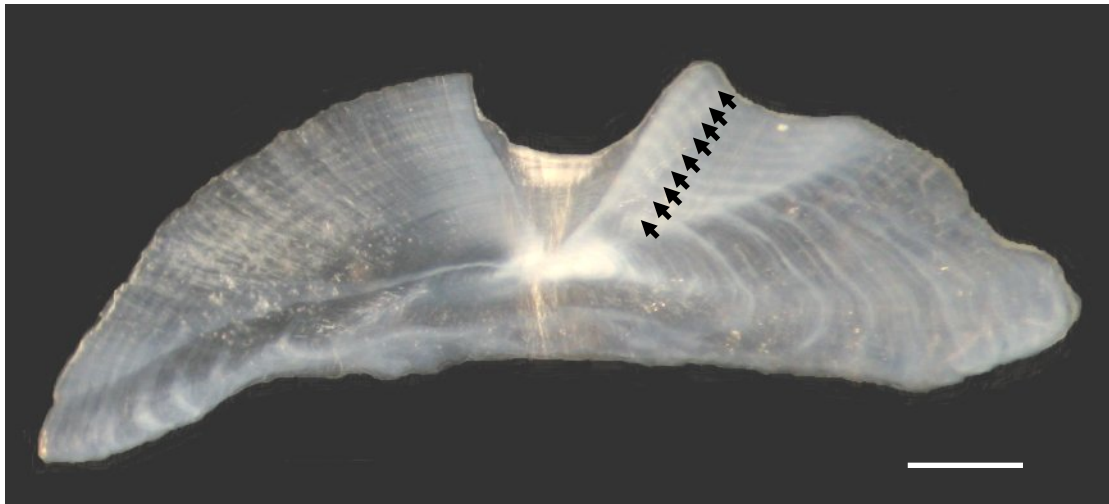


Figure 2.5. Section of a sagittal otolith of red throat emperor estimated to have been nine years old from Glow Reef in the Townsville region of the Great Barrier Reef. Arrowheads indicate annual opaque increments and the path along which they were counted. Scale bar = 1mm.

Sectioned otoliths from common coral trout were read by at least two independent, experienced readers. If the counts from the two readers were the same, the age was

accepted. If the counts differed, a third count was made by a third independent, experienced reader. If the third count matched either the first or second count, that count was accepted. If there was no agreement between any two of the three readers, a final count was made by all three readers together. If no agreement could be reached on this final count, the otolith was discarded.

Sectioned otoliths from maori wrasse were read three times by a single experienced reader. In cases where the disparity between counts was 20% or greater, an additional count was made by a second observer.

All sectioned otoliths from barramundi cod were read twice by a single experienced reader. If the counts from the two readings were the same, the age was accepted. If the counts differed, a third count was made by the same reader. If the third count matched either the first or second count, that count was accepted. If there was no agreement among counts, the otolith was discarded.

Sectioned otoliths of red throat emperor and blue-spot coral trout were read only once by a single experienced reader.

Whole otoliths

All whole otoliths from red throat emperor were examined in random order with no prior knowledge of location of capture or fish length. Counts of opaque increments in whole otoliths were made from the nucleus to the dorso-posterior edge, on the convex face of the otolith (Figure 2.6).

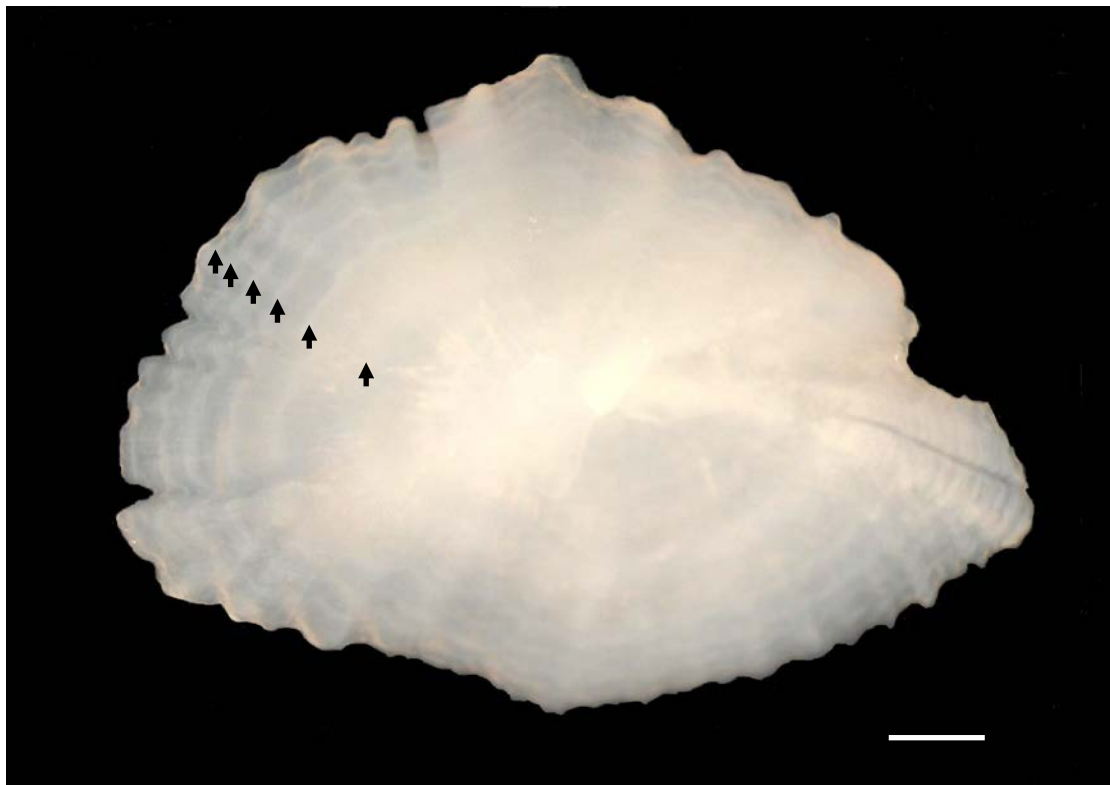


Figure 2.6. Whole sagittal otolith of red throat emperor estimated to have been six years old from Reef 21-133 in the Storm Cay region of the Great Barrier Reef. Arrows indicate annual opaque increments and the path along which they were counted. Scale bar = 1mm.

Similar to counts from sectioned otoliths, the opaque increment closest to the margin of whole otoliths was only counted if completely formed. Otoliths were only read once by a single experienced reader.

Gonad processing and histology

Prior to any reproductive staging, gonads from all species were dried of excess fixative, weighed to the nearest 0.1g and sexed macroscopically where possible. Medial samples from all gonads were used for histological examination. Transverse sections were taken from the medial sample of one gonad lobe and placed in histological cassettes and stored in 70% alcohol for 2 hours prior to transferring to an automatic tissue processor. Cassettes were then placed in a Labec Vacuum Setup for 30 minutes to completely remove all water from the tissue and infiltrate with paraffin wax (Winsor 1994). Tissue sections were embedded in paraffin and sectioned at 5µm thickness. All sections were stained using Myer's Haematoxylin and Young's Eosin-Erythrosin and mounted with DPX resin (Winsor 1994).

Reproductive staging

Each gonad section was examined under high power microscope to determine sex. Sections were read in random order without prior knowledge of the location of capture or the size or age of the fish to prevent biases in interpretation. Individuals were classified into developmental categories adapted from Moe (1969). Oocyte and spermatogenic stages were adapted from Ferreira (1995), Samoilys and Roelofs (2000), Adams *et al.* (2000) and Bean *et al.* (2003). Ovaries were qualitatively classified by the most advanced oocytes present (West 1990), including the presence of postovulatory follicles. Germinal characteristics which may indicate prior spawning, such as the presence of brown bodies, atretic oocytes vascularisation, and the relative thickness of the gonad wall (Sadovy and Shapiro 1987), were also noted.

3. Regional patterns in stock abundance, age, growth, mortality and reproductive biology of red throat emperor (*Lethrinus miniatus*) on the Great Barrier Reef

Ashley J. Williams, Campbell R. Davies, Bruce D. Mapstone, Kyi Bean, Cameron D. Murchie, Andrew Tobin

3.1 Introduction

Red throat emperor (*Lethrinus miniatus*) is an important species within the commercial, recreational, and charter sectors of the GBR CRFFF. Annual commercial catches have steadily increased from around 400 t in 1988 to over 800 t in every year since 2001 (Slade and Williams 2002, QDPI&F unpublished data). The annual harvest of red throat emperor by recreational anglers was estimated to be at least 240 t in 1999 (Higgs 2001). Currently, there are no catch estimates for red throat emperor available for the charter sector, but red throat emperor are known to be a primary target species for many charter operations on the GBR (Green *et al.* in prep).

Concerns have been expressed about the sustainability of harvest rates for red throat emperor within the CRFFF (Williams and Russ 1994). Fishers with significant history within the fishery relate experiences of localised depletion, quoting areas of usually reliable catches that have recently produced relatively poor catch rates. These concerns are generally based upon fisher anecdote with individuals from all fishing sectors lamenting catches that used to be. A small but steady decline in catch rates of red throat emperor since 1992 is apparent from commercial catch records reported in the Queensland Department of Primary Industries and Fisheries compulsory commercial logbooks (Slade and Williams 2002, QDPI&F unpublished data). It is not clear whether these declines are a result of natural decadal-scale changes in abundance or a consequence of increased fishing pressure.

There have been a number of major changes to management of the CRFFF recently, including the implementation of an Individual Transferable catch Quota (ITQ) system for the management of all commercially harvested reef fish. Within the ITQ system, a Total Allowable Commercial Catch (TACC) has been established for three species groups, including red throat emperor, which has been assigned an annual TACC of 700 t. Other management changes relevant to red throat emperor include an increase in the minimum legal size from 35 cm to 38 cm TL, a reduction in the recreational possession limit from 10 fish to 8 fish, and the implementation of three nine-day spawning closures in October, November and December of each year. Although not developed specifically as a fisheries management tool, the introduction of the Representative Areas Program by the GBRMPA has resulted in a significant reduction in the area of the GBRMP in which fishing is permitted.

The current management of the CRFFF assumes that the demography of important target species, such as red throat emperor, does not vary substantially over the species range, and that fish populations on the GBR represent a single homogeneous stock. While initial genetic research has suggested the existence of a single genetic stock of red throat emperor on the GBR (van Herwerden *et al.* 2003, Chapter 4), preliminary demographic research has demonstrated significant variation in age, growth and mortality of red throat emperor among regions of the GBR (Williams 1997, Williams *et al.* 2003). The existence of regional variation in demography of red throat emperor may reflect regional differences in productivity,

which will have important implications for assessment and management of the fishery.

The primary objective of this chapter was to examine the regional patterns in demography of red throat emperor on the GBR by consolidating and expanding on the preliminary demographic research of Williams *et al.* (2003), which was limited to only a single year of data and estimates of only a few age-based demographic parameters. Importantly, we examine regional patterns in demography by using data collected from reefs that have been closed to fishing for at least 10 years. We estimate a range of demographic parameters (relative abundance and biomass indices, age structure, rates of growth and mortality, and sex-specific reproductive traits) from data collected annually from these reefs over a six year period (1995 – 2000) among three regions spanning over 500 km of the GBR.

3.2 Methods

Sample collection

Effects of Line Fishing Experiment

Samples of red throat emperor were collected from three discrete regions of the Great Barrier Reef (Townsville, Mackay and Storm Cay) over six years from 1995 to 2000 during the Effects of Line Fishing (ELF) Experiment catch surveys (Davies *et al.* 1998), as described in Chapter 2. Samples were not collected from the Lizard Island region (fourth region in ELF Experiment), as the distribution of red throat emperor does not extend north of about Cairns. The three regions, therefore, cover most of the distribution of red throat emperor on the GBR (Figure 2.1), which is restricted to the southern 50% of the GBR.

Only samples collected from reefs that were closed to fishing were used to estimate demographic parameters, as the objective of this chapter was to obtain estimates of natural variability in populations in the absence of effects such as fishing. Two reefs within each of the three regions (Table 3.1) were chosen, as these reefs were the only reefs to be closed throughout the ELF Experiment, and had been closed for 10-12 years prior to the ELF Experiment (Mapstone *et al.* 2004). The number of red throat emperor collected from each reef in each year is given in Table 3.1. Individual reefs within each region were treated as replicates in each analysis for the comparison among regions.

Catch and effort data were collected during ELF catch surveys as outlined in Chapter 2. Details of otolith and gonad processing and estimation of age, sex and reproductive stage are also outlined in Chapter 2.

Additional sampling

Additional samples of red throat emperor were required to estimate some of the reproductive parameters that could not be estimated from samples collected from the ELF experiment. Additional samples of red throat emperor containing smaller, immature individuals were collected from the Capricorn Group in the far southern region of the GBR (see Chapter 2 for details). Size and age information from these smaller individuals was necessary to estimate the size and age at maturity, as very few immature red throat emperor were collected from ELF catch surveys. Samples of red throat emperor were also collected monthly from the commercial fishing fleet over a two year period (see Chapter 2 for details), primarily for the estimation of the spawning season, as ELF catch surveys did not sample in all months of the year.

Table 3.1 Number of red throat emperor collected from two reefs within each of three regions of the Great Barrier Reef. Samples were collected as part of the Effects of Line Fishing Experiment.

Year	Townsville		Mackay		Storm Cay	
	Glow Reef	Dip Reef	20-142	21-137	21-132	21-131
1995	71	53	56	97	59	29
1996	31	15	51	56	43	29
1997	91	33	40	38	48	50
1998	44	26	45	41	82	50
1999	65	27	106	102	138	66
2000	34	16	81	86	140	62
Total	336	170	379	420	510	286

Relative abundance and biomass

Catch per unit effort (CPUE) indices were used as proxies for relative abundance and relative biomass for each reef. CPUE indices were calculated as numbers (abundance) or weight (kg biomass) of legal-sized (≥ 350 mm TL), under-sized (<350 mm FL) and all-sized red throat emperor caught per hour of fishing per reef per year. Fishing effort was stratified by block (area fished) and depth at each reef (see Chapter 2 for details), ensuring that fishing was distributed evenly both among and within reef areas. Thus, for each reef, CPUE indices were assumed to represent the relative abundance and biomass of red throat emperor.

Relative abundance and biomass estimates were compared among regions and years using two-factor repeated measures ANOVAs with Region as the between-subject fixed factor, Year as the within-subject fixed factor, and reef-specific estimates of abundance and biomass as replicates.

Age structure

Three parameters describing the age structure for red throat emperor were estimated for each reef: 1) mean age (the average age of all fish from each reef), 2) A_{90} (the 90th percentile age - a conservative estimate of longevity), and 3) age frequency distributions for each reef. Mean age and A_{90} were compared among regions and years using two-factor repeated measures ANOVAs with Region as the between-subject fixed factor, Year as the within-subject fixed factor, and reef-specific estimates of mean age and A_{90} as replicates.

Age frequencies were pooled across years and reefs to obtain region-specific age frequency distributions due to relatively low sample sizes in most age classes. In pooling age frequencies across years it was necessary to assume that rates of recruitment and mortality were consistent among years for each reef. Multi-dimensional contingency tables were then used to compare age frequency distributions among regions. Age classes 3 years and younger and age classes 10 years and older were pooled into 3⁻ and 10⁺ age class due to low frequencies in the tails of the age distributions and to ensure that the same range of age classes were compared among regions.

Growth

The parameter estimates from the Schnute (1981) growth function suggest the von Bertalanffy growth function (VBGF) provides the best fit to length-at-age data for red throat emperor from most reefs sampled in the ELF experiment (Williams 2003, Williams *et al.* 2003), and was the model used here for consistency and validity of regional growth comparisons. Length-at-age data were pooled across years to obtain sufficient sample sizes to estimate growth for each region, and because Williams (2003) demonstrated that patterns of growth for red throat emperor did not differ significantly across years. The VBGF was fitted by nonlinear least-squares regression of fork length on age for each region. The form of the VBGF used to model length-at-age data was,

$$L_{t,r} = L_{\infty,r} \left(1 - e^{-K_r(t-t_{0,r})} \right) \quad (3.1)$$

where:

$L_{t,r}$ is the length-at-age t for region r ,

$L_{\infty,r}$ is the mean asymptotic fork length for region r ,

K_r is the rate at which L_{∞} is approached for region r , and

$t_{0,r}$ is the age at which the sampled fish have a theoretical length of zero for region r .

VBGF's were compared among regions using likelihood ratio tests (Kimura 1980), which are considered the most reliable procedure for such comparisons (Cerrato 1990). A common range of age classes was used in each analysis to assure validity of the comparisons (Haddon 2001).

Regional patterns in growth were further examined by comparing the approximate 95% confidence ellipses for the VBGF parameter estimates of L_{∞} and K among regions (Draper and Smith 1966, Kimura 1980). Using this technique to compare growth parameters requires the VBGF parameter t_0 to be constrained to the same value for all growth curves being compared. A common value for t_0 was obtained for each region by fitting an unconstrained VBGF to the size-at-age data from all regions. The constraining of t_0 usually alters estimates of L_{∞} and K due to the correlation among VBGF parameters. Consequently, the results from this technique for growth comparison are not always consistent with results from the likelihood ratio tests. Furthermore, estimates of the differences among growth curves will be more conservative (i.e. less likely to be different) when t_0 is constrained to the same value for all curves due to the correlation among VBGF parameters.

Mortality

The CPUE of fish sampled in each age class was used as an index of relative abundance of each age class for each region, assuming catchability was constant among age classes and years for all age classes fully recruited to the gear. Estimates of mortality were made using age-based cohort-specific catch curves (Beverton and Holt 1957, Ricker 1975) where the natural log-transformed CPUE was regressed on age class, and total mortality (Z) was estimated as the absolute value of the regression slope. In this case Z was taken as an approximation of M , because

fishing mortality (F) was assumed to be negligible on these reefs because they were closed to fishing.

A major assumption in using catch curves to estimate mortality is that all age classes used in the regression are equally selected by the sampling gear used. Williams (2003) estimated that the age at which red throat emperor are fully selected by the gear used in this study was six years. Accordingly, catch curves were used to estimate rates of mortality for cohorts aged six years or older in 1995. Rates of mortality were only estimated for those cohorts with at least one fish captured in each subsequent year. Hereafter, each cohort will be referred to by the age of fish in the cohort in 1995. For example, the cohort aged 6 years in 1995 through 11 years in 2000 will be referred to as the 6yo cohort.

Sample sizes were sufficient to estimate cohort-specific mortality for the 6yo -10yo cohorts in the Townsville region, 6yo - 9yo cohorts in the Storm Cay region, and the 6yo and 8yo cohorts in the Mackay region. These data were analysed using three separate ANCOVAs for: a) comparison of the regression slopes of the 6yo and 8yo cohorts among all three regions; b) comparison of the regression slopes of 6yo - 9yo cohorts between the Townsville and Storm Cay regions; and c) comparison of the regression slopes of cohorts 6yo -10yo in the Townsville region only. For all ANCOVAs, Region was a fixed factor, Cohort was a fixed factor and Age was the covariate. The interaction between the factors and the covariate provided the tests for significant differences among regression slopes. Sources of any suggested differences were identified by Least Significant Difference (LSD) adjusted multiple comparisons (Milliken and Johnson 2001).

Reproductive biology

A number of reproductive parameters were estimated for red throat emperor, including spawning season, size and age at maturity, size and age at sex change, and sex ratios. To estimate these parameters, red throat emperor gonads were removed, processed and staged as described in Chapter 2. Five female and four male stages were identified through histology (Table 3.2 and 3.3). For analyses, female stages IVa and IVb were treated as a single 'ripe' stage, due to the relatively low number of stage IVb females. Similarly, male stages IIa and IIb also were treated as a single stage in analyses, as both are resting stages.

Spawning season

The spawning season for red throat emperor was estimated from monthly samples collected from the commercial line fishing fleet (see Chapter 2 for details). These samples were divided into a northern and southern area, which allowed for a spatial comparison of the spawning season of red throat emperor on the GBR. For a comparison with the locations sampled during the ELF Experiment catch surveys, the Townsville region is located within the northern area, and the Mackay and Storm Cay regions are located within the southern area.

Table 3.2. Description of histological features of ovarian developmental stages of red throat emperor (based on Bean *et al.* 2003).

Developmental Stage	Histological description
I. Immature	Ovary dominated by pre-vitellogenic oocytes (gonia, chromatin nucleolus, early peri-nucleolus and late peri-nucleolus stages). Inter-lamellar mesenteries are filamentous or absent. No evidence of prior spawning in the form of brown bodies, atretic vitellogenic oocytes, or intra-lamellar muscle bundles.
II. Resting	Ovary dominated by pre-vitellogenic oocytes. Evidence of prior spawning indicated by the presence of brown bodies, atretic vitellogenic oocytes, post-ovulatory follicles and intra-lamellar muscle bundles.
III. Ripening	The most advanced oocytes present are at yolk vesicle stage. Atretic oocytes and/or brown bodies may be present.
IVa. Ripe	Ovary is in active vitellogenesis with yolk globule and migratory nucleolus stage oocytes present. Atretic oocytes and brown bodies are rare and inter-lamellar mesenteries thin.
IVb. Hydrated	Ovary contains hydrated oocytes as well as some yolk globule and migratory nucleolus stage oocytes. Post-ovulatory follicles may be present and atretic oocytes and brown bodies are rare.

Table 3.3. Description of histological features of testicular developmental stages of red throat emperor (based on Bean *et al.* 2003).

Developmental Stage	Histological description
I. Spent	Testis is loose and disrupted containing few spermatocysts of any sperm stage. Sperm sinuses are empty or collapsed.
IIa. Post-spawn resting	Spermatocysts no longer loose or disrupted and are separated by scar tissue. Earlier sperm stages are common.
IIb. Pre-spawn resting	Testis contains densely packed spermatocysts of spermatogonia, spermatocytes and spermatids. Spermatozoa occurred most frequently in spermatocysts alongside inter-lamellar mesenteries. Sperm has not filled the sperm sinuses.
III. Ripe	Testis dominated by spermatozoa both within spermatocysts and filling all sperm sinuses. Early stages of sperm development are rare and occur along the peripheral margins of the gonad lamellae.

A gonosomatic index (GSI: gonad weight / whole body weight * 100) was calculated for each sample, which provided a relative measure of reproductive stage. Whole body weights of these samples were not available directly, as commercial fishers provided only filleted 'frames'. Consequently, whole body weights were estimated using the relationship between fork length and total weight obtained from fish collected during ELF experiment catch surveys. The relationship used was, $W = 8.04 \times 10^{-6} L^{3.127}$, where W is fish weight in grams and L is the fork length in millimetres. It was assumed that estimates of total weights would suffice for estimates of GSI because only the temporal patterns in GSI, rather than the absolute values of GSI, were required to determine the spawning season. Where only one gonad lobe was available, due to damage during processing, gonad weight was estimated by multiplying the weight of the single lobe by two. It was assumed that this provided a reasonably accurate measure of gonad weight, as the two gonad lobes are generally equal in size for red throat emperor (Bean *et al.* 2003).

Mean monthly GSI values for mature fish were plotted separately for males and females from each area (north and south, Chapter 2) to determine the peak spawning period for red throat emperor. The proportion of samples in each mature female and male reproductive stage in each month were also plotted for each area to examine the ovarian and testicular development patterns throughout the year, and the degree of spawning activity occurring in each month in each area.

Size and age at maturity

A sample of red throat emperor from the Capricorn Group in the far southern region of the GBR (see Chapter 2 for details) was used to estimate size and age at maturity. A spatial comparison of the size and age at maturity was not possible due to the lack of small individuals collected from both the ELF experiment catch surveys and commercial line fishers. The size and age at maturity for red throat emperor from the Capricorn Group was estimated using the logistic equation,

$$P_m = (1 + e^{-\ln 19(m-m_{50})/(m_{95}-m_{50})})^{-1} \quad (3.2)$$

where:

P_m is the proportion of mature fish in age or 10 mm length class m ;

m_{50} is the age or length at 50% maturity; and

m_{95} is the age or length at 95% maturity.

Size and age at sex change

Size and age at sex change for red throat emperor were estimated from samples collected during ELF experiment catch surveys (see Chapter 2 for details). Data were pooled across years to increase sample sizes for each reef. The size at sex change was estimated for each reef and region using the logistic equation,

$$P_s = (1 + e^{-\ln 19(s-s_{50}^r)/(s_{95}^r-s_{50}^r)})^{-1} \quad (3.3)$$

where:

P_s is the proportion of males in age or 10 mm length class s ;

s_{50}^r is the age or length at which 50% of the population are males from reef or region r , and

s_{95}^r is the age or length at which 95% of the population are males from reef or region r .

Likelihood ratio tests (Haddon 2001) were used to test for differences in the size and age at sex change among regions.

Sex ratio

Sex ratios for red throat emperor were estimated from samples collected during ELF experiment catch surveys (see Chapter 2 for details). The sex assigned from histology was used to calculate the sex ratios (Female/Male) for each reef and region. Sex ratios were compared among regions and years using a two-factor repeated measures ANOVA with Region as the between-subject fixed factor, Year as the within-subject fixed factor, and reef-specific sex ratios as replicates.

3.3 Results

Relative abundance and biomass

The abundance of red throat emperor varied with Region in interaction with Year for legal-sized ($F_{10,15} = 3.51$, $p = 0.014$), under-sized ($F_{10,15} = 2.78$, $p = 0.036$), and all-sized ($F_{10,15} = 3.61$, $p = 0.013$) fish. Similarly, the biomass of red throat emperor varied with Region in interaction with Year for legal-sized ($F_{10,15} = 3.78$, $p = 0.010$), under-sized ($F_{10,15} = 3.57$, $p = 0.013$), and all-sized ($F_{10,15} = 3.80$, $p = 0.010$) fish. The abundance and biomass was lowest in the Townsville region for under-sized fish in all years, and lowest for legal-sized and all-sized fish in all years except for 1995, 1997 and 1998 (Figure 3.1). The abundance and biomass of legal-sized and all-sized fish was generally highest in the Mackay region in 1995 and 1996, and highest in the Storm Cay region in 1998 and 1999 (Figure 3.1). The largest difference for legal-sized and all-sized fish occurred in 2000 when the abundance and biomass was nearly four times greater in the two southern regions compared with the Townsville region (Figure 3.1).

Age structure

The mean age of red throat emperor varied significantly among regions consistently across years (Region main effect - $F_{2,3} = 28.70$, $p = 0.011$). Mean age was significantly higher in the Townsville region than in the Storm Cay region, which in turn had a significantly higher mean age than the Mackay region (Figure 3.2). Similarly, A_{90} varied significantly among regions consistently across years (Region main effect - $F_{2,3} = 11.99$, $p = 0.037$). A_{90} was significantly higher in the Townsville and Storm Cay regions than in the Mackay region (Figure 3.2).

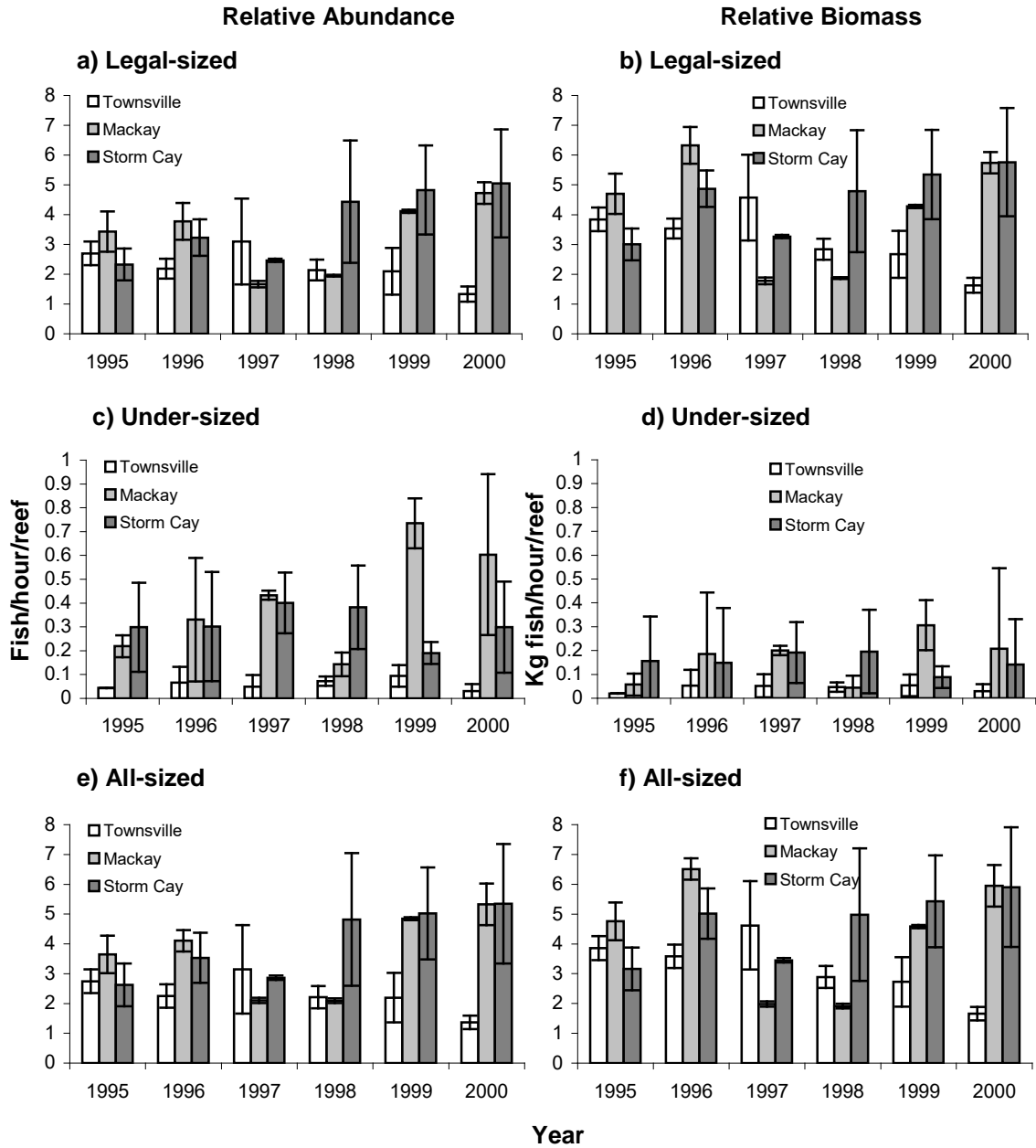


Figure 3.1. Relative abundance and biomass indices of red throat emperor from reefs within three regions of the Great Barrier Reef (Townsville, Mackay and Storm Cay) from 1995 to 2000. Three groups of catch are shown: legal sized catch (a-b), under-sized catch (c-d), and total catch (e-f). Error bars are standard error.

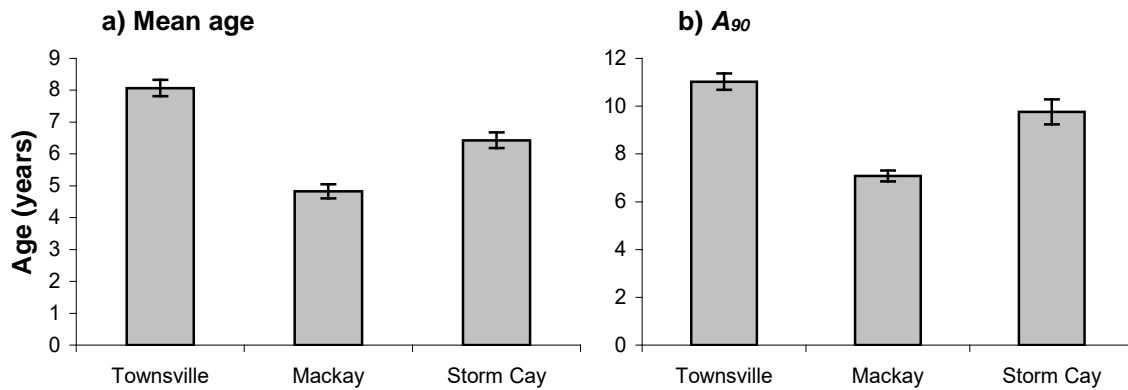


Figure 3.2. Mean age (a) and A_{90} (b) for red throat emperor sampled from three regions of the Great Barrier Reef (Townsville, Mackay and Storm Cay). A_{90} was estimated as the 90th percentile age for reefs within each region across six years (1995-2000). Error bars are standard error.

Age frequency distributions for red throat emperor varied significantly among all regions ($\chi^2 = 491.93$, $p < 0.001$) and between all pairs of regions (Townsville vs Mackay: $\chi^2 = 477.05$, $p < 0.001$; Townsville vs Storm Cay: $\chi^2 = 186.24$, $p < 0.001$; Mackay vs Storm Cay: $\chi^2 = 114.42$, $p < 0.001$). The modal age was 6 years in the Townsville region and 4 years in the Mackay and Storm Cay regions (Figure 3.3). Generally, the relative frequency of older (> 6 years) fish was greater in the Townsville region than in the Mackay and Storm Cay regions (Figure 3.3). The oldest individuals, however, were in the Storm Cay region where a small number of fish were present in age classes 15 – 20 years (Figure 3.3). The relative frequency of younger (> 4 years) fish was greater in the Mackay region than in the Townsville and Storm Cay regions (Figure 3.3).

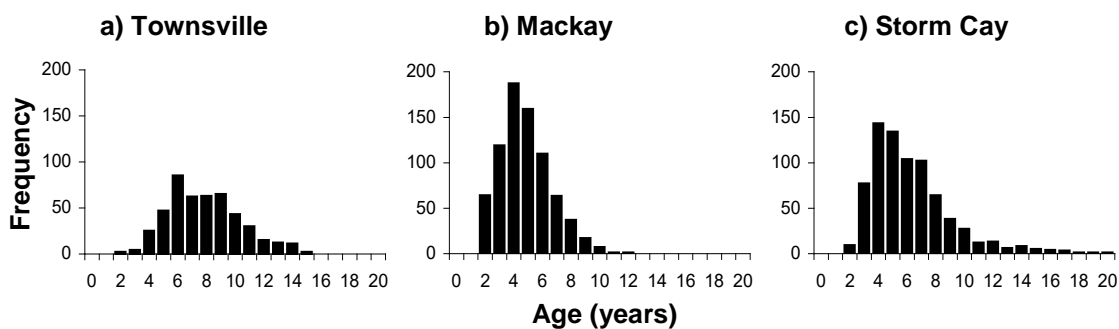


Figure 3.3. Age frequency distributions for red throat emperor pooled across six years (1995-2000) and across two reefs within the Townsville (a), Mackay (b), and Storm Cay (c) regions of the Great Barrier Reef.

Growth

There was considerable variability in the length-at-age of red throat emperor from all regions (Figure 3.4). The growth patterns for red throat emperor for each region were generally of asymptotic form, except for the Mackay region (Figure 3.4), where fewer fish sampled over 10 years resulted in less asymptotic growth.

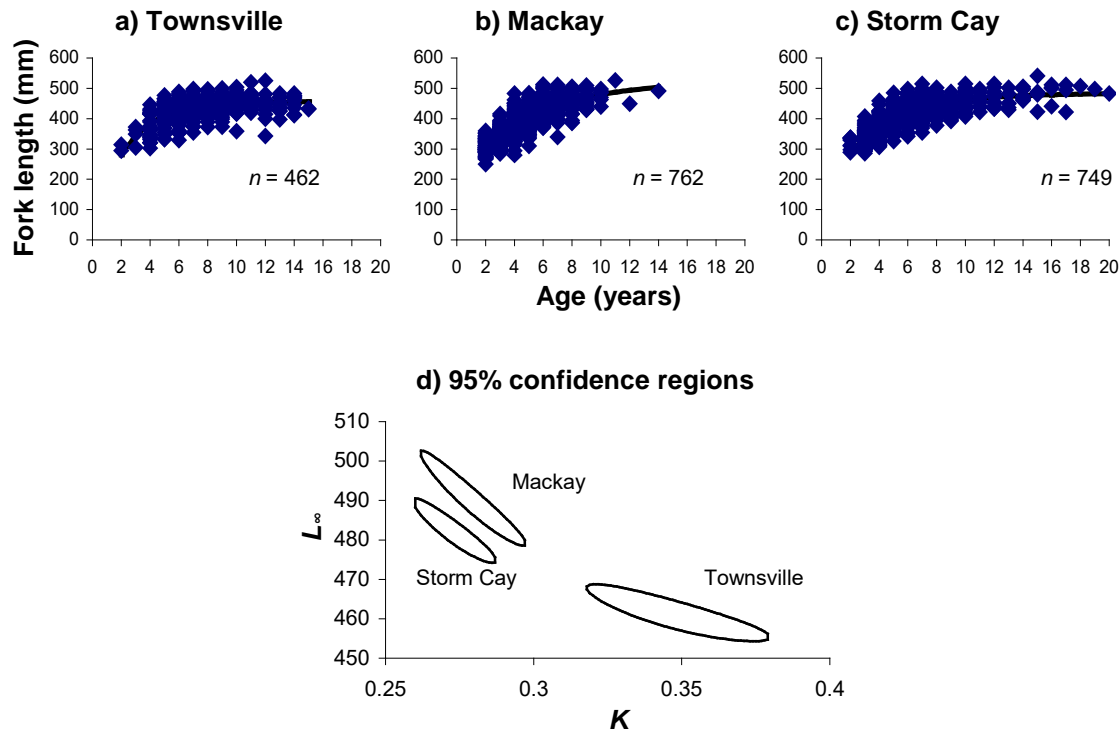


Figure 3.4. Length-at-age data and estimated von Bertalanffy growth curves for the Townsville (a), Mackay (b), and Storm Cay (c) regions of the Great Barrier Reef. Data were pooled across two reefs within each region and over the years 1995 to 2000. Approximate 95% confidence regions (d) of the parameters L_{∞} and K for red throat emperor for the three regions. Common values of the VBGF parameter t_0 were used to estimate confidence regions (see text for details).

Likelihood ratio tests indicated that patterns of growth for red throat emperor differed significantly among all regions (Table 3.2). The estimate of L_{∞} was significantly higher in the Mackay region than the Storm Cay region, which in turn had a significantly higher L_{∞} than the Townsville region (Table 3.3). The estimate of K was significantly higher in the Townsville region than the Storm Cay region, which in turn had a significantly higher K than the Mackay region (Table 3.3). There was no overlap in estimates of the 95% confidence regions for region-specific VBGF parameters L_{∞} and K (Figure 3.4), which is consistent with the results of the likelihood ratio tests.

Table 3.2 Results of likelihood ratio tests comparing von Bertalanffy growth function (VBGF) parameter estimates for red throat emperor among three regions of the Great Barrier Reef. χ^2 = likelihood ratio chi-square statistic. Each comparison tests the hypothesis that the three VBGF parameters L_∞ , K and t_0 are the same for each curve being compared.

Age Classes (years)	Comparison	df	χ^2	p
2 – 14	All regions	6	78.25	<0.001
2 – 14	Townsville vs Mackay	3	42.71	<0.001
2 – 15	Townsville vs Storm Cay	3	34.50	<0.001
2 – 14	Mackay vs Storm Cay	3	41.66	<0.001

Table 3.3 Estimates of the von Bertalanffy growth function (VBGF) parameters for three regions of the Great Barrier Reef. All length-at-age data were pooled across six years (1995-2000). L_∞ = mean asymptotic fork length, K = von Bertalanffy growth coefficient, t_0 = theoretical age at length zero.

Region	L_∞	K	t_0	n
Townsville	455.92	0.45	-0.12	462
Mackay	524.34	0.20	-2.41	762
Storm Cay	484.27	0.26	-1.49	749

Mortality

Cohort-specific mortality varied substantially among regions, but not among cohorts in any region or overall. There was no significant interaction between cohort and region and ANCOVA indicated mortality rates did not differ significantly between the 6yo and 8yo cohorts over all regions (Region*Cohort*Age interaction, Table 3.4).

Table 3.4 Analysis of Covariance comparing estimates of cohort-specific mortality of red throat emperor between the 6yo and 8yo cohorts and among the Townsville, Mackay and Storm Cay regions of the Great Barrier Reef. Estimates of cohort-specific mortality (M) for each region, and results of Least Significant Difference (LSD) multiple comparisons among regions are also presented.

Test	Source of variation	df	MS	F	p
Adjusted means	Region	2	1.213	4.022	0.035
	Cohort	1	0.168	0.556	0.465
Slopes	Age	1	16.293	54.046	<0.001
	Region*Age	2	1.616	5.360	0.014
	Cohort*Age	1	0.221	0.732	0.403
	Region*Cohort*Age	2	0.620	2.057	0.155
	Residual error	19	0.301		

LSD test for differences among regions:

Townsville ($M = 0.35$) Storm Cay ($M = 0.52$) Mackay ($M = 0.98$)

The average mortality rates of these three cohorts, however, were significantly different among regions (Region*Age interaction, Table 3.4). LSD adjusted multiple comparisons indicated mortality was significantly higher in the Mackay region ($M = 0.98$), than in the Townsville ($M = 0.35$) or Storm Cay ($M = 0.52$) regions (Figure 3.5).

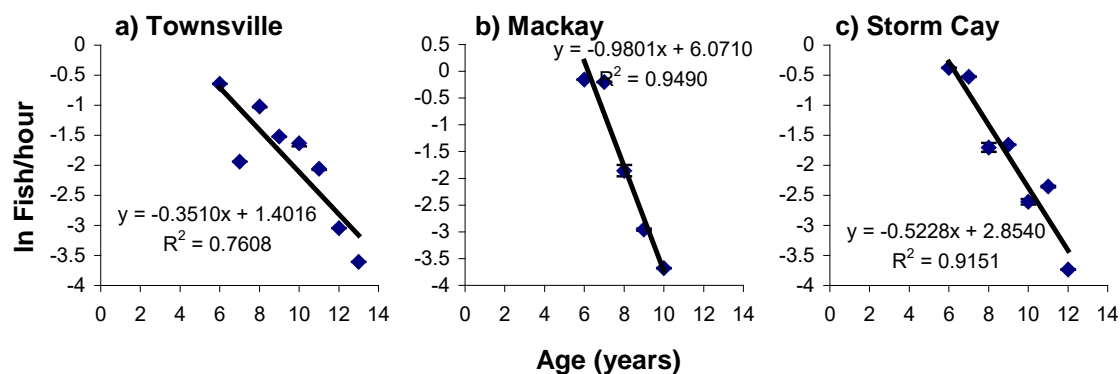


Figure 3.5. Cohort-specific catch curves for red throat emperor from three regions of the Great Barrier Reef, Townsville (a), Mackay (b), and Storm Cay (c). Catch curves were averaged over two cohorts aged 6 years (6yo cohort) and 8 years (8yo cohort) in 1995 (see methods for more details). Catch rates (Fish/hour) were used as a proxy for abundance. Error bars are standard errors.

Mortality rates did not differ significantly among cohorts 6yo-9yo in the Townsville and Storm Cay regions (Region*Cohort*Age interaction, Table 3.5). Furthermore, mortality rates for the 6yo-9yo cohorts did not differ significantly between the Townsville ($M = 0.32$) and Storm Cay ($M = 0.33$) regions (Region*Age interaction, Table 3.5, Figure 3.6).

Table 3.5 Analysis of Covariance comparing estimates of cohort-specific mortality of red throat emperor among the 6yo-9yo cohorts and between the Townsville and Storm Cay regions of the Great Barrier Reef.

Test	Source of variation	df	MS	F	p
Adjusted means	Region	1	0.058	0.155	0.696
	Cohort	3	0.072	0.192	0.901
Slopes	Age	1	18.422	49.150	<0.001
	Region*Age	1	0.026	0.069	0.795
	Cohort*Age	3	0.080	0.212	0.887
	Region*Cohort*Age	3	1.008	2.691	0.062
	Residual error	33	0.301		

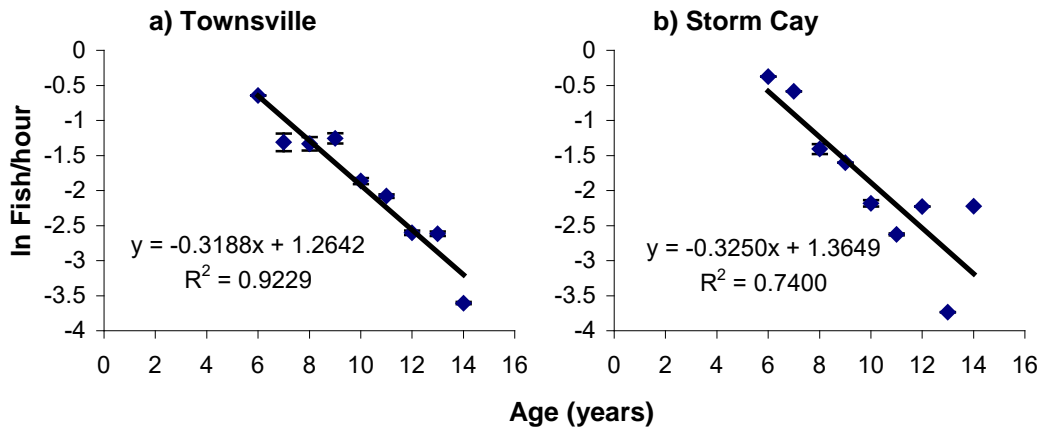


Figure 3.6. Cohort-specific catch curves for red throat emperor from two regions of the Great Barrier Reef, Townsville (a) and Storm Cay (b). Catch curves were averaged across four cohorts aged 6 years (6yo cohort) to 9 years (9yo cohort) in 1995 (see methods for more details). Catch rates (Fish/hour) were used as a proxy for abundance. Error bars are standard errors.

Finally, mortality rates did not differ among cohorts 6yo-10yo in the Townsville region (Table 3.6), and the estimate of M pooled across these cohorts in the Townsville region was 0.30 (Figure 3.7).

Table 3.6 Analysis of Covariance comparing estimates of cohort-specific mortality of red throat emperor among the 6yo-10yo cohorts in the Townsville region of the Great Barrier Reef.

Test	Source of variation	df	MS	F	p
Adjusted means	Cohort	4	0.294	1.303	0.304
Slopes	Age	1	12.883	57.194	<0.001
	Cohort*Age	4	0.192	0.853	0.509
	Residual error	19	0.225		

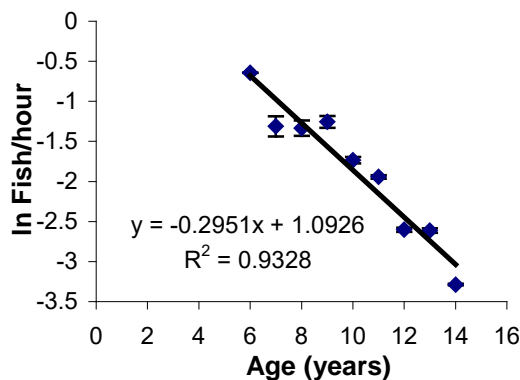


Figure 3.7. Cohort-specific catch curves for red throat emperor from the Townsville region of the Great Barrier Reef. The catch curve was averaged across five cohorts aged 6 years (6yo cohort) to 10 years (10yo cohort) in 1995 (see methods for more details). Catch rates (Fish/hour) were used as a proxy for abundance. Error bars are standard errors.

Spawning season

Mean monthly GSI values for mature females were highest in July to October in the northern area and July to September in the southern area (Figure 3.8). The mean monthly GSI values for males were highest in July to October in both areas (Figure 3.8).

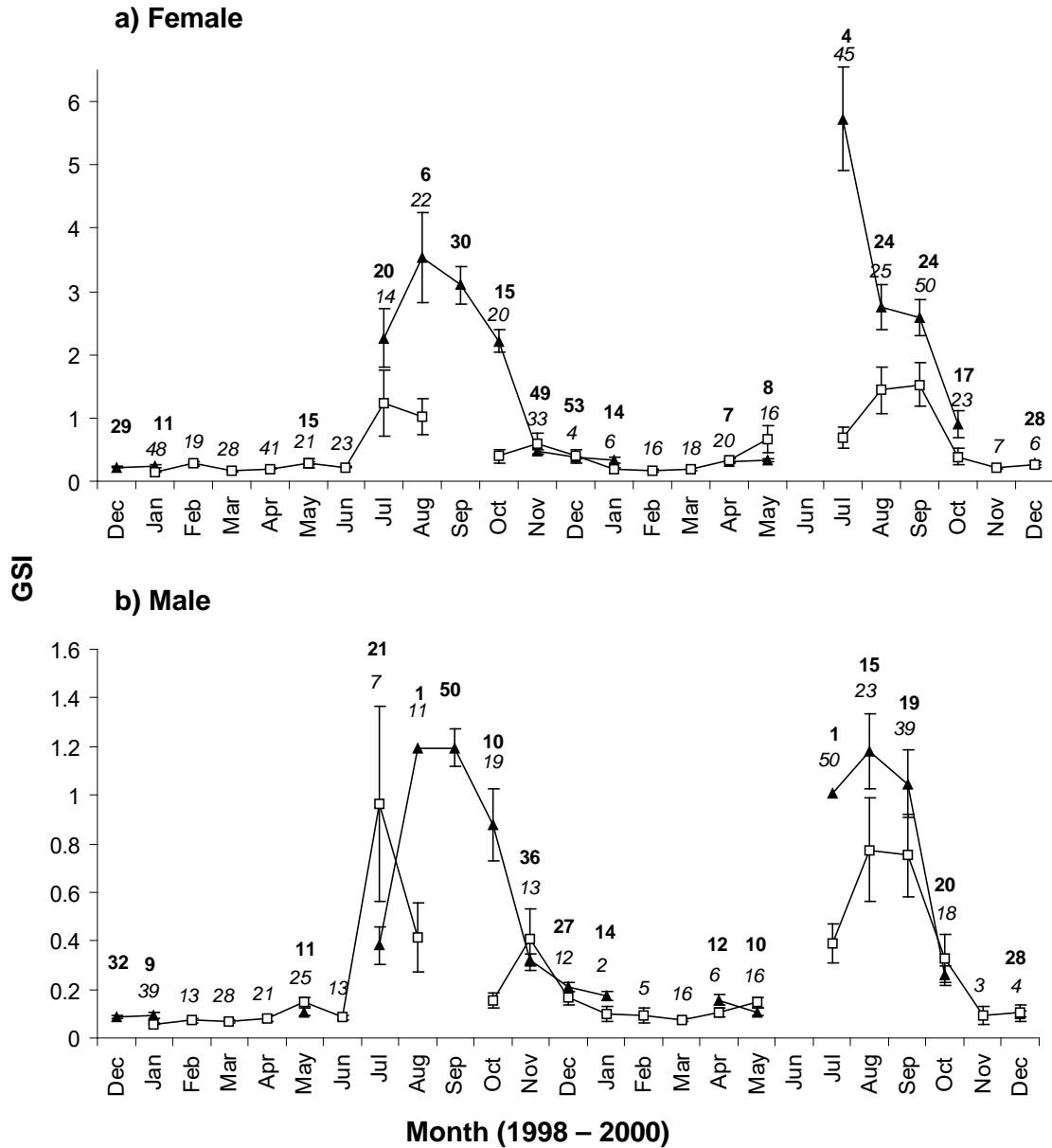


Figure 3.8. Mean monthly gonosomatic index (GSI) values for mature female (a) and male (b) red throat emperor within two regions of the Great Barrier Reef representing the north (▲) and south (□) of red throat emperor distribution. Error bars are standard errors. Sample sizes for the northern (**bold**) and southern (*italics*) regions are indicated above data points for each month.

It was not possible to verify whether spawning commenced in July or June in either area, due to missing data in June 1999 in the northern area and June 2000 in both areas. Based on GSI, however, it appears that the spawning season for red throat emperor is similar in both areas of the GBR and spans at least three to four months.

Average GSI for both females and males were higher in the northern area compared with the southern area during the spawning season (Figure 3.8).

The monthly trend in the frequency of mature ovarian stages suggested a similar temporal pattern in spawning activity to the monthly GSI values for both areas (Figure 3.9). There was some evidence of spawning in the months of January, April, May, and November in the northern area, but the majority of spawning activity occurred in the months of July to October (Figure 3.9). In the southern area, a relatively large proportion of ripe females were present in the months of May and November suggesting a slightly protracted spawning season in this area, although again the majority of spawning-ready individuals occurred between July and September (Figure 3.9).

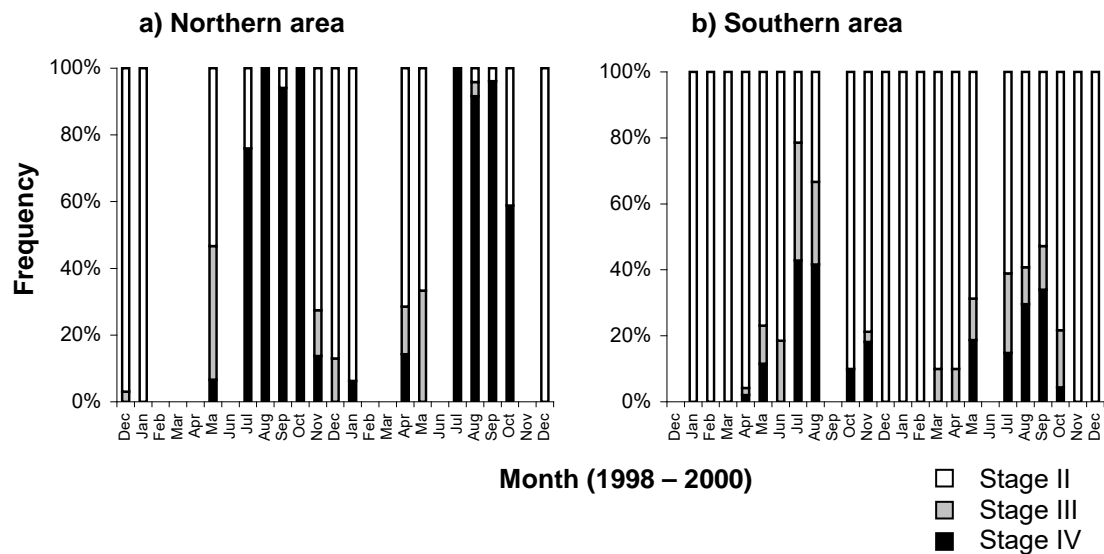


Figure 3.9. Monthly frequencies of mature ovarian stages of red throat emperor within two areas of the Great Barrier Reef representing the north (a) and south (b) of the red throat emperor distribution. Stage descriptions are provided in Table 3.2.

There was a large difference between the northern and southern areas in the proportion of ripe females during the peak spawning months (Figure 3.9). Between 59% and 100% of females were ripe during the peak spawning months in the northern area whereas no more than 43% of females were ripe in any month in the southern area (Figure 3.9). This large difference between areas was not an expected result. The relationship between size and reproductive stage was examined to determine if the low number of ripe females in the southern area was related to the size of ripe females. The proportion of ripe (stage IVa and b) ovaries during the spawning season was relatively consistent among size classes in the northern area and exceeded 70% of all ovaries in all but one size class (Figure 3.10). In contrast, the proportion of ripe ovaries during the spawning season in the southern area generally increased with size, and ripe ovaries did not exceed 50% of all ovaries until the 450 mm FL size class (Figure 3.10). Ripe females were observed at a much smaller size in the northern area (280 mm FL) compared with the southern area (350 mm FL).

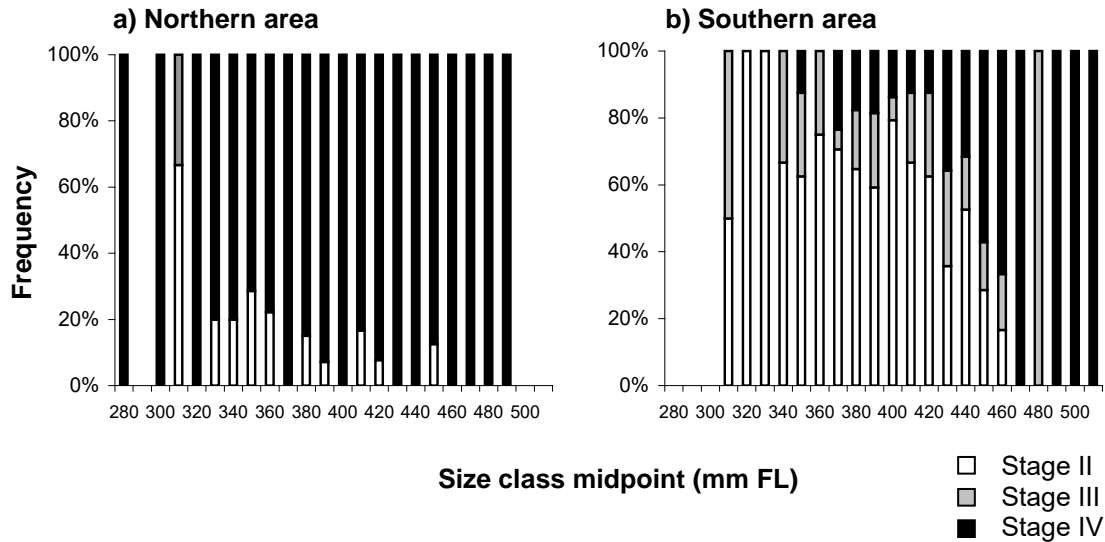


Figure 3.10. Proportion of each developmental stage for red throat emperor ovaries collected during the peak spawning months (Jul. – Oct.) in 10mm size classes within two areas of the Great Barrier Reef representing the north (a) and south (b) of red throat emperor distribution.

Males appeared to be capable of spawning over an extended period of time either side of the spawning season (as defined by the presence of active females) in both areas, as indicated by the monthly trend in the frequency of testicular stages (Figure 3.11). Greater than 50% of males had mature sperm present in all months except December and January in the northern area and December through March in the southern area (Figure 3.11).

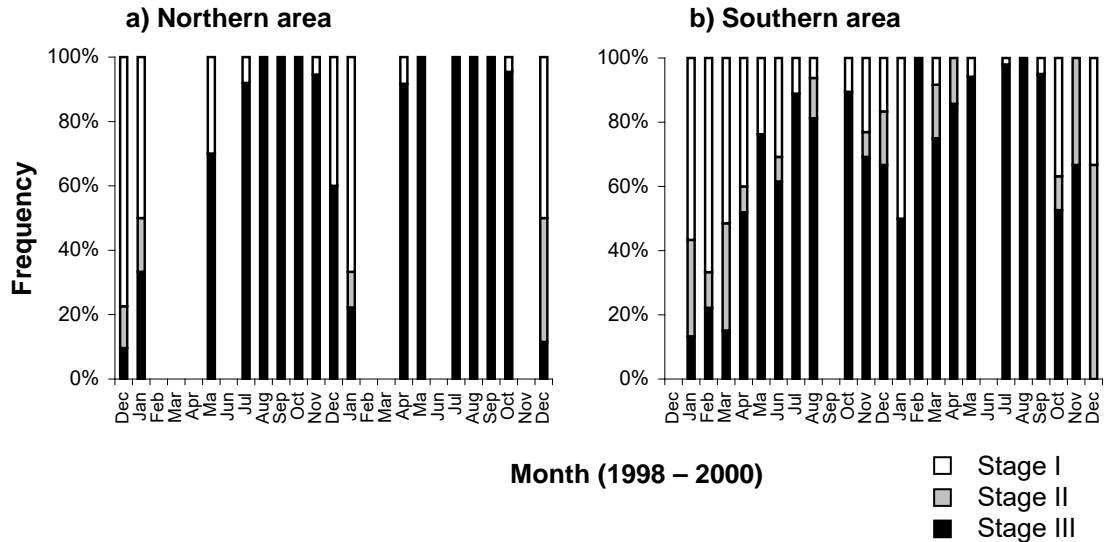


Figure 3.11. Monthly frequencies of testicular stages of red throat emperor within two areas of the Great Barrier Reef representing the north (a) and south (b) of the red throat emperor distribution. Stage descriptions are provided in Table 4.2.

Size and age at maturity

Samples collected from reefs in the Capricorn Group ranged in size from 179 mm to 460 mm FL and from 0⁺ to 6 years of age (Figure 3.12). The smallest and youngest mature female in the sample was 250 mm FL and 1 year of age, while the largest and oldest immature female was 313 mm FL and 2 years old (Figure 3.12). The size and age at which 50% of the sample was mature, estimated from the logistic function, was 280 mm FL and 1.2 years of age (Figure 3.12; Table 3.7), and 95% of individuals would be expected to be mature at 333 mm FL and 3.1 years of age (Table 3.7).

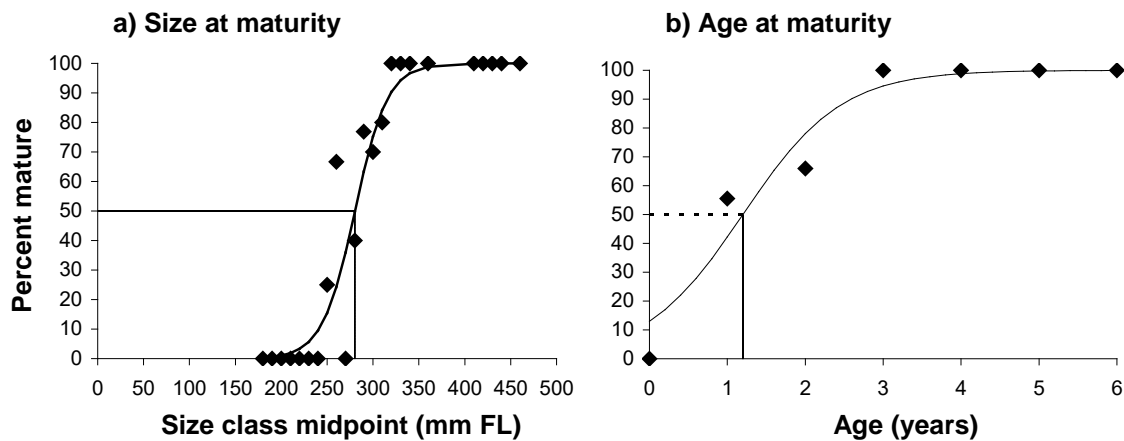


Figure 3.12. Percentage of mature female red throat emperor and estimated logistic maturation schedules for the Capricorn Group region of the Great Barrier Reef related to size (a) and age (b). Dotted lines indicate size (a) and age (b) at 50% maturity. Parameters of the maturation functions are provided in Table 3.7.

Table 3.7. Parameters of age and size-specific maturity schedules for red throat emperor populations in the Capricorn Group region of the GBR estimated by logistic regression. (m_{50} and m_{95} are the age or length at 50% and 95% maturity respectively).

	m_{50}	m_{95}	R^2
Age-specific	1.2 years	3.1 years	0.94
Size-specific	280 mm FL	333 mm FL	0.92

Size and age at sex change

There was a large overlap in the size distributions of males and females in all regions, although females dominated the smaller size classes and males dominated the larger size classes (Figure 3.13). Likelihood ratio tests indicated the pattern in the size at sex change differed significantly among all three regions and between all region pairs (Table 3.8). Pairwise comparisons between regions indicated that the size at which 50% (s_{50}) and 95% (s_{95}) of the population were male varied significantly among all regions ($p < 0.001$), except between the Townsville and Storm Cay regions, where the size at 50% sex change (s_{50}) did not differ significantly.

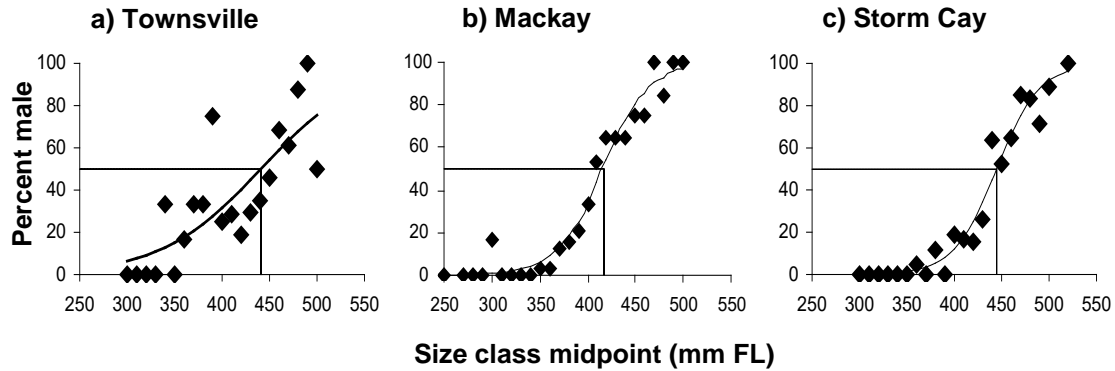


Figure 3.13. Percentage of male red throat emperor in each size class and estimated sex change schedules from the Townsville (a), Mackay (b) and Storm Cay (c) regions of the Great Barrier Reef. Parameters of the sex change functions are provided in Table 3.9.

The size at 50% sex change was 25 mm greater in the Townsville region and 28 mm greater in the Storm Cay region compared with the Mackay region (Figure 3.13, Table 3.9). Furthermore, the size at which males first appeared in the population was smaller in the Mackay region (300 mm FL) compared with the Townsville (340 mm FL) and Storm Cay (360 mm FL) regions (Figure 3.13). There was also a greater proportion of females in some larger size classes in the Townsville region compared with the Mackay and Storm Cay regions (Figure 3.13), which resulted in a substantially higher estimate of s_{95} for the Townsville region (Table 3.9).

Table 3.8 Results of likelihood ratio tests comparing logistic functions of the proportion of male red throat emperor in each size and age class among three regions of the Great Barrier Reef. χ^2 = likelihood ratio chi-square statistic. Each comparison tests the hypothesis that the logistic parameters s_{50} and s_{95} (size or age at which 50% and 95% of the population are male, respectively) are the same for each function being compared.

	Size range (mm)	Age range (years)	Comparison	df	χ^2	p
Size at sex change	300-500		All regions	4	29.44	<0.001
	300-500		Townsville vs Mackay	2	13.62	0.001
	300-500		Townsville vs Storm Cay	2	9.62	0.008
	300-500		Mackay vs Storm Cay	2	36.43	<0.001
Age at sex change		3-9	All regions	4	24.74	<0.001
		3-9	Townsville vs Mackay	2	18.61	<0.001
		3-14	Townsville vs Storm Cay	2	10.08	0.007
		2-9	Mackay vs Storm Cay	2	15.62	<0.001

Table 3.9. Parameters of age- and size-specific sex change for red throat emperor from three regions of the Great Barrier Reef. s_{50} and s_{95} are the length or age at which 50% and 95% of the population are males, respectively.

Region	Size-specific sex change			Age-specific sex change		
	s_{50}	s_{95}	R^2	s_{50}	s_{95}	R^2
Townsville	441 mm	596 mm	0.63	13.25 y	38.72 y	0.34
Mackay	416 mm	488 mm	0.97	5.54 y	8.90 y	0.95
Storm Cay	445 mm	511 mm	0.96	9.46 y	22.76 y	0.43

Similar to the size distributions, there was a large overlap in the age distributions of males and females in all regions (Figure 3.14). Females dominated the younger age classes and males dominated the older age classes in the Mackay and Storm Cay regions, but in the Townsville region, males did not dominate all of the older age classes. Likelihood ratio tests indicated that the pattern in the age at sex change differed significantly among all three regions and between all region pairs (Table 3.8). Pairwise comparisons between regions indicated that the age at which 50% (s_{50}) and 95% (s_{95}) of the population were male varied significantly among all regions ($p < 0.001$). The age at 50% sex change was almost 4 years older in the Storm Cay region and almost 8 years older in the Townsville region than in the Mackay region (Figure 3.14, Table 3.9). The age at which males first appeared in the population was youngest in the Mackay region (2 years), oldest in the Townsville region (4 years) and intermediate in the Storm Cay region (3 years) (Figure 3.14). The significant proportion of females in the older age classes, particularly in the Townsville region, was not expected for a protogynous species, and resulted in a substantially higher estimate of s_{95} for the Townsville region (Table 3.9).

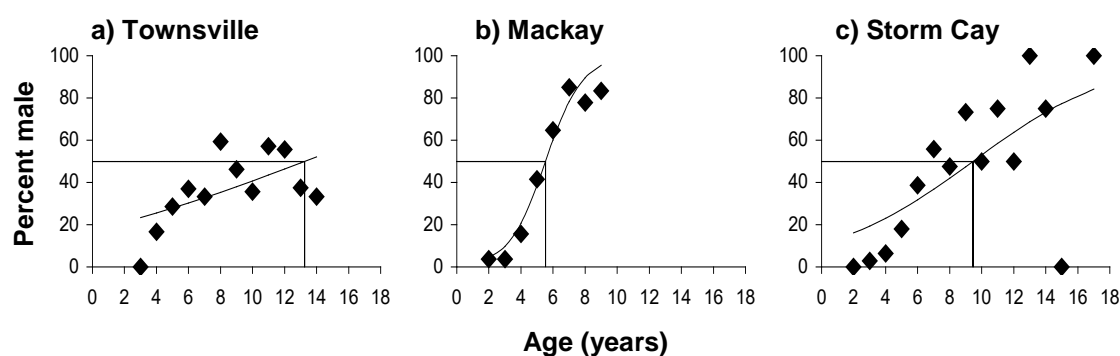


Figure 3.14. Percentage of male red throat emperor in each age class and estimated sex change schedules from the Townsville (a), Mackay (b) and Storm Cay (c) regions of the of the Great Barrier Reef. Parameters of the sex change functions are provided in Table 3.9.

Sex ratios

The sex ratio of red throat emperor was female biased in all regions (Figure 3.15). Sex ratios varied significantly among regions consistently across years (Region main effect - $F_{2,3} = 14.48$, $p = 0.03$). The sex ratio was significantly more female biased in the Mackay (2.78) and Storm Cay (2.77) regions than in the Townsville (1.39) region (Figure 3.15). The less female biased sex ratio in the Townsville region was most

likely due to the lower proportion of smaller (predominantly female) fish in the Townsville region relative to the two southern regions (Figure 3.3).

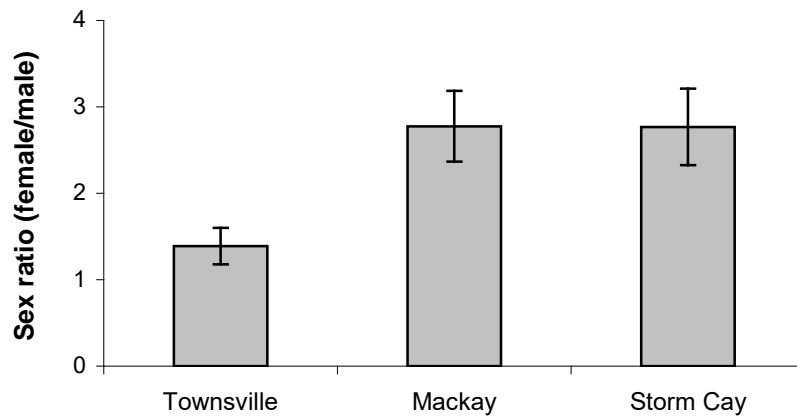


Figure 3.15. Sex ratios of red throat emperor from three regions of the Great Barrier Reef. Data were pooled across two reefs within each region and over three years (1998 – 2000). Error bars are standard errors.

3.4 Discussion

This study has demonstrated that the abundance, distribution and population biology of red throat emperor varies significantly and substantially among regions of the Great Barrier Reef, confirming the preliminary finding of Williams *et al.* (2003) and extending this to include reproductive parameters. Significant regional variation was found in all demographic parameters compared among the Townsville, Mackay and Storm Cay regions. While some parameters differed significantly among all three regions (mean age, age frequency distributions, growth, and size and age at sex change), others differed significantly between two of the three regions (abundance, biomass, A_{90} , mortality, and sex ratios) (Table 3.10).

Table 3.10. Summary of regional patterns in demographic parameters for red throat emperor among regions of the Great Barrier Reef

Parameter	Townsville	Mackay	Storm Cay
Relative Abundance	low	high	high
Average age	high	low	intermediate
Longevity	high	low	high
Age distribution	flat, low % <4yo	left skew, high % <4yo	left skew, moderate % <4yo
Growth	smaller	larger	intermediate
Mortality	low	high	intermediate
Size at sex change	high	low	intermediate
Age at sex change	high	low	intermediate
Sex ratio	female biased	high female bias	high female bias
Proportion of ripe females	high	low	low

The Townsville and Mackay regions consistently showed the greatest difference for each demographic parameter, with parameter estimates for the Storm Cay cluster often being intermediate to these two regions. This indicates that the observed differences did not relate simply to a linear latitudinal gradient among the three regions.

Other demographic parameters (spawning season, proportion of spawning females and size and age at maturity) were not able to be estimated for any of the three regions sampled by the ELF catch surveys, due to the selectivity of the sampling gear and frequency of sampling. The spawning season and proportion of spawning females, however, were able to be estimated and compared across two broad areas of the GBR covering the majority of the distribution of red throat emperor. The spawning season was found to be consistent between both areas, while a significantly larger proportion of spawning females were found in the northern area compared with the southern area. Estimates of the size and age at maturity were only possible for a single location on the GBR (Capricorn Group), and thus spatial comparisons were not possible.

The significant regional variation in demographic parameters of red throat emperor suggests that there are likely to be substantial differences in productivity and dynamics among the three regions. The results for the Townsville region suggest relatively low productivity, slower population turnover and potentially inconsistent, episodic recruitment. In contrast, the Mackay region appears to be characterised by high productivity (larger size and potentially consistent high recruitment) and high rates of turnover. The results for the Storm Cay region indicate that it is generally intermediate between the other two regions, having larger fish, higher rates of mortality and a greater proportion of young fish than the Townsville region, but greater longevity and lower mortality than the Mackay region.

There are a range of potential explanations for these observed patterns that were discussed in detail by Williams (2003). These include regional variation in general biological production due to differences in environmental conditions or habitats and/or regionally distinct populations of red throat emperor with intrinsic population parameters. The results of the stock structure component of this project, using genetic and microchemical methods (van Herweden *et al.* 2003, Chapter 4), indicate that the likelihood of multiple reproductively isolated stocks of red throat emperor on the GBR is low. This is also consistent with the results of other studies of stock structure and gene flow of fish and invertebrate populations on the GBR (Doherty *et al.* 1995, Dudgeon *et al.* 2000). It appears more likely that the observed differences in population parameters reflect a single spatially structured stock, with the observed spatial structure related to meso-scale (> 100 km) patterns in productivity, variation in recruitment (Doherty 1991, 2002, Doherty and Fowler 1994), and potentially large-scale ontogenetic migration of red throat emperor (Williams 2003).

Unlike most smaller reef fish, the relatively deep open sand/rubble areas between reefs, which often extend for several kilometres, do not appear to create a boundary for the movement of red throat emperor, as they are commonly caught in areas of sand and shoal between reefs to depths of at least 128m (Williams and Russ 1994, Newman and Williams 1996). One hypothesis, proposed by Williams (2003), is that large-scale net movement of adult red throat emperor occurs on the GBR in a general northerly direction, towards the Townsville region. Central to this hypothesis is the influence of the East Australian Current on the GBR, which results in a general southerly flow of water over the regions in this study (Wolanski 2001). As a result, net transport of red throat emperor larvae on the GBR is predicted to occur in a southerly

direction, and subsequent recruitment to be consistently higher in the southern regions.

A number of factors are consistent with this hypothesis. Firstly, the greater abundance of smaller and younger fish, and greater overall abundance, in the southern regions suggests that recruitment is significantly higher in these regions than in the Townsville region. Secondly, historically higher catches and catch rates of red throat emperor recorded from the Mackay and Storm Cay regions of the GBR compared with the Townsville region (Mapstone *et al.* 1996a) suggest higher average levels of recruitment in southern regions of the GBR. Thirdly, the significantly greater proportion of spawning fish in the northern area compared with the southern area suggests that a large proportion of red throat emperor larvae on the GBR may originate from the northern area. Net movement of adult red throat emperor towards the northern extreme of their distribution may represent an evolutionary advantage for the species to maintain its current distribution on the GBR. Finally, the high estimate of natural mortality in the Mackay region ($M = 0.98$) corresponds to a loss of nearly 70% of a cohort each year. It seems likely that this estimate is an overestimate given red throat emperor on the GBR has a potential longevity of 20 years, and estimates of natural mortality for other large reef fish with similar longevities typically range between 0.1 and 0.5 (Munro and Williams 1985, Russ *et al.* 1998, Newman *et al.* 2000a,b, Kritzer 2002). Net emigration of older fish from the Mackay region would explain the lack of older fish and unrealistically high estimate of M for this region.

Several outstanding questions need to be resolved, however, to determine the validity of the movement hypothesis. Movement rates of red throat emperor within and among regions of the GBR need to be quantified. This does not only involve elucidating latitudinal movement patterns, but also includes determining the extent to which red throat emperor move across the continental shelf, and the identification of the juvenile habitat. Ontogenetic cross-shelf movement on the GBR have been documented for mangrove jack (*Lutjanus argentimaculatus*) (Russell *et al.* 2003) and suggested for other large lutjanids including red emperor (*L. sebae*), and small and large-mouth nannygai (*L. erythropterus* and *L. malabaricus*) (Williams 1991, Williams and Russ 1994), but is unknown for red throat emperor. Tagging studies generally have been unsuccessful at tracing movements of red throat emperor on the GBR (Brown *et al.* 1994) because of remarkably low recapture rates. The development of new tagging techniques with the ability to track large-scale movement patterns of fish would be a profitable area for further research. An understanding of the movement patterns of red throat emperor, in conjunction with regional estimates of demographic parameters, would greatly assist the development of spatially explicit stock assessments.

The development of stock assessments usually requires reliable estimates of reproductive output (spawning stock biomass). It will be important, therefore, to determine why a significant proportion of mature female red throat emperor do not spawn each year in the southern area of the GBR, as estimates of reproductive output usually assume that all mature females in a population participate in spawning each year. Clearly, the results from this project suggest that the reproductive output of red throat emperor would be significantly overestimated for the southern area of the GBR, and stock assessments would significantly overestimate potential yields, if all females were assumed to be spawning each year. Why most smaller female red throat emperor do not spawn during some years, prior to reaching a certain size, is unclear, but for other species, spawning omission has been linked to low food availability (Pollock 1984, Burton 1994, Burton *et al.* 1997), reduced water temperature (Chauvet 1991) and geographic position at the edge of the species distribution (Fennessy and Sadovy 2002).

In addition to providing statistical comparisons of population parameters among regions of the GBR, this project has substantially extended the existing knowledge of the general biology of red throat emperor on the GBR. Specifically, this project has expanded the preliminary work by Williams *et al.* (2003) by consolidating estimates of age structure, growth and mortality of red throat emperor over a period of six years, and providing estimates of additional demographic parameters including relative abundance, biomass, spawning season, maturity, sex change and sex ratio.

Specific restrictions for red throat emperor on the GBR include a minimum size limit of 380 mm TL (approximately 350 mm FL) for all fishers, which is intended to allow 50% or more of fish to reach maturity and spawn before becoming vulnerable to the fishery. Based on the maturity estimate from the Capricorn Group, the current minimum size limit appears to be meeting the stated objective, as 100% of females were found to be mature at 350 mm FL. However, this estimate of maturity was obtained from a single region of the GBR. It will be important to determine whether maturity varies among regions of the GBR to establish whether the current minimum size limit is appropriate for all regions of the GBR.

The use of a minimum size limit is complicated by the finding that 50% of females in the southern area of the GBR do not spawn in all seasons until they reach approximately 450 mm FL. From a management perspective, the females that do not spawn in a given season are effectively 'immature' for the years they do not contribute to egg production. Therefore, although the current minimum size limit may be allowing 100% of females to reach maturity before becoming vulnerable to the fishery, it is likely that many of these females, at least in the southern area of the GBR, do not spawn before being caught. The use of a minimum size limit for red throat emperor is further complicated by the protogynous sexual strategy of red throat emperor (changing sex from female to male). The majority of the male population of red throat emperor are vulnerable to harvest (>350 mm FL), and therefore red throat emperor may be particularly vulnerable to sperm limitation arising from overfishing of males. An increase in the current minimum size limit, or the introduction of a maximum size limit, are two mechanisms that may offer some protection from harvest to a proportion of the male population.

Recently, a spawning closure for the GBR Line Fishery has been implemented for three nine-day periods around the new moons in October, November and December. The closures are intended to protect the spawning activity of reef fish, particularly spawning aggregations of the main target species, coral trout. Red throat emperor, however, will gain little, if any, protection of spawning activity from the closures, as they do not coincide with the peak spawning period for red throat emperor (July – October). Furthermore, the efficacy of the spawning closures depends on more than aligning the closures with peak spawning periods. For spawning closures to be most effective (i.e. more effective than closures at other times), there must be evidence of intentional targeting of spawning aggregations or an increase in catchability of a species during the spawning season. There is little documented evidence consistent with either of these scenarios for red throat emperor or any other species in the CRFFF (Mapstone *et al.* 2001).

4. Stock structure of red throat emperor (*Lethrinus miniatus*) in the Great Barrier Reef Region based on microsatellite and otolith microchemistry analyses

Campbell R. Davies, John D. Benzie, Lynne van Herwerden, Ashley J. Williams, Cameron D. Murchie and Bruce D. Mapstone

4.1 Introduction

One of the main challenges to stock assessment is the definition of a unit stock (Beverton and Holt 1957). In the case of demersal reef fish, this requires determining both the distance and direction of movement of dispersive larvae that may maintain high levels of connectivity between groups of geographically separated, less dispersive adults (Begg *et al.* 1999, O'Connell and Wright 1997). In the absence of comprehensive tagging data, genetic and microchemical methods are increasingly being used to infer connectivity between geographically separated adults and, hence, stock structure.

Current fisheries management regulations for red throat emperor (*Lethrinus miniatus*) on the Great Barrier Reef (GBR) are based on the assumption that the species forms a single reproductive unit ("panmictic stock"). Consistent with this assumption, management measures such as size, effort and catch limits are applied uniformly across the full geographic range of the fishery (Mapstone *et al.* 1996c). Evidence to date suggests that the adults of most large reef fish species have restricted movement ranges (Beinssen 1989, Davies 1995, 2000, Samoilys 1997a, Zeller 1997, Zeller and Russ 1998). Gene flow between reef associated adult populations is generally considered to occur through larval dispersal (Doherty *et al.* 1995).

Adult red throat emperor does, however, occur in deeper water (> 100m) on patchy hard ground in inter-reef areas (Williams and Russ 1994, Newman and Williams 1996). The extent to which individuals may move between individual reefs, or from inter-reef areas up onto reefs, is unknown (Davies 1995, Williams 2003). If this sort of movement was to occur to a significant degree, it would promote random mating and, at high enough rates, would maintain gene flow sufficiently to maintain a panmictic stock.

Previous work on the age, growth and mortality of red throat emperor indicates significant differences in the estimated mean age, rate of total mortality and rate of growth of red throat emperor among three regions on the GBR (Williams 1997, Williams *et al.* 2003, Williams 2003, Chapter 3, this report). These patterns may reflect regional differences in productivity, harvest patterns or the existence of separate isolated populations (stocks). Which of these alternatives is actually correct has important implications for the assessment of stock(s), the potential effects of fishing on the stock(s) and management of the fishery in the GBR. The early evidence of regional difference in population parameters (Williams 1997, Williams *et al.* 2003) provided the primary need for this stock structure component of the current project.

There are a range of methods that may be used to examine stock structure in fish populations, including genetic techniques, otolith microchemistry techniques, paratsites, otolith morphology, meristics and ecto-parasites. Microsatellites are nuclear markers and have a higher mutation rate relative to mitochondrial DNA (Burg *et al.* 1999). We considered that these characteristics would provide the greatest likelihood of detecting potential differences in the genetic composition among the red

throat emperor populations due to relatively recent geographic or ecological separation since the last significant change in sea level inundated the GBR lagoon. As the microsatellite genetic technique had not been applied to reef fish previously, it was necessary to first develop a set of microsatellite “markers” that could be used for red throat emperor (van Herwerden *et al.* 2000). Following development of the markers we used them to examine the extent of any genetic differences among adult red throat emperor populations in three different regions of the GBR (van Herwerden *et al.* 2003). In addition to this primary question of stock structure of red throat emperor, we used the same markers to examine the evolutionary phylogeny of the five coral trout species that occur on the GBR (van Herwerden *et al.* 2002). The results of this additional component of the genetics and the use of these markers in other studies of reef fish are not discussed further here.

The use of otolith microchemistry in the study of stock structure of fish populations is a developing field. It is based on the premise that differences in the environmental and or ecological conditions among different geographic locations will result in differences in the chemical composition of the otoliths or other bony structures in the fish. If this premise holds, then it should be possible to identify individuals from different geographic areas by the microchemical “signature” in their otoliths. Otolith microchemistry cannot be used to estimate the level of connectivity between geographically separated populations in the same way as genetic methods, such as microsatellites. It can, however, provide correlative evidence which may be used in conjunction with other observations to infer stock structure. The technique has been applied most extensively for species which exhibit ontogenetic shifts in habitat, such as between estuarine, or coastal waters and offshore marine waters. A significant advantage of the approach is it’s relatively low cost in comparison to genetic approaches such as microsatellites and other molecular markers.

In this component of the project we used both microsatellite markers and otolith microchemistry to test the hypothesis that the red throat emperor populations in three regions of the GBR represent a single reproductive unit, or a panmictic stock. In order to incorporate the greatest geographic range possible, we collected samples from reefs in one additional location in the far south-eastern Swains reefs for this component of the project (Chapter 2). The microsatellite genetics was done on samples from each of two reefs in the Townsville and Mackay clusters of the ELF Experiment and the two reefs from the south-eastern Swains. The otolith microchemistry approach was applied to these same reefs and, in addition, two reefs from the Storm Cay cluster of the ELF Experiment in the north-east Swains reefs.

4.2 Methods

Sample collection

A total of 573 mature adult red throat emperor (*Lethrinus miniatus*) were collected by line fishing from two individual platform coral reefs in each of three regions of the Great Barrier Reef, Australia, i.e. 6 locations in total as part of research surveys in August 1998 (see Chapter 2, Davies *et al.* 1998). The timing of the surveys coincided with the peak spawning period for red throat emperor in the three locations sampled and all fish were in mature and in spawning condition. Williams *et al.* (2003) had demonstrated significantly different population demographics in these three regions, and no significant differences between the four reefs sampled within each region. In the present study, samples were obtained from reefs previously characterised by Williams *et al.* (2003) in the Townsville and Mackay and Storm Cay regions and an additional two reefs at the Southern extreme of the Swains region (Sweetlip and Sandshoe) were sampled to maximise the geographic range covered in the stock structure component of the project. In the case of the microsatellite analyses, there were sufficient resources to analyse samples from Townsville, Mackay and the Swains reefs.

Following capture, all fish were immediately placed in brine-ice slurry where they were kept for a maximum of three hours before being returned to the main vessel for processing. Samples of muscle tissue and fin were taken from each fish using a clean blade, rinsed in fresh seawater. Samples were put into coded plastic vials and placed back on the ice slurry until sampling was completed. The vials were then placed in liquid nitrogen where they were stored for the duration of the field exercise. The heads of the sampled fish were retained and frozen and otoliths subsequently extracted in the laboratory (see below).

Microsatellite genetics

The development of the microsatellite markers used here is described in van Herwerden *et al.* (2000). DNA was extracted from samples stored at -70°C using standard phenol/chloroform techniques (Sambrook *et al.* 1989). Procedures for polymerase chain reaction (PCR) amplification and genotyping of samples at nine microsatellite loci were followed as presented in van Herwerden *et al.* (2000). Microsatellites were detected using 5' fluoro-labelled primers for the amplification, followed by polyacrylamide gel electrophoresis and visualisation using ABI 377 sequencing apparatus and ABI software (Genescan and Genotyper).

Estimates of exact tests were performed using Markov chain approximations to determine the probabilities that loci were in Hardy-Weinberg equilibrium, as implemented in the program GENEPOP 3.1d (Raymond and Rousset 1995). These tests were done across populations for each locus and across loci for each population. Fisher's method was used to assess genotypic disequilibrium by determining exact P-values for each locus pair across all populations. Significance levels were corrected for simultaneous multiple tests following Rice (1989).

Because we cannot be certain that the geographic assignment of individuals to populations represents a "biologically significant" population, we used the Bayesian clustering approach implemented in STRUCTURE (Pritchard *et al.* 2000) to determine whether the given assignment of individuals to populations is consistent with the genetic information, as characterised by the set of allele frequencies at all unlinked microsatellite loci conforming to Hardy-Weinberg equilibrium. These

analyses were done with a “burnin” period setting of 10^5 and 10^6 or 10^7 Monte Carlo Markov Chain (MCMC) repetitions in order to estimate the number of populations (K). Each of these analyses was run independently at least three times for all possible *a priori* values of K, specified as K = 1, 2, 3, 4, 5 or 6. Posterior probabilities of the number of populations, $\ln \Pr(X | K)$ were compared at each *a priori* K. The smallest value of K is considered “correct”, if several of the $\Pr(X | K)$ estimates are similar (Pritchard *et al.* 2000).

Population genetic structure was further investigated by analysis of molecular variance (AMOVA) (Weir and Cockerham 1984, Excoffier *et al.* 1992, Weir 1996) using the F_{ST} analogue, ϕ_{ST} implemented in ARLEQUIN 2.000 as per Raymond and Rousset (1995). This was done to partition the genetic variation into that occurring within (Fis) and among (Fst) locations sampled. The significance of the Fst values was evaluated by performing (at least 1000) Monte-Carlo permutations of alleles across locations, as implemented in the program ARLEQUIN ver. 2.00 (Schneider *et al.* 2000). Rst values were not determined here, as several of the loci contained imperfect repeats that were either compound or interrupted (van Herwerden *et al.* 2000), making the use of the stepwise mutation model inappropriate. Estimates of gene flow were not made as they are not considered necessary at best and misleading at worst (Whitlock and McCauley 1999).

Otolith microchemistry

Microchemistry was completed for a subset of the same red throat emperor samples used in the genetic analyses collected from two reefs within each of three regions (Townsville, Mackay and Swains), and samples from additional reefs within the Storm Cay region in 1999 (Table 1) (see Chapter 2). Unfortunately, samples for the whole otolith analyses were not available for one of the Storm Cay reefs (21-139). Two forms of solution-based inductively coupled plasma mass spectrometry (ICP-MS) microchemistry were done: whole otolith, in which the entire otolith is dissolved to provide an integrated signal over the entire life of the fish; and adult-juvenile, in which the outer (adult) and inner (juvenile) sections of the otolith were dissolved and analysed independently to provide information on potential differences between the adult and juvenile stages of the life cycle.

Whole sagittal otoliths were removed from samples of red throat emperor using plastic forceps to avoid contamination of otoliths, rinsed in Milli-Q water to remove membranous tissue, and placed in acid washed vials. For the whole otolith analysis, otoliths were then sonicated for 5 minutes using an ultrasonic bath, triple rinsed in Milli-Q water and left in a laminar flow cabinet to dry for 24 hours. Otoliths were dissolved in 1 ml ultrapure HNO_3 before dilution with Milli-Q water to a total of 5 ml. The sample solution was then further diluted with 1% HNO_3 to a ratio of 1:10 for trace elements and 1:1000 for Sr and Ca. For the otoliths used in the adult-juvenile comparison, the juvenile portion of each otolith, including the otolith nucleus, was carefully removed using a diamond blade jewellery saw, and stored in acid washed vials. The adult portions that were cut away to reveal the juvenile portion were stored in separate acid washed vials. Adult and juvenile otolith portions were then prepared separately for analyses following the same preparation procedure used for the whole otolith analyses.

Samples were analysed by solution-based ICP-MS at the Advanced Analytical Centre, James Cook University. Solution based ICP-MS was used in preference to laser ablation ICP-MS (as originally proposed) following discussions with a prominent researcher in the field (Prof. Cynthia Jones, Applied Marine Laboratory, Old Dominion University, Norfolk), who suggested that concentrations of many trace

elements in fish from the GBR may be below detection limits for laser-based techniques. The ICP-MS was calibrated at the start of each sample processing session or when showing signs of significant instrumental drift.

The initial analysis of 16 elements (Mg, Al, Cr, Mn, Fe, Co, Ni, Cu, Zn, As, Rb, Sr, Cd, Ba, Pb, Ca) indicated that three elements (Sr, Ba, Ca) were present above detectable limits and would be useful for further analysis. The other elements were frequently below detection limits, showed poor reading precision or were likely to be confounded by interferences with other elements. The major isotope of Strontium (Sr^{88}) was analysed, but the minor isotopes for Calcium (Ca^{40}) and Barium (Ba^{55}) were analysed due to potential interferences of the major isotopes of Ca and Ba with other elements.

Table 4.1. Samples sizes of whole otoliths and adult and juvenile sections of otoliths of red throat emperor from reefs within four regions of the Great Barrier Reef used for microchemistry analysis.

		<i>Whole otolith</i>	<i>Adult-Juvenile sections</i>
Region	Reef	<i>n</i>	<i>n</i>
Townsville	Glow	20	10
	Dip	20	10
Mackay	20-137	10	10
	Bax	10	10
Storm Cay	21-132	20	10
	21-139	-	10
Swains	Sandshoe	10	10
	Sweetlip	10	10

Whole otolith analyses

For all analyses, concentrations of Ba and Sr were expressed as a ratio to Ca. Ratios of these elements for the whole otoliths were compared between reefs within regions and among regions using two separate MANOVAs with Region as a fixed factor and Reef as a random factor nested in Region. The first MANOVA tested for differences in elemental signatures between reefs within the Townsville, Mackay and Swains regions and among these regions, The Storm Cay region was omitted from this analysis due to the lack of samples for the second reef in this region for the whole otolith samples. To test for overall regional effects the second MANOVA tested for differences in elemental signatures among the Townsville, Mackay, Storm Cay and Swains regions, with only one replicate for the Storm Cay region. Wilks' Lambda criterion was used to test for group differences in the MANOVAs. *A posteriori* univariate ANOVAs were used to explore patterns for each of the elements separately when significant effects were indicated in the MANOVAs. Tukey's honestly significant difference (HSD) test was used to determine which means differed (when more than 2 means) following significant effects in the ANOVAs.

Adult-Juvenile section analyses

Concentrations of Ba and Sr, expressed as a ratio to Ca, were compared between adult and juvenile otolith sections (Stage), between reefs within regions and among regions using MANOVA with Region and Stage as a fixed factors and Reef as a random factor nested in Region. Wilks' Lambda criterion was used to test for group differences in the MANOVAs. Sums of squares and degrees of freedom of interactions were pooled where the *F*-ratios of interaction effects were ≤ 1 . Pooling increases the degrees of freedom for the denominator and consequently the power of the test of remaining (unpooled) effects in the analyses. *A posteriori* univariate ANOVAs and Tukey's honestly significant difference (HSD) test were used to examine the source of significant effects as describe above.

4.3 Results

Population Structure from microsatellite markers

Genetic variation

The nine microsatellite loci used in this study were highly polymorphic, ranging from 15 (37rte) to 54 (80rte) alleles at each locus over all samples, and from seven (37rte) to 42 (80rte) alleles within individual locations (Table 4.2). Many rare alleles were detected in the majority of loci. Expected heterozygosities ranged from 0.54 (37rte) to 0.95 (19rte) (Table 4.2). Allele frequency distributions were generally multimodal, with the exception of locus 37rte, which was unimodal. Allele frequencies were similar for all locations sampled.

Deviations from Hardy-Weinberg and linkage equilibrium

Five of the nine microsatellite loci (bst233, 19rte, 23rte, 37rte and 95tgrte) were in Hardy-Weinberg equilibrium ($P > 0.05$) in every population, while three loci (58rte, 80rte, and 90rte) each showed significant deviations ($P < 0.05$) in only two populations (Table 4.2). In contrast, 67rte showed significant deviations in every population. All deviations resulted from heterozygote deficits, due to the presence of null alleles. This locus was therefore excluded from further analyses. The Mackay reef 20-137 population showed heterozygote deficiency at three loci (19rte, 37rte and 90rte) in addition to 67rte (Table 4.2).

Five out of 216 exact tests for linkage-disequilibrium between loci were significant ($P < 0.05$) after correcting for multiple simultaneous tests. Different pairs of loci produced these significant values in different sub-populations (58rte and 95tgrte, and 23rte and 80rte, in Sandshoe; 23rte and 90rte in Bax; 58rte and 67rte in Glow and 37rte and 67rte in Dip), which suggests that the relevant loci are not strongly linked, rather they may reflect stochastic associations in different populations.

Inter-population genetic structure

Four loci (37rte, 58rte, 67rte and 90rte) had *F_{st}* values that were significantly different from zero (Table 4.3). Genic differentiation was significant for the same four and an additional two loci (80rte and 95tgrte). *F_{st}* values were not significantly different from zero for the remaining five of the nine loci examined, and for the mean *F_{st}*.

The three statistically significant pairwise *F_{st}* values all indicated differences between the Reef 20-137 samples from Mackay with the Sandshoe (Swains), Bax (Mackay), and Glow Reef (Townsville) samples (Table 4.4). Therefore differences were observed between 20-137 and one location from each of the three regions (and

therefore of all three different demographic types identified by Williams (1997)). Mantel tests for any association of F_{st} values with geographical separation of the regional pairs were not significant ($P > 0.05$).

All Bayesian clustering analyses for $K = 4, 5,$ and 6 produced variable estimates of $\ln \Pr(X|K)$ which were not consistent across runs (Table 4.5). However, for $K = 1, 2$ and 3 estimates of $\ln \Pr(X|K)$ were reasonably consistent across runs, especially for $K = 1$ (Table IV). Additionally, the largest estimated $\Pr(X|K)$ was obtained for $K = 1$, which also had the smallest variance for the likelihood of K being what it was specified to be *a priori*, which was approximately 22 – to 150 – fold less than the variances for any other K values tested (Table 4.5). Mean alpha values were always > 1 and varied greatly during the course of each run and between multiple re-runs for the same value of K , suggesting that there isn't any real population structure in the data, but extensive "admixture" between locations sampled (Pritchard *et al.* 2000). Allele frequencies from the six locations were not correlated to any particular one of the *a priori* specified populations when $K > 1$, indicating that none of the locations sampled had unique allele frequencies relative to the other samples (Table 4.5).

AMOVA analyses showed that virtually all the genetic variation detected in the data was within locations (99.74%, $p \geq 0.023$), whilst almost no variation was attributed among regions or among locations within regions (Table 4.6).

Table 4.2. Genetic diversity and deviation from Hardy-Weinberg equilibrium in six populations of red throat emperor. Data provided are the number of individual fish sampled (n), the number of alleles (k), expected gene diversity (H_e), observed gene diversity (H_o) and correlation of alleles within individuals (F_{is}) at each of the nine loci screened. [* allelic frequencies not in Hardy-Weinberg equilibrium ($P < 0.05$, after Bonferroni correction)].

Locus	Swains		Mackay		Townsville	
	Sandshoe	Sweetlip	Bax	20-137	Glow	Dip
bst233						
n	105	83	100	99	102	84
k	24	20	20	24	23	19
H_e	0.895	0.897	0.897	0.899	0.910	0.911
H_o	0.933	0.866	0.84	0.909	0.882	0.952
F_{is}	-0.042	0.035	0.064	-0.011	0.031	-0.045
19rte						
n	105	83	100	98	102	83
k	29	27	28	30	32	29
H_e	0.857	0.95	0.94	0.929	0.931	0.929
H_o	0.914	0.98	0.95	0.889	0.951	0.881
F_{is}	0.025	-0.023	-0.007	0.048	-0.018	0.057
23rte						
n	104	83	100	98	102	83
k	15	14	14	16	15	17
H_e	0.857	0.878	0.85	0.848	0.863	0.869
H_o	0.895	0.902	0.90	0.848	0.863	0.833
F_{is}	-0.042	-0.035	-0.054	0.002	0.001	0.038

Table 4.2. (cont'd)

Locus	Swains		Mackay		Townsville	
	Sandshoe	Sweetlip	Bax	20-137	Glow	Dip
37rte						
n	105	83	100	99	102	82
k	9	7	7	8	9	10
He	0.638	0.561	0.62	0.535	0.637	0.619
Ho	0.581	0.524	0.72	0.555	0.696	0.655
Fis	0.097	0.068	-0.166	-0.043	-0.096	-0.059
58rte						
n	105	83	100	97	102	84
k	11	10	10	11	10	13
He	0.752	0.756	0.68	0.687	0.637	0.714
Ho	0.733	0.756	0.52	0.545	0.520	0.631
Fis	0.032*	0.007	0.233	0.208*	0.189	0.123
67rte						
n	105	82	100	97	98	81
k	23	19	20	20	20	20
He	0.819	0.805	0.87	0.838	0.765	0.821
Ho	0.495	0.549	0.62	0.727	0.578	0.548
Fis	0.395*	0.321*	0.286*	0.137*	0.247*	0.334*
80rte						
n	101	83	96	99	101	81
k	42	31	34	36	36	33
He	0.876	0.890	0.85	0.929	0.892	0.881
Ho	0.848	0.915	0.77	0.818	0.824	0.750
Fis	0.035	-0.022	0.095	0.115*	0.082*	0.144
90rte						
n	105	83	100	99	102	84
k	12	13	14	13	12	12
He	0.752	0.780	0.81	0.788	0.784	0.798
Ho	0.829	0.829	0.80	0.747	0.863	0.833
Fis	-0.105	-0.063	0.008	0.052*	-0.096	-0.044*
95tgrte						
n	105	83	97	99	102	83
k	15	14	13	13	14	16
He	0.714	0.756	0.71	0.717	0.745	0.667
Ho	0.724	0.890	0.79	0.758	0.755	0.714
Fis	-0.015	-0.184	-0.113	-0.061	-0.014	-0.064

Table 4.3. Population structure of six red throat emperor populations along the Great Barrier Reef. F_{st} measures the genetic differentiation between subpopulations, assuming the infinite alleles model; genic differentiation P values (+/- standard error) determined by 1000 Markov chain iterations, 100 batches; $4N_e\mu$: four times the product of effective population size and mutation rate of microsatellite markers. * $P < 0.05$, *** $P < 0.001$. The mean F_{st} and p values, determined using Fisher's method, were for combined loci

locus	F_{st}	Genic differentiation	$4N_e\mu$
bst233	-0.001 ^{NS}	0.789 (.029)	36
19rte	-0.000 ^{NS}	0.455 (.035)	48
23rte	-0.002 ^{NS}	0.883 (.018)	24.8
37rte	0.008***	0.000 (.000)	6
58rte	0.006***	0.000 (.000)	9.6
67rte	0.010***	0.000 (.000)	18.4
80rte	0.002 ^{NS}	0.038 (.013)	31.2
90rte	0.001*	0.017 (.006)	14.8
95tgrte	0.000 ^{NS}	0.019 (.007)	10
Mean	0.003 ^{NS}		22

Table 4.4. Pairwise differentiation of populations with F_{st} values below the diagonal. ** $P < 0.01$, *** $P < 0.001$.

Population	Sandshoe	Sweetlip	Bax	20-137	Glow	Dip
Sandshoe	-					
Sweetlip	0.001	-				
Bax	0.003	0.001	-			
20-137	0.006***	0.003	0.005**	-		
Glow	0.003	0.002	0.002	0.006***	-	
Dip	0.001	0.000	0.000	0.002	0.003	-

Table 4.5. Partitioning of genetic variation, as detected by AMOVA, when samples were grouped *a priori* on the basis of region (Swains, Mackay and Townsville).

Source of variation	Df.	SS	Variance component	p-value	Percentage of variation
Among groups	2	73.768	0.023 Va	0.247	0.10
Among populations	3	84.265	0.033 Vb	0.176	0.15
Within populations	1140	24821.760	21.773 Vc	0.023	99.74
Total	1145	24979.760			

Microchemistry

Whole otoliths

The results of the MANOVA identified a significant difference in elemental signature in whole red throat emperor otoliths between reefs within regions, but not among regions (Table 4.6). Univariate analyses of variance (ANOVAs) indicated that these differences were due to significant variation in both Ba and Sr among reefs within regions (Table 4.7).

Table 4.6. Results of MANOVA comparing elemental signatures from solution-based ICP-MS of whole red throat emperor otoliths between two reefs in each of three regions of the Great Barrier Reef (Townsville, Mackay and Swains).

Factor	Wilks' Lambda	F	Num df	Den df	p
Region	0.4751	0.45	4	4	0.770
Reef(Region)	0.1913	31.30	6	146	<0.0001

Ba concentrations were significantly different between reefs in the Townsville and Mackay regions, but not between reefs in the Swains region (Figure 4.1). Ba concentrations were significantly higher for Dip reef than Glow reef in the Townsville region ($F_{1,38} = 89.46$, $p < 0.001$), and significantly higher for 21-137 than Bax reef in the Mackay region ($F_{1,18} = 8.26$, $p = 0.01$). Sr concentrations were significantly different between reefs in the Townsville and Swains regions, but not between reefs in the Mackay region (Figure 4.2). Sr concentrations were significantly higher for Dip reef than Glow reef in the Townsville region ($F_{1,38} = 148.82$, $p < 0.001$), and significantly higher for Sweetlip reef than Sandshoe reef in the Swains region ($F_{1,18} = 8.71$, $p = 0.009$). The results for the Storm Cay reef, for which samples were available, are included in figure 4.1 and 4.2 and indicate values similar to those for the other reefs in the southern two clusters and Glow Reef in the Townsville cluster.

Table 4.7. Results of ANOVAs comparing elemental signatures from solution-based ICP-MS of whole red throat emperor otoliths from two reefs in each of three regions of the Great Barrier Reef (Townsville, Mackay and Swains).

Dependent variable	Factor	df	MS	F	p
Ba ($\mu\text{g/g Ca}$)	Region	2	2.34×10^{-5}	1.20	0.413
	Reef(Region)	3	1.94×10^{-5}	52.22	<0.0001
	Error	74	3.70×10^{-7}		
Sr ($\mu\text{g/g Ca}$)	Region	2	1.252	1.09	0.440
	Reef(Region)	3	1.144	95.47	<0.0001
	Error	74	0.012		

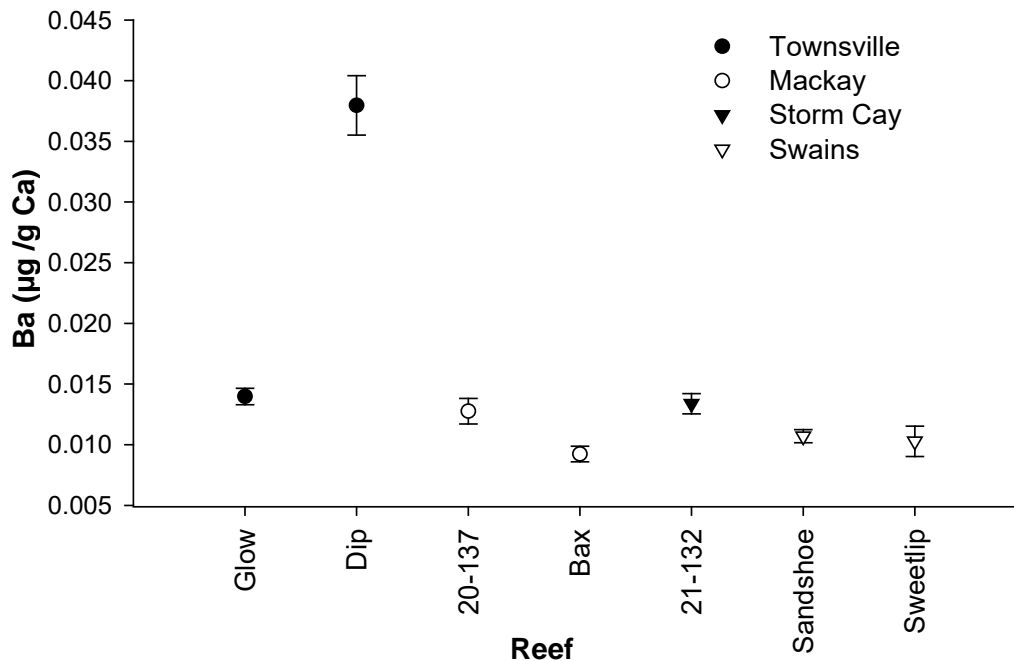


Figure 4.1. Mean concentration of Ba relative to Ca from solution based ICP-MS of whole otoliths of red throat emperor collected from two reefs in each of three regions (Townsville, Mackay and Swains) and one reef within the Storm Cay region of the Great Barrier Reef. Error bars are standard error.

Adult and juvenile sections of otoliths

The results of the MANOVA identified a significant difference in elemental signature in red throat emperor otoliths between adult and juvenile otolith sections (Stage), though the differences varied with region (Region*Stage interaction; Table 4.7). ANOVAs indicated that these differences were due to significant variation in Ba between adult and juvenile otolith portions in interaction with regions (Region*Stage interaction; Table 4.8) and differences in Sr between adult and juvenile otolith

portions and among reefs within regions (Main effects of Stage and Reef (Region); Table 4.8).

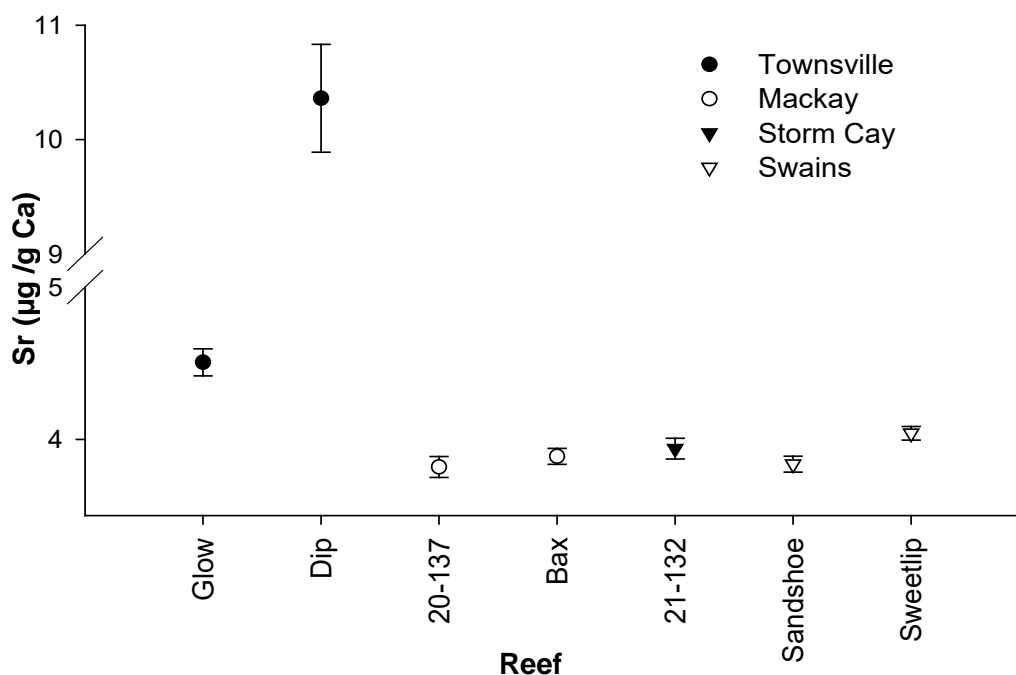


Figure 4.2. Mean concentration of Sr relative to Ca from solution based ICP-MS of whole otoliths of red throat emperor collected from two reefs within each of three regions (Townsville, Mackay and Swains) and one reef within the Storm Cay region of the Great Barrier Reef. Error bars are standard error.

Although differences in Ba concentrations between adult and juvenile otolith portions were apparent in most regions, differences were significant for the Townsville region only ($F_{1,38} = 9.085$, $p = 0.005$), where the Ba concentrations were significantly higher for juvenile sections than for adult sections (Figure 4.3). Sr concentrations were significantly and consistently higher for adult sections than for juvenile sections for all reefs and regions (Table 4.8, Figure 4.4). Sr concentrations were also significantly higher for 21-139 than for 21-132 in the Storm Cay region ($F_{1,38} = 8.252$, $p = 0.007$), but did not differ significantly between reefs in any other region (Figure 4.5).

Table 4.7. Results of MANOVA comparing otolith elemental signatures from solution based ICP-MS of adult and juvenile portions of otolith of red throat emperor (Stage), between two reefs in each of four regions of the Great Barrier Reef (Townsville, Mackay, Storm Cay and Swains), and among regions. Only final analyses resulting from pooling terms with $F \leq 1$ are shown.

Factor	Wilks' Lambda	F	Num df	Den df	p
Region	0.0863	2.40	6	6	0.155
Reef(Region)	0.9026	1.93	8	296	0.058
Stage	0.7543	23.95	2	147	<0.0001
Region*Stage	0.8621	3.77	6	294	0.001

Table 4.8. Results of ANOVAs comparing elemental signatures from solution based ICP-MS of adult and juvenile portions of otoliths of red throat emperor (Stage) between two reefs in each of four regions of the Great Barrier Reef (Townsville, Mackay, Storm Cay and Swains), and among regions.

Dependent variable	Factor	df	MS	F	p
Ba ($\mu\text{g/g Ca}$)	Region	3	8.03×10^{-6}	6.40	0.053
	Reef(Region)	4	1.26×10^{-6}	0.66	0.624
	Stage	1	1.04×10^{-6}	0.54	0.462
	Region*Stage	3	9.67×10^{-6}	5.05	0.002
	Error	148	1.92×10^{-6}		
Sr ($\mu\text{g/g Ca}$)	Region	2	0.020	0.60	0.649
	Reef(Region)	3	0.033	3.33	0.012
	Stage	1	0.471	47.41	<0.0001
	Region*Stage	3	0.025	2.57	0.057
	Error	148	0.010		

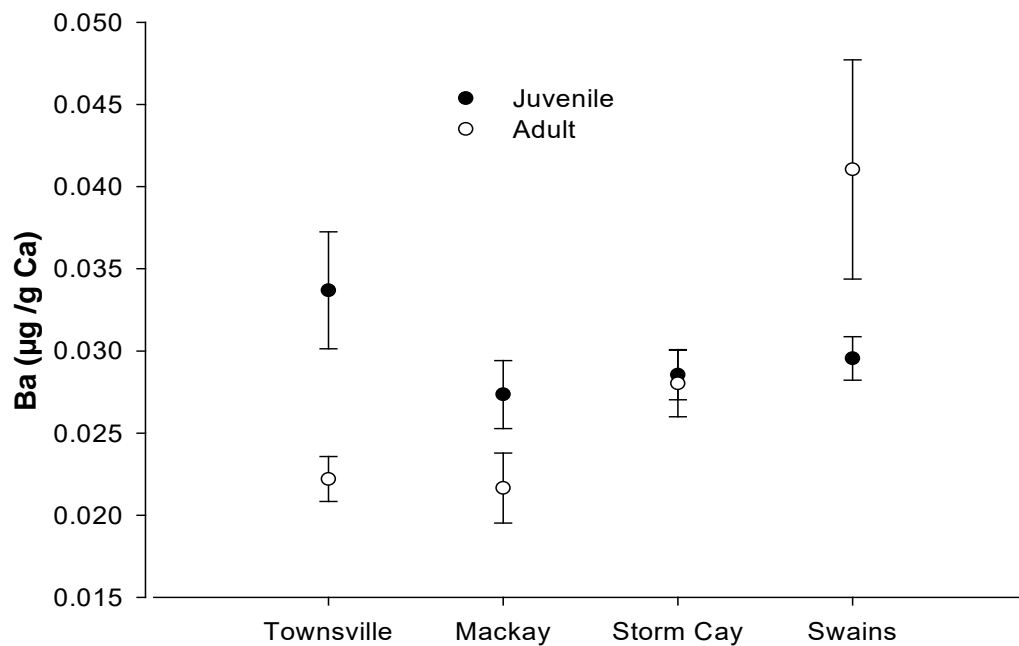


Figure 4.3. Mean concentration of Ba relative to Ca from solution based ICP-MS of adult and juvenile portions of otoliths of red throat emperor pooled across two reefs in each of four regions (Townsville, Mackay, Storm Cay and Swains) of the Great Barrier Reef. Error bars are standard errors.

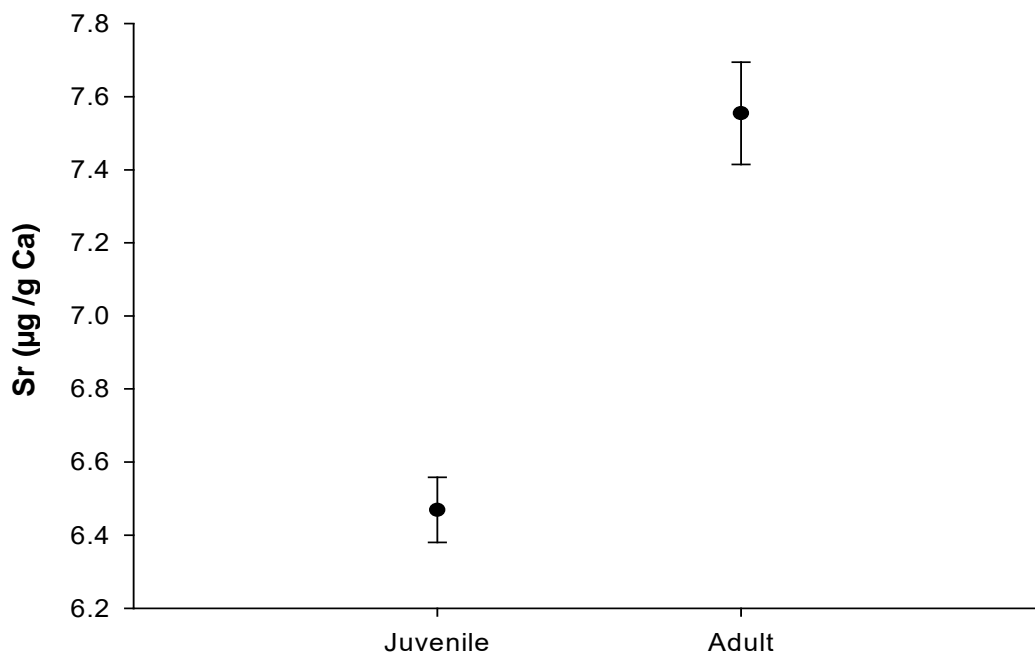


Figure 4.4. Mean concentration of Sr relative to Ca from solution based ICP-MS of adult and juvenile portions of otoliths of red throat emperor pooled across two reefs and four regions (Townsville, Mackay, Storm Cay and Swains) of the Great Barrier Reef. Error bars are standard error.

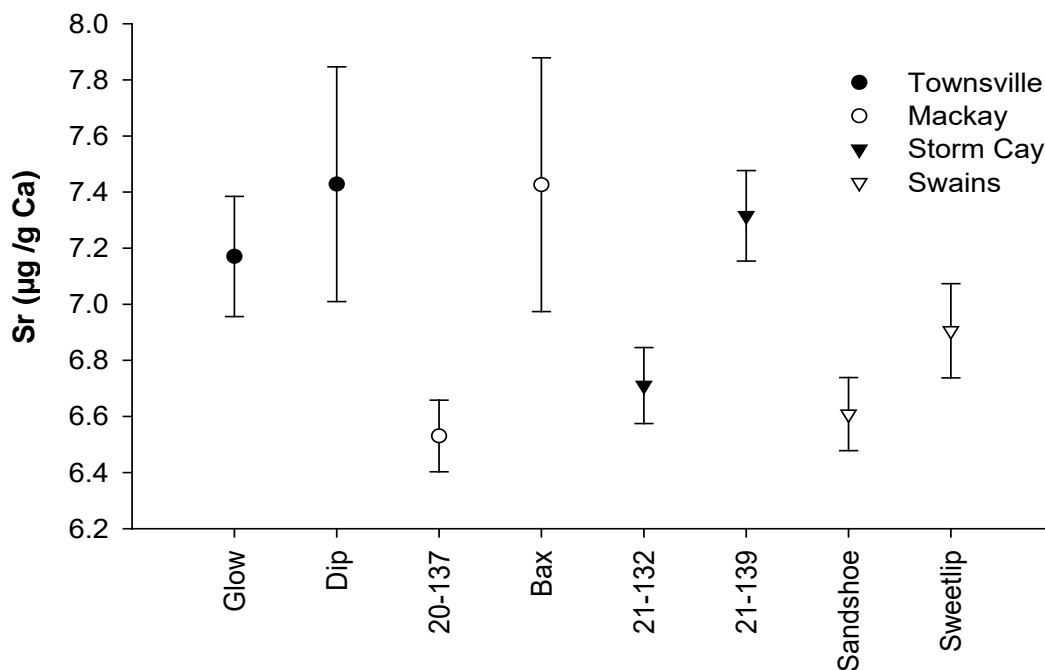


Figure 4.5. Mean concentration of Sr relative to Ca from solution based ICP-MS of adult and juvenile portions of otoliths of red throat emperor collected from two reefs within each of four regions (Townsville, Mackay, Storm Cay and Swains) of the Great Barrier Reef. Data are pooled across juvenile and adult otolith portions. Error bars are standard error.

4.4 Discussion

Microsatellite genetics

Overall, the results of the microsatellite study are consistent with red throat emperor on the GBR being a single panmictic stock. While there is some evidence of genetic structuring, based on F_{st} values for some loci only, there were statistically significant differences between some populations for allele frequencies, or mean allele size, at some loci only. There were also significant deviations in allele frequencies from those expected under conditions of Hardy-Weinberg equilibrium at some loci. Although statistically significant, even after Bonferroni correction, these results reflected minor shifts in gene frequencies of rare alleles and were not consistent from locus to locus or population to population. This suggests that there is no major spatial structuring of red throat emperor populations, with the possible exception of populations from Reef 20-137 from the Mackay region and Sandshoe Reef from the Swains region.

Bayesian clustering indicated extensive mixing between all locations and suggested there is no substructure to the red throat emperor population on the GBR. AMOVA analyses indicated extensive and significant heterogeneity within locations, but not between locations or regions. Accordingly, only the within - population component of genetic variance was statistically significant ($p = 0.023$). This suggests that substantial levels of gene flow occur between all regions sampled on the GBR.

The lack of consistency in the locations and loci showing genetic differentiation suggests no strong structuring that might indicate other processes, such as selection, were operating consistently on a subset of loci. This result, the lack of differentiation at the other loci, and the lack of significant population differentiation when averaged over all loci, means that we cannot reject the null hypothesis that red throat emperor populations along the Great Barrier Reef form a single genetic stock. This conclusion is strongly supported by both Bayesian clustering and AMOVA analyses.

The existence of a single stock is not unexpected, as pelagic larvae, not only of red throat emperor, but of many other species of marine organisms, generally maintain genetic connectivity amongst populations on the GBR (e.g. Benzie 1994, Doherty *et al.* 1995, Ayre and Hughes 2000, Dudgeon *et al.* 2000). There are, however, counter examples demonstrated by some marine gastropods, with and without pelagic larval dispersal (see Kyle and Boulding 2000), and for some brooding/spawning coral species (Ayre and Hughes 2000) where there is not high connectivity among populations throughout the GBR. Additionally, red throat emperor adults, unlike some other reef fish adults, commonly inhabit deeper water (up to 130 m) in inter-reef areas (Newman and Williams 1996), which suggests that adult movement, in addition to larval dispersal, may contribute to maintaining connectivity between locations and regions on the Great Barrier Reef (Williams 2003, Chapter 3). Furthermore, conditions associated with climatological events such as ENSO cycles and cyclonic events may produce sporadic episodes of greater mixing between long-lived red throat emperor adults from different regions of the GBR, which would be sufficient to maintain genetic homogeneity among populations in different regions.

Demographic studies of red throat emperor (Williams 1997, 2003, Williams *et al.* 2003, Chapter 3) have demonstrated significant differences in growth and size, age structure and mortality between the Mackay region and Townsville and Swains regions. Specifically, fish from the Mackay region on average reached a larger asymptotic size and were younger than those caught in the Townsville region, and the parameters for the Swains populations were intermediate. In contrast, all demographic parameters were similar among the four reefs within each of the

regions sampled (Williams 1997, Williams *et al.* 2003). The demographic data is indicative of the existence of different stocks of *L. miniatus* in Townsville, Mackay and the Swains. The results of the microsatellite survey provide strong evidence that the demographic differences between populations are likely to have an environmental (or mixed environmental and genetic origin) rather than solely a genetic one. It is possible that the outcome of a genetic study of this population using genetic loci under selection may produce a different outcome. This result does not depend on demonstrating random mating. None of the minor evidence consistent with some (stochastic) genetic structuring matched populations showing genetic differences with populations that differed in demography (based on F_{st} statistics), except possibly for Reef 20-137 from the Mackay region and Sandshoe Reef from the Swains region. For example, significant genetic differences were found at some loci between populations within regions (and which had similar demography), and no genetic differences were found between populations in different regions, which had different demography (such as Bax Reef from the Mackay region and either Glow or Dip Reefs from the Townsville region).

Otolith microchemistry

The results for the whole otolith microchemistry for barium (Ba) and strontium (Sr) did not indicate any consistent variation among the four regions (Townsville, Mackay, Storm Cay and Swains). One reef in the Townsville region (Dip) had substantially, and significantly, higher concentrations of Ba and Sr. This may be associated with the position of Dip Reef on the edge of the outer-shelf (see Figure 2.1) and, presumably, the greater influence of Coral Sea water properties, relative to other reefs included in the study.

The results for the juvenile-adult otolith sections were more complicated, although they too did not indicate a regional pattern consistent with that observed in the population parameters. Concentrations of Sr were consistently significantly higher in the adult portion of the otolith, while there was the suggestion of a north-south trend in the difference in the concentration of Ba. Barium was significantly higher in the juvenile portion in the Townsville region, not different in the Mackay and Storm Cay regions and lower, although not significantly, for the southern Swains. This pattern suggests that of a north-south, cross-shelf process may be influencing the elemental composition. Unfortunately, in the absence of meso-scale oceanographic data on water properties and information on the distribution of juvenile red throat emperor interpretation of these patterns is entirely speculative.

While the results from the otolith microchemistry were inconclusive, in terms of assisting with the interpretation of the spatial patterns of the adult component of the red throat emperor population, they may prove more useful in attempts to understand the distribution of juvenile component. Our preliminary results demonstrate a clear difference in the concentration of Sr between the adult and juvenile sections of the otolith. This may be evidence in support of the contention that for the first year or two of their life-cycle red throat emperor inhabit substantially different habitats to the adult phase. Further detailed work is required to establish whether this extrapolation based on these preliminary findings holds. However, given the relative importance of red throat emperor to all sectors of the fishery and the continuing lack of information on the distribution and abundance of newly settled and juvenile red throat emperor, some priority should be given to research that will improve our understanding of this important stage of the life-cycle.

It is important to note that phenotypic/demographic variation, which has traditionally been used to identify stocks in fisheries, may be influenced by both environmental

and genetic factors (Swain and Foote 1999). Population differentiation identified by morphological differences between populations has often not been confirmed by genetic studies (reviewed by Swain and Foote 1999). Indeed, phenotypic plasticity results when variable environmental factors affect the differential expression of genes common to both “stocks”, as has been experimentally verified (Taylor *et al.* 1996). The patterns we have observed for red throat emperor on the GBR are consistent with a greater emphasis on environmental effects shaping the demography of populations from different regions, and a single genetic stock of this species on the GBR. The estimates of population parameters provided in Chapter 3 and Williams (2003) provide the basis for developing spatially explicit assessment models, examining further the potential causal mechanisms and evaluating the performance of alternative management strategies in light of this regional variation.

5. Age, growth, mortality, and reproduction for maori wrasse (*Chelinus undulatus*), barramundi cod (*Cromileptes altivelis*) and blue-spot coral trout (*Plectropomus laevis*) on the Great Barrier Reef

Campbell R. Davies, J. Howard Choat, Bruce D. Mapstone, Ashley J. Williams, Gary Carlos, Cameron D. Murchie and John Ackerman

5.1 Introduction

The primary interest in large reef fishes currently lies in evaluating their vulnerability and resilience to fishing. This reflects the perception that large size may be associated with combinations of life history features that make large species more vulnerable to overfishing and local depletion (Jennings *et al.* 1999, Roberts and Hawkins 1999, Sadovy and Vincent 2002). For example, size may be positively correlated with maximum age (Donaldson and Sadovy 2001) and time to maturity, and negatively with somatic growth rate, rates of recruitment and population increase (Jennings *et al.* 1999, Roberts and Hawkins 1999). There is also concern that sex change, a characteristic of many species of reef fish, may predispose fishes to additional risk of overfishing (Roberts and Hawkins 1999, Sadovy and Vincent 2002). Despite increasing interest in the population dynamics of large reef fishes, few age-based studies exist that provide the necessary information for evaluating the hypothesis on life history features of large reef fish species. It is unknown, for example, whether large size is indeed associated with increased longevity or whether there are any important correlations with growth rate, longevity and sex reversal in large protogynous hermaphroditic reef fish. In this chapter we present the results of an initial study on the growth, longevity and reproductive biology of maori wrasse, *Chelinus undulatus*, barramundi cod, *Cromileptes altivelis* and the blue-spot coral trout, *Plectropomus laevis*, on the Great Barrier Reef (GBR). There is no age-based biological information available for any of the three species.

The maori wrasse is one of the largest teleost fishes associated with coral reef environments. A summary of the biological characteristics of maori wrasse is as follows. The species geographical distribution extends through the Red Sea, Indian and Pacific oceans to the Line, Marshall, Cook and Tuamotu islands. Over this range the species occurs in relatively shallow reef areas achieving a maximum recorded size and weight of 229cm and 190 kg (Randall *et al.* 1997, Sadovy *et al.* 2003). This record is, however, unconfirmed and individuals greater than 150 cm are rare even in unfished areas of the Pacific and Indian Oceans (Choat *et al.* unpublished data). There are currently no published estimates of rates of growth, longevity or natural mortality. There is, however, a general perception that the species is likely to be long-lived (possibly reaching one hundred years) with corresponding low rates of growth and natural mortality (e.g. Johannes and Riepen 1995). Evidence suggesting maori wrasse are protogynous hermaphrodites has been presented by Donaldson and Sadovy (2001), which indicates size for female sexual maturation is 400-600 mm. As with most cheiline wrasses, the diet of maori wrasse is dominated by benthic reef invertebrates (Randall *et al.* 1978).

Fishing associated with the live reef fish trade in south-east Asia and the Pacific has reputedly resulted in declines in size structure and abundance of maori wrasse in south-east Asian waters. As a result, maori wrasse was recently listed as "endangered" in the IUCN Red Book (Cornish 2004). At the commencement of this study, maori wrasse was taken by line and spear (recreational sector only) in the

CRFFF on the Great Barrier Reef. It accounted for a relatively small proportion of the commercial line catch (Mapstone *et al.* 1996c) even following the shift to marketing live fish (Mapstone *et al.* 1998a). The harvest of the species was regulated by a minimum size limit of 750 mm and a bag limit of 1 for the recreational fishery. More recently, regulations included in the final management plan for the fishery have banned the taking of this species and barramundi cod in all sectors of the fishery.

Knowledge of the abundance, distribution and biology of barramundi cod on the GBR, and elsewhere, is also very limited. It is a cryptic reef serranid and, as such, is difficult to survey for estimating abundance. It has a reported maximum size of approximately 650 mm (Randall *et al.* 1997) and, while a highly prized species, has represented a very small percentage of the commercial and recreational catch (Mapstone *et al.* 1996c). Their cryptic nature, low abundance in catches (and therefore the perception that the species is relatively uncommon) and its high value in the live reef fish trade has led to considerable concern that the species is particularly vulnerable to over fishing.

The blue-spot coral trout is the largest of the coral trout species from the GBR and has been reported to reach sizes in excess of 100 mm TL (Randall *et al.* 1997). It has a strong cross-shelf gradient in abundance, being most common on outer-self GBR reefs and Coral Sea platform reefs, relatively common on mid-shelf reefs and rare on inner-shelf reefs (Ayling and Ayling 1992, Mapstone *et al.* 1998b). Of the three species investigated in this chapter, blue-spot coral trout is the most common species in commercial catches (Mapstone *et al.* unpublished data).

The primary aim of this study was to obtain age-based information on the life history features maori wrasse, barramundi cod and blue-spot coral trout to assess their conservation and fishery status on the GBR. This included estimates of maximum age, rates of growth and mortality, and the relationship between age and size with respect to female maturity and the recruitment of males (i.e. sex change from female to male) into the sampled populations. While the study focussed on populations of these species on the GBR, it is likely that the results will inform the debate of the conservation and fisheries status of maori wrasse and barramundi cod in other parts of their geographic range.

5.2. Methods

Maori wrasse

With the exception of one juvenile (73 mm FL) obtained from Bali (aquarium dealer), all maori wrasse sampled for demographic information were obtained from the northern and central regions of the Great Barrier Reef from 14° to 22° S. A total of 178 samples were obtained between 1995 and 2002. The sources of the samples partitioned by sampling method and locality are as follows:

- CRC Reef Effects of Line Fishing Experiment. 120 individuals ranging from 360-1290 mm FL by line fishing. Sampling localities; Mid and outer shelf Great Barrier Reef from 14° to 22° S. (Individual sample sites available);
- JCU Marine Biology demography program. 37 individuals ranging from 243 to 1110 mm FL by spearing. Sampling localities Mid and outer shelf Great Barrier Reef from 14° to 18° S;

- Commercial fishers. 10 individuals ranging from 720-1383 mm FL by line-fishing. Mid and outer shelf Great Barrier Reef from 14° to 20° S;
- Recreational fishers. Seven individuals ranging from 560-1420 mm FL by spearing. Inner and Mid shelf Great Barrier Reef from 14° to 20° S;
- Aquarium trade. Two individuals 62 and 73 mm FL by netting. Bali and northern Great Barrier Reef;
- GBRMPA Aquarium. Two individuals 990 and 1275 mm FL.

Validation of periodicity of otolith increments

Validation of the annual periodicity of increments observed in sagittal otoliths was accomplished by tetracycline marking of individuals maintained in an aquarium. Given the large size and relative rarity of maori wrasse, a field based validation program was not possible. Two adult individuals injected with oxytetracycline were maintained in a circulating seawater system tank with a capacity of 160,000 litres circulated through a biological filtration system and algal scrubbers 6-8 times per 24 hrs. Details for each individual were as follows:

Individual 1, an adult male (900 mm FL), was captured on the GBR (18° S) on 12/10/97, transported in an aerated tank to the aquarium at James Cook University on 14/10/97, injected with tetracycline and released into the main tank. A second adult individual captured at the same site was also injected and placed in the aquarium system on 14/10/97. The first individual was maintained for 1176 days, and following a second injection of tetracycline on 25/11/99 was sacrificed on 31/7/00. At this time, individual 1 was 995 mm FL and 19.8 kg. The second individual died 24/8/98 and was 944 mm FL. Strong tetracycline bands were observed in the sectioned sagittal otoliths of each individual with individual 1 recording two clear bands.

The model of Cappelletti *et al.* (2000) was used to obtain estimates of the periodicity of opaque increment completion. In summary, this model proposes that if each translucent/opaque increment (one cycle) is equivalent to one year, then the distance from the tetracycline mark to the outer edge of the otolith, divided by the width of the last complete cycle should equal the time from mark to recapture. Following Cappelletti *et al.* (2000) the initial fractions (*IF*) and final fractions (*FF*) of otolith growth were estimated as:

$$IF = (R_a - T)/(R_a - R_{a-1}), \text{ and} \quad (5.1)$$

$$FF = (R - R_a)/(R_a - R_{a-1}), \quad (5.2)$$

where:

a = the age of the fish;

R = radius to the edge;

R_a = radius to the final opaque zone; and

T = radius to the OTC mark.

The cycle frequency (V) estimates the number of increment cycles completed per year as:

$$V = (IF + FF + N) / L, \quad (5.3)$$

where:

N = number of full increment cycles outside the OTC mark; and

L = the time at liberty.

Age and growth

Fork length (FL) of all individuals was measured to the nearest millimetre. Sagittal otoliths were removed, cleaned and stored dry. The procedures for otolith processing and sectioning are provided in Choat *et al.* (2003) and Chapter 2.

Size and age data from the collected samples were used to construct size and age frequency distributions. An additional size frequency distribution was obtained from visual surveys in 1994/95 and 2001. These surveys consisted of replicated belt transects (400 x 20 m) with start and finish points determined using a Global Positioning System (GPS) receiver. All maori wrasse greater than 300 mm FL were counted within the transect area and FL estimated to the nearest 100 mm. Size frequencies were compared between the sampled population and visual surveys.

Estimates of growth were obtained by fitting the VBGF to size-at-age data as for red throat emperor (Section 3.2, Eqn. 3.1). Because VBGF parameter estimates can be sensitive to the range of ages and sizes used (Ferreira and Russ 1994, Craig 1999), t_0 was constrained to 62 mm, which was the size of the smallest individual for which size and age data were available.

Mortality

Total mortality (Z) and survivorship rates (S) were calculated in two ways i) using log-linear regression analyses of age frequency data (catch curves) where $S = e^{-Z}$, and ii) $Z = \ln(100) / t_{max}$, where t_{max} is the estimated maximum longevity. Fish younger than five years were excluded from catch curve analysis, as they were not considered to be representatively sampled.

Reproductive biology

Gonads were dissected from the body cavity from freshly caught, or in a minority of cases frozen fish, and weighed to the nearest gram. Estimates of the size and age at maturity were obtained by examining the size and age of immature females and the relationship between ovary weight and FL. Estimates of the size and age at sex change were obtained by examining the size and age of the smallest males sampled.

Diet

Dietary analyses were carried out on specimens captured on reef fronts during daylight hours of 1000 to 1700hrs. These did not include individuals associated with reproductive activity. Contents of the entire alimentary tract were removed and preserved in 10% formaldehyde. Contents were identified to genus where feasible and percentage cover of each identity, as a proxy for volume, was estimated using

the transect methodology of Choat and Clements (1992) and expressed as mean % cover.

Barramundi cod and blue-spot coral trout

The majority of samples of barramundi cod and blue-spot coral trout were obtained from the clusters of six reefs in four regions of the Great Barrier Reef (Lizard Island, Townsville, Mackay and Storm Cay) over six years from 1995 to 2000 during the Effects of Line Fishing (ELF) Experiment catch surveys (Davies *et al.* 1998), as described in Chapter 2. Additional samples of barramundi cod were provided by commercial and recreational fishers and recreational spear fishers. There were insufficient samples of either species from any one reef or region to allow robust comparisons of spatial differences in population parameters. Therefore all analyses have been done on the pooled samples over the entire sampling period.

Samples were measured, weighed, processed for otoliths and gonads and age, sex and reproductive status determined as described in Chapter 2. Estimates of growth, mortality and reproductive parameters were obtained using the same methods applied to red throat emperor (Chapter 3) using the pooled sample over the sampling period for each species and without any regional spatial comparison. In addition, the variation in size and age at sexual maturity and distribution of maturity stages was examined for the two colour phases (“blue-spot” and “footballer”) of the blue-spot coral trout.

5.3. Results

Summary of biological samples

A summary of the samples collected and processed for each species is provided in Table 5.1.

Table 5.1: Summary of samples of maori wrasse (*Chelinus undulatus*), barramundi cod (*Cromiletes altevelis*) and blue-spot coral trout (*Plectropomus laevis*) collected by line and spear fishing between 14° – 22° S on the Great Barrier Reef for estimation of age, growth and reproduction. Details of collection methods and permits given in text.

Species	Samples	Otoliths	Gonads	Gut contents
Maori wrasse	178	163	135	17
Barramundi Cod	228	199	107	-
Blue-spot coral trout	945	346	480 ¹	-

¹ Sample size for length-based reproductive parameters = 480. Sample size for age-based reproductive parameters = 164.

Maori wrasse

Validation of periodicity of otolith increments

Sectioned otoliths had a highly characteristic appearance with a deep sulcal groove on the medial face of the sagitta of larger individuals. Growth increments were visible as opaque bands in the matrix of the sectioned otolith when viewed under transmitted light. Opaque increments characteristically became more narrowly spaced toward the medial region of the sagitta and were readily counted on either

side of the sulcal groove (Figure 5.1). Specimens collected as far north as 15° N displayed well defined increments in sectioned sagittae.

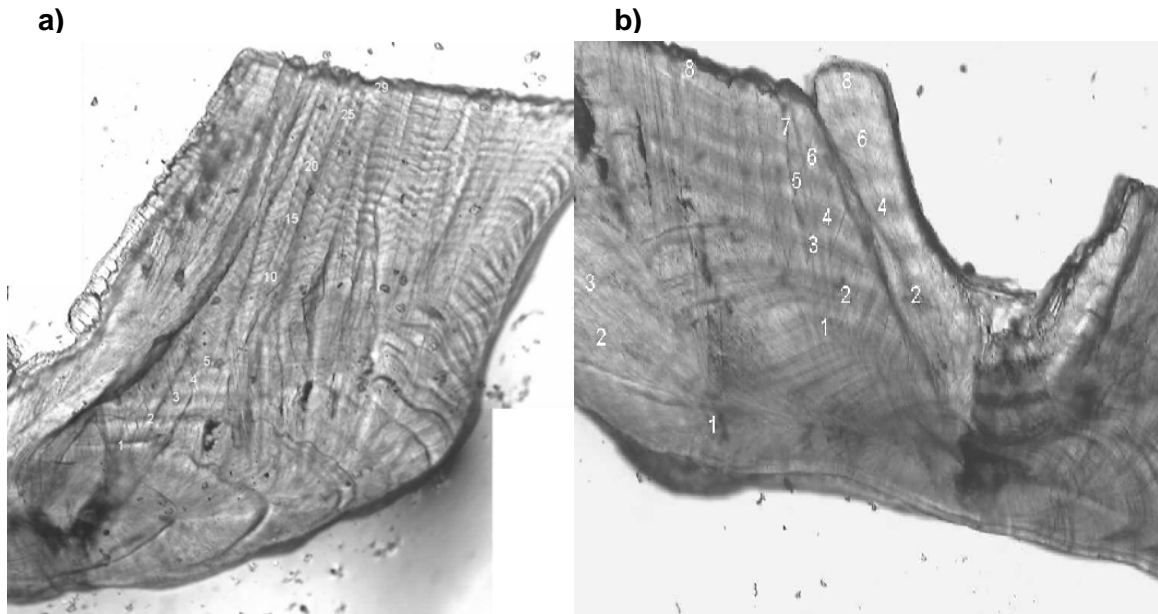


Figure 5.1. Sectioned sagittal otoliths of a 29 year old female maori wrasse (765 mm FL) (a) and an 8 year old female maori wrasse (565 mm FL) (b), with positions of each opaque increment indicated.

Tetracycline injections of two individuals were carried out in order to validate the annual frequency of opaque increments seen in sections of sagittal otoliths. The first (double injected) showed two clear tetracycline marks under fluorescent light (Figure 5.2).

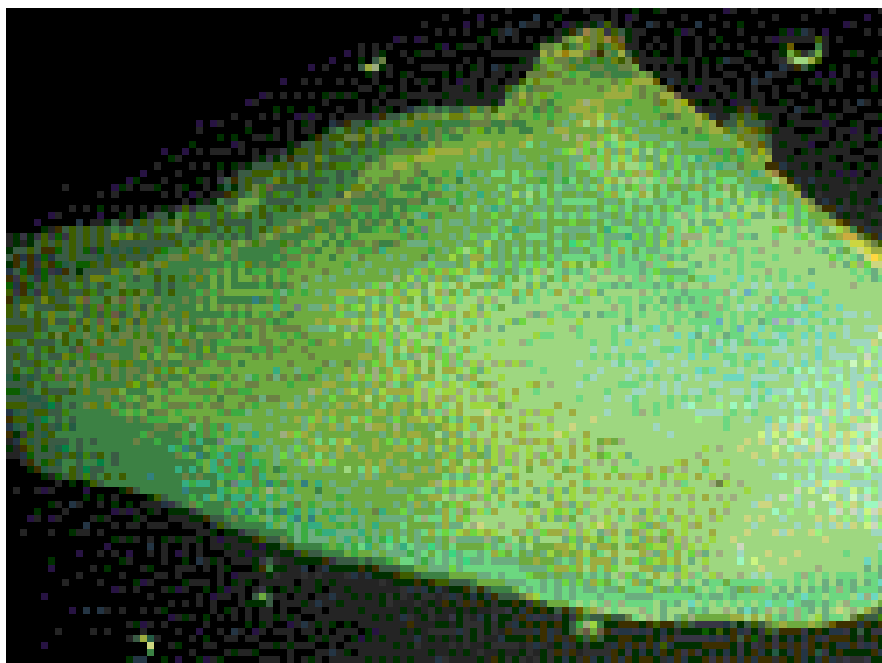


Figure 5.2. Sectioned sagittal otolith of a maori wrasse (995 mm FL) double injected with oxytetracycline (visible as two yellow bands at margin of otolith).

The second individual showed a single clear tetracycline band. The estimated cycle frequency (V, Cappo *et al.* 2000) for formation of opaque check marks was estimated as 1.06 yrs and 1.10 years respectively. Based on this result, the opaque increments observed in sectioned sagittae were identified as annual increments.

Age and Growth

Maori wrasse sampled for this study showed a strongly right-skewed size frequency distribution (Figure 5.3). The majority of sampled individuals were between 400-600 mm FL with a modal length of 500-600 mm. Very few specimens < 300 mm FL were collected. This reflects the cryptic behaviour of juvenile maori wrasse and their habitat preferences; sheltered lagoonal environments vs exposed reef slopes for adults. Preliminary observations suggested that the dominance of individuals between 400-600 mm FL and the long tail of uncommon, larger individuals reflected size frequency in the field.

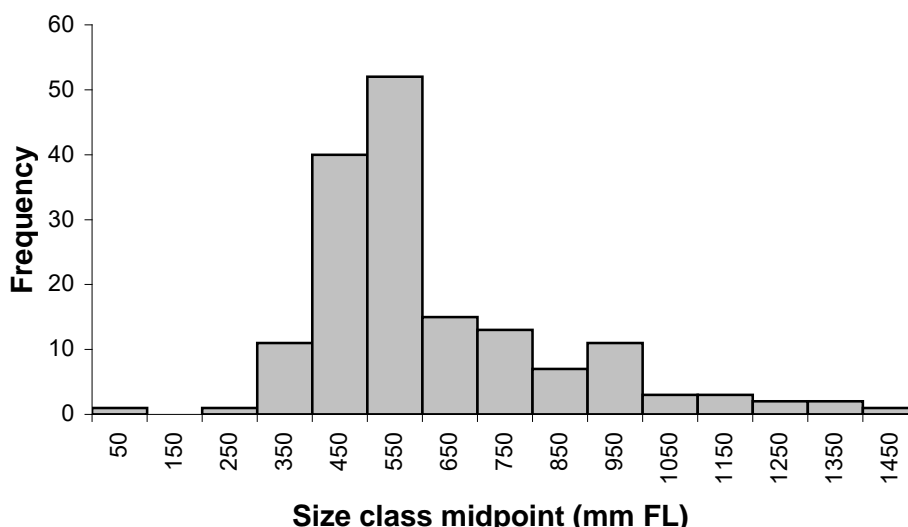


Figure 5.3. Size frequency distribution of maori wrasse samples used in this study.

Visual surveys

The size frequencies of fishes estimated from visual surveys of reef front and reef pass populations on the northern reefs of the GBR showed the same general structure as the catch sample; populations dominated by small individuals and relatively low numbers of large fish (Figure 5.4). The main difference was that the sample obtained from line and spear fishing showed a greater proportion of small individuals (< 450 mm FL) than recorded in the visual surveys. This is explicable in terms of the more cryptic behaviour of small females, which means they may be under-represented in the visual surveys. The maximum size of males obtained from catch data was also greater than observed in counts.

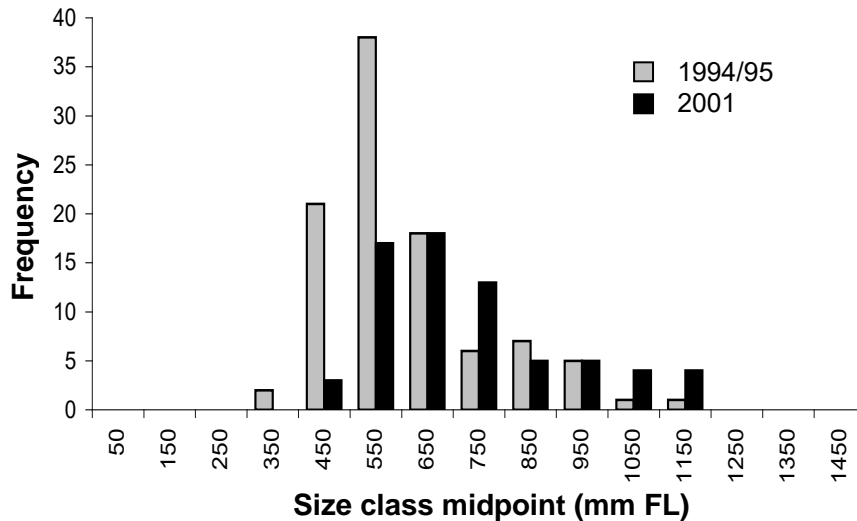


Figure 5.4. Size frequency distributions for maori wrasse from underwater visual surveys conducted on a number of reefs on the northern Great Barrier Reef in 1994/95 (and 2001).

A size at age plot was constructed using the 164 individuals for which age estimates were obtained. The plot exhibited increasing variability in the relationship between size and age. Partitioning the plot by sex demonstrated that this variability was due to increasingly divergent growth trajectories between males and females (Figure 5.5). We analysed the size-at-age data in two ways. Fitting separate VBGF to male and female data gave L_{∞} estimates of 75.9 cm FL for females, and 229.3 cm FL for males. These estimates confirm the asymptotic growth pattern for females relative to males, resulting in a 3 fold difference in L_{∞} between the sexes. Males were first recorded in the sample population at an age of 9 years and at a size of 73.0 cm FL. Due to the pattern of female-male sex change comparative VBGF estimates for k and t_0 have little meaning. For both sexes linear plots adequately described the size at age relationships for sexually mature individuals over the age distribution sampled. For females the range of ages was from 6 (see below) to 32 years, in males from 9 (the youngest male recruit in the population) to 25 years. For sexually mature females the relationship between age and size was $y = 19.76x + 3687.9$, $r^2 = 0.74$, for males $y = 44.59 + 285.4$, $r^2 = 0.71$. Estimated growth rates for each sex expressed in mm yr^{-1} (females 19.7 ± 2.1 , males 44.6 ± 14.4) showed male growth rates were approximately double those of females resulting in relatively young but large males.

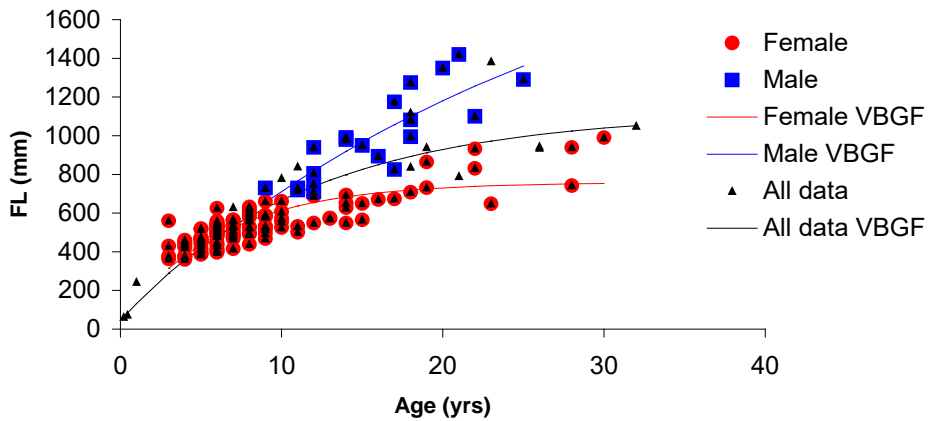


Figure 5.5. Size-at-age plots with VBGF partitioned by sex for maori wrasse. Middle fitted line is VBGF for entire sample. For all curves, t_0 was constrained to 62 mm FL.

Mortality

Total instantaneous mortality was estimated by catch curve analysis using age classes six years and older. The annual mortality estimate from the regression analysis was 0.11 suggesting that less than 3.5% of maori wrasse from the study population live beyond 30 years (Figure 5.6). A second mortality estimate, using an estimate of t_{max} of 32 years, gives an estimated mortality rate of 0.14 with less than 1.5% of the population living to 30 years. Both results suggest that very few maori wrasse in the study area achieve an age of greater than 30 yrs.

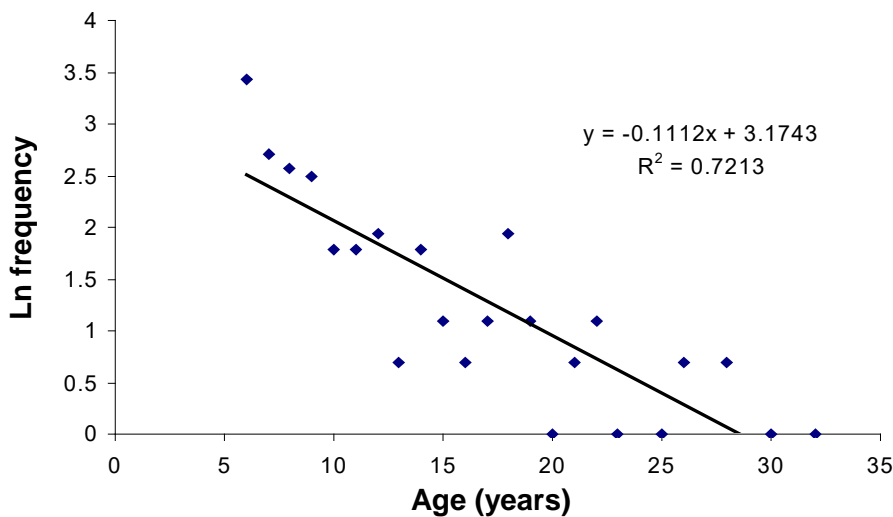


Figure 5.6. Catch curve for estimation of total mortality of maori wrasse aged 6 to 32 years sampled from the Great Barrier Reef.

Reproductive biology

Analysis of gonad weights for both females and males revealed the same bipartite relationship between ovary and testis weight and fish size observed in other protogynous labroid fishes (Figure 5.7). There were insufficient numbers of immature females in the sample to estimate size and age at maturity statistically. More than 50% of females were mature in all size classes sampled. The smallest and youngest mature females were 360 mm FL and 3 yo, while the largest and oldest immature females were 709 mm FL and 8 yo, which suggests that maturity takes place over a wide size and age range, and can occur as early as 360 mm and 3 years of age. Ovary weight abruptly increased at approximately 550 mm FL and at an age between 6-7 years indicating that female sexual maturity may first occur, on average, at around this combination of ages and sizes.

There were insufficient numbers of males in the sample to estimate the size and age at sex change. The youngest male observed in the population was 9 years and approximately 700 mm FL. In both sexes, the relationship between gonad weight and fork length was highly variable. For ovary weight an exponential equation was fitted; for testis weight the most appropriate equation was linear. In both instances the r^2 values were relatively low. As with many protogynous species, the relationship between testis weight and body length was linear but highly variable. The differing relationships between ovary (exponential) and testis (linear) weights and body length in maori wrasse are characteristic of a number of protogynous species.

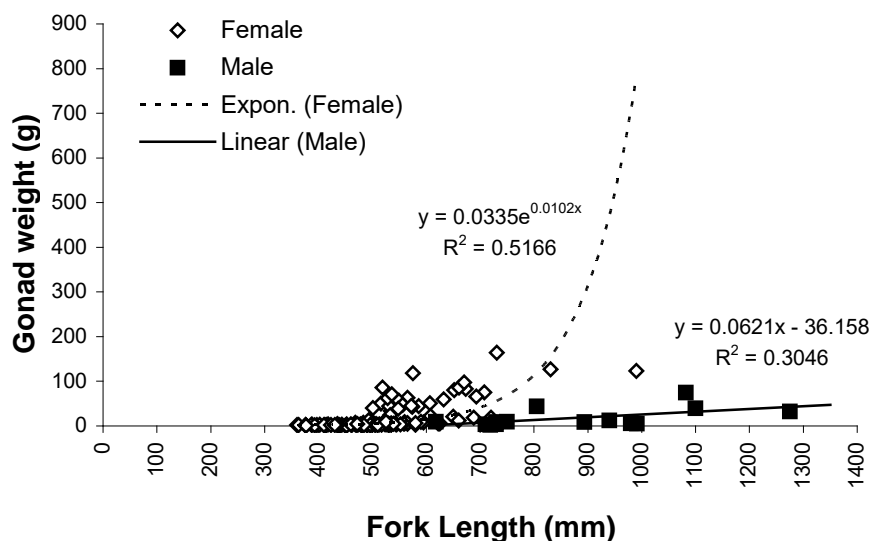


Figure 5.7. Relationship between gonad weight and length for maori wrasse partitioned by sex.

Diet

Analysis of alimentary tract contents of 17 individuals collected by spearing confirmed a diet dominated by larger invertebrates (molluscs, crustaceans and echinoderms) with some evidence of feeding on benthic fishes (Figure 5.8). The proportions of the prey items recorded from northern Australian fishes were remarkably similar to those collected in a study of prey items sampled from more broadly distributed populations of maori wrasse; invertebrates 79 vs 77%, fish 19 vs 22% (Randall *et al.* 1978). Maori wrasse is confirmed as a predator of large benthic invertebrates, primarily gastropods and crustaceans with relatively few echinoderms.

Although *Acanthaster planci* was common at the northern reef sampling sites, no *A. planci* material was found in the gut contents.

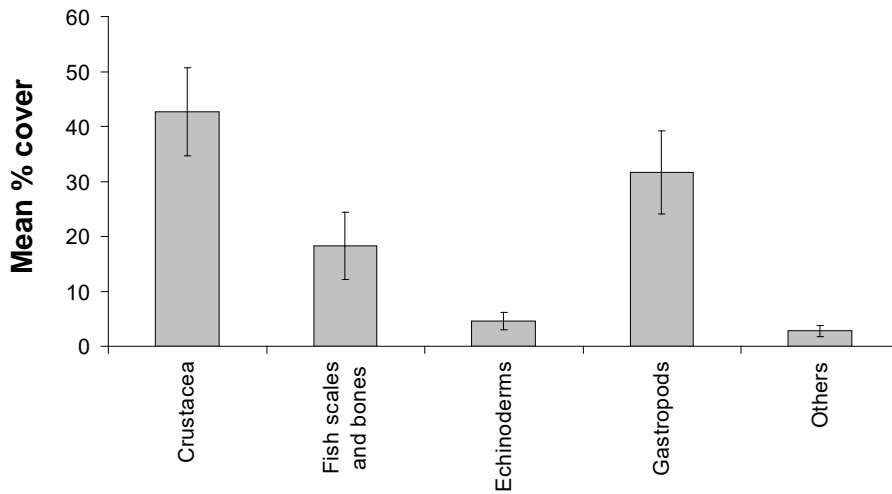


Figure 5.8. Summary of stomach contents of maori wrasse $n = 17$. Error bars are standard error.

Barramundi Cod

Age and Growth

A total of 228 barramundi cod were sampled, ranging in size from 350 to 710 mm FL and from 1 to 19 years of age (Figure 5.9). The majority of samples were between 430 and 610 mm FL and 4 and 13 years of age. The under-representation of small young fish in the sample is likely to be due to the cryptic nature, and perhaps alternative habitat preferences, of this component of the population. The age distribution of the sample suggests that barramundi cod are not fully selected by the sampling gear until about 6 years of age.

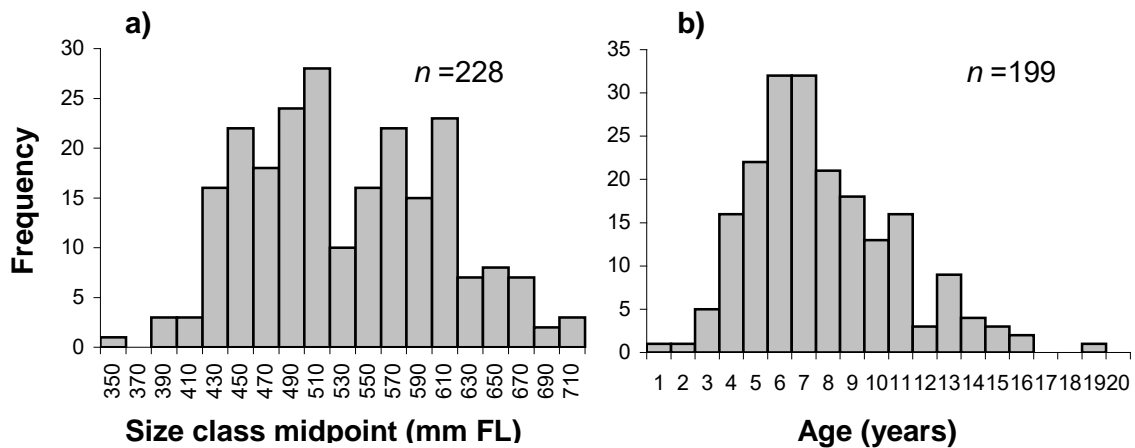


Figure 5.9. Length (a) and age (b) frequency distributions of barramundi cod sampled from the Great Barrier Reef. Data were pooled across reefs and years from 1995 – 2001.

The size related bias is also evident in the length-at-age distribution (Figure 5.10) in the rapid contraction in the size range in each age class from age six and younger. This is most likely the result of gear selectivity and, hence, only the fastest growing individuals from these age classes are represented in the sample.

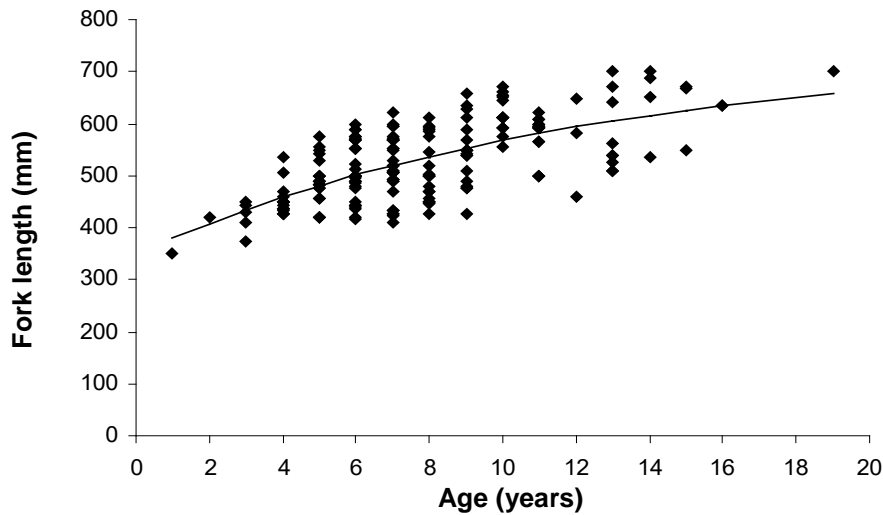


Figure 5.10. Length-at-age data and estimated von Bertalanffy growth curve for barramundi cod sampled from the Great Barrier Reef. Data were pooled across reefs and years from 1995 – 2001.

Estimates of von Bertalanffy growth parameters for the fit illustrated in Figure 5.10 are provided in Table 5.2. These estimates should be treated with some caution given the associated sampling biases noted above. Attempts to deal with the biased distribution in the size-at-age in the younger age classes, by constraining the value of t_0 , resulted in even poorer fits.

Notwithstanding this, the distribution of the data indicate a period of relatively rapid growth to around 500 mm FL between 0 and 6 years of age followed by a general reduction in growth rate and a flattening of the growth curve.

Mortality

Total instantaneous mortality was estimated by catch curve analysis using age classes 6 to 19 years (Figure 5.11). The linear regression for the catch curve provided a reasonably good fit ($r^2 = 0.91$) to the log frequency of the age data for the pooled sample and an estimate of total mortality of 0.28.

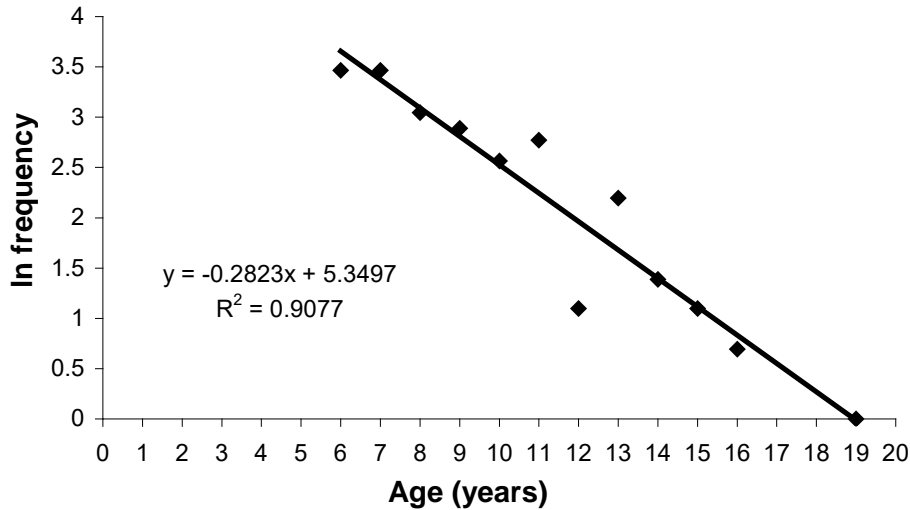


Figure 5.11. Catch curve for estimation of total mortality of barramundi cod sampled from the Great Barrier Reef. Data were pooled across reefs and years from 1995 – 2001.

Table 5.2. Estimated von Bertalanffy growth parameters for barramundi cod and blue-spot coral trout from nonlinear least squares minimisation, including goodness of fit and sample size.

Parameter	Barramundi cod	Blue-spot coral trout
L_{∞} (mm FL)	738	948
K (year ⁻¹)	0.08	0.14
t_0 (years)	-7.68	-1.71
r^2	0.45	0.71
n	198	346

Reproductive biology

There were no immature barramundi cod in the sample. Hence it was not possible to estimate size at maturity statistically. However, the smallest (mature) female sampled was 350 mm FL, indicating that first maturity is likely to occur at no larger than 350 mm FL.

The parameter estimates for the size and age at sex change for barramundi cod are given in Table 5.3 and fits of the logistic model to the size and age at sex change illustrated in Figures 5.12 and 5.13, respectively. Sex change occurred over a broad range of lengths (410 – 610mm FL, Figure 5.12) and ages (4 – 13, Figure 5.13), indicating a degree of plasticity in the timing of sex change.

It is also worth noting that several bisexual individuals were identified. The bisexual stage is defined by the presence of both male and female germinal tissue that shows no sign of degeneration in either tissue type, as is the case for the transitional stage (see *Reproductive staging*, chapter 6).

Table 5.3. Parameters of age- and size-specific maturity and sex change for barramundi cod and blue-spot coral trout. m_{50} and m_{95} are the age or length at 50% and 95% maturity respectively, and s_{50} and s_{95} are the length or age at which 50% and 95% of the population are males, respectively. Estimates of m_{50} and m_{95} are not available for barramundi cod due to lack of immature individuals in the sample.

	m_{50}	m_{95}	s_{50}	s_{95}
Barramundi cod				
Size-specific (mm FL)	-	-	542 mm	716 mm
Age-specific (years)	-	-	8.2 years	13.7 years
Blue-spot coral trout				
Size-specific (mm FL)	391	618	828	940
Age-specific (years)	2.22	4.77	11.70	18.56

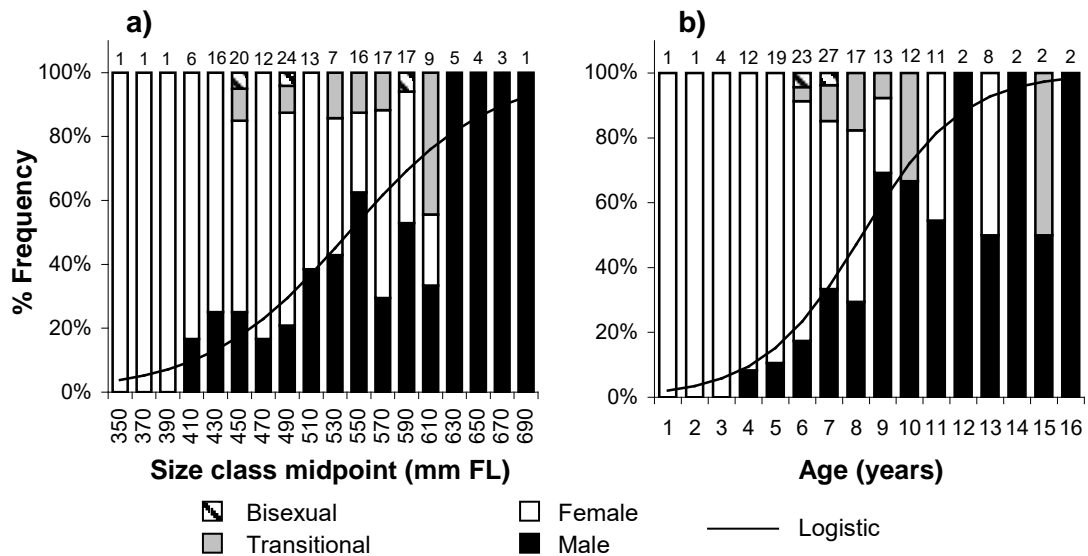


Figure 5.12. Proportion of male, female, transitional and bisexual barramundi cod in each size (a) and age (b) class and estimated logistic function fitted to the proportion of males (relative to females). Parameters of the logistic functions are given in Table 5.3.

Blue-spot coral trout

Age and Growth

A total of 945 blue-spot coral trout were sampled over the course of the project with otoliths and reliable ages obtained for a sub-sample of 346. The size range of the sample was from 220mm FL to 930mm FL, and the age range of the sample was from 1 year to 18 years (Figure 5.13). It is likely that the upper ends of both the size and age range of the sample are negatively biased due to the tendency for very large, and presumable old, blue-spot coral trout to be difficult to capture using either line for spear fishing techniques.

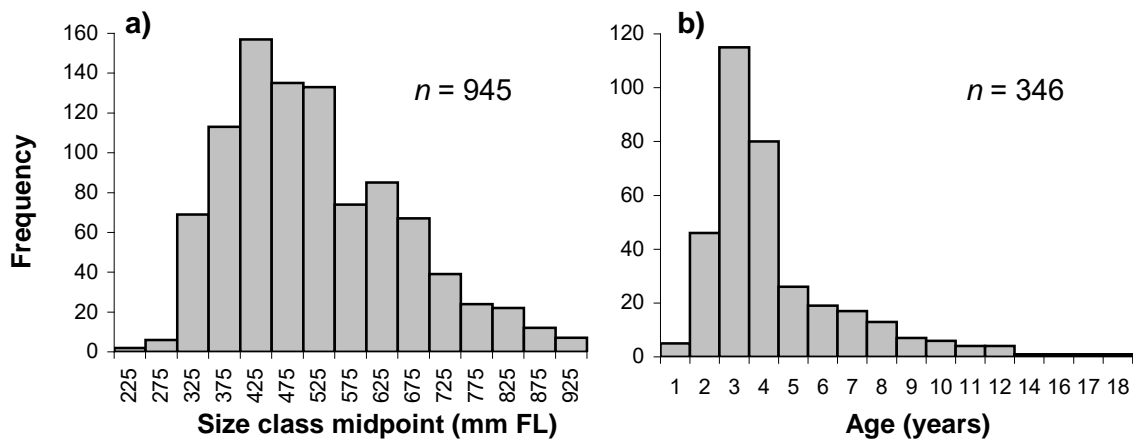


Figure 5.13. Length (a) and age (b) frequency distributions of blue-spot coral trout sampled from the Great Barrier Reef. Data were pooled across reefs and years from 1995 – 2000.

The fact that the majority of reefs surveyed for the ELF experiment are mid-shelf reefs is also likely to result in a bias toward smaller, younger fish, as blue-spot coral trout generally, and larger individuals in particular, are more common on outer-shelf reefs (Ayling and Ayling 1992, Mapstone *et al.* 1998b). The majority of fish sampled were relatively evenly distributed between 300mm and 700 mm FL (Figure 5.13). The distribution of ages, however, was significantly skewed toward the younger age classes with age classes older than 9 accounting for less than 10% of the sample (Figure 5.13).

There was substantial variation in length-at-age in most age classes, with length ranges of approximately 300mm to 700mm FL for age classes 3-5 years (Figure 5.14).

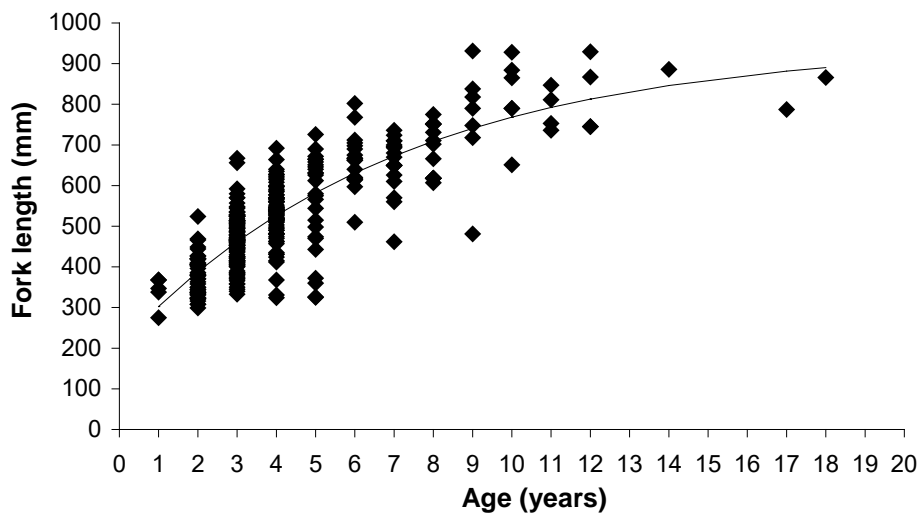


Figure 5.14. Length-at-age data and estimated von Bertalanffy growth curve for blue-spot coral trout sampled from the Great Barrier Reef. Data were pooled across reefs and years from 1995 – 2000. VBGF parameters are given in Table 5.2.

Although not representatively sampled, the length-at-age in the first two to three years indicates rapid growth with an estimated average size at three years of approximately 480 mm FL, and a significant proportion of individuals reaching more than 550mm FL within three years (Figure 5.14).

The rate of growth appears to reduce around 9-10 years of age. Although, this may to some extent be exaggerated due to an under-representation of larger, fast growing individuals in these age classes as a result of selectivity of the sampling methods. The estimates of von Bertalanffy parameters are given in Table 5.2, with L_{∞} and K estimates as 948mm FL and 0.14, respectively.

Mortality

Total instantaneous mortality was estimated by catch curve analysis using two age ranges: 3-18; and 3-14 years. The latter was done as a sensitivity analysis to examine the effect of the last three age classes for which the frequencies were one. The estimated total mortality using the complete sample (ages 3-18) was 0.32 (Figure 5.15). Excluding the last four age classes resulted in the estimate increasing to 0.39 (Figure 5.15).

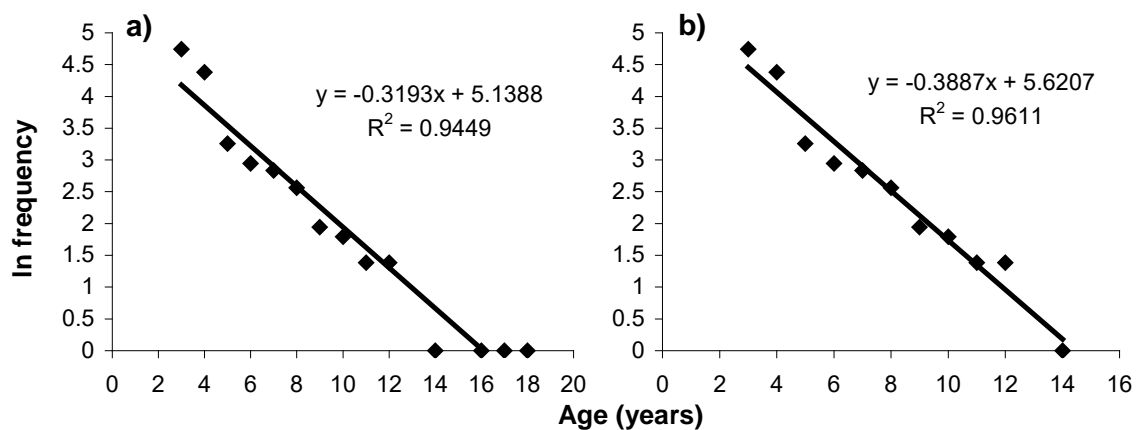


Figure 5.15. Catch curve for estimation of total mortality of blue-spot coral trout aged 3 to 18 years (a) and 3 to 14 years (b) sampled from the Great Barrier Reef. Data were pooled across reefs and years from 1995 – 2000.

Reproductive biology

The estimated size and age at 50 % maturity were estimated to be 391mm and 2.22 years, respectively (Table 5.3, Figure 5.16). While there were sufficient immature fish in the sample to estimate the parameters of the logistic function, the likely under-representation of individuals less than 300 mm and 0-2 years of age means that these estimates may be slightly biased as the inflection in the curve is not well defined for the length based estimate, or at all for the age-based estimate.

The proportion of female, bisexual, transitional and male stages of reproductive status by length and age, as well as the fit of the logistic function, are given in Figure 5.17.

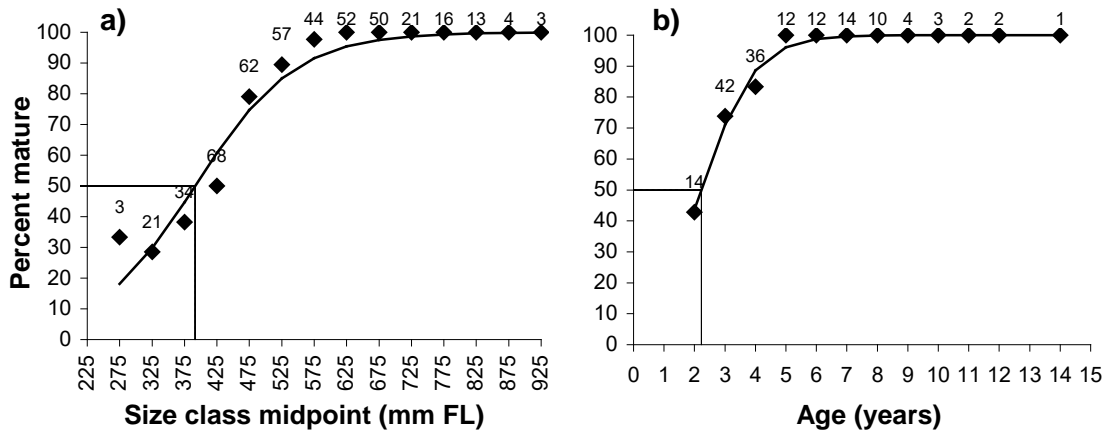


Figure 5.16. Percentage of mature females in each size (a) and age (b) class and estimated logistic maturation schedule for blue-spot coral trout from the Great Barrier Reef. Dotted line indicates size (age) at 50% maturity. Sample sizes for each size (age) class are shown above each bar. Data were pooled across reefs and years from 1995 – 2000. Parameters of the maturation function are provided in Table 5.3.

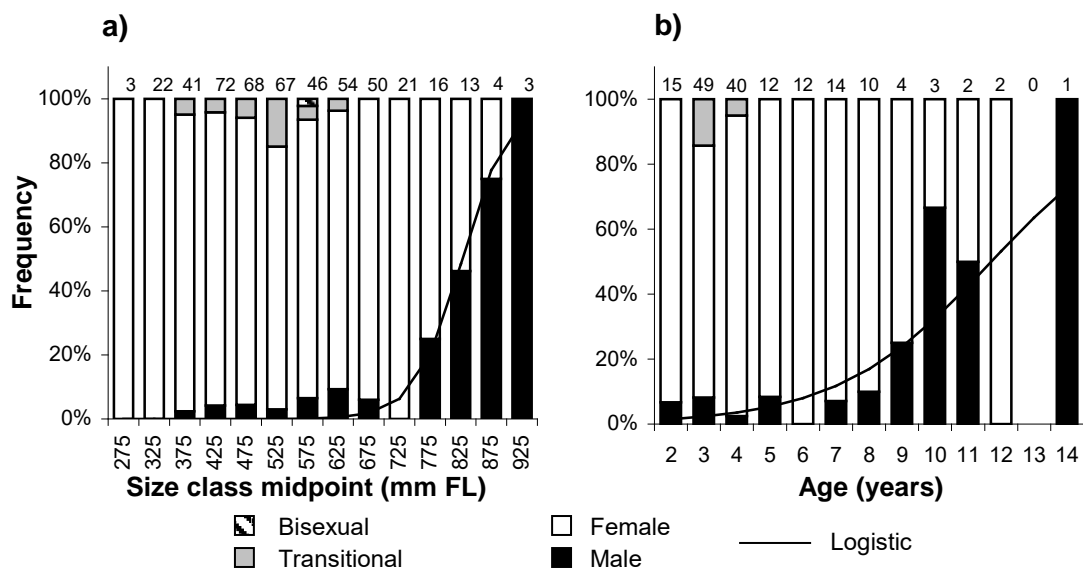


Figure 5.17. Proportion of male, female, transitional and bisexual blue-spot coral trout in each size (a) and age (b) class and estimated logistic function fitted to the proportion of males (relative to females). Sample sizes for each size (age) class are shown above each bar. Parameters of the logistic function are given in Table 5.3.

Estimates of length and age at sex change are given in Table 5.3. It is evident from the distribution of males and females among length and age classes (Figure 5.17) that females dominate all but the very largest and oldest size and age classes. Males constitute less than 10% of the sample for all size classes below 750mm FL and of the total sample. Length at 50% sex-change was estimated to be 828mm FL and age at sex change 11.70 years.

The distribution of the “footballer” and “blue-spot” colour morphs by length and age are presented in Figure 5.18. The “footballer” colour morph, while observed in all

length classes and most age classes, is more common in the smaller length classes and younger age classes. A significantly larger proportion of the “footballer” colour morph were immature (>40%) relative to the “blue-spot” colour morph (<10%), which was dominated by mature females (Figure 5.19).

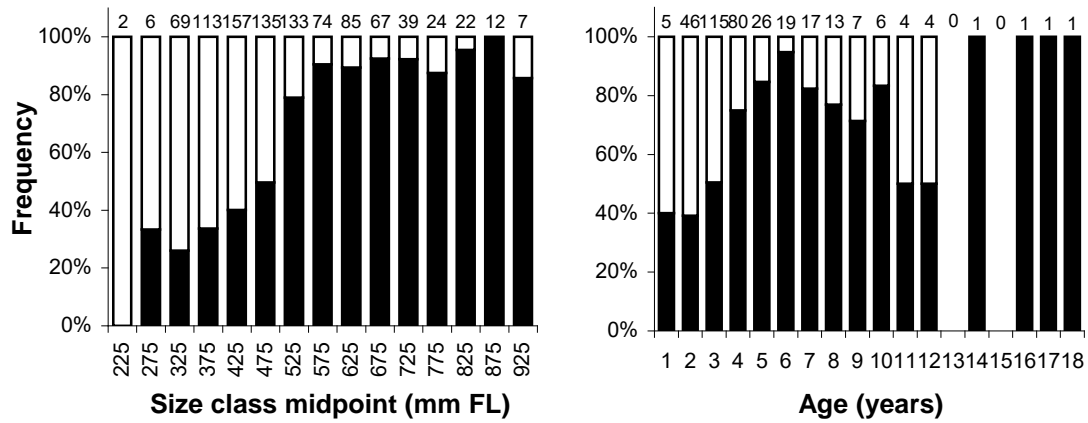


Figure 5.18. Proportion of blue-spot coral trout in each colour phase, footballer (□) and blue-spot (■) by size (a) and age (b) class. Sample sizes for each size (age) class are shown above each bar.

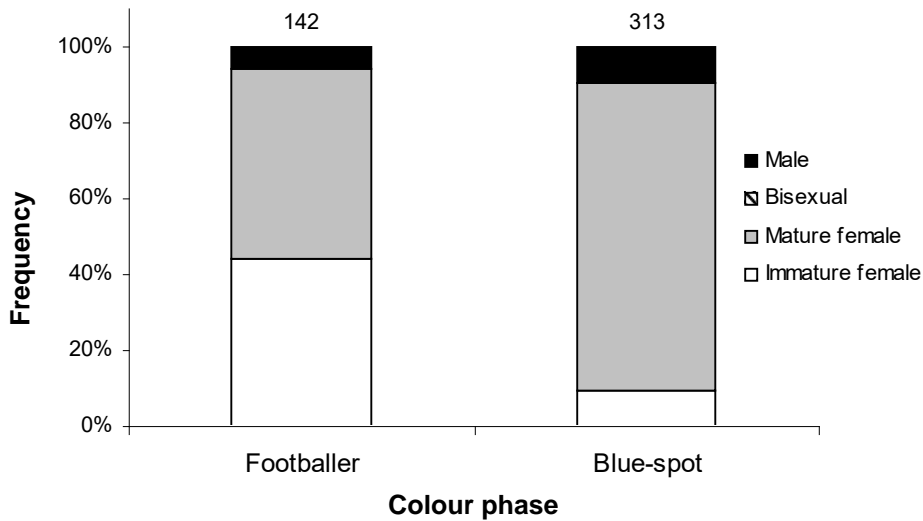


Figure 5.19. Proportion of male, female, transitional and bisexual blue-spot coral trout in each colour morph (Footballer, Blue-spot). Sample sizes for each colour phase are shown above each bar.

Discussion

Increasing levels of local, national and international concern about the vulnerability of maori wrasse and barramundi cod to over fishing, particularly in the face of the rapid expansion of the live reef fish trade, was the primary motivation for this component of the project. In addition, given its larger maximum size and, presumably, different demography relative to the other species of coral trout on the GBR, similar concerns had been raised for the potential for over-harvest of the blue-spot coral trout.

We have provided age-based estimates of essential population parameters (longevity, growth, mortality, size and age at maturity and sex change) for each of the target species from samples collected over a large section of the GBR. Importantly, we have also convincingly validated the annual periodicity of the bands in otoliths of the maori wrasse, providing a sound basis for further age-based assessments of this high value, iconic species. Efforts should continue to provide similar validations for the other species.

Each of these species is considered “large” by demersal reef fish standards; all having a maximum length of greater than 750mm FL, with the maori Wrasse and blue-spot coral trout reaching more than 1000mm FL. Somewhat contrary to expectation, the maximum age for each species is relatively modest: 32, 19 and 18 years for the maori wrasse, barramundi cod and blue-spot coral trout, respectively. Reported maximum lengths and ages for other target and bycatch species in the reef line fishery are given in table 5.4 for comparison.

Table 5.4. Maximum reported length and age for target and common bycatch species in the reef line fishery on the Great Barrier Reef (data from ELF Experiment).

Species	Length _{Max} (mm FL)	Age _{Max} (years)	Source
Common coral trout (<i>Plectropomus leopardus</i>)	650	17	(Lou <i>et al.</i> 2005, ELF Project, unpublished data)
Red throat emperor (<i>Lethrinus miniatus</i>)	550	20	(Williams 2003)
Stripey bass (<i>Lutjanus carponotatus</i>)	350	18	(Davies 1995, Kritzer 2001, 2002)
Blue-spot rock cod (<i>Cephalopholis cyanostigma</i>)	360	42	(Mosse 2001, Mosse and Davies, in review)
Footballer rock cod (<i>Epinephelus fasciatus</i>)	360	20	(ELF Project, Unpublished data)

This comparison (Table 5.4) indicates that a range of species with maximum lengths considerably less than these three species addressed by this chapter have similar, or greater longevity, than those reported here. Comparisons among a number of groups of reef fishes indicate that i) the range of life spans varies greatly among and within different families, and ii) there is only a very loose relationship between age and size (e.g. Choat *et al.* 1996, Hart and Russ 1996, Newman *et al.* 2000a,b).

Potential taxonomic explanations for the combination of fast growth and modest longevity evident for maori wrasse are discussed briefly below and in more detail by Choat *et al.* (in review). The patterns of growth for barramundi cod and blue-spot coral trout demonstrate the range of variability within one family of commercially important reef fishes; many large species of serranids are relatively short lived (< 20 years) and fast growing (e.g. Ferreira and Russ 1992, 1994, Sheaves 1995), while small species may have extended life spans (>40 years) (e.g. Mosse 2001, Mosse and Davies in review). These results reiterate the need for age-based estimates of population parameters as a basis for assessing the conservation and resource status of reef fish populations.

The results presented here demonstrate that these species, the maori wrasse in particular, are not as long-lived as some have considered (e.g. Johannes and Riepen 1995, Sadovy *et al.* 2003). It is important, however, to keep the historical development of the reef line fishery on the GBR in mind when interpreting these results for each species. The samples of each species included in this study were obtained from both reefs open to and closed to fishing. In addition, fishing had been prohibited on the closed reefs for 12 years prior to the collection of these samples. Before this all reefs were open to fishing. Hence, the estimates of longevity are likely to be under-estimates, and unlikely to be representative of an unfished equilibrium population, as the populations have been protected from fishing for less than the estimated longevity of any of the species. Obtaining unbiased estimates of longevity (and other age-based population parameters) will require that populations are protected and monitored from fishing for at least several generations. In lieu of such information, the estimates of longevity provided here should be considered minimum estimates. Similarly, the estimates of mortality for each species will be influenced by the historical and current levels of fishing effort.

A number of other aspects of the biology and ecology of these species are likely to render them potentially vulnerable to over harvest in a multi-species fishery, such as the reef line fishery, and make the assessment and management of these species problematic. Principle among these are: i) their low abundance and overlapping distribution with the target species of the fishery, ii) the difficulty and/or expense associated with obtaining accurate estimates of abundance, iii) their propensity to form aggregations to spawn (particularly in the case of maori wrasse and blue-spot coral trout), and iv) their protogynous hermaphroditic reproductive strategy. Although both the maori wrasse and barramundi cod are now listed as 'no take' species for the CRFFF, they will remain a bycatch species in the fishery, as the fishing gear used in all sectors of the fishery will continue to catch both species. Understanding the potential impact of bycatch mortality be important to consider, particularly with respect to requirements under the *Environmental Protection and Biodiversity Conservation Act 1999* for all export fisheries to be conducted in a manner that does not threaten bycatch species. The information from this project for these species provides a basis for such assessments.

Maori wrasse

There is also considerable concern within the international conservation and scientific community about the viability of populations of maori wrasse and barramundi cod on south-east Asian coral reefs, where they are heavily targeted as part of the Asian live reef fish trade, often using destructive fishing practices (Johannes and Riepen 1995, Lee and Sadovy 1998). As noted above it is primarily this concern that has led to maori wrasse being listed in Appendix II of CITES, which means a permit is required for any trading of this species. Similar concerns about their potential vulnerability to overfishing, the lack of information on their basic biology and their high value as a

tourist drawcard has resulted in the harvest of this species and the barramundi cod being prohibited in the reef line fishery.

Animals can achieve large size through rapid growth resulting in large but relatively young individuals. Alternatively growth may be slower but increased longevity may provide an opportunity to reach large sizes. Both scenarios require periods of indeterminate growth over much of the life span. Such growth patterns are characteristic of labrid fishes, which contrast with those exhibited by many acanthurids, lutjanids some pomacentrids and serranids that achieve ages in excess of 30 years while maintaining relatively small body sizes (Choat and Robertson 2002, Meekan *et al.* 2001, Mosse 2001, Newman *et al.* 2000b). Given the large size achieved by maori wrasse, it is of considerable interest to consider the underlying mechanism leading the species life-history strategy.

Large size in the study populations of maori wrasse is attributable to a relatively rapid growth rate associated with an indeterminate pattern of growth, especially in males. The achievement of large size is associated with a modest life span with a maximum of 32 years for females and only 25 years for males. In the case of males, the maximum life span following recruitment via sex reversal was 16 years, during which time growth was essentially linear. The patterns revealed for maori wrasse are similar to those seen in other labrid fishes: demography with fast, indeterminate growth and relatively short life spans implying relatively rapid population turnover.

Large size in fishes has important management implications (Dulvy *et al.* 2003). For coral reef fishes, most interest has been focussed on fishes of the families Serranidae and Labridae (Sadovy *et al.* 2003). Large size, (defined here as a maximum total length of >750 mm) has been recorded from a variety of labrid species although the demographic data necessary to identify the underlying population dynamics are sparse. It is now possible to put the issue of large size in maori wrasse into a more general context by examining the evolutionary and habitat relationships that underlie size distributions in labrid fishes.

The lack of a consolidated taxonomic base and unresolved phylogenetic relationships of labroid fishes has hindered such an approach previously. Recent reviews of the taxonomy and phylogeny of scarids (parrotfishes) and labrid (wrasses) fishes (Parenti and Randall 2000, Clements *et al.* 2004) indicate that the maori wrasse is atypical. It is a significant outlier in terms of its maximum size relative to other species of tropical wrasses of the same genus (*Chelinus*) which has an average size of 330 mm FL and appears to be more closely related evolutionary to the ecologically and morphologically similar species of parrot fish on the GBR (humpheaded parrot fish, *Bolbometopon muricatum*, and the bicolour parrot fish, *Cetoscarus bicolour*).

A recent review of maori wrasse biology and fishing practices leaves little doubt that this species is impacted by commercial fishing in the western Pacific and SE Asia (Sadovy *et al.* 2003). Sadovy *et al.* (2003) invoke conservative life history features, including slow growth and extended life spans, as one of the reasons for the deleterious impacts of fishing. Hostetter and Munroe (1993) have made similar arguments relating to life history features in large labrids. An analysis of the large temperate labrine *Tautoga onitis* recorded a maximum age of 25 years. The maximum age attributed to *T. onitis* species is 34 years (Cooper 1967). The greatest size and age achieved by the species occurred in males (Hostetter and Munroe 1993). Hostetter and Munroe (1993) reviewed growth rates and life spans in other large temperate-water labrids. Two conclusions were drawn from their comparative study: i) for northern temperate labrids, growth rates were slow and associated with

extended longevity; and ii) these characteristics may be an inherent feature of large-sized labrids in general. More recent analyses of longevity in coral reef fishes, however, (Newman *et al.* 1996, Newman *et al.* 2000b, Mosse 2001, Meekan *et al.* 2001, Choat and Robertson 2002) shows that 30 years is not old in relative terms. Moreover, growth rates in labrids even in cold water species (Hostetter and Munroe 1993, Gordo *et al.* 2000) appear to be comparatively rapid.

What other factors then are potentially responsible for the impacts of fishing on maori wrasse populations? The size and age-specific distribution of sexes in maori wrasse supports the conclusion of protogyny (Sadovy *et al.* 2003) in this species. Complex sexual ontogenies could increase the impact of fishing (Roberts and Hawkins 1999). The demographic characteristics of males in the study population, however, suggest that maori wrasse is capable of a rapid response to male depletion, by shifting of the age of transition and by rapid growth of recently transformed males. Sadovy *et al.* (2003) also presented information on male size distribution that suggested some flexibility in the size at sexual transition. The age at first maturity (5-7) years is relatively late, 20% of the female life span as opposed to 5–6% of the female life span observed in other reef fishes with life spans in excess of 30 years (Choat and Robertson 2002). Initial observations of spawning behaviour, however, suggest that small individuals (450 mm FL) are involved in pair spawning episodes with very large males (R. Fitzpatrick pers com).

Three features of maori wrasse biology appear to be a major significance in terms of response to fishing. Firstly, as expected from the negative relationship between size and abundance in reef fishes (Dulvy *et al.* 2003); adult maori wrasse are relatively rare even in undisturbed habitats. Sadovy *et al.* (2003) recorded densities of approximately 10 individuals per hectare in unfished areas, and 4-5 individuals in lightly fished areas. High abundance records of up to 27 individuals per hectare (Sadovy *et al.* 2003) require confirmation. Secondly, the size-at-age distribution confirms that not all individuals change sex and the oldest members of the population are females in the 800-900 mm size range. These individuals have very large ovaries and have the potential to contribute disproportionately to the overall reproductive output of the population. As the size distributions from catch records and underwater surveys demonstrate, however, (Sadovy *et al.* 2003, Figure 5.1) individuals in this size range are extremely rare. Thirdly, the shallow depth range (2-30m) of this species, the tendency to occupy shallow sleeping site on reef fronts and an aggregative and highly visible spawning behaviour makes maori wrasse highly accessible to fishing at all stages of its adult life cycle.

Finally, there is evidence of specific habitat requirements for the juvenile stages of some species of large labrids. Most adult maori wrasse are observed on reef fronts and passes on exposed slopes with relatively low coral cover. Estimates of abundance by size classes have shown an association between juvenile maori wrasse and coral cover (Sadovy *et al.* 2003). In this example, the correlates of high coral cover were sheltered environments such as lagoons. Confirmatory evidence was obtained from the Cocos-Keeling Island in 2002 where, in extensive surveys of the reef system, the only habitat in which juvenile maori wrasse were observed was sheltered lagoonal areas. Large numbers of juveniles (30-100 mm FL) were recorded from shallow algal dominated lagoon habitats in the reef system. Similar patterns were also observed for the hump-headed parrotfish, *Bolbometopon muricatum*.

Mumby *et al.* (2004) noted recently that juveniles of one of the largest Caribbean labrids, *Scarus guacamaia* were associated with mangroves, in contrast to adults that were most abundant on open reef habitats. Destruction of the juvenile habitat was related to reductions in adult numbers at a Caribbean study site. If disjunct habitat

distributions for juveniles and adults are a consistent feature of the ecology of large labrids, then destruction of juvenile habitats may be a contributing influence to reductions in adult numbers. This might be especially marked in areas where habitats preferred by juveniles are close to coastal areas with high human population densities, such as throughout much of SE Asia and the populated Pacific Islands.

This study establishes the age-based demographic information that will provide a framework for understanding the capacity of maori wrasse to respond to fishing impacts and other disturbances. Four additional areas of research are identified: i) A more comprehensive analysis of the reproductive biology, including histological studies to confirm the estimates of size and age of first female maturity and the mechanism of male recruitment; ii) Estimates of age and sex-specific growth rates, life spans and mortality rates from other localities, including the western Pacific and the Indian Oceans, to put the GBR populations in a broader biogeographical context; iii) Abundance and size estimates based on a standardised methodology partitioned by habitat from a range of localities including the western Pacific and the Indian Oceans; and iv) A more detailed analysis of the demographic and abundance data to provide a framework for predicting responses of maori wrasse populations to variations in fishing rates.

Barramundi cod

Of the three species addressed by this component of the project, the barramundi cod is the one of which we know the least in terms of basic biology and ecology. We have demonstrated it has a longevity of at least 19 years, is a protogynous hermaphrodite that grows rapidly during the first few years of life, matures relatively small (< 330 mm FL) and young (<2 years) and changes sex at approximately two-thirds of its maximum size (540 mm FL) and about half its maximum age (8-9 years). These characteristics are similar to what we know of other serranids (Ferreira and Russ 1994, Ferreira 1995, Sheaves 1995, Adams 2002) with the pattern of growth appearing to be more asymptotic, similar to the *Cephalolus* species serranids than the larger *Epinephelus* species. Given the limited size and selective nature of the sample available to estimate the parameters, some caution should be exercised when using them. Despite this limitation, the data and results of the analysis do provide useful information to better understand the biology of the barramundi cod and important issues for future research.

The size and age distributions and the distribution of size-at-age indicate that a large proportion of the population below 450 mm FL and six years of age are not selected by the gear, or are not available on the reefs sampled. The majority of samples were collected using 8/0 hooks and 80 lb hand lines, which was standard gear in the commercial fishery at the commencement of the study. The cryptic nature of the species and, in particular small individuals, means conventional visual surveys as used for the ELF Experiment do not provide useful estimates of abundance and distribution (Mapstone *et al.* 1998a). It may be possible to obtain estimates of abundance and size structure using dedicated survey designs involving intensive searches (J.H. Choat/R.Pears *pers comm.*), however, the cost-effectiveness of such methods in the context of the whole fishery are not known. Catch rates from the commercial fishery and the ELF Catch Surveys suggest that average abundance is many times lower than other serranid species, such as the coral trout (*P.leopardus*, *P.maculatus*, *P.laevis*). This combination of characteristics is likely to make the barramundi cod particularly susceptible to overfishing in a multi-species line fishery without species specific regulations. As noted above, under the new management plan for the reef line fishery the taking of this species is prohibited. In this case, the

primary concern for management is whether the release mortality is sustainable and the extent of any illegal harvest.

Blue-spot coral trout

Low abundance relative to target species and the difficulty associated with reliably estimating abundance will tend to make the cost of robust assessments of stock status and sustainable yields of blue-spot coral trout prohibitive. While it can be argued that this is no longer required in the case of maori wrasse and barramundi cod on the GBR, given their protected status under the new management plan, it is a current management issue in terms of sustainable levels of harvest for the blue-spot coral trout. This species is currently harvested and marketed as “coral trout” along with the principle target species, the common coral trout, *Plectropomus leopardus*, and the bar-cheek coral trout, *P. maculatus* (Mapstone *et al.* 1996a, Williams and Slade 2002).

We have demonstrated that the longevity of the blue-spot coral trout is at least 18 years, which is one year greater than that recorded for the common coral trout (Chapter 6). There are reasons to believe this is an underestimate of the true longevity for this species. As noted, it is likely that the larger size ranges for this species have not been fully sampled in the current study due to the difficulty in catching large individuals with the standardised gear used for the ELF catch surveys and the mid-shelf position of the majority of the reefs involved in the ELF Experiment. The estimates of reproductive parameters also support the assertion that the estimate of longevity may be negatively biased. They indicate that the blue-spot coral trout matures and changes sex at a greater length and age than the common coral trout (Chapter 6, Ferreira 1995, Adams 2002), which would be consistent with a greater longevity than the common coral trout. In addition, the very low proportion of males in the samples and the lack of evidence of primary males (see Chapter 6, Adams 2002) suggest that the blue-spot coral trout may have a different, and possibly less flexible, reproductive strategy than the common coral trout.

This combination of life history traits combined with low abundance and the likelihood of similar vulnerability to the fishery as the common coral trout, suggest the blue-spot coral trout will be prone to over-harvest in the absence of species specific harvest regulations. The current management plan addresses this need, in part, by setting a minimum size limit for blue-spot coral trout of 500 mm FL, relative to 380 mm FL for the common coral trout. This change was a direct outcome of research done as part of this project (Adams 2002) and, given the results of additional analysis presented here, this minimum size limit is likely to provide sufficient protection to allow the majority of female blue-spot coral trout to spawn at least once before being vulnerable to harvest. The question remains, however, as to whether this measure on its own will be sufficient to limit the effects of fishing to sustainable levels given the protogynous reproductive strategy of the species and the putative importance of the contribution of large individuals to the total reproductive output of fish populations (Berkeley *et al.* 2004, Palumbi 2004). In this regard, the significant areas of platform reefs now closed to all forms of fishing as part of the GBRMPA Representative Areas Program should provide a level of protection to the components of the stock contained within them. Gaining a better understanding of the nature and extent of the interaction between populations of large serranids, such as the blue-spot coral trout, in these closed areas and the areas open to fishing, should continue to be a priority for future research.

In particular, we consider the investigation of relative cost-effectiveness of permanent or rotational systems of spatial closures, in combination with or independent of

conventional input and output control systems, for diverse multi-species fisheries to be a high research priority for fisheries and conservation management. The outputs and information base established as part of this and the broader ELF project, provide a sound basis for this work.

6. Regional patterns in the reproductive biology of common coral trout (*Plectropomus leopardus*).

Ashley J. Williams, Samantha Adams, Bruce D. Mapstone, Campbell R. Davies, and Cameron Murchie

6.1 Introduction

The common coral trout (*Plectropomus leopardus*) is the most abundant coral trout species on the GBR and is the main target species in the GBR CRFFF. Other coral trout species, including blue-spot trout (*P. laevis*), barred-cheek trout (*P. maculatus*), and passionfruit trout (*P. areolatus*), are caught less frequently and are usually grouped together with common coral trout into a generic 'coral trout' group in catch records. Annual commercial catches of coral trout have steadily increased from around 800 t in 1988 to over 2000 t in 2001 (Samoilys *et al.* 2002, QDPI&F unpublished data). Annual commercial fishing effort for coral trout has also increased significantly during this time from around 11,000 days fished in 1988 to over 30,000 days fished in 2001 (Samoilys *et al.* 2002, QDPI&F unpublished data). The rapid expansion in the trade of live reef fish from the GBR since the early 1990's and the significantly higher market value for live coral trout contributed largely to this increase in commercial fishing effort (Mapstone *et al.* 2001). The annual harvest of coral trout by recreational anglers was estimated to be around 300 t in 1997 and 1999 (Higgs 1999, 2001). Currently, there are no catch estimates for coral trout available for the charter sector, but coral trout are known to be a primary target species for many charter operations on the GBR (Green *et al.* in prep).

Concerns have been expressed about the sustainability of harvest rates for coral trout due to significant declines in catch rates since the early 1990's (Samoilys *et al.* 2002). In response to these concerns, a new management plan for the CRFFF was implemented in 2004. Management changes relevant to coral trout included a Total Allowable Commercial Catch (TACC) of 1300 t for coral trout, a reduction in the recreational possession limit from 10 fish to 7 fish, and the implementation of three nine-day spawning closures in October, November and December of each year. Although not developed specifically as a fisheries management tool, the introduction of the Representative Areas Program by the GBRMPA has resulted in a significant reduction in the area of the GBRMP in which fishing is permitted.

The current management of the CRFFF assumes that the demography of important target species, such as coral trout, does not vary substantially over the species range, and that fish populations on the GBR represent a single homogeneous stock. Currently, there are no data available on the genetic structure of coral trout populations on the GBR to indicate whether distinct genetic stocks exist. Recently, however, Mapstone *et al.* (2004) demonstrated significant variation in abundance and mean size and age of common coral trout among four regions of the GBR. Research on the reproductive biology of common coral trout has also demonstrated significant regional variation in sex ratios, mean size of females and mean age of transitional (sex changing individuals) (Adams 1996, Adams *et al.* 2000). The existence of regional variation in demography of common coral trout may reflect regional differences in productivity, which will have important implications for assessment and management of the fishery.

The primary objective of this chapter was to examine the regional patterns in reproductive biology of common coral trout on the GBR by consolidating and expanding on the research of Adams *et al.* (2000), which was limited to only a single

year of data and two regions (Townsville and Storm Cay) of the GBR. Importantly, we examine regional patterns in reproductive biology by using data collected from reefs that have been closed to fishing for at least 10 years. We estimate a range of reproductive parameters (spawning season, size and age at maturity, size and age at sex change and sex ratios) from data collected annually from these reefs over a six year period (1995 – 2000) among four regions spanning over 1000 km of the GBR.

6.2 Methods

Sample collection

Effects of Line Fishing Experiment

Samples of common coral trout were collected from four discrete regions of the Great Barrier Reef (Lizard Is., Townsville, Mackay and Storm Cay) over six years from 1995 to 2000 during the Effects of Line Fishing (ELF) Experiment catch surveys (Davies *et al.* 1998), as described in Chapter 2. For brevity, common coral trout will be referred to as coral trout for the remainder of this chapter. Size-based parameters were estimated from samples collected from 1995 to 2000, while age-based parameters were estimated from the 1995-1999 samples, as otoliths had not been read for samples collected in 2000 at the time of this report.

Only samples collected from reefs that were closed to fishing were used to estimate reproductive parameters, as the objective of this chapter was to obtain estimates of natural variability in populations in the absence of effects due to fishing. Two reefs within each of the three regions (Table 6.1) were chosen, as these reefs were the only reefs to be closed throughout the ELF Experiment, and had been closed for 10-12 years prior to the ELF Experiment (Mapstone *et al.* 2004). The number of coral trout collected from each reef in each year is given in Table 6.1. Individual reefs within each region were treated as replicates in each analysis for the comparison among regions. Details of otolith and gonad processing and estimation of age, sex and reproductive stage are outlined in Chapter 2.

Table 6.1. Number of common coral trout collected from two reefs within each of four regions of the Great Barrier Reef. Samples were collected as part of the Effects of Line Fishing Experiment. When sample sizes exceeded 300 for a reef in a given year, fish were released and only length data were recorded for these individuals.

Year	Lizard Is.		Townsville		Mackay		Storm Cay	
	MacGillivray Reef	South Direction	Glow Reef	Dip Reef	20-142	21-137	21-132	21-131
1995	45	145	186	90	258	318	356	287
1996	-	49	148	50	258	175	290	241
1997	79	63	168	138	140	85	146	224
1998	72	126	181	163	202	155	146	281
1999	53	138	225	115	227	146	300	295
2000	44	78	188	104	211	192	231	278
Total	293	599	1096	660	1296	1071	1469	1606

Additional sampling

An additional sample of 307 coral trout were collected from a group of mid-shelf reefs located north of Townsville in the Central Section of the GBR (see Chapter 2 for details). These samples were collected monthly, primarily for the estimation of the spawning season, as ELF catch surveys did not sample in all months of the year.

Reproductive staging

A number of reproductive parameters were estimated for coral trout, including spawning season, size and age at maturity, size and age at sex change, and sex ratios. To estimate these parameters, coral trout gonads were removed, processed and staged as described in Chapter 2. For samples collected from the ELF catch surveys, combinations of histological and macroscopic techniques were used to reproductively stage coral trout, as sampling took place during the spawning season for coral trout, when the majority of the population was reproductively active, making macroscopic staging of ripe females (gonad large, yellow with visible eggs) possible. Histological techniques were used to stage the monthly samples of coral trout.

Females and transitional individuals were classified histologically into developmental categories adapted from Moe (1969) (Table 6.2). Reproductive staging of males was more problematic than for females and transitionals and often reliant on appraisal of the general gonad morphology rather than germinal cell types alone. Accordingly, more detailed criteria were developed to stage males (Table 6.3). Images of all above reproductive stages can be found in Adams (1996, 2002 and 2003) and Samoilys and Roelofs (2000). Males that showed no evidence of prior spawning as a female (e.g., presence of degenerating ripe oocytes) were present in the samples, suggesting direct male development after gonadal differentiation as an immature female. However, the historical immature female lumen was maintained in the male testis together with peripheral sperm sinuses in the ex-ovarian wall. Therefore, primary males were only distinguishable whilst undergoing male sexual maturation in an immature female ovary at young ages (categorised as immature males, Table 6.3) and early after sexual differentiation where the female ovary clearly showed no signs of previous spawning as a female (primary males, Tables 6.2 and 6.3). Primary males could not be distinguished from secondary males with increasing time from sex differentiation.

A number of mature bisexual individuals were identified (Table 6.4). Bisexual individuals were those fish which had both male and female germinal tissue present, yet showed no sign of degeneration in either (as in transitionals). Bisexuals were categorised mature and ripe if both mature oocytes (yolk globule, migratory nucleolus – stage 4) and spermatozoa were present. Following this, the bisexuals were placed in male or female categories depending on which germinal tissue was most advanced. For example, a mature female, ripe bisexual was a bisexual with healthy hydrated eggs present amongst proliferating spermatocysts where the spermatozoa had not yet reached the sperm sinuses. A mature running ripe bisexual was where hydrated eggs (which occasionally appeared in the lumen) occurred together with proliferating spermatogenesis to the point where spermatozoa reached the sperm sinuses.

Reproductive stages of mature females (Ripe, Resting, Spent) and males (Ripe, Resting, Spent) were grouped as mature females and males respectively for analysis. Mature bisexual and immature individuals were not analysed statistically due to small sample sizes.

Table 6.2. Developmental stages of female and transitional common coral trout based on histological examination. Reproductive criteria were adapted from Moe (1969), Hastings (1981)^a, Sadovy and Shapiro (1987)^b, Shapiro *et al.* (1993)^c, Burton *et al.* (1997)^d, Sadovy and Colin (1995), Adams (1996) and Adams (2003)^e.

Developmental stage	Histological description
Immature female	Ovary small, tightly packed and dominated by previtellogenic, primary growth stage oocytes (chromatin nucleolus and perinuclear stage). Thin gonad wall ^d . <i>No evidence</i> of prior spawning in the form of post ovulatory follicles, atretic vitellogenic (yolk globule and/or migratory nucleolus, brown bodies or intralamellar muscle bundles ^c in the gonad. Precursory sperm sinuses (PSS) can be present in some individuals ^e .
Mature, resting female	Ovary dominated by previtellogenic, primary growth oocytes (chromatin nucleolus and perinuclear stage) with a thick gonad wall ^d . Evidence of recent prior spawning indicated by the presence of intralamellar muscle bundles ^c . PSS can be present in some individuals.
Mature, spent female	Ovary generally disorganized, dominated by previtellogenic, primary growth oocytes (stages 1 and 2). Evidence of recent prior spawning indicated by atretic vitellogenic (yolk globule and/or migratory nucleolus) oocytes. Obvious intralamellar muscle bundles ^c present. PSS can be present in some individuals.
Mature, ripe female	Ovary in active vitellogenesis. Oocytes present in all stages of development; Cortical alveolus and vitellogenic oocytes dominate the ovary.
Mature, running ripe female	Ovary in active vitellogenesis as in ripe females although migratory nucleolus stage oocytes have become hydrated.
Transitional	<u>Essential criteria:</u> Degenerating vitellogenic oocyte stage 4 in the presence of proliferating testicular tissue ^b , where spermatozoa have not yet proceeded to fill the dorsal sperm sinuses ^a and/or proliferation of testicular tissue in a female ovary that has gonadal characteristics of a mature resting female (see above). Spermatogenesis had progressed to at least the spermatid stage. <u>General descriptors:</u> Dorsal sperm sinuses are present in all transitionals. Thin bands of primary and secondary spermatocyte, spermatid and spermatozoa spermatocysts present and often closely associated with peripheries of gonad wall.

Table 6.3. Developmental stages of male common coral trout based on histological examination. Spent males may be incomplete or complete, although resting incomplete males cannot be distinguished from transitionals. Reproductive criteria were adapted from Moe (1969), Hastings (1981), Sadovy and Shapiro (1987), Shapiro *et al.* (1993), Burton *et al.* (1997), Adams (2003)^a and Adams (1996)^b.

Developmental stage	Histological description
Immature male ^a	Proliferation of spermatogenesis (primary and secondary spermatocytes spermatids and spermatozoa) in an immature female ovary (see table 1 for immature female), however spermatozoa have not yet reached the precursory dorsal sperm sinuses.
Mature ripe male (incomplete) ^{b,8}	Dorsal sperm sinus (DSS), formed and filled with spermatozoa, gonad dominated (>50%) by previtellogenic ovarian tissue. Atretic oocytes may be present. Males may be primary or secondary.
Mature ripe male (complete) ^f	Gonad dominated (<50%) by spermatogenetic tissue, central and dorsal sperm sinuses filled with spermatozoa, pre-vitellogenic oocytes may still be present, spermatogonia, spermatocytes and spermatids may be present. Males may be primary or secondary.
Spent	Spermatozoa rare and not in major sperm sinuses, testis disorganised and vascularised, well developed stromal tissue, major sperm sinuses collapsed, columnar epithelial lining of major sperm sinuses prominent, brown bodies common.
Resting male (pre-or post-spawning)	Differs from Spent males in that the testis has minimal vascularisation and is compact, spermatozoa rare and not in major sperm sinuses, primary and secondary spermatocytes dominate.

⁸ The terms 'incomplete' and 'complete' are strictly descriptive morphological terms (i.e. non-functional) that refer to the proportion of the testis still containing previtellogenic oocytes. This allows hypotheses to be made as to the proximity of the male to sex differentiation and/or change (Adams 2003).

Table 6.4. Developmental stages of bisexual common coral trout gonads based on histological examination. Reproductive criteria were adapted from Moe (1969), Hastings (1981), Sadovy and Shapiro (1987), Shapiro *et al.* (1993), Burton *et al.* (1997), Sadovy and Colin (1995)^a and Fennessy and Sadovy (2002)^b.

Developmental stage	Histological description
^{a,b} Immature bisexual (describes presence of germ cells only, non functional)	Gonad was characterised as an immature female ovary (as above) yet spermatocysts of primary and secondary spermatocytes present ^a . Neither germ cell showed any sign of degeneration or proliferation ^a (unlike transitionals and immature males).
^{a,b} Mature, ripe bisexual (directional development uncertain)	Gonad had shared features of mature ripe females and ripe males. Ovary was in active vitellogenesis where yolk globule and/or migratory nucleolus stage oocytes were the most advanced oocyte present and showed no sign of degeneration. Proliferating spermatocysts lined the gonad peripheries to the centre of the gonadal lobes although spermatozoa were not present in the dorsal sperm sinus.
Mature female, ripe bisexual	Gonads had shared features of mature ripe bisexual where by sperm was proliferated in the presence of active vitellogenesis yet oogenesis had progressed to the point where hydrated eggs were present, spermatocysts of all sperm stages line the gonad peripheries to the centre of the gonadal lobes. However, spermatozoa were not present in the dorsal sperm sinus.
Mature male, ripe bisexual	Gonad had shared features of mature ripe bisexual whereby sperm was proliferating in the presence of active vitellogenesis (yolk globule and/or migratory nucleolus stage most advance oocyte present) yet spermatogenesis had progressed to the point where spermatozoa are present in the dorsal sperm sinuses. Spermatocysts of all stages line the gonad peripheries to the centre of the gonadal lobes although spermatozoa were not present in the dorsal sperm sinuses.
Mature, running ripe bisexual	Hydrated oocytes were present, sometimes in the lumen, along-side active spermatogenesis. Well-developed sperm sinuses were filled with spermatozoa.

Spawning season

It was not possible to estimate the spawning season for coral trout from samples collected through the ELF Experiment, as ELF catch surveys did not sample in all months of the year. The spawning season for coral trout was estimated from monthly samples collected from a group of mid-shelf reefs north of Townsville in the Central

Section of the GBR (see Chapter 2 for details). A spatial comparison of the spawning season was not possible as monthly samples were collected from only one location.

A gonosomatic index (GSI: gonad weight / whole body weight x 100) was calculated for each individual fish, which provided a relative measure of reproductive stage. Mean monthly GSI values for mature fish were plotted separately for males and females to determine the peak spawning period for coral trout. The proportion of samples in each mature female and male reproductive stage in each month were also plotted to examine the ovarian and testicular development patterns throughout the year, and the degree of spawning activity occurring in each month.

Size and age at maturity

There were insufficient immature females collected in any region to estimate size and age at maturity for coral trout by fitting a logistic function to the proportion of mature females in each size and age class. Estimates of the size and age at maturity for coral trout were inferred from examination of the size and age range of immature females.

Size and age at sex change

Size and age at sex change for coral trout were estimated by fitting a logistic function to the proportion of mature females in each size and age class for each region using equation 3.3 (Chapter 3). Data were pooled across years to increase sample sizes for each reef. Likelihood ratio tests (Haddon 2001) were used to test for differences in the size and age at sex change among regions. The presence or absence of transitional and bisexual individuals in each size and age class also provided an estimate of the size and age range over which sex change occurs.

Sex ratio

The sex assigned from histology was used to calculate the operational sex ratios (mature female/male) for each reef within each region. An average sex ratio was calculated for MacGillivray reef in 1996 (when no sampling occurred on this reef) by averaging the sex ratio across all years and both reefs in the Lizard Island region. Sex ratios were compared among regions and years using a two-factor repeated measures ANOVA with Region as the between-subject fixed factor, Year as the within-subject fixed factor, and reef-specific sex ratios as replicates. Data were square root transformed to satisfy the assumptions of ANOVA.

6.3 Results

Spawning season

Average GSI for females was significantly higher than for males in all months sampled in each year (Figure 6.1). Although data were missing for several months in each year, mean monthly GSI values for mature females were highest in September and October in 1998 and 2000 and October and November in 1999 (Figure 6.1). The mean monthly GSI values for males followed a very similar pattern to females, with higher mean GSI values in September and October in 1998 and 2000 and October and November in 1999 (Figure 6.1). It was not possible to verify whether spawning commenced before September in 1998 or after October in 2000, as no samples were collected in these months.

The monthly trend in the frequency of mature ovarian stages suggested a similar, but slightly extended, temporal pattern in spawning activity to the monthly GSI values (Figure 6.2).

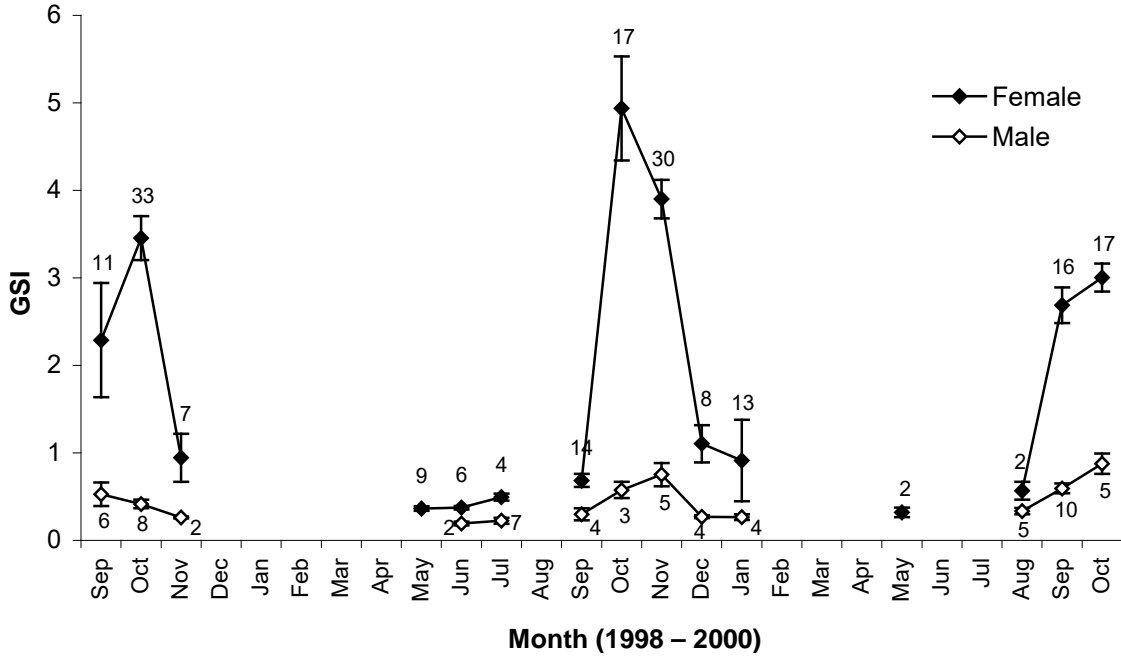


Figure 6.1. Mean monthly gonosomatic index (GSI) values for mature female and male common coral trout from the Central Section of the Great Barrier Reef. Error bars are standard errors. Sample sizes are indicated above (females) and below (males) data points for each month.

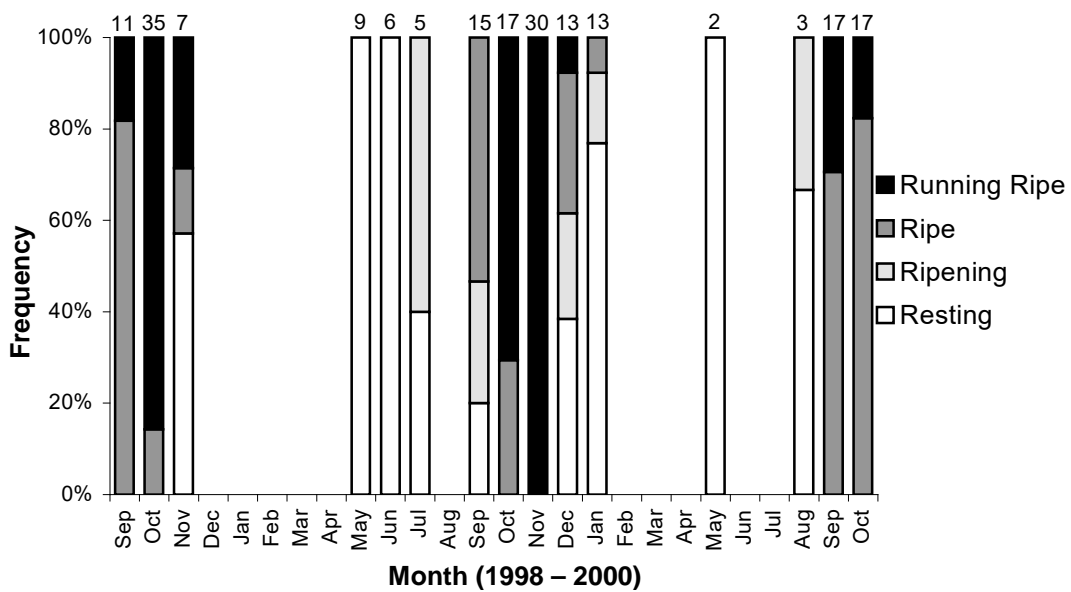


Figure 6.2. Monthly frequencies of mature ovarian stages of coral trout from the Central Section of the Great Barrier Reef. Stage descriptions are provided in Table 6.2.

Running ripe females were present between September and November in 1998, September and October in 2000 and between October and December in 1999 (Figure 6.2). Similar to the GSI data, it was not possible to verify whether spawning females were present before September or after November in 1998 or after October in 2000, as no samples were collected in these months. From the available GSI and ovarian stage data, however, it appears that the majority of spawning activity for coral trout occurs between September and December in the Central Section of the GBR.

Size and age at maturity

A small number of immature females were present in each region (Figure 6.3 and 6.4). It was not possible to estimate the size or age at which 50% of the population were mature for any region, as there was no size or age class where more than 50% of females were immature, except where the sample size was one (Figure 6.3 and 6.4).

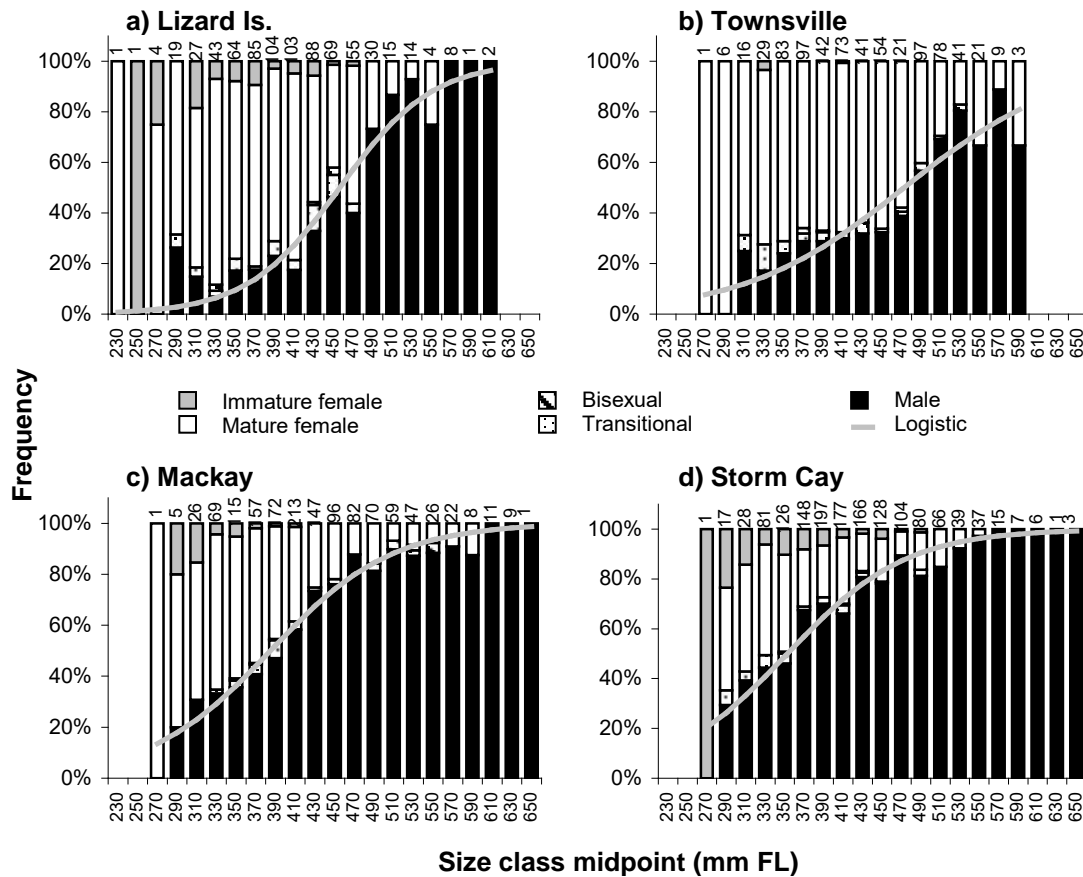


Figure 6.3. Proportion of male, transitional, bisexual and mature and immature female common coral trout in each size class and estimated logistic function fitted to the proportion of males (relative to females) in Lizard Is. (a), Townsville (b), Mackay (c) and Storm Cay (d) regions of the Great Barrier Reef. Sample sizes for each size class are shown above each bar. Data were pooled across two reefs within each region and across years (1995-2000). Parameters of the logistic function are given in Table 6.6.

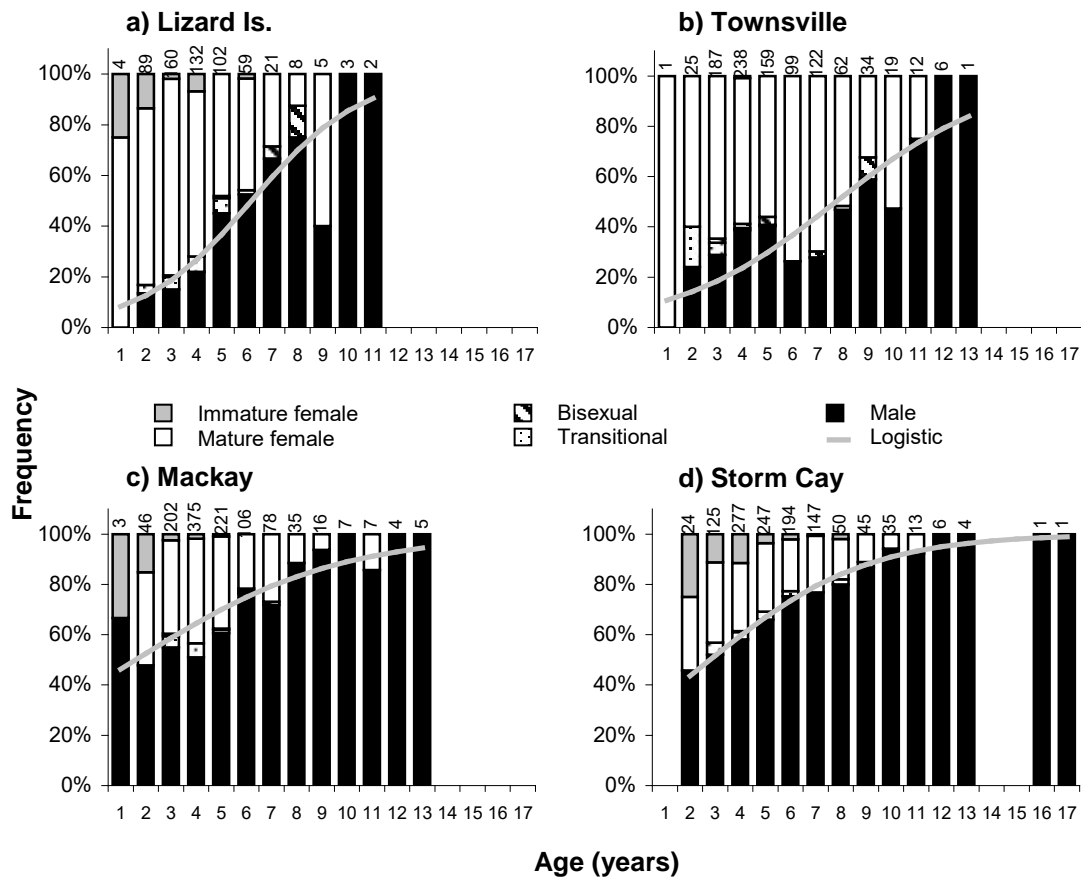


Figure 6.4. Proportion of male, transitional, bisexual and mature and immature female common coral trout in each age class and estimated logistic function fitted to the proportion of males (relative to females) in Lizard Is. (a), Townsville (b), Mackay (c) and Storm Cay (d) regions of the Great Barrier Reef. Sample sizes for each size class are shown above each bar. Data were pooled across two reefs within each region and across years (1995-2000). Parameters of the logistic function are given in Table 6.6.

Across all regions, the size and age of immature females ranged widely from 250-490 mm FL and 1-8 years respectively (Figure 6.3 and 6.4). There were substantially fewer immature females in the Townsville region (0.2%) than in any other region (Lizard Is 4.4%, Mackay 2.0% and Storm Cay 5.7%). Furthermore, mature females did not appear in the Townsville region until 330 mm FL and four years of age, which was substantially larger and older than for the other three regions (Figure 6.3 and 6.4). Across all regions, mature females were present in the smallest size class (230 mm FL) and age class (1 year) (Figure 6.3 and 6.4).

Size and age at sex change

There was a large overlap in the size distributions of males and females in all regions, although females dominated the smaller size classes and males dominated the larger size classes (Figure 6.3). Likelihood ratio tests indicated that the pattern in the size at sex change differed significantly among all four regions and between all region pairs (Table 6.5). Pairwise comparisons between regions indicated that the size at which 50% of the population were male (s_{50}) differed significantly between all region pairs ($p < 0.001$), except between the Lizard Island and Townsville regions. The size at which 95% of the population were male (s_{95}) differed significantly

between the Townsville region and all other regions ($p < 0.001$), but did not differ significantly between any other region pairs.

Table 6.5 Results of likelihood ratio tests comparing logistic functions of the proportion of male common coral trout in each size and age class among four regions of the Great Barrier Reef. χ^2 = likelihood ratio chi-square statistic. Each comparison tests the hypothesis that the logistic parameters s_{50} and s_{95} (size or age at which 50% and 95% of the population are male, respectively) are the same for each function being compared.

	Size range (mm)	Age range (years)	Comparison	df	χ^2	p
Size at sex change	270-590		All regions	6	88.69	<0.001
	270-590		Lizard Is vs Townsville	2	8.37	0.02
	270-610		Lizard Is vs Mackay	2	34.10	<0.001
	270-610		Lizard Is vs Storm Cay	2	47.43	<0.001
	270-590		Townsville vs Mackay	2	40.55	<0.001
	270-590		Townsville vs Storm Cay	2	51.59	<0.001
	270-650		Mackay vs Storm Cay	2	15.01	<0.001
Age at sex change		2-11	All regions	6	51.70	<0.001
		1-11	Lizard Is vs Townsville	2	7.28	0.03
		1-11	Lizard Is vs Mackay	2	19.19	<0.001
		2-11	Lizard Is vs Storm Cay	2	16.29	<0.001
		1-13	Townsville vs Mackay	2	28.09	<0.001
		2-13	Townsville vs Storm Cay	2	28.33	<0.001
		2-13	Mackay vs Storm Cay	2	0.16	0.92

Generally, the size at which 50% of the population are male was between 70 and 120 mm greater in the two northern regions (Lizard Island and Townsville) compared with the two southern regions (Mackay and Storm Cay) (Figure 6.3, Table 6.6). Although significant, the difference in the size at 50% sex change between the Mackay and Storm Cay regions was only around 30 mm (Figure 6.3, Table 6.6). There were a greater proportion of females in some larger size classes in the Townsville region compared with the other three regions (Figure 6.3), which resulted in a substantially higher estimate of s_{95} for the Townsville region (Table 6.6).

Similar to the size distributions, there was a large overlap in the age distributions of males and females in all regions (Figure 6.4). Females dominated the younger age classes up to 6 years of age in the Lizard Island region and up to at least 9 years of age in the Townsville region (Figure 6.4). In contrast, males dominated all age classes except for 2 year olds in the Mackay and Storm Cay regions (Figure 6.4). Likelihood ratio tests indicated that the pattern in the age at sex change differed significantly among all four regions and between all region pairs except between the Mackay and Storm Cay region (Table 6.5). Pairwise comparisons between regions indicated that the age at which 50% of the population were male (s_{50}) differed significantly between all region pairs ($p < 0.001$), except between the Lizard Island and Townsville regions and the Mackay and Storm Cay regions. The age at which

95% of the population were male (s_{95}) differed significantly between the Townsville and Lizard Island regions and between the Townsville and Storm Cay regions ($p < 0.001$), but did not differ significantly between any other region pairs.

Generally, the age at which 50% of the population are male was between 3 and 6 years older in the two northern regions (Lizard Island and Townsville) compared with the two southern regions (Mackay and Storm Cay) (Figure 6.4, Table 6.6). The greater proportion of females in some older age classes in the Townsville region compared with the other three regions (Figure 6.3) resulted in a substantially higher estimate of s_{95} for the Townsville region (Table 6.6).

Table 6.6. Parameters of age- and size-specific sex change for common coral trout from four regions of the Great Barrier Reef. s_{50} and s_{95} are the length or age at which 50% and 95% of the population are males, respectively.

Region	Size-specific sex change			Age-specific sex change		
	s_{50}	s_{95}	R^2	s_{50}	s_{95}	R^2
Lizard Island	456 mm	595 mm	0.94	6.17 y	12.51	0.82
Townsville	473 mm	713 mm	0.89	7.73 y	17.10 y	0.80
Mackay	385 mm	567 mm	0.97	1.60 y	13.43 y	0.76
Storm Cay	353 mm	532 mm	0.94	2.80 y	12.00 y	0.98

Sex ratio

The sex ratios of coral trout varied significantly among regions consistently across years (Region main effect – $F_{3,4} = 14.26$, $p = 0.01$). The sex ratio was significantly more female biased in the Lizard Island and Townsville regions than in the Mackay and Storm Cay regions ($p < 0.05$, Figure 6.5). Furthermore, the sex ratio of coral trout was consistently female biased in the Lizard Island and Townsville regions and consistently male biased in the Mackay and Storm cay regions over the six years from 1995 to 1999 (Figure 6.5).

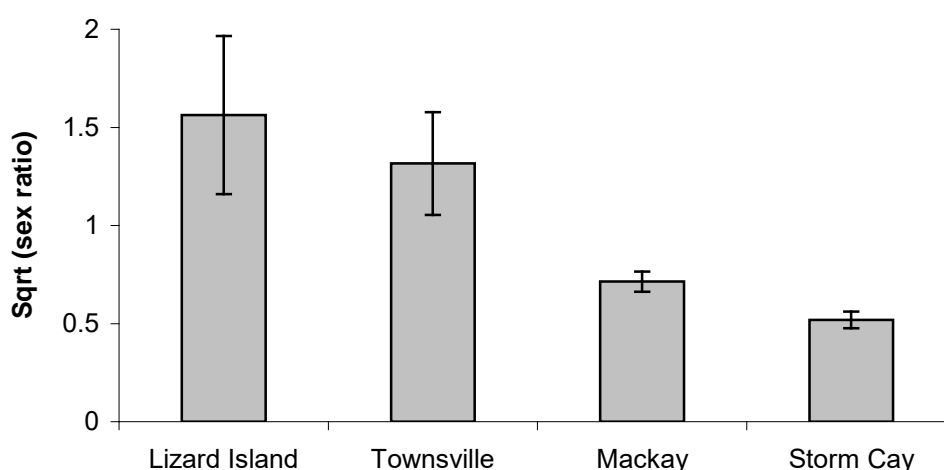


Figure 6.5. Sex ratios (female/male) of coral trout from four regions of the Great Barrier Reef. Data were pooled across two reefs within each region and over six years (1995 – 2000). Error bars are standard errors.

6.4 Discussion

This study has demonstrated that the reproductive biology of coral trout varies significantly and substantially among regions of the Great Barrier Reef, confirming the preliminary finding of Adams *et al.* (2000) and extending this to include two additional regions (Lizard Island and Mackay) of the GBR. Estimates of the size and age at sex change and sex ratios of coral trout in the two northern regions (Lizard Island and Townsville) differed substantially and consistently from estimates for the two southern regions (Mackay and Storm Cay). Populations of coral trout in the two northern regions changed sex at a significantly larger size and older age than populations in the two southern regions. Consequently, sex ratios were more female biased in the northern regions than in the southern regions. Furthermore, sex ratios were significantly female biased in the two northern regions and significantly male biased in the two southern regions.

The spawning season and size and age at maturity were not able to be estimated for any of the four regions sampled by the ELF catch surveys, due to the selectivity of the sampling gear and frequency of sampling. From additional samples, however, the spawning season was estimated to occur between September and December on a group of reefs within 80km of the Townsville region. Ferreira (1995) reported spawning of coral trout during the same months on reefs in the Lizard Island and Townsville regions in the early 1990's, suggesting the spawning season of coral trout may be temporally and spatially consistent between these two regions. The size and age at which 50% of coral trout reach maturity could not be estimated directly, but the low proportion of immature females in the smallest size classes and youngest age classes suggest that coral trout may, on average, mature at less than 250 mm FL and 1 year of age. Adams (1996) estimated, although not statistically, that coral trout mature at approximately 270 mm FL and 2 years of age in the Townsville and Storm Cay regions from a sample of smaller individuals collected by spearfishing in 1995 (Welch 2001). It will be necessary to analyse statistically a sample of smaller and younger coral trout from different regions of the GBR to accurately estimate regional patterns in the size and age at maturity.

Similar to red throat emperor (Chapter 3), the significant regional variation in reproductive parameters of coral trout suggests that there are likely to be substantial differences in productivity and dynamics among the four regions. Reproductive output may be significantly greater in the northern regions where there is a high proportion of females, compared with the southern regions where the proportion of females is lower. Furthermore, recent research on other species has demonstrated that larger and older females, which for coral trout are more prevalent in the northern regions, produce larvae with significantly greater rates of growth and survival (Berkeley *et al.* 2004, Palumbi 2004). Counteracting this potential for increased production in the northern regions is the significant regional variation in abundance of coral trout on the GBR. Mapstone *et al.* (2004) found that the abundance of coral trout was up to 3 times higher in the southern regions compared with the northern regions. Quantifying the reproductive output of coral trout in each region of the GBR will help elucidate regional patterns in productivity of coral trout on the GBR.

Adams (2003) demonstrated that the sexual pattern in common coral trout is diandric protogynous hermaphroditism, whereby males are derived directly from immature females as well as through sex change from mature females. This diandric sexual pattern may explain, in part, the strong regional pattern in size and age at sex change and the unusual occurrence of male biased sex ratios in the Mackay and Storm Cay populations. Diandric protogynous hermaphrodites have the potential to form male biased sex ratios during the spawning season as primary males group or

sneak spawn with females (1 female with many males or 1 pair with sneaker males) (Warner 1995). We hypothesise that populations of coral trout in the southern regions of the GBR may utilise this reproductive strategy to a greater extent than populations in the northern regions, resulting in significantly more smaller and younger males in the southern regions. Further work is necessary, however, on the fine scale variation in testis characteristics of coral trout throughout the spawning season to test this hypothesis.

This project also identified the presence of mature, ripe bisexual individuals, which suggests that sex change in coral trout may be extremely rapid, and individuals may be able to function as both male and female within one spawning season. Further work is necessary on the gonoduct structure of the mature bisexual individuals determine the functional sex of running ripe bisexual individuals.

In addition to providing statistical comparisons of reproductive parameters among regions of the GBR, this project has highlighted the extreme flexibility in reproductive biology of coral trout, and substantially extended the existing knowledge of the general biology of coral trout on the GBR. This project has expanded the preliminary work by Adams *et al.* (2000) by providing quantitative estimates of the size and age at sex change in coral trout populations, and extending estimates of reproductive parameters to include other regions of the GBR.

Conclusion

Through this project we have attempted to address a number of high priority research needs identified by fisheries and conservation managers and stakeholders in the Great Barrier Reef region. We have done this effectively by building on the focus and operational support available through the ELF Experiment and collaborations among research, industry and management partners in the CRC Reef. In short, we addressed four significant questions in this report.

The first and second questions focussed on red throat emperor. Firstly, are the strong regional patterns in age, growth and mortality of red throat emperor identified by Williams et al. (2002) consistent over years, and secondly, are these differences most likely to be the result reproductively isolated stocks or other factors operating in each region? We have clearly demonstrated (Chapter 3) that these differences have been consistent between 1995 and 2000 and as such are likely to reflect real differences in current population structure and productivity among regions of the GBR. The results of the stock structure component of the project strongly suggest that red throat emperor form a single panmictic stock on the GBR, and that the differences are most likely due to environmental differences or historical effects of fishing among regions. The quantitative description of these regional differences will inform the development and evaluation of stock assessment methods for red throat emperor currently underway. The results of this component of the study have also informed the parameterization of population dynamics model of red throat emperor in the related multi-species management strategy evaluation project. The use of the outcomes of this project in these two related exercises will provide for their direct translation into specific advice for the future management of red throat emperor on the GBR. Notwithstanding the outcomes of those exercises, the obvious conclusion from this project is that some form of regional harvest controls may be required in order to account for the regional differences in population parameters.

The third question related to general concern whether the harvest of Maori wrasse, barramundi cod and blue-spot coral trout was sustainable and the lack of information on their basic biology. Does the basic biology of these high profile species make them particularly vulnerable to overfishing? We have provided age-based estimates for the important population parameters and confirmed the protogynous reproductive strategy for each species. These results indicate each species is likely to be vulnerable to over fishing in multi-species fisheries in which the primary target species is many times more abundant. While the recently implemented prohibition of harvest of Maori Wrasse and barramundi cod is likely to provide the necessary protection for these species, the current arrangements for the blue-spot coral trout may need to be reviewed in light of these results, in particular whether historical and current regulations sufficiently protect the male component of the population.

The last question addressed the regional and seasonal variation in reproduction of the common coral trout (Chapter 5) and red throat emperor (Chapter 3). In both cases there was evidence of significant regional variation in the population sex structure, which further demonstrates the need to incorporate regional considerations in the assessment of sustainable catch limits and management of the harvest of the primary target species.

Benefits

The outcomes of this research will be of direct benefit to fisheries (Queensland Department of Primary Industries and Fisheries) and conservation (Great Barrier Reef Marine Park Authority) managers, the commercial, recreational and charter boat sectors of the reef line fishery and conservation NGOs concerned with the conservation of biodiversity on the GBR.

The information provided on the stock structure and regional variation in population parameters of red throat emperor (and reproductive strategies of coral trout) are currently being used in the development of multi-species management strategy evaluation models of coral trout and red throat emperor to evaluate alternative management strategies in a multi-species context and will also support the development of quantitative stock assessment models to estimate sustainable levels of harvest for red throat emperor (QFS).

We have also provided the first age-based parameter estimates for three high profile by catch/by product species in the fishery. This information will inform the assessment of the sustainability of harvest of blue spot coral trout and of levels of by-catch Maori wrasse and barramundi cod for strategic assessment under the EPBC Act. It will also inform the development of management approaches for these species in other jurisdictions (e.g. WA, SE Asia, Pacific Islands).

Further Development

There are a number of areas that this and related projects have highlighted for future work. These include:

- Plausible conceptual and quantitative models for the movement and spatial structure of red throat emperor on the GBR
- Spatial stock assessment models for red throat emperor to estimate long term sustainable yields
- Integrated tagging and monitoring studies of red throat emperor to provide estimates of rates of movement at a range of spatial scale relevant to the management of the fishery and closed areas.
- Identification of juvenile habitat for the red throat emperor
- Development and evaluation of monitoring, assessment and management strategies for data poor, multi-species fisheries
- Further theoretical and empirical research on the response of protogynous species to fishing.

References

- Adams, S. 1996. The effects of reef zoning and region on the sexual structure of *Plectropomus leopardus* populations on the Great Barrier Reef. Honours Thesis, Department of Marine Biology, James Cook University, Townsville.
- Adams, S.A. 2002. The reproductive biology of three species of *Plectropomus* (Serranidae) and responses to fishing. PhD Thesis, School of Marine Biology and Aquaculture, James Cook University, Townsville.
- Adams, S.A. 2003. Morphological ontogeny of the gonad of three plectropomid species through sex differentiation and transition. *J. Fish Biol.* 63: 22-36.
- Adams, S.A., Mapstone, B.D., Russ, G.R., and Davies C.R. 2000. Geographic variation in the sex ratio, sex specific size, and age structure of *Plectropomus leopardus* (Serranidae) between reefs open and closed to fishing on the Great Barrier Reef. *Can. J. Fish. Aquat. Sci.* 57: 1448-1458.
- Anon. 1997. Research needs and priorities for the management of Queensland's fisheries. Queensland Fisheries Management Authority.
- Ayling, A.M., and Ayling, A.L. 1992. Abundance, distribution and length frequencies of a group of large piscivorous fishes, *Plectropomus* spp. (Pisces: Serranidae) on the Great Barrier Reef. Unpublished report to GBRMPA.
- Ayre, D.J., and Hughes, T.P. 2000. Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution* 54: 1590-1605.
- Bean, K., Davies, C.D., Mapstone, B.D., Murchie, C.D., and Williams, A.J. 2003. Gonad development and evidence of protogyny in the red-throat emperor on the Great Barrier Reef. *J. Fish Biol.* 62: 299-310.
- Begg, G.A., Friedland, K.D., and Pearce, J. B. 1999. Stock identification and its role in stock assessment and fisheries management: an overview. *Fish. Res.* 43: 1-8.
- Beinssen, K. 1989. Heron Reef demersal reef fish movement study. Unpublished report to GBRMPA
- Benzie, J.A.H. 1994. Patterns of gene flow in the Great Barrier Reef and Coral Sea. In: Beaumont, A.R. (Ed) Genetics and evolution of aquatic organisms. pp 67-79. Chapman and Hall, London.
- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85: 1258-1264.
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. *Fish. Invest. Ser. II Mar. Fish. G.B. Minist. Agric. Fish. Food* 19, 533 pp.
- Brown, I.W., Doherty, P., Ferreira, B., Keenan, C., McPherson, G., Russ, G., Samoilys, M., and Sumpton, W. 1994. Growth, reproduction and recruitment of Great Barrier Reef food fish stocks. Fisheries Research and Development Corporation Final Report. Project no. 90/18.
- Burg, T.M., Trites, A.W. and Smith, M.J. 1999 Mitochondrial and microsatellite DNA analyses of harbour seal population structure in the northeast Pacific Ocean. *Can. J. Zool.* 77: 930-943.
- Burton, M.P.M. 1994. A critical period for nutritional control of early gametogenesis in female winter flounder, *Pleuronectes americanus* (Pisces: Teleostei). *J. Zool.* 233: 405-415.
- Burton, M.P.M., Penney, R.M., and Biddiscombe, S. 1997. Time course of gametogenesis in Northwest Atlantic Cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* 54: 122-131.
- Cappo, M., Eden, P., Newman, S.J., and Robertson, S. 2000. A new approach to validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. *Fish. Bull.* 98: 474-488.

- Cerrato, R.M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47:1416-1426.
- Chauvet, C. 1991. Statut d'Epinephelus guaza (Linnaeus, 1758) et elements de dynamique des populations méditerranéen et atlantique. In: Boudouresque, C. F., Avon, M., Gravez, V. (eds) Les Espèces Marines à Protéger en Méditerranéen (GIS Posidonie: France), p 255-275.
- Choat, J.H., and Clements, K.D. 1992. Diet in odacid and aplodactylid fishes from Australia and New Zealand. *Aust. J. Mar. Freshwat. Res.* 43: 1451-1459.
- Choat, J.H., Axe, L.M., and Lou, D.C. 1996. Growth and longevity in fishes of the family Scaridae. *Mar. Ecol. Prog. Ser.* 145: 33-41.
- Choat, J.H., and Robertson, D.R. 2002. Age-based studies. In: Sale, P. F. (Ed) Coral reef fishes. Dynamics and diversity in a complex ecosystem. Academic Press, London, pp 57-80.
- Choat, J.H., Robertson, D.R., Ackerman, J., and Posada, J. 2003. An age-based demographic analysis of the Caribbean stoplight parrotfish *Sparisoma viride*. *Mar. Ecol. Prog. Ser.* 246: 265-277.
- Choat, J.H., Davies, C.R., Ackerman, J., and Mapstone, B.D. In review. Demography of a large teleost, *Chelinus undulatus* with a review of size distribution in labrid fishes. Submitted to *Mar. Ecol. Prog. Ser.*
- Clements, K.D., Alfaro, M.E., Fessler, J., and Westneat, M.W. 2004. Relationships of the temperate Australasian labrid fish tribe Odacini (Perciformes; Teleostei) *Mol. Phyl. Evol.* 32: 575-587.
- Cooper, R.A. 1967. Age and growth of the tautog, *Tautoga onitis* (Linnaeus) from Rhode Island. *Trans. Am. Fish. Soc.* 96: 134-142.
- Cornish, A. 2004. *Cheilinus undulatus*. In: IUCN 2004. 2004 IUCN Red List of Threatened Species. www.redlist.org.
- Craig, P.C. 1999. The von Bertalanffy growth curve: When a good fit is not good enough. *The ICLARM Quarterly.* 22: 28-29.
- Davies, C.R. 1995. Patterns of movement of three species of coral reef fish on the Great Barrier Reef. PhD Thesis, Department of Marine Biology, James Cook University, Townsville.
- Davies, C.R. 2000. Inter-reef movement of the common coral trout, *Plectropomus leopardus*. A report to the Great Barrier Reef Marine Park Authority. Research publication No. 61, 50 pp.
- Davies, C.R., Mapstone, B.D., Ayling, A., Lou, D.C., Punt, A., Russ, G.R., Samoily, M.A., Smith, A.D.M., Welch, D.J., and Williams, D.McB. 1998. Effects of line fishing experiment 1995-1997: Project structure and operations. Supplementary to progress report. CRC Reef Research Centre, Townsville, Australia, 28 pp.
- Doherty, P.J. 1991. Spatial and temporal patterns of recruitment. In: Sale P.F. (ed) *The ecology of fishes on coral reefs*. pp. 261-293. Academic Press, San Diego.
- Doherty, P.J. 2002. Variable replenishment and the dynamics of reef fish. In: Sale, P. F. (ed) Coral reef fishes. Dynamics and diversity in a complex ecosystem. Academic Press, London, p 327-355.
- Doherty, P., and Fowler, T. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science* 263: 935-939.
- Doherty, P.J., Planes, S., and Mather, P. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier Reef. *Ecology* 76: 2373-2391.
- Donaldson, T.J. and Sadovy, Y. 2001. Threatened fishes of the world: *Cheilinus undulatus* Rüppell, 1835 (Labridae). *Env. Biol. Fish.* 62: 428.
- Draper, N.R., and Smith, H. 1966. Applied regression analysis. Wiley and Sons, New York.

- Driml, S.M. 1997. Dollar values and trends of major direct uses of the Great Barrier Reef Marine Park. Research Publication No. 56. Great Barrier Reef Marine Park Authority, Townsville.
- Dudgeon, C.L., Gust, N., and Blair, D. 2000. No apparent genetic basis to demographic differences in scarid fishes across continental shelf of the Great Barrier Reef. *Mar. Biol.* 137: 1059-1066.
- Dulvy, N.K., Sadovy, Y., and Reynolds, J.D. 2003. Extinction vulnerability in marine populations. *Fish and Fisheries* 4: 25-64.
- Excoffier, L., Smouse, P., and Quattro, J. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction sites. *Genetics* 131: 479-491.
- Fennessy, S. and Sadovy, Y. 2002. Reproductive biology of a diandric protogynous hermaphrodite, the serranid *Epinephelus andersoni*. *Mar. Freshwater Res.* 53: 147-158.
- Ferreira, B.P. 1995. Reproduction in the common coral trout *Plectropomus leopardus* from the central and northern Great Barrier Reef. *Bull. Mar. Sci.* 56, 653-669.
- Ferreira, B.P., and Russ, G.R. 1992. Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the central Great Barrier Reef, Australia. *Aust. J. Mar. Freshw. Res.* 43: 1301-1312.
- Ferreira, B.P., and Russ, G.R. 1994. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus*, (Lacepede, 1802) from Lizard Island, Northern Great Barrier Reef. *Fish. Bull.* 92: 46-57.
- Fisher, R., and Bellwood, D.R. 2002. The influence of swimming speed on sustained swimming performance of late-stage reef fish larvae. *Mar. Biol.* 140: 801-807.
- Fisher, R., Bellwood, D.R., and Job, S.D. 2000. Development of swimming abilities in reef fish larvae. *Mar. Ecol. Prog. Ser.* 202: 163-173.
- Gordoa, A., Moli, B., and Raventos, N. 2000. Growth performance of four wrasse species on the north-western Mediterranean coast. *Fish. Res.* 45: 43-50.
- Green, B, Troy, S., and Mapstone, B.D. In prep. A description of the Great Barrier Reef charter fishery. CRC technical Report.
- Haddon, M. 2001. Modelling and quantitative methods in fisheries. Chapman and Hall. London, 406 pp.
- Hart, A.M., and Russ, G.R. 1996. Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus*. *Mar. Ecol. Prog. Ser.* 136: 25-35.
- Hastings, P. A. 1981. Gonad morphology and sex succession in the protogynous hermaphrodite *Hemianthias vivianus* (Jordan and Swain). *J. Fish Biol.* 18, 443-454.
- Higgs, J. 1999. Experimental recreational catch estimates for Queensland residents. Results from the 1997 diary round. RFISH technical report no. 2. Queensland Fisheries Service, Australia.
- Higgs, J. 2001. Recreational catch estimates for Queensland residents. Results from the 1999 diary round. RFISH technical report no. 3. Queensland Fisheries Service, Australia.
- Hostetter, E.B., and Munroe, T.A. 1993. Age, growth, and reproduction of tautog *Tautoga onitis* (Labridae: Perciformes) from coastal waters of Virginia. *Fish. Bull.* 91: 45-64.
- James, M.K., Armsworth, P.R., Mason, L.B., and Bode, L. 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proc. R. Soc. Lond., Ser. B: Biol. Sci* 269: 2079-2086.

- Jennings, S., Reynolds, J.D., and Polunin, V.C. 1999. Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conservation Biology* 13: 1466-1475.
- Johannes, R.E., and Riepen, M. 1995. Environmental, economic, and social implications of the live reef fish trade in Asia and the western Pacific. Report to the South Pacific Commission and the Nature Conservancy. 81 p.
- Kimura, D.K. 1980. Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* 77: 765-776.
- KPMG Consulting 2000. Economic and financial values of the Great Barrier Reef Marine Park. Research Publication No. 63. Great Barrier Reef Marine Park Authority, Townsville.
- Kritzer, J.P. 2001. Patterns of spatial variation in the population biology of a coral reef fish and implications for metapopulation dynamics. PhD Thesis, School of Marine Biology and Aquaculture, James Cook University, Townsville.
- Kritzer, J.P. 2002. Variation in the population biology of stripey bass *Lutjanus carponotatus* within and between two island groups on the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 243: 191-207.
- Kritzer, J.P. 2004. Sex-specific growth and mortality, spawning season, and female maturation of the stripey bass (*Lutjanus carponotatus*) on the Great Barrier Reef. *Fish. Bull.* 102: 94-107.
- Kritzer, J.P., Davies, C.R. 2005. Demographic variation within spatially structured reef fish populations: when are larger-bodied subpopulations more important? *Ecological Modelling* 182: 49-65.
- Kritzer, J.P., Davies, C.R., and Mapstone, B.D. 2001. Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. *Can. J. Fish. Aquat. Sci.* 58:1557-1568.
- Kyle, C.J., and Boulding, E.G. 2000. Comparative population genetic structure of marine gastropods (*Littorina* spp.) with and without pelagic larval dispersal. *Mar. Biol.* 137: 835-845.
- Lau, P.F. and Parry-Jones, R. 1999. The Hong Kong trade in live reef fish for food. TRAFFIC East Asia and World Wide Fund for Nature, Hong Kong.
- Lee, C., and Sadovy, Y. 1998. A taste for live fish: Hong Kong's live reef fish market. *Naga, ICLARM* 21(2): 38-42.
- Leis, J.M., and Carson-Ewart, B.M. 1999. In situ swimming and settlement behaviour of larvae of an Indo-Pacific coral-reef fish, the coral trout *Plectropomus leopardus* (Pisces: Serranidae). *Mar. Biol.* 134: 51-64.
- Lou, D.C., Mapstone, B.D., Russ, G.R., Davies, C.R., and Begg, G.A. 2005. Using otolith weight–age relationships to predict age-based metrics of coral reef fish populations at different spatial scales. *Fish. Res.* 71: 279-294.
- Mapstone, B.D., McKinlay, J.P., and Davies, C.R. 1996a. A description of the commercial reef line fishery logbook data held by the Queensland Fisheries Management Authority. Report to the Queensland Fisheries Management Authority. 480pp.
- Mapstone, B.D., McKinlay, J.P., and Davies, C.R. 1996b. Summary report on A description of the commercial reef line fishery logbook data held by the Queensland Fisheries Management Authority. Report to the Queensland Fisheries Management Authority. 36pp.
- Mapstone, B.D., McKinlay, J.P., and Davies, C.R. 1996c. A description of the commercial reef line logbook data held by the Queensland Fisheries Management Authority: Description of the fishery. pp54-61 in Queensland Fisheries Management Authority. 1996. The Queensland tropical coral reef fin fish fishery – Discussion Paper No. 2. Queensland Fisheries Management Authority. 68pp.

- Mapstone, B.D., Davies, C.R., and Robertson, J.W. 1997. The effects of line fishing on the Great Barrier Reef: available evidence and future directions. Proceedings of the Great Barrier Reef science, use and management conference. Vol 1, pp178-192.
- Mapstone, B.D., Davies, C.R., Lou, D.C., Punt, A.E., Russ, G.R., Ryan, D.A.J., Smith, A.D.M., Williams, D.McB. 1998a. Effects of line fishing experiment 1995-1997: progress report. CRC Reef Research Centre, 86 pp.
- Mapstone, B.D., A.M. Ayling and J.H. Choat. 1998b. Habitat, cross shelf, and regional patterns in the distributions and abundances of some coral reef organisms on the northern Great Barrier Reef, with comment on the implications for future monitoring. Research Publication No. 48. Great Barrier Reef Marine Park Authority. Townsville. 71pp.
- Mapstone, B.D., Davies, C.R., Slade, S., Jones, A., Kane, K.J. and Williams, A.J. 2001. Effects of live fish trading and targeting spawning aggregations on fleet dynamics, catch characteristics and resource exploitation by the Queensland commercial demersal reef line fishery. Fisheries Research and Development Corporation Project no. 96/138. CRC Reef Research Centre, Townsville, Australia.
- Mapstone, B.D., Davies, C.R., Little, L.R., Punt, A.E., Smith, A.D.M., Pantus, F., Lou, D.C., Williams, A.J., Jones, A., Ayling, A.M., Russ, G.R., and MacDonald, A.D. 2004. The effects of line fishing on the Great Barrier Reef and evaluations of alternative potential management strategies. CRC Reef Research Centre Technical No. 52. CRC Reef Research Centre, Townsville, Australia.
- Meekan, M.G., Ackerman, J.L., and Wellington, G.M. 2001. Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Mar. Ecol. Prog. Ser.* 212: 223-232.
- Milliken, G.A., Johnson, D.E. 2001. Analysis of messy data, volume III: Analysis of covariance. Chapman and Hall/CRC Press, New York, 624 pp.
- Moe, M.A. Jr. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. *Fla. Dep. Nat. Resour. Mar. Lab. Prof. Ser.* 10:1-95.
- Mosse, J.W. 2001. Population biology of *Cephalopholis cyanostigma* (Serranidae) on the Great Barrier Reef. PhD Thesis, School of Marine Biology and Aquaculture, James Cook University, Townsville.
- Mosse, J.W. and Davies, C.R. In review. The extended life of a small serranid, the blue-spotted rockcod, *Cephalopholis cyanostigma*, from the Palm Islands, on the central Great Barrier Reef. Fisheries Bulletin.
- Mumby P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., Wabnitz, C.C., and Llewellyn, G. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427: 533-536.
- Munro, J.L., and Williams, D.McB. 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. Proceedings of the fifth international coral reef congress, Tahiti. Vol. 4: Symposia and Seminars (B) - Seminar C, p 545-578.
- Newman, S.J., and Williams, D.McB. 1996. Variation in reef associated assemblages of the Lutjanidae and Lethrinidae at different distances offshore in the central Great Barrier Reef. *Env. Biol. Fish.* 46: 123-138.
- Newman, S.J., Williams, D.McB., and Russ, G.R. 1996. Age validation, growth and mortality rates of the tropical snappers (Pisces: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef. *Aust. J. Mar. Freshw. Res.* 47: 575-584.
- Newman, S.J., Cappo, M., and Williams, D.McB. 2000a. Age, growth, mortality rates and corresponding yield estimates using otoliths of the tropical red snappers, *Lutjanus erythropterus*, *L. malabaricus* and *L. sebae*, from the central Great Barrier Reef. *Fish. Res.* 48: 1-14.

- Newman, S.J., Cappo, M., and Williams, D.McB. 2000b. Age, growth and mortality of the stripey, *Lutjanus carponotatus* (Richardson) and the brown-stripe snapper, *L. vitta* (Quoy and Gaimard) from the central Great Barrier Reef, Australia. *Fish. Res.* 48: 263-275.
- O'Connell, M. and Wright, J.M. 1997. Microsatellite DNA in fishes. *Rev. Fish Biol.* 7: 331-363.
- Palumbi, S.R. 2004. Fisheries Science: Why mothers matter. *Nature* 430: 621-622.
- Parenti, P., and Randall, J.E. 2000. an annotated checklist of the species of the labroid fish families Labridae and Scaridae. *Ichthyol. Bull.* 68: 1-97.
- Pollock, B.R. 1984. Relations between migration, reproduction and nutrition in yellowfin bream *Acanthopagrus australis*. *Mar. Ecol. Prog. Ser.* 19: 17-23.
- Pritchard, J.K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.
- Punt, A.E., Smith, A.D.M., Davidson, A.J., Mapstone, B.D. and C.R. Davies. (2001). Evaluating the scientific benefits of spatially explicit experimental manipulations of common coral trout, *Plectropomus leopardus*, populations on the Great Barrier Reef, Australia. p. 67-103. In: G.H. Kruse, N. Bez, A. Booth, M.W. Dorn, S. Hills, R.N. Lipcius, D. Pelletier, C. Roy, S.J. Smith and D. Withrell [Ed.]. University of Alaska Sea Grant, AK-SG-01-02, Fairbanks
- QFS 2003. Fisheries (Coral reef fin fish) Management Plan 2003. Queensland Fisheries Service, Queensland Government, Australia.
- Randall, J.E., Head, S.M., and Sanders, A.P.L. 1978. Food habits of the giant humphead wrasse, *Cheilinus undulatus* (Labridae). *Env. Biol. Fish.* 3:235-238.
- Randall, J.E., Allen, G.R., and Steene, R.C. 1997. Fishes of the Great Barrier Reef and Coral Sea, 2nd Ed. Crawford House Press, Australia.
- Raymond, M., and Rousset, F. 1995. Genepop ver 3.1. Montpellier: Institut des Sciences de l'Evolution, Université de Montpellier.
- Rice, W.R. 1989. Analysing tables of statistical tests. *Evolution* 43: 223-225.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191: 382 pp.
- Roberts, C.M., and Hawkins, J.P. 1999. Extinction risk in the sea. *TREE* 14: 241- 246.
- Russ, G.R., Lou, D.C., Higgs, J.B., and Ferreira, B.P. 1998. Mortality rate of a cohort of the coral trout, *Plectropomus leopardus*, in zones of the Great Barrier Reef Marine Park closed to fishing. *Mar. Freshwater Res.* 49: 507-511.
- Russel, D.J., McDougall, A.J., Fletcher, A.S., Ovenden, J.R. and Street, R. 2003. Biology, management and genetic stock structure of mangrove jack, (*Lutjanus argentimaculatus*) in Australia. Fisheries Research Development Corporation Final Report Project No. 1999/122.
- Sadovy, Y., and Colin, P.L. 1995. Sexual development and sexuality of the Nassau grouper. *J. Fish. Biol.* 46: 961-976.
- Sadovy, Y., and Shapiro D.Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia* 1: 136-156.
- Sadovy, Y.J., and Vincent, A.C.J. 2002. Ecological issues and the trades in live reef fishes. In: Sale, P.F. (Ed) Coral reef fishes: Dynamics and diversity in a complex ecosystem Academic Press, London, pp 391-420.
- Sadovy, Y., Kulbicki, M., Labrosse, P., Letourneur, Y., Lokani, P., and Donaldson, T.J. 2003. The humphead wrasse, *Chelinus undulatus*: Synopsis of a threatened and poorly known giant coral reef fish. *Rev. Fish Biol. Fish.* 13: 327-364.
- Sambrook, J., Fritch, E.F., and Maniatis, T. 1989. Molecular cloning: A laboratory manual, 2nd edn. New York, Cold Spring Harbor Laboratory Press.

- Samoilys, M.A. 1997a. Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. *Coral Reefs* 16: 151-158.
- Samoilys, M.A. 1997b. Periodicity of spawning aggregations of coral trout *Plectropomus leopardus* (Pisces: Serranidae) on the northern Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 160: 149-159.
- Samoilys, M.A., and Roelofs, A. 2000. Defining the reproductive biology of a large serranid, *Plectropomus leopardus*. CRC Reef Research Centre Technical Report No. 31, CRC Reef Research Centre, Townsville, Australia.
- Samoilys, M.A., and Squire, L.C. 1994. Preliminary observations on the spawning behavior of coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. *Bull. Mar. Sci.* 54: 332-342.
- Samoilys, M., and Pollard, D. 2000. *Cromileptes altivelis*. In: IUCN 2003. 2003 IUCN Red List of Threatened Species.
- Samoilys, M., Slade, S.J., and Williams L.E. 2002. Coral trout. In L.E. Williams (Ed) Queensland's fisheries resources. Current condition and recent trends 1988-2000, Department of Primary Industries: Brisbane, Australia, pp. 75-79.
- Schneider, S., Roessli, D., and Excoffier, L. 2000. ARLEQUIN ver 2.000. A software for population genetics data analysis. Geneva, Genetics and Biometry Laboratory, Department of Anthropology and Ecology, University of Geneva.
- Schnute, J. 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.* 38: 1128-1140.
- Shapiro, D.Y., Sadovy, Y.M., and McGehee, A.M. 1993. Size composition and spatial structure of the annual spawning aggregation of the red hind, *Epinephelus guttatus* (Pisces: Serranidae). *Copeia*. 399-406.
- Sheaves, M. 1995. Large lutjanid and serranid fishes in tropical estuaries: Are they adults or juveniles? *Mar. Ecol. Prog. Ser.* 129: 31-40.
- Shulman, M.J., and Birmingham, E. 1995. Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. *Evolution* 49: 897-910.
- Slade, S.J., and Williams, L.E. 2002. Red throat emperor. In L.E. Williams (Ed) Queensland's fisheries resources. Current condition and recent trends 1988-2000, Department of Primary Industries: Brisbane, Australia, pp. 80-83.
- Stobutzki, I.C. 1998. Interspecific variation in sustained swimming ability of late pelagic stage reef fish from two families (Pomacentridae and Chaetodontidae). *Coral Reefs* 17: 111-119.
- Stobutzki, I.C., and Bellwood, D.R. 1994. An analysis of the sustained swimming abilities of pre- and post-settlement coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 175: 275-286.
- Stobutzki, I.C., and Bellwood, D.R. 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar. Ecol. Prog. Ser.* 149: 35-41.
- Swain, D.P., and Foote, C.J. 1999. Stocks and chameleons: the use of phenotypic variation in stock identification. *Fish. Res.* 43: 113-128.
- Taylor, E.B., Foote, C.J., and Wood, C.C. 1996. Molecular genetic evidence for parallel life history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). *Evolution* 50: 401-416.
- UNESCO 2003. Properties inscribed on the World Heritage List. UNESCO 1972 Convention concerning the protection of the world cultural and natural heritage. World Heritage Centre, Paris, France. 20pp.
- van Herwerden, L., Benzie, J., Peplow, L., and Davies, C.R. 2000. Microsatellite markers for coral trout (*Plectropomus laevis*) and red throat emperor (*Lethrinus miniatus*) and their utility in other species of reef fish. *Mol. Ecol.* 9:1929-1931.

- van Herwerden, L., Davies, C.R., and Choat, J.H. 2002. Phylogenetic and evolutionary perspectives of the Indo-Pacific grouper *Plectropomus* species on the Great Barrier Reef, Australia. *J. Fish Biol.* 60: 1591-1596.
- van Herwerden, L., Benzie, J., and Davies, C. 2003. Microsatellite variation and population genetic structure of the red throat emperor on the Great Barrier Reef. *J. Fish Biol.* 62: 987-999.
- Wachenfeld, D.R., Oliver, J.K., and Morrissey, J.I. 1998. State of the Great Barrier Reef World Heritage Area 1998. Great Barrier Reef Marine Park Authority, Townsville, Australia.
- Warner, R.R. 1995. Large mating aggregations and daily long-distance spawning migrations in the blueheaded wrasse, *Thalassoma bifasciatum*. *Env. Biol. Fish.* 44: 337-345.
- Weir, B.S. 1996. Genetic data analysis II: Methods for discrete population data. Sunderland, MA, Sinauer Assoc. Inc.
- Weir, B.S., and Cockerham, S.S. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38: 1358-1370.
- Welch, D.J. 2001. Bias in size and age samples of *Plectropomus leopardus*, taken by line fishing among regions and management zones of the Great Barrier Reef. MSc Thesis, Department of Marine Biology and Aquaculture, James Cook University, Townsville.
- West, G. 1990. Methods of assessing ovarian development in fishes: A Review. *Aust. J. Mar. Freshw. Res.* 41: 199-222.
- Whitlock, M.C., and McCauley, D.E. 1999. Indirect measures of gene flow and migration. $F_{st} \neq 1/(4nm+1)$. *Heredity* 82: 117-125.
- Williams, A.J. 1997. Spatial variation in population structure of the Red Throat Emperor, *Lethrinus miniatus*, among regions and management zones on the Great Barrier Reef. Honours Thesis, Department of Marine Biology, James Cook University, Townsville.
- Williams, A.J. 2003. Spatial patterns in population biology of a large coral reef fish: what role can movement play? PhD Thesis, School of Marine Biology and Aquaculture, James Cook University, Townsville.
- Williams, A.J., Davies, C.R., Mapstone, B.D., and Russ, G.R. 2003. Scales of spatial variation in demography of a large coral-reef fish-an exception to the typical model? *Fish. Bull.* 101: 673-683.
- Williams, A.J., Davies, C.R., Mapstone, B.D. In press. Variation in the periodicity and timing of increment formation in red throat emperor (*Lethrinus miniatus*) otoliths. Submitted to *Mar. Freshw. Res.*
- Williams, D.McB. 1991. Patterns and process in the distribution of coral reef fishes. In: Sale P. F. (ed.). The ecology of fishes on coral reefs. Academic Press, San Diego, p 437-474.
- Williams, D.McB., and Russ, G.R. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Report to the Great Barrier Reef Marine Park Authority.
- Williams, L.E. 2002. Line fisheries of Queensland. In: Williams, L.E. (ed) Queensland's fisheries resources. Current condition and recent trends 1988-2000. pp. 63-65. Department of Primary Industries, Queensland.
- Winsor, L. 1984. Manual of basic zoological microtechniques for light microscopy. James Cook University Library, Townsville, Australia.
- Winsor, L. 1994. Tissue processing. In: Woods, A. E., Ellis, E. C. (Eds). Laboratory histopathology: a complete reference. Churchill Livingstone, Edinburgh, 42 pp.
- Wolanski E.J. (ed) 2001. Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef. CRC Press.

- Wolanski, E., Doherty, P., and Carleton, J. 1997. Directional swimming of fish larvae determines connectivity of fish populations on the Great Barrier Reef. *Naturwissenschaften* 84: 262-268.
- Zeller, D.C. 1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Mar. Ecol. Prog. Ser.* 154: 65-77.
- Zeller, D.C. 1998. Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. *Mar. Ecol. Prog. Ser.* 162: 253-263.
- Zeller, D.C., and Russ, G.R. 1998. Marine reserves: Patterns of adult movement of the coral trout (*Plectropomus leopardus*) (Serranidae). *Can. J. Fish. Aquat. Sci* 55: 917-924.

Appendix A: Intellectual Property

No patentable or marketable products or processes have arisen from this research. Intellectual property accruing from the analysis and interpretation of raw data collected as part of this project vests jointly with the Fisheries Research and Development Corporation, The CRC Reef, AIMS, James Cook University, the Great Barrier Reef Marine Park Authority, the Principal and Co-Investigators and the graduate students.

Appendix B: Staff

Principle Investigator: Campbell Davies

Co-Investigators: John Benzie
J. Howard Choat
Bruce Mapstone
Gary Russ
Melita Samoily⁹
Andrew Tobin
Ashley Williams

Liaison Officer: Annabel Jones

Project Staff: Kyi Bean
Lynne van Herwerden
Cameron Murchie
Lesa Peplow
David Welch
Ashley Williams

PhD Students Samantha Adams
Ashley Williams
Bob Mosse
Jake Kritzer

⁹ Dr Samoily was a co-investigator on the original proposal but took up a position in Canada during the early stages of the project. Dr Tobin took up her responsibilities in 2000.