Climate change and the aquatic environment – the future for fish and fisheries: ASFB 2010

FINAL REPORT

John D. Koehn and Jarod Lyon

June 2011





Australian Government

Fisheries Research and Development Corporation

Project No. 2010/301

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2010/301 ASFB 2010 Climate change and the aquatic environment – the future for fish and fisheries.

PRINCIPAL INVESTIGATOR: Jarod LyonADDRESS:Arthur Rylah InstitutePO Box 137Heidelberg VIC 3084Telephone: 03 94508600 Fax: 03 94508799

Objectives

To host the The 2010 Australian Society for Fish Biology Symposium *Climate Change and the Aquatic Environment – the future for fish and fisheries.* The aims of the symposium were to:

- 1. Present an overview of the perceived effects of climate change on fish and fisheries in freshwater, estuarine and marine environments
- 2. Provide scientific predictions about the future of our aquatic world, fish biodiversity and fisheries
- 3. Discuss potential approaches for reducing human impacts and threats of climate change on fish and aquatic habitats
- 4. Provide a forum for stakeholders to present their vision of the fish and fisheries of our planet in 20 years.

NON TECHNICAL SUMMARY:

FRDC provided funding to support the organisation and hosting of the 2010 Australian Society for Fish Biology (ASFB) workshop on *Climate Change and the Aquatic Environment – the future for fish and fisheries* held at the Melbourne Museum, Carlton, Melbourne, 12-14 July 2010. A comprehensive science program was developed involving invited keynote speakers recognised internationally for their expertise in their particular research field with presentations addressing eight key areas:

- How is climate changing in aquatic environments?
- Future climate change modelling, predictions, and adaptation options.
- Have there been range shifts for Australian fishes in response to climate change?
- Climate-induced degradation and loss of critical fish habitats.
- Climate change and fish reproduction.
- Implications of climate change for fisheries and aquaculture in the Pacific region.
- Effects of global warming and ocean acidification on fish early life histories.
- How do fish figure in climate change models?

These presentations resulted in 6 draft keynote papers which will be accompaniesd by a further 6 invited papers and published as a special edition of *Marine and Freshwater Research* in 2011.

The keynote papers are:

- 1. Observed climate change in Australian aquatic environments by Janice M. Lough, Alistair J. Hobday, David Jones
- 2. Projected climate change in Australian aquatic environments by Alistair J. Hobday, Janice M. Lough
- 3. Effects of climate change on fish reproduction and early life history stages by Ned W. Pankhurst, Philip L. Munday
- 4. Have there been range shifts for Australian fishes in response to climate change? by *David Booth, Nick Bond, Peter Macreadie*
- 5. Contribution of climate change to degradation and loss of critical fish habitats in Australian aquatic environments. by Morgan S. Pratchett,, Line K. Bay, Peter C. Gehrke, John D. Koehn, Kate Osborne, Robert L. Pressey, Hugh P.A. Sweatman and David Wachenfeld
- 6. Aquatic Ecosystems, Communities and Populations: Advances in Modelling the Effects of Climate Change for Australia and the Tropical Pacific by *Éva Plagányi, Johann Bell, Rodrigo Bustamante, Jeffrey M.* Dambacher, Darren Dennis, Cathy Dichmont, Leo Dutra, Beth Fulton, Alistair Hobday, Ingrid van Putten, Franz Smith, Tony Smith, Shijie Zhou

These papers will also be accompanied by introductory and synthesis papers.

Overall the event was an outstanding success, attracting over 180 delegates, including 90 students representing major research and educational institutions and management agencies from across Australia and New Zealand, as well as international delegates and industry representatives. The keynote speakers also participated in a public lecture that was attended by over 200 people.

These draft papers were completed within 12 months of the event and will be a lasting legacy of this symposium. The introductory and synthesis papers will be made open access.

OUTCOMES ACHIEVED

The Workshop provided researchers and industry with an understanding of the latest science on climate change ensuring a rapid uptake of this knowledge into fisheries management. The symposium will have a demonstrable impact on future climate change research being undertaken in Australia. Ultimately it will result in greater collaboration and partnerships across institues, States and between marine, estuarine and freshwater disciplines and leading to improved research outcomes.

KEYWORDS: Climate change, impacts on fisheries, marine, freshwater

SPECIAL CONDITIONS

Nil

INTELLECTUAL PROPERTY ISSUES ARISING:

Nil

CONTACT WITH BENEFICIARIES:

Beneficiaries will be contacted when the *Marine and Freshwater Research* special edition is printed (expected Aug-Sept 2011).

VARIATIONS TO PROJECT:

There were some minor variations in timelines approved for the production of this final report necessary due extended reviews and production of draft papers.

Acknowledgements

The authors of this report wish to thank the authors of all publications submitted for this special issue, and the anonymous reviewers who so constructively improved the papers. Thanks goes to Australian Society for Fish Biology Conference and organising committee led by Martin Gomon, participants at the conference and *Climate change and the aquatic environment: the future for fish and fisheries* symposium held at the Melbourne Museum, Carlton, Melbourne, 12-14 July 2010 and the symposium steering committee. Other key sponsors of this event were the Museum of Victoria and Department of Sustainability and Environment, Victoria.

Background

The Australian Society for Fish Biology Annual Conference and workshop provides an opportunity for scientists, managers and industry to come together and discuss the most recent developments in fish and fisheries science. Conferences and workshops such as this are a key component of the skill development of people in the sector, particularly offering students and young scientists the opportunity to obtain new ideas in a relaxed and informal setting.

While there is a lot of general talk on climate change, *Climate change and the aquatic environment: the future for fish and fisheries* symposium aimed to present some credible science and predictions that can be used as a synopsis of the likely impacts on fish and fisheries. In particular, stock assessment analyses should consider the implications of climate change when predicting future population biomass.

The 2010 Conference and Symposium aimed to reduce registration costs to enable a wider section of the Fisheries scientific community to attend. Reducing costs is especially important in attracting large numbers of students to the conference, which was the most affordable in over ten years. This reduction in registration costs was possible due to reduced overheads (such as the omission of paid conference organisers) and the involvement of key sponsors such as FRDC.

Need

Climate change will have many impacts on marine and freshwater ecosystems, and on human uses of them. Improved scientific support for policy and management decision-making in the face of these potential impacts is essential. In response to this need, interdisciplinary research teams have been formed around the world to analyse data and develop models to explore the likelihood and nature of future ecosystem states and strategies for sustainable use of such resources in these future states.

There are likely to be significant climate change impacts on the biological, economic, and social aspects of Australian fisheries. Both positive and negative impacts are expected, and impacts will vary according to changes in the regional environment: south-east fisheries are most likely to be affected by changes in water temperature, northern fisheries by changes in precipitation, and western fisheries by changes in the Leeuwin Current.

There may be new opportunities for some wild fisheries where tropical species shift southward. There will also be many challenges, (such as that faced by the Tasmanian salmon aquaculture industry due to Atlantic salmon being cultivated close to their upper thermal limits of optimal growth). Nevertheless, it is important that there is potential for adaptation measures to be employed by fishery industries. There is a need in fisheries and aquaculture management to better integrate the effects of climate variability and climate change in establishing harvest levels and developing future strategies. This will enhance the resilience of marine biodiversity and the adaptive capacity of the fisheries and aquaculture industries.

This symposium provided a forum for scientists and policymakers to discuss the potential impacts of climate change on marine and freshwater ecosystems and our uses of these ecosystems, and to consider the strategies that society can take to be prepared for anticipated impacts. Quantitative studies of the potential impact of climate change on fish and fisheries throughout the Australia will be featured.

Objectives

To host the The 2010 Australian Society for Fish Biology Symposium *Climate Change and the Aquatic Environment – the future for fish and fisheries.* The aims of the symposium were to:

- 1. Present an overview of the perceived effects of climate change on fish and fisheries in freshwater, estuarine and marine environments
- 2. Provide scientific predictions about the future of our aquatic world, fish biodiversity and fisheries
- 3. Discuss potential approaches for reducing human impacts and threats of climate change on fish and aquatic habitats
- 4. Provide a forum for stakeholders to present their vision of the fish and fisheries of our planet, and particulalry Australia, in 20 years.

Methods

Unlike previous years where the ASFB conference and workshop have been held as separate events, this symposium on Climate change was embedded within the conference schedule. This involved 8 keynote speakers that introduced each day (2-3 each morning), followed by the general conference papers. The general conference papers included all aspects of fish and fisheries, but many also included a climate change theme. The keynote speakers also took part in a public lecture held on the first night, which was cosponsored by the Museum of Victoria. The final keynote session involved a panel discussion that captured the main points of the presentations and combined them into a short synopsis of the current situation and the way forward.

The integrated symposium enabled a topic of national significance to be discussed in an open forum, led by internationally acclaimed experts. Valuable knowledge was acquired and key contacts were established by fisheries biologist and managers.

In the past, many workshop proceedings have been of variable quality and often disappear into the grey literature. The scientific output of this symposium will be of a quality that means it can be published in a peer reviewed journal as a special edition of CSIRO journal *Marine and Freshwater Research*.

Day	Time	Presentation title	Keynote speaker (bold) and co authors
Monday 12 July	1100-1130	How is climate changing in aquatic environments?	Janice Lough
Monday 12 July	1130-1200	Future climate change – modelling, predictions, and adaptation options.	Alistair Hobday, David Jones
Monday 12 July	1200-1230	Have there been range shifts for Australian fishes in response to climate change?	David Booth, Nick Bond
Tuesday 13 July	0900-0930	Climate-induced degradation and loss of critical fish habitats.	Morgan Pratchett, Peter Gehrke
Tuesday 13 July	0930-1000	Climate change and fish reproduction.	Ned Pankhurst
Tuesday 13 July	1000-1030	Implications of climate change for fisheries and aquaculture in the Pacific region.	Johann Bell
Wednesday 14 July	0900-0930	Effects of global warming and ocean acidification on fish early life histories.	Philip Munday
Wednesday 14 July	0930-1000	How do fish figure in climate change models?	Éva Plagányi, Beth Fulton, Ingrid van Putten
Wednesday 14 July	1000-1030	Panel discussion	Chaired by John Koehn with all available speakers

Climate change and the aquatic environment – the future for fish and fisheries. Keynote speaker program.

The CV's of keynote speakers are included in Appendix 3.

Results/Discussion

The Australian Society for Fish Biology Annual Conference for 2010 was held at the Melbourne Museum, Carlton Gardens, Melbourne, Australia from Monday through Wednesday, 12–14 July 2010. Over 180 people, representing major research and educational institutions and management agencies from across Australia and New Zealand, as well as international delegates and industry representatives attended the event. The conference with its integrated symposium focused on a subject of current universal importance presents a unique opportunity for organisations and agencies wishing to bring their products and services to the attention of these groups.

Keynote papers

Paper Title			r Title	Authors	
How	is	climate	changing	aquatic	Lough, Hobday

environments?	Jones
Projected climate change in Australian	Hobday and Lough
aquatic environments.	
Effects of global warming on fish reproduction and early life histories.	Pankhurst and Munday
Have there been range shifts for Australian fishes in response to climate change?	Booth, Bond and Macreadie
Contribution of climate change to degradation and loss of critical fish habitats in Australian aquatic environments.	Osborne, Pressey, Sweatman,
Modelling the effects of climate change on aquatic ecosystems and their dependent communities in Australia and the Pacific	Dambacher, Dennis, Dichmont,

Abstracts of these papers are included in Appendix 4 and full draft papers in Appendix 5.

In addition, the following papers which were not contributed by keynote speakers will also be added to this special edition.

Climate change and the aquatic environment – the future for fish and fisheries in Australia.	Koehn
Using species distribution models to infer environmental filters and climate induced range shifts	Bond, Thomson Reich and Stein
Fish out of water: impacts, adaptations and climate change in Australia's freshwater fish	Morrongiello, Beatty, Bennett, Crook, Ikedife, Kennard, Kerezsy, Lintermans, McNeil, Pusey and Rayner
Impacts of climate change on aquatic ecosystems of the Murray-Darling Basin Effects of climate change on estuaries	Balcombe, Sheldon , Marsh , Bond , Bernays, Hadwen, Capon, Kennard Gillanders et al.
Climate change and Australian fishes: it is having impacts now - are we ready to adapt?	

The keynote speakers also participated in a public leacture that was attended by over 200 people.

Benefits and Adoption

The main benefits of the 2010 Australian Society for Fish Biology *Climate* change and the aquatic environment – the future for fish and fisheries in Australia relate to the exposure of the latest science on climate change across a broad range of disciplines: researchers, managers and industry stakeholders. As evidenced by the number and quality of presentations, the large number of workshop participants (about 180), attendance at the public lecture (>200) and the positive feedback from attendees it is clear that there was considerable interest in the area. The event was of an exceptionally high standard in terms of venue, organisation, scientific program and social functions.

Beneficiaries of the conference were State and Federal management agencies with responsibilities for management of biodiversity and fisheries resources in aquatic environments. The primary outcome of the conference will be an enhanced understanding of the impacts of climate change for managing the sustainability of species in Commonwealth-managed fisheries. Attendees from different fisheries orgnisations from around Australia benefited directly by learning about potential impacts of climate change and the new techniques and approaches possible for dealing with it through fisheries management. This will lead to greater consideration of potential climate change impacts and encourage researchers and managers to develop greater predictive capabilities.

Students were, in particular, be encouraged to participate in the conference to discuss their current research and learn about potential approaches to their work and about work prospects for the future.

All major sponsors of the conference were acknowledged within each Keynote address and in each paper published in *Marine and Freshwater Research*.

Further Development

In relation to this project there is no further development required. However, we believe that the integrated approach to organising the event, with effective promotion strategies targeted at government, educational and industry sectors is a model for future conferences. Specifically, we were successful in attracting a strong representation of post-graduate students and university researchers, groups that have much to offer to fisheries science and management, especially given the need to consider information needs in the context of ecosystem based fishery management. The use of a public lecture was very successful in promoting the symposium and its sponsors and conveying current science to 'the real world'. The objective of having an output as a peer reviewed publication (and indeed, in this case as a special edition of a journal) promoted the calibre of keynote speakers and provides and ongoing, tangible contribution to the science in this field.

Planned Outcomes

While the Australian Society for Fish Biology is a professional, independent, non-profit, non-commercial and non-aligned organization, it is recognised that outcomes from annual conferences and symposiums will be relevant to many state and national organizations. As such, the 2010 symposium will be take into account the following overarching themes.

1. The impacts of climate change have the potential to lower productivity and increase biosecurity risk within the freshwater and marine environments. Industry will increasingly need to enhance its drought preparedness capacity. At the same time, climate change also presents opportunities to increase production where there is a secure water supply.

2. The increasing global demand for food and fibre is resulting in increased competition from developing countries with low labour costs and changing production structure. Opportunity exists to capitalise on 'clean and green' reputation and innovative product development, as consumers both domestically and internationally focus on purchasing high-quality, value-added products that are ethically and sustainably produced.

3. Discovery-oriented science and quick uptake of improved technology by enterprises offer greater scope to further boost productivity and production. This includes more efficient use of water.

4. Population growth is putting strain on fisheries habitats and resources as urbanisation intensifies. To address these challenges an evidence and riskbased approach to protect habitats and fish stocks as needed. New avenues need to be pursued to foster efficiency and greater profitability in the commercial sector and growth in the recreational sector, while continuing to ensure the sustainable use of fisheries resources and habitats.

5. Major biosecurity incidents will likely become more frequent as the movement of products and people around the world increases, climates and environments change and market requirements intensify. There are opportunities to reduce the impacts of biosecurity events on our economy, environment and way of life through more co-ordinated prevention, detection and response activities across Australia.

Conclusion

The 2010 Australian Society for Fish Biology *Climate change and the aquatic environment – the future for fish and fisheries in Australia* symposium was an outstanding success at all levels. In terms of promotion and sponsorship the Organising Committee was able to attract a large number of government, university and industry sponsors. In terms of registrants, it was attended by over 180 delegates. Of particular significance was the large number of international delegates (around 25) and the large student representation (about 90), which represent the future of fish and fisheries research in Australia. The symposium program included many extremely quality presentations by many of Australia's most productive and innovative researchers. The publication of the symposium proceedings in a peer reviewed journal represent an important and tangible output of a timely amalgamation of the current knowledge of climate change and its impacts on fish and fisheries. In this respect it is evident that Australian scientists and technology providers are at the forefront in many areas and that there are considerable opportunities for collaboration and partnerships.

References

- Booth D., Bond N. and Macreadie P. Have there been range shifts for Australian fishes in response to climate change?
- Hobday A. J. and, Lough J. M. Projected climate change in Australian aquatic environments
- Lough, J. M. Hobday A. J. and, Jones David Observed climate change in Australian aquatic environments
- Pankhurst N. W.and Munday P. L.Effects of climate change on fish reproduction and early life history stages
- Plagányi É., Bell J., Bustamante R., Dambacher, J. M. Dennis, Darren Dichmont, Cathy Dutra Leo, Fulton Beth, Hobday A., van Putten, I. Smith,
 F. Smith, T. and Zhou S. Aquatic Ecosystems, Communities and Populations: Advances in Modelling the Effects of Climate Change for Australia and the Tropical Pacific
- Pratchett, M. S., Bay L. K, Gehrke P. C., Koehn J. D., Osborne K., Pressey, R. L. Sweatman H. P.A. and Wachenfeld D. Contribution of climate change to degradation and loss of critical fish habitats in Australian aquatic environments.

Other references are included in individual papers (Appendix 4).

Appendix 1: Intellectual Property

This is not applicable to this project. Information will be made freely available through the special edition of *Marine and Freshwater Research*.

Appendix 2: Staffing

The ASFB organising committee consisted of Dr Martin Gomon, Dr John Koehn, Dr Di Bray, Dr Alison King, Dr David Crook, Dr Patrick Coutin, Cr Charles Todd, Jarod Lyon, Dr Steve Swearer, Natalie Calder, Dr Jodi Kemp, Vennessa Thompson, Fern Hames, Jason Lieschke, Adrian Flynn. Dr John Koehn convened the *Climate change and the aquatic environment: the future for fish and fisheries* symposium. The Symposium steering committee: John Koehn (Chair), Philip Munday, Alistair Hobday, Ned Pankhurst, Dave Crook, Jeff Leis.

Appendix 3: Draft Inform article – free public lecture

Free lecture: "Climate change and the aquatic environment – the future for fish and fisheries"

Monday 12th July, 6-7.30 pm Age Theatre, Melbourne Museum, Carlton Gardens, Rathdowne St, Carlton.

The Australian Society for Fish Biology (ASFB) is holding its 2010 Annual Symposium next week at Museum Victoria's Carlton venue, Melbourne Museum. This annual meeting draws together fish and fisheries experts from all over the world to present the latest in research findings. A strong theme at this meeting is the impact of climate change on fishes and fisheries stocks. Major sponsors for this event are the Department of Sustainability and Environment, Museum of Victoria and the Fisheries Research and Development corporation.

In order to bring this information to the public arena, the ASFB and Museum Victoria are sponsoring a public lecture featuring some of Australia's leading fish and fisheries experts as keynote speakers.

The evening will present three keynote speakers and be chaired by Dr John Koehn (Arthur Rylah Institute for Environmental Research, DSE, Victoria) and introduced by Dr Mark Norman, Head of Sciences at Museum Victoria. It will conclude with a round table discussion by the participants, stirred on by questions from the audience.

Speakers:

- Dr Mark Norman (Museum Victoria) "The fishes on our doorstep - Victoria's rich fish fauna"
- Dr Alistair Hobday (Climate Adaptation Flagship, CSIRO) "Whats happening, how do we know, how do we predict?"
- Dr Philip Munday (James Cook University, Townsville) "Fish in hot water"
- Dr Éva Plagányi (Wealth from Oceans Flagship, CSIRO) "Fried fish and frazzled people – are we ready for climate change?"

While there is considerable public discussion on climate change, this lecture will bring together credible science and scientific predictions on the likely impacts on our marine and freshwater environments, fish and fisheries. These speakers will summarise evidence on the anticipated impacts on fishes and fisheries, providing a personalised perspective on the issues. Topics to be covered will include:

- the impacts on fish habitats
- effects of temperature on reproduction, larval development and physiology

- aquaculture and subsistence fisheries in the region
- fish stocks
- fish distributions (including invasive species)
- early life histories
- data, modelling and predictions

The public lecture is a free event and no booking is required. Come early as seats may be limited.

Appendix 4: Draft Media release

The forthcoming symposium *Climate change and the aquatic environment* – *the future for fish and fisheries* will be part of the the Australian Society for Fish Biology for the Society's 2010 Annual Conference to be Melbourne, Victoria, from Monday 12th to Wednesday 14th July 2010.

While there is a lot of general talk on climate change, this symposium aims to present some credible science and predictions that can be used as a synopsis of the likely impacts on fish and fisheries. It will:

- Relate to marine and freshwater, fish and fisheries;
- Be about science not policy;
- Provide scientifically credible information.

The symposium is to be embedded within the general conference schedule and will be supported by a range of other presentations on climate change and general fish and fisheries science. It will involve 8 keynote speakers that will present talks demonstrating how changes will impact on fish and fisheries, providing a personalised perspective on the issue. Topics such: as the impacts on fish habitats, physiology, aquaculture, subsistence fisheries, fish stocks, fish distributions (including invasive species), early life histories and data, modelling and predictions intend to be covered. The final keynote session will involve a panel discussion that captures the main points of the presentations.

Keynote speaker	Presentation	
Janice Lough	How is climate changing in aquatic environments?	
Alistair Hobday	Future climate change – modelling, predictions, and adaptation options.	
David Booth	Have there been range shifts for Australian fishes in response to climate change?	
Morgan Pratchett	Climate-induced degradation and loss of critical fish habitats.	
Ned Pankhurst	Climate change and fish reproduction.	
Johann Bell	Implications of climate change for fisheries and aquaculture in the Pacific region.	
Philip Munday	Effects of global warming and ocean acidification on fish early life histories.	
Éva Plagányi	How do fish figure in climate change models?	
all available speakers	Panel discussion	

Several of the keynote speakers will also take part in a public lecture to be held on Monday 12th July, sponsored by the Australian Society for Fish Biology and the Museum of Victoria.

The expected high quality of scientific output from this symposium will be of a quality that it can be published in a peer reviewed journal and will include several theme papers and a short synopsis paper of the current situation and the way forward.

It is expected that this symposium will provide an important contribution to the understanding of this important topic.

Sponsorship for this 2010 Australian Society for Fish Biology Conference and Symposium is supported by funding from FRDC on behalf of the Australian Government and the Department of Sustainability and Environment on behalf of the Victorian Government.

Appendix 4: *Symposium keynote speakers*

David Booth Department of Environmental Sciences, University of Technology Sydney. PO Box 123, Broadway NSW 2007, Australia. David.Booth@uts.edu.au



David Booth is Professor of Marine Ecology at University of Technology, Sydney, and Chair of the Scientific Advisory Committee, Sydney Institute of Marine Sciences. He has published over 60 papers and book chapters on reef fish ecology, specialising in recruitment processes and the effects of environment, including climate change factors on dispersal and behaviour of coral reef fishes.

Alistair Hobday Climate Adaptation Flagship, CSIRO Marine and Atmospheric Research. Hobart TAS 7001, Australia. Alistair.Hobday@csiro.au





Dr Alistair Hobday is a Senior Research Scientist at CSIRO Marine and Atmospheric Research. His research spans a range of topics, including spatial management and migration of large pelagic species, environmental influences on marine species, and the impacts of climate change on marine resources. He leads the Marine Climate Impacts area within the CSIRO Climate Adaptation National Research Flagship, and has been co-editor of two recent reports on the impacts of climate change on (i) fisheries and aquaculture, and (ii) Australian marine life. He is a member of the steering committee for the international GLOBEC program CLIOTOP (Climate Impacts on Top Ocean Predators). **Janice Lough** Australian Institute of Marine Science. PMB 3, Townsville MC, QLD 4810, Australia. j.lough@aims.gov.au



Dr Janice Lough is a Senior Principal Research Scientist at the Australian Institute of Marine Science and a Partner Investigator with the ARC Centre of Excellence for Reef Studies. A climatologist by training, she currently specialises in identifying the nature and consequences of a rapidly changing global climate for coral reef ecosystems and determining climate and environmental histories of the past several centuries from the annual records contained in massive coral skeletons

Philip Munday James Cook University. Townsville QLD 4811, Australia. Philip.munday@jcu.edu.au





Philip Munday is a Professorial Research Fellow at James Cook University, Townsville. His research focuses on understanding and predicting the impacts of climate change on populations and communities of coral reef fishes, both directly through changes in the physical environment and indirectly through effects on coral reef habitat. Using laboratory and field experiments he is investigating the effects of increased temperature and ocean acidification on reef fish populations and testing their capacity for acclimation and adaptation to a rapidly changing environment. He has published over 80 papers on reef fish ecology, including major reviews and research papers on climate change and marine fishes. **Morgan Pratchett** ARC Centre of Excellence for Coral Reef Studies, James Cook University. Townsville QLD 4811, Australia. morgan.pratchett@jcu.edu.au





Associate Professor Morgan Pratchett is a principal research fellow with the ARC Centre for Coral Reef Studies, James Cook University, researching the effects of disturbances and community resilience in coral reef ecosystems. His current research focuses on critical aspects of coral reef habitats that influence the structure and abundance of coral reef fishes, and assessing the vulnerability of coral reef habitats to increasing temperatures and ocean acidification. Morgan has published >60 papers and is the lead author on several recent reviews documenting diverse effects of climate change on coral reef organisms and ecosystems.

Ned Pankhurst Griffith University, Gold Coast campus, Gold Coast, Qld 4222 n.pankhurst@griffith.edu.au



Professor Ned Pankhurst's research centres on the reproductive physiology of fish, with areas of expertise in reproductive physiology and endocrinology of

tropical damselfishes, broodstock management and induced spawning of fishes in aquaculture, development of new marine species for aquaculture, and climate change and fish reproduction. He has published 150 papers and reviews in refereed scientific journals, and supervised ~ 40 Honours, Masters and PhD students. He is currently Deputy Vice-Chancellor (Research) at Griffith University, Queensland.

Johann Bell Secretariat of the Pacific Community. B.P. D5, 98848 Noumea Cedex, New Caledonia. johannb@spc.int





Dr Johann Bell is a Senior Fisheries Scientist with the Strategic Engagement, Policy and Planning Facility at the Secretariat of the Pacific Community (SPC) in New Caledonia. He has been doing and supervising research for the sustainable development of small-scale fisheries and coastal aquaculture in the Pacific and in Asia for 17 years. His recent research interests are in the areas of restocking and stock enhancement of coastal fisheries, planning the use of fish for food security, and climate change and fisheries. Johann is currently leading a comprehensive assessment of the vulnerability of fisheries and aquaculture in the Pacific to climate change. This assessment involves contributions from more than 70 scientists from about 30 institutions.

Éva Plagányi Wealth from Oceans Flagship, CSIRO Marine and Atmospheric Research. Cleveland, QLD 4163, Australia. <u>Eva.Plaganyi-lloyd@csiro.au</u>



Dr Éva Plagányi is a Research Team leader and senior scientist at CSIRO Marine and Atmospheric Research. Her research interests focus on quantitative modelling of renewable biological resources, ranging from stock assessment modelling, management strategy evaluation to the development

of ecosystem models. She was contracted by the FAO (Food and Agriculture Organisation, Rome) to author a global review of models for an ecosystem approach to fisheries. She is using modelling approaches to investigate climate change impacts on fisheries.

Appendix 6:

Abstracts from the keynote papers from ASFB 2010 Climate change and the aquatic environment – the future for fish and fisheries.

Observed climate change in Australian aquatic environments

Janice M. Lough, Alistair J. Hobday, David Jones

Abstract The consequences of human activities that have led to increases in the concentrations of greenhouse gases in the atmosphere are already being felt in marine and terrestrial environments. These greenhouse gases have already trapped more energy in the global climate system resulting in observed warming of global land and sea temperatures. An estimated 30% of the extra atmospheric carbon dioxide has been absorbed by the oceans and increased their acidity. Thermal expansion of the oceans and some melting of land-based ice have already caused sea level to rise. Significant climate changes have now been observed across Australia and its surrounding coastal seas. The clearest signal is warming of air and sea temperatures; further, the observed rates of warming have accelerated since the mid-20th century. Ocean warming has been greater than the global average around Australia, and most intense in waters off south-east Australia. Changes that can be attributed to climate change in the hydrological regime are more difficult to differentiate from natural variability in Australia, as there is high inter-annual variability in this "land of drought and flooding rains". That said, trends towards significantly drier winters in the south-west of Western Australia and part of southern Australia over a long period of time appear to be largely attributable to human-induced changes in the climate system. Attribution is less clear for recent trends towards wetter and drier conditions in northwest and along the east coast, respectively. Even without significant changes in average rainfall, warmer air temperatures increase evaporative losses and thus enhance the intensity of recent droughts, and reduce river flows. Sustained and co-ordinated monitoring of the physical environment, especially lacking for Australia's freshwater ecosystems, is important to assess the magnitude and biological consequences of ongoing changes.

Projected climate change in Australian aquatic environments

Alistair J. Hobday, Janice M. Lough

Abstract Changes in the physical environment of aquatic systems that are consistent with climate change have already been reported from around Australia. These have, or are expected to have impacts on a range of marine and freshwater species. The magnitude of future impacts depends on future environmental conditions. Projections of the future state of marine and freshwater environments can be obtained in several ways, including qualitative knowledge of the earth system, interpolation of historical trends, and dynamical projection using global climate models. Downscaling of model results is often necessary before they are useful to aquatic biologists,

managers and planners, and can be achieved via statistical or dynamical models. Here we show results of projections for a range of environmental variables for Australian marine and freshwater environments using several of these approaches and discuss the limitations and uncertainties that accompany such projections. In the ocean, warmer sea surface temperatures are projected around Australia but particularly for south-eastern Australia, with the slowest rates of warming for the upwelling regions of western Victoria. The East Australia Current will transport greater volumes southward, while the Leeuwin Current may weaken. Sea levels will rise around the country, although regional projections are not yet considered reliable. On land, air temperatures will rise and rainfall is generally projected to decline across much of Australia in coming decades. Together these changes will result in reduced runoff and hence stream flow and lake storage. The impact of these changes for marine and freshwater species will result in changes to their distribution, abundance, physiology and phenology. Adaptation to these changes is possible for some species and the humans that rely on them, but will be limited by the rate of the projected change, and the investment available to respond. Adaptation efforts under future climate change are expected to be local. At present, however, local projections are generally considered less certain than those for large spatial and temporal scales.

Effects of climate change on fish reproduction and early life history stages

Ned W. Pankhurst, Philip L. Munday

Abstract Seasonal change in temperature has a profound effect on the regulation of reproduction in most fish species. Increasing temperatures cue reproductive development and spawning in many spring spawning species, and falling temperatures stimulate reproductive processes in autumn spawners. Elevated temperatures truncate spring spawning and delay autumn spawning. Increases in environmental temperatures will have an impact on reproductive patterns but the nature of these effects will depend on the period and amplitude of the temperature increase, and will range from phase-shifting of spawning within the annual cycle to complete inhibition of reproductive activity. This latter effect will be most marked in species which for any reason are constrained in their capacity to shift geographic range. Studies on a variety of taxa across diverse habitats and a wide temperature range have all shown similar (usually inhibitory) effects of elevated temperature albeit about different environmental set points. The effects are generated through the endocrine (hormonal) system, and it is increasingly clear that in adult females, this resides strongly in the inhibition of ovarian estrogen production. Larval fishes are usually more sensitive than adults to environmental fluctuations. Consequently, these early life history stages might be especially vulnerable to rapid climate change. In addition to direct effects on embryonic duration and egg survival, increasing temperature has a range of consequences for early life history stages, including influencing size at hatching, developmental rate, pelagic larval duration and probability of survival, all of which have important ecological ramifications. Relatively little is known about the effects of ocean acidification on fish reproduction and early life history development, although

most of the available evidence suggests that developmental processes are relatively tolerant to mild changes in pH. However, ocean acidification may pose a significant threat through its capacity to alter larval behaviour and impair sensory capabilities. These effects in turn could have significant impacts on population replenishment and connectivity patterns of marine fishes.

Have there been range shifts for Australian fishes in response to climate change?

David Booth, Nick Bond, Peter Macreadie

Abstract One of the most obvious and expected impacts of climate change on organisms is a shift in distributional range. For fishes, this is a complex consequence of how various life history stages interact with the environment; for instance, how fish larval dispersal is affected by climate-change alterations in ocean currents and water temperature. Here, we first survey the world- and Australian literature on climate-change effects on fish range, contrasting freshwater and marine studies, and show that very few definitive studies exist to date. Next we review the range of climate-change drivers in Australian coastal marine, estuarine, and freshwater ecosystems, and evidence for whether these have affected life history traits that may lead to range shifts. We then review the few definitive studies of fish range shifts in Australia and their links to climate change. Finally we discuss the direct and indirect approaches, including co-opting government and museum fish databases, to elucidating range shifts, and make recommendations for future work, including linking and standardising various databases to provide evidence of future range shifts.

Contribution of climate change to degradation and loss of critical fish habitats in Australian aquatic environments.

Morgan S. Pratchett,, Line K. Bay, Peter C. Gehrke, John D. Koehn, Kate Osborne, Robert L. Pressey, Hugh P.A. Sweatman and David Wachenfeld

Abstract Australia's aquatic ecosystems are unique, supporting a high diversity of species and high levels of endemism, but are extremely vulnerable to the major environmental changes expected to occur due to climate change. This review assesses climate-induced changes to structural habitats that have occurred in different aquatic ecosystems. For the most part, climatic impacts are difficult to discern against the background of habitat degradation caused by more direct anthropogenic impacts. However, climate impacts will become more pronounced with ongoing increases in temperature, changes in water chemistry, sea level rise, altered rainfall, increased severity of tropical storms, and changes to ocean currents. Each of these factors is likely to have specific effects on ecosystems, communities or species, and their relative importance varies with habitat. In the Murray-Darling Basin, the greatest concern relates to declines in surface water availability and riverine flow, which will be exacerbated by declining rainfall and increased evaporative loss. On the Great Barrier Reef, increasing temperatures, storm severity and

ocean acidification contribute to sustained and ongoing loss of coral and other habitat forming organisms. Despite the marked differences in major drivers and consequences of climate change, the solution is always the same. Greenhouse gas emissions need to be reduced as a matter of urgency, whilst simultaneously minimizing non-climatic causes of habitat degradation. Together, these actions will maximize opportunities for adaptation by species and increase the resilience of ecosystems.

Aquatic Ecosystems, Communities and Populations: Advances in Modelling the Effects of Climate Change for Australia and the Tropical Pacific

Éva Plagányi, Johann Bell, Rodrigo Bustamante, Jeffrey M. Dambacher, Darren Dennis, Cathy Dichmont, Leo Dutra, Beth Fulton, Alistair Hobday, Ingrid van Putten, Franz Smith, Tony Smith, Shijie Zhou

Abstract Climate change presents significant challenges to modelling and managing aquatic resources. Equilibrium assumptions common in many modelling approaches need to be replaced by formulations that allow for changing baselines, and integration of ongoing changes and adaptations by species, ecosystems and humans. As ecosystems change, so will the ways humans use, monitor and manage them; adaptive management loops may be one solution that deserves more prominence in the management toolbox. Models are critical tools for giving us an early understanding of the challenges to be faced by integrating observations and examining possible solutions. We review modelling tools currently available to simulate the effect of climate change on marine and freshwater ecosystems, and the implications for Non-linearities management of their natural resources. confound interpretations and hence adaptive management responses should be robust to surprises. An improvement in the ability to model the effects of climate change from a social and economic perspective is necessary. The outputs from "end-to-end" and socio-ecological models can potentially inform planning, in both Australia and the Pacific region, about how best to build resilience to change. Lessons from this region can guide increased use of models to test options for managing aquatic resources world-wide.

Appendix 7: Draft Symposium papers submitted to *Marine and Freshwater Research*

Observed climate change in Australian aquatic environments

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ABSTRACT

The consequences of human activities that have led to increases in the concentrations of greenhouse gases in the atmosphere are already being felt in marine and terrestrial environments. These greenhouse gases have already trapped more energy in the global climate system resulting in observed warming of global land and sea temperatures. An estimated 30% of the extra atmospheric carbon dioxide has been absorbed by the oceans and increased their acidity. Thermal expansion of the oceans and some melting of land-based ice have already caused sea level to rise. Significant climate changes have now been observed across Australia and its surrounding

coastal seas. The clearest signal is warming of air and sea temperatures; further, the observed rates of warming have accelerated since the mid-20th century. Ocean warming has been greater than the global average around Australia, and most intense in waters off south-east Australia. Changes that can be attributed to climate change in the hydrological regime are more difficult to differentiate from natural variability in Australia, as there is high inter-annual variability in this "land of drought and flooding rains"¹. That said, trends towards significantly drier winters in the south-west of Western Australia and part of southern Australia over a long period of time appear to be largely attributable to human-induced changes in the climate system. Attribution is less clear for recent trends towards wetter and drier conditions in northwest and along the east coast, respectively. Even without significant changes in average rainfall, warmer air temperatures increase evaporative losses and thus enhance the intensity of recent droughts, and reduce river flows. Sustained and co-ordinated monitoring of the physical environment, especially lacking for Australia's freshwater ecosystems, is important to assess the magnitude and biological consequences of ongoing changes.

INTRODUCTION

Global climate warming is not a future event – observations and impacts from around the world show that in recent decades the fingerprint of climate change is apparent (e.g. Root et al 2003). The decade 2000-2009 was the warmest in the instrumental record period globally (Arndt et al., 2010) and across Australia (Bureau of Meteorology/CSIRO 2010). Humans, and the natural and managed ecosystems that we rely upon, are adapted to operate within a limited range of prevailing local climatic conditions – the coping range (Jones and Mearns 2005). These typical conditions are what we expect the weather to be like at a particular location and time of year based many years of observations and includes both the average and the range of variability from year-to-year (**Figure 1**). A climate change is, therefore, a significant change in what we expect the weather to be like at a particular location and season (Mitchell et al., 1966). The change could be in average values and/or in the variability about the average, i.e. the range of extremes, and takes the

¹ Dorothea MacKellar (1904) My Country

system outside its coping range. Determining the nature and significance of climate changes requires long, homogeneous observations of the physical environment (e.g. Manton et al 2001).

Climate change is not new – global and regional climates have varied in the past over a range of timescales due to several causes such as El Niño-Southern Oscillation events, Pacific Decadal Oscillation, volcanic aerosols and the amount of incoming solar radiation (Le Treut et al., 2007). We have, however, entered a new era of rapidly changing global climate as a consequence of human activities, where unlike previous warming, increases in atmospheric carbon dioxide (CO₂) concentration is preceding temperature change. Human activities over recent centuries are increasing the concentrations of greenhouse gases in the atmosphere (Forster et al., 2007). This is changing the global energy budget (Trenberth et al., 2009) and causing current global warming (Trenberth et al., 2007). The atmospheric concentration of the main greenhouse gas, CO₂ has increased by ~40% since the late 18th century and is now at its highest concentration in at least the last 800,000 years (Luthi et al., 2008). Not only are atmospheric concentrations of greenhouse gases rising but the rate of increase is accelerating (Figure **2a).** The annual mean growth rate of CO_2 was 2.0 ppm.yr⁻¹ for 2000-2007 compared to an average annual growth rate of 1.5 ppm.yr⁻¹ from 1990-1999 (Canadell et al., 2007). In addition, about a third of the extra CO2 in the atmosphere has been absorbed by the oceans (if this had not occurred warming would have been greater) and is changing their chemistry (Figure **2b**) with significant consequences for marine calcifying organisms (e.g. Doney et al., 2009). Combining instrumental observations of air temperatures over land and sea surface temperatures clearly shows the world has been warming since the mid 19th century and that the rate of warming is accelerating (**Figure** 3). These trends cannot be explained as artefacts of measurement, despite the best hopes of climate deniers (Jones et al., 2005).

Rapid global climate change is already occurring (Allison et al., 2009; Steffen, 2009) with significant consequences for freshwater resources (Bates et al.,

2008a). What changes have already been observed that might affect Australia's marine and freshwater aquatic environments? In this paper we review recent observational evidence for significant changes in Australia's surface climate. Is surface climate already changing as projected by global climate models (**Hobday et al., this volume**)? Current climate changes are set against the backdrop of the driest inhabited continent on earth with exceptionally high natural inter-annual rainfall variability that places Australia on the "climate change front line" (Palutikof, 2010).

The high natural variability in the Australian climate means assessing changes in the physical environment requires long periods of homogeneous instrumental observations. The availability of such data for all components of the physical environment of Australia's aquatic environments varies. The Bureau of Meteorology provides extensive and accessible surface climate data sets (e.g. air temperature, rainfall, sea surface temperatures, sea-level pressure, tropical cyclone activity) that allow examination of temporal and spatial patterns and trends (Jones et al., 2009; Alexander et al., 2010). Additional observations are available from oceanographic databases; however, the more recently available satellite observations are too short to detect robust trends that allow attribution. A centrally coordinated and standardized database for Australian freshwater resources is only now being developed (www.bom.gov.au/water) and data are currently scattered amongst various regional archives. We, therefore, use air temperatures and rainfall as "proxies" for surface climate conditions that might affect freshwater environments.

MARINE ENVIRONMENTS

Temperature, freshwater input, sea level, ocean chemistry, the frequency of extreme events all control the makeup and physiological processes (e.g. distribution, ranges, community composition, community dynamics, seasonal timing of spawning etc) of species in Australia's marine ecosystems (e.g. Poloczanska et al., 2007; Hobday et al., 2008). Here we describe these

physical changes around Australia; other papers in this issue describe the resulting biological changes (**add refs later**).

Sea surface temperatures

Significant warming is already evident in Australia's surrounding oceans (Lough 2009). Globally, sea surface temperatures (SSTs) at comparable latitudes to Australian waters have significantly warmed (Figure 4a) with recent average temperatures (1980-2009) 0.41°C warmer than in the early 20th century (1910-1939). Over the same period, the warming of Australian waters have been of greater magnitude, 0.57°C (Figure 4b). The rate of warming around Australia in all seasons has accelerated in recent decades and also shows a spatial signature with greatest warming off the southeastern and southwestern coasts (Figure 4c). For tropical coastal waters, this warming has already resulted in southward shifts of climate zones by >200 km along the east coast and by ~100 km along the west coast (Lough, 2008). The evidence for significant ocean warming both at the surface and through the water column is supported by both global SST compilations and continuous in situ coastal observations (e.g. Holbrook and Bindoff, 1997; Alory et al., 2007; Ridgway, 2007; Caputi et al., 2009). This warming has been accompanied by increasing sea surface salinity (Pearce and Feng, 2007; Thompson et al., 2009), which is related to a world-wide signature (Helm et al., 2010).

Sea level

Globally, average sea level has risen about 20 cm since the late 19th century (**Figure 5a**), largely due to thermal expansion with a relatively minor contribution, so far, from melting land ice (Bindoff et al., 2007). The rate of sea-level rise has accelerated recently and is now at the upper end of IPCC AR4 projections (Rahmstorf et al., 2007; Church et al., 2008). Although based on monitoring systems that only started in the early 1990s (see National Tidal Centre: <u>www.bom.gov.au/oceanography</u>), making the significance of trends difficult to confirm, observed recent sea-level rise

around Australia's coastline has been lower along the central east coast and greater along the western and north coasts (**Figure 5b**).

Sea-level rise is not, therefore, uniform. The Indian Ocean, for example, shows considerable spatial complexity in recent observed sea-level changes, partly due to changes in atmospheric circulation patterns (Han et al., 2010). Rising sea level also affects the frequency of extreme sea level events affecting the coast. Sydney and Fremantle both have long-term records back to the 1920s and these show that the occurrence of extreme sea level events (defined by the 0.01 percentile) has become three times more frequent in the period after 1950 compared to earlier years (Church et a., 2006).

Ocean currents

Australia is unique with warm, poleward-flowing currents along both its eastern (East Australian Current, EAC) and western (Leeuwin Current) coasts which results in, for example, significant coral reefs and coral communities along both coastlines (Lough, 2008). Evidence is emerging for significant changes in the EAC which, over the period 1944-2002, has increased its southward penetration by ~350km, bringing warmer and saltier waters further south (Ridgway 2007; Hill et al., 2008). The oceanography of some of Australia's marine environments, such as the Great Barrier Reef, are especially complex (Steinberg, 2007) and require improved understanding of the linkages between large-scale and meso and lower scale processes to begin to document potential changes in circulation patterns (e.g. Weeks et al., The nationally co-ordinated and standardised ocean observing 2010). (Integrated Marine Observing systems System, IMOS. http://www.imos.org.au/) will significantly improve our understanding of ocean circulation changes.

Ocean chemistry

Changes in water chemistry, as a result of the oceans absorbing about a third of the extra anthropogenic carbon dioxide injected into the atmosphere, are highly likely to have significant consequences throughout Australia's marine ecosystems, especially those involving organisms that form skeletons and shells (Kleypas et al., 2006; Hoegh-Guldberg et al., 2007; Moy et al., 2009). Assessing baseline conditions. changes and potential biological consequences requires long-term monitoring of the chemistry of Australia's marine waters. We do not, for example, have the long-term perspective available from the Bermudan (BATS http://bats.bios.edu/) or Hawaiian (HOTS http://hahana.soest.hawaii.edu/hot/) ocean chemistry time series (e.g. Dore et al., 2009). To date, assessments of change in Australian and much of the world's oceans have relied on repeat oceanic observations rather than continuous time series (e.g. Borges et al., 2008; Takahashi et al., 2009). We still know very little about baseline and variation in ocean chemistry conditions in Australian waters, which appear to be particularly complex in tropical coral reef ecosystems (e.g. Gagliano et al., 2010). Improving the observational record of ocean chemistry around Australia is a significant focus of IMOS.

FRESHWATER ENVIRONMENTS

Australia's freshwater environments range from ephemeral billabongs and inland lakes, seasonal creeks and rivers, to permanent tropical rivers. High interannual variation in rainfall leads to a range of species and systems that can cope with water shortage, however, the combination of landscape modification as a result of European settlement and agriculture, and climate change is stressing many systems. Flow into rivers is related to air temperatures, rainfall, and extreme events (cyclones and storms).

Surface air temperatures

Warming of air temperatures over land areas is one of the clearest signals of a rapidly changing climate system and rates of warming are greater than for the oceans. Globally, air temperatures over the period 1980-2009 are 0.62°C warmer than 1910-1939 (**Figure 6a**). Over the same time period, air temperatures over Australia warmed by 0.70°C (**Figure 6b**). As with SSTs in Australian waters, air temperatures over the continent are warming faster than the global average. Warming is evident across almost the entire country (**Figure 6c**) and the rate of warming has accelerated in recent decades (Lough, 2009). Observed warming is now clearly attributable to increases in atmospheric greenhouse gas concentrations both globally (Trenberth et al., 2007) and across Australia (Karoly and Braganza, 2005).

Warming air temperatures across Australia are resulting in changes in temperature extremes which match model expectations (Alexander et al., 2007; Alexander and Arblaster, 2009). Higher mean maximum and minimum temperatures are leading to more hot days and warm nights and fewer cool days and cold nights across Australia (Chambers and Griffin, 2008; Hennessy et al., 2008). Trewin and Vermont (2010), for example, examined record high and low temperatures over the period 1957-2009, when mean daily maximum and minimum air temperatures warmed by ~0.7-0.8°C. They found that record low temperature extremes dominated the earlier part of the record and record high temperature extremes dominated the most recent decades. Thus, for example, the most extreme maximum daily temperatures occurred on average 13.3 times per decade (20.4/decade for extreme lows) from 1957-1966 but for 1997-2009 the highs occurred almost twice as frequently (22.5/decade) and the lows almost half as frequently (9.3/decade).

Rainfall and river flow variability

Rainfall is highly seasonal and exhibits high inter-annual variability across much of Australia. Australian freshwater ecosystems are sensitive to both seasonal flows, e.g. in the dry tropics of northern Australia (Abrantes and Sheaves, 2010; NALWS 2009) and to recent droughts in southern Australia, the effects of which being compounded by human interventions in natural river systems (e.g. Bond, et al., 2008). Highly variable river flows regulate many processes in freshwater environments and the spatial and temporal variability both seasonally and inter-annually play a significant role in shaping ecosystem dynamics (e.g. Leigh et al., 2010; Puckridge et al., 2010). Although of primary interest for freshwater ecosystems, the extent to which we can develop a coherent view of river flow variations across Australia is still limited by the lack of a nationally-integrated and centralized data repository although this is now being developed (www.bom.gov.au/water). We,

therefore, focus on the high-quality observations of rainfall provided by the Australian Bureau of Meteorology as a "proxy" for river flows.

Although clear evidence is now emerging for a recent acceleration in the global hydrological cycle (Helm et al., 2010), assessing the magnitude and significance of observed rainfall changes across Australia is hampered by the high interannual rainfall variability. High rainfall variability results in Australian river flows being amongst the most variable in the world (Finlayson and McMahon (1988). Seasonal, inter-annual and longer-term rainfall variability across Australia is largely controlled by several external factors recently summarized by Risbey et al. (2009). El Niño-Sothern Oscillation (ENSO) events have long been recognized (e.g. Troup 1966; Allan et al., 1996) as the primary source of inter-annual variability across much of the country, though with effects varying across seasons and region. Again river flows in eastern Australia stand out in a global context as being particularly sensitive to ENSO events (Ward et al., 2010). The Madden-Julian Oscillation (MJO) primarily affects within season variability of the northern Australian summer monsoon (Wheeler et al., 2009). The Indian Ocean Dipole (IOD) primarily affects winter (June to October) rainfall in the southwest and southeast where rainfall is also influenced by the Southern Annular Mode (SAM).

The strength of the linkages (teleconnections) between ENSO events and Australian rainfall waxes and wanes on interdecadal time scales as modulated by the Pacific Decadal Oscillation (PDO; Mantua et al., 1997; Power et al., 1999). During PDO cool phases the teleconnections between ENSO and eastern Australian rainfall tend to be stronger, with more coherent rainfall anomalies and higher rainfall variability compared to PDO warm phases (Kiem et al., 2003; Meinke et al., 2005). La Niña events that occur during PDO cool phases result in river floods of twice the magnitude of regular La Niña events (Verdon et al., 2004).

In addition, although showing several common features, no two El Niño or La Niña events evolve in exactly the same way (Trenberth and Stepaniak, 2001).

More recently it has been suggested that ENSO events have shifted from those dominated by warming or cooling centred in the eastern equatorial Pacific to events (termed ENSO-Modoki) characterised by warming or cooling in the central equatorial Pacific (Ashok et al., 2007). Whether this is a "global warming" signal is, as yet unclear, but the two flavours of ENSO appear to produce different rainfall anomaly patterns across Australia. ENSO-Modoki are associated with greater rainfall anomalies across northwest and northern Australia (to the northern Murray-Darling Basin) compared to the traditional ENSO where the main effects (droughts or floods) are seen in eastern Australia (Cai and Cowan, 2009; Taschetto and England, 2009a).

Rainfall changes

Compilations of reliable observations by the Bureau of Meteorology allow assessment of spatial and temporal variations in Australian rainfall, with confidence, back to the early 20th century (Jones et al., 2009). As noted by Hennessy et al (2008; CSIRO/BOM 2007; Gallant et al., 2007), given the high degree of interannual and decadal variability, assessing the reality and significance of frequency of rainfall extremes and changes in average rainfall are more difficult and particularly dependent on the chosen analysis period, e.g. much of eastern Australia experienced wetter conditions in the 1950s and 1970s (Lough, 2007) (**Figure 7**). There is, therefore, some disagreement in published analyses of Australian rainfall trends as to the nature and significance of recently observed trends and whether they can be attributed to global climate change. It is important to note, that even if rainfall is unchanged, warmer air temperatures lead to increased evaporation of water; coupled with increased demands by human societies and population growth climate change will significantly alter inland river systems.

The trend to wetter summer conditions in northwest Australia appears to be a relatively clear (Shi et al., 2008; Smith et al., 2008) as do winter rainfall declines in southwest Western Australia and part of southwest of southeastern Australia. Winter rainfall variations in the latter two regions are linked as rainfall-bearing disturbances typically track across both regions.

The recent winter rainfall declines in the two areas have been plausibly linked to significant southward shifts in these rainfall-bearing disturbances and storms. This appears to be part of significant changes in the larger-scale atmospheric circulation patterns with higher sea-level pressure over southern Australia, a more intense sub-tropical ridge along the east coast and more positive phase of SAM which reflects a contraction southwards of the main Southern Hemisphere westerly wind belt (Larsen and Nicholls, 2009; Alexander et al., 2010; Hope et al., 2010; Nicholls, 2010). The 15-20% decline in winter rainfall since the 1970s has been suggested to have changed the hydrological regime of southwestern WA from perennial to ephemeral streams (Petrone et al., 2010) and is also associated with significant (up to 50%) reductions of inflows into dams (Bates et al., 2008b).

Widely-reported declines in eastern Australian rainfall (e.g. CSIRO, 2007) appear, at least for Queensland, to be largely confined to the southeastern part of the state and only become apparent when records from the late 20th century are considered (Smith, 2004; Taschetto and England, 2009a, b). Steffen (2009) suggests that the "drying connection" in northern and eastern Australia is "not yet clear" and attribution of recent east coast rainfall declines are confounded by decadal influences with higher rainfall characterising the 1950s and 1970s.

Recent reductions in rainfall are, however, compounded by warming air temperatures (Nicholls, 2004) and this leads to a greater reduction in river flows than caused by reduced rainfall alone, due to evaporation as water moves across the landscape. For the Murray-Darling Basin, Cai and Cowan (2008), examining the 2001-2007 drought, found that a warming of 1°C resulted in 15% reduction in inflows. Streamflows decreased by 55% for the Murray-Darling Basin whilst rainfall declined by only 11%, as a result of this temperature effect (Steffen 2009). Similarly, Murphy and Timbal (2008) provided evidence that recent drought conditions in southeast Australia were more extreme than earlier rainfall deficits due to warmer air temperatures.

Tropical cyclones

Large volumes of freshwater can be deposited via rainfall during extreme events, such as tropical cyclones, which subsequently floods the landscape and flows into rivers and lakes. There is still debate as to whether we are seeing any significant changes in the occurrence and frequency of tropical cyclone activity globally (e.g., Emanuel, 2005; Elsner et al., 2008). Nicholls et al. (1998) provided evidence of an apparent decline in numbers of weak tropical cyclones in the Australian region over the period 1969/70 to 1996/96 based on satellite observations. They suggested that this trend was, in part, due to improved discrimination through time of tropical cyclones from other tropical storms but also noted a weak increasing trend for the most intense tropical cyclones. Comparing the east and west Australian tropical cyclone regions, Hassim and Walsh (2008), examining the period 1969/70 to 2004/2005, provide some evidence that the number, duration and maximum intensity of severe tropical cyclones off WA have been increasing since the 1980s but in the eastern region the number has decreased with no obvious trend in either intensity or duration. There has been no observed change in the latitudinal distribution of tropical cyclone activity.

IMPROVED MONITORING FOR AUSTRALIA'S AQUATIC ENVIRONMENTS

Climate change impacts cannot be detected without long-term observations because oceanic properties vary significantly across a range of spatial and temporal scales (Thompson et al., 2009)

To predict the biological consequences of ongoing climate change we need sustained monitoring to determine average conditions, seasonal cycles and inter-annual and longer term variability and detect trends in Australia's aquatic environments – this information will also be critical in management responses to climate variability and change (e.g. Murray-Darling Basin Authority 2010). The extent to which we can do this varies considerably. Australia has, for example, many high-quality, homogenous and ongoing records of weather elements over land that allows detection and, in some cases, attribution of recent trends in air temperatures and rainfall. Global compilations of ships-of-

opportunity measurements at sea (now routinely blended with satellite observations), especially of surface water temperatures, also provide a high level of confidence in the nature and significance of recent warming trends in Australian marine waters.

There is, however, much room for improvement and we can never underestimate the value of establishing and maintaining long-term monitoring stations with common sampling techniques and data quality standards (e.g. Pearce and Feng, 2007). Maintenance of just four coastal monitoring sites for over 60 years has provided significant insights into both physical and chemical changes in the marine environment (Thompson et al., 2009), yet also leaves considerable uncertainty in other regions. Achieving comprehensive geographic coverage in a country the size of Australia is a challenge but "necessary if we wish to understand the impacts of climate variability and the consequent implications for our marine ecosystems" (Thompson et al., 2009).

The Integrated Marine Observing System (IMOS) has set a new standard for observing and understanding processes in Australia's varied marine environments that can provide the necessary data to link physical and biological processes (e.g. Lough et al., 2010). The value of the IMOS initiative will only increase through time and thus it is essential that the national commitment for its ongoing support and funding is maintained. The publicly accessible data will be critical not only for attributing changes in the environment, but for interpreting changes in the biology of adjacent systems.

For Australia's freshwater environments, there have been many calls for more organized and integrated monitoring (e.g. Davies et al., 2010; Lake et al., 2010; Tomlinson et al. 2010). As noted by Bond et al (2008) the responses by both scientists and resource managers to drought in our freshwater environments have to date, been "haphazard and uncoordinated". We are, for example, unable to examine long-term changes in freshwater temperatures which have been shown to be also warming in parts of the USA and Europe (e.g. Webb and Nobilis, 2007; Kaushal et al., 2010). The

establishment in New Zealand of the National River Water Quality Network, which undertakes standardised physical and chemical monitoring of 77 sites on 35 rivers now provides continuous time series back to 1989 (http://www.niwa.co.nz/our-science/freshwater/our-services/water-qualitymonitoring-and-advice/national-river-water-quality-network-nrwqn). As with any monitoring program the value of sustained high-quality measurements only increases with time and the New Zealand example allows insights into biological, physical and chemical linkages and changes which would not be obtainable otherwise (e.g. Scarsbrook et al., 2000, 2003).

Australia is not bereft of significant observations of the physical, chemical and biological characteristics of its freshwater environments, some of which extend back to the early 20th century (e.g. river flows). To date, however, such data are scattered through State and Territory water authorities and individual scientists' or scientific organizations' research programs. The future does look brighter with the recent establishment within the Australian Bureau of Meteorology of the Australian Water Resources Information System (AWRIS; www.bom.gov.au/water) as a consequence of the Water Act At the core of the AWRIS will be a centralized and nationally-2007. consistent system for storage and retrieval of current and historical water Amongst its many objectives, of particular significance for data. understanding change in Australia's freshwater environments are the commitments to modernise and extend water monitoring systems and provide a centralised data base of river flows and water quality parameters.

SUMMARY

Observational records show that both global climate and that of the Australian region are already significantly changing due to human activities changing the composition of the atmosphere and changing the energy balance of the global climate system. The extent to which observed significant changes (detection) can be attributed to human-induced changes in the atmospheric composition of greenhouse gases (attribution) (Hegerl et al., 2007) varies between marine and freshwater systems, as well as regionally. It is very likely that the widespread warming of air temperatures across Australia and surface ocean

temperatures in the surrounding seas can be attributed to human-induced Similarly the observed increase in northwest summer radiative forcing. rainfall and decreased winter rainfall in the southwest of Western Australia and southeastern Australia are consistent with greenhouse gas forcing (Nicholls 2006; Steffen 2009). Attribution of recent east coast rainfall declines are, however, confounded by decadal influences with higher rainfall characterising the 1950s and 1970s. Even without significant changes in average rainfall totals, warmer temperatures are already exacerbating the severity of Australian droughts (Ummenhofer et al., 2009), significantly affecting the availability of freshwater resources. In both marine and freshwater systems, these physical changes are projected to continue for the next 50-100 years (Hobday et al., this volume), and both human and biological systems will be challenged in their ability to adapt. Without successful greenhouse gas mitigation, significant disruption to Australia's aquatic environments is almost certain.

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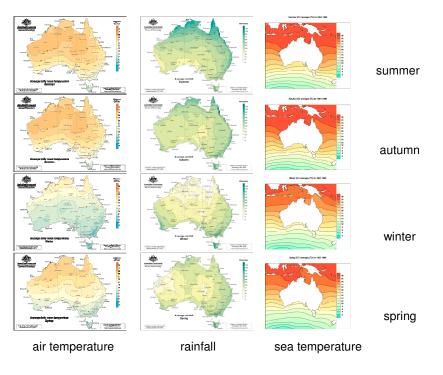


Figure 1

Figure 1: Climate averages, 1961-1990, for Australia for summer, autumn, winter and spring and air temperatures, rainfall and sea surface temperatures (Data source: BOM).

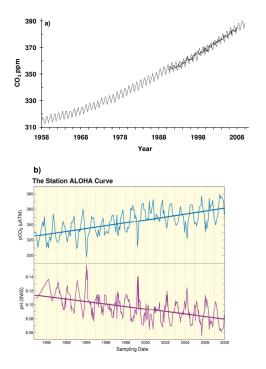


Figure 2

Figure 2: Monthly atmospheric carbon dioxide concentration (ppm) for a) Mauna Loa, Hawaii (grey, 1958-2009) and Cape Ferguson, Queensland (black, 1991-2008). (Data source: World Data Centre for Greenhouse Gases <u>http://gaw.kishou.go.jp/cgi-bin/wdcgg</u>), and b) monthly observations of partial pressure of seawater CO₂ and pH measured in situ at Station ALOHA, northern Pacific, 1988-2007 (adapted from Dore et al., 2009).

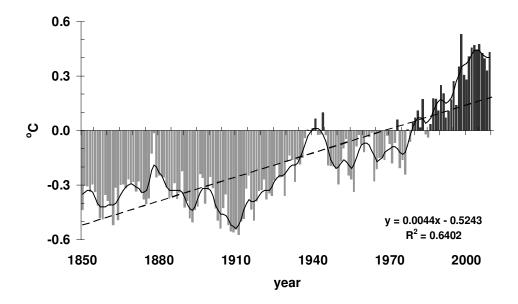


Figure 3: Annual global land and sea temperature anomalies (from 1961-1990 mean): 1850-2009. Thick line is 10-year Gaussian filter emphasising decadal variability; dashed line is linear trend (Data source: HadCRUTV3, <u>www.cru.uea.ac.uk</u>; Jones et al., 1999; Brohan et al., 2006; Rayner et al., 2003, 2006).

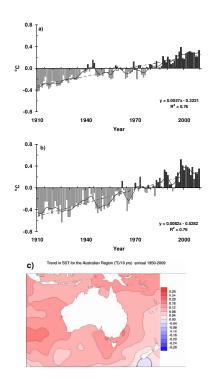


Figure 4: Annual sea surface temperature anomalies (from 1961-1990 mean), 1910-2009 for a) global oceans, 45°N-45°S, b) Australian region (see Figure 1), and c) linear trend (°C/decade) of annual sea surface temperatures, 1950-2009 (Data source: HadISST, Bureau of Meteorology). Thick line is 10-year Gaussian filter emphasising decadal variability; dashed line is linear trend.

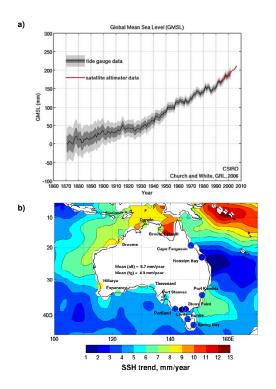


Figure 5: a) Global sea level, 1870-2006 (from Church & White, 2006 www.cmar.csiro.au/sealevel, and b) net relative sea-level trend, mm.yr⁻¹, early 1990s through June 2009 (Bureau of Meteorology, www.bom.gov.au/oceanography).

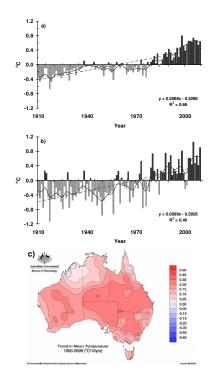


Figure 6: Annual air temperature anomalies over land (from 1961-1990 mean), 1910-2009 for a) global land area, b) Australia, and c) linear trend (°C/decade), 1950-2009 (Data sources: HadCRUV v3, Bureau of Meteorology). Thick line is 10-year Gaussian filter emphasising decadal variability; dashed line is linear trend.

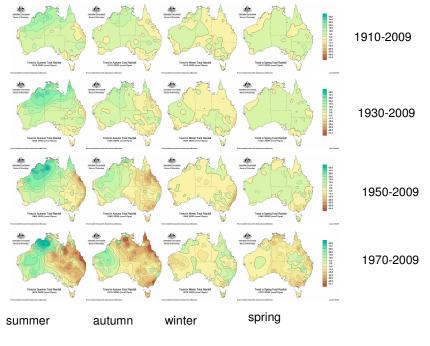


Figure 7: Linear trends in seasonal rainfall totals (mm/decade) for time periods 1910-2009, 1930-2009, 1950-2009 and 1970-2009 (Date source: BOM).

Projected climate change in Australian aquatic environments

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ABSTRACT

Changes in the physical environment of aquatic systems that are consistent with climate change have already been reported from around Australia. These have, or are expected to have impacts on a range of marine and freshwater species. The magnitude of future impacts depends on future environmental conditions. Projections of the future state of marine and freshwater environments can be obtained in several ways, including qualitative knowledge of the earth system, interpolation of historical trends, and dynamical projection using global climate models. Downscaling of model results is often necessary before they are useful to aquatic biologists, managers and planners, and can be achieved via statistical or dynamical models. Here we show results of projections for a range of environmental variables for Australian marine and freshwater environments using several of these approaches and discuss the limitations and uncertainties that accompany such projections. In the ocean, warmer sea surface temperatures are projected around Australia but particularly for south-eastern Australia, with the slowest rates of warming for the upwelling regions of western Victoria.

The East Australia Current will transport greater volumes southward, while the Leeuwin Current may weaken. Sea levels will rise around the country, although regional projections are not yet considered reliable. On land, air temperatures will rise and rainfall is generally projected to decline across much of Australia in coming decades. Together these changes will result in reduced runoff and hence stream flow and lake storage. The impact of these changes for marine and freshwater species will result in changes to their distribution, abundance, physiology and phenology. Adaptation to these changes is possible for some species and the humans that rely on them, but will be limited by the rate of the projected change, and the investment available to respond. Adaptation efforts under future climate change are expected to be local. At present, however, local projections are generally considered less certain than those for large spatial and temporal scales.

Additional Keywords: Australian marine and freshwater fishes, climate change impacts, future climate scenarios, global climate model

INTRODUCTION

The climate of Australia's marine environments has already changed compared with historical baselines (Ridgway 2007; Pearce and Feng 2007; Lough 2008; Poloczanska *et al.* 2009; Lough *et al.*, this volume). On both coasts, water temperatures have warmed and salinity has increased in the poleward-flowing currents (Ridgway 2007; Pearce and Feng 2007). In the ocean surrounding Australia, these physical changes are coincident with biological changes in a range of marine species, including changes in local abundance, geographic range, phenology, and community structure (e.g. Hobday *et al.* 2007; Poloczanska *et al.* 2007; Ling 2008; Poloczanska *et al.* 2009; Figueira and Booth 2009; Last *et al.* 2010; Pitt *et al.* 2010). It seems clear that climate is already affecting many marine fishes and other organisms.

Given the physical changes observed over the Australian continent, for example in air temperature and rainfall (e.g. Hughes 2003; CSIRO 2007; Nicholls 2006; Hennessey et al. 2007), it is likely that freshwater environments such as rivers and lakes, are also being impacted, although the evidence is less coherent (Lough et al., this volume). Changes in land cover have exacerbated the effects of warmer temperatures due to climate change resulting in longer-lasting and more severe droughts (e.g. Deo et al. 2009; Ummenhofer et al. 2009). The droughts and general drying in some parts of the country reduce runoff into fish habitats such as rivers and lakes. Victoria has seen a decline in autumn rainfall of 40% in the period 1950-2006 (Cai and Cowan 2008). In the Murray-Darling basin rainfall declined by 11%, yet river flow has declined 55% below the long-term average (Steffan 2009). In recent years an increase of 1 °C in air temperature has been associated with a 15% reduction in stream flow (Cai and Cowan 2008). In south-western WA, stream flow and water storage in dams and reservoirs has fallen dramatically since the early 1900's, from some 338 GL to less than 90 GL for the period 2001-2006 (Steffen 2009).

Given the historical emissions of greenhouse gases that have already occurred, and the observed climate changes to date, future changes are inevitable (IPCC, 2007; Solomon *et al.* 2009). At a global scale, climate change that takes place due to increases in carbon dioxide concentration is

largely irreversible for 1,000 years after emissions stop (Solomon *et al.* 2009). Sea level, temperature and ocean pH will continue to change over the coming centuries (IPCC 2007). While some may consider these projections confronting, and even suggest that action is futile, there is still opportunity to limit future impacts below dangerous levels (e.g. Schneider 2009). Importantly, planning for adaptation responses requires information on the expected condition of future ocean and freshwater environments. Timely development of appropriate adaptation strategies should increase the flexibility in management of vulnerable species and ecosystems (Hulme 2005). Thus, access to information on future climate is critical for many biologists working to determine species and ecosystem impacts. In this paper, we first explain how climate projections are obtained, discussing some of the associated caveats and limitations, and then provide a range of projections for Australia's aquatic environment. Given the rapid progress in development of climate projections, improving the ability of aquatic scientists, managers and policy makers to access the most up-to-date and appropriate projections will lead to a range of benefits in delivering better biological projections, and is a major goal of this paper.

Projecting future conditions

One way to estimate future environmental conditions is simply to extrapolate based on historical trends. This approach is not widely used, however, as it would only be useful over short periods of time and may not incorporate dynamical changes in the ocean-atmosphere system. Future conditions for the Earth's climate system will depend not only on the response to changes in greenhouse gas concentration and radiative forcing, but also on how humans respond through changes in technology, economies, lifestyle and policy. Because a range of futures are possible, and a variety of approaches were being used by climate modelers, the Intergovernmental Panel on Climate Change (IPCC) commissioned development of a range of future emission scenarios to be used for driving global circulation models (see Figure 1 in Moss *et al.* 2010). The most recent set of scenarios were presented in the Special Report on Emissions Scenarios (SRES) for use in the Third Assessment Report (TAR) in 2001 and were also used for the Fourth

Assessment Report (AR4) in 2007 (IPCC 2007) (**Figure 1**). These scenarios represent a range of warming, and have been widely used in biological studies (e.g. Hobday 2010). Low (e.g. SRES BI, CO₂ concentration stable at 549 ppm by 2100 and global temperatures ~2-4 °C higher), medium (e.g. A1B, CO₂ concentration at 717 ppm by 2100 and global temperatures ~3-5 °C higher) and high (e.g. A1FI, CO₂ concentration at 970 ppm by 2100 and global temperatures ~5-6 °C higher) scenarios are often used in projection studies as a way of bracketing the future change, although given present rates of greenhouse gas emission and observed climate change (Rahmstorf *et al.* 2007; Le Quéré et al 2009), low scenarios are now seen as less realistic.

Unfortunately, just as biologists and other "user" scientists were becoming familiar with these scenarios and their nomenclature, an updated set of scenarios is being used for IPCC AR5, based on radiative forcing (Moss et al. 2010). Radiative forcing describes an external change in the radiation balance, such as changes in atmospheric concentrations of greenhouse gases. Positive forcing indicates warming of the earth system. These new scenarios, known as RCP (representative concentration pathways) with a similarly confusing nomenclature, differ from the SRES set in that they include scenarios that allow for climate change mitigation and adaptation (Figure 1). While the currency has changed (gas concentration (ppm) to radiative forcing (W m⁻²)), the SRES and RCP's are related, in that increasing concentrations of greenhouse gases affects the balance between incoming solar radiation and outgoing heat radiation which determines the Earth's average temperature. Previously, SRES greenhouse gas concentrations were converted to radiative forcing of the climate system using radiation conversion codes located within each GCM, which represented an unnecessary additional source of variation now removed under the RCP approach. Biologists will likely continue to use the SRES scenarios for some time, as many climate models and projections that are available for wide use are based on these scenarios. Such a transition period occurred when the IS92 scenario set used in the Second Assessment Report of 1995 was superceded by the SRES set (e.g. Poloczanska et al. 2007).

As these scenarios are global and based on changes in greenhouse gas concentrations (SRES) or radiative forcing (RCP), the changes are converted into a range of relevant variables at finer scales using Global Climate Models (GCM, also General Circulation Models) developed by a number of research organisations around the world. These models are based on the general principles of fluid dynamics and thermodynamics and had their origin in weather prediction (Stute *et al.* 2001). GCMs describe the dynamics of the atmosphere and ocean in an explicit way, at horizontal space scales of 1-3 degrees, and with varying numbers of vertical layers in the ocean and atmosphere, and provide a way to run quantitative experiments on climate conditions during the past, present, and future. Advances in development of GCM's used for climate modeling are typically oriented around the IPCC reporting timelines, with transition periods as for emission scenarios when both old and new models are available to the wider research community.

Uncertainties in future projections based on climate models should not be underestimated, and result from a combination of scenario uncertainty (what will be the future level of greenhouse gas emissions), climate sensitivity to these emissions, difference between climate models (e.g. how they incorporates ocean-land-atmosphere processes), and model scale (IPCC 2007). While single model-scenario combinations may have considerable uncertainty, there are a number of approaches to improve confidence in future projections such that dependent biological projections can be useful. What is clear from analyses of model outputs is that rates of warming are projected to continue to the end of this century, unless major mitigation efforts are successful (Schneider 2009).

Which model to use and how to get it

Biologists can be challenged in several ways in their attempts to use data from the range of available GCM's. Model selection and validation, model scale, and model access can all be problematic. The first two issues will be discussed briefly before we describe how to access model data and use examples to illustrate potential future environmental conditions in Australian aquatic environments.

Not all climate models perform equally well for all variables in all regions. While the ability of models to project future conditions cannot be assessed, performance in reproducing current climate conditions and historical patterns can be assessed. For example, Suppiah et al. (2007) used statistical methods to test how well 23 AR4 models simulated observed average patterns of mean sea-level pressure, temperature and rainfall over the Australian region. They then used the 15 best models to derive projections for 2030 and 2070 for the variables of interest. This process, known as validation, is considered best practice when attempting to use GCM's to forecast future conditions. Unfortunately, the observational data to validate models is often not available for aquatic biologists, nor is it within their typical skill set. Thus, using a suite of models to make an ensemble average will be the best available option for marine and freshwater researchers, although there is some debate as to whether this approach provides the most robust projections for regionally-specific climate change projections (Perkins and Pitman, 2009; Pierce et al. 2009; Shukla et al. 2009; Smith and Chandler, 2010). While the resolution of climate models is improving, model scale is still considered coarse (~100-200 km) with regard to representation of the environments that many aquatic biologists are interested in (< 10 km). Thus, downscaling of climate models is considered necessary before projections are meaningful.

In this context, downscaling is the process of transforming information from coarse resolution GCMs to a finer regional spatial resolution. Downscaling is necessary where the mesoscale processes (in the ocean these operate at length scales of < ~100 km) are very sensitive to local climate, and the drivers of local climate variations, such as topography, are not captured at coarse scales. There are two broad categories of downscaling: dynamic (which simulates physical processes at fine scales) and statistical (which transforms coarse-scale climate projections to a finer scale based on observed relationships between the climate at the two spatial resolutions) (e.g. Whetton *et al.* 2005; Schmidli *et al.* 2008; Vasilaides *et al.* 2009; Tabor and Williams 2010).

Dynamical downscaling uses regional climate models (RCMs) to translate the large-scale weather and ocean evolution from a GCM into a

physically consistent evolution at higher resolution (Tabor and Williams 2010). Marine RCM's represent the processes that are sub-grid scale in the GCM's, which makes them computationally expensive, as they solve multiple equations regarding the transfer of heat and energy in multiple depth layers at time steps as short as 30 minutes. Statistical downscaling is based on empirical relationships between the regional climate (e.g. local sea surface temperature) and large-scale predictor variables (e.g. heat content in the tropical ocean) derived from the GCM. Advantages include computational simplicity and that large-scale predictors can be relatively robust in terms of the relationship with local variables. Different relationships occur in different regions, thus downscaling must be calculated anew for each study region. This approach assumes that the relationship between large scale processes and local variables is stationary over time (Tabor and Williams 2010) (**Figure 2**).

The primary source of information on future projections comes from the output of GCM's, for example the set of IPCC AR4 models. The volume of data from these GCMs can be overwhelming and disparate in file structure and notation. Central repositories were established to facilitate access to consistently formatted AR4 suite of models (www2pcmdi.llnl.gov/esg data portal), however, even downloading and accessing complete suites of data is difficult for biologists with limited programming skills. Recently, data portals have been developed that allow extraction of the desired data without downloading the raw files (e.g. http://www.ipccdata.org/ddc visualisation.html). These raw data are coarse in time (e.g. monthly fields) and space and in the case of marine waters, do not resolve mesoscale features such as eddies, coastal upwelling, boundary currents, or fronts (Figure 3 A). At this resolution, only broad latitudinal patterns of warming can be seen.

Secondary processing of GCM data by GCM-literate groups (e.g. Whetton *et al.* 2005; Tabor and Williams 2010; Harwood *et al.* 2010) offers some options for biologists, however, the flexibility of data selection and limited number of variables available can be problematic. A set of GCM ensembles for the Australian region were released in 2007, and allow web-

based access to a limited set of variables for a range of time periods and seasons (<u>www.climatechangeinaustralia.gov.au</u>). For marine users, only a single variable is available (sea surface temperature), although wind speed projections also cover the ocean region, and for freshwater biologists only proxies such as air temperature, solar radiation, potential evapotranspiration and rainfall are available. The resolution in these products is again quite coarse, and mesoscale features are not resolved (**Figure 4**).

Finer scale data are currently available via rescaled GCMs (statistical downscaling based on pattern matching in OzClim and OzClim for Oceans, <u>www.csiro.au/ozclim/home.do</u>; Whetton *et al.* (2005)) again with a limited number of variables for aquatic users (marine: sea surface temperature, temperature at a depth of 250 m, and salinity; freshwater: rainfall, potential evapotranspiration, air temperature). While the resolution is improved, mesoscale features are still not resolved, although in the ocean, the major boundary currents on the east and west coasts of Australia can be detected (**Figure 3 B**). This data source may be the most generally useful for biologists seeking general patterns of future change, and has been widely used to inform managers and policy makers in a range of terrestrial sectors. More recently, even finer scale downscaling for terrestrial variables has been completed using the OzClim data with a topographical correction at a scale of 1 km² (Harwood *et al.* 2010)

Dynamical downscaling approaches using regional climate models for the Australian region are "experimental" only at present. For example, in the ocean, the Bluelink model (Oke *et al.* 2008) has been nested in the CSIRO Mk3.5 model and has a limited number of future years of data at a 10 km resolution, that are useful in projecting future habitat distribution (e.g. Hartog *et al.* 2010). Mesoscale features are resolved (e.g. **Figure 3 C**), although there are ongoing challenges with evaluating the reliability of the downscaling (Chamberlin *et al.* in review; R. Matear, pers comm.). Tabor and Williams (2010) discuss some additional limitations with downscaling GCM's to finer resolution.

We now illustrate some of the future projections for Australian aquatic environments out to the year 2100 based on a variety of these approaches. We encourage biologists to become primary users of climate model output, through one of the access options described above. Both absolute values and relative changes compared to a baseline period are used by biologists for both experimental studies and for predictive biological models, and we use both styles of projection in the following sections.

AUSTRALIA'S FUTURE AQUATIC CLIMATE

At a national scale, a recent summary by the CSIRO and the Bureau of Meteorology (BOM) indicate that Australian average air temperatures are projected to rise by 0.6 to 1.5 °C by 2030 (State of the Climate 2010). If global greenhouse gas emissions continue at current levels, warming is projected to be in the range of 2.2 to 5.0 °C by 2070. Warming is projected to be lower near the coast and in Tasmania and higher in central and north-western Australia. These changes will be felt through an increase in the number of hot days. Thus, drying and decreased runoff into freshwater habitats is also likely. While direct projections of stream flow are not available, historical relationships between declines in rainfall and stream flow suggest a 1:4 reduction ratio is realistic (e.g. Steffen 2009).

Warming is also expected in seas around Australia. By the 2030s SSTs are projected to be ~1 $^{\circ}$ C warmer (relative to 1980-1999) around Australia, with slightly less warming in southern Australia. By the 2070s, SSTs are projected to be between 1.5-3.0 $^{\circ}$ C warmer with slightly less warming to the south of the continent and greatest warming east/northeast of Tasmania (Poloczanska *et al.* 2007; Lough 2009).

Marine environments

The marine environments of Australia range from coastal bays and estuaries, nearshore shallows and reefs, across the continental shelf to the deep ocean where depths exceed 3000 meters (e.g. Poloczanska *et al.* 2007). Monitoring in this environment has not been comprehensive, and many gaps in time series and spatial coverage exist (e.g. Lough *et al.*, this volume). The advent of satellite-based measurements has allowed synoptic coverage, but only of near-surface properties such as temperature, ocean colour and sea surface height. Thus, projections of change in variables derived via GCMs cannot always be validated against historical observations. Here we provide

examples of projected future change in sea surface temperature, ocean currents, ocean chemistry and extreme events.

Sea surface temperature

Sea surface projections based on a suite of climate models downscaled with the OzClim approach (Whetton *et al.* 2005) show considerable variability in some parts of Australia, such as north-western Australia (**Figure 5**). In southeast Australia, there is more agreement between model projections, and warming appears in all model realizations. When an ensemble average is generated, south-east Australia shows the greatest projected rate of warming to the end of this century. By 2050, average temperatures in this region are projected to be 2 °C warmer than the 1990-2000 average (**Figure 6**). In contrast, much less warming is evident in the upwelling regions of western Victoria, which has been attributed to increased upwelling (Hobday *et al.* 2007). Biologists seeking to determine appropriate temperature rises to use in experimental work should select a range of temperatures around a mean value in their region of interest to account for inter-model variability, and to ensure that results remain relevant, even as projections change.

Sea-level

Globally, sea-levels are currently rising at the upper end of current projections (Rahmstorf et al. 2007). Sea-level will continue to rise during the 21st century and beyond in response to increasing concentration of greenhouse gases. The IPCC projections are for a global sea-level rise of 18 cm to 79 cm by 2095 compared to 1990 (IPCC 2007; Church et al. 2009). However, there is limited understanding of the response of ice sheets to global warming and a larger rise is possible. Rising sea-levels will result in inundation of low-lying coastal regions and greater coastal erosion, which will be particularly critical for estuarine habitats, critical nursery areas for many marine fishes. Coastal sea-level rise and resulting impacts are elevated during storm events and at times of high tides. Where coastlines are highly modified, such as in the densely populated south-east of Australia, the ability of coastal species and habitats such as mangroves, to naturally adapt to sea-level rise, and migrate landwards, is reduced; a process referred to as the 'coastal squeeze' (Church et al. 2009). As for temperature, sea-level rise will not be uniform around Australia, however, confidence in regional projections is low, as GCM's show little agreement at this scale (Church et al. 2009). That caveat noted, the average from 17 climate model simulations based on the A1B scenario suggest a higher than global average sea-level rise off the south-east coast of Australia for both 2030 and 2070 (see Church *et al.* 2009).

Ocean currents

The observed warming along the east coast of Australia is associated with systematic changes in the surface currents; including strengthening of the East Australia Current (EAC) and increased southward flow as far south as Tasmania (Cai *et al.* 2005; Poloczanska *et al.* 2007; Ridgway 2007). Historical change in the EAC has been explained by a southward migration of the high-latitude westerly wind belt south of Australia (Cai 2006). In turn, this movement of the wind belt has been attributed to both ozone depletion and increases in greenhouse gases (Ridgway and Hill, 2009). Climate model simulations show consensus that these trends will continue over the next 100 years, with Cai *et al.* (2005) projecting a 20% increase in the mean flow of the EAC by 2070. This continued intensification will compound the direct regional warming due to increased solar radiation received at the surface. This east coast region is projected to remain a globally important hotspot of climate change for at least the next 50 years (Hobday and Pecl, in review).

Along the west coast of Australia, the Leeuwin Current (LC) also carries warm water southwards, but the smaller transport volume of this current makes projection more difficult than for the EAC (Hobday *et al.* 2007; Poloczanska *et al.* 2007). Over the period from the mid-1970s to mid-1990s, a trend of subsurface cooling in the equatorial western Pacific, coupled with a weakening trend of the Pacific trade winds was transmitted into the southeast Indian Ocean and the LC region and caused a multi-decadal weakening of the LC strength. Since the mid-1970s, the volume transport in the LC has declined by 10-30%, and thus its southward heat transport has also declined (Feng and Weller 2009). Despite this decline in transport, there have been

persistent warming trends and an increase in salinity in the LC and associated shelf waters over the past 50 years (Pearce and Feng 2007).

While change in the LC is difficult to directly project from climate models due to scale issues, more recent analysis of climate model simulations suggest that reductions of trade wind strength in the tropical Pacific, increase in the frequency of Indian Ocean Dipole events, and the upward trend of the Southern Annual Mode in recent decades are mostly due to the effect of increased greenhouse gases in the atmosphere. Climate model projections suggest these climate trends will likely continue in the future so, on the basis of these various indicators , the LC could continue to weaken slowly in future years (Feng and Weller, 2009).

In the south, the Great Australian Bight region will experience more westward transport from the Indian Ocean as global temperatures rise, but a reduction in the strength of the LC will mean reduced coastal flow to the east. Along the northwest and northeast coasts an increase in the northward flow water has been projected (Poloczanska *et al.* 2007).

Ocean chemistry

The pH of the surface oceans is projected to decrease by 0.2 - 0.3 units by 2100 (Orr *et al.* 2005; Howard *et al.* 2009). As for sea-level, regional projections around Australia are difficult to make, and global averages are the most robust estimates currently available, because surface ocean chemistry largely tracks atmospheric concentrations of CO₂. That said, spatial variation in projected change around Australia does exist, and a single model projection is used as an example (**Figure 7**). Oceanic pH is lower in northeast Australia, and continues to decline to lower levels by 2100. The aragonite saturation state is initially higher in northern Australian waters, but is projected to drop below 3 by 2060. Calcite saturation state also declines to the end of the century (**Figure 7**).

Of critical importance for marine calcifying organisms is when pH drops to levels where waters become under-saturated in carbonate (in the form of the more soluble aragonite or less soluble calcite), as without additional energy being expended to maintain structural carbonate, weaker structures result (e.g. Doney *et al.* 2009) and even dissolution is possible (e.g. Howard *et al.* 2009). Around Australia, the time at which saturation states approach these thresholds varies (**Figure 7**).

The acidity of ocean waters, and the saturation states, can vary on daily, seasonal and interannual time scales, and much work remains to be done to understand the effect of variation in pH for biology. In the high-latitude Southern Ocean aragonite saturation thresholds may be crossed in winter by around 2040 (McNeil and Matear 2008). By 2100, the entire Southern Ocean surface (south of the Polar Front) is projected to become under-saturated for aragonite (Orr et al. 2005). Declining aragonite saturation states in tropical waters have already been implicated in declining coral growth rates (De'ath et al. 2009), and this trend is expected to continue, threatening the structure of coral reef communities as they exist today (Hoegh-Guldberg et al. 2007). Tropical fish may also be impacted, in ways that are only becoming apparent as a result of novel experiments (e.g. Munday et al. 2009; Pankhurst and Mundy, this volume). Aragonite saturation horizons will occur at shallower depths in future, especially in the Antarctic and Australian southern margins, threatening a wide range of larval and adult benthic and pelagic calcifying organisms (e.g. Przeslawski et al. 2009; Sheppard Brennand et al. 2010).

Freshwater environments

Climate projections for freshwater environments are not available at a national scale. Water bodies such as rivers and lakes are below the resolution of gridcell based climate models, and trend or statistical analysis is required to generate local projections based on proxy data such as air temperature, solar radiation, evaporation rates, and rainfall. General patterns are illustrated for air temperature and rainfall, with additional data projections freely and easily available, as described in previous sections.

Surface air temperatures

Air temperatures in the Australian region are projected to continue to warm through the 21st century with a magnitude comparable to the global average.

The land area is projected to warm more than the surrounding ocean with slightly less warming in coastal regions and Tasmania (see Lough 2009). Ensemble forecasts based on multi-modal averages show that warming relative to the 1980-1999 baseline is greatest in northwestern Australia, with an increase of 2.5 °C by 2050 based on a medium emission scenario (A1B) for the average set of models (**Figure 8**). Given current trends in global warming (Rahmstorf *et al.* 2007; Le Quéré et al 2009), patterns observed from higher emission scenarios (A1FI) are also likely. Similar patterns based on analyses presented in Suppiah *et al.* (2007) are obtained using the OzClim online scenario generation tool for individual models and range of scenarios (www.csiro.au/ozclim). The spatial resolution in both projection sets is coarse, and for some biological uses will not be suitable for resolving differences at local scales.

Rainfall and river flow variability

Rainfall is generally projected to decline over most of Australia, with a small increase in the far north according to some models (Poloczanska et al. 2007). Confidence in these projections is, however, less than for temperature changes as evidenced by much lower agreement between different models on rainfall outcomes. Even without significant changes in rainfall amounts, the effectiveness of rainfall will decrease due to warmer temperatures as has already been observed in the observation climate record (Lough et al., this volume). At a regional scale, by 2070 for a medium emission scenario (SRES A1B), annual rainfall is projected to decline by 5-10% for south-east Australia and by 10-20% for south-west Australia (**Figure 9**) (Suppliah *et al.* 2007). High emissions scenarios show these reductions occurring earlier: between 2030 and 2050. Seasonal differences are also apparent, with winter rainfall declining over most of the country, while summer rainfall may increase in some parts of northern Australia (Suppiah et al. 2007. see www.climatechangeinaustralia.gov). Salinity problems, which can occur throughout all parts of a river system, and have been noted as problematic in south-west Australia and the Murray Darling regions may be exacerbated by changes in rainfall, temperature and stream flows (Pratchett et al, this volume). Lower flows and higher temperatures may also reduce water quality within the catchment. For example, low flows, higher temperatures and elevated nutrients create a more favourable environment for potentially harmful algal blooms.

Projections of rainfall and temperature at finer scales, to 1 km², are being generated for a number of regions based on the OzClim data, and involve combining a pattern of observed historical rainfall distribution with the coarser OzClim projections. This "correction", can be used to generate finer patterns. Corrections for topography have also been used (e.g. Harwood *et al.* 2010; **Figure 10**) and the software to generate these downscaled scenarios is publicly available <u>http://www.csiro.au/products/OzConverter-Software.html</u>). These maps show that regional differences in climate change can be dramatic. Generating historical data at fine resolution also requires statistical interpolation of data, as the stations collecting these data are not distributed at this scale, and so errors can also be introduced (e.g. Chiew *et al.* 2008). Generating fine scale projections is likely to advance local adaptation, but issues of "reliability" should lead to caution in using these as they become available in future.

Extreme events

Climate change is speeding up the global hydrological cycle and, as a result, more intense storms are projected to occur, although this is an area of considerable debate amongst scientists, even for the historical record (e.g. Graham and Diaz 2001; Emanuel 2005). In the Australian region there is for decline the frequency evidence а in of tropical cyclones (http://www.bom.gov.au/cyclone/climatology/trends.shtml). Some climate models project that although there maybe fewer tropical cyclones in the future, those that do occur will be of higher intensity (Poloczanska et al. 2007; IPCC 2007). Increased wind speed has also been detected in some climate models, but future projections regarding extreme events must be viewed cautiously at this time. Accepting this caveat, increases in storm intensity have been coupled with sea-level trends to model coastal impacts. For example, McInnes et al. (2003) used a regional climate model for northeast Australia, and showed that projected increases in cyclone intensity can result in a storm surge event with a return period of 100 years, becoming a 55-year event by 2050 and a 40-year event when sea-level rise is included. On land,

greater fire activity could contaminate water catchments with sediment and ash, while floods may be more intense if projections of increased storm intensity are correct. With regard to future impacts, an important area of research for biologists is to determine the relative influence of extreme events versus long-term gradual changes in environmental conditions in driving population responses.

PROSPECTS FOR AUSTRALIAN AQUATIC ECOSYSTEMS

As summarized by Lough *et al.* (this volume), changes in the physical environment of aquatic ecosystems have already been observed around Australia. Drastic cuts in global greenhouse gas emissions are necessary to curtail the impact of future change. Even with such commitments, due to inertia in the climate system, warming and sea-level rise will continue over the 21st century. The projections for Australian marine systems show warmer temperatures, rising sea-level, and lower pH in the coming years, while for freshwater systems, inferences based on declining rainfall in many parts of the country suggest that stream flow and lake levels will also decline in these locations.

In order to improve performance of GCMs and use of GCM-based projections, improved resolution of mesoscale processes is critical. One way to achieve this is to link regional climate models with GCMs to project impacts at a regional scale (e.g. Hartog et al. 2010). A challenge given the computing time this involves is to generate a suitable suite of scenario-model combinations so that future conditions and associated uncertainty can be assessed. To improve confidence in model-based projections, historical validation is important (Smith and Chandler 2010). In the case of Australia, this means a commitment to maintaining critical in situ ocean climate observations, now realistic under the IMOS program (www.imos.org.au). These provide important verification for longer-term but less spatially detailed datasets, ground-truthing of satellite observations and linking the physical and biological components of the marine environment at scales relevant to the physiological processes of marine organisms (Lough 2009; Lough et al. 2010). Equally important is to continue to maintain high-quality remote sensing for Australian waters. Integration of both *in situ* and remote-sensed products with longer-term data sets will be valuable to many users.

A critical question for aquatic biologists working on climate change impacts centers on the adaptation potential of impacted species and habitats. Vulnerability assessments (e.g. Hobday *et al.* 2007; Marshall and Johnson 2007) rely on estimates of present or future exposure to climate change to determine species or habitat vulnerability. Similarly, information on future physical changes is a pre-requisite to more detailed study of biological impacts, such as quantitative population models (e.g. Wolf *et al.* 2010). These more detailed biological models are necessary to consider the effect of adaptation options, and tradeoffs between competing human needs. With improved physical information on historical and future trends, and awareness of how to use the available information, the impacts of climate change for Australian aquatic environments can be better predicted, and effective and cost-efficient adaptation options implemented to "manage the avoidable", while continuing to implement mitigation efforts to "avoid the unmanageable" (SEG 2007).

ACKNOWLEDGEMENTS

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FIGURE LEGENDS

Figure 1. Climate change scenarios used to generate projections. **A**. Scenarios (SRES) used for the third and fourth assessment reports of the IPCC, with change expressed in greenhouse gas concentration (CO₂ concentration) or temperature, as in this panel. **B**. New generation scenarios being used for the fifth IPCC assessment report, known as Representative

Concentration Pathways, with change measured in units of radiative forcing (Moss *et al.* 2010).

Figure 2. Downscaling from a GCM to generate finer scale predictions using a regional climate model or statistical interpolation.

Figure 3. Resolution in projected sea surface temperature. **A.** Example data from global climate model showing projected average sea surface temperature for spring (months Sept-Nov) for the decade 2031-2040 from the CSIRO Mk3.5 model. **B.** Example of statistically downscaled data available via the OzClim approach showing projected average sea surface temperature for April for the decade 2031-2040 downscaled from the CSIRO Mk3.5 model. **C.** Example of dynamically downscaled data showing sea surface temperature data from the Bluelink model forced by GCM data in the month "April 2064".

Figure 4. An example of predicted sea surface temperature based on the ensemble mean of multiple global climate models. Projections are given relative to the period 1980-1999 and give an estimate of the average climate around 2030, 2050 and 2070, based on the mid-point of the spread of model results. Low emissions is the B1 scenario, medium is A1B and high is A1FI. (Source: www.climatechangeinaustralia.gov.au)

Figure 5. Model variability in sea surface temperature projections using the OzClim suite of nine models and the A1B scenario for the month of January in the year 2050.

Figure 6. Ensemble average monthly sea surface temperatures based on the A1B scenario for the year 2050, based on all nine models in the OzClim suite.

Figure 7. Projected pH, $CO_3^{2^-}$, calcite (OCA) and aragonite (OAR) saturation state at the surface around Australia for each decade 2000 to 2100, based on

the IS92 scenario (~SRES A2) and the French ISPL model. Data courtesy of Richard Matear (CSIRO) and Lenton *et al.* (in review).

Figure 8. Projected annual air temperature change for the 50th percentile of climate models. Extracted from <u>www.climatechangeinaustralia.gov</u>

Figure 9. Projected annual percentage rainfall change for the 50th percentile of climate models for the periods 2030, 2050, and 2070 for low, medium and high emissions scenarios. Source: <u>www.climatechangeinaustralia.gov</u>

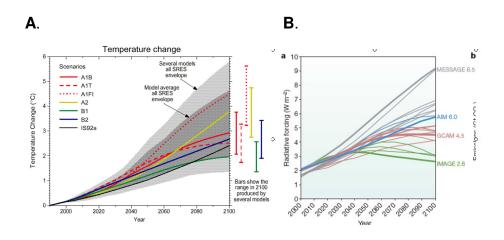


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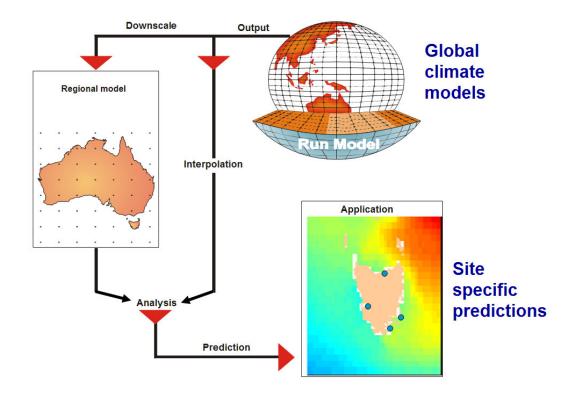


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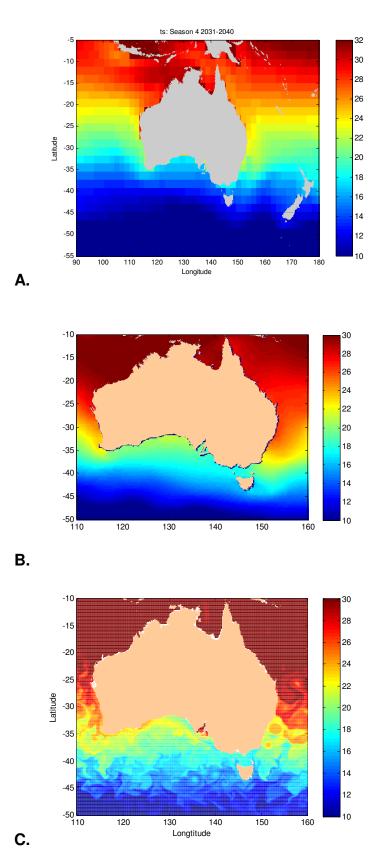


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statistically downscaled data available via the OzClim approach showing projected average sea surface temperature for April for the decade 2031-2040 downscaled from the CSIRO Mk3.5 model. Generated with ReefClim_plotv2.m, as per instructions in ASFB presentation. **C.** Example of dynamically downscaled data showing sea surface temperature data from the Bluelink model forced by GCM data in the month "April 2064". Data generated using code in the figures ppt.

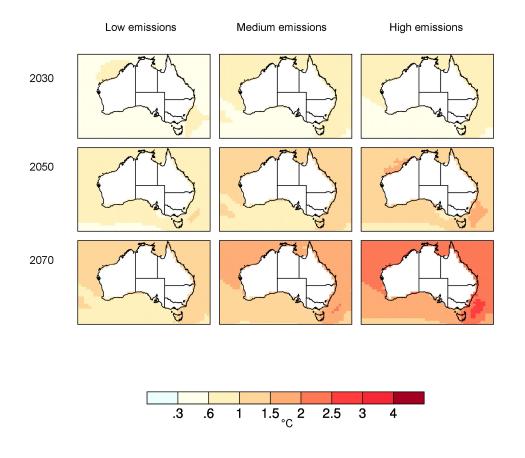


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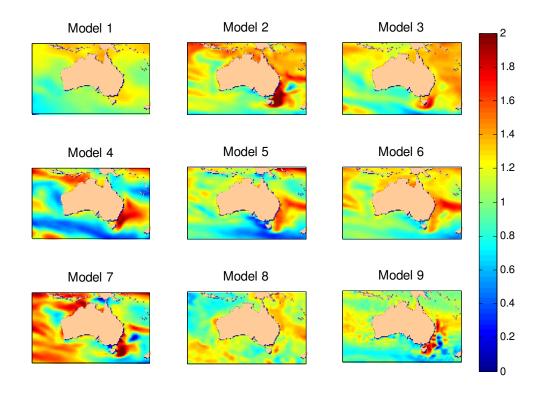


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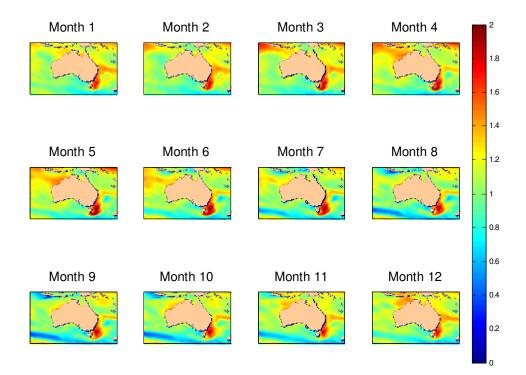


Figure 6. Ensemble average monthly sea surface temperatures based on the A1B scenario for the year 2050, based on all nine models in the OzClim suite. Generated with ReefClim_Plot_mean.m

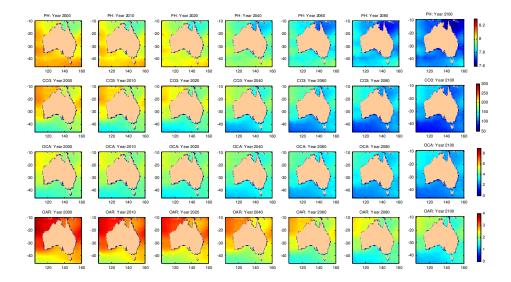


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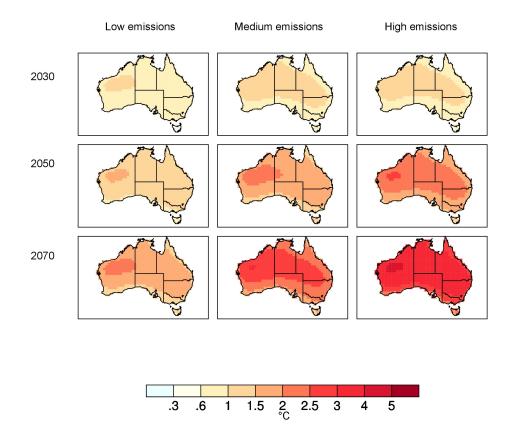


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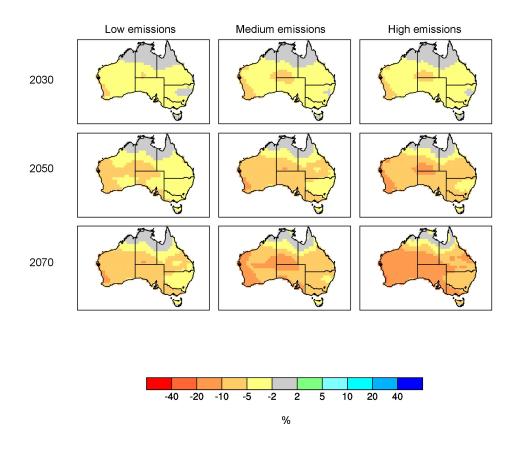


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Effects of climate change on fish reproduction and early life history stages

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Running Head: Climate change and fish reproduction

Abstract.

Seasonal change in temperature has a profound effect on reproduction in fish. Increasing temperatures cue reproductive development in spring spawning species, and falling temperatures stimulate reproduction in autumn spawners. Elevated temperatures truncate spring, and delay autumn spawning. Temperature increases will affect reproduction but the nature of these effects will depend on the period and amplitude of the increase, and range from phase-shifting of spawning to complete inhibition of reproduction. This latter effect will be most marked in species which are constrained in their capacity to shift geographic range. Studies from a range of taxa, habitats and temperature ranges all show inhibitory effects of elevated temperature albeit about different environmental set points. The effects are generated through the endocrine system, particularly through the inhibition of ovarian estrogen production. Larval fishes are usually more sensitive than adults to environmental fluctuations, and might be especially vulnerable to climate change. In addition to direct effects on embryonic duration and egg survival, temperature also influences size at hatching, developmental rate, pelagic larval duration and survival. A companion effect of marine climate change is

ocean acidification which may pose a significant threat through its capacity to alter larval behaviour and impair sensory capabilities. This in turn impacts on population replenishment and connectivity patterns of marine fishes.

Additional keywords: temperature, spawning, estrogens, acidification, larval behaviour.

Introduction

Temperature is a fundamental physical regulatory factor in the lives of fishes and this effect is expressed particularly strongly in the control of all reproductive processes from gamete development and maturation, ovulation and spermiation, spawning, embryogenesis and hatching, to larval and juvenile development and survival. In reproductively mature adults, temperature is generally considered to be a secondary cue to photoperiod in phasing reproductive seasonality but it has a major role in synchronising the final stages of reproductive maturity, and also in truncating reproductive episodes (reviewed in Pankhurst and Porter 2003). The effects of temperature can be differentially expressed depending on when in the annual thermal cycle spawning normally occurs, with increasing spring temperatures being required to cue maturation in spring and early summer spawners (eg. Stacey 1984; Scott and Pankhurst 1992; Shimizu 2003), but elevated temperatures delaying the onset of maturation and ovulation in autumn spawning species (reviewed in Pankhurst and King 2010). Temperature has a similarly important role in the modulation of post-fertilization processes both through its rate-determining effects on embryogenesis and hatching (Pauly and Pullin 1988) and subsequent larval development (Howell et al. 1998), growth (Jobling 1997) and survival (Sponaugle and Cowen 2006).

Complications in the assessment of the effects of temperature in the natural environment arise from the fact that much of our current understanding is generated from controlled laboratory experiments that typically test thermal tolerances rather than behavioural preferences. For example, studies on salmonids show that there is often a wide gap between tolerance and preference profiles. Atlantic salmon *Salmo salar* have upper

thermal tolerances in the 22-24°C range (Barton 1996) but ocean range preferences for 4-10°C (Reddin *et al.* 2000) and similar effects are reported for other salmonids (reviewed in Pankhurst and King 2010). This means that temperatures that might not be high enough to elicit tolerance-related responses in captivity can induce significant preference-related effects in the natural environment. Single domain temperature experiments also generally ignore the synergistic interaction of temperature with other physical and biotic variables. Temperature effects on reproduction can be differentially expressed under different photoperiod regimes (Pankhurst and Porter 2003) and recent experiments on tropical damselfish show that temperature effects are modulated by nutritional status (Donelson *et al.* 2010). Finally, some species exhibit variation in thermal reaction norms across their geographic range that indicates some capacity for acclimation and adaptation to temperature gradients (Angilletta 2009; Gardiner *et al.* 2010), and potentially to a changing climate.

The effects of climate change on aquatic species will vary with latitude, habitat, water column characteristics, and in riverine systems, flow regimes. However, some general expectations of climatic change are for possible phase shifting of seasonal temperature profiles, elevated seasonal maxima and minima, and as a consequence of increases in atmospheric CO_2 , increasing ocean acidification. Riverine habitats are likely to experience elevated temperatures in association with decreased flow rates and increasing incidence of hypoxic conditions, but with guite marked regional differences in effect. For example, tropical NE Australia is predicted to experience increased rainfall and flow regimes whereas both are likely to be markedly reduced in SW Australia (reference this volume). A reasonable prediction is that the effects of temperature change on reproduction will be most widespread in marine systems, but probably most extreme in riverine systems. Lacustrine habitats will experience a range of effects depending on lake inflows, water column structure and lake basin topography (Wahl and Loffler 2009). In addition to increases in temperature, elevations in atmospheric CO₂ means that marine systems will also be affected by ocean acidification which has the potential to directly influence reproduction and

early life stages of marine species (Ishimatsu *et al.* 2008), and to interact with the effects of temperature (Pörtner and Farrell 2008).

With the caveats noted above, the implication is that any changes in thermal regime occasioned by climate change will have major consequences for fish reproduction and that these effects will be exercised across all stages of the reproductive process (Graham and Harrod 2009; Jonsson and Jonsson 2009; Pankhurst and King 2010). The extent of those effects will be determined by a range of factors including specific physiological tolerances, capacity for acclimation and adaptation, scope for behavioural avoidance, capacity to extend or shift ranges, and when in the reproductive cycle that any thermal challenge occurs. The possible outcomes range from extremes of complete reproductive and recruitment failure to changes in seasonal phasing of reproduction and possible increases in species range (Munday *et al.* 2008a). This review examines the basis for some of these effects at the level of the individual and the possible consequences for population level events in terms of adult reproduction, and subsequent egg, larval and juvenile development and survival.

Reproduction

Endocrine control of reproduction

Changes in environmental variables are transduced into effects on reproductive processes through the hypothalamo-pituitary-gonadal (HPG) axis. This begins with hypothalamic synthesis and synaptic release of peptide gonadotropin releasing hormones (GnRH) onto the gonadotropic cells of the pituitary gland where they stimulate the synthesis and release of the protein hormones, follicle stimulating hormone (FSH) and luteinising hormone (LH) (reviewed in Planas and Swanson 2008; Levavi-Sivan *et al.* 2010; Zohar *et al.* 2010). In many species there is also inhibitory tone imposed by the action of dopamine (DA)-secreting neurones, with the release of FSH and LH being dependent on the balance between GnRH stimulation and DA inhibition (reviewed in Dufour *et al.* 2010). GnRH-pituitary interaction is further modulated by melatonin produced by the light-sensitive pineal gland by as

yet poorly understood mechanisms (reviewed in Migaud *et al.* 2010), by the kisspeptin system through direct effects on the activity of GnRH-producing neurones (reviewed in Akazome *et al.* 2010) and by the feedback effects of gonadal steroids (reviewed in Pankhurst 2008).

FSH is involved in stimulating the early stages of gamete development and LH in the control of maturational events, with both exercising their effects at the gonadal level through binding with G protein-coupled membrane-bound receptors in the ovary and the testis, giving rise to an increase in intracellular cAMP levels (Planas and Swanson 2008). This in turn results in the activation of protein kinases and the susbesequent de novo synthesis and releases of gonadal steroids through the sequential cleavage of the base molecule cholesterol. In males, the predominant steroids produced are the androgens, testosterone (T) and its more biologically active metabolite 11ketotestosterone (11KT); females also produce T but this is further metabolised to the estrogen 17β -estradiol (E₂). Both sexes also produce a progesterone-like maturational steroid (typically 17,20β-dihydroxy-4-pregnen- $[17,20\beta P]$ or $17,20\beta,21$ -trihydroxy-4-pregnen-3-one $[20\beta-S]$) in 3-one response to gonadal stimulation by LH (Pankhurst 2008). The actions of gonadal steroids include the stimulation of gametogenesis in both sexes, spermiation in males and vitellogenesis (yolk accumulation) and oocyte maturation in females, as well as regulating secondary sexual characters and a suite of sexual behaviours (Pankhurst 1998; 2008). A key step in the reproductive development of females is the stimulation by E₂ of hepatic synthesis of the egg yolk precursor vitellogenin (Vtg) which is released into the plasma from where it is taken up by the developing oocytes. E_2 also stimulates the ovarian and hepatic synthesis of zona pellucida proteins (ZP) that will ultimately form the chorion (egg shell) of the ovulated ovum (Tyler et al. 2000; Babin et al. 2007; Modig et al. 2007)

Temperature and the HPG axis

Temperature change has the capacity to affect the HPG axis at multiple sites through its reaction rate-determining effects on hormone synthesis and action, and its effects on hormone structure. This is reflected in a minimum temperature threshold for most endocrine events, increasing hormone synthesis, activity and metabolism across the physiological tolerance range and decreasing activity at the top end of that range (Pankhurst and King 2010). Inhibitory effects at higher temperature may arise from conformational changes in proteins (eg. FSH, LH and their receptors, steroid synthesizing enzymes), and also the increasing tendency for steroid hormones to form water-soluble conjugates at high temperatures (reviewed in Van Der Kraak and Pankhurst 1997). Steroid conjugates (usually sulphates or glucuronides) suffer the dual fate of no longer being soluble in (and able to pass through) cell membranes to gain access to their intracellular receptors, and of being more available for kidney filtration and excretion in the urine, significantly reducing their plasma residence times.

Irrespective of the mechanisms involved, it is clear that thermal inhibition of reproduction is present across a wide spread of taxa, habitats and temperature ranges with the main difference between species being the absolute temperature at which the suppressive effects occur (Table 1). In cold temperate and sub-Arctic species, the inhibitory effects typically appear at temperatures of 11-12°C, among cold temperate species at around 18°C, for temperate species at about 24°C and tropical species at 30°C and above (Table 1). This supports the view that all species are likely to show similar responses to rising temperatures but that the thresholds for these effects will vary in relation to specific thermal tolerance ranges. There is also some evidence that that ranges over which normal function can be maintained may be broader in cool water and temperate species, than among tropical species (Donelson *et al.* 2010).

More detailed understanding of the mechanisms involved in the thermal inhibition of reproductive processes is derived mainly from studies on temperate species, with most evidence from studies on salmonids. Arctic charr *Salvelinus alpinus* held at 10°C (a temperature that suppresses normal ovulation) show greater responsiveness (LH secretion and subsequent ovulation) to synthetic analogs of GnRH (GnRHa) combined with the dopamine antagonist pimozide, than GnRHa alone, suggesting that part of the inhibitory mechanism involves increases in dopamine inhibition at the

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level of the pituitary (Gillet and Breton 2009). In Atlantic salmon *Salmo salar*, elevated summer and autumn temperatures inhibit the activity of the steroid converting enzyme P_{450} aromatase (arom) and the subsequent ovarian synthesis of E_2 from androgen precursors. This in turn results in reductions in the hepatic synthesis of Vtg and subsequent reductions in final egg size, fertility and survival. Exposure to elevated temperature during vitellogenesis also results in reduced affinity of hepatic E_2 -receptors. Exposure to elevated temperatures at the completion of vitellogenesis (late autumn), inhibits the synthesis of the maturational steroid 17,20 β P and subsequent progression of oocytes through final oocyte maturation (the resumption of meiosis) and ovulation (reviewed in Pankhurst and King 2010).

Similar effects are seen in non-salmonids, with wolffish Anarhichas lupus showing reduced plasma levels of T and E₂, retarded ovulation, and reduced fertility and survival (Tveiten and Johnsen 2001; Tveiten et al. 2001), red seabream Pagrus major, showing inhibition of expression of genes coding for arom and 11β -hydroxylase (which mediates the conversion of T to 11KT) (Lim et al. 2003), and freshwater pejerrey (Odontesthes bonariensis) showing reduced plasma levels of E₂ in females, and T in males (Soria et al. 2008). At higher levels in the HPG axis, red seabream exposed to typical summer temperatures (which truncate normal spawning) showed reduced central expression of genes for GnRH and its pituitary receptor, and reduced pituitary expression of the β -subunit gene for LH (LH β) (Okuzawa *et al.* 2003). Similarly, pejerrey displayed reduced expression of LH β and the receptor for FSH in females exposed to moderate elevations in temperature (Soria et al. 2008). There is also some evidence that high temperature has the capacity to interfere with the transduction of photoperiod signals to the reproductive axis although as noted earlier, the mechanism in fish is still not well understood. The amplitude of the nocturnal surge in melatonin in fish is greater at higher temperature and if as in some birds, melatonin exerts its role through stimulation of factors that inhibit GnRH synthesis (reviewed in Migaud et al. 2010), then temperature-regulated increases in melatonin secretion could also result in an inhibitory effect at the pituitary level. With the caveat that the understanding of all of the possible effects of temperature on reproductive

physiology is not complete, it is clear that temperature regulates reproduction at multiple sites in the reproductive pathway (Fig. 1).

Stress and reproduction

An alternative, non-exclusive explanation for the inhibitory effects of elevated temperature is the possibility that thermal inhibition occurs through activation of the hormonally-mediated stress response. Stress is in turn known to have marked inhibitory effects on reproduction in fish (Pankhurst and Van Der Kraak 1997; Leatherland et al. 2010; Schreck 2010). Stress stimulates activation of an acute catecholamine-mediated response that has the primary effect of rapidly increasing energy availability and the delivery of O₂ to the tissues, followed by a longer and more sustained activation of the hypothalamic-pituitary-interrenal (HPI) axis, resulting in plasma elevations of the steroid cortisol in teleosts and chondrosteans, and 1αhydroxycorticosterone in elasmobranchs (reviewed in Pankhurst 2011). Short term increases in corticosteroids increase the availability of a variety of energy substrates but longer term exposure to elevated cortisol results in suppressive effects on a range of functions including reproduction, growth and immune function (Pankhurst 2011). Some of the longer term effects can be explained by the largely catabolic effects of cortisol but stress is also capable of suppressing plasma levels of T and E_2 in as little as 15-30 mins after the imposition of stress (Haddy and Pankhurst 1999) and there is equivocal evidence that this rapid effect is the direct result of cortisol action (Pankhurst *et al.* 1995).

A consideration for the role of stress in temperature-mediated suppression of reproduction is whether environmental temperature change actually stimulates a stress response. Increases in temperature can be an effective stressor in the laboratory context (Pankhurst 2011) but elevations in temperature that occasion inhibition of reproduction in broodstock Atlantic salmon do not result in significant elevations of plasma cortisol (Pankhurst *et al.* under review) strongly suggesting that the marked inhibitory effects observed in salmonids are not being exercised through the HPI axis. There is also the consideration as to whether environmental conditions are routinely stressful for fish in the natural environment, and the conclusion is that there is not strong evidence for initiation of stress responses under quite wide ranges of environmental conditions (Schreck 2010; Pankhurst 2011). The caveat here is that events that do stimulate stress responses in free ranging vertebrates from other classes are typically associated with extreme weather events. For fish populations this is likely to coincide with storms and floods when sampling from wild populations is generally precluded (Pankhurst 2011). However, environmental changes predicted for riverine environments such as increasing temperatures, decreased flow rates and O₂ saturation (reference this volume) may well generate conditions that do stimulate activation of the HPI axis and a reasonable prediction is that this will contribute to reproductive suppression in these environments, separately or additively to direct thermal effects on reproductive endocrine processes.

Additional considerations

Despite the general consistency of the effects of elevated temperature on reproduction described above, data from an increasing number of studies suggest that there will be subtleties in the way that these effects are likely to be expressed. This in turn is going to make the precise nature of effects arising from climate change harder to predict. A first consideration will be when in the reproductive cycle thermal challenge occurs. Studies on austral stocks of Atlantic salmon have shown that females are reasonably robust in terms of their response to elevated temperature for much of the summer and autumn, but highly sensitive to thermal disruption in February during a period of substantial oocyte growth and gonadal reorganisation (King *et al.* 2007). The implication is that elevated temperature may have more, or less benign effects depending on whether or not it consistently occurs across this period of heightened sensitivity.

Temperature change may also have differential impacts on sympatric species with different seasonal spawning patterns. For example, spiny damselfish *Acanthochromis polyacanthus* spawn in spring and early summer on Australia's Great Barrier Reef, and show temperature inhibition of ovarian steroidogenesis above 30°C (Donelson *et al.* 2010; Pankhurst *et al.* in press).

In the same regions, humbug dascyllus *Dascyllus aruanus* spawn later in the summer when temperatures are typically higher, and don't show evidence of inhibition of steroidogenesis until temperatures of 33°C (Pankhurst *et al.* in press). This suggests that as in temperate species (Pankhurst and Porter 2003) increasing temperature plays a normal role in truncating spawning episodes in spring spawners, and cueing the onset of spawning in summer spawners. Under this scenario, the effects of any increase in temperature will depend on when in the reproductive cycle the increase occurs and when in the year spawning normally occurs. For example, a higher summer maximum may have negligible effects on spiny damselfish reproduction if it occurs during a period when spawning is normally suppressed, but might reduce a spring spawning window if the rate of the spring increase in temperature became steeper, i.e. the effects will be strongly dependent not only on the absolute temperature but also the annual pattern of thermal change.

The response to thermal stress may also be variable within the same population. Recent work with Atlantic salmon shows that the effect of summer and autumn exposure to high temperature $(22^{\circ}C)$ is partially determined by the age class of broodstock. Both first-spawning season (maiden) and second-spawning season (repeat) females show depression of plasma E_2 and Vtg levels, reduced expression of Vtg and ZP genes, delay in maturation and ovulation and reduced fertility and egg survival (Pankhurst *et al.* under review). However, repeats show higher fertility and survival than maidens for reasons that are not clear but may relate to overall larger egg size and maternal endowment with vitellogenin. A similar effect operating in natural populations would generate differential impacts depending on the age structure of the population, and one prediction might be that heavily fished populations dominated by younger fish might have heightened susceptibility to thermal disruption of reproduction.

Within-population variability is also likely to occur as a function of individual nutritional status. It is well known that there is a tightly-coupled relationship between nutritional status and reproductive output (Lambert *et al.* 2000); however, experiments with spiny damselfish have shown that high nutritional status confers some protection from the inhibitory effects of

exposure to high temperature (Donelson *et al.* 2010). The basis for the effect is not known but may be related to the permissive effects that a number of nutritionally-regulated endocrine factors (eg. thyroid hormones, insulin-like growth factor I) exert on the HPG axis (reviewed in Pankhurst *et al.* 2008). On this basis, another prediction might be that temperature effects on reproduction of natural populations will be exacerbated if there is a concurrent negative impact on food availability.

An observation based on the consistent effect of increasing temperature in inhibiting gonadal arom activity in fishes, is that arom suppression will have at least two additional significant effects on reproduction based on the roles of arom in sex determination, and sex inversion respectively (Pankhurst et al. in press). Phenotypic sex in fish can be quite labile during the period of primary sex determination such that female phenotypes emerge in the presence of brain arom-dependent estrogen synthesis, and males in the absence of arom activity (reviewed in Devlin and Nagahama 2002). Higher temperatures inhibit arom activity and drive sex determination towards the male phenotype (reviewed by Guiguen et al. 2010). A prediction here is that increasing sea temperatures will increase the proportion of fish developing as male, even within the thermal range over which reproductive performance can be maintained. The possible impacts of this on population resilience are not known. Similarly, many teleost species undergo sex inversion (Frisch 2004), with the presence of gonadal arom activity maintaining the ovarian condition in protogynous species, and being requisite for the transition from male to female in protandrous species. The primary control mechanism appears to be mainly exercised by social context (eg. Munday et al. 2006) but the underlying physiological mechanism is strongly dependent on the subsequent activation, or inhibition of arom activity. The prediction here is that thermal inhibition of arom activity may generate premature transition from female to male in protogynous species, and inhibition of transition to female in protandrous species, even in the presence of the appropriate social context. Here also, the possible impacts at population level are not known.

Ocean acidification and reproduction

Uptake of additional CO₂ at the ocean surface, due to increasing concentrations of CO₂ in the atmosphere, is causing ocean pH to decline and reducing the carbonate ion concentration of the shallow ocean. This process, know as ocean acidification, is considered to be a serious threat to marine species, especially for calcifying species that require carbonate ions to form their shells and skeletons (Hoegh-Guldberg et al. 2007; Fabry et al. 2008). Elevated PCO₂ can also have a direct physiological effect on aquatic species through disruption of acid-base balance and limiting oxygen supply (Pörtner et al. 2004; Pörtner and Farrell 2008). The effects of increasing PCO₂ in water is probably of greater concern than reducing pH per se, because of the high permeability to biological tissue of gaseous CO₂ relative to hydrogen ions (Brauner 2009). Indeed, experiments with red seabream (Pagrus major) demonstrate that larval fish are more sensitive to the effects of acidification with CO₂ than to the same pH achieved with mineral acids (Kikkawa et al. 2004). Increased tissue PCO₂ causes acidosis (lowering of pH and accumulation of bicarbonate), which can be detrimental to many cellular processes, including protein synthesis, enzymatic function and oxygen transport (Pörtner et al. 2004). Fish compensate for acidosis by acid-base equivalent ion transport from the body to the environment, mostly across the branchial epithelium, and to a lesser extent via the kidneys and intestine (Claiborne et al. 2002).

In general, fishes appear to be more tolerant to increases in ambient CO_2 than many invertebrates (Ishimatsu *et al.* 2008; Widdicombe and Spicer 2008), possibly because of their well-developed mechanisms for acid-base regulation (Pörtner *et al.* 2004; Melzner *et al.* 2009). However, very little is known about the effects that chronic exposure to levels of PCO_2 predicted to occur over the next 50-100 years (up to ~1000ppm CO_2) might have on fish reproduction. The few preliminary studies available suggest the impacts might not be substantial. Sperm motility of the flounder *Limanda yokohamae* is arrested by mild increases in PCO_2 (Inaba *et al.* 2003), but similar effects were not observed in 10 other species from a range of families (Inaba *et al.* 2003), or in the Baltic cod, *Gadus morhua* (Frommel *et al.* 2010). Sensitivity of fish eggs to elevated CO_2 varies markedly between species, but species

tested to date typically have 24h LC50 (lethal concentration resulting in 50% mortality) values well above 10,000ppm CO_2 (Ishimatsu *et al.* 2008). Furthermore, Munday *et al.* (2009a) did not detect any effect of exposure to 1000ppm CO_2 on the embryonic duration or survival of clownfish (*Amphiprion percula*) eggs. Eggs of pelagic spawners might be more sensitive to CO_2 stress than the eggs of benthic spawners such as clownfishes, because pelagic eggs probably experience less fluctuation in environmental *P*CO₂ than eggs on the benthos, but this hypothesis has not been adequately tested.

One potential concern is that higher PCO_2 may limit the scope for aerobic performance in adults (Pörtner and Farrell 2008), which could affect reproductive output. Aerobic scope of two tropical cardinalfishes, *Ostorhinchus doederleini* and *O. cyanosoma*, declined by 33% and 47%, respectively, when they were exposed to ~1000ppm CO₂ at the average summer temperature (29°C) for the study population and at temperatures up to 3°C above average (Munday *et al.* 2009b). Whether such a loss in aerobic capacity has an effect on reproduction is unknown, but it is reasonable to suspect that it might. For example, collapse of aerobic scope in association with anomalously high water temperature has been linked to failed migration (and thus spawning) in sockeye salmon, *Oncorhynchus nerka* (Farrell *et al.* 2008). The possible effects of elevated CO₂ on endocrine pathways that mediate reproduction in fishes are currently unknown.

Early Life History stages

Effects on egg incubation

Egg are one of the most thermally sensitive life stages in fishes and tolerance limits appear to be within $\pm 6^{\circ}$ C of the spawning temperature for many species (Rombough 1997). Small increases in temperature can dramatically increase egg mortality, especially in tropical species (Gagliano *et al.* 2007). Consequently, survivorship to hatching could decline as oceans and rivers warm, unless species adjust the timing of spawning to suit the optimal temperature for embryo development. Such shifts appear likely because gametogenesis is highly temperature sensitive in many fish species (discussed above) and breeding may cease before critical thermal limits for egg survival are reached. For example, the critical temperature for gametogenesis of brook trout *Salvelinus fontinalis* is approximately 2°C lower that the thermal limit for normal development of fertilized eggs (Rombough 1997). Nevertheless, some species spawn at suboptimal temperatures and may suffer reduced embryonic survival as a result, both because increased temperature during ovulation can reduce gamete viability (van der Kraak and Pankhurst 1997) and because increased temperature during embryogenesis increases mortality (Gillet *et al.* 1996; Pankhurst and Thomas 1998; Janhunen *et al.* 2010).

Temperature also has a highly significant effect on the rate of embryonic development. For many species, embryonic developmental rate more than triples for each 10°C increase in temperature (i.e. $Q_{10} > 3$) (Rombough 1997). Increased developmental rate means that the incubation period declines as average water temperature increases. Incubation period is also dependent on egg size, with larger eggs (often benthically spawned) taking longer to develop than small eggs (often pelagically spawned) (Pauly and Pullin 1998). Consequently, increased temperature may advance hatching by minutes to hours in small eggs, and by hours to days in large eggs, with the effects being most marked in cold water species with long incubation periods (Rombough 1997). Whether shorter incubation periods affects individual fitness may depend on the potential for a mismatch between the timing of hatching and favourable conditions for larval survival. For example, hatching of benthic eggs often occurs at night when larvae are less susceptible to visual predators (Roberston 1991; Michael 2008). At least in some species, hatching can be cued by environmental factors that are not temperature dependent, such a diurnal light cycles, which may help ensure larvae hatch at the appropriate time even if they are competent to hatch earlier.

Effects on larvae

Temperature affects metabolism, growth, developmental rate and stage duration of larval fishes (reviewed by Houde 1989; Blaxter 1992; Benoit *et al.* 2000). Metabolic rate measured as mass-specific oxygen consumption increases sharply with increasing temperature in larval fishes, although

responses vary considerably among species (Houde 1989; Rombough 1997). Higher metabolic rates mean that fish have higher basal energy demands at higher temperatures. Larval growth rate also increases with temperature for both temperate (Blaxter 1992; Benoit *et al.* 2000) and tropical species (McCormick and Molony 1995; Meekan *et al.* 2003; Green and Fisher 2004), with temperature explaining up to 89% of variation in growth rates among cohorts of some species (Sponaugle and Cowen 2006). Thermal reaction norms of growth in larval fish tend to be approximately linear until the lethal upper thermal limit is reached, at least in the majority of species studies to date (Rombough 1997; Sponaugle and Cowen 2006). This contrasts with thermal reaction norms of growth in juveniles and adults, which usually decline well before the lethal thermal limit is reached (e.g. Munday *et al.* 2008b). As a result we might expect that larval growth rates will tend to be maintained as water temperatures increase due to global warming, even if temperatures exceed optimum conditions for some other life processes.

Developmental rate increases and therefore stage durations are shorter in warmer water. The time until yolk absorption, metamorphosis and pelagic larval duration (PLD) are all negatively correlated with temperature, both within (Rombough 1997; Fuiman et al. 1998; Green and Fisher 2004) and among species (Houde 1989; Benoit et al. 2000). In one of the clearest examples of this effect, PLD of reef fishes is closely correlated with temperature in a range of species (McCormick and Molony 1995; Green and Fisher 2004; Sponaugle and Cowen 2006). There are also strong correlations between PLD and growth rates, with fast growing larvae often exhibiting shorter larval durations (Houde 1989; McCormick and Molony 1995; Benoit et al. 2000; Green and Fisher 2004; Sponaugle and Cowen 2006). The relationship between growth rate and PLD will influence size at settlement, which is often variable between cohorts (Fuiman et al. 1998; Sponaugle and Cowen 2006) because these rates are not perfectly reciprocal and because growth also depends on a range of other factors, such as food supply. Larger size at settlement may offer some survival advantages (Sogard 1997), however, small individuals settling in warmer conditions may grow faster after

settlement and quickly reach equivalent sizes to fish that settle in cooler conditions (Sponaugle and Cowen 2006).

Mortality rates are usually very high during the larval phase, therefore, faster growth and reduced PLD at higher temperatures might increase larval survivorship (Houde 1989; Bergenius et al. 2002; O'Connor et al. 2007). Across a broad range of species the slope of the relationship between PLD and temperature is steepest in cool water species (O'Connor et al. 2007) and small increases in water temperature might be expected to have the greatest effect on high latitude species. However, even among tropical fishes, PLD can decline by 4-8% per ^oC (Munday et al. 2009c), which could have a significant effect on survivorship. Within the temperature range currently experienced by reef fishes, warmer years generally appear to favour good recruitment events for a variety of species (Meekan et al. 2001; Wilson and Meekan 2002; Cheal et al. 2007), which is consistent with the hypothesis that reduced PLD tends to increase larval survivorship. Recruitment of the bluehead wrasse Thalassoma bifasciatum in the Florida Keys increases with temperature, but also becomes more variable at high temperatures (Sponaugle and Cowen 2006), possibly because of increased risk of starvation in warm water cohorts. Although the growth rate of marine fish larvae increases with temperature, growth efficiency does not (Houde 1989; Rombough 1997). Furthermore, larvae require more food at higher temperatures to sustain higher metabolic rates. As a result, larvae are more susceptible to starvation at higher temperatures and this may explain observations of more variable recruitment and episodes of recruitment failure during periods of anomalously high water temperature. For example, recruitment of most reef fish species failed in French Polynesia during a warm El Nino period (Lo-Yat et al. in press), suggesting that either reproduction or larval survival of a broad range of species was dramatically reduced at high summer temperatures.

Together, these observations demonstrate that increased temperatures will affect the life history and demography of larval fish, possibly affecting recruitment success and population dynamics. Small increases in temperature might tend to favour recruitment in some species, especially at higher latitudes. Larger temperature increases could lead to recruitment

failures, especially at low latitudes, and at time or places where food supply is limited (Munday *et al.* 2008a). Larval success and patterns of recruitment will also be strongly affected by the effects of temperature on reproduction, which is likely to be one of the first processes impacted by increasing water temperature. A summary of the demonstrated and possible effects of increased temperature and PCO_2 on early life history traits is shown in Fig. 2.

Ocean acidification and early life history stages

Larval stages are predicted to be more sensitive to elevated PCO₂ than adults because they have a larger surface area to volume ratio, and thus are more susceptible to changes in ambient conditions, and because they might have less developed mechanisms for acid-base balance compensation (Fabry et al. 2008; Ishimatsu et al. 2008; Melzner et al. 2009). Acid-base balance in adult fish is mostly maintained by ion transport across the gills (Claiborne et al. 2002). Although very little is known about the mechanisms and pathways of acid-base regulation in larval fishes, it is clear that they must be capable of acid-base homeostasis (Brauner 2009). Indeed, the early ontogenetic development of gills in larval fish may be more important in ionoregulation and maintaining acid-base balance than for oxygen delivery (Fu et al. 2010). Similar to the egg stage, the 24h LC50 for larval fish is generally above 10,000ppm CO₂ for the few species tested to date (Kikkawa et al. 2003; Ishimatsu et al. 2008). Furthermore, two recent studies have not detected significant negative effects on life history traits of larval reef fishes reared in conditions simulating near-future CO₂ in the ocean. Munday *et al.* (2009a) did not detect negative effects on the size at hatching, growth rate, size at settlement, or critical swimming speed of clownfish Amphiprion percula larvae reared from hatching in seawater aerated with up to 1000ppm CO₂. Similarly, juvenile spiny damselfish Acanthochromis polyacanthus reared for 3 weeks at up to 850ppm CO_2 were the same size as fish reared in current-day CO_2 controls, did not suffer higher mortality, and exhibited no differences in skeletal or otolith development compared with controls (Munday et al. 2011). Although more studies are required, the limited evidence available to date suggests that PCO₂ levels predicted to occur in the ocean during the next 50100 years might not have a serious effect on the growth and development of larval fishes.

A potentially serious consequence of rising PCO_2 is that it can affect the olfactory system of some marine fishes, rendering them unable to distinguish between ecologically important chemical cues (Munday et al. 2009d). Clownfish larvae reared at 1000ppm CO₂ exhibited a broad attraction to any chemical cue presented in binary-choice flume trials and became attracted to chemical cues that they avoided when reared in control seawater. At 1000ppm CO₂ they became attracted to the smell of inappropriate habitats (Munday et al. 2009d), could no longer discriminate the smell of kin versus non-kin (Munday et al. 2009d), and became attracted to the smell of predators (Dixson et al. 2010). At even higher PCO₂ (~1700ppm) they failed to respond to any chemical cues, indicating complete impairment of the olfactory system. In subsequent experiments, Munday et al. (2010) showed that: 1) olfactory impairment of larval clownfishes and damselfishes (Pomacentrus wardi) occurred at 700-850ppm CO₂, 2) behaviour of larval damselfish was altered in their natural coral reef habitat, and 3) that this caused a 5-9 fold increase in mortality from predation compared to controls. These results suggest that increased PCO_2 in the ocean could have a significant effect on the successful replenishment of reef fish populations, although the effects on predators and the outcome of predator-prey interactions when both partners have been exposed to elevated CO₂ have not yet been tested. Ecological connectivity between fish populations could also be significantly affected if exposure to elevated CO₂ impairs navigation and homing abilities of larval fishes as suggested by the original studies (Munday et al. 2009c).

The physiological mechanisms responsible for impairment of olfactory sensitivity and changes in behaviour of larval fish exposed to elevated CO_2 are currently unknown, but do not appear to be related to changes in the chemical stimuli, or abnormal developmental of the sensory system. Neither control nor CO_2 treated fish alter their responses to chemical cues when presented in acidified versus control water (Munday *et al.* 2010; Dixson *et al.* 2010), indicating that elevated CO_2 affects the fish, not the chemical cue

itself. No modification of the sensory epithelium was apparent in CO_2 treated fish (Munday *et al.* 2009d) and these fish regained their normal sensory ability after two days in control water (Munday *et al.* 2010). It is possibly that the effects on behaviour and olfactory ability be related to incomplete acid-base compensation or some other effect of elevated CO_2 on the nervous system, but this has yet to be examined.

Acclimation and Adaptation

Many fish species have geographic ranges spanning a considerable gradient in average, maximum and minimum temperature, suggesting some capacity for acclimation or adaptation to temperature change (Munday et al. 2008a). There is evidence that thermal exposure history can moderate subsequent responses to increasing temperature. Populations of bullhead Cottus gobio harvested from a stream system which had a less variable annual thermal range (4.5-11.5°C) than another (0.5-19.2°C) were found to be less robust in resisting the inhibitory effects of high temperature (Reyjol et al. 2009). Similarly, populations of four species of reef fish from two families (Apogonidae and Pomacentridae) on the northern Great Barrier Reef (GBR) exhibited poorer performance at high temperatures compared with fish from the southern GBR that experience a more variable thermal range (Gardiner et al. 2010). This indicates that local populations of these species are either acclimated or adapted to the local thermal environment, and that populations from more variable environments might have enhanced capacity to cope with future thermal stress.

Although acute thermal stress often depresses reproduction, long-term exposure to higher temperatures can confer some improvement through acclimatory processes. For example, laboratory experiments on spiny damselfish show that fish reared at higher temperature since birth have a greater capacity to maintain reproduction at temperatures over 30°C compared with individuals that have only a few weeks thermal acclimation (Donelson *et al.* 2011; unpublished data). Furthermore, the thermal history of the parents is important, with embryos and larvae from parents reared at high

temperatures exhibiting greater thermal tolerance or improved performance at high temperatures in a number of species (Rombough 1997).

In addition to acclimatory responses due to thermal exposure history, individuals within a population can exhibit different thermal preferences (ie. individual genetic variability), and different populations can be locally adapted to different thermal regimes (Crawshaw and O'Connor 1997; Farrell *et al.* 2008; Munday *et al.* 2008a). This variation provides the raw material for selection of more tolerant genotypes. The potential for genetic adaptation to rapid climate change depends on a range of factors, including the amount of adaptive genetic variation present, effective population sizes, generation time, and connectivity between populations that can aid in the spread of tolerant genotypes (Skelly *et al.* 2007; Munday *et al.* 2008a, 2009c) . Unfortunately much of this information is unknown for both marine and freshwater fishes and should be a priority area for future research.

Conclusion

It is clear that climate change will, or already is affecting reproductive and early life history events of most fishes, at a variety of levels and through a range of mechanism which as our understanding develops are emerging as increasingly complex. These include the interplay of changes in physical variables with the characteristics of the habitat, when in the reproductive cycle thermal challenge occurs, when during the year that spawning occurs, whether events are extreme enough to initiate a physiological stress response, the energy status and reproductive age of the fish, and the thermal exposure history and adaptive capacity of the individual or the population. There is also the very strong suspicion that we are substantially underinformed in terms of being able to make useful predictions about likely effects beyond general assumptions, except for the relatively few species that have received the bulk of research attention. This in turn places limitations on the capacity to develop specific options as management strategies. This raises the wider observation that temperature is one of the most fundamental variables affecting the lives of fishes but we still know discouragingly little about its effects.

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Table 1. Summary of inhibitory effects of elevated temperature on reproduction across a range of species, habitats and thermal ranges.

Species Arctic charr <i>Salvelinus alpinus</i>	Habitat Cold temperate/sub Arctic freshwater	Effects Inhibition of LH secretion, ovulation (10- 11°C)	<i>,</i> 0
Wolffish Anarhichus lupus	Cold temperate/sub Arctic marine	Reduced steroid (T and E_2) production, ovulation, fertility and survival (12°C)	Johnsen 2001;
Lake whitefish <i>Coregonus lavaretus</i>	Cold temperate lacustrine	Delayed ovulation and spawning	Wahl and Löffler 2009
Atlantic salmon <i>Salmo salar</i>	Cold temperate anadromous	Reduced Vtg and ZP gene expression, steroid $(T, E_2 \text{ and } 17,20\beta P)$ production, aromatase activity, ovulatory frequency, fertility, egg survival $(18^{\circ}C)$	9
Rainbow trout Oncorhynchus	Temperate freshwater		Pankhurst <i>et al.</i> 1996; Pankhurst

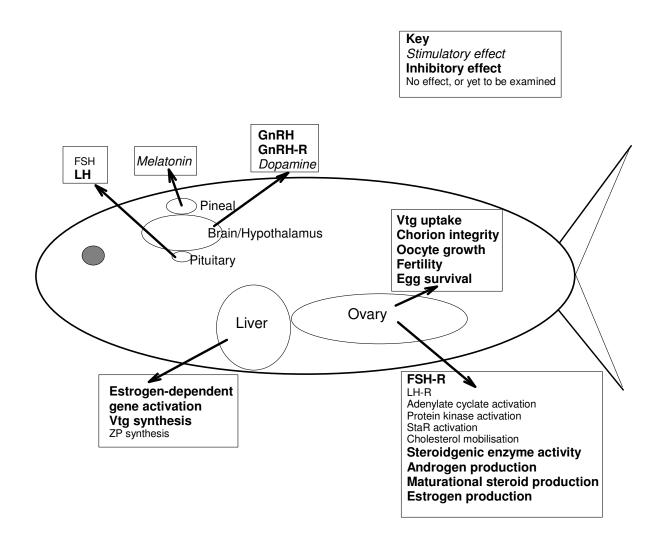
Temperatures above which effects occur (where known)

mykiss		17,20βP), fertility and survival (18-21°C)	and Thomas 1998
Red seabream <i>Pagrus major</i>	Temperate marine	Aromatase and 11β- hydroxylase inhibition (24°C)	Lim <i>et al.</i> 2003
Pejerrey Odontesthes bonariensis	Warm temperate freshwater	Reduced LH β -subunit and FSH-receptor gene expression, T and E ₂ levels, fertility (24°C)	Soria <i>et al.</i> 2008
Spiny damselfish Acanthochromis polyacanthus	Tropical marine	$\begin{array}{llllllllllllllllllllllllllllllllllll$	2010; Pankhurst et
Humbug dascyllus Dascyllus aruanus	Tropical marine	Reduced E_2 production (33°C)	Pankhurst <i>et al.</i> in press

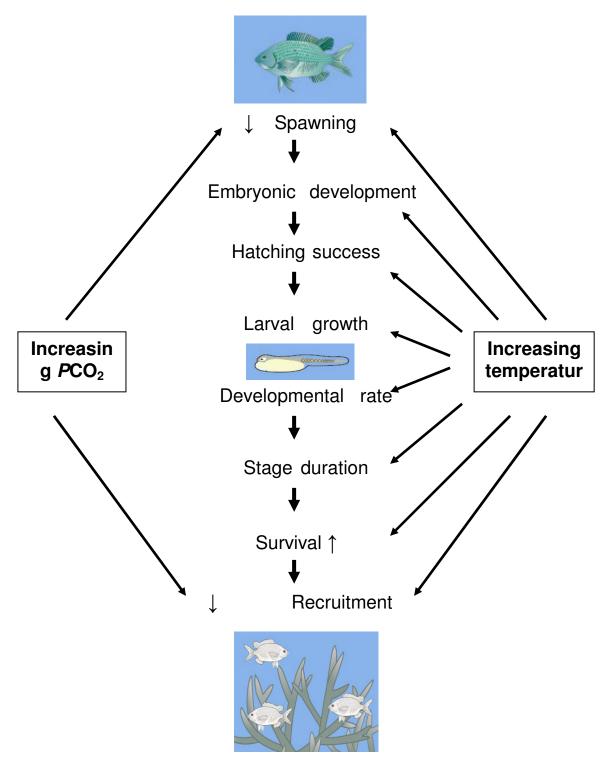
Captions for Figures

Fig. 1. Schematic summary of the effects of above normal temperature on reproductive processes in teleosts fish. Components in bold are inhibited by high temperature, items in italics are stimulated at high temperature, normal text means no measurable effect or yet to be investigated. Abbreviations are defined in the text.

Fig. 2. Physiological and ecological responses to increased water temperature and elevated PCO_2 during the early life history of fishes. \uparrow = increasing rate, \downarrow = decreasing rate, \uparrow = rate may increase or decrease depending on other environmental parameters.









Have there been range shifts for Australian fishes in response to climate change?

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Abstract. One of the most obvious and expected impacts of climate change on organisms is a shift in distributional range. For fishes, this is a complex consequence of how various life history stages interact with the environment; for instance, how fish larval dispersal is affected by climate-change alterations in ocean currents and water temperature. Here, we first survey the worldand Australian literature on climate-change effects on fish range, contrasting freshwater and marine studies, and show that very few definitive studies exist to date. Next we review the range of climate-change drivers in Australian coastal marine, estuarine, and freshwater ecosystems, and evidence for whether these have affected life history traits that may lead to range shifts. We then review the few definitive studies of fish range shifts in Australia and their links to climate change. Finally we discuss the direct and indirect approaches, including co-opting government and museum fish databases, to elucidating range shifts, and make recommendations for future work, including linking and standardising various databases to provide evidence of future range shifts.

Additional Keywords: Australian marine and freshwater fishes, climatechange impacts, range shifts

Introduction

'Most, if not all, organisms could (but rarely do) spread beyond their current ranges until they are stopped by inhospitable environments, competitively superior species, or physiological limits' (Poore and O'Hara 2007)

Simply defining distributional range has a history of conflict in the ecological literature. From early definitions such as from (Elton 1924) which stated that range encompasses broad geographic limits inside which the species may be found more or less permanently distributed, it has been unclear how species whose range fluctuates widely on a seasonal basis, or whose offspring disperse well beyond core adult range (Andrewartha and Birch 1954) can be captured in such a definition. This poses a significant challenge in examining range shifts in fish across marine, estuarine, and freshwater environments.

Marine reef fish species are characterised by a bipartite life cycle (Leis 2006) with larvae as the dispersive phase, sometimes moving 1000s of km after hatching. This makes range measurement especially difficult. Fig 1a shows a model with an example of marine reef fish distribution highlighting core breeding range and layers extending to peripheral recruitment habitat. Which part of this constitutes range must be defined. Depth distributions may differ across latitudinal ranges (Kingsford and Carlson 2010); Malcolm, Jordan *et al.* 2010)} so surveying must incorporate this, and while usually quite sedentary and persistent, recruit densities may fluctuate widely within and among years (Booth, Figueira *et al.* 2007).

In contrast, many estuarine and freshwater fish populations are not at spatial equilibrium; that is, their ranges expand and contract regularly. These expansion/contraction events reflect the dynamic nature of each of these environments. Estuaries occupy relatively small, transitional zones between land and sea, and are subjected to marine influences, such as waves, tides,

and saltwater incursion; and freshwater influences, such as freshwater runoff, which bring influxes of nutrients and sediments – all of which create physical barriers that influence dispersal, feeding, reproduction, and other life history parameters of estuarine fish. What's more, these influences change over short (e.g. seasonal) and long (e.g. ENSO cycles) time scales, and at local (within estuaries) and regional (between estuaries) spatial scales. A key challenge for defining range in estuarine fish then becomes separating temporary vagrancy, which relates to tolerance, from actual range shifts, which requires long-term persistence through adaptation (Davis and Shaw 2001). For the purpose of this review, we define a fish as having an 'estuarine-range' if it spends the majority of its life cycle in a semi-enclosed body of water where fresh and salt water meet, though we note that there are other 'estuarine-dependent' fish species (e.g., diadromous fish species) that may show range shifts in response to climate change.

In freshwater systems, and arid zone rivers in particular, interannual variation in rainfall and runoff generate highly dynamic patterns of habitat persistence with periodic contractions to isolated refugia resulting in highly variable occupied ranges through time (Arthington, Balcombe *et al.* 2005; Bunn, Thoms *et al.* 2006; Unmack 2001).

Thus, across marine estuarine and freshwater systems a mix of high dispersal rates and potential vagrant populations coupled with high levels of temporal environmental variability present a challenging backdrop against which to distinguish the effects of a changing climate. Below we review the available evidence for range shifts among fishes generally, as well as more specifically within an Australian context, as well as summarising the various approaches that have, or could be, used in the future to detect or predict such shifts.

Meta-analysis of worldwide climate-change range shift studies in fishes

Surprisingly, very few fish studies worldwide adequately show range shifts, let alone indisputable links to climate change. Meta-analysis of ISI database Web of Science (Fig 2) shows several trends using appropriate key words. Overall fish studies on range shifts are under 100 to date, most are marine, few are estuarine or freshwater, but numbers have increased rapidly in the last decade, partly fuelled by the climate change debate. About 10% of these studies are Australian. Only one quarter of the studies involve extensive field sampling of ranges, while a further 1/4 incorporate some field data into predictive or descriptive models. Given the importance of evaluating range shifts to understanding the impacts of climate change on the environment and its economic value, this paucity of empirical data is worrying.

The best available evidence of climate-related range shifts have made opportunistic use of rigorous historical data on fish catches, which are then compared to contemporary fish catches and linked with changing water temperatures. For example, Perry et al. (2005) used a commercial fishery data set from the North Sea to show that two-thirds of exploited and non-exploited species have shifted in mean latitude or depth during 1977 to 2001. Similarly, Nye et al. (2009) analysed temporal trends in fish stocks in the Northeast U.S. continental shelf during 1968 to 2007 and identified poleward shifts of many stocks in relation large-scale temperature increases and changes in ocean circulation.

Such examples from estuarine systems are rare; however, Fodrie et al. (2010) quantified changes in fish assemblages within seagrass meadows of estuaries (albeit a rather loose definition of estuary; Able 2005) within the Gulf of Mexico between 1970s and 2006-07 and identified a suite of tropical and subtropical species that were present in the latter sampling period, but not in the former, which they attributed to regional increases in air and sea surface temperatures (>3°C) during the 30 year period.

In freshwater systems there are a number of long-term studies linking patterns of climate variability to periodic shifts in demographic processes. For example, in a 30 year study of brown trout *Salmo trutta* populations in north west England Elliott *et al.* (1997) showed a clear impact of drought years on survivorship and recruitment, and many more studies demonstrate the influence of climatic variables in explaining historic distributional patterns (e.g. Minns and Moore 1995). Depending on the way in which a species range is characterised, there is also some evidence that periodic droughts will extirpate local populations, particularly at the margins of a species distribution

(e.g. Balcombe and Closs 2004; Closs and Lake 1996). Fragmentation of populations during mega-droughts or wet-dry cycles may last sufficiently long to promote genetic divergence (Douglas, Brunner *et al.* 2003; Faulks, Gilligan *et al.* 2010a). Evidence for recent range shifts, however, is limited. (Daufresne, Lengfellner *et al.* 2009) analysed trends in the distribution of fish in the Rhone River in France, and observed longitudinal changes in the distribution of thermophilic fish – chub and barbell, which began to replace dace in more northerly upstream habitats. These shifts were correlated with changes in water and atmospheric temperatures over the same period, and appeared independent of changes linked to more localised aspects of river hydrology and thermal pollution. Similarly, Boughton et al. (2005) implicate climatic factors in the northward range shift of rainbow trout *Oncorhynchus mykiss* in California, although anthropogenic barriers to migration are seen as the primary driver of population declines.

Key climate-change impacts that can affect life history and range

Many of the environmental drivers that would be expected to link to shifts in range or large scale abundance of fish species are climate-change related, and each of these may impinge differently depending on life history stage or habitat. These drivers, and their links to life history events that shape range, are summarised in Table 1 and described below.

Water temperature

For ectotherms such as fishes, water temperature and its links to metabolism and swimming ability, is a key environmental variable. For marine fish larvae, swimming speed and consequent dispersal are positively affected by temperature (O'Connor, Bruno *et al.* 2007) but opposing this is the inverse relationship between water temperature and days to metamorphosis, by which time larval reef fish must have located suitable adult habitat. The sum of these temperature influences, along with ocean current speed, will determine the dispersal envelope (e.g.,(O'Connor, Bruno *et al.* 2007). (Pearce and Hutchins 2009) present a 25 year dataset on recruitment of the tropical damselfish *Abudefduf vaigiensis* to Rottnest Island, SE Western Australia which correlates well with temporal patterns of sea surface temperature (SST), which suggests a net dispersal increase with rise in SST. For fishes advected well outside their adult ranges, an "overwintering bottleneck" may occur where winter water temperatures appear to have a severe modifying effect on densities (e.g., (Figueira and Booth 2010). Projections of an average 2°C rise in winter water temperatures off the SE Australian coast by 2008 suggest that overwintering may be a regular occurrence for a suite of coral reef fishes by then, with consequent range shifts likely. Differences in general temperature tolerances among fish species may also indicate shifts in range and assemblage structures under future climate change. For instance, a suite of reef fishes restricted to the southern GBR have little scope for southern range shift due to unsuitable habitat and may drastically contract in range (Munday, Jones et al. 2007). Species with shifting distributions in relation to changes in water temperature can have faster life cycles and smaller body sizes than nonshifting species (Perry, Low et al. 2005).

For estuarine fish, temperature (along with salinity) is one of the key determinants influencing both their distribution (e.g. Harrison and Whitfield 2006) and abundance (e.g. Power and Attrill 2003), especially those that live in shallow estuaries with irregular riverine flow or exchange with the sea (e.g. coastal lagoons). Temperature affects physiological processes in estuarine fish; including, maturation, feeding and growth (Gill, Wise *et al.* 1996; Power and Attrill 2002; Power and Attrill 2007). There is also evidence that temperature indirectly determines the distribution of fish within estuaries through its influence on resource distribution (Attrill and Power 2002; Attrill and Power 2004), though links of temperature driven range shifts in estuarine fish are lacking.

Thermal constraints are equally important in freshwater environments, and the range of most species is probably limited to some extent by either upper or lower temperature tolerances, although these can be extreme. For example the upper and lower LD_{50} temperatures for spangled perch, one of Australia's most widespread fish species, span a range from 5-39 deg C, and it is only in the very south that the lower temperature bounds impact upon the species

range (Llewellyn 1973). Together with species such as golden perch, rainbowfish and some gudgeon species, spangled perch may therefore expand southward under a warming climate, although such trends may be constrained by reduced streamflows, particularly in smaller rivers. In contrast, a number of cool water native species including river and two-spined blackfish, trout cod and Macquarie Perch will likely contract in range toward more southerly and/or higher altitude streams. Effects of increasing temperature will also be exacerbated by reduced flow volumes, and in some lower altitude catchments a lack of suitable upstream refuges may lead to local extinction from some catchments. Increasing temperatures will also extirpate brown and rainbow trout from some streams potentially reducing their competitive and predatory impacts on small native fish such as galaxids (Closs and Lake 1996). The effects of temperature on growth rates may also have indirect impacts by altering reproductive output and competitive interactions (e.g. Morrongiello, Crook et al. 2010).

Freshwater Flow

Estuarine fishes

Estuarine fish abundances are linked to annual fluctuations in freshwater discharge (Cyrus and Blaber 1992). Levels of freshwater runoff are determined by climate (e.g. rainfall), hydrological characteristics in a given area (e.g. dynamics of drainage channels), and anthropogenic activities (particularly farming practises that influence water extraction from rivers and nutrient input from land runoff). Salinity is the main physical parameter that influences demographic processes in fish and is linked with freshwater input; however, freshwater flow also influences turbidity, pH, and temperature. In contrast to northern hemisphere estuaries, Australian estuaries, are characterised by irregular freshwater flow regimes (Roy, Williams *et al.* 2001). This has become particularly noticeably in south eastern Australia with recent drought conditions (which have been linked to climate change) causing declining abundances of estuarine fish (Gillson, Scandol *et al.* 2009).

including the timing of spawning (e.g. Newton 1996), the buoyancy of eggs

and early stages (e.g. Mackenzie, Gislason *et al.* 2007), shifts in the amount and location of suitable spawning grounds (Nicholson, Jenkins *et al.* 2008), and the movement patterns of fish (e.g. Childs, Cowley *et al.* 2008). Freshwater inputs can also affect survival, particularly during major pulse events or low rainfall periods, which can cause mass mortality of fish (Chuwen, Platell *et al.* 2007). Although there is good theoretical basis to predict that changes in freshwater input to coastal systems due to climate change will alter the ranges of estuarine fish, experimental evidence is lacking. Most research to date on the effects of freshwater inputs has come from descriptive and small-scale experiments (Gillanders and Kingsford 2002); however, increasing use of acoustic tracking technology is allowing better coupling of patterns of fish movements with freshwater flow into estuaries (e.g. Hindell 2007; Hindell, Jenkins *et al.* 2008).

Spatial patterns of runoff are a major determinant of fish distributions in rivers and streams – especially river size (mean discharge), patterns of flow variability (from daily to interannual time-scales) and the presence or absence of particular flow events such as overbank floods and periods of cease to flow (Bunn and Arthington 2002; Poff and Allan 1995). These various components of the flow regime strongly influence habitat availability and water quality, and can influence a range of life-history processes. Floods in particular are an important trigger for spawning in some species and deliver a pulse of energy to rivers that drives productivity in the channel. A number of studies have demonstrated the importance of cease to flow events in excluding certain species from some rivers (e.g. Bond, McMaster *et al.* 2010; Dodds, Gido *et al.* 2004). Such patterns likely arise from both direct habitat loss and the rapid changes in water quality (increasing temperatures and decreased dissolved oxygen) when flows cease (Boulton and Lake 1990).

Habitat loss

In coastal reefs, despite some climatic buffering, large-scale habitat changes have occurred and are expected to occur under climate change, largely as a result of water temperature rises. For example, coral bleaching is now widespread, and can result in dramatic loss in reef fishes (Booth and Beretta 2002). So far this has lead to drastic local reductions in range of some species, but not yet in a biogeographically significant way, i.e., widespread range shifts (see discussion in (Munday, Jones et al. 2007) for coral reef fishes). Key temperate marine habitats are shifting in response to climatechange related sea surface temperature shifts. (Ling, Johnson et al. 2009) have demonstrated that urchin (mainly Centrostephanus rodgersii) barrens, a key coastal reef habitat in SE Australia, are expanding polewards into SE Tasmania, at the expense of kelp (e.g. Ecklonia sp., Phyllospora sp.). Reef fish assemblages differ greatly among these habitats. In New South Wales, (Gillanders and Kingsford 1998) found small blue groper Achoerodus viridis in greater numbers in kelp beds than in adjacent urchin barrens, although the species appeared to be flexible in its use of habitats on reefs, suggesting that populations would persist if urchin barrens expanded in an area. In northeastern New Zealand, some species of reef fish have shown similar patterns, while others were more closely linked to kelp or urchin barrens (Anderson and Millar 2004). Parma microlepsis in NSW have been shown to depend on barrens habitat (Holbrook, Kingsford et al. 1994). Therefore, range shifts of habitat-specific species of fish can be expected (see (Last, White et al. 2010).

Urbanisation of estuarine shorelines has caused widespread habitat loss worldwide, including Australia (Edgar, Barrett *et al.* 2000), and climate change will exacerbate further losses through a variety of environmental drivers (e.g., increases in water temperature, sea level rise, etc.) discussed herein (Kennish 2002). Direct physical impacts are associated with coastal development (e.g. installation and construction of docks, piers, and boat ramps), and indirect causes of habitat loss include dredging, pollution, and destructive fishing. Loss of estuarine habitats have far reaching ecological ramifications; for estuarine fish, the most obvious outcome is a loss of available habitat, which is especially consequential for fish that use estuarine habitats as a nursery ground during their juvenile stages of development – of which there are many Australian species (Gillanders, Able *et al.* 2003; Meynecke, Lee *et al.* 2008). Estuarine fish may also be indirectly impacted through changes in trophic cascades. For example, Edgar and Barrett (2000)

showed that urbanisation of Tasmanian estuaries caused changes in sediment composition from sandy to muddy beds, and a concomitant shift benthic community assemblages (which are an important food source for estuarine fish).

In a global context habitat loss through human alteration of catchments is regarded as the major threat to freshwater biodiversity (Sala, Chapin *et al.* 2000), and a number of authors have highlighted the potential for negative interactions between existing anthropogenic stress and climate change (Palmer, Reidy *et al.* 2007). In many parts of Australia existing hydrologic stress due to human water use is already high, and these impacts are likely to intensify under expected climate scenarios (CSIRO 2008). Together with land-use change and other anthropogenic impacts hydrologic alteration has already led to substantial range contractions for many freshwater fish in Australia (Mallen-Cooper 1992). Habitat loss from sedimentation and channel alteration will likely interact with hydrologic stress to further decrease habitat availability in many rivers, as has been observed during recent drought periods in southeastern Australia (Bond and Lake 2005).

Sea level rise

Sea-level rise is likely to have strong indirect effects on fish production through its affects on key estuarine fish habitats, namely mangroves, seagrass, and saltmarsh (Bond and Lake 2005; Kennish 2002). Theoretically, these habitats have the potential to adapt to sea level rise by slowly migrating up the shore (Haslett, Strawbridge *et al.* 2001), but their ability to do this depends on land being available for a landward progression – i.e. sediment accretion rates need to keep up with rising sea levels (Kennish 2001). In addition, there mustn't be physical barriers (e.g. bulkheads, rock walls) to block habitat migration up the shoreline.

In Australia, mangrove stands are increasing in area at the expense of saltmarsh in the southeast, and key saltmarsh habitats are shrinking (Saintilan and Williams 1999). Saltmarsh is a nursery for crab zoea (larvae) production so in turn acts as a key food source for estuarine fishes ((Mazumder, Saintilan *et al.* 2006)). Sea level rise in Australia may also

directly affect estuarine and marine fish during their pre- and post-settlement phases. For example, Jenkins et al. (1997) showed that spatial and temporal variability in recruitment of a temperate, seagrass-associated fish (King George whiting, *Sillaginodes punctata*) was largely determined by physical processes, including residual sea-level (caused by changes in barometric pressure). Other Australian commercial species that might be similarly affected include pink snapper (*Pagurus auratus*), southern sea garfish (*Hyporhamphus melanochir*), Australian herring (*Arripis georgianus*), whiting and mullet (Fletcher and Head 2006)

Ocean currents and wind patterns

Western (EAC) and Eastern (LC: Leeuwin) Boundary currents bracket Australia and are expected to alter under climate change scenarios. The strength of the LC is influenced by ENSO-related thermocline anomalies, and may be weakening, while the EAC is projected to strengthen and drive further poleward into Tasmanian waters by late this century (Ridgway 2007)The LC and its interannual variability have profound impacts on marine ecosystems off the west and south coasts of Australia. For example, high recruitment of the western rock lobster (Panulirus cygnus) fishery of Western Australia is influenced by a stronger LC and the associated warmer water temperatures (Caputi, de Lestang et al. 2009). The strengthening EAC will lead to higher SSTs in SE Australian waters but also advect tropical and subtropical fauna Especially for the EAC, strengthening and southward extent are poleward. likely and have already occurred due to climate change. This of course interacts with water temperature (see above) but also increases potential for warmer-water species to move south through advantages to larval dispersal. On the flip side, southern species may find it difficult to disperse north or even maintain range possibly precipitating a shift south.

Changes in wind strength and direction are predicted under climate change scenarios, which can affect mixing and circulation of water. In Port Phillip Bay (Victoria, Australia), post-larval abundances of King George whiting (*Sillaginodes punctata*) in seagrass sites are strongly correlated with zonal westerly winds (Jenkins 2005; Jenkins, Black *et al.* 1997).

Acidification

Recently, increased ocean CO₂ through climate change, resulting also in pH drops, has been shown to affect homing in coral reef fishes ((Munday, Dixson et al. 2010)) but the generalisation of these results to marine fishes in general and the implications to range shifts are unknown at present. Relative to ocean and freshwater systems, the effects of acidification on estuarine fishes have been largely ignored. However, recent data from the Puget Sound, a large estuary complex in the U.S. Pacific Northwest, suggests that ocean acidification accounts for 24-49% of the pH decrease relative to pre-industrial values, and up to 49-82% for a doubling of atmospheric CO₂ (Feely, Alin et al. 2010). It is difficult to know whether estuarine fish will respond in similar ways to fresh and marine fishes given that most of the literature has focussed on responses (e.g. reproduction, early development, growth and behaviour) of marine and freshwater fish to prolonged CO₂ exposure (Ishimatsu, Hayashi et al. 2008), whereas estuarine fish are more likely to be exposed to pulses in CO_2 exposure due to the highly dynamic nature of estuarine environments. Acidification of rivers in Australia will most likely arise as a result of decreasing river flows exposing acid sulphate soils rather than from increased CO2 absorption, as evidenced by recent events in parts of the Lower Murray River (Fitzpatrick, Thomas et al. 2009). Reinundation of acid sulphate soils leads to rapid oxidation resulting low oxygen concentrations as well as low pH and have caused severe fish kills (Lamontagne, Hicks et al. 2004). Fish such as the already threatened Murray Hardyhead (*Craterocephalus fluviatilis*), which inhabitat shallow floodplain wetlands along the lower Murray River are particularly at risk.

Approaches to range shift detection in Australian fishes

Our review has uncovered almost no direct evidence that range shifts in Australian fish species has occurred, let alone examples related to climate change. Much anecdotal evidence of species local extinctions exists, but the lack of scientifically-rigorous monitoring is apparent. Nonetheless there are numerous clearly identified mechanisms by which climate change is expected to induce range shifts across marine, estuarine and freshwater environments. The few reliable studies are summarised here, along with examples of a range of indirect approaches to inferring range shifts or predicting likely range shifts in response to climate change drivers.

Direct field census vs. recorded change in environmental variables

One of the rare examples of direct evidence of a relationship between faunal changes and climate change drivers in Australia is that of (Stuart-Smith, Barrett *et al.* 2010) who used over 100 underwater surveys to compare assemblages on Tasmanian rocky reefs between the early 1990's and 2005. Long term SST monitoring at Maria Island showed SST rises of up to 1 °C over the curse of the study but the authors concluded that reef communities had remained relatively stable over that time. Significantly, however, ranges of several key eastern marine fishes had shifted south. For instance, the weed whiting *Siphonognathus attenuates* and luderick *Girella tricuspidata* southern range edges shifted over 2 degrees off eastern Tasmania, and two previously-absent eastern species, the crimsonband wrasse *Notolabrus gymnogenis*, and the marblefish *Aplodactylus lophodon* were observed in 2005.

Probably the most compelling and comprehensive example of demonstrated range shifts of fishes in Australia is reported in (Last, White *et al.* 2010). This study also monitored Tasmanian coastal fish distributions but included data since the late 1800s using multiple methods (e.g., spearfisher records, commercial fisheries data, scientific surveys, REDMAP data) to quantify perceived changes in ichthyofauna. Indeed, 61 of 300 fish species off coastal Tasmania had undergone significant shifts in range and/or abundance. Some losses (e.g. 5 predatory fish species) were attributed to exploitation, but 45 species (in 21 families) showed range shifts likely to be related to climate change (SST increases).

Existing databases

Commercial catch databases

Given the generational nature of fishing fleets, it is likely that commercial fishers can provide anecdotal accounts of climate related range shifts that may serve to trigger further investigation of changes in fish ranges. Of course, comparison of past and present fish catches are susceptible to sampling artefacts, especially in commercial fishing records, whereby fishing gears change through time, or where earlier records fail to report fish lacking commercial value (Byrkjedal, Godo et al. 2004). An example of the use and limitations of such datasets comes from the NSW commercial catch database housed and maintained at NSW Department of Innovation and Investment. This database is divided by fishery, such as estuarine haul, and by latitude. From 1940-1960 no effort data were recorded, while from 1961-1997 effort data were not reliable in most cases. For the whole database, catch was not only related to availability but also to market preferences, circumstances of fishers and changes in legislation. Despite these issues, (Gillson, Scandol et al. 2009) were able to use the estuary database to explore how catches of key commercial fish species caught by gillnet varied with river flow. Booth (unpub. data) has used the database, in consultation with NSW Industry and Investment specialists, to look at catch and CPUE changes across time in key species that may alter distribution with climate change (e.g. Fig 3a).

Recreational catch and "citizen-science" databases

Where scientific databases are lacking, and provided data can be crossreferenced and calibrated, various recreational fishing databases can be useful to determination of species range shifts, which can then be related to climate drivers. First, records from fishing competitions, where catches are carefully recorded, including weights and identifications, can be valuable despite obvious biases (e.g., fish samples are biased towards larger individuals or desirable species). Such competitions are held regularly and in the same place, including spearfisher, game fishing and other marine competitions. Provided the researcher is allowed access and understands limitations, these can be useful (Steffe, Murphy et al. 2005). New online websites public (e.g., REDMAP www.REDMAP.org.au) coordinate widespread fish observations across a range of amateur fishing, diving, and scientific observers and have the potential to capture new appearances and range shifts of fishes in coastal marine habitats. 'Reeflife' surveys (Edgar, Barrett *et al.* 2009) have combined rigorous experimental design and data manipulation and storage with amateur diver training to survey habitat and key fish and invertebrate species around southern (and more recently northern) Australia. The consistent methodology and frequent surveys make it an excellent vehicle to detect range shifts.

Museum and government collection databases

Museums sponsor expeditions/collecting trips around the Australian coast and in freshwater habitats and the archived specimens and data collected could be of value in mapping ranges and range shifts of fishes. On the plus side, the collections are often quantitative (e.g., rotenone stations), specimens are usually accurately identified, locations are often revisited over decades, and specimens are usually accessed into collections so can be recovered for measurement later. Similarly, most government agencies maintain databases of fish survey records from government and university research programs. Historically these have been an underutilised resource, but increasingly they are being used as a source of data for examining species distribution patterns via more quantitative modelling approaches (e.g. Bond, Thomson et al. submitted; Growns 2008). Shortcomings in relying on these sources of data include the range of sampling approaches used, varied sampling objectives and variable collection intensity, all of which may render them inadequate for detection of range shifts. Nonetheless, in some cases even cursory examinations of these sorts of databases can reveal interesting trends, for example latitudinal changes in the proportion of tropical species over decadal time scales based on data from Australian Museum rotenone collections stations from coastal NSW sites from the 1960s to the present (Figure 3b).

Combining data on past and present distributions with expected habitat/environmental driver changes to demonstrate/predict range shifts

Another indirect approach to monitoring range shifts is to overlay known physiological limits of the taxon in question on current/historical distribution maps and to extrapolate distribution changes based on projections of how the environmental variable in question is predicted to change (e.g., cane toad invasions: (Shine 2010)). (Cheung, Lam et al. 2009)) used a dynamic bioclimate envelope model to project range shifts of over 1000 exploited fishes and invertebrates using past data and future models of values for key ocean environment variables such as SST, sea ice cover, salinity and upwelling. That is, they couple past distribution change with these environmental variables to project future changes. Laboratory data on physiological tolerances to key environmental drivers can supplement and refine these models. For example, (Hofmann 2005) used biochemical and molecular techniques to gain into the role of temperature in setting species' distribution patterns in the marine environment, and (Barnes, Griffiths et al. 2009) inferred range-limits based on physiological tolerances in benthic Arctic marine invertebrates. However, these lab approaches should be used with care. For instance, vagrant damselfishes (Abudefduf vaigiensis) can survive under laboratory conditions down to at least 15[°]C (Figueira, Biro *et al.* 2009) but the same species disappears in the field below 17⁰C (Booth unpub. data; See Figure 4).

Other indirect approaches

Demographic and physiological models: While correlative approaches have been widely used to infer potential range shifts in fish, changes in physiological costs and demographic processes such as survivorship or reproductive output may also lead to eventual population losses and hence range contractions (e.g. Perry and Bond 2009; van Winkle, Rose *et al.* 1997). While relatively data intensive, physiological and demographic models (collectively referred to as bottom up or mechanistic approaches) are more likely to reveal ecological surprises, as long-term population viability is effectively an emergent property of the model rather than a set of constraints imposed as part of the model, as is the case in bioclimatic modelling approaches.

Paleoecology: Interrogating palaeoecological data to understand contemporary and future biotic responses to climate change offers an increasingly promising approach, especially when data records extracted from lake and marine sediments because of their ability to log climate change and concomitant biological responses (Willis, Bailey et al. 2010). The obvious advantage of paleoecological data sets is that they have the capacity to record ecological and evolutionary processes over time scales that far exceed most observational records. For example, Newbrey et al. (2009) used fossil fish material from the Cretaceous Dinosaur Park Formation of Alberta (Canada) to document the presence of members of the Characiformes (relatives of the piranha and neon tetras) in North America in the Late Cretaceous, a time of significantly warmer global temperatures than now. Fish otoliths, which can act as records of growth, chemical environment and lifehistory events are well-preserved in sediments, aboriginal middens etc. and show great promise as paleogological tools to detect climate change and range shifts. In addition to understanding the geographical range of fish, paleoecological data can be used to make inferences about the temporal range of fish (e.g. Murray and Wilson 2009; Read, Bellwood et al. 2006).

Genetics: The genetic structure of populations can provide information on the potential biogeographic history of organisms. In aquatic environments, range expansion and contraction events can be inferred by matching information on the phylogenetic separation of taxa with information on oceanic circulation and physical barriers that might limit dispersal (e.g. Ayre, Minchinton *et al.* 2009; Barber, Palumbi *et al.* 2000; Dawson 2001; Faulks, Gilligan *et al.* 2010b). Such approaches are now widespread, but there is also an increasing move toward relying not only on the use of neutral markers to assess historical patterns of gene flow, but toward the detection of genes that are actively being selected for along environmental gradients. This is an area that offers considerable promise in terms of understanding variation in the adaptation potential of not only different taxa but also different populations distributed in different geographic areas (Hoffmann and Willi 2008).

Conclusions and recommendations

While the resolution and availability of past and predicted data on climatechange environmental variables is rapidly increasing with advances in technology, (e.g., satellite SST and ocean colour data), biological data such as fish distributions are much sparser and more field labour-intensive. Matching the temporal and spatial resolution of the "independent" and "response" variables is problematic. We conclude that at present the knowledge of actual fish ranges in all 3 habitats, especially non-commercial species, is poor. Key guidebooks (e.g. (Gomon, Glover *et al.* 1994)) and distribution websites (e.g., FishBase [www.fishbase.org] and Biomaps [www.biomaps.net.au]) provide information on regional distributions and range edges of marine species but it is unclear how accurate and recent all of these sources are in their field monitoring of range edge.

One approach would be to target key regions and habitats for intensive monitoring. Climate change hotspots, such as coastal waters off SE and SW Australia for marine and estuarine, would be important for marine and estuarine species. In freshwater systems, less heavily regulated river basins may provide independent measures of climate change impacts, but in many cases it will be modified river systems where climate impacts are greatest (Palmer, Reidy *et al.* 2007). Threatened habitats such as urbanised estuaries vulnerable to sea level rise and vanishing kelp habitats (East and West coast) could also be targeted. Key commercial fish species may be prone to shifting away from the economic zones of States or even National waters, so research on these could be targeted. Range-shifters could be considered "invasive species" and stronger collaboration with biosecurity researchers (and their access to funds!) would be useful.

While many non-specific databases have problems with data accuracy, georeferencing etc. they clearly have much to offer in terms of examining largescale and long-term trends in fish occurrence patterns. It is important that such databases are adequately maintained and we recommend a national approach to calibrating/cross-referencing databases in future. The newly-formed National Climate Change Adaptation Research Facility (NCCARF) would be an excellent vehicle to investigate such data set consolidation.

Given Australia's position as a world "hotspot" for climate change and our relatively advanced knowledge of key species, we have an exciting opportunity to lead worldwide in understanding climate-change induced range shifts of marine and freshwater fishes.

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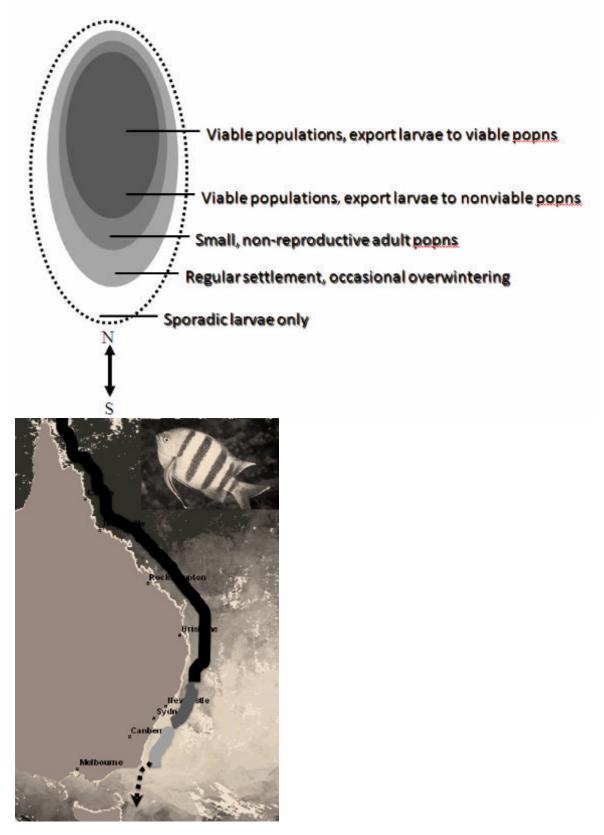
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Figures



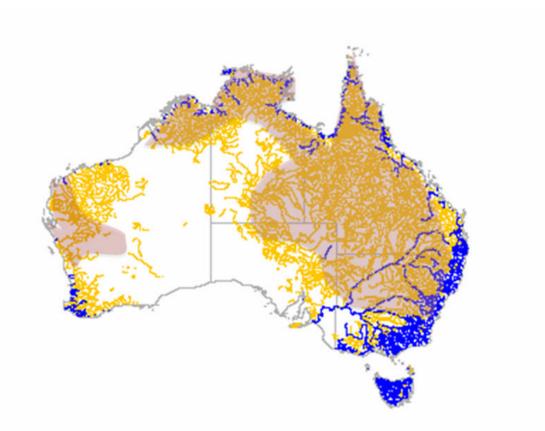


Figure 1: example ranges of Australian fish species

(a) Coastal Marine vagrant tropical fishes [upper panel shows a model for distribution, lower panel shows, for SE Australia, distribution layers as per above example for the sergeant-major damselfish (*Abudefduf vaigiensis*) Booth unpub. data.

(b) Distribution of spangled perch (*Leioptherapon unicolour*) through large parts of inland Australia where few rivers are perennial (yellow drainage lines) and hence distributions are patchy and expand and contract in relation to wet/dry cycles.

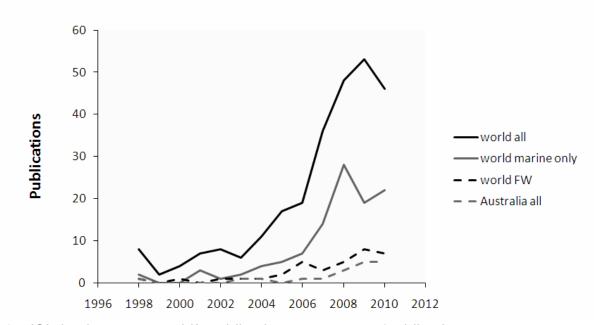


Figure 2: ISI database range shift publications 1996-2010 (publications per year), using keywords fish* and climate change and (range* or distribution) and (shift or edge or change).

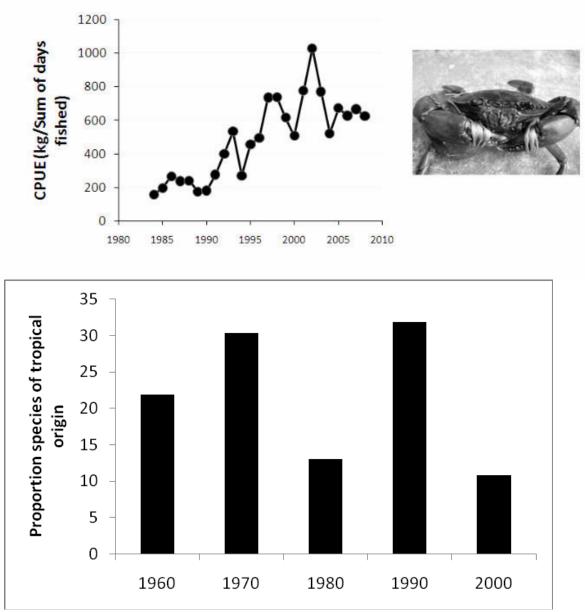


Figure 3: (a) Change in mudcrab CPUE in estuarine and ocean haul fisheries in NSW waters since 1985 (source NSW Industry and Investment (Fisheries) database)

(b) Decadal changes in species collected of tropical origins from Australian museum rotenone collection stations in SE Australia.

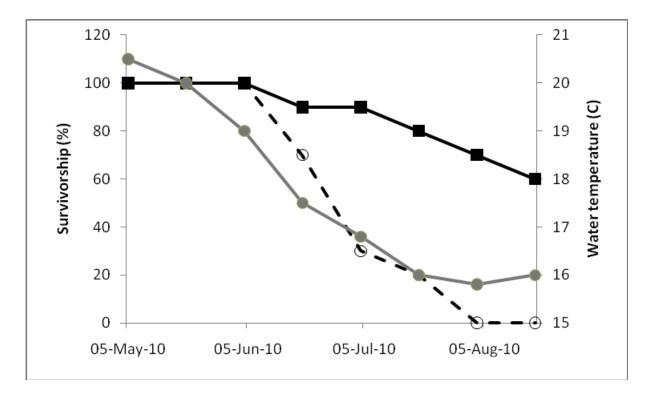


Figure 4: Example of differing laboratory vs. field physiological response. For the vagrant tropical damselfish *Abudefduf vaigiensis* in temperate SE Australia, survivorship under lab conditions is 60% down to 15C, whereas fish from the same cohort in the field disappear below 17C. (adapted from (Figueira, Biro *et al.* 2009)and Booth unpub. data).

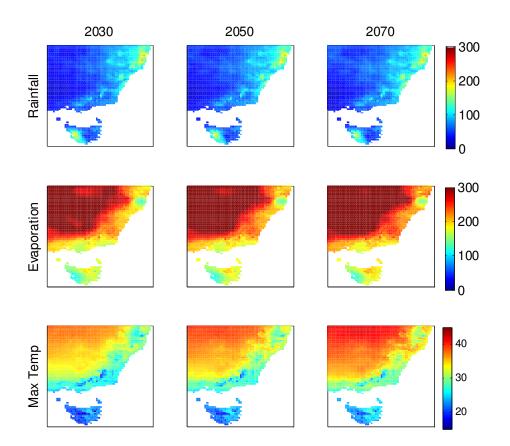


Figure 9. Projected January rainfall, evaporation and maximum temperature for the periods 2030, 2050, and 2070 based on downscaled data from the CSIRO mk3.5 climate model and the A1FI SRES scenario (data courtesy Tom Harwood, CSIRO).

CONTRIBUTION OF CLIMATE CHANGE TO HABITAT DEGRADATION AND LOSS IN AUSTRALIAN AQUATIC ENVIRONEMENTS.

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Australia's aquatic ecosystems are unique, supporting a high Abstract. diversity of species and high levels of endemism, but could be extremely vulnerable to the major environmental changes expected to occur due to climate change. This review assesses climate-induced changes to structural habitats that have occurred in different aquatic ecosystems. For the most part, climatic impacts are difficult to discern against the background of habitat degradation caused by more direct anthropogenic impacts. However, climate impacts will become more pronounced with ongoing increases in temperature, changes in water chemistry, sea level rise, altered rainfall, increased severity of tropical storms, and changes to ocean currents. Each of these factors is likely to have specific effects on ecosystems, communities or species, and their relative importance varies with habitat. In the Murray-Darling Basin, the greatest concern relates to declines in surface water availability and river flows, which will be exacerbated by declining rainfall and increased evaporative loss. On the Great Barrier, increasing temperatures lead to increased incidence and severity of coral bleaching, thereby contributing to sustained and ongoing coral loss. Despite the marked differences in major drivers and consequences of climate change, the solution is always the same; immediately reducing greenhouse gas emissions whilst minimizing nonclimatic causes of habitat degradation to maximize ecosystem resilience. In the short-term, management must also attempt to facilitate the adaptation of species and ecosystems to inevitable climate change.

INTRODUCTION

In aquatic habitats, as on land, anthropogenic climate change is having

significant and appreciable effects on ecosystems, communities and species (Walther et al. 2002; Parmesan and Yohe 2003; Hoegh-Guldberg and Bruno 2010; major effects include declines in biodiversity and productivity (O'Reilly et al. 2003), changes in taxonomic composition and community dynamics (Hughes et al. 2003; Xenopoulos et al. 2005; Ficke et al. 2007), and shifts in the geographic ranges, distribution and abundance of species (Perry et al. 2005; Balston 2009; Pitt et al. 2010). Aquatic habitats may be even more vulnerable, and changing more rapidly as a consequence of recent climate change, compared to terrestrial ecosystems (Richardson and Poloczanska 2010). However, research on the effects of climate change in aquatic ecosystems lags behind that of terrestrial ecosystems. The number of marine and freshwater studies included in the Fourth Assessment Report of the IPCC (Rosenzweig et al. 2007) was <0.3% that of land-based studies, reflecting a general imbalance in levels of scientific research undertaken in aquatic versus terrestrial systems (Richardson and Poloczanska 2010). Understanding of the effects of climate change in aquatic ecosystems is also difficult due to the i) size and/ or complexity of aquatic ecosystems, ii) inherent variability in environmental conditions, and iii) limited long-term records of environmental conditions (Richardson and Poloczanska 2010).

Although there is a strong terrestrial bias in documented effects of anthropogenic climate change on natural ecosystems and organisms (Parmesan 2007; Richardson and Poloczanska 2010), climate change has had significant, and often spectacular, impacts in marine and freshwater ecosystems. In 1998, for example, warm ocean waters caused extensive bleaching and widespread mortality of scleractinain corals throughout the world (Goreau et al. 2000; Wilkinson 2000). Links between increasing ocean temperatures and regional-scale bleaching of scleractinian corals are incontrovertible (Hughes et al. 2003; Hoegh-Guldberg et al. 2007), and climate-induced coral bleaching has greatly exacerbated ongoing declines in the abundance of habitat-forming scleractinian corals at many locations (Hoegh-Guldberg 1999; Wilkinson 2004). In freshwater ecosystems, climate change poses a direct threat to the existence of many habitats, and habitat degradation and loss is already a major threat for threatened fish species from freshwater ecosystems, wetlands and estuaries (Figure 1). The combined effects of sea level rise, reduced rainfall, and increased drought severity place many coastal freshwater habitats and species at increased risk of saline intrusion (Bayliss et al. 1997; Mulrennan and Woodroffe 1998; Hitchcock 2004). Extinction rates of freshwater fishspecies are equal or higher than those of many terrestrial taxa (Heino et al. 2009), and are expected to increase in coming decades by the impacts of climate change. (Xenopoulos *et al.* 2005).

The vulnerability of aquatic ecosystems to global climate change is due to the profound influence of environmental conditions (especially temperature, water flow and/ or nutrient availability) on biological and ecological processes, and the sensitivities of species within these systems. Coral reefs are considered to be among the most vulnerable ecosystems to climate change (Walther *et al.* 2002), owing to thetemperature sensitivities of corals, which may bleach and die when sea temperatures exceed normal local limits by as little as 1.0°C (Jokiel and Coles 1990). There are few other ecosystems in which the major habitat-forming organisms function so close to their upper

thermal limit. Vulnerability of aquatic habitats to climate change is further heightened due to the degraded state of many aquatic habitats (e.g. Valiela *et al.* 2001; Schindler 2001, Hughes *et al.* 2003, Worm *et al.* 2006). For the most part, effects of climate change compound upon habitat degradation and species losses that have occurred as a result of anthropogenic disturbances, such as species exploitation, pollution and habitat modification (e.g. Schindler 2001; Hughes *et al.* 2003). This is particularly so for freshwater and estuarine ecosystems that are impacted by surrounding development and land and water use.

Climate change may impact on any number of the ecological processes (e.g. nutrient cycling, energy transfer, sediment transport, recruitment or dispersal of biota), structural or biological components (e.g. communities or individual species) of aquatic habitats. For fishes, climate change will have both direct and indirect effects (Roessig et al. 2004; Munday et al. 2008; Pratchett et al. 2009). Being ectotherms, changes in temperature will have direct effects on fish physiological condition, oxygen consumption, developmental rate, growth, swimming ability, reproductive performance and behaviour (e.g. Van der Kraak and Pankhurst 1997). Changes to water chemistry, (especially reductions in pH) which are expected to occur with current levels of greenhouse gas emissions, have also been shown to interfere with sensory abilities of some marine fishes (e.g. Munday et al. 2009), which may have important ramifications for settlement and survivorship (Dixson et al. 2010). However, the most immediate effects of climate change on fishes are likely to be indirect, caused by changes in availability, structure, and connections between critical habitats. Climate induced changes to habitat structure have already been recorded in many aquatic ecosystems, where they have had significant effects on both abundance and diversity of fishes (Swales *et al.* 1999; Wilson *et al.* 2006; Pratchett *et al.* 2008).

The purpose of this review is to consider effects of climate change on the habitat structure of aquatic ecosystems within Australia, comparing the major drivers of climatic impacts across freshwater ecosystems, tidal wetlands, seagrass beds, tropical coral reefs, and temperate rocky reefs (Table 1). Australia's aquatic ecosystems are unique, supporting a high diversity of species and high levels of endemism (Unmack 2001; Poloczanska et al. 2007), and could be extremely vulnerable to the major environmental changes expected to occur in some locations (Poloczanska et al. 2007). In general, there is very limited data available with which to assess the effects of climate change on aquatic ecosystems in Australia, especially compared to Europe and North America (Hughes 2003; Poloczanska et al. 2007). Two notable exceptions are the Great Barrier Reef (GBR), and the Murray-Darling Basin (MDB), for which anthropogenic threats and changes in ecosystem state have been documented for >100 years (e.g. Murray-Darling Basin Commission 2004a, 2004b; Daley and Griggs 2006, 2008). Within each of these distinct and iconic systems, the recent and observable effects of climate change will be compared to degradation and loss of critical fish habitats caused by other more direct anthropogenic disturbances. The projected effects of climate change will also be considered to assess their likely impacts in coming decades.

Major drivers of climatic impacts in different aquatic ecosystems

The two main consequences of anthropogenic climate change are i)

increases in average atmospheric temperatures, and ii) increases in atmospheric concentrations of greenhouse gases, mainly CO_2 . In aquatic ecosystems, increasing atmospheric temperatures will warm surface waters of oceans, lakes and rivers (Levitus *et al.* 2000). However, aswater has a higher heat capacity than air, this means that increases in water temperatures will lag behind that of atmospheric temperatures (Lough 2007). A significant component of anthropogenically produced CO_2 (approximately one third, thus far) is that it also dissolved in the world's oceans, lakes and rivers (Roessig *et al.* 2004). Additional CO_2 dissolved in the ocean reacts with seawater to form weak carbonic acid, causing pH to decline and reducing the availability of dissolved carbonate ions required by many marine calcifying organisms (e.g. corals, other invertebrates, and coralline algae) to build their shells or skeletons (Orr *et al.* 2005).

Other environmental changes linked to global climate change that will effect aquatic habitats include increased severity of tropical cyclones (Madin and Connolly 2006), reduced overall rainfall, more extreme rainfall events, or altered rainfall patterns (especially long dry spells) (CSIRO 2008), sea level rise (Short and Neckles 1999), and changes to ocean circulation and current patterns (Munday *et al.* 2008, 2009). Tropical cyclones are expected to become more intense in a warmer world (Webster *et al.* 2005), causing greater damage to key habitat-forming species, such as corals and seagrasses (Madin and Connolly 2006). Sea level rise will lead to a redistribution of intertidal and shallow coastal habitats, as well as increase seawater intrusion into estuaries and the lower reaches of rivers (Short and Neckles 1999). Changes to ocean circulation and current patterns will alter

dispersal of marine larvae (Munday *et al.* 2008, 2009), and combined with reductions in vertical water mixing, will limit the supply of nutrients and subsequent productivity. Changes to temperatures and flows in freshwater ecosystems are also likely to alter processes such as productivity and the downstream drift of larvae (Lake 2003). A complete loss of freshwater may occur for some habitats such as wetlands. Each of these factors is likely to have specific effects on ecosystems, communities or species, but their relative importance will vary greatly among habitats (Table 1).

Freshwater ecosystems

For freshwater systems the most critical factor affecting habitat structure, as well as nutrient loading, transport of materials and organisms, is the amount of rainfall that runs off the land surface to form streamflow (Walker et al. 1995). Variation in river flow over time scales from days to decades is also very important in setting the dynamic equilibrium among habitat patches (Thorp et al. 2006). Changes in flow dynamics resulting from climate change will therefore have profound effects on riverine habitats and the fishes that depend upon them (Walker et al. 1995; Meyer et al. 1999). Xenopoulos et al. (2004) suggested that 75% of freshwater fish throughout the world will become extinct through part of their range by 2070 because of reduced river discharges. Australia has large areas of dryland rivers and highly variable flow regimes that are prone to periods of low/no flows (Walker et al. 1995). Hence, reductions in river flows under a drier climate regime (CSIRO 2008) are likely to exacerbate the existing declines in fish species richness attributable to reduced flows. Reductions to river flows due to water extraction has already been shown to impact native fishes in lowland

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reaches of the Murray-Darling River system (Gehrke and Harris 2000). Despite predictions of reduced total rainfall, increased intensity of rainfall may also result in increased turbidity from suspended sediments transported from surrounding catchments. The resultant reduced light penetration for photosynthesis by macrophytes, phytoplankton and benthic algae may potentially lead to shifts in primary production in aquatic food webs. Decreased rainfall and higher temperatures will increase the rsik of fires within the catchment and resultant eroding sediments can lead to fish kills and the smothering of habitats (Lyon *et al.* 2007)

Increased river temperatures are likely to affect the distribution of freshwater species, leading to vertical contraction of cold-water species, accompanied by an potential upstream range extension of warm-water species (Buisson et al. 2008). Warming effects are likely to be exacerbated where clearing of riparian vegetation reduces shading of the water surface (Rayne et al. 2008). Warmer temperatures and increased evaporation rates, combined with a drier climate across much of Australia, will result in increased drying of wetlands and waterholes in ephemeral rivers, and may result in some permanent habitats becoming intermittent (Kennard et al. 2010). Some intermittent freshwater habitats may also cease to exist, have ezxtended dry periods or will become much rarer leading to smaller geographic ranges of certain species or reduced connectivity among populations. While increases in temperatures may allow southerly extensions to the range of some marine species (Booth et al. in review), the discontinuous nature of freshwater catchments can prevent similar range changes and indeed may lead to range reductions for many species (Bond et al. in review). For the most part, these

effects will compound upon pre-existing threats associated with water extraction and aquifer draw-down, especially in dry inland areas (e.g. central Queensland).

Of the 46 fish species listed under the Australian Environment Protection and Biodiversity Conservation (EPBC) Act 1999 (www.environment.gov.au/biodiversity/threatened/index.html) most (56%) are from freshwater habitats (Figure 1). The primary cause of declines in the geographic range and/ or overall abundance of these freshwater fishes is habitat degradation or loss (Figure 1; Pollard et al. 1990). The other major contributor to increased extinction risk of freshwater fishes in Australia is the introduction of exotic species or translocation of Australian native species, which predate on or compete with native species (e.g. Ingram et al. 1990). Pollard et al. (1990) suggested that 34% of Australia's freshwater fishes were already threatened by habitat loss, invasive species, and/ or overfishing.

Tidal wetlands

The major structural habitat components in tidal wetlands are plant species (saltmarshes and mangroves) and are therefore, very responsive to climate related changes in atmospheric temperature, CO₂ concentrations, rainfall and freshwater input (Lovelock and Ellison 2007). However, the greatest effect of climate change on tidal wetlands (including, mangroves and salt marshes) is expected to arise due to increasing sea level. Mangrove trees are well adapted to being inundated with salt water, but growth of trees declines and/ or forests retreat landward with increasing frequency and duration of inundation. Previous episodes of sea level rise have led to proliferation of mangroves in northern Australia (e.g. Woodroffe 1990).

However, development and modification of coastal habitats has resulted in loss of wetlands, disruption to connectivity, enhanced nutrients, and physical barriers that reduce the potential for landward migration of wetlands along much of Australia's coastline (Lovelock and Ellison 2007), referred to as "coastal squeeze" (Doody 2004). In Australia, current rates of sea level rise are estimated to be 0.3 - 0.5 mm/ year, which is much lower than most global estimates. However, mangroves are already progressing landward and encroaching on saltmarsh environments at many locations along Australia's south-east coast (Saintilan and Williams 1999), which may be partly due to sea-level rise. Since 1983, 14% of Australia's mangrove habitat has been lost (Valiela et al. 2001), and a further 231km² is destroyed each year (Valiela et al. 2009) mostly due to land reclamation and deforestation. Globally, Nicholls et al. (1999) calculated that 13-31% of tidal wetlands have already been lost, but only 0-2% of this habitat loss was attributable to sea level rise. With current rates of deforestation, Valiela et al. (2009) suggested that mangroves would have been lost before the major impacts from projected sea level rise become fully apparent.

Tidal wetlands are an important component of coastal ecosystems in providing a buffer zone between freshwater and marine environments. Mangroves and saltmarshes are capable of high rates of denitrification and intercept land-based nitrates, thereby protecting coastal seagrass meadows from excessive eutrophication (Valiela *et al.* 2009). Saltmarsh and mangrove sediments also retain many industrial contaminants (e.g. heavy metals), which would otherwise affect marine ecosystems (Twilley 1995). There is also a strong positive relationship between the areal extent of wetlands and the productivity of adjacent seagrass meadows (Valiela *et al.* 2009). Tidal wetlands (including associated estuarine areas) are also an important habitat in their own right, supporting up to 300 species of fishes (mainly in tropical environments) and up to 290kg of fish biomass per hectare (Blaber, 2002). The nutrient rich water of wetland dominated estuaries support many commercially important fish species. Along the Queensland coast, Manson *et al.* (2005) demonstrated that fisheries catch of barramundi (*Lates calcarifer*) were positively correlated with the local extent of mangroves. It is generally suggested that tidal wetlands provide subsidies (both in terms of nutrients and larval production) to other coastal habitats, whereby strong connectivity between mangroves and seagrasses, or mangroves and coral reefs leads to increases in overall productivity (Mumby *et al.* 2004).

Increasing loss of tidal wetlands has significant ecological and geophysical impacts, including destabilization of coastal shorelines and sediments. increased contamination and eutrophication of coastal ecosystems, leading to lower productivity and loss of habitat for fishes, as well as many other important species, such migratory shorebirds (Valiela et al. 2009). For the 14 threatened fishes from Australian tidal wetlands and estuaries, major threats relate habitat loss and overfishing (Figure 1). The management actions required for increasing resilience of tidal wetlands to climate change, and especially increasing sea level, are i) minimise deforestation and land reclamation to preserve existing wetland habitats, and ii) recognise and facilitate landward migration of tidal habitats, thereby enabling natural and autonomous adaptation to climate change.

Seagrass beds

Seagrass beds are a unique and important coastal habitat, formed by the growth of flowering plants (as distinct from algae or seaweed) in shallow sandy habitats throughout tropical and temperate biomes (Dennison 2009). Seagrasses as a whole are particularly sensitive to a wide range environmental changes resulting from climate change, including changes in temperature, salinity, water clarity and nutrient loads, elevated CO₂ concentrations and ocean acidification, sea level rise, the frequency and/ or severity of cyclones, and ocean circulation (e.g. Short and Neckles 1999; Waycott et al. 2007). In part, increases in CO₂ concentrations may actually increase growth and productivity of seagrasses. The major effect of climate change is expected to be a shift in the relative abundance of seagrass species, with increased abundance of more ephemeral species (Waycott et al. 2007). Complete loss of seagrasses is expected to be localized (e.g. at the mouths of rivers) and may be offset by increases in the extent of seagrasses in areas where seagrass growth is currently limited by nutrient availability (Waycott et al. 2007). However, the total areal extent of seagrass beds is declining at 1.5% (or 110 km² per year) across the continent, mainly due to direct disturbances (Waycott et al. 2009), excessive eutrophication, sedimentation and disease (Orth et al. 2006; Waycott et al. 2009).

Australia has some of the most extensive and diverse seagrass beds in the world. On the Great Barrier Reef, the total area of seagrass beds is twice that of coral-dominated habitat (Dennison 2009). Moreover, extensive seagrass beds in southeast Australia support one third of all seagrass species (Carruthers *et al.* 2007). However, Kirkman (1997) estimated that the total area of seagrass beds in Australia declined by 1,450 km² (or >20%) between 1986 and 1996, mostly in the tropics and mostly due to cyclonic disturbances. Recovery of tropical seagrasses subject to anthropogenic disturbances or cyclones is generally very rapid, but recovery has been hampered in some areas by habitat degradation (increasing sedimentation) and declining water quality. In temperate waters (e.g. Western Port in Victoria), where direct anthropogenic disturbances have killed off large areas of seagrass, there is limited prospect of recovery (Dennison 2009).

Seagrass habitats are an important component of coastal ecosystems, contributing greatly to productivity of coastal ecosystems. While very sensitive to excessive nutrient loads, seagrasses also trap considerable nutrients arising from terrestrial and estuarine habitats (Orth *et al.* 2006). Seagrasses represent an important source of food for several threatened species, including dugongs and sea turtles (Waycott *et al.* 2009). They may also serve as nursery grounds for economically or functionally important fishes that otherwise reside on coral reefs or other inter-connected habitats (Mumby *et al.* 2004). Localised declines in some fishes have been observed following the reduction in seagrass areas (Butler and Jernakov 1999; Walker *et al.* 2006). It remains to be tested however, what proportion of coastal fishes are specifically reliant on non-reefal habitats such as seagrass beds, and whether these fishes could utilize alternative habitat-types if seagrass beds were unavailable (e.g. Mumby *et al.* 2004).

Coral reefs

Climate change is widely recognised as the most important emerging threat to coral reef ecosystems and there are many ways that climate change will impact on coral reef species, communities and ecosystems (Hughes *et al.* 2003; West and Salm 2003; Hoegh-Guldberg et al. 2007; Wachenfeld et al. 2007). The most devastating effects of climate change, so far, have been large-scale and severe episodes of coral bleaching resulting from increasing sea surface temperatures (Goreau et al. 2000). In 1998, coral bleaching occurred in >50 countries throughout the world, killing up to 90% of leading to marked changes in the taxonomic composition of coral assemblages (e.g. Riegl and Purkis 2009). Given projected increases in sea surface temperatures, if corals are unable to acclimatize or adapt, coral bleaching events become more frequent and more severe through time (Hoegh-Guldberg 1999; Donner et al. 2005). By 2050, most coral reefs are expected to be subject to annual thermal anomalies equivalent to those experienced in 1998 (Hoegh-Guldberg 1999), suggesting that mass bleaching will occur at intervals much less than the time required for corals (populations and communities) to recover from successive major bleaching events (Donner et al. 2005). Effects of increasing temperature will also be further exacerbated by ocean acidification (Hoegh-Guldberg et al. 2007), which reduces coral growth and increases susceptibility to coral bleaching.

Coral loss, and associated changes in biological and physical structure of coral reef habitats, has an important influence on the abundance and diversity of coral reef fishes (Wilson *et al.* 2006; Pratchett *et al.* 2008). Declines in coral cover have direct effects on the abundance of reef fishes, especially among coral-dependent species (e.g. Kokita and Nakazono 2001; Munday 2004; Pratchett *et al.* 2004). Extensive coral loss may also result in declines in habitat and topographical complexity (Sheppard *et al.* 2002; Graham *et al.* 2007), which are critical for sustaining high diversity of reef fishes and other reef-associated organisms (Wilson *et al.* 2006; Pratchett *et al.* 2009). When coral loss is combined with structural collapse of reef habitats, such as from storms, up to 65% of reef fishes may experience declines in abundance (e.g. Jones *et al.* 2004). Increasing frequency and severity of mass-bleaching events are clearly linked to climate change (Walther *et al.* 2002; Hughes *et al.* 2003) and the longer-term future is potentially catastrophic, not just for corals, but for coral reef fishes as a well.

Globally, corals reefs are facing significant and accelerating coral loss. Wilkinson (2004) estimated that 20% of the world's coral reefs have already been destroyed, whereby coral cover has declined by >90% and there is limited prospect of recovery. Coral cover has declined by 20-90% on a further 50% of the world's coral reefs, and these reefs may be destroyed by 2050 (Wilkinson 2004). One global mass-bleaching event in 1998 contributed greatly to coral reef degradation (Wilkinson 1999), especially in the Indian Ocean (e.g. Graham et al. 2008). However, coral reef degradation is mostly concentrated in east Africa, south-east Asia, and the central and southern Caribbean (Wilkinson 1999). All these areas have relatively large human populations living adjacent to coral reef habitats, and have also had a long history and high levels of exploitation (e.g. Pandolfi et al. 2003), indicating that coral loss is caused, or at least precipitated, by anthropogenic disturbances. It is likely however, that climate related changes in temperature and sea water chemistry will contribute greatly reef degradation in coming decades (Hoegh-Guldberg 1999; Wilkinson 1999). In part, anthropogenic degradation and the increased fragmentation of coral reef habitats have greatly eroded reef resilience and making coral reef habitats much more susceptible to future

climate change (Hughes et al. 2003).

Temperate rocky reefs

Australia has high biodiversity and endemicity of temperate marine flora (e.g. Kerswell 2006), which is considered to be very vulnerable to increasing ocean warming (Wenberg et al. 2009). Marine algae with latitudinal ranges centered in temperate Australia are generally cold-water specialists and cannot survive in warmer waters. Accordingly, the geographic ranges of some of these habitat-forming algae have contracted southwards over the last few decades (Wenberg et al. 2009), exhibiting an adaptation strategy for temperate species to avoid increasing temperatures. However, given the lack of landmasses and associated shallow coastal habitats to the south of Australia, most species will have limited opportunity for further poleward shifts in their latitudinal ranges to accommodate further increases in ocean temperatures. Increasing ocean temperatures may also lead to southern range extensions for potentially devastating marine invasive species (Thresher et al. 2003; Ling et al. 2009), which may be further enhanced by strengthening of the East Australian Current (EAC). Invasive species are one of the greatest contemporary threats to global biodiversity and climate change is expected facilitate establishment and expansion of many new species on temperate reefs (Wenberg et al. 2009). Climate change (specifically, increasing temperatures and strengthening of the EAC) has been directly linked to changes in distribution and abundance of herbivorous species along the south-east coast, which have contributed to declines in the abundance of giant kelps (Edgar 1999; Ling et al. 2009).

The abundance of giant kelp (Macrocysitis pyrifera) has declined

dramatically over the past 30 years, especially in south-eastern Tasmania (Edgar 1997). In the 1950's the total area of kelp forests in Australia was estimated to 120 km² Cribb (1954), but more recent estimates of 8 km² in 1986 (Sanderson 1987), and 0.5 km² in 1988/89 (SeaCare, pers.comm.), point to a major loss of giant kelp. A number of factors may account for these dramatic losses, including increased penetration and influence of the EAC southwards along the east coast of Tasmania, which has increased water temperatures by 1.5°C since 1940 (Edgar 1999; Crawford *et al.* 2000). The currents and increased temperatures facilitated local increases in the abundance of the black sea urchin (*Centrostephanus rodgersii*), which feeds on giant kelp (Edgar 1999). Further contributors to declines in abundance of giant kelp are marine pollution, and the introduction of the Japanese Kelp (*Undaria pinnatifida*), which has colonized many areas formerly occupied by *M. pyrifera* (Sanderson 1987).

Globally, loss of kelp and macroalgal environments has resulted from increased disease, herbivory, physiological stress, and/ or interactions among these processes (Steneck *et al.* 2002). At lower latitudes, periodic deforestations result from anomalies in temperature, salinity or nutrients that either kill kelps directly or trigger diseases that may kill physiologically-stressed plants. At higher latitudes (40–60°), herbivory by sea urchins is the most common and most important agent of kelp deforestation. Both these effects may be linked to sustained and ongoing climate change, though loss of kelp forests and changes in habitat conditions of temperate rocky reefs, has been most pronounced in areas adjacent to urban centres, caused by coastal development, oil spills, fisheries depletion of apex predators and

invasions of introduced species. In heavily urbanized areas of Japan, for example, terrestrial deforestation and damming of rivers reduced availability of iron and humic substances necessary for kelp development (e.g. Suzuki *et al.* 1995). Loss of habitat-forming algae has important consequences for local biodiversity and ecological function (Steneck *et al.* 2002). Most notably, kelp forests concentrate and magnify secondary production, thereby supporting complex food webs in coastal zones. Kelp forests also provide habitat to high diversity and abundance of marine organisms, including mammals, fishes, crabs, sea urchins, and molluscs (Mann 1973). Losses of kelp forests and temperate macroalgal habitats are expected continue, if not accelerate, due to climate change and human population growth (Steneck *et al.* 2002), contributing to widespread degradation of coastal habitats.

Observed versus predicted climate impacts

Global climate change is being caused by anthropogenic forcing of the climate system (Houghton *et al.* 2001), and not only are atmospheric concentrations of greenhouse gases rising, but the rate of increase is accelerating (e.g. Canadell *et al.* 2007). Similarly, increases in atmospheric temperatures are expected to continue throughout next century, and are likely accelerate over the next two decades due to continued increases in greenhouse gas emissions and the inertia in the climate system (Houghton *et al.* 2001). As a consequence, even if climatic impacts are not yet apparent (or have had minor influence compared to other more direct anthropogenic disturbances) the effects of global climate change on ecosystems, communities and species will become greater over time . Accordingly, this section explores both current (observed) and projected effects of climate

change in two specific aquatic systems: the Murray-Darling Basin; and the Great Barrier Reef. These are both large, relatively well-studied systems, of considerable ecological and economic importance to Australia.

The Murray-Darling Basin

The Murray-Darling basin (MDB) is one of the world's largest catchments, covering more than 1 million km^2 and $1/7^{\text{th}}$ of the area of mainland Australia (Crabb 1997). Ranging over 13 degrees of latitude (from 24°S to 37°S) and up to 2,000 meters in altitude, the MDB experiences a wide range of climatic conditions. The MDB comprises 24 major rivers grouped into the Darling, Murrumbidgee, and Murray River systems. The rivers are fed mainly by rainfall on the western slopes of the Great Dividing Range. The average annual river flow of the MDB (10,00-22,000 GL pa) is low by world standards (Maheshwari et al. 1995), but inter-annual variability in flow is extremely high, especially within the drier and temperate regions of the basin (Walker et al. 1995). In the extreme, many major riverbeds become completely dry, which causes extensive mortality of resident fishes (Figure 2). Drought is a recurrent, natural event in the Murray-Darling Basin, and the native fish have evolved to cope with periodic reductions in habitat and river flow (Lintermans and Cottingham 2007; Bond et al. 2008). However, water extraction and flow regulation, for the purposes of agriculture, have greatly intensified the effects of droughts (e.g. Bond et al. 2008).

The MDB catchment yields \$10 billion of agricultural produce annually, accounting for 40% of the Australia's agricultural production. Approximately, 80% of the MDB has been cleared for agriculture, mostly for dryland grazing,

but there are also small areas of intensive horticulture, cotton and cereal crops, which are heavily reliant on irrigation (CSIRO 2008). Current water use accounts for 48% of surface water availability across the entire MDB, representing an increase of >500% since 1925 (CSIRO 2008). Ground water extraction has also increased (doubling in just the last 10-20 years), although records of groundwater use are limited (CSIRO 2008). River flows are also highly regulated and there is intense and increasing competition between water resource development and environmental needs (Walker 1985, 1992).

The MDB is inhabited by 46 native fish species (Lintermans 2007), most of which have declined in abundance or become highly restricted in their spatial distribution throughout the past century (Murray-Darling Basin Commission 2004a, 2004b; Lintermans and Cottingham 2007). Fifty seven percent of these species are now listed as threatened under either Federal or State legislation (Lintermans 2007)In 2005-2007, fishes of the MDB were comprehensively sampled as part of the Sustainable Rivers Audit (Davies et al. 2010). Native fishes were not caught in many (43%) of the sample sites and zones where they were predicted to occur, and the biomass of exotic species often exceeded that of native species (Davies et al. 2010). The overall abundance of native fishes in the MDB is suggested to have declined to about 10% of pre-European levels (MDBC 2004). These declines are linked to a range of threats including declining river flows, an overall scarcity of surface water habitats and limited flows during severe droughts. During droughts, the habitats available for fish are reduced and isolated, and their quality (including water quality) deteriorates through time (Lintermans and Cottingham 2007; Figure 2). Moreover, crowding of fish in refugia may

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increase exposure to alien species, and increases competition, predation and diseases (Lintermans and Cottingham 2007). It is during these periods when agricultural demands for water are at their peak that environmental flows are critical to reduce damage to important aquatic ecosystems, communities, and species (Bond *et al.* 2008).

Observed climate impacts

Surface water availability is a major limiting factor for freshwater habitats in the MDB, and is influenced by a number of different climatic drivers, including atmospheric temperatures and seasonal patterns of rainfall. Average annual rainfall in the MDB in the 10-years to 2006 (440 mm) was 4% lower than the annual average for the period 1985 to 2006 (CSIRO 2008). These data are consistent with projected declines in average annual rainfall throughout Australia due to global climate change. However, there is high inter-annual and inter-decadal variability in rainfall for the MDB, and similar periods of low rainfall occurred in the 1890s, 1940s, 1960s, and 1980s. Recent declines in average rainfall during the 'millenium' drought may or may not reflect global climate change, but average annual runoff recorded since 1997 to 2006 is 21% below the long-term average, and unprecedented in the historical (>100 year) record (CSIRO 2008). As a dryland river system, average evaporation is very high (94% of precipitation) and runoff averages only 4% of precipitation (Davies et al. 2010). CSIRO (2008) attribute marked declines in runoff to disproportionate declines in autumn and early winter rainfall in the southern MDB. As a consequence, the soils are less saturated, and together with moderate declines in winter rainfall, this greatly reduces

runoff. Increasing atmospheric temperatures and declines in vegetative cover of catchments may also exacerbate declines in runoff (Chiew *et al.* 1995).

Declines in runoff attributable to recent climate change (and specifically, temporal shifts in major rainfall periods) contribute significantly to documented changes in surface water availability (Figure 3; Van Dijk *et al.* 2006). However, reductions in river flows attributable to climate change are likely have had lesser impacts on freshwater habitats, were it not for the very high levels of water extraction, retention and diversion across the MDB (CSIRO 2008).

Non-climatic threats

Major threats to the freshwater habitats and fishes in the MDB have been well documented (e.g. Cadwallader 1978; Koehn and O'Connor 1990; Murray-Darling Basin Commission 2004a; Davies *et al.* 2010). Foremost among these threats are: i) changes to flow regimes, including reduced flow due to water retention and diversion, and limited seasonal variability in flow rates; ii) habitat degradation, including removal of riparian zones, removal of structural woody habitat and increasing sedimentation; iii) declines in water quality, due to addition of cold water (from dam relseases), pesticides, nutrients, sediment and other contaminants; iv) barriers to longitudinal and lateral connectivity (dams, weirs and culverts), v) historical over-fishing, and vi) high densities of non-native species. The relative importance of these different threats varies among native fish species, but regulation of water flows has had far-reaching effects and has greatly reduced overall resilience of freshwater habitats (Gehrke and Harris 2001). Gehrke and Harris (2001)

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showed that regulated rivers contained a higher proportion of non-native fishes compared to unregulated rivers, and also had lower than expected diversity of fishes in their lower reaches.

Degradation and loss of freshwater habitats in the MDB has been occurring for more than a century, and must be substantially reversed in order to re-establish viable populations for most native fishes (MDBC 2004b). The MDB Ministerial Council *Native Fish Strategy* (MDBC 2004b) aims to rehabilitate native fish communities to >60 per cent of their pre-European abundance and distribution. The major interventions required to achieve this aim include i) restoration of habitats and ii) restoration of environmental flows, which together are expected to increase the abundance of native fishes in MDB by at least 45%. It is clear however, that restoration and maintenance of historical flow rates will be increasingly challenged by ongoing climate change (Van Dijk *et al.* 2006).

Future climatic impacts

Recent declines in rainfall in MDB cannot be unambiguously be linked to climate change (e.g. Lough *et al.* In review), but it is expected because Australia will become progressively drier in coming decades. Projected declines in total rainfall over the next 20-50 years (especially in the south-eastern section of the Basin) will reduce river flows by 5-15% (Van Dijk *et al.* 2006). It is important to note, however, that even if rainfall is unchanged, increasing atmospheric temperatures will reduce inflows to freshwater environments due to increasing evaporative water loss (Cai and Cowan 2008). The impact of climate change on water use is also likely to be

significant (Van Dijk *et al.* 2006). Reduced rainfall and increased temperatures will increase the demand for irrigation water and reduce the amount of water in storage. Coupled with increasing water demands, climate change will put increasing pressure on environmental flows critical for sustaining freshwater habitats in the MDB. Other potential effects include decreases in the frequency and magnitude of floodplain inundation, increased salinity, altered sediment and nutrient delivery, and increased incidence of algal blooms (Van Dijk *et al.* 2006). Poor water quality can lead to an increased incidence of fish kills (Koehn 2005).

The overall effects of climate change on the MDB will largely depend on other activities being undertaken to reduce water use. Ironically, strategies to mitigate the effects of climate change may exacerbate some impacts on freshwater systems. Tree plantations established to sequester CO₂ emissions intercept rainfall and reduce runoff from forested catchments, also have the potential to significantly further reduce streamflows (Hafi *et al.* 2010).

THE GREAT BARRIER REEF

Australia's Great Barrier Reef (GBR) is the largest coral reef system in the world, comprising approximately 2,900 individual reefs spanning 14 degrees of latitude and stretching 2,100 kilometres from north to south. The GBR Marine Park was established in 1975 under the GBR Marine Park ACT, and was declared world's largest World Heritage Area in 1981 (Wachenfeld *et al.* 2009). On July 1st 2004, 33% of the area encompassed within the GBR Marine Park was designated as "no-take" (up from 4.5%), including >20% protection for each of 70 distinct bioregions (Fernandes *et al.* 2005). This increased level of protection was partly motivated by increased recognition of threats posed to the GBR from declining water quality, commercial and recreational fishing, and global climate change (Olsson *et al.* 2008). The new network of no-take areas was a key step towards increasing the resilience of the GBR whilst maintaining important goods and services that are provided by this system (Fernandes *et al.* 2005). In contrast to the MDB, the GBR contains a total of about 2000 marine fish species

The GBR provides significant social and economic benefits to Australia. Tourism activities on the GBR contribute \$6.1 billion per annum directly to the Australian economy, and employs an estimated 63,000 people (Wachenfeld et al. 2009). Commercial fishing in the GBR generates a further \$119 million per annum, and employs 3,600 people (Wachenfeld et al. 2009). There is also a significant value associated with intangible benefits (ie. nonuse values) associated with maintaining the "near-pristine" status of the GBR (Oxford Economics 2009). However, increasing use of the GBR places considerable pressure on the overriding conservation objective of the GBR Marine Park Authority, to ensure its ecological sustainability (Day 2009). The ecological status, as well as the economic value, of the GBR, is also likely to be undermined by sustained and ongoing global climate change. However, climate change also provides additional incentive to improve current management of the GBR, whereby local actions (e.g. improved water quality and reduced threats to reef habitats) could greatly increase coral reef resilience (Marshall and Schuttenberg 2006). For example, Wooldridge (2009) estimated that significant improvements in water quality on the inshore GBR would enable local corals to withstand a further 2.0-2.5°C of temperature rise.

Observed climate impacts

As for coral reefs globally, the most obvious sign of climatic impacts on the GBR are recent increases in the incidence and severity of coral bleaching (Table 2). While coral reef habitats account for <7% of the area encompassed within the GBR Marine Park, they are an ecologically and economically important component of this system (e.g. Pratchett et al. 2008). Moreover, coral reef habitats are extremely vulnerable to local changes increasing temperatures and ocean acidification (Walther et al. 2002; Hoegh-Guldberg et al. 2007). Major instances of coral bleaching have been recorded at fairly regular intervals on the GBR, extending back to 1980, when conspicuous bleaching of common corals (mostly, Acropora and Montipora) was first noted at several isolated reefs between Townsville and Cairns (Oliver 1985). Since then, successive bleaching episodes have tended to occur over increasing geographic scales, affecting greater number of reefs, greater numbers of coral species and colonies, with increased severity (Table 2; Oliver et al. 2009). Australia was largely spared during the 1998 global mass-bleaching, which caused extensive bleaching in virtually every region of the world, and killed up to 90% of corals, especially in the Indian Ocean (Wilkinson 2004). On the GBR, bleaching was conspicuous and widespread in 1998, but bleached corals recovered well (Wilkinson 2004) and overall mortality rates were generally very low (Maynard et al. 2008; Anthony and Marshall 2009).

The most extensive and most severe bleaching episode to affect the GBR occurred in 2002 (Berkelmans *et al.* 2004; Maynard *et al.* 2008), corresponding with the highest sea surface temperatures (often >33^oC)

recorded on the GBR. During this event, bleaching was recorded at 54% of reefs surveyed across the length and breadth of the GBR (Berkelmans *et al.* 2004). As with previous bleaching events, bleaching was more extensive and more severe on inshore reefs compared to offshore reefs (Berkelmans *et al.* 2004), but there is little data on mortality versus recovery of bleached corals (Baird and Marshall 2002; Maynard *et al.* 2008). The most recent bleaching event, in 2006, was mostly restricted to the southern GBR (south of 20°S), and effects were highly localised (Weeks *et al.* 2008). At the Keppel Islands, >90% of corals bleached in 2006 and 40% of corals subsequently died (Diaz-Pulido *et al.* 2009). Elsewhere (e.g. Heron Island) coral bleaching was very minor, owing to the frequent intrusions of cooler oceanic waters (Weeks *et al.* 2008). Effects of coral bleaching are typically very patchy within and among reefs of the GBR, which may promote persistence of species and also enhances recovery and resilience of coral communities (Oliver *et al.* 2009).

History of habitat degradation

The GBR has been subject to a long history of exploitation and anthropogenic degradation, especially on nearshore reefs. Coastal populations of indigenous Australians have harvested food from the GBR for millennia, though exploitation of many species (e.g. turtles, dugongs, sea cucumbers) and degradation of reef habitats increased significantly following European settlement (Daley *et al.* 2008). Importantly, introduction of sheep and cattle in many major catchments adjacent to the GBR was initiated in the 1860's, after which, there was a doubling of sediment loads introduced to the GBR lagoon during major flood events (McCulloch *et al.* 2003). Although no longer pristine, the GBR has much lower levels of depletion for carnivores, herbivores, and architectural species, compared to other major reef ecosystems (Pandolfi *et al.* 2003).

Inshore reefs of the GBR tend to be much more degraded (Pandolfi et al. 2003), having less coral and more macroalgae, compared offshore reefs (e.g. Wismer et al. 2008). These cross-shelf differences are to be expected given natural gradients in terrestrial versus ocean influences, as well as important differences in the composition of fish assemblages (Hoey and Bellwood 2008). However, the lack of corals on inshore reefs may have been exacerbated by anthropogenic activities (agriculture and development) in adjacent catchments. Photographic records of inshore reefs spanning >100 years, reveal long-term changes in habitat structure at some sites (Wachenfeld 1997). At Stone Island, for example, photographs taken by Saville-Kent in 1890 reveal extensive cover of branching corals on the exposed reef flat. Comparable photographs of the same reef flat taken in 1994, do not show any corals, but patches of macroalgae interspersed across a mud flat (Figure 4a). The long-term changes in habitat structure most likely reflects chronic stresses associated with declining water quality (De'Ath and Fabricius 2010; Hughes et al. 2010). However, detailed analyses of historical photographs by Wachenfeld (1997) revealed that these changes were not consistent across all locations, and many inshore reefs retain similar habitat structure to that recorded pre-1950s (Figure 4b).

More recently (mostly since 1960), there has been as accelerated rates of loss of coral cover across the GBR due to a combination of natural and anthropogenic disturbances. Bellwood et al. (2004) suggested that average coral cover declined >40% from 1960 to 2000, and attributed these losses to cumulative effects of increasing outbreaks of the corallivorous crown-of-thorns starfish (Acanthaster planci) and coral bleaching. Broad scale and ongoing monitoring by the Australian Institute of Marine Science (e.g. Sweatman et al. 2008), shows that coral cover on the GBR is highly dynamic, caused by interreefal variation in the effects of (and recovery from) several different types of disturbance, including cyclones, outbreaks of *A. planci*, bleaching and coral disease. Overall, coral cover has shown a systematic (though very moderate) decline through time, which is mainly attributable to the effects of cyclones (especially cyclone Hamish in 2009) and outbreaks of A. planci, rather than climate related disturbances (Figure 3; Osborne et al. in review). Similarly, Bruno and Selig (2007) showed that climate change played a minimal part in protracted coral declines apparent across much of the Pacific. It is incontrovertible that regional scale incidences of mass-bleaching are caused by climate related increases in sea-surface temperatures (Hughes et al. 2003), but bleaching currently accounts for <6% of recorded coral loss on the GBR (Figure 3). Climate change may have also exacerbated coral loss attributable to coral disease (Bruno et al. 2007) and/ or cyclones (Webster et al. 2005), but it is difficult to assess the proportional contribution of climate change to these effects.

Future climatic impacts

Climate impacts on Australia's coral reefs have so far been relatively minor compared to the extent of coral loss caused by other natural and anthropogenic disturbances (Figure 3). Climate change related increases in sea-surface temperatures and declines in ocean pH are however, expected to increasingly impact coral reefs in the future (Hoegh-Guldberg 1999; Hoegh-Guldberg *et al.* 2007). Climate projections suggest that mass bleaching will become a bi-annual phenomenon by 2030 if corals do not acclimatise or adapt (Donner *et al.* 2005). Increased thermal tolerances of 0.5°C -1.0°C by 2050 could delay projected bleaching events by 5 years, possibly allowing impacted reefs some recovery between major disturbances. The future cover and species composition of scleractinian corals and the ecosystems they support will critically depend on their ability to adjust to current rates of ocean warming and acidification. Despite this, very few data exist upon which to evaluate the adaptive capacity of coral communities, species or populations to these trends.

Communities can adapt to climate change through shifts in community composition towards more tolerant species. (e.g. Hughes *et al.* 2003). Shifts in community species composition following bleaching have been widely documented (e.g. Edwards *et al.* 2001; Loya *et al.* 2001). Recovery of reefs may occur through the growth of more resilient survivors (Loya *et al.* 2001) or through recruitment and recovery of fast growing but often more sensitive species (Edwards *et al.* 2001; Pratchett *et al.* 2008). Therefore, while climate change is expected to change the community composition of reef corals it is not yet clear whether a shift towards more tolerant species will occur.

Coral populations can acclimatise or adapt by increasing the frequency of more tolerant individuals (genotypes) within populations. While increases in the thermal tolerances of some coral populations have been observed following major bleaching events (e.g. Maynard et al. 2008), no study to date has directly linked differences in allelic frequencies to thermal tolerance in coral (Maynard et al. 2008). D'Croz and Mate (2004) found genetic divergence between Caribbean populations of P. damicornis in cooler and warmer reef areas with corresponding thermal tolerances. Edmunds (1994) found that rates of natural bleaching differed among genotypes in M. annularis but did not associate tolerance with specific alleles. Corals may also gain increased thermotolerance by changing their dominant symbionts towards types with greater thermal tolerances, a process termed "symbiont shuffling" (e.g. Berkelmans and van Oppen 2006). While there are limits to thermal acclimatisation through symbiont shuffling (ie. 1.5°C when dominated by GBR D type instead of C2 type) field evidence suggests that reef wide changes in dominant Symbiodinium type can offer corals some short-term protection against predicted temperature increases (Jones et al. 2008). However, it should be noted that symbiont shuffling is likely to come at a fitness cost with D-type dominated corals growing at a slower rate than those dominated by clade C Symbiodinium (Jones and Berkelmans 2010).

The potential for adaptation of corals, and the time scales over which this can occur, can be modelled if quantitative genetic estimates of heritability are known. Heritability describes the amount of genetic variation in a population natural selection can act upon (i.e. additive genetic variation result in offspring with intermediate appearance to parents). At present, only two studies have estimated heritability in any coral trait (Csaszar *et al.* 2010; Meyer *et al.* 2009). Both studies found significant heritability in molecular and physiological traits of both host and symbionts suggesting the potential for genetic adaptation in these traits. Estimates of heritability of more coral traits, as well as links between these traits and fitness (e.g. growth and survival) in a variety of temperature and PH scenarios are required before effective modelling of coral's responses to climate change effects can occur.

Managing effects of climate change

Clearly, urgent action is required to minimise global greenhouse gas emissions and thereby reduce longer-term climatic impacts on Australia's aquatic ecosystems. However, drastic reductions in emissions, even if implemented immediately, will not guarantee the persistence of ecosystems, communities and species that are already being affected by global climate change and will be affected for some time into the future. It is predicted, for example, that global atmospheric temperatures will increase by >1°C by the end of the century, regardless of any future emission scenarios, and Australia's climate is currently warming faster than the global average (Lough *et al. in review*). Reductions in global greenhouse gas emissions may limit extreme changes in environmental conditions and reduce rates of change to which species must adapt to survive. In the short-term, however, management must attempt to facilitate the adaptation of species and ecosystems to inevitable climate changes.

Management will need to be both non-spatial and spatial (Figure 5), although this section focuses principally on spatial management interventions. Non-spatial management approaches are often (though not always), applied without being area-specific. Some examples for aquatic ecosystems are: regulation for sustainable harvest of species; reduced bycatch; quarantine arrangements to prevent the arrival of invasive species; environmental water allocations; and strategies to reduce water extraction from streams and wetlands for agricultural and urban uses. As a last resort, *ex situ* conservation might be necessary to avoid extinction of some species (e.g. translocations) for which spatial management options have been exhausted (e.g. Shoo *et al.* in review).

Four kinds of spatial management are distinguished here that can help to promote adaptation of aquatic ecosystems and species to climate change (Figure 5). In practice, these would be applied in various combinations, and often with the support of policy, regulation and other non-spatial approaches. The conventional, and still important approach to conservation, has been to establish protected areas to represent examples of ecosystems (Figure 5 -Box 1), few ecosystems, however, can be managed for conservation in their entirety (Margules et al. 2002). Protected areas are not particularly applicable to habitats such as rivers, which are long and linear and subjected to upstream and downstream influences (Koehn 2004). More recently, however, conservation planning has begun to address a variety of spatially explicit management actions in addition to protected areas (Joseph et al. 2008). Given the likely effects of climate change in altering the distributions of species, the value of managing present occurrences of aquatic ecosystems requires some consideration. The protection of areas, however, remains an important tool in a changing climate management, especially to to ensure that refugia, or areas that might be buffered from the effects of climate change, are effectively managed. Examples of this may be: are occurrences of mangroves that might undergo relatively mild effects of climate change (McLeod and Salm 2006), and coral reefs that are buffered from rising sea surface temperatures by cool upwellings and other physical factors (Marshall and Johnson 2007; Ban *et al.* in review). An additional reason is to enhance the resilience of ecosystems to the effects of climate change. For coral reefs, spatial management can promote recovery of corals after bleaching events by maintaining healthy populations of herbivorous fish to reduce algal growth and grouping protected reefs such that bleached reefs are well supplied with coral propagules from unaffected reefs (Obura 2005). The protection of refuge pools in rivers or wetlands can allow opportunities for recolonisation under higher flows.

Resilience to climate change is likely to be an important goal of spatial management for aquatic ecosystems generally. Among the factors determining resilience are the attributes of the species (Crook *et al.* 2010) and the functional integrity of ecosystems. This can be expected to minimize the impacts of climate change on ecosystems or confer the ability to recover from those impacts. Stressors that can be directly managed, such as water extraction, sedimentation and eutrophication, should therefore be limited or reduced (Hughes *et al.* 2003) and fishing mortalities minimised (Bellwood *et al.* 2004; Marshall and Schuttenberg 2006). A related emerging trend toward management for resilience is the increasing attention given to spatial planning for the persistence of processes (Pressey *et al.* 2007). Recent work, for example, has begun to address time-series data and quantitative conservation objectives related to the spatio-temporal dynamics of sea

surface temperature anomalies and risk of coral bleaching (Game *et al.* 2008; Ban *et al. in review*).

Direct spatial management of examples of aquatic ecosystems (Figure 5 - Box 1) can also involve restoration. Spatial priorities can be identified, for example, to replant mangroves (McLeod and Salm 2006), to reverse the impacts of engineering works such as drainage and floodgates in coastal wetlands (Pressey and Middleton 1982) or enhance structural woody habitats (Nicol *et al.* 2004). Considerations would include the historical condition of the ecosystems prior to disturbance, the feasibility of returning areas to their predisturbance states, the cost of the interventions, and proximity to spatial management actions for other ecosystems. The success of some recovery actions such as revegetation could be compromised under climate change scenarios.

Given that ecosystems are not self-contained units, a complementary management approach is to consider the requirements of species with life histories that involve moving between ecosystems (Figure 5 - Box 2). This is important for freshwater systems (Dudgeon *et al.* 2006) where diadromous fish species undertake extensive longitudinal migrations between headwaters and the estuaries or the open ocean (Beger *et al.* 2010). Functional riverine connectivity is essential to ensure that movements can continue. It is also important for the marine realm, where proximity of different ecosystems can determine the composition and abundance of species in each (Skilleter *et al.* 2005; Mumby 2006). Fully integrated management of aquatic ecosystems would also recognize the dependence of many terrestrial species on

freshwater and marine systems (Dudgeon *et al.* 2006; Beger *et al.* 2010). Essentially, this approach to management requires knowledge of the complementary nature of particular ecosystems and ecosystem functions and appropriate conservation actions in each. Under climate change, it will also require some understanding of how each of the ecosystems, and the biological connections between them, might change.

Climate change implies changes to both the distribution of species and ecosystems, so management for climate change must anticipate these changes and consider the areas to which aquatic ecosystems and species might move (Figure 5 - Box 3). One application of this approach would be to identify intertidal wetlands with the potential to move landward, because of lack of adjacent development or seawalls, and to protect both these wetlands and the inland areas that they will occupy with higher sea levels (McLeod and Salm 2006). A related application is the translocation of species. As problematic as this might appear, this may be the only prospect for the survival of species that are unable to disperse unassisted in responding to future suitable climates. Some progress has been made toward rigorous assessment of options and risks for translocation (Hoegh-Guldberg *et al.* 2008).

Even more so than in the terrestrial realm, aquatic ecosystems can be adversely affected by distant anthropogenic threats that may be compounded by climate change. The impacts of distant threats are particularly obvious in large catchments from which sediment, nutrients and toxins can affect freshwater, estuarine and marine ecosystems downstream (Brodie *et al.* 2009). Management approaches are therefore needed for areas expected to influence aquatic ecosystems, often from afar (Stoms et al. 2005), and these will be more effective with understanding of the influence of climate change on land use and runoff (Figure 5 - Box 4). In some regions, climate change will increase human needs for water and perhaps exacerbate the effects of reduced rainfall and run-off (Abell 2002). In other regions, the distributions and types of land uses will be adjusted to altered climates, with implications for surrounding ecosystems (Dudgeon et al. 2006). In this context, management of activities in catchments could reduce nutrient runoff to inshore marine waters and lessen the effects of high sea temperatures on coral bleaching (Marshall and Johnson 2007; Wooldridge and Done 2009). Ideally, management actions in catchments would integrate diverse objectives, including conservation of terrestrial ecosystems, reduced disturbance of freshwater ecosystems, and providing appropriate water quality to nearshore marine ecosystems. This would allow managers to more cost-effectively address multiple objectives by identifying all areas that they contributed to.

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Table 1. Differential effects of climate change on Australian aquatic habitats. Major changes are expected to occur across aquatic habitats as a result of degradation or loss of key structural species, but the major climatic effects and associated drivers vary greatly.

Habitats	Critical habitat	Current threats	Major climatic effects	Key drivers
Freshwater systems	rivers and wetlands	Water extraction (irrigation), habitat modification,loss of connectivity	Reduced runoff,river flows, wetland areas	Reduced rainfall
Tidal Wetlands	Mangroves and saltmarshses	Deforestation and habitat modification	Increasing tidal inundation	Sea level rise
Seagrass beds	Seagrasses	Increasing sedimentation and nutrient discharge	Increasing physical disturbance	Increasingly severe storms and cyclones
Coral Reefs	Scleractinian corals	Cyclonic disturbances and outbreaks of coral-eating starfishes	Coral bleaching and loss of physical habitat structure	Ocean warming and acidification
Temperate Reefs Giant kelp and Mai macroalgae		Marine pollution and pest species	Shifts in geographical ranges for habitat- forming species	Ocean warming and strengthening of the EAC

Table 2. Recorded instances of mass coral bleaching on the Great Barrier Reef, since 1979. Seasonal "paling" of some coral colonies occurs in nearly all years, but specific instances of mass-bleaching, whereby multiple colonies and species are simultaneously affected has occurred 9 times (at intervals of 1-6 years). Data presented shows the percentage of reef considered that had conspicuous evidence of bleaching, as well as the percentage of reefs with severe (>60%) bleaching.

Year	n	Bleaching recorded	Severely bleached	Key Reference(s)
1980	5	100%	0%	Oliver 1985
1982	14	100%	7%	Oliver 1985
1983	14	100%	0%	Oliver 1985
1987	21	81%	0%	Oliver <i>et al.</i> 2009
1992	24	30%	0%	Oliver <i>et al.</i> 2009
1994	40	10%	0%	Oliver <i>et al.</i> 2009
1998	654	42%	18%	Berkelmans and Oliver 1999
2002	641	54%	18%	Berkelmans <i>et al.</i> 2004
2006	35	56%	9%	Weeks <i>et al.</i> 2008

Aquatic Ecosystems, Communities and Populations: Advances in Modelling the Effects of Climate Change for Australia and the Tropical Pacific

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ABSTRACT

Climate change presents significant challenges to modelling and managing aquatic resources. Equilibrium assumptions common in many modelling approaches need to be replaced by formulations that allow for changing baselines, and integration of ongoing changes and adaptations by species, ecosystems and humans. As ecosystems change, so will the ways humans use, monitor and manage them; adaptive management loops may be one solution that deserves more prominence in the management toolbox. Models are critical tools for giving us an early understanding of the challenges to be faced by integrating observations and examining possible solutions. We review modelling tools currently available to simulate the effect of climate change on marine and freshwater ecosystems, and the implications for management of their natural resources. Non-linearities confound interpretations and hence adaptive management responses should be robust to surprises. An improvement in the ability to model the effects of climate change from a social and economic perspective is necessary. The outputs from "end-to-end" and **Fisheries Research House** 25 Geils Court, Deakin ACT

socio-ecological models can potentially inform planning, in both Australia and the Pacific region, about how best to build resilience to change. Lessons from this region can guide increased use of models to test options for managing aquatic resources world-wide.

Keywords: adaptive management, climate change, socio-economics, ecosystem models, Australian fisheries, Pacific Island countries and territories, qualitative models, end-to-end models

Introduction

Climate change is already occurring worldwide and together with a range of existing threats and pressures presents significant challenges in terms of how we model and manage aquatic resources. The diversity of Australian marine and coastal ecosystems also makes management challenging, with many resource users spanning multiple systems. These systems range from tropical to temperate to sub-Antarctic, from deep-sea to coastal estuaries, and the largest coral reef system in the world (Great Barrier Reef). These ecosystems are occupied by unique fauna and flora (Poloczanska *et al.* 2007; Chambers *et al.* in review; Butler *et al.* 2010).

Poleward boundary currents on both coasts lead to temperature change hotspots in the south-eastern and south-western regions of Australia (Hobday and Pecl in review). The observed rate of temperature change in these hotspots over the past 100 years is up to four times the global average rate of warming (Ridgway 2007; Pearce and Feng 2007). These changes have resulted in southward expansion of a range of taxa, including fish (Last *et al.* 2010) and reef and intertidal invertebrates (Ling *et al.* 2009; Pitt *et al.* 2010). In northern Australia, Lough (2008) reported significant warming and expansion of temperate zones relative to tropical zones, which has also been shown to affect tropical fish distribution (Figueria and Booth 2009).

In addition to ocean warming, a number of other climate-related changes in the ocean are projected to affect species, ecosystems and humans, including winds, upwelling, mixing, pH and terrestrial inputs (e.g. Poloczanska *et al.* 2007). Lough *et al.* (this volume) report that rates of change have accelerated in the last part of the 20th century, and the fingerprint of climate change is clearly detectable in the physical changes occurring in marine and freshwater systems. Future climate-related changes in the ocean will continue to challenge marine managers - Hobday *et al.* (this volume) indicate the changes in future climate are likely to continue to move "ecosystem" zones and their fauna.

For the tropical Pacific, the changes to the surface climate and ocean projected to occur under the IPCC A2 emissions scenario are described by Lough *et al.* (in press) and Ganachaud *et al.* (in press). By 2035, air and sea surface temperatures are expected to increase by $0.5-0.8^{\circ}$ C and rainfall by 5-15%. There is also the possibility that cyclones may progressively become more intense in the subtropics (Pittcock *et al.* 2006). Decreases in pH by 0.2-0.3 units by 2050 and 2100 are expected to reduce the availability of carbonate ions and the saturation of aragonite, essential for the formation of reef-building corals, to marginal levels by 2050, and low to risky levels by 2100.

Modelling tools can give us an early understanding of the challenges that these important climate changes will pose for marine and freshwater resources and the communities that depend on them, and offer a way to examine and test possible solutions. Models such as Atlantis have verified their utility as tools for ecosystem-based management (EBM), as illustrated by the application of Atlantis-SE to support the strategic restructuring of southeast Australian federal fisheries (Fulton *et al.* 2010). Continued development of both qualitative and quantitative models is necessary as equilibrium assumptions are limiting when applied to climate change problems, and many feedbacks are now seen as critical when evaluating the adaptation elements of climate change. Australia is well-placed in terms of its current toolbox of approaches for both inland aquatics ecosystems (MacDonald *et al.* 2006; Tomlinson and Davis 2010) and coastal-marine ecosystems (MacDonald *et al.* 2006;

Smith *et al.* 2007), particularly in regard to attempts to model the impacts of climate change from a social and economic perspective (e.g. Olsson *et al.* 2008).

Extending the scope of modelling approaches will allow more potential interactions involving climate change, and possible ways to build the resilience of both natural resources and the communities that depend on them, to be identified. This is essential not only for Australia, but also the neighbouring Pacific Island countries and territories (PICTs), where future development and food security depend heavily on sustainable and innovative use of fisheries resources (Bell *et al.* 2009; Gillett 2009; Gillett and Cartwright 2010). For PICTs, for example, modelling is needed to identify the relationships between (1) fishing effort, stocks, catch and markets; (2) the effects of key drivers such as human population growth, habitat degradation and climate change on these relationships, and (3) the potential for practical adaptations to address the consequences of these drivers.

In this paper, we evaluate the ability of a range of modelling approaches to increase understanding of the effects of climate change in the context of maintaining food resources and economic development, with a focus on selected Australian and tropical Pacific ecosystems. There are unique challenges affecting these regions as well as lessons of global relevance. We present a broad overview of the tools available, ranging from single-species quantitative models to full ecosystem models, qualitative modelling approaches, human behaviour modelling as well as semiqualitative and quantitative risk assessments (Table 1). In each instance we draw on selected examples of the approach rather than attempting to comprehensively document the full range of approaches and applications. We characterise approaches along axes of physical, biological, and human complexity (Fig. 1) and explore how extensions of current approaches across different axes might enhance their relevance in modelling climate change impacts and scenarios.

Recognising that climate change will impact all aquatic ecosystems, and that there are often strong links between marine and freshwater systems, we also include an overview of the current status of coastal zone models. We define the coastal zone as a continuum between catchments, freshwater streams, estuaries and nearshore

waters, or the catchment-to-coast (CtoC) domain. We use this to highlight current challenges and to simulate the processes required for operational management or strategic policy to assess the effects of climate change in fisheries and aquaculture. We conclude with a discussion of the role modelling approaches play in informing planning about how best to build resilience to changes in the distribution and abundance of key natural resources, and maintain the current benefits of fisheries.

1. Characterising models along axes of physical, biological, and human complexity

The kinds of models required and their utility under any scenario are a function of the questions to be addressed (Plagányi 2007; Fulton 2010). Hence, we first acknowledge that there is no single optimal model structure and that a range of models will be needed to address climate change impacts on marine ecosystems. This structure can range from simple to highly complex models in space and time, as well as qualitative through to quantitative approaches. Qualitative techniques are generally more subjective, and use more words than numbers, than their quantitative counterparts, but there is nonetheless a continuum between these approaches. Recognising that there are time and money constraints to building new models, we commence with three examples of single-species biological assessment models that have been extended in ways that enhance their utility as tools for understanding climate change impacts. At the opposite extreme, we discuss the current state of development of end-to-end models (see Travers *et al.* 2007; Rose *et al.* 2010), defined as models that attempt to span entire systems and include all major relevant processes (Fulton 2010).

To what extent have these highly complex frameworks expanded to incorporate the social and economic representations that are required to simulate in a comprehensive way climate change impacts on aquatic ecosystems and dependent communities? While many people involved in modelling (scientists, managers, resource users) have known that systems are impacted by multiple stressors, it is only recently that this has become tractable in models. Computing power and combining multiple resolutions of processes has been critical in this breakthrough

(e.g. Fulton 2010). Recognising it is important to consider all significant pressures on a system, such coupled models can play an important role in representing more realism in a system and simulating cumulative impacts (e.g. Halpern *et al.* 2008). These models highlight that thresholds that appear to be avoided if factors (such as climate variables) are considered separately, are passed when multiple factors are considered (Casini *et al.* 2008; Lindegren *et al.* 2009).

1.1. Extensions to single-species bio-centric models

Under changing climate, there is a need to modify fisheries stock assessments and to test the robustness of their management recommendations to future climatic variations. Such variations may impact particularly strongly on survival rates and carrying capacities for larval and juvenile fishes (Walters and Parma 1996). Simulation analyses can test the efficacy of different exploitation rate policies – for example, Walters and Parma (1996) demonstrated that constant fraction harvest policies perform well under strongly autocorrelated interannual variations in recruitment as might be expected under climate change. Single-species bio-centric models are often used as part of a Management Strategy Evaluation (MSE) framework (see Section 5). MSEs are a valuable tool that can be used to assess the robustness of alternative management strategies to the effects of climate change (e.g. A'mar *et al.* 2009).

The Torres Strait tropical rock lobster *Panulirus ornatus* illustrates potential challenges in terms of how to model and manage aquatic resources. The fishery is managed by Australia and Papua New Guinea. It is one of the most important fisheries, both commercially and culturally, to Torres Strait Islanders. It is simultaneously a valuable resource for Papua New Guinean stakeholders and contributes to regional food security. The involvement of a number of different sectors in the fishery as well as multi-jurisdictional and cross-border considerations epitomise the need for incorporating the human dimension in the fisheries management sphere. This is even more necessary under a climate change scenario in which this northern neighbour may be at even greater risk from climate change impacts than Australia itself (see e.g. Pernetta 1992; Hughes *et al.* 2003). Modelling

initiatives are needed to explore and inform on adaptation options pertinent to both countries as well as the different Australian sectors of the fishery, which are predicted to respond differently to climate change impacts (Plaganyi *et al.* in review).

As with most fisheries, the management process has focused on collection and analysis of key biological information, which in turn informs annual assessments of resource status and sustainable catch levels. To address questions related to climate change, there is a need to expand such analyses along the physical and human complexity dimensions (Fig. 1b). Given logistical constraints, there is a need for creative thinking and practical solutions and, where possible, collection of new data. Historically, fisheries management has generally only considered the target species, and habitat and other influential environmental factors have not been included explicitly in fishery assessments.

In most cases, we lack adequate baseline information for monitoring environmental change. Monitoring of the Torres Strait rock lobster population was initiated in 1989 to provide indices of recruiting and fished lobster abundance (Pitcher *et al.* 1992; Ye *et al.* 2005). During the lobster surveys divers concurrently record habitat data, primarily to inform future sampling strategies, but also to provide information on changes that could influence lobster abundance. These surveys are thus able to provide benchmark information for long-term assessments of climate impacts.

Significantly, the medium term habitat trends reflect the observation of substantial coral bleaching in 2010 (Plaganyi *et al.* in prep). It is not likely that the lobster population will be impacted by any resultant coral mortality, given the low mean cover of coral and the lack of association between *P. ornatus* and coral communities. However, the cause of coral bleaching may directly or indirectly influence lobster abundance. Monitoring and understanding the extent and impacts of coral bleaching has become increasingly important as coral reefs are threatened globally (Hughes *et al.* 2003; Hoegh-Guldberg *et al.* 2007). Empirical data are required to test the accuracy of models assessing climate impacts on fisheries, both in the concept phase and the future monitoring phase. However, it is often not logistically possible to monitor all associated environmental factors as part of a fishery assessment. Thus

the qualitative habitat data recorded concurrently during Torres Strait lobster surveys may prove useful for future climate impact modelling and stresses the more general need for appropriate data collection to complement research on implications of climate change.

As an example of a method for extending existing models along the physical and human complexity axes, Plaganyi *et al.* (in review) mapped a range of plausible climate impacts onto the life history parameters of *P. ornatus*, assessed the population level consequences of these effects and used an input-output economic analysis to quantify the resultant socio-economic effects to fishers, their communities and national economies. By integrating qualitative and quantitative approaches, and linking disparate methodologies, a useful start can be made to model climate change impacts.

1.2 A ROLE FOR BIOPHYSICAL MODELS

Coupling environmental dynamics to biological systems and species is a strong area of research and tool development (e.g. Cowen *et al.* 2006; Cury *et al.* 2008; Fulton 2010). One such approach is used in Australia for the management of tuna species. A single-species habitat prediction model is used for the current management and to project climate-related distribution changes for yellowfin tuna (YFT, *Thunnus albacares*) and southern bluefin tuna (SBT, *Thunnus maccoyii*) in eastern Australia (Hartog *et al.* in press). Capture of SBT is regulated by quota, as is access to regions likely to contain SBT (Hobday and Hartmann 2006; Hobday *et al.* 2010). A habitat prediction model combining data from an ocean model and pop-up satellite archival tags is used to define habitat zones based on the probability of SBT occurrence. The zones display a distinct seasonal cycle driven by the seasonal southward expansion and northward contraction of the East Australia Current (EAC) and, as a result, access by fishers to particular ocean regions changes seasonally (Hartog *et al.* in press).

This simple biophysical model was also used to consider the future change in distribution of these two species compared to the present, and to explore the potential future impact on fishers and management. Economic factors were not modelled explicitly in this approach. Future ocean predictions from the CSIRO

Bluelink ocean model coupled with a Global Climate Model for the year 2064 were used to generate habitat projections. As the ocean warms on the east coast of Australia and the EAC extends southward, the dual-species model projects that the suitable habitat for SBT and YFT will move further south. An increase in the overlap of SBT and YFT habitat is also expected to occur throughout the management season, due to regional variation of each species' habitat. These results illustrate that a management trade-off exists between restricting fisher access to SBT habitat and allowing access to YFT habitat. Management options to address this trade-off include varying the spatial restrictions on fish capture based on the seasonal variability of the overlap, and redeployment of the fleet to the north to avoid interaction with the more southern SBT. Results from these simple models can aid management when only biological considerations are important, but when economic factors are relevant, alternative approaches are needed.

1.3 Bio-economic models

The inclusion of economics and spatial dynamics into the conservation management of marine natural resource has been developed for the past 2-3 decades (e.g. Wilen and Brown 1986; Sanchirico and Wilen 1999; Smith *et al.* 2009). In Australia this approach has been adopted as policy (DAFF 2007), with target reference points now required to be based on achieving economic objectives while limit reference points are to be set so as to achieve conservation objectives. The NPF is the first major fishery with harvest control rules that explicitly account for both biological and economic factors (Dichmont *et al.* 2010). Although technically challenging (Dichmont *et al.* 2010), it does show that the incorporation of the economic dimension is feasible and that it is possible to explicitly represent the economic consequences of changes in resource status.

In terms of use as a tool for understanding climate change impacts, the NPF model is well placed to represent economic considerations, but cannot forecast how climate change is likely to influence resource status without incorporating more physical and biological complexity (Fig. 1b). The effects of climate on prawns are well documented (Vance *et al.* 1985). These impacts not only directly affect the migration patterns of some of the species, but also their seagrass or mangrove nursery

grounds (Vance *et al.* 1985; Rothlisberg *et al.* 1988). This example highlights the need to integrate and link freshwater and marine ecosystems because of the important role of catchment hydrodynamics (specifically rainfall-runoff) affecting the prawn fishery in the southern Gulf of Carpentaria (GoC) (Rothlisberg *et al.* 1996; Toscas *et al.* 2009). Thus the next logical step in model complexity is to include more of the ecosystem processes.

1.4 Ecosystem Models

Ecosystem models are seeing increased use in fisheries and are a valuable strategic tool for integrating information and understanding of climate change effects in a way that is difficult to achieve otherwise. Indeed, there are in excess of 20 well-developed fisheries ecosystem models currently in use (Plagányi (2007). Fisheries ecosystem models are generally defined as all fisheries models that include more than a single species, recognising that there is a continuum of model categories. Ecosystem models face many challenges given their complexity and associated uncertainty, and these become stretched further still when incorporating the additional uncertainties associated with representing climate change scenarios.

Travers *et al.* (2007) review the major process-based approaches used for marine ecosystem modelling, together with providing suggestions for extending and coupling these approaches to better assess the effects of climate change and fishing on ecosystem dynamics. Ecopath with Ecosim (Christensen and Walters 2004) has been widely used to tease apart the effects of fishing and environmental change and as such is an important tool for investigating climate change effects (MacKinson *et al.* 2009). In this paper we provide brief discussion of two approaches only, ranging from intermediate to high complexity, currently under development in Australia.

Climate change impacts on exports of freshwater flow volume from catchments may be a key driver and integrator of the catchment-to-coast-marine ecosystem. Modelling of links between catchment dynamics and the NPF, is being advanced using an approach termed Models of Intermediate Complexity for Ecosystem assessments (MICE), often also referred to as Minimally Realistic Models (MRMs) (Punt and Butterworth 1995; Plagányi 2007). MICE are intended to represent the critical parts of the system (restricting focus within an ecosystem to represent a limited number of species and processes most likely to have important interactions with key system components of interest. In general, these approaches consider fewer components than other end-to-end approaches, more fully account for uncertainty and are formally fit to data. They have utility in a climate change context in terms of a fairly rigorous approach that is tailored to represent the key physical and chemical processes of concern, but few approaches have thus far included the human dimension.

1.5 The cumulative nature of impacts

Understandably, there is a desire to make evaluation of a new problem as simple and straightforward as possible. This has seen the initial consideration of climate threats treated directly and in isolation from other pressures (Hobday 2010). However, the dynamics of real systems are the expression of cumulative impacts, where thresholds are passed which are assumed to be safely avoided if factors are considered separately. Crain et al. (2008) found that cumulative effects in individual studies were generally synergistic, but could also be additive or antagonistic. Consequently, it is important to consider all pressures on a system (Halpern et al. 2008, 2009). This is important as it can identify when one pressure (e.g. acidification) modifies what are considered "safe" levels of pressure from another source (e.g. fisheries). For instance, Fulton et al. (in press) found that the level of fishing pressure that was sustainable under projected global climate change was as much as 35% lower than under current conditions. However, cumulative effects can also see the moderation of one factor by another. For example, Fulton (unpublished) has found that increases in productivity in some systems under climate change can potentially moderate or offset declines due to the effects of acidification, at least at the level of functional groups. Perhaps most importantly, the inclusion of cumulative effects highlights the non-linear (typically skewed) responses of different parts of coupled social-economic-ecological systems (e.g. Brown et al. 2010).

Models can play an important role in synthesising and understanding the role of climate impacts over and above other anthropogenic impacts and environmental changes. Representation of the synergistic or moderating influence of several impacts acting in combination is usually only possible using coupled or end-to-end models. Simulations using these models may usefully inform simpler models - models that focus on selected drivers and impacts in isolation need to bear in mind the possibility that responses might differ in reality given cumulative impacts.

The models discussed so far have ignored (biophysical) or included to a limited extent (end-to-end) the involvement of humans in natural aquatic systems. Understanding interactions between human and ecological systems becomes increasingly important in order to anticipate and respond to the impact of climate change on aquatic ecosystems and dependent communities.

2. Characterising human behaviour models along complexity axes

Across the range of current existing models, from biological stock assessment models, through to larger ecosystem and end-to-end models, the human dimension has typically been restricted to a small component of marine resource users (mainly commercial fishers), with the behaviour of these users explained predominantly in terms of economics. This is an important start, but in a climate change context it would be insightful to more explicitly include other users, as well as other aspects of human behaviour such as social, psychological and anthropological considerations. These aspects are increasingly incorporated in large end-to-end models under development in Australia. These models provide an integrated synthesis of ecosystems across a range of dimensions and as such are a valuable tool for exploring, for example, the efficacy of different management and adaptation options on linked social-economic-ecological systems. However, it is not always possible to invest the time and resources required to develop such complex models, and hence in Section 3 we provide a complimentary example as to how a simpler qualitative modelling approach can usefully link the social-economic-ecological systems and guide the development of adaptations to climate change.

Modelling human behaviour in fisheries has concentrated on changes to fleets over time and space (Venables *et al.* 2009). This uses fine scale (e.g. with Vessel Monitoring Systems) and/or broad scale (e.g. logbooks) to produce statistical models of past human behaviour but with terms that can allow for costs and learning (Venables *et al.* 2009). These models would need to be adapted to climate where fisher behaviour may potentially not reflect the past.

How else can we progress models along the human dimension axis? Models that include a behavioural aspect based on economic considerations have become common over the past three decades (van Putten *et al.* in review). These models focus largely on location choice decisions but also increasingly aim to explain compliance, discarding, entry and exit, and investment behaviour. Not only has the focus on behaviour other than location choice grown, but efforts to incorporate considerations from the other social sciences, explaining other aspects of human behaviour and their drivers, has increased. A comprehensive overview of all human behaviour modelling approaches is beyond the scope of this paper. Instead, we review approaches that have been used in existing economic-ecological systems models. We also focus on some tools that are less commonly used but have significant potential to increase understanding of fisheries-related climate change impacts - such as network analysis, Bayesian Networks (BNs) and Agent Based Models (ABMs).

2.1 Macro, meso, and micro scale economic models

Economic models used in the context of climate change and fisheries resources have been applied at the macro, meso, and micro scale, or rather at country, region or sector, and fleet or fisher level, respectively. Economic models can be used to not only assess the likely impacts of climate change, but also to assess potential human behaviour and thus adaptation options.

At the highest (macro) level, input-output analysis is a modelling tool that deterministically depicts relationships between industries of an economy and predicts the effect of changes within this economy. Although input-output models operate

mostly at the macro level they are also useful for assessing regional or sectoral economies and can be effectively used for planning purposes. As such, they are useful tools in the context of climate change - not only can the consequences of climate change on fisheries be assessed in terms of the resultant socio-economic effects on fishers, their communities and national economies, they can be used for adaptation planning. For example, Norman *et al.* (2010) assessed changes in the level of fishing effort, the location of vessels, and the location of fish farms following a range of possible changes in the abundance and distribution of Australian wild and farmed fisheries due to climate change. Although these macro level models are useful for assessing the potential impact of climate change on the fisheries resource, they do not in themselves explain behaviour.

At the micro level, economic theories underpin models of fisher behaviour. These fisher behaviour models have been incorporated in bio-economic models in climate change assessments (e.g. Dichmont et al. 2010). In the past, the most common approach to studying fisher decision-making was based on micro-economic theory, and the assumption that fishers maximize profit. However, increasingly, models seek to explain how fishers develop expectations, and how these influence their choices e.g. by using expected utility theory or Random Utility Models (RUMs). RUMs allow incorporation of both monetary and non-monetary attributes of choices, as well as individual characteristics of decision-makers, including attitudes towards risk, variability in information levels, or the role of normative and social influences on decision-making. There are a number of useful reviews of behavioural drivers of fleet dynamics (van Putten et al. in review), decision making under uncertainty (Holland 2008), and bio-economic modelling approaches (Prellezo et al. 2009). Moreover, quantitative models of fisher behaviour and fishing fleets are available for a range of fisheries around the world (e.g. Vermard et al. 2008). In Australia, models such as that applied to the NPF have made substantial advances in modelling economic considerations in the context of climate change. Using statistical or Markov chain fleet level approaches have made models more realistic as they rely less on historical information that could be less applicable in non-linear climate change scenarios.

Integrated social-economic-ecological models are thus increasingly capable of explicitly representing human behaviour. But understanding how effective and adaptive management systems are requires a broader representation of human behaviour and integration of social and economic fisher behaviour models.

2.2 Other ways to model human behaviour

There are multiple tools for modelling human behaviour that include drivers other than economics, and in a fisheries context social network analysis, BNs, and ABMs have been applied to better represent other domains of human behaviour. These models operate mostly, but not exclusively, at the micro level, i.e., the level of the individual fisher or fleet. The popularity of these alternative modelling tools is partly due to the flexibility in the way they can combine theories of human behaviour originating in different domains of social science. These modelling tools can combine data from biophysical and social sciences and uncertainty can be considered.

Social network models, analogous to food-webs and predator-prey relationships (e.g. Dambacher et al. 2010), provide insight into the characteristics of a connected system and the behaviour of actors within that system. Quantitative measures of interactions between actors in a social network allow analysis of the structure and dynamics of the network, the connections, and the actors within the network. Social network analyses in both a fisheries and climate change context (e.g. Tompkins and Adger 2004) have mostly been of a gualitative nature and fisheries-related social network analyses have mostly been undertaken outside Australia, with only one example of quantitative Australian fisheries-related network analysis (van Putten et al. in press). Nevertheless, social networks strongly influence behaviour and have been found to influence compliance (Palmer 1991; Ramirez-Sanches and Pinkerton 2009), fishing success (Meuller et al. 2008), and decision making in co-management arrangements (Crona and Bodin 2006), and affect trade (Weisbush et al. 2000; Kirman 2001). Empirically-based, guantitative models of social and trade networks are effective tools in determining impact of management changes. For example, van Putten et al. (in press) used network analysis to analyse economic, social and cultural changes resulting from the introduction of Individual Transferable Quota

(ITQ) management to a Tasmanian rock lobster fishery. These empirically-based, quantitative models are particularly powerful in a climate change context, as they can help explain behaviour, project management outcomes, and can be incorporated into social-economic-ecological models.

In social network modelling, like its biological equivalent, nodes are linked to each other by means of directed or undirected connections that can be mapped and measured. Where the links between nodes in a network are causal, conditional probability tables can be developed that form the basis of BNs. In a fisheries context, a Bayesian approach has been used with the network structure and connections represented spatially, based on the geographic proximity between fishers, to model the effect of information access on fishing success (Little et al. 2004). If a fisher is spatially close to many other fishers, they are assumed to have access to more fishing information which increases their fishing success. Similarly, if a fisher is connected to a 'good' fisher from whom they obtain information, this may increase their fishing success. Thomas et al. (2009) used a Bayesian approach to link catchments to the Great Barrier Reef and understand the socio-economic tradeoffs associated with managing for resilient Great Barrier Reef communities, given the threat posed by climate change. The strength in BNs lies is the fact that quantitative and qualitative data from biophysical and social science can be combined, and uncertainty is explicitly considered in the models (e.g. Ticehurst et al. 2007; Castelletti and Soncini-Sessa 2007; Thomas et al. 2009).

In the economic models discussed in 2.1, it is generally assumed that fishers operate in a consistent manner based on the incentives they face. In ABMs, the range of drivers may be increased and non-deterministic outcomes reflected. ABMs can be used to simulate and assess the overall effect of interactions between individuals in the model and evaluate non-linearity in the system. This is particularly relevant as fishers do not all respond in a similar manner and are faced with different levels of information, different information processing abilities, and different constraints (social and/or economic). While there has been a growing number of theoretical studies using ABMs (Maury and Gascuel 2001; Millischer *et al.* 2006; Soulié and Thébaud 2006; Thébaud and Soulié 2008), empirical applications are still the exception (Dreyfus-Leon 1999; Helu *et al.* 1999; Little *et al.* 2004; Little *et al.* 2009) as they are data intensive (especially in cases where the population is large) and computationally demanding. However, the ability to evaluate a system's non-linearities and thresholds is particularly relevant in a fisheries and climate change context.

2.3 Combining human and biophysical models

End-to-end models attempt to represent entire systems by coupling physical, biological and human components (Rose et al. 2010; Fulton 2010). Increasingly these are moving from standard abiotic drivers, such as riverine and atmospheric inputs, winds, irradiance, precipitation and major water body features (e.g eddies or upwelling, or temperature and salinity profiles) to include properties relevant to global change such as alkalinity, sea-level rise and the effects of storms. The treatment of these new factors has been fairly simple to date (e.g. Fulton (in press) used simple functional forms to represent the effects of changes in these physical properties on biological components of marine ecosystems), but is likely to be refined as understanding grows. The models are also being refined ecologically. Many already include processes from across marine and coastal foodwebs (from the microbial scale to top predators) and the main refinements entail more sophisticated representation of features such as relationships between water column properties and rates of growth, consumption, reproduction, mortality and behaviour (e.g. Fasham 1993; Doney 1996; Fulton et al. 2003; Batchelder and Kashiwai 2007; Flynn 2010; Wild-Allen et al. 2010).

Anticipating and responding to the impact of climate change on aquatic ecosystems and dependent communities is a problem that requires consideration of the interaction between human and ecological systems. This problem is often approached in modelling frameworks that attempt to provide precise projections to guide research programs and management interventions, but in meeting the goal of precision, the focus quickly turns to addressing uncertainty in model parameters, and the importance of uncertainty in the structure of the model itself is often overlooked. Recent initiatives have seen the coupling together of models in a complex interactive adaptive form, using a MSE framework. This enables resolution of climate impacts (e.g. production forcing function on a food web) and other spatial management strategies (MPAs, closures), at reasonably small spatial scales, as has been developed for northern Australia (Bustamante *et al.* 2010). The operating model (or virtual resource) is an Ecospace model of the Gulf of Carpentaria that draws together 30 years of surveyed biophysical data collections. Allied to this Ecospace model, is also a multiple single species-taxa model that is designed to investigate the effects of trawling (Dichmont *et al.* 2008). In the management module, there is a full bio-economic model of the different models, as well as changes to the fleet behaviour, a two-tiered fleet dynamics model is used (Venables *et al.* 2009).

3. Overview of additional approaches for modelling climate change impacts

There has been considerable research in Australia and the neighbouring Pacific aimed at assessing the vulnerability of marine ecosystems (e.g. Johnson and Marshall 2007; Hobday *et al.* 2008). There has similarly been good progress in translating this understanding into models capable of simulating changes in resource abundance and the consequences for dependent communities. But integration of vulnerability assessments and models capable of simulating climate change impacts in the coastal domain seems to be lagging slightly. Accordingly, we overview potential requirements for integrated catchment-to-coast models to assess the effects of climate change, and evaluate the extent to which current approaches meet these requirements.

Recognising that ecological risk assessment approaches have been widely adopted within Australia, we provide an overview of the current developments and future challenges related to applications of this suite of approaches under changing climate. Finally, we illustrate the utility of qualitative models as a tool for simulating the effects of climate change on aquatic ecosystems and their dependent communities, focusing on evaluating and mitigating impacts on food security.

3.1 Linking land-sea impacts

The negative effects of climate change in Australia and the Pacific threaten fisheries and aquaculture developments in the coastal zone. Changes in climate are projected to modify rainfall patterns and promote sea-level rise (Lough *et al.* in press; IPCC 2007). These changes will likely increase erosion within catchments (Gehrke *et al.* in press) and impact shore stability. An early period of destabilising sedimentation in the CtoC domain is anticipated as catchment streams and shorelines adjust to new and changing base levels (Dutra and Haworth 2008; Baker *et al.* 2001; Martin *et al.* 2003). As there is a range of "dependence" of biological resources on CtoC processes, the consequences of how climate change may influence these as a result of altered catchment/coastal processes will vary depending on the number of species/resources and their relative economic/consumptive value (Fig. 2).

In addition to climate change, there are other factors influencing the coastal zone that should be included in any effort to understand coastal zone dynamics. For instance, this is the region most Australians choose to live and its population is expected to continue to grow in the future (Australian Bureau of Statistics 2010). Population growth promotes catchment disturbances, such as conversion of forests to agricultural fields and urban areas, changing water flows and riverside habitats. More people also increase demands for housing, food, water, and recreation, thus requiring construction of infrastructure (e.g. farms, dams, aquaculture, housing, road network). These developments often increase sediment, nutrient and other chemical levels in the CtoC domain with inevitable negative impacts on the surrounding landscape and ecosystems (Vörösmarty 2010).

Physical and biophysical simulation models used in the CtoC domain have been used to inform operational and legislative decisions (e.g. Wild-Allen *et al.* 2010; van Daalen *et al.* 2002; Xu *et al.* 2009; Caitcheon *et al.* 2001). However, there is a strong need for a common framework to address issues related to the effects of climate change on fisheries and aquaculture in the CtoC domain in an integrated manner, instead of modelling each part separately and leaving a third party to decipher the links. Moreover, there is also a need to understand how humans would react to climate impacts on the biophysical realm and economic costs associated with these changes.

The rationale of an integrated CtoC model is a continuous linkage through water flow from catchments to the coast. Sediments, nutrients and chemicals are washed from catchments into watercourses, which carry these constituents to estuaries and the coast, influencing ecosystems in their way, affecting human denizens who depend on these resources

economically (e.g. for income/subsistence) and for social purposes (e.g. recreation). In this context, models should be used to systematically organise data, assumptions and knowledge to inform a decision for management or development and implementation of strategic policies (Jakeman *et al.* 2008).

The integration of CtoC biophysical models is important because in addition to the link between freshwater and coastal systems through water flow, there are feedbacks between the coast and catchments during extreme events, such as storms and higher than normal tides, where saltwater can flow to freshwater streams impacting freshwater ecosystems (Gehrke *et al.* in press). The feedback can also occur through management actions. For instance, if environmental degradation in coastal waters is associated with poor catchment practices, management measures may be implemented to improve catchment conditions. These links are more evident if one wants to understand the consequences of predicted sea-level rises associated with global warming, with consequent increases in salinity and erosion at estuaries and further upstream, which has the potential to negatively affect mangroves and coral reefs.

The requirements of a CtoC model to understand the effects of climate change on fisheries/aquaculture are depicted in Table 2 and descriptions of modelling approaches are provided in Appendix I. Given limited resources, it is likely that the scope of the linked models would have to range from semi-quantitative, to minimum realistic quantitative models up to full ecosystem models. It would then be necessary to evaluate the strength and weaknesses of each type of model to determine which would be best to use.

Are we ready for climate change in the coastal domain? In terms of individual models to simulate catchment/freshwater or estuarine/marine processes we suggest that the answer is yes. There are several models that can be used to evaluate the effects of climate change in catchments, estuaries and coastal water (see http://wiki.csiro.au/confluence/display/C2CCOP/Inventory+of+C2C+models). However, if we consider the coastal zone as a continuum between catchments and the coast, integration of multiple models is needed. This is required in order to simulate the processes required for operational management or strategic policy to assess the effects of climate change in

fisheries and aquaculture. Therefore, despite some recent efforts to integrate CtoC models (e.g. Wulff *et al.* 2007; Cannard *et al.* in prep.; Ellis *et al.* in prep; Dutra *et al.* in prep), large challenges need to be overcome before these approaches can effectively model climate change in the coastal domain.

3.2 Risk Assessment approaches to climate

Australia's fisheries are, in general, relatively small and low volume, with high diversity of target or bycatch species. Due to cost of assessment, risk-based approaches have been developed to assess ecological risk from fishing and prioritize management responses (Fletcher 2005; Hobday *et al.* in press; Smith *et al.* 2007; Zhou and Griffiths 2008). These approaches underpin the Ecosystem-Based Fisheries Management (EBFM) approach in Australia at both a state and national level. Attempts to generalize these risk-based approaches to include climate risks have so far met with limited success, in part because data to estimate sensitivity to climate impacts are lacking. Nevertheless, the same EBFM frameworks could still be used because climate is just another driver, so the challenge is as much to develop integrated risk frameworks, as it is to develop climate-based risk frameworks.

Historically, the concept of risk assessment has been implicitly but crucially embedded in fisheries management. The classical single species stock assessment is a rigorous risk assessment that defines the probability of a specific management objective not being achieved. In the last decade, risk assessments have been extended to a wider range of aquatic components, including: target species; by-product and by-catch species; threatened, endangered and protected species (TEP species); habitats (Williams *et al.* in press) and communities (Astles *et al.* 2006; Fletcher 2005; Hobday *et al.* 2007; Smith *et al.* 2007; Stobutzki *et al.* 2002; Zhou *et al.* 2007, 2009, 2010). Some of these tools have the capability to incorporate climate change into the model and have been applied to assess the impact of climate change on marine ecosystems.

In particular, an Ecological Risk Assessment for Effects of Fishing (ERAEF) framework has the capability to assess the ecological effects of fishing under

changing climate (Hobday *et al.* 2007, in press; Smith *et al.* 2007). The ERAEF framework is a hierarchical approach that starts from a qualitative analysis, through a semi-quantitative analysis, to a quantitative analysis (Smith *et al.* 2007). For example, "Productivity Susceptibility Analysis (PSA)" is based on scoring each species on a number of productivity (ability of the unit to recover from impact; \approx resilience) and susceptibility (exposure of the unit to impact; \approx vulnerability) attributes following Stobutzki *et al.* (2001). More quantitative methods, such as Sustainability Assessment for Fishing Effects (SAFE), are useful for assessing risk for data-poor bycatch species (Zhou and Griffiths 2008; Zhou *et al.* 2009, 2010). The SAFE framework consists of two key components: an indicator and reference points, where environmental variables, including climate changes, are readily included in both components.

There have been some efforts to extend ERAEF for vulnerability assessments for marine climate change (Richardson *et al.* 2010). Recently, an Integrated Risk Assessment for Climate Change (IRACC) was developed and applied to assess the vulnerability of sharks and rays on Australia's Great Barrier Reef (GBR) to climate change by merging a traditional climate change vulnerability framework with approaches from ERAEF (e.g. PSA) (Chin *et al.* 2010). This semi-quantitative assessment identified exposure factors, at-risk species and their key biological and ecological attributes, critical habitats and ecological processes, and major knowledge gaps. Consequently, the IRACC can provide a foundation upon which to develop climate change response strategies.

Similarly, the quantitative ERAEF (i.e., SAFE) can accommodate climate change, particularly when linking to fishing effect because climate change typically alters species sensitivity to other external stressors. For example, species spatial distribution is one of the key factors in SAFE that determine its risk to fishing impacts. Climate changes have been known to alter species distribution, often through species-specific physiological thresholds of temperature and precipitation tolerance (Walther *et al.* 2002) or life history traits (Crozier *et al.* 2008; Munday *et al.* 2008). The use of

biological reference points in SAFE to gauge a species' vulnerability to external stressors can be derived as a function of basic life history parameters of each species (e.g. temperature influences on somatic growth - Pauly 1980; Quinn and Deriso 1999).

3.3 Qualitative models – their role and applications

In qualitative modelling the focus is on understanding the influence of model structure on system feedback, and how this feedback affects the behaviour of the system. Qualitative modelling permits inclusion of variables that are important but cannot be measured, and variables of disparate form, thus supporting conceptual syntheses across disciplines. Qualitative models are descriptions using signed digraphs of the variables and relationships within a system, where the links between variables describe either positive (\rightarrow) or negative (—•) direct effects (Fig. 3a). These links can be used to describe one- or two-way interactions in ecological or socio-economic (Fig. 3b) systems, or modified interactions where interaction strengths are modified by the magnitude of a variable (Fig. 3c).

From the signed digraph we can ascertain the feedback properties of a system, which can provide insight into its ability to achieve or maintain an equilibrium, or the likely response and future state of the system if it is perturbed (Dambacher *et al.* 2002, 2003). In Fig. 3a, the pair-wise relationship between variables X and Y creates a negative feedback cycle (i.e., $X \rightarrow Y - \bullet X$) that contributes to stability. Here, a shock to the system that decreases X will result in a decrease in Y, which can translate to an eventual increase in X and a return to its former level of abundance. In Figure 3b, positive feedback between the variables can lead to unhindered growth or decay depending on the source of the input, and the system can only be restrained by the degree to which there is self-regulation (i.e., density-dependent growth or external control) in each of the variables.

To illustrate the utility of qualitative models for guiding the development of adaptations by Pacific Island countries and territories to climate change, a qualitative model was constructed of the principle variables controlling food security for coastal communities in PICTs. The effects of subsistence and artisanal fisheries on fish stocks were portrayed through the variables of fishing effort, catch and the market value of catch (Dambacher *et al.* 2009). Fishing effort directly increases catch and exerts a rate of mortality on the demersal fish and near-shore pelagic fish (including tuna) stocks that dominate coastal fisheries in the region (Pratchett *et al.* in press), although the effect of the coastal fishery on the large stocks of tuna in the region (Lehodey *et al.* in press) is negligible and is omitted in subsequent analyses. The benefits of catch support fishing effort and food security, but high levels of catch suppress its market value.

Some of the main drivers of the system are human population density, habitat degradation and climate change. These drivers 'feedback' on the system in positive and negative ways. An increased human population creates increased demand for food, leading to an increase in fishing effort. It also contributes to degradation of habitats supporting demersal fish stocks, such as coral reefs. Climate change is expected to have a positive effect on pelagic fish stocks (tuna) in 2035 throughout the Pacific, but by 2100 the effects are projected to become negative in the western Pacific (Lehodey *et al.* in press). Climate change is also expected to have a direct negative effect on demersal fish through alterations to reproduction and recruitment, and an indirect negative effect on demersal finfish by exacerbating habitat degradation (Pratchett *et al.* in press; Hoegh-Guldberg *et al.* in press).

The feedback properties of the model system (Fig. 4) indicate a moderate potential for stability (Dambacher *et al.* 2003). Positive destabilizing feedback is associated with increases in human population, leading to increased fishing effort, catch, food security, and thus even greater increases in human population. This feedback subsystem is augmented by the shorter-length positive feedback between fishing effort and catch. In its present configuration, higher-level system feedback is regulated only by negative feedback cycles associated with habitat degradation or depletion of demersal reef stocks.

The effect of these drivers, and possible adaptations, on food security of coastal communities in PICTs was analysed by assessing the qualitative response of food security to perturbation scenarios based on all possible combinations of the driver

and adaptation variables. These perturbation scenarios were applied to models that represented the eastern or western Pacific in 2035 and 2100. However, because human populations in coastal areas are projected to increase substantially only in the western Pacific (Melanesia) (SPC 2008), an increase in human population was not included in the perturbation scenarios for the eastern Pacific. The total number of positive and negative effects on food security generated from the perturbation scenario was summed, and the sensitivity of the results to specific drivers and adaptations, or combinations of them examined. The analysis of the perturbations and adaptations indicate that:

- 1) The contribution of catch to food security in the western Pacific is generally likely to be lower than in the eastern Pacific.
- There are no adverse or unintended consequences for food security in any combination of the proposed adaptations.
- 3) In general, more adaptations resulted in better outcomes for food security.
- 4) Integrated coastal zone management appeared to generate the greatest positive effect on food security across all perturbation scenarios.

The effects of climate change on fisheries resources and socio-economic systems in all types of models for PICTs will be improved by access to the outputs of coupled atmosphere-ocean climate models that have been 'downscaled' to focus on areas of most interest to managers in PICTs. This information is now being assembled by Australia's Pacific Climate Change Science Programme (www.pacificclimatechangescience.org).

4. OVERVIEW OF TOOLBOX FOR CLIMATE MODELLING

Figure 1 shows a schematic representation of modelling approaches along axes of physical, biological, and human complexity. Here, we are using the term 'complexity' as a conceptual way to roughly illustrate the relative amount of detail incorporated in the model structure (e.g. number of interactions, relationships, entities, parameters). For example, climate models tend to have a large amount of physical complexity, with little biological or human complexity involved (e.g. limited biological feedbacks, emission scenarios). In contrast, single species stock assessment models can have

a large amount of biological detail, with little detail of physical or human complexity. Ecosystem modelling approaches (e.g. MICE and Atlantis) vary in the degree of representation of biological, physical, and human complexity. For addressing aspects of climate change, these types of models could be more valuable by extending across different axes to be more relevant. For example, the ability of climate models to include more biological complexity is likely to be more valuable for more accurately representing changes in the biogeochemical environment and feedbacks with ocean production. Similarly, single-species stock assessment models that incorporate a greater degree of physical environmental parameters may have utility in forecasting recruitment events or different rates of juvenile mortality under different climate regimes. In contrast, given their already expansive biophysical coverage and the importance of human decisions and responses in dictating pressure on ecosystems, ecosystem modelling approaches that are likely to have a role in affecting adaptive management responses under climate change will need to incorporate a greater amount of detail in representing the complexity of the human system.

Modelling of the human dimension has thus far focused predominantly on incorporating economic factors or a subset of human behaviour (usually motivated on economic grounds). But there is still a long way to go in terms of representing other aspects of the human dimension such as developing social models of networks, relationships and factors such as resilience, psychological models incorporating attitudes and personality types and anthropological models to simulate morals and norms as well as cultural considerations. These aspects will likely be sequentially added to end-to-end models, but simultaneously may need to be given higher priority in some systems than in others. For example, models to inform strategic planning associated with the Torres Strait rock lobster fishery would need to be cognisant of the important cultural role of this resource to traditional users in the region.

There is a disparity between models developed for marine ecosystems and those centred on the coastal domain such that it is currently difficult to link and integrate models of the two systems, despite the linkages between the systems. Although many CtoC models provide excellent and detailed representation of physical processes, few models are at an appropriate scale for holistically simulating the links between physical drivers, biological productivity and the resultant social and economic consequences for stakeholders. There is a need to critically evaluate the suitability in terms of scale and breadth of representation of CtoC models that have utility in a climate change context.

Recognising that it is not always possible, or even desirable, to keep increasing the complexity of modelling approaches, other approaches such as risk assessment methods or qualitative models may be a more appropriate tool in some contexts. These tools permit more rapid assessment of likely impacts under changing climate, and are able to more simply represent key drivers in the biological, physical and human dimensions. Similarly, qualitative modelling of the form of the example presented here permit fairly rapid exploration of the broad benefits of a range of adaptation options.

5. RESEARCH FOR ADAPTATION IN AUSTRALIA AND THE TROPICAL PACIFIC

Research into adaptation options for marine and freshwater environments is relatively scant, and has focused to date on assessing impacts (e.g. Hobday *et al.* 2007) and vulnerability (e.g. Hobday *et al.* 2008). Identifying adaptation options is the next step (e.g. Hobday and Poloczanksa 2010). The outputs from the models discussed in this paper can potentially contribute to so-called directed adaptation in which management or incentives direct resource users to a desired outcome. Models can also be used to test for negative outcomes arising from other adaptation options.

Adaptation options should address both short- the longer-term effects of climate change through measures that promote resilience in bio-physical and socioeconomics systems (Grafton 2010). For example, the qualitative modelling approach outlined in Section 3.3 was useful in capturing the inter-relationships between climate change, population growth and food security affecting Pacific Island countries and territories. Possible adaptations to maintain or increase access to fish for food security include integrated coastal zone management, the use of low-cost, inshore Fisheries Research House fish aggregation devices (FADs) to increase the catch of near shore pelagic fish, small-pond aquaculture and post-harvest processing of tuna caught around FADs (SPC 2008; Bell *et al.* 2009).

Long-term observations of variation in the micronekton of the tropical Pacific Ocean will help modellers bridge the gap between ocean models and the population dynamics of tuna under climate change (Lehodey *et al.* 2008, 2010, in press). Acoustic methods promise to be of great use here, although there is an urgent need to verify them with direct observations of micronekton (Kloser *et al.* 2009). Long-term monitoring is also required to separate the effects of climate change on coastal fisheries from other drivers, such as habitat degradation and overfishing.

Many Pacific Island societies have a history of watershed management and resource tenure that extends for 100's to 1000's of years – embodied in concepts such as *pauva* (Solomon Islands), *ahupua'a* (Hawai'i), *ki uta ki tai* (Aotearoa/New Zealand)(Berkes, *et al.* 2000; Townsend, *et al.* 2004). Although there remain a number of challenges for integrating catchment-to-coast models to capture biogeochemical and ecological processes, a better understanding of how Pacific cultures traditionally relate to the land and sea may increase the relevance of modelling results to local communities and inform a more holistic approach to resource management and climate adaptation strategies for PICTs.

As ecosystems change, so will the ways humans use, monitor and manage them, and adaptive management loops will need to be an indispensible part of the management toolbox. An effective means of exploring the potential outcomes of adaptive management is management strategy evaluation, which involves modelling each step of the formal adaptive-management approach (Walters 1986) and evaluating the consequences of a range of management strategies or options. Reviews of this approach are given in Butterworth and Punt (1999), Smith *et al.* (1999), Sainsbury *et al.* (2000) and Rademeyer *et al.* (2007). Briefly, it makes explicit tradeoffs across a range of management options and is a valuable tool for checking the robustness of management measures to inherent uncertainties in all inputs and assumptions used (Cooke 1999). There is increasing uptake of this approach in both

the coastal and marine domains. Its potential to readily incorporate the human dimension enables visualisation of trade-offs in biological, economic and social dimensions arising from different climate adaptation options.

Discussion

Modelling is a valuable tool for understanding and seeking solutions to the significant challenges posed by climate change at several levels. There is a need for focused and integrated research capable of translating changes in physical variables into evaluations of changes in ecosystem functioning and impacts on dependent and affected communities. Australia and the neighbouring tropical Pacific region are using modelling tools ranging from qualitative to fully quantitative approaches (Table 1), and from simple to complex models.

PICTs have limited scientific capacity and will continue to need assistance from first world nations, such as Australia, to identify the vulnerability of their fisheries and aquaculture sectors, and the adaptations needed to maintain the benefits from fisheries resources in the face of climate change. Qualitative modelling can be used to engage other disciplines (e.g., agriculture) and include broader socio-economic contexts (e.g., diversification of livelihoods into other sectors, community-based planning for sustainable resource use) in the modelling exercise. This can contribute to assessing the trade-offs associated with a range of development and adaptation options in response to changing climate.

There is a range of "dependence" of biological resources on catchment/coastal processes (Fig. 2) and the links between marine, coastal and freshwater processes – which all respond differently to climate change – cannot be ignored for some species and systems. The priority accorded to understanding these links will be dictated by the biodiversity value and economic value of the resources (Fig. 2). In some situations, economic values might have relatively greater importance from the perspective of direct fishery profits and revenue, or because of the central role of marine resources in providing food security. Progress in understanding these links is

currently impeded to some extent by difficulties in linking and integrating marine and coastal models.

Different approaches have utility in different contexts, and in some cases the utility can be improved by expanding one or more of the biological, physical and human complexity dimensions (Fig. 1). Universally, there is a shortage of suitable data to adequately inform and validate understanding. The modelling examples and approaches we summarised (Table 1) differ in their data requirements and there is a need to identify critical data gaps, as well as to revisit old data from new perspectives.

In general, although advances have been made in accurately modelling physical and biological processes, much work remains in terms of representing complex components of human behaviour, such as psychological and anthropological factors. There is potential for further development and increased uptake of approaches such as social network analyses. Simultaneously, there is a need for gradual expansion of the number and types of users represented in models.

End-to-end models are at the forefront of approaches capable of integrating effects from the lowest biophysical levels through to the efficacy of adaptation options and governance structures to respond to climate change impacts. However, these models require substantial resources to develop and implement, and it is encouraging that the toolbox of available approaches also includes simpler qualitative models and risk assessment approaches that can usefully inform managers and stakeholders about a range of relevant issues. The suitability of different models and approaches depends on the context and underlying objectives and our examples demonstrate that models of climate change impacts can, for example, inform understanding of ecosystem impacts, risks to individual species, changes in the economic gains of stakeholders, adaptation options and the risks to food security.

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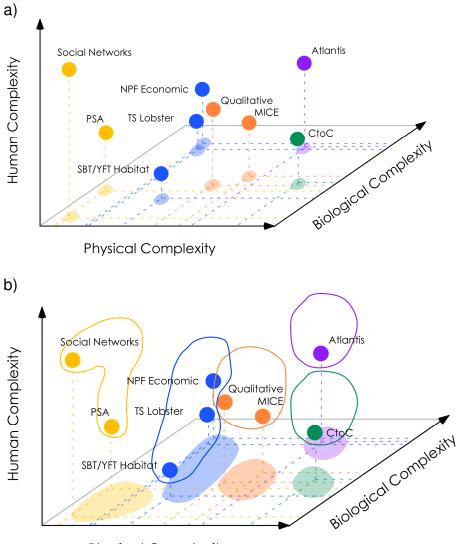
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Model	Model description	Fishery / Region	References
Atlantis	3D end-to-end model	Southeast Australia	Fulton <i>et al.,</i> 2007, in press
Coupled Models (spatial MSE)	Integrated spatial-explicit multi-model framework. 2D end-to-end modelling system	Northern Prawn Fishery	Bustamante <i>et al.</i> 2010
CtoC	Decision support Tool for Management Strategy Evaluation that integrates biophysical, social perception and economic models	South East Queensland, Australia	Ellis <i>et al.,</i> in prep.; Cannard <i>et al., in</i> <i>prep.;</i> Tickell <i>et al., in</i> <i>prep;</i> Dutra <i>et al., in</i> <i>prep;</i> Perez <i>et al., in</i> <i>prep.</i>
Ecosim	Trophodynamic	Several systems	Griffiths et al. 2008,
Ecospace	Trophodynamic 2D model	Several	Fulton in press Gribble 2003 Bulman <i>et al.</i> , 2006a Bulman 2006 Fulton in press, Bustamante <i>et al.</i> unpublished.
InVitro	Agent-based end-to-end	Ningaloo-Exmouth region * Northwest shelf Australia *	Fulton <i>et al.,</i> 2009, in press Gray <i>et al.,</i> 2006 Little <i>et al.,</i> 2006
NPF fishery	Size-structured population model coupled with economic model; MSE framework	Northern Prawn Fishery	Dichmont <i>et al.</i> 2008, 2009
PSA	Semi-qualitative risk assessment	More than 30 Commonwealth fisheries	Stobutzki <i>et al</i> . 2001
Qualitative model using signed digraphs	Qualitative Model of variables controlling food security for coastal communities	Pacific Island countries and territories	Dambacher <i>et al.</i> 2009; this paper
Quota trade networks affecting fisheries	Quantitative network analysis		Van Putten <i>et al</i> . in press
SAFE	Quantitative risk assessment	Dozen major Commonwealth fisheries	Zhou and Griffiths 2008
Southern rock	Empirical analysis of fishing	Tasmania	van Putten <i>et al.</i> in
lobster Torres Strait lobster	business data Stock assessment model	Torres Strait	press Plaganyi et al. 2010

Table 1. Summary of models (listed alphabetically) discussed in the text in relation to their potential to address climate change impacts.

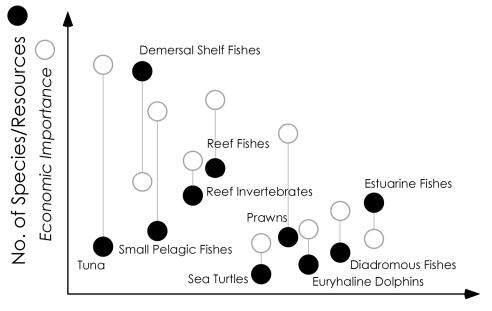
Simulation	Process detail		
requirement			
Land-use/runoff	Soil characteristics, land cover and catchment runoff		
Hydrodynamics	A catchment/freshwater model should be able to represent at least catchment flows that generate information on the runoff of sediments, nutrients and other chemicals. Receiving water models should be able to simulate 3-D processes, such as mixing, turbulence/re-suspension of sediments, layering/stratification, sea level rise and biochemical process representation.		
Transport	The origin and fate of sediments and nutrients in the CtoC domain are essential to understand the effects of climate variability and changes in land-use.		
Physio-chemical water quality constituents	Variables, such as pH, redox potential, temperature and salinity should be included in integrated CtoC models to assist in the prediction of impacts of physio-chemical variables in high value ecosystems, which provide foodstuff, and aquaculture farms.		
Biogeochemistry	Simulation of reactive transport and transformation of common parameters such as nitrogen, phosphorus, oxygen, carbon and inorganic suspended solids, and assimilation of nutrients by primary producers. Simulating parameters such as bacteria, pathogens, algae and zooplankton is also highly desirable.		
Ecological relations	Simulation of higher order functions, such as predator-prey interactions between fish and invertebrates is desirable. Requires ability to quantify interaction strength to characterise competition, facilitation, and predator-prey interactions. Information on key rate processes (e.g. respiration, growth) and dependence on physical environmental factors are needed for predictions of how climate change may influence organisms at a physiological level and how this scales to population/ecosystem effects.		
Social-Economic Relationships	Information on social and economic networks, behavioural roles of humans, and decision rules around resource use and management will be necessary as part of an overall predictive framework (e.g. MSE, adaptive management cycles). Incorporation of cultural contexts and sociological values will also underpin models that support policy and institutional/management frameworks.		

Table 2. Requirements for integrated "catchment-to-coast" (CtoC) models to assess effects of climate change on fisheries and aquaculture.



Physical Complexity

Fig. 1. (a) Schematic representation of modelling approaches discussed in this paper distributed along axes of physical, biological and human complexity. The term "complexity" refers broadly to the amount of detail incorporated in the model structure, thus for example, biological complexity could be in terms of the number of species groups or the detail included for a single group. (b) Schematic illustration of ways to increase the value of these types of models for addressing aspects of climate change by extending across different axes. Modelling approaches that are likely to have a role in affecting adaptive management responses under climate change will need to incorporate a greater amount of detail in representing the complexity of the human system.



Dependence on "Catchment"/Coastal Processes

Fig. 2. Schematic representation of the dependence of species/resources on "catchment"/coastal processes relative to the number of species (i.e. biodiversity value) *versus* the economic/consumptive importance (i.e. revenue, sustenance). These values are likely to vary in different regions around Australia and across Pacific Island countries and territories. Climate change is also likely to shift the position of these in terms of the number of resources and/or their relative importance (see e.g. Brown *et al.* 2010).

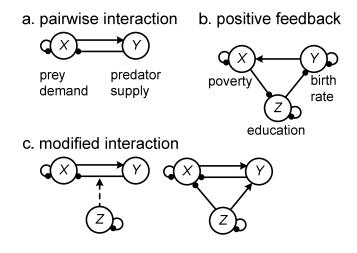


Fig. 3. Signed digraphs showing relationships between variables (open circles), with a link ending in an arrow representing a positive direct effect, and a link ending in a filled circle representing a negative direct effect; negative self-loops denote self-regulation in a variable. a) A pair-wise interaction with a positive and negative link can represent a biological relationship, such as predation, or an economic one, such as product supply and demand. Other possible biological relationships include competition (-,-), mutualism (+, +), commensalism (+, 0), and amensalism (-, 0). b) Example of positive or self-enhancing feedback within a socio-economic system. c) A modified interaction, in which variable *Z* enhances the strength of the pair-wise interaction of *X* and *Y*, as denoted by a dash-lined link. The product of this modifying link with either of the two pair-wise links creates direct effects of *Z* on variables *X* and *Y* (Dambacher and Ramos-Jiliberto 2007).

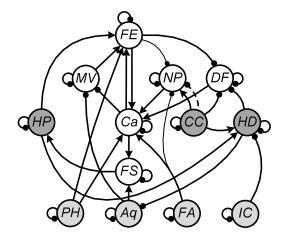


Fig. 4. Signed digraph model of factors affecting the use of fish for food security by coastal communities in Pacific island countries and territories under the IPCC A2 emissions scenario. As in Figure 1, with circles representing major variables that regulate delivery of protein from fish and invertebrates to human populations; darklyshaded circles (HP, CC and HD) represent pressures and drivers for the system, and lightly-shaded circles represent possible interventions (adaptations) to improve food security (PH, Aq, FA and IC). Thin-lined links entering near-shore pelagic fish (mainly tuna) indicate negligible levels of fishing mortality. Note that in 2035 the effects of climate change on stocks of near shore pelagic fish are projected to be positive across the entire tropical and subtropical Pacific, however, the effects change by 2100; they remain positive in the eastern Pacific, but, as denoted by the dashed-line link, are expected to be negative in the western Pacific (Lehodey et al. in press). Aq, aquaculture; Ca, catch; CC, climate change; DF, demersal fish and invertebrates associated with coral reefs; FE, fishing effort; FA, fish aggregation devices; FS, food security; HD, habitat degradation; HP, human population; IC, integrated coastal-zone management; MV, market value of catch; NP= near-shore pelagic fish; PH, post-harvest processing.